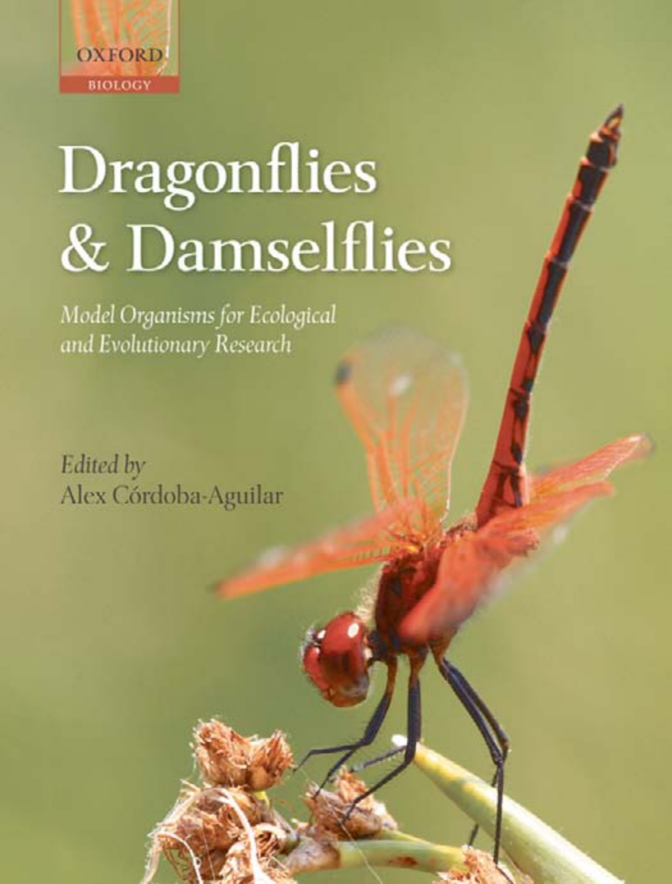

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BIOLOGY

Dragonflies & Damselflies

Model Organisms for Ecological and Evolutionary Research

Edited by
Alex Córdoba-Aguilar

Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research

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Dragonflies and Damselflies

Model organisms for ecological and evolutionary research

EDITED BY

Alex Córdoba-Aguilar

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Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.
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Published in the United States
by Oxford University Press Inc., New York

First published 2008

British Library Cataloguing in Publication Data
Data available

Library of Congress Cataloging in Publication Data
Data available

Typeset by Newgen Imaging Systems (P) Ltd., Chennai, India
Printed in Great Britain
on acid-free paper by
CPI Antony Rowe, Chippenham, Wiltshire

ISBN 978–0–19–923069–3 (Hbk)

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To the memory of Phil Corbet.
For many of us, his writings were a source of inspiration
and his friendship an enormous treasure

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Foreword

The conspicuous behaviour of adult dragonflies, as well as the modest number of species in the order Odonata, make these insects unusually accessible to the investigator. During the last 50 years or so an impressive amount of information has been gathered regarding the behaviour and ecology of these handsome insects, and this has recently been made available in the form of a comprehensive review (Corbet 2004). Most of this information, necessarily, has been in the form of factual observations of the conduct of dragonflies under natural conditions; that is, descriptions of how these insects behave in nature. Observations of this kind, often the product of great skill and dedication, provide the foundation needed for the construction of theoretical models which represent a further step towards elucidating the strategies that enable us to rationalize patterns of behaviour in terms of evolutionary pressures. A few pioneers have already ventured along this fruitful path. For adult dragonflies, Kaiser (1974), Ubukata (1980b), Poethke and Kaiser (1985, 1987), and Poethke (1988) modelled the relationship between territoriality and density of males at the reproductive site, Marden and Waage (1990) likened territorial contests to wars of attrition in the context of energy expenditure, and Richard Rowe (1988) explored the mating expectation of males in relation to the density and oviposition behaviour of females. In 1979 Waage provided the first, and probably still the most convincing, evidence for any taxon of the mechanism by which males gain sperm precedence, thereby opening the way for testable hypotheses for modelling mechanisms of sperm displacement and therefore male–female competition. Using simulation models, Thompson (1990) elucidated the relationship between weather, daily survival rate, and lifetime egg production. For larvae, Lawton's (1971) estimation of the energy budget of a coenagrionid made possible the tracking of energy flow from egg to adult, Thompson (1975) and Onyeka (1983) characterized functional-response distributions during feeding, Pickup and Thompson (1990) and Krishnaraj and Pritchard (1995) used such information as a variable to model the effects of food and temperature on growth rate, and Glenn Rowe and Harvey (1985) applied information theory to agonistic interactions between individuals.

With these examples to provide inspiration, and with a rich lode of factual information ready to be mined, today's biologists are supremely well placed to make further progress in the fields of modelling and evolutionary research using odonates subjects. The contributions in this book constitute convincing testimony to this assessment and to the suitability of dragonflies as models for elucidating the proximate and ultimate forces that give direction to their behaviour, morphology, and ecology.

Any advance in knowledge and understanding that helps to place greater value on dragonflies and the natural world in which they live can only serve to heighten our awareness of the urgent need to conserve those species that are still with us. This book will surely contribute towards that end and I wish it great success.

Philip S. Corbet
University of Edinburgh
Phil Corbet died on February 18.

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Contents

Contributors

Bradley R. Anholt, Department of Biology,
University of Victoria, Box 3020 Stn CSC,
Victoria, British Columbia, Canada V8W 3N5
anholt@uvic.ca
Adolfo Cordero Rivera, Grupo de Ecoloxía
Evolutiva, Departamento de Ecoloxía e Bioloxía
Animal, Universidade de Vigo, E.U.E.T.
Forestal, Campus Universitario, 36005
Pontevedra, Spain
adolfo.cordero@uvigo.es
Alex Córdoba-Aguilar, Departamento de Ecología
Evolutiva, Instituto de Ecología, Universidad
Nacional Autónoma de México, Apdo. Postal
70–275, Ciudad Universitaria, México D.F.,
04510, México
acordoba@ecologia.unam.mx
Philip H. Crowley, Department of Biology,
101 T H Morgan Building, Lexington,
KY 40506, USA
pcrowley@email.uky.edu
Patrick W. Crumrine, Department of Biological
Sciences & Program in Environmental Studies,
Rowan University, Glassboro, NJ 08028, USA
crumrine@rowan.edu
Marjan De Block, Laboratory of Aquatic
Ecology and Evolutionary Biology,
University of Leuven, Ch. Deberiotstraat 32,
3000 Leuven, Belgium
marjan.deblock@bio.kuleuven.be
Mark R. Forbes, Department of Biology, Carleton
University, 1125 Colonel By Drive, Ottawa,
Ontario, Canada K1S 5B6
mforbes@connect.carleton.ca
Johanna Honkavaara, Section of Ecology,
Department of Biology, University of Turku,
FI-20014, Finland
johhon@utu.fi
Frank Johansson, Department of Ecology and
Environmental Science, Umeå University, 90187
Umeå, Sweden
frank.johansson@emg.umu.se
Walter D. Koenig, Hastings Reservation
and Museum of Vertebrate Zoology,
University of California Berkeley, 38601 E.
Carmel Valley Road, Carmel Valley,
CA 93924, USA
wicker@berkeley.edu
Janne S. Kotiaho, Department of Biological and
Environmental Science, P.O. Box 35, 40014,
University of Jyväskylä, Finland
jkotiaho@bytl.jyu.fi
John H. Matthews, WWF Epicenter for
Climate Adaptation and Resilience
Building, 1250 24th Street, NW, Washington,
D.C. 20037, USA
john.matthews@wwfus.org
Michael L. May, Department of Entomology,
Rutgers University, New Brunswick, NJ 08901,
USA
mimay@rci.rutgers.edu
Mark A. McPeek, Department of Biological
Sciences, Dartmouth College, Hanover, NH
03755, USA
mark.mcpeek@Dartmouth.edu
Dirk Johannes Mikolajewski, Department of
Animal and Plant Sciences, University of
Sheffield, Western Bank, The Alfred Denny
Building, Sheffield S10 2TN, UK
d.mikolajewski@daad-alumni.de
David J.S. Newman, Exeter Health Library,
Royal Devon and Exeter Hospital, Exeter
EX2 5DW, UK
david.newman@rdeft.nhs.uk
Beat Oertli, University of Applied Sciences of
Western Switzerland, Ecole d'Ingénieurs HES
de Lullier, 150 route de Presinge, CH-1254 Jussy,
Geneva, Switzerland
beat.oertli@etat.ge.ch

Markus J. Rantala, Section of Ecology,
Department of Biology, University of Turku,
FI-20014, Finland
mjranta@utu.fi

Tonia Robb, Department of Biology, Carleton
University, 1125 Colonel By Drive, Ottawa,
Ontario, Canada K1S 5B6
trobb@connect.carleton.ca

Michael J. Samways, Centre for Invasion Biology,
Department of Conservation Ecology and
Entomology, Faculty of AgriSciences, University
of Stellenbosch, Private Bag X1, Matieland 7602,
South Africa
samways@sun.ac.za

Martín Alejandro Serrano-Meneses,
Departamento de Ecología Evolutiva, Instituto
de Ecología, Universidad Nacional Autónoma
de México, Apdo. Postal 70–275, Ciudad
Universitaria, México D.F., 04510, México
mserrano@ecologia.unam.mx

Tom N. Sherratt, Department of Biology, Carleton
University, 1125 Colonel By Drive, Ottawa,
Ontario, Canada K1S 5B6
sherratt@ccs.carleton.ca

John P. Simaika, Centre for Invasion Biology,
Department of Conservation Ecology and
Entomology, Faculty of AgriSciences, University
of Stellenbosch, Private Bag X1, Matieland 7602,
South Africa
simaikaj@sun.ac.za

Robby Stoks, Laboratory of Aquatic Ecology and
Evolutionary Biology, University of Leuven,
Ch. Deberiotstraat 32, 3000 Leuven, Belgium
Robby.stoks@bio.kuleuven.be

Jukka Suhonen, Section of Ecology, Department
of Biology, University of Turku, FI-20014, Finland
juksuh@utu.fi

Erik I. Svensson, Section of Animal Ecology,
Ecology Building, 223 62 Lund, Sweden
erik.svensson@zooekol.lu.se

Paul V. Switzer, Department of Biological
Sciences, Eastern Illinois University, Charleston,
IL 61920, USA
pvswitzer@eiu.edu

Tamás Székely, Department of Biology and
Biochemistry, University of Bath, Claverton
Down, Bath BA2 7AY, UK
bssts@bath.ac.uk

Katja Tynkkynen, Department of Biological
and Environmental Science, P.O. Box 35,
40014, University of Jyväskylä, Finland
katynkky@bytl.jyu.fi

Hans Van Gossum, Evolutionary Ecology
Group, University of Antwerp,
Groenenborgerlaan 171, B-2020 Antwerp,
Belgium
Hans.VanGossum@ua.ac.be

Robin J. Wootton, School of Biosciences,
University of Exeter, Exeter EX4 4PS, UK
r.j.wootton@exeter.ac.uk

CHAPTER 1

Introduction

Alex Córdoba-Aguilar

Fifteen years ago, the time when I started thinking about possible ideas to develop for my university degree dissertation, I became fascinated by the flying damselfly and dragonfly adults I found during my field trips to the riverine areas around Xalapa, my hometown in Mexico. I must admit that although this inclination was influenced initially by my like for these animals, I soon realized I was on the right path in using them to test important theoretical questions in ecology and evolution. I was lucky not only because much information was already known about them but also because important advancements could still be achieved with relatively little money and time. In a way, I found out that I could make a scientific career by using these animals, and realizing this at a young age was valuable. Paradoxically, given the considerable amount of information already published, I wondered why there was no single textbook summarizing the scientific discoveries and advancements using damselflies and dragonflies as study animals while similar treatises were available for other taxa (e.g. Bourke and Franks 1995, Field 2001). This feeling started because it was easy to see that odonates had been and are still used to test several theories and hypotheses, and have therefore become ancillary pieces in the construction of ecological and evolutionary theory. Take as an example the fundamental discovery of a copulating damselfly male being able to displace the previous male's sperm from the female vagina, by Waage (1979), an idea that provided important grounds for sperm competition theory, and which fostered research on similar morphological and physiological adaptations in other taxa (Simmons 2001). Although a few books on odonate ecology and evolution were available or have appeared lately (e.g. Corbet 1999), they have overemphasized the fascination of these animals as study subjects without admitting their limitations. The idea of the book I had in mind was to fill two gaps: first, to take a theory-based perspective rather than a taxon-based approach, where enquiry was the prevailing thread for reasoning; and, second, to show the merits of the subject as well as its limitations. The present book was written in this spirit, which is why, to my knowledge, it is different from other odonate books.

Odonates have been prime subjects for research in recent decades. One way of testifying this is by checking the number of recent papers on ecology and evolution where odonates have figured. I carried out this inspection by looking at those cases where these animals have been used as the main research subject. For this I searched in some of the most prominent ecology and evolution journals from the last 14 years. I intentionally did not examine applied journals (such as medical and agronomical) that would not utilize odonates, given their restricted relevance in human affairs. Furthermore, I only selected the numbers of the most widely used insect orders. The results appear in Figure 1.1. As can be observed, and although the absolute numbers are not impressive, odonates have a respectable and regular (in terms of time) place in ecology and evolution disciplines when compared with other insect orders. This despite the astonishingly low diversity of the Odonata compared with, for example, Coleoptera, Diptera, and Lepidoptera, which are some of the most diverse orders in the Animal Kingdom. The contribution that odonates have made to evolution and ecology disciplines (as will also be corroborated in the following chapters)

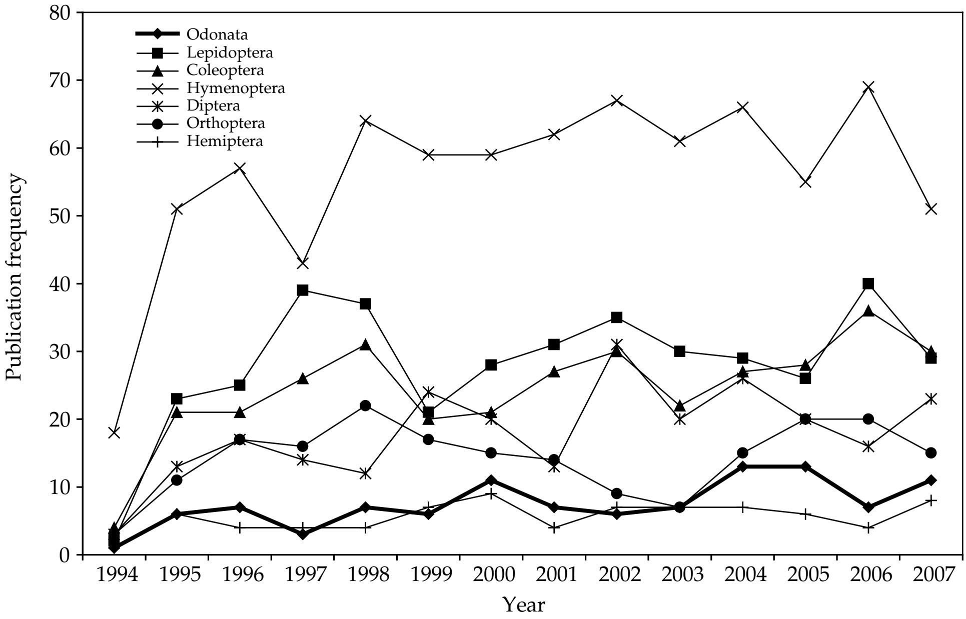

Figure 1.1 Publication frequency in seven selected insect orders (where the insect order was used as the main study subject), including Odonata, in the following journals: *Ecology*, *Evolution*, *Journal of Evolutionary Biology*, *American Naturalist*, *Animal Behaviour*, *Behaviour*, *Ethology*, *Behavioral Ecology*, *Journal of Ethology*, *Ecological Monographs*, *Journal of Animal Ecology*, *Ethology Ecology & Evolution*, and *Global Change Biology*.

is therefore immense. This contribution has been particularly evident for specific issues such as sexual selection, the evolution of flight, community ecology, and life-history theory. Curiously, however, I do not believe that there are many people working on these animals, compared with other taxonomic groups, a fact that is reflected by the relatively low number of contributors to this book (and actually, several of us appear repeatedly in different chapters). This means, first, that despite being very few (and stubborn, possibly), we believe firmly that odonates are good study models offering, as I have said before, potentially fruitful scientific careers; and second, that new workers are scarce, but that the ones who remain indeed make their name working on these animals.

In planning this book, I sought to invite those people to contribute whose efforts have been essential in testing and constructing new ideas. These researchers could directly provide a more straightforward understanding of their discoveries and outline the issues to be addressed in the future. I have encouraged these colleagues to base their writing on theories and hypotheses, and to allow readers to see the pros and cons of using odonates as study subjects, so that we do not appear too optimistic. Readers, I hope, will find this balance in most chapters. As for the subject matter, I tried to gather together the major theoretical and applied topics in which odonates have played a prominent role. Although I have discussed this with other colleagues, I take any blame for any possible bias in these topics and any that have been omitted. If this project proves to be successful, I will include those other topics in future editions. Readers will find two arbitrary sections in this book: ecology and evolution. Of course, the border between these sections is blurred for many chapters and better justice would have been served to include them in a major section called evolutionary ecology. However, as this does not apply to all chapters, I preferred to stick to my arbitrary but still useful resolution. Each chapter had a word limit and was sent out for review, a painful process for everyone but especially the editor. My sincere thanks and, particularly, apologies to everyone—authors and reviewers mainly—for my messages that flooded their e-mail accounts. Although they accepted my requests quite happily without exception, there were times at which I imagined that reading my name had a frightening effect on some of these people.

This project started a year and half ago and included far more people than I initially thought. I am very grateful to Brad Anholt, Wolf Blanckerhorn, Andrea Carchini, Andreas Chovanec, Adolfo Cordero-Rivera, Phil Crowley, Hugh Dingle, Henry Dumont, Roland Ennos, Mark Forbes, Rosser Garrison, Greg Grether, John Hafernik, Richard Harrington, Paula Harrison, Frank Johansson, Vincent Kalkman, Walter Koenig, Shannon McCauley, James Marden, Andreas Martens, Mike May, Soren Nylin, Beat Oertli, Stewart Plaistow, Andy Rehn, Mike Ritchie, Richard Rowe, Albrecht Schulte-Hostedde, Laura Sirot, Robby Stoks, Jukka Suhonen, John Trueman, Karim Vahed, Steven Vamosi, Hans Van Dyck, Hans Van Gossum, Rudolf Volker, and Robin Wootton, who gracefully assisted me when reviewing the different chapters, on some occasions reviewing more than one chapter or reading the same chapter more than once. I thank Blackwell Publishing, Chicago University Press, Elsevier, the Royal Society, and Scientific Publishers for allowing to use some figures. Erland R. Nielsen was very generous in giving me free access to use his fantastic pictures. During this winding path, I was gracefully assisted by Raúl I. Martínez Becerril, my laboratory technician. The chief of my department, Daniel Piñero, was very encouraging by allowing me not to be in my work place on many days when I was working at home. My graduate and postgraduate students also deserve a place during the more hysterical moments of this project, for understanding my hurry in attending to their experiments and theses. Helen Eaton and Ian Sherman from Oxford University Press were outstanding in providing help during all stages, including editorial and personal situations that arose during these months. Finally, the long nights and early mornings would have been far harder had I not been accompanied by Ana E. Gutiérrez Cabrera. She, more than anyone, suffered this book by taking good care of me and acted as the great loving partner that she has always been. Her company and words were the most gratifying formula each day.

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SECTION I

Studies in ecology

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CHAPTER 2

Mark–recapture studies and demography

Adolfo Cordero-Rivera and Robby Stoks

Overview

Population ecology is concerned with estimates of the composition and size of populations and the processes that determine their dynamics. To this aim, population ecologists must track wild animals over their lifetimes, and this task is only possible if animals are marked individually and can be recaptured afterwards. Odonates are convenient model organisms for mark–recapture studies, and one of the classic models to analyse mark–recapture histories (the Manly–Parr model) was developed to analyse data on a small coenagrionid damselfly, *Ischnura elegans*. Mark–recapture methods on odonates are successful because they are marked easily and remain near water bodies, allowing high recapture rates. In recent years the focus in mark–recapture models has switched from estimates of population size to estimation of survival and recapture rates and from testing hypotheses to model selection and inference. Here we review the literature on mark–recapture studies with odonates, and suggest areas where more research is needed. These include the effect of marking on survival and recapture rates, differences in survival between sexes and female colour morphs, the relative importance of processes in the larval and adult stages in driving population dynamics, and the contribution of local and regional processes in shaping metapopulation dynamics.

2.1 Introduction

Populations may show considerable temporal and spatial variation in abundance. Population ecology deals mainly with the temporal changes in abundance and their underlying mechanisms. The factors that cause a change in population size are of interest for basic and applied ecology. To understand their causes and implications, we need precise estimates of the fundamental demographic processes as provided by population parameters. Four main processes are responsible for change in abundance: birth and immigration increase numbers, whereas mortality and emigration reduce them. It is obvious that in almost all cases ecologists cannot count all the animals in a given population, and therefore samples must be taken as a means of estimating population size. A myriad of ecological sampling methods has been developed (e.g. Southwood and Henderson 2000), and mark–recapture methods are among the most powerful.

Marking wild animals allows researchers to estimate population densities and key demographic parameters including survival rates, longevity, and emigration rates. Marking allows a portion of the population to be recognized, and if certain assumptions are met (Box 2.1), repeated sampling produces reliable estimates of many population parameters. All methods developed so far, even the most sophisticated, are derivations of the Lincoln–Peterson index, which is based on a simple comparison of proportions: the ratio of marked animals (m) to total animals captured (n) in the (i+1) th sample, should equal the ratio in the population; that is, the number released (r) on the ith sample in relation to the whole population (N).

Box 2.1 Basic assumptions of mark–recapture models, and the suitability of odonates for this kind of research

The basic tenet of mark–recapture methods is that marking does not affect survival, emigration, or recapture rates of animals. This is obvious because all estimates of population parameters depend on ratios of marked to unmarked animals, or animals marked on a given occasion compared with those marked on other occasions. Strictly speaking, all the estimates obtained by these methods only apply to the subset of the population that has been marked, and we can only assume that these estimates also apply to the population as a whole. The main assumptions of Cormack–Jolly–Seber methods (CJS methods; see text for details) are the following (adapted from Arnason *et al.* 1998). These have been termed the iii assumptions by Lebreton *et al.* (1992): independence of fates and identity of rates among individuals. Violations of these assumptions can be tested with specific software (e.g. U-Care; Choquet *et al.* 2005).

Assumption	**Comment**
No mark loss and correct recording of marks	Odonates can be marked with numbers on their wings, and if marking is made with care, then marks remain until death, unless wings are broken. Marking tenerals can produce wing deformation making numbers illegible. Teneral odonates can be retained for some hours in a cool box, and then marked safely. Marking larvae will produce mark loss at the moment of moulting, but at least in the last instar, lost marks could be recovered easily, and using multistate models, an estimation of survival rate can be obtained (e.g. Besnard *et al.* 2007).
Homogeneity of capture probability for all animals alive just before sample *i*	Probability of capture should not depend on previous history. So-called trap-happiness (i.e. the increased recapture probability of already marked animals), and the opposite should be avoided. In the case of odonates, given that capture (or resighting) is made without trapping, catchability should be the same for different age classes, sexes, sizes, and so on. There is evidence for a sex difference in capture probabilities. Because of this, sex should be taken into account when analysing data. If many animals move between different places and sampling only includes one of these places, then emigration is non-permanent, in the sense that animals can only be captured while they remain in the sampled area. This violates the homogeneity-of-capture assumption. Populations of odonates rarely have a large fraction of transients, and if sampling includes all the main breeding sites, then this problem is minimized. If there is heterogeneity of capture probabilities, the use of Pollock's (1982) robust method is recommended.
Homogeneity of survival for all animals in the population just after sample *i*	Survival curves for adult odonates are typically type II (age-independent mortality; see Figure 2.5). Nevertheless, animals marked immediately after emergence are less likely to be resighted. Marking only adults or only tenerals, or taking age into account in the analyses, should solve this issue. It is very important to note that weather has a strong effect on activity and hence survival of adult odonates. Therefore studies should be long enough to include periods of favourable and unfavourable weather, to obtain biologically relevant estimates of population parameters.

Obviously, this holds only if several assumptions are met (Box 2.1), the most important being that marking does not change life expectancy or recapture rates of marked animals (see, for example, Arnason *et al.* 1998). Pollock (1982) developed a model that is robust to heterogeneity in recapture probabilities. This model requires primary (for example, months) and secondary sampling periods close to each other in time, such as several consecutive days, and assumes that the population is constant over the secondary sampling periods within a primary sampling period. Population parameters can be estimated by exploiting the two levels of sampling, using models for closed populations allowing for unequal catchability. This method produces less biased estimates than the Cormack–Jolly–Seber (CJS) method (Pollock 1982), and to our knowledge has never been applied to odonates. Further details of specialized mark–recapture methods can be found in the literature (Seber 1982; Lebreton *et al.* 1992).

2.1.1 Odonates as models for mark–recapture studies

Historically, odonates have been inspiring as model organisms to use in the development of mark–recapture methods because large data-sets are relatively easy to obtain. One classical method to analyse mark–recapture data was developed to deal with survival rates of age classes in *Ischnura elegans*. Mike Parr was one of the first to study population dynamics of adult odonates systematically (e.g. Parr 1965). While he was analysing survival rates of *I. elegans*, he met Brian Manly, a statistician, and they jointly published a suitable method to take into account daily variation in survival rate (Manly and Parr 1968), only 3 years after the classic works on this matter by Jolly (1965), Cormack (1965), and Seber (1965). Additionally, in an extensive study of a community of odonates, Van Noordwijk (1978) developed a regression method to analyse mark–recapture data, again using odonates as the model system.

The use of mark–recapture methods in Odonata has become firmly entrenched. Of the 1210 and 146 papers in *Odonatologica* (1972–2006) and *International Journal of Odonatology* (1998–2006) respectively, about 10% of papers used marked animals during the 1970s and 15–30% during the 1980s. Both journals show similar patterns: 17% of papers that use marked animals are about demographics of adult populations and 66–71% deal with behaviour (Figure 2.1). These numbers show clearly that odonates (especially zygopterans) are good models for mark–recapture experiments.

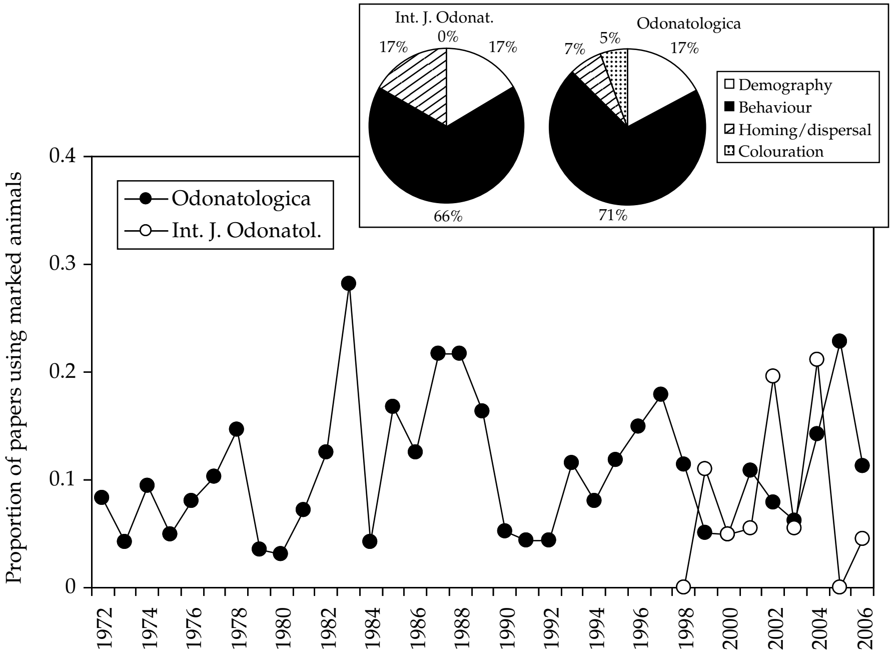

Figure 2.1 The suitability of odonates as model organisms for mark–recapture studies as inferred from the proportion of papers using marked animals in *Odonatologica* and *International Journal of Odonatology*. This proportion was about 10% in both journals. Note that marking is used mainly for behavioural studies. During the sampling periods there were 1210 and 146 papers published in *Odonatologica* (1972–2006) and *International Journal of Odonatology* (1998–2006), respectively.

The first obstacle in acquiring demographic data was using a method of marking that allows for unique recognition of individuals in the field. Borror (1934) was probably the first to use marking techniques to study an odonate population. In the summers of 1931 and 1932 he marked 830 adults of *Argia moesta*, and recaptured 178 (21%), discovering that the adults of this species do not fly long distances and live for up to 24 days. He also discovered that *A. moesta*, as many other damselflies, undergoes ontogenetic colour changes during maturation. Borror marked adults by applying different combinations of dots of india ink to the wings with a small pointed stick. Since Borror's study, several authors have developed new methods for marking. Before the appearance of felt-tipped permanent markers, researchers used delicate methods to apply a code of colours to different wings, allowing visual recognition of previously marked animals. The amount of demographic and behavioural information collected using these time-consuming and delicate methods of marking is impressive (e.g. Corbet 1952; Jacobs 1955; Pajunen 1962; Moore 1964; Bick and Bick 1965; Parr 1965).

In more recent years, marking has been more easily achieved by writing a number on the wings using permanent markers (Figure 2.2), thus allowing for a more rapid and efficient means of marking of large numbers of individuals. For example, Van Noordwijk (1978) marked over 7000 adults of several species in 2 months; and Watanabe *et al.* (2004) more than 13 000 adults of *Sympetrum infuscatum* over several years. More imaginative methods are still being designed, some very suitable to study migration/dispersal (see Chapter 6 in this volume). To batch-mark large numbers of larvae Payne and Dunley (2002) added rubidium (as RbCl) to the water, increasing the body concentration of Rb to several hundred times that in the water. These high concentrations persist in adults and would therefore allow a precise study of dispersal (provided the adults are recaptured). In another example, adult *Coenagrion mercuriale* were marked by applying ink that fluoresces in ultraviolet light, and searched for at night with a black light lamp (Hunger 2003). This method not only allowed finding roosting areas, but yielded an unexpected behavioural observation: three marked individuals were found in copula at night! The continuing refinement of modern technology will allow other unforeseen discoveries about dragonfly behaviour, including the use of miniaturized radio-emitters, which has been applied successfully to large odonates (Wikelski *et al.* 2006).

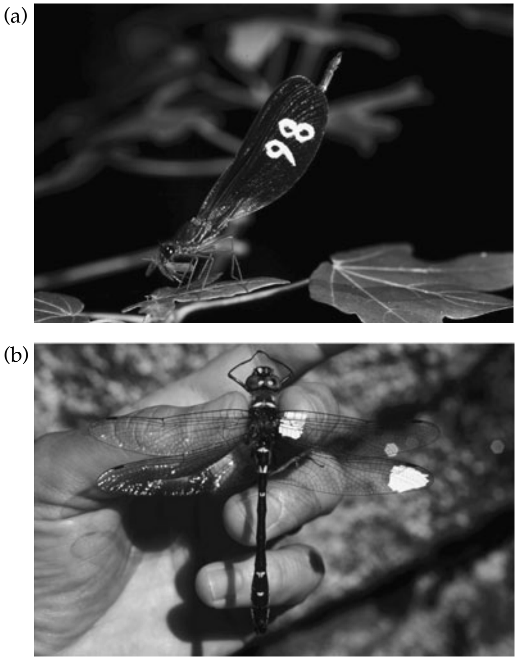

Figure 2.2 Adult odonates can be marked by writing a number on the wing using a permanent marker. This is easy to do but has the disadvantage that individuals must be recaptured or observed at very close distances to read the number. An alternative is to use coloured dots applied to different parts of the wing, so that the code can be recognized even when the animal is flying. (a) *Calopteryx haemorrhoidalis*; (b) *Macromia splendens*. Photographs: A. Cordero.

2.2 A review of population ecology studies with odonates

The four demographic parameters—birth, death, immigration, and emigration rates—are amenable to study with mark–recapture methods. Here we discuss sex ratios, longevity and survival rates, recapture rates, and the effect of marking. Migration is covered elsewhere in this volume (see Chapter 6).

2.2.1 Sex ratio

Except under local mate competition, or other particular situations (Hardy 2002), the primary sex ratio (i.e. sex ratio at egg fertilization) should be 1:1. Several mechanisms can nevertheless produce changes in this primary sex ratio during ontogeny. For instance, if embryonic mortality is sex-biased, the sex ratio at birth will deviate from 1:1. In these cases, sex-ratio biases may occur not only at birth but also at later stages of an organism's life cycle. Identifying such biases is crucial as they may have large implications. For instance, they may seriously reduce effective population size and shape the intensity of sexual selection.

Odonates cannot be sexed morphologically at egg hatching, so direct information on primary sex ratio is lacking. However, diploid organisms typically have a sex ratio close to unity. Studies where freshly hatched larvae were reared in isolation and with low mortality indeed suggest that primary sex ratios for odonates are close to one. For example, studies on *Lestes viridis* where 95.3–99.7% of the larvae survived until they were sexed showed a sex ratio of 51.3–52.6% males (De Block and Stoks 2003, 2005).

A comprehensive review of sex ratio at emergence in odonates (Corbet and Hoess 1998) found that males are slightly more frequent than females in Zygoptera, whereas the opposite is true in Anisoptera (Figure 2.3a). This is clear even in large samples (over 1000 exuviae). Therefore, at this point of the life cycle, odonates show somewhat skewed sex ratios. Nevertheless, when adult animals are marked in field studies, the pattern is more male-biased, with a sex ratio, on average, of 64.5% males (range, 54.3% in Platycnemididae to 83.4% in Corduliidae; Figure 2.3b). The numerical predominance of males in adult odonates has been known for a long time (e.g. Tillyard 1905), and there are many hypotheses to explain this phenomenon.

Some authors have stated that the observed male-biased adult sex ratio should be considered an artefact due to the more cryptic behaviour and colouration of females and their differential habitat use, causing recapture probabilities to be typically lower in females than in males (e.g. Garrison and Hafernik 1981). However, male-biased sex ratios are also observed in studies where recapture probabilities were similar in both sexes (e.g. Anholt *et al.* 2001). Moreover, modern methods used to estimate male and female population sizes are robust against differential recapture probabilities (Anholt 1997; Anholt *et al.* 2001; Stoks 2001a). This topic makes clear the need to use methods that estimate survival independently of recapture probabilities in all future studies.

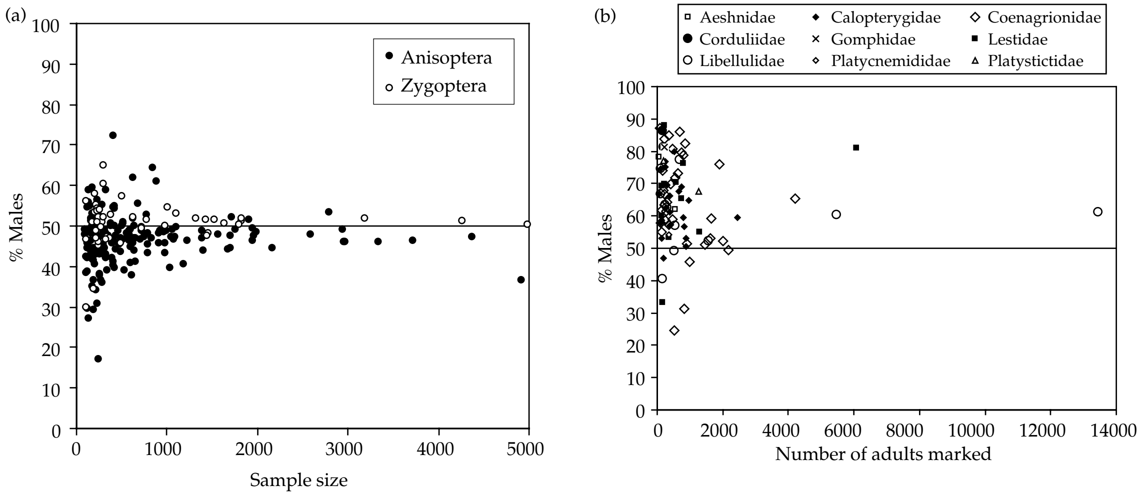

Figure 2.3 (a) Sex ratio at emergence in odonates, plotted as a function of sample size. Data include 194 records compiled by Corbet and Hoess (1998) and 16 further records not included in that paper. (b) Sex ratio among adult odonates marked in field studies, plotted as a function of sample size. Data include 86 records of 54 species from nine families.

Several hypotheses have been put forward to explain the male-biased adult sex ratios in odonates and other insects and we review them here for damselflies. We base our comments largely on a study of the damselfly *Lestes sponsa* (Stoks 2001a, 2001b), unless otherwise stated, because no other studies have dealt in detail with this problem.

- *There may be a male-biased sex ratio at emergence.* As discussed above there is usually a slight bias in male damselflies at emergence. However, typically this bias is too low to explain the observed male-biased adult sex ratios in the field.
- *Males and females may not emerge synchronously.* This would result in temporarily biased sex ratios or permanent biases given time-dependent survival probabilities. Male damselflies often emerge slightly before females in laboratory rearing experiments (e.g. De Block and Stoks 2003). However, the field study on *L. sponsa* failed to detect a sex effect on emergence date despite high sample sizes. Moreover, even if males emerge on average 2 days earlier than females, it seems implausible that this would result consistently in higher survival rates for males.
- *Females have a longer maturation period.* This indeed has been observed in several studies. For example, in *L. sponsa* female maturation times averaged 2 days longer than male maturation times. These differences would need, however, to be combined with unrealistically low daily survival rates for males to explain the shift in sex ratio (see also Anholt 1997).
- *Immature females have higher mortality rates.* In accordance with their larger mass increase during maturation (Anholt *et al.* 1991), immature females have higher foraging rates than immature males (Stoks 2001b). Because active foraging is generally associated with a higher vulnerability to predation (e.g. Werner and Anholt 1993), this should result in a lower survival probability in immature females, which was detected in one out of two study years for *L. sponsa* (see also Anholt 1991, for *Enallagma boreale*). The combination of slightly longer maturation times in females (19 compared with 17 days) coupled with slightly lower daily survival probabilities during maturation (0 95 compared with 0.98) was sufficient to generate a shift from an even sex ratio at emergence towards a male-biased sex ratio of about 2:1 in adults. Note that sex-biased dispersal is not considered a separate hypothesis causing male-biased sex ratios. Damselflies typically only show natal dispersal (Corbet 1999). If females are more likely to disperse, all else being equal, this would result in some populations being female biased. However, this has never been observed in lestid populations (Jödicke 1997; R. Stoks, personal observation). Any female bias in natal dispersal must therefore be associated with higher mortality to result in male-biased population sex ratios (see also Fincke 1982).
- *Mature females have lower survival probabilities.* In some populations lower survival probabilities in mature females have been observed (see below). However, the pattern is far from general (see Figure 2.4, below), and also, where no sex differences in adult survival were present, male-biased sex ratios were still observed.

Taken together, several factors may contribute to the typically male-biased sex ratios in adult damselfly populations; however, several of them (sex ratio at emergence, maturation times) are on their own insufficient to cause the pattern. The most plausible mechanism is driven by the lower survival probabilities of females during maturation, which is likely due to higher mortality rates by predation. Unfortunately, the immature stage is notoriously difficult to study and so far we lack direct evidence for higher predation rates on immature females. Kéry and Juillerat (2004) conclude that more sex-ratio studies in odonates are needed to assess under what conditions uneven sex ratios occur. We believe that sound manipulative experiments where predation rates are manipulated directly in large insectaries may prove rewarding for this (e.g. De Block and Stoks 2005).

2.2.2 Longevity and survival rate

One of the obvious advantages of marking wild animals is that their longevity can be measured from multiple recapture experiments. Nevertheless, mark–recapture studies are likely to underestimate actual adult longevity for three reasons: because the date of marking will usually not be the date of emergence; because the last sighting will be unlikely to be the date of death (this is especially true for animals marked close to the end of the field work); and finally because animals can emigrate and therefore spend part of their lives uncatchable. Even with these limitations, marking is the best way to estimate important life-history parameters of adult odonates. Literature on mean and maximum longevity of odonates has been reviewed by Corbet (1999). He found that the average lifespan of Anisoptera is 11.5 days, and that of Zygoptera 7.6 days, with maximum longevities in the range of 17–64 days and 15–77 days respectively.

Our review of the literature indicates that many data exist for Zygoptera, but good estimates of lifespan are scarce for Anisoptera. Figure 2.4a shows patterns in mean and maximum longevity from 43 studies of 36 species. These data suggest goals for future studies. First, the duration of mark–recapture experiments should be at least 1 month for Coenagrionidae, 45 days for Calopterygidae and a minimum of 2 months for Lestidae and Libellulidae. Only studies of this length can produce reliable estimates of longevity, because weather has a tremendous effect on survival, and a short study is more likely to be done under atypical

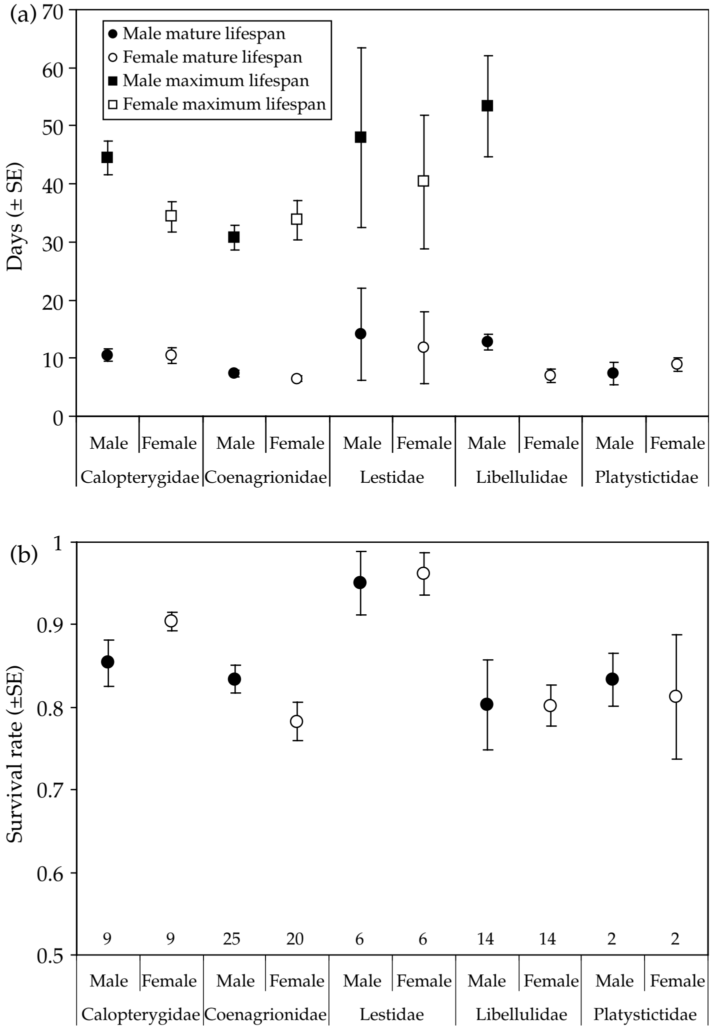

Figure 2.4 Survivorship estimated from mark–recapture data of adult odonates. (a) The mean and maximum lifespan of adult odonates. A summary from 43 studies that report data for 36 species from five families. (b) Daily survival rate (φ) (mean±SE). Numbers at the base of the graph indicate sample size (in this case, the number of estimates of φ, irrespective of the species identity). Data from 32 studies, 16 of which are presented in Table 2.1.

weather conditions. Second, Lestidae are probably the most long-lived odonates from temperate latitudes, but the great variance between studies suggests that some species have been tracked for too short a period. Third, the scarcity of data for Anisoptera (except Libellulidae) makes generalization about this suborder more difficult. And finally, almost no data exist on population parameters for tropical families (for an exception see Garrison and González-Soriano 1988), some of which have populations in danger of extinction (see the reports in Clausnitzer and Jödicke 2004).

Field surveys with multiple sessions of capture–recapture provide an easy estimation of survival rates. Modern mark–recapture methods allow a separation of survival and recapture rates using CJS models to analyse recapture histories (Lebreton *et al.* 1992). Our review of the literature shows 32 papers that report survival and/or recapture rates for 35 species from eight families. Although recent papers use CJS models, papers published before the 1990s usually estimated survival rates from the method of Jolly (1965) or Manly and Parr (1968), but all were included in our survey. Unfortunately, most of these studies do not report standard errors, and some only show data for one sex. Table 2.1 summarizes all the studies (16) that did report standard errors directly, or allowed us to estimate them from their data. Figure 2.4b shows that the average survival rate is higher for males than females within Coenagrionidae, but the opposite occurs in Calopterygidae. These data suggest a strong effect of sex on survival rate, and also a sex × family interaction. Given the heterogeneity of methods used to estimate survival rates and standard errors among studies, a meta-analysis of survival rates, as has been completed recently for the spotted owl (*Strix occidentalis*; Anthony *et al.* 2006), seems premature for odonates. This topic is suitable for further studies.

2.2.3 Recapture rate

Many authors have stated that male and female odonates have different recapture rates (e.g. Utzeri *et al.* 1988). Recently, Beirinckx *et al.* (2006) reviewed the literature on mark–recapture experiments of damselflies and, using a meta-analysis, found that the likelihood of recapturing an animal at least once was higher for males than for females. They attributed this difference to higher female-biased dispersal. However, this recapture rate is a combination of the probability of an animal surviving after marking, and its probability of being resighted, provided it remains at the sampling area. Therefore, the alternative explanation of female-biased mortality (which is very likely in Coenagrionidae, see above) cannot be discarded because only the proportion of individuals recaptured was used for their meta-analysis.

The (scarce) data available in Table 2.1 indicate that males always exhibit higher recapture rates, but the difference between sexes depends on the family (Coenagrionidae: 0.266 in males compared with 0.152 in females; Lestidae: 0.317 compared with 0.119; Libellulidae: 0.727 compared with 0.200).

2.2.4 The effect of marking

As we have already noted, mark–recapture studies allow estimation of population parameters, provided that appropriate conditions are met (Box 2.1). The act of marking the animal, which requires capture and handling, can cause slight damage (Cordero-Rivera *et al.* 2002) and modify behaviour. This immediate effect of marking seems negligible in some species, particularly Calopterygidae, which are so territorial that males return almost immediately to their favourite perch, and within minutes of marking can court females. However, even under these circumstances, a marking effect cannot be discarded. For instance, Beukema (2002) found that in male *Calopteryx haemorrhoidalis* the apparent survival rate was 94% (i.e. the disappearance rate was 6% per day), but from day 0 (marking) to 1 it was 84% (i.e. a disappearance rate almost three times greater). This marking effect has been found repeatedly in odonates (Parr and Parr 1979; Banks and Thompson 1985; Fincke 1986). Figure 2.5 shows two typical examples with *Ischnura elegans* and *Ceriagrion tenellum*. Very few studies have analysed in detail whether marking has a significant effect on adult odonates, but given the relevance of this topic to obtaining reliable population parameters (Box 2.1), future studies should pay more attention to this (for an exception see Bennett and Mill

Table 2.1 Daily survival and recapture rates estimated from multiple capture–recapture experiments of adult odonates. Only studies that reported standard errors for both sexes are included. Some of the studies did not separately estimate capture rates, and therefore the reported survival rate is likely an undertestimate.

Species	Family	Mating system	Survival rate				Recapture rate				Reference
			Males	SE	Females	SE	Males	SE	Females	SE	
Calopteryx haemorrhoidalis	Calopterygidae	Territorial	0.910	0.120	0.920	0.140					Cordero 1989
Calopteryx haemorrhoidalis		Territorial	0.940	0.047	0.890	0.032					Cordero 1989
Calopteryx haemorrhoidalis		Territorial	0.839	0.037	0.857	0.047					Cordero 1999
Calopteryx japonica		Territorial	0.820	0.090	0.930	0.020					Watanabe *et al.* 1998
Calopteryx japonica		Territorial	0.870	0.060	0.870	0.050					Watanabe *et al.* 1998
Calopteryx virgo		Territorial	0.860	0.046	0.950	0.074					Cordero 1989
Calopteryx xanthostoma		Territorial	0.660	0.176	0.890	0.223					Cordero 1989
Mnais pruinosa		Territorial	0.843	0.168	0.889	0.399					Nomakuchi *et al.* 1988
Argia chelata	Coenagrionidae	Territorial	0.850	0.030	0.860	0.040					Hamilton and Montgomerie 1989
Ceriagrion tenellum		Non-territorial	0.905	0.018	0.880	0.026	0.158	0.024	0.076	0.013	Andrés and Cordero-Rivera 2001
Coenagrion puella		Non-territorial	0.860	0.014	0.860	0.014	0.500	0.062	0.238	0.081	Anholt *et al.* 2001
Enallagma hageni		Non-territorial	0.800	0.030	0.850	0.030					Fincke 1986
Ischnura elegans		Non-territorial	0.812	0.031	0.579	0.086	0.141	0.048	0.141	0.048	Anholt *et al.* 2001
Ischnura elegans		Non-territorial	0.960	0.118	0.898	0.093					Cordero *et al.* 1998
Pyrrhosoma nymphula		Territorial	0.794	0.334	0.675	0.638					Bennett and Mill 1995
Lestes disjunctus	Lestidae	Non-territorial	0.759	0.028	0.831	0.087	0.341	0.079	0.105	0.061	Anholt 1997
Lestes sponsa		Non-territorial	0.981	0.032	0.981	0.032	0.293	0.012	0.132	0.014	Stoks 2001a, 2001b
Libellula fulva	Libellulidae	Territorial	0.880	0.010	0.830	0.020					Boano and Rolando 2003
Libellula fulva		Territorial	0.910	0.010	0.850	0.030					Boano and Rolando 2003
Orthetrum coerulescens		Territorial	0.953	0.020	0.953	0.020	0.610	0.030	0.200	0.030	Kéry and Juillerat 2004
Orthetrum coerulescens		Territorial	0.928	0.020	0.928	0.020	0.700	0.030	0.170	0.030	Kéry and Juillerat 2004
Orthetrum coerulescens		Territorial	0.855	0.040	0.855	0.040	0.870	0.060	0.230	0.070	Kéry and Juillerat 2004
Sympetrum darwinianum		Non-territorial	0.828	0.067	0.719	0.292					Watanabe and Taguchi 1988
Sympetrum eroticum		Non-territorial	0.974	0.079	0.879	0.090					Watanabe and Taguchi 1988
Sympetrum infuscatum		Territorial	0.300	0.220	0.660	0.400					Watanabe *et al.* 2004
Sympetrum infuscatum		Territorial	0.400	0.120	0.660	0.080					Watanabe *et al.* 2004
Sympetrum parvulum		Non-territorial	0.870	0.043	0.829	0.090					Watanabe and Taguchi 1988
Sympetrum pedemontanum		Non-territorial	0.805	0.068	0.721	0.053					Watanabe and Taguchi 1988

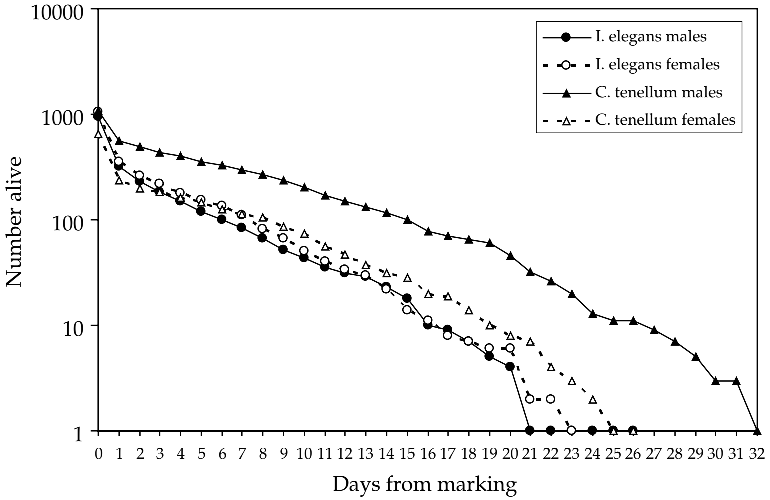

Figure 2.5 The effect of marking is clearly visible in the difference in slope in the apparent survival curve of two damselfly species from day 0 (marking) to 1, compared with successive days. Data from Cordero *et al.* (1998) and Andrés and Cordero-Rivera (2001).

1995). One possibility is to estimate the weight of marks and their aerodynamic effect. Another interesting topic is to use different colours on the same study and estimate the effect of colour on recapture rates.

There are two explanations for the marking effect. Either handling during marking increases mortality, or it elicits dispersive behaviour, each of which could result in captured animals avoiding specific sites where they were originally marked (Mallet *et al.* 1987), and therefore be less likely to be recaptured. To test these two alternatives, Cordero (1994) studied several species maintained in insectaries in the laboratory. Results were clear: immediate mortality after marking was almost null, discarding the first alternative. Therefore, we conclude that handling for marking produces stress and many individuals leave the site. This marking effect offers interesting insights into the learning capacity of insects, and suggests they are able to associate a traumatic experience with a particular site, as has been shown for *Heliconius* butterflies by Mallet *et al.* (1987). Whether marked adults permanently emigrate or simply leave the reproductive site for a few days is unknown, because dispersal patterns are difficult to study. In any case, this temporary migration violates the assumptions of mark–recapture methods, and increases the likelihood that an individual dies before returning to the reproductive site, where marking typically occurs.

2.3 Conclusions and lines for future research

We have shown that odonates are good models for mark–recapture studies, and useful for testing biological hypotheses with modern CJS models (Lebreton *et al.* 1992). Large data-sets exist and more will likely be available in the future, but few have been analysed within the framework of generalized linear models, and the model-selection paradigm that has been shown to be so successful in wildlife research (Burnham and Anderson 1998).

We believe that the duration of mark–recapture experiments should be adjusted to the maximum longevity of a target species, to obtain reliable estimates of population parameters. Furthermore, we have identified a clear lack of information on the most speciose and endangered groups, those of tropical regions. Long-term studies of odonates from rainforest areas are remarkably difficult to complete (see for example Fincke and Hadrys 2001), but it is very unlikely that patterns extracted from temperate (seasonal) areas could be generalized to tropical families.

One of the long-standing problems of odonate biology, namely what causes male-biased sex ratios in adult populations, is still not solved. To disentangle mortality from dispersal, studies of several breeding habitats, within a distance that odonates can cover, are the most promising lines of research. Further studies that manipulate predation pressure directly could give direct information on the putative role of sex-biased mortality by predation.

Additionally, the act of marking, which requires capture and handling, produces a significant change in behaviour that has also been recognized in long-lived butterflies (Mallet *et al.* 1987). The effect of marking is underexplored but, given its implications, offers important rewards for the future. For instance, an attempt to re-introduce an endangered damselfly to its former habitat found a large marking effect (Hannon and Hafernik 2007), indicating the need of a better knowledge of this effect for conservation biology projects.

Capture–mark–recapture studies have dealt almost exclusively with adults. A challenging issue is to develop procedures to extract population parameters from larval populations, which have the advantage of being closed populations. Such information could set the stage in assessing the relative importance of processes within larval and adult stages in driving population dynamics. The survival rate from last instar larvae to adults could be estimated using multistate models, allowing for mark loss, which unavoidably occurs at emergence. This procedure has been applied successfully to immature grasshoppers (Besnard *et al.* 2007). Odonates would be suitable models, because exuviae are concentrated in time and space, and therefore marks could be recovered easily.

Tackling the above-mentioned issues is crucial to further exploit odonates as model organisms in testing general ecological and evolutionary hypotheses that require precise and unbiased population parameters. Odonates may seem especially useful in following areas of research that in our opinion are underexplored. First, recent capture–mark–recapture models allow incorporation of continuous covariates (e.g. body size, asymmetry), which are very powerful for evaluating sexual and survival selection on phenotypic traits in natural populations and which can be used to test specific selection hypotheses. This would further strengthen the use of odonates as model systems in sexual selection (see Chapter 12). Second, as discussed in Chapter 17, odonates have proven to be successful model organisms when studying the evolutionary ecology of colour polymorphism. Large capture–mark–recapture studies could add insight to the extent of whether these morphs are selectively neutral with regard to survival. Third, natural habitats are increasingly becoming smaller and isolated, making a metapopulation perspective increasingly appealing and necessary to evaluate aspects such as regional viability of species (Watts *et al.* 2004). Given the relative ease of obtaining estimates of population parameters, and to a lesser of extent population exchange, capture–mark–recapture studies for several populations may give further insight to fundamental research topics including the contribution of local and regional processes in shaping metapopulation dynamics.

Acknowledgements

We are very grateful to Rosser Garrison, John Hafernik, and an anonymous referee for their comments and useful suggestions. We thank Marjan De Block for providing sex-ratio data and Carlo Utzeri for helping us to obtain some papers. ACR was supported by research grants from the Spanish Ministry of Education and Science (grants PB97–0379, BOS2001–3642, and CGL2005–00122). RS was supported by research grants from the Flemish Government (FWO-Flanders) and the KULeuven Research Fund (OT and GOA).

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CHAPTER 3

Structure and dynamics of odonate communities: accessing habitat, responding to risk, and enabling reproduction

Patrick W. Crumrine, Paul V. Switzer, and Philip H. Crowley

Overview

Studies on odonates, particularly odonate larvae, have played an important role in identifying factors that influence the structure and dynamics of ecological communities. In this chapter, we highlight the key abiotic and community-level interactions that determine odonate community structure. We focus on three important life-history-based issues central to odonate communities: habitat access, response to risk during the larval stage, and emergence and reproduction. We approach each issue by considering relevant ecological theory and identify and review empirical studies with odonates that address hypotheses raised by theoretical studies. For habitat access, a dominant role is played by hydroperiod, because it underlies the transition from mainly invertebrate predators to insectivorous fish predators and imposes a significant abiotic constraint on larval development. Habitat access may be strongly influenced by dispersal behaviour, which in turn may be related to the degree of habitat specialization, but few studies have been able to connect dispersal behaviour with predation and larval performance. As larvae, odonates must respond to risk imposed by predators. The types of predators present, such as fish, other odonate species, and conspecifics, strongly influence the level of risk. Consequently, we focus on the primary ecological interactions that occur within odonate communities, including intraguild predation, interference competition, and cannibalism, which seem to play a more important role in structuring odonate communities than exploitative competition. In most cases body size, which is affected by the relative growth and phenology of species in the community, strongly impacts the direction and intensity of these ecological interactions. Finally, we consider how the adult stage may be affected by the larval stage and how it may affect the community interactions at the larval stage. The role of adults in odonate community ecology has received much less attention than that of larvae. However, larval interactions can influence the body size and emergence time of adults, which may have a direct impact on adult fitness. Furthermore, interactions among heterospecific adults, which are driven primarily by constraints imposed by their mating and sensory systems, may affect the relative spatial and temporal distribution of sympatric species. Although numerous short-term studies at relatively small spatial scales have been conducted with odonate larvae, we still know very little about the relative impacts of competition, cannibalism, and predation on odonate population dynamics and community structure in natural systems. Long-term studies at multiple life-history stages and levels of organization are required to generate a more complete understanding of odonate communities, and of ecological communities in general.

3.1 Introduction

What factors determine the structure of ecological communities? This simple question has been the topic of extensive research and considerable controversy, but a set of general laws or principles that can be applied to most or all communities remains elusive. The general paradigm guiding research in this area suggests that there is a distinct species pool for every biogeographic area determined by the processes of speciation, extinction, and migration, and each species in the pool can colonize habitats selectively within the biogeographic area (McPeek and Brown 2000). Following colonization, abiotic factors (e.g. temperature, pH, dissolved oxygen content, dissolved solutes, and hydroperiod) and biotic interactions (e.g. predation, competition, parasitism, and disease) determine which species will persist at any given location (Corbet 1999). Co-existence among species competing for limited resources has historically been viewed in terms of niche differentiation over evolutionary time (see McGill *et al.* 2006), but recent work has begun to examine patterns in odonate communities using neutral models of community structure (e.g. Hubbell 2001; Leibold and McPeek 2006). These two perspectives are not necessarily mutually exclusive and, when taken together, may offer more explanatory power than when considered separately.

Odonate communities can be found in a wide array of freshwater systems dependent on biotic and abiotic constraints. Lentic and lotic systems ranging in physical scale from tree holes to large lakes and rivers and in temporal scale from ephemeral or seasonal to permanent can be hospitable to odonates. The distributions of these different odonate communities on the landscape are in flux under the influence of climate change, habitat alteration, invasive species, and other factors strongly linked to anthropogenic influence.

In this chapter, we identify and review three major issues in contemporary odonate community ecology primarily in lentic ecosystems: habitat access, response to risk in the larval stage, and emergence and reproduction. Of these three, we focus most on how larvae respond to risk because that phenomenon has received the most attention to date and is likely to play the largest role in structuring odonate communities. By 'odonate communities' here, we mean co-existing odonate populations and their connections to significant predators and essential prey; we make no attempt to address the many other species of known influence on odonates, primarily because they seem less likely to have major impact at the community level. We focus on the insights that studies with odonates have yielded in these general areas and highlight where additional work is needed to elucidate mechanisms underlying odonate community structure. In taking this approach we consider relevant ecological theory and discuss how results of experimental and observational studies with odonates relate to predictions of community ecology theory. We also discuss the potential for studies with odonates to improve our understanding of major patterns in communities in light of recent advances in the field.

3.2 Habitat access

3.2.1 Dispersal

Upon emergence, odonates may stay in the natal area or disperse to adjacent habitats. Adult dragonflies are generally strong fliers capable of long-distance flight, including true seasonal migration (Corbet 1999). Adult dispersal may, however, be costly because insect flight imposes significant energetic costs and may increase the probability of predation by aerial predators such as hawks (Jaramillo 1993). In landscapes where habitat quality is more variable over space than over time, selection acts to limit dispersal rates (Levin *et al.* 1984) and this pattern can lead to the evolution of habitat specialization. Alternatively, females may use dispersal as a bet-hedging strategy to increase the chance that at least some of her offspring survive, particularly if local environmental quality is poor or highly variable (Hopper 1999).

Moving to adjacent habitats may expose larval offspring of dispersing females to predators to which they are poorly adapted and/or habitats with sub-optimal physical characteristics, particularly with respect to hydroperiod. In field experiments with damselflies (McPeek 1989) and dragonflies (McCauley 2007), habitat generalists found with both fish and invertebrate top predators were more likely to disperse from natal sites relative to habitat specialists co-existing with a single predator type. Habitat generalists also dispersed greater distances and were more likely to colonize newly created artificial habitats than habitat specialists (McCauley 2007). Habitat specialists co-existing with fish or invertebrate predators also tend to be more vulnerable to alternative predator types (Stoks and McPeek 2003; McCauley 2007). This latter point is particularly important to the evolution and maintenance of dispersal behaviour and ultimately the composition of odonate communities because vulnerability to predation acts to reinforce the limited dispersal of habitat specialists (McCauley 2007).

On the landscape level, odonate communities are arranged in a meta-community structure (McCauley 2006) as viable aquatic habitats (ponds and lakes) within a terrestrial matrix. Such partially connected habitats can be viewed as sources or sinks as a function of hydroperiod and predator type (De Block *et al.* 2005). The spatial arrangement of available habitats in the landscape influences whether a habitat will be colonized by dispersers. Species richness of odonate communities in habitats disconnected by distance or physical barriers from sources is lower than in habitats with less isolation (McCauley 2006).

3.2.2 Oviposition sites and the importance of hydroperiod

Female odonates dispersing from natal habitats are then faced with a second question. Of the available habitats in the landscape, which should receive eggs? Oviposition site selection dictates the type of environment odonate larvae will experience and acts as an additional biological filter on larval odonate community composition. Selection of oviposition sites is influenced by proximate cues such as reflective properties of water (Bernath *et al.* 2002), physical dimensions of the water body (Corbet 1999), and presence of emergent aquatic vegetation (Rouquette and Thompson 2005). The proximate cues are likely related to ultimate factors influencing the probability of larval survival. For some species there may be special requirements for oviposition; for example, *Anax junius* oviposits endophytically (inside leaf tissue) and thus requires aquatic vegetation. Aquatic vegetation also increases the structural complexity of the aquatic environment and provides refuge from predation for larval odonates (Johansson 2000). Odonates appear primarily to use visual and tactile senses to select oviposition sites, but their ability to detect and respond to the chemical presence of fish predators seems to be weak at best (McPeek 1989).

Hydroperiod plays a major role in structuring not only odonate communities but also lentic aquatic communities in general (Wellborn *et al.* 1996). At one end of this environmental gradient are small pools that may persist for only a matter of days or weeks, whereas at the other end of the continuum are large lakes that endure for thousands of years. Wellborn *et al.* (1996) identify two important transitions that affect the structure of invertebrate communities along this gradient: a permanence transition and a predator transition. These transitions delineate three distinct habitat types: temporary habitats, permanent fishless habitats, and permanent habitats with fish. Odonate communities are present in each habitat type but the quality of these habitat types differs considerably for different odonate species, shifting community composition (Stoks and McPeek 2003). The predation regime shifts from dominance by invertebrates (especially large dragonflies) to vertebrates (especially insectivorous fish) with increasing system permanence along the hydroperiod gradient (Stoks and McPeek 2003, 2006).

Aquatic habitats along the permanence gradient can act as sinks or sources for certain odonate species based on their ability to cope with environmental constraints. Pools that persist only for a matter of days or weeks are effectively sinks for most odonate species unless eggs and/or larvae have the capability to endure long-term dry conditions or larvae are capable of developing extremely fast. Permanent habitats with fish predators, to the extent that they attract ovipositing females of the relevant species, tend to be sinks for species poorly adapted for co-existence with fish but sources for those compatible with this predator type.

3.3 Responding to risk

3.3.1 Lifestyles, hydroperiods, and predation regimes

A short hydroperiod imposes a significant abiotic constraint on larval development and has strongly influenced the evolution of life-history strategies in species that occupy habitats prone to drying. These habitats also generally lack fish predators; thus, the fitness benefits of exploiting this habitat type can be substantial. Odonate species exploiting these habitats rely on egg diapause, larval aestivation, and migration to cope with the constraints imposed by hydroperiod, issues addressed more thoroughly by Stoks *et al.* (see Chapter 4 in this volume). In temporary habitats, selection favours individuals that can develop rapidly, and species with this life-history trait tend also to be highly active in gathering required food resources.

In permanent habitats with fish predators, selection favours individuals with less active lifestyles, and consequently the duration of the larval stage for odonate species in this habitat type tends to be longer (Corbet 1999; Johansson 2000). This slow/fast lifestyle dichotomy is supported by a large number of studies with larval odonates (e.g. McPeek 2004; Johansson *et al.* 2006). Some Libellulids (e.g. *Pachydiplax longipennis*, *Erythemis simplicicollis*, and *Perithemis tenera*) appear to be particularly effective colonizers of temporary habitats, with some species able to complete larval development in as few as 4 weeks (Corbet 1999). Colonizing temporary habitats may also allow some species to complete more than one generation per year. Some species may be univoltine at northern latitudes and unable to exploit temporary ponds because environmental conditions do not allow larvae to complete larval development, but multivoltine at more southern latitudes where environmental conditions permit them to exploit habitats with limited hydroperiods. In between the ephemeral and fish-dominated extremes lie permanent fishless bodies of water where large dragonflies usually act as top predators (Johnson and Crowley 1980; McPeek 1998; Stoks and McPeek 2003). Species that possess the ability to complete larval development in temporary habitats are also common in permanent fishless systems.

In habitats lacking fish, odonates often function as top predators, particularly those highly active species that rely heavily on visual cues when foraging, but benthic sprawlers and burrowers are also prevalent is these habitats (Corbet 1999). Aeshnids such as *A. junius*, *Anax longipes*, and *Aeshna mutata* and large active libellulids such as *Tramea lacerata* (e.g. see McPeek 1998) have a considerable top-down impact on composition in North American odonate communities. Some other species (e.g. *Plathemis lydia*, *Enallagma aspersum*, *Enallagma boreale*, and *Lestes congener*) are able to persist with odonate top predators, whereas other species (e.g. *Epitheca cynosura*, *Celithemis elisa*, *Enallagma triviatum*, *Enallagma civile*, and *Lestes vigilax*) are found in much greater abundance in systems with fish top predators (Johnson and Crowley 1980; McPeek 1998; Stoks and McPeek 2006).

Studies by McPeek and colleagues (e.g. Stoks and McPeek 2003, 2006; Chapter 5 in this volume) have demonstrated elegantly that groups of *Lestes* and *Enallagma* damselflies segregate among ponds along the permanence gradient. *Enallagma* species require 10–11 months for larval development at temperate latitudes and are thus restricted to relatively permanent habitats; in contrast, some *Lestes* species are able to complete larval development in 2–3 months and can thus occupy habitats with a wider range of hydroperiods. Among both genera, there are species that have evolved to co-exist with dragonfly *or* fish predators.

But, in contrast to *Lestes* and *Enallagma* species, *Ischnura* species are able to co-exist with both fish and dragonfly predators (Johnson and Crowley 1980; McPeek 1998, 2004). *Ischnura* species are more vulnerable to predation than *Enallagma* species in a given habitat due to their higher activity level, but they also have faster developmental rates in these habitats (Pierce *et al.* 1985; McPeek 1998). Interestingly, higher activity levels in *Ischnura* species may not translate into higher feeding rates; rather, *Ischnura* species are superior at converting food into biomass under the risk of predation (McPeek 2004).

Flexible anti-predator behaviours allow some odonates to survive in the presence and absence of fish predators. *P. longipennis* is also a habitat generalist with respect to predator type (Johnson and Crowley 1980; Hopper 2001). In laboratory experiments, Hopper (2001) demonstrated that in the presence of fish chemical cues *P. longipennis* reduced activity level regardless of whether they were from ponds with or without fish. Similarly, in the absence of fish chemical cues, individuals from both habitat types actively moved away after a simulated attack. Habitat specialists largely excluded from habitats with fish, such as *A. junius*, tend not to respond as strongly to the presence of fish chemical cues. This may explain why *A. junius* is not successful in these habitats (Crumrine 2006) or may reflect a lack of selection pressure on a species that so rarely must contend with predaceous fish. In a similar vein, morphological plasticity may also influence the distribution of odonates across the landscape. Morphological plasticity, particularly for the size of abdominal spines which reduce vulnerability to fish predators, may allow some odonates to exploit habitat types with fish or invertebrate top predators (e.g. Johansson 2002). However, in species for which this trait is fixed and individuals have spines, it reduces the survival of individuals in the presence of invertebrate predators (morphological defences are described more thoroughly in Chapter 10).

3.3.2 The interference–predation continuum

Intraguild predation (IGP) and interference competition are particularly common in assemblages of odonate larvae, and their prevalence is strongly influenced by larval size distributions within and among populations (Hopper *et al.* 1996; Crumrine 2005). Consequently these interactions have a strong impact on the size structure and relative abundances of species within larval odonate communities. The prevalence of IGP (including cannibalism) and interference competition (both within and between species) blurs the distinction between competition and predation in odonate communities. Interference competition is traditionally viewed as a non-lethal direct interaction between individuals that has negative effects on feeding rates and potentially on growth and development as well. When interactions among similarly sized conspecifics are considered along a continuum from the absence of interaction at one end of the continuum to cannibalism at the other end, cannibalism can be viewed as an extreme form of interference competition. Cannibalism can also be viewed as a form of opportunistic predation that reduces the number of potential competitors and triggers both behavioural and density-mediated indirect effects in food webs. Some, but perhaps not all, of the local density effects resulting from cannibalism may be mimicked by injury and avoidance behaviour resulting from interference.

IGP combines elements of both competition and predation and occurs when two species (hereafter called species A and species B) interact as predator and prey, respectively, but also engage in competition for similar resources (Polis *et al.* 1989) (Figure 3.1). IGP is prevalent among odonates because of the wide range of body sizes usually present in larval assemblages. IGP almost always results from larger individuals consuming smaller heterospecifics and is thus almost exclusively asymmetrical, but the direction of IGP between two species may shift over ontogeny. For example, it may be possible for a large, late-instar damselfly larva (species B) to consume a small, early-instar dragonfly larva (species A), especially if the damselfly overwinters and the dragonfly completes development within a single season (Figure 3.1). However, during a majority of the warm season, individuals of species A may be much larger than species B, reversing the advantage. The overall net effect of species A on B and vice versa over the entire larval period has been difficult to address adequately in empirical studies (but see Wissinger 1992).

3.3.3 Theory and IGP

Simple mathematical models suggest that asymmetric IGP should persist only (1) when intermediate predators are more effective exploitative competitors than top predators for shared prey, (2) when top predators gain significantly from consuming intermediate predators, and (3) at intermediate levels of shared prey abundance (Holt and Polis 1997). At low levels of shared prey abundance, intermediate predators are predicted to exclude top predators via exploitative competition, while at high levels of shared prey abundance top predators are expected to exclude intermediate predators via apparent

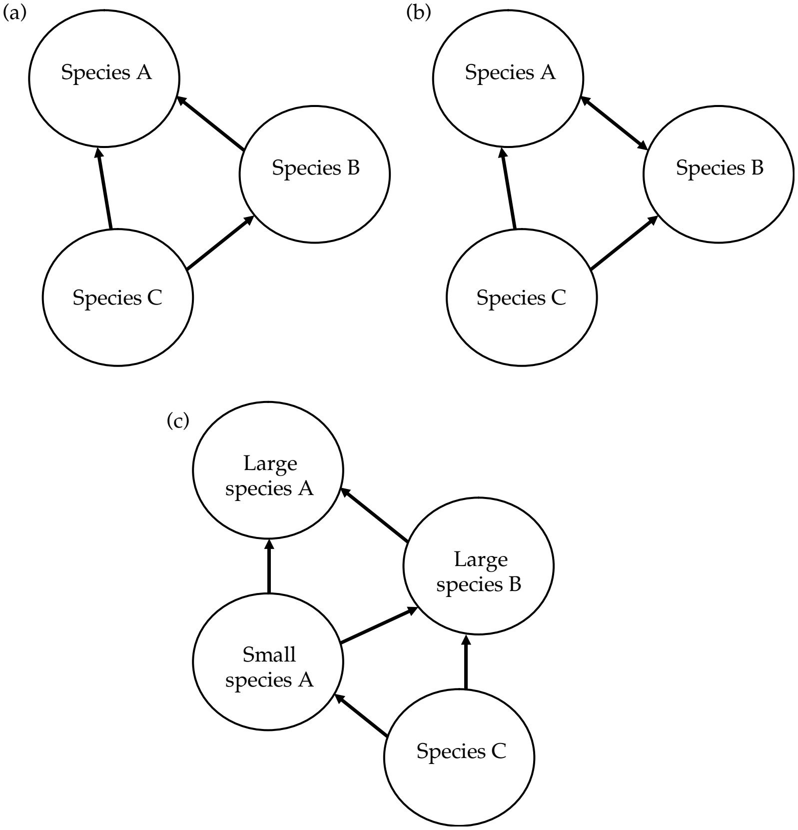

Figure 3.1 Simplified configurations of IGP in three-species food webs. Arrows indicate the potential flow of energy through each system. (a) Asymmetric IGP. Species A, usually a larger top predator, is capable of consuming species B, usually a smaller intermediate predator, and species C, the shared prey. The intermediate predator is only capable of consuming shared prey. (b) Symmetric IGP, also termed mutual IGP. Both predators are capable of consuming each other and may often be similar in size. (c) Size-structured IGP with two size classes of the top predator (species A). As predators grow they may also change their diet. Small species A consumes shared prey but larger species A exclude shared prey from their diet and include both conspecifics and large species B. This is one of many IGP scenarios that may exist in odonate communities with size-structured predators that undergo life-history omnivory.

competition (Holt and Polis 1997). Taken together, these conditions severely limit the conditions under which one would expect IGP to persist in natural communities; however, IGP is widespread and occurs in terrestrial, marine, and aquatic communities (Polis *et al*. 1989).

Some authors have hypothesized that elements of biological realism omitted from these initial theoretical formulations of IGP—such as size/stage structure, phenological asynchrony, adaptive anti-predator behaviour, and alternative prey—should promote co-existence between predators engaged in strong IGP. Both theoretical and empirical studies lend some support to this hypothesis (Holt and Polis 1997; Mylius *et al.* 2001; Crumrine 2005; Rudolf 2007). The considerable size structure present within and between species in odonate communities coupled with ontogenetic diet shifts (Werner and Gilliam 1984) may thus facilitate co-existence. Subsequent theoretical work by Rudolf (2007) suggests that size-structured cannibalism, likely to be prevalent in odonate communities, has much stronger effects on co-existence in IGP systems relative to the size-structured systems modelled by Mylius *et al.* (2001).

Explicit tests of the predictions of IGP theory are difficult to carry out with larval odonates, because experimental systems rarely meet the assumptions of mathematical models, and their predictions often address population dynamics over multiple generations or even evolutionary time scales. Furthermore, some researchers have suggested that conclusions of short-term experiments bear little relationship to predictions of equilibrium models of IGP, because many experiments only quantify attack rates and fail to consider conversion efficiency (Briggs and Borer 2005). Nevertheless, experiments and field studies with larval odonates have illuminated many basic features of IGP, and conclusions drawn from these experiments have greatly enhanced our understanding of the importance of IGP in structuring aquatic communities.

3.3.4 Cannibalism and IGP

In IGP systems, cannibalism could promote the survival of intermediate predators by (1) reducing the overall number of top predators that are recruited to larger size classes, (2) reducing encounter rates between small top predators and intermediate predators if small top predators reduce their activity level in the presence of larger conspecifics, and (3) reducing the attack rate on intermediate predators by top predators that feed cannibalistically (Crumrine and Crowley 2003; Crumrine 2005). This latter interaction is often termed an alternative prey effect and can have a positive impact on both intermediate predators and shared prey. In an IGP study using larval odonates, Crumrine (2005) demonstrated that intraspecific interactions between two size classes of larval *A. junius* top predators promoted the survival of an intermediate predator, larvae of the dragonfly, *P. longipennis*, relative to treatments with a single size class of *A. junius*. Ultimately, these interactions are likely to promote the co-existence of predators engaged in strong IGP (see Rudolf 2007).

3.3.5 Size structure, phenology, and IGP

In Central American neotropical tree-hole systems, IGP can be particularly influential in determining odonate community structure. Odonate predators that utilize these unique and limited habitats include the pseudostigmatid damselflies *Mecistogaster ornata*, *Mecistogaster linearis*, *Megaloprepus coerulatus*, and the aeshnid dragonfly *Gynacantha membranalis* (Fincke 1992). *M. coerulatus* deposits more eggs in large tree holes than small tree holes (Fincke 1994). Small tree holes (those under 1 litre) tend to be occupied by a single predator, and size-dependent IGP determines which odonate predators are likely to persist in these habitats (Fincke 1992, 1999). Individuals (in this case *Mecistogaster* species) that have a developmental head start generally cannot be trumped by individuals arriving later (Fincke 1994). Therefore *Mecistogaster* species tend to emerge from smaller tree holes (Fincke 1992). In larger tree holes, priority effects are less important because greater food availability allows later-arriving *M. coerulatus* (and presumably *G. membranalis* as well) to achieve high growth rates, surpassing *Mecistogaster* in size and eliminating them from these larger habitats via IGP (Fincke 1992). Surprisingly, smaller *M. coerulatus* can also sometimes kill larger *Mecistogaster* species in large tree holes (Fincke 1994).

Clearly, IGP in odonate communities is heavily influenced by the size structure of interacting populations and their spatial and temporal overlap. To capture the size-structure component present in many assemblages of larval odonates, Wissinger (1992) proposed an index of the opportunity (IOP) for IGP for a community of larval odonates inhabiting a pond in temperate North America. This index is preferable to conventional spatiotemporal indicies (e.g. Hurlbert's index L; Hurlbert 1978) for quantifying the potential for IGP in a speciose assemblage of predators because it considers encounters between species on a size-specific basis. This analysis elegantly demonstrates the influence of phenology on the potential for IGP (Wissinger 1992). Species that begin development earlier in a seasonal growth interval than others are more likely to act as intraguild predators in larval odonate communities (Benke *et al.* 1982; Wissinger 1992) and can sometimes exclude guild members that begin development later (Fincke 1992). Not surprisingly, *T. lacerata* and *A. junius* were identified as having strong potential to act as intraguild predators, particularly *T. lacerata* because of its greater habitat overlap with other odonates in the community. Both species are larger than most other odonates at a given instar and thus strongly influence overall odonate community structure.

Recent theoretical work on the effects of ontogenetic diet shifts on food web dynamics suggest that life-history omnivory can reduce the likelihood of co-existence in unstructured IGP systems (Van de Wolfshaar *et al.* 2006). These results contrast with the predictions of previous models and a thorough examination of the impact of life-history omnivory on community structure is necessary to develop a cogent theoretical framework for size-structured interactions in odonate communities.

3.3.6 Responses to predation risk

The degree to which larval odonates are susceptible to IGP depends on both anti-predator behaviour and habitat use. Laboratory and field experiments with several *Aeshnid* species demonstrate that smaller conspecifics tend to reduce activity level in the presence of larger conspecifics, but this can come at a foraging cost (Van Buskirk 1992; see also the modelling study of Crowley and Hopper 1994; but see Ferris and Rudolf 2007 for a counter example). This response is also true for odonate larvae in the presence of larger heterospecifics (Crumrine and Crowley 2003). Reduced activity level may also be coupled with a shift in habitat in the presence of predatory heterospecific and conspecific odonates. A number of laboratory experiments have shown that individuals vulnerable to IGP will spatially segregate themselves from larger individuals (Crumrine and Crowley 2003; Suutari *et al.* 2004). Field observations further support the hypothesis that spatial segregation between size classes promotes the survival of smaller conspecifics (Wissinger 1992).

3.3.7 Multi-predator effects

Predicting how multiple predators influence prey survival has been a persistent challenge for ecologists. Simply combining the effects of individual predators on prey survival can generate erroneous predictions of the effects of those predators when in combination (Sih *et al.* 1998). Deviations in prey survival above and below levels predicted by independent (multiplicative) risk models are termed risk reduction and risk enhancement, respectively (Sih *et al.* 1998; Crumrine and Crowley 2003). Experimental work indicates that risk reduction is quite common in aquatic communities and particularly so in odonate communities (e.g. Crumrine and Crowley 2003). Much of the experimental work examining these effects has focused on short-term responses, so using these results to explain longer-term population dynamics may be problematic.

In most studies with larval odonates, risk reduction occurs when asymmetric IGP leads to density-mediated indirect effects; that is, top predators reduce the density of intermediate predators thus indirectly promoting shared prey survival. Trait-mediated indirect effects are also mechanisms that may lead to risk reduction and occur when intermediate predators reduce activity level and foraging rates in the presence of top predators. Some studies suggest that the magnitude of trait-mediated effects is similar to, if not stronger than, density-mediated effects (Crumrine and Crowley 2003; Preisser *et al.* 2005). The strength of risk reduction in experimental studies should be stronger when IGP is mutual (i.e. the two predators in the system are capable of consuming one another). In this case, density- and trait-mediated effects can be transmitted through both predators and could have a substantial positive effect on shared prey survival. On the other hand, with little IGP or interference between predators, the higher overall predator density should reduce survival of shared prey. Although IGP is an interaction that involves both competition and predation between guild members, most IGP studies have focused on the predation component of this interaction. Examining the prevalence and intensity of competition in odonate communities outside of context of IGP has, however, been a fruitful area of research.

3.3.8 Interference competition and the threat of cannibalism

Theoretical models demonstrate that the risk of cannibalism and inter-odonate predation can translate into interference competition, with potentially slowed development and reduced survival to emergence (Crowley and Hopper 1994). Results of field studies support the general conclusion that both intra- and interspecific interference competition is a pervasive interaction in odonate communities and has been a critical factor in the evolution of odonate life histories (Crowley *et al.* 1987). Whether competition actually occurs between species with these attributes often depends on population density and prey availability.

A number of studies suggest that interference competition rather than exploitative competition plays a more influential role in structuring larval odonate communities, but the degree to which odonates are actually food-limited under field conditions remains to be fully elucidated. Larval damselflies are generally thought to be food-limited in the field (Crowley *et al.* 1987). Anholt (1990) contends that food limitation is probable based on overlapping size distributions of damselflies emerging from a pond and those emerging from experimental cages where density-dependent food limitation was observed. McPeek (1998), however, provides evidence from field enclosures in fishless systems that damselfly larvae are not food-limited, whereas those in ponds with fish are food-limited and engage in both exploitative and interference competition. The prevalence of interference competition in odonate communities thus suggests that larvae must take risks and expose themselves to competitors (and potential cannibals) to acquire food. From this perspective, food is limited because it not abundant enough in the microhabitats that would spare them exposure to enemies.

In neotropical tree-hole systems exploitative competition is more apparent in small habitats (under 1 litre) where food can be limited, and this may also restrict the number and size of individuals emerging from these habitats (Fincke 1992). In temperate systems, seasonal fluctuation in prey availability also affects competition within and between species, and competition can be more intense in spring rather than summer/fall, when prey is more abundant (Wissinger 1989). Experiments excluding fish predators suggest that fish can ameliorate the intensity of resource competition in odonate communities by limiting the density of potential competitors (Morin 1984). Although resource competition has been detected among larval odonates in several field and laboratory experiments, the impact of this interaction appears to influence larval growth rates more strongly than community structure (Wissinger 1992); but several studies have failed to detect evidence for exploitative competition in odonate communities altogether (Johnson *et al.* 1985; Pierce *et al.* 1985).

There is also some conflicting evidence for the prevalence and importance of interference interactions under laboratory and field conditions. Several studies suggest that high density may lead to reduced foraging rates via interference competition and mortality via cannibalism (Johnson *et al.* 1985; Pierce *et al.* 1985; Van Buskirk 1992), whereas other studies have failed to detect any relationship between interference interactions and foraging rate (Baker 1989; Anholt 1990). It is possible that variation among species is responsible for these conflicting results (Baker 1989).

Interference interactions that reduce prey consumption can have negative effects on larval odonates, but aggressive interactions between individuals, including cannibalism, are pervasive in odonate assemblages. Larval odonates are generalist predators that consume most prey items smaller than themselves, including other odonates (Corbet 1999). Cannibalism and intra-odonate predation can reduce the likelihood of exploitative competition between individuals (Polis 1981; Fincke 1994) and accelerate growth rates among surviving individuals (Hopper *et al.* 1996). When the threat of predation causes smaller conspecifics to reduce foraging activity, intermediate predators may benefit (Crumrine and Crowley 2003). Thus, cannibalism and intra-odonate predation may act to limit the population size of predators that have the potential to eliminate other species from communities and can act as a stabilizing feature at the community level (Rudolf 2007).

3.3.9 Studying larval communities in the laboratory and field

Despite a few exceptions (Morin 1984; McPeek 1998), the vast majority of the experimental studies examining the impacts of predation and competition in larval odonate communities have focused on the more logistically feasible small scales in space and time. Odonate community ecologists have generally relied on comparative approaches (e.g. examining species assemblages in systems with and without fish) to distinguish patterns in the field and have then conducted simple experiments to characterize the mechanisms underlying those patterns. Although this approach has been successful, a future challenge for odonate community ecologists will be to carry out whole-pond manipulations (e.g. Hall *et al.* 1970). For example, the impact of a cohort of migratory *A. junius* on odonate community structure could be estimated by covering some ponds in the landscape and preventing oviposition while leaving other ponds open for oviposition. Field stations with arrays of artificial and semi-natural ponds would be ideal sites to carry out these types of manipulations. This approach will allow ecologists to study the biotic processes that influence odonate community structure in a much more complex but potentially meaningful way.

3.4 Enabling reproduction

3.4.1 Consequences of larval odonate communities for adults

Up to this point, much of this review has addressed how interactions among odonate larvae affect larval growth and survival. Larval community interactions, however, may also have important consequences for the adults and their terrestrial communities. For example, larval conditions can affect the number of adults emerging, the size and condition of adults, or the timing of adult emergence (e.g. De Block and Stoks 2005; Knight *et al.* 2005). Body size and condition may be important for the ultimate fitness of males and females of many odonate species (e.g. Contreras-Garduño *et al.* 2006), and a shift in emergence time may put adults, or the offspring of those adults, at a disadvantage for competition and survival.

Few studies have addressed these potential connections between community processes at the larval and adult stages, with two notable exceptions. Knight *et al.* (2005) connected the consequence of fish predation on larval odonates with the reproductive success of terrestrial plants surrounding the ponds. They found that the insect pollinator communities visiting St. John's wort (*Hypericum fasciculatum*) varied qualitatively and quantitatively between ponds, with differences in both who visited (Diptera at ponds with fish, Hymenoptera at ponds without fish) and how many visited (lower visitation rates occurred at plants by ponds containing fish). These differences were a likely result of fish predation on larval odonates, because ponds with fish had fewer larval and adult odonates than ponds without fish, and pollinators were observed both to avoid plants at which odonates were present and to be eaten by odonates. Most interestingly, the changes in pollinator communities apparently affected the seed set of the plants, with *Hypericum* plants surrounding ponds without fish being significantly more pollen-limited than individuals surrounding ponds with fish.

Moreover, De Block and Stoks (2005) found that interactions among larvae may have consequences for adult characteristics. They found that larval *Lestes viridis*, when subjected to nutritional constraints, emerged relatively late and at a smaller adult size. These characteristics subsequently affected the mating success of adults. In addition, there were lasting effects of larval history on mating success that were not explained by size and time of emergence. Therefore, although De Block and Stoks (2005) varied the nutritional regime directly, it seems plausible that if interactions among heterospecific larvae caused the changes in nutritional intake instead, then similar consequences on adult fitness would be observed.

3.4.2 Interactions among adult odonates

As terrestrial adults, odonates serve as both predators (e.g. Kauppinen and Mappes 2003) and prey (e.g. Rehfeldt 1992). Consequently, in a broad community perspective, adult odonates have the potential to impact those prey and predator populations; however, to our knowledge, studies rarely have examined whether this impact is realized (but see the study by Knight *et al.* 2005 above). Also, although adults, like larvae, may attack both heterospecifics (Corbet 1999) and conspecifics (e.g. Cordero 1992), reports of such predation are relatively uncommon. This lack of information may indicate that IGP and cannibalism at the adult level are likely to have limited effects on odonate communities, or, as with the broader community effects, may simply indicate a lack of attention. Note that one important difference in any IGP that exists between odonate adults compared with odonate larvae is that size asymmetries will consistently favour one species over another, because the relative size of heterospecific adults will not vary with their age.

Within the odonate community, at the adult level the most important effects seem to be the result of interference competition. This competition may occur at foraging sites (e.g. Baird and May 2003), but typically occurs among territorial males at the breeding site and can take two forms. First, adults of one species may actually exclude heterospecific males from a breeding site (e.g. Moore 1964) or from preferred locations or perches within a breeding site (e.g. Worthen and Patrick 2004). The second form of interference is less 'intentional' and seems to result in mistaken species recognition by males. Adult males detect females and competing males primarily by vision, and, as a result, many species have colours and patterns on their bodies and wings that serve as species- and sex-specific signals (Corbet 1999). However, some signal similarity often exists among species, which, in combination with sensory constraints on discrimination and probable time constraints on a male to interact quickly with a female or intruding male (Switzer and Eason 2000), can lead to interactions among heterospecifics. Reports of heterospecific pursuits and territoriality are common among odonates (Corbet 1999), and these mistakes seem to occur most frequently among species similar in size and colour (Corbet 1999; Schultz and Switzer 2001; Tynkkynen *et al.* 2006).

Although reports of such 'mistakes' are common, few studies have examined the costs or consequences of these mistaken interactions. In one of the only studies of the costs of heterospecific interactions among adults, Singer (1990) studied the costs of imprecise discrimination among three sympatric species of *Leucorrhinia* dragonfly. He found that males of all three species would attempt to mate with heterospecific females and would chase heterospecific males both while defending their territory and while mate-guarding a conspecific female. Of these interactions, the most significant costs were incurred when a male was mate-guarding against a heterospecific male; in these cases, the energetic costs and risk of injury were relatively high because of high-intensity interactions, and the guarding male would occasionally lose his mate to a conspecific male while he was preoccupied with chasing a heterospecific male (Singer 1990). Singer (1990) proposed that although these costs may be high, sensory constraints on the discrimination ability of males may favour low levels of species discrimination, because those males that take the time to discriminate conspecifics from heterospecifics may miss their opportunity to defend their mate or territory.

If heterospecific interactions are costly among odonate adults, one would predict they might lead to evolutionary changes in behaviour, morphology, or life history in ways that minimized these costs. However, to date relatively few studies have tried to connect interactions among heterospecific adults with the evolutionary consequences of these interactions, and the future study of these consequences promises to be a fruitful area of research. For the interacting species, the consequences of their interactions may affect both selection on the sexual signals and the spatial and temporal distribution of adults. Below we discuss these two potential consequences.

3.4.3 Selection on sexual signals

The sexual signals of adults may currently be under natural or sexual selection (e.g. Grether 1997; Svensson *et al.* 2006). From a community perspective, one would predict that if costs of heterospecific interactions are high enough, then species for which such mistakes are highly likely will have signals that have been under divergent selection. This could be examined at a crude level by comparing signal similarity among sympatric versus allopatric species.

More directly, however, recent studies by Tynkkynen and colleagues (2004, 2005, 2006; Chapter 11 in this volume) on sympatric *Calopteryx splendens* and *Calopteryx virgo* have examined current selection on signals as a result of interspecific interactions. These species have pigmented spots on their wings, and wing-spot size is related to the amount of aggression directed mistakenly toward heterospecifics, with large-spotted *C. splendens* more closely resembling the spots of *C. virgo* and receiving more aggression from *C. virgo* males as a result. This heterospecific aggression has important effects on *C. splendens*; territorial spacing is related to the relative wing-spot size of neighbours and the number of territorial *C. splendens* increased after removal of *C. virgo* (Tynkkynen *et al.* 2006). Perhaps most interestingly, this aggression may result in negative selection on wing-spot size in *C. splendens*, because the size of *C. splendens* wing spots is lower with higher population sizes of *C. virgo* (Tynkkynen *et al.* 2004). Also, directional selection on *C. splendens* spot size was dependent on the relative abundance of *C. virgo*, such that at low relative abundance there was positive directional selection and at high relative abundance selection was positive (Tynkkynen *et al.* 2005). Furthermore, this pattern of directional selection was not present among populations in which *C. virgo* had been removed experimentally (Tynkkynen *et al.* 2005).

3.4.4 Spatial and temporal distribution of adults

If adults of one species exclude adults of other species from the breeding sites (Moore 1964) or from preferred locations within breeding sites (e.g. De Marco and Resende 2004), and if female oviposition behaviour is affected by male location, then adult interactions could drive the initial distribution of larvae. For example, we could speculate that these competitive interactions among adults may result in less preferred larval habitat being used by one of the species, which could have a negative impact on larval growth and survival. Furthermore, if larval movement is limited, any shift in the spatial distribution among species could affect which species are present to interact in any particular location. Therefore, either through decreased growth and survival or through simply not being present, the adult interactions within a breeding site may affect interactions among the odonate larval community, which could, in turn, affect population sizes and the characteristics of individuals (e.g. size, time of emergence, etc.) within those populations.

Adults may avoid costly heterospecific interactions by adjusting their breeding time, either within a day or within a season. Within a day, many species have characteristic times during which they visit the same breeding site (Corbet 1999). Differences among sympatric species in phenology (e.g. Ferreras-Romero and Corbet 1995) may be caused by a number of factors, but one possibility is avoidance of heterospecific interactions at the adult stage. Michiels and Dhondt (1987) found evidence that three sympatric *Sympetrum* species partitioned their adult activity via daily, seasonal, and habitat characteristics, and suggested that this was to limit heterospecific interactions at the adult stage. The question that clearly needs to be studied is whether temporal overlap, either within a day or within a season, is less for species that have the highest potential for negative heterospecific interactions as adults and to what extent the overlap is facultative, such that populations in which interacting species are both present exhibit less overlap than that among sites in which only a single species is present.

Answering such questions about temporal overlap would require at least two pieces of information. First, one would need an index of potential adult interaction, which could change depending on the focus. For example, if testing the idea that within-day partitioning was due to avoiding the costs of mistaken heterospecific pursuits, one could calculate either a qualitative or quantitative index based on size, colour, and pattern. Second, one would need to quantify the extent of temporal overlap of each species and relate this to their index of potential adult interaction. For a strong test of adult interactions driving temporal patterns, one could conduct removal or exclusion experiments, removing focal species from study ponds and comparing the partitioning of time to that found in ponds in which the adult odonate community was intact. If interactions among adults do drive shifts in phenology, then one would predict that the larval communities would differ as well. Differences in size and age distributions of odonate larvae would occur among communities with different temporal overlap, and those differences would, in turn, drive the type and extent of interactions among those larvae.

3.5 Bringing communities into focus

Conflicting evidence for the importance of various abiotic factors and biotic interactions in determining the structure of odonate communities is apparent. In some communities exploitative competition plays a significant role, but in many others interference, predation, and the direct and indirect effects of hydroperiod are clearly more influential. These conflicts are not unique to odonate communities, and developing a set of general laws that can explain community structure, in a broad sense, has been problematic for researchers. Elucidating the factors that determine community structure is possible for individual communities, but it is difficult to transfer this understanding to other communities because rules are often contingent on local conditions (Simberloff 2004). In fact, the apparent complexity of ecological communities has prompted Lawton (1999) to suggest that 'community ecology is a mess' and that researchers in this area should 'move on to macroecology'. Despite some researchers' frustration with community ecology, ecologists are making significant advances in developing a robust predictive theory of community ecology and several recent syntheses and reviews have proposed novel approaches to help further our understanding of community ecology (Hubbell 2001; McGill *et al.* 2006).

Neutral theory, based on the null assumption that the probability of survival and reproduction is identical for all species in a community and that trophically similar species are ecological equivalents, has recently challenged the long-established paradigm of niche theory (Hubbell 2001). Neutral community models have been effective at predicting a number of fundamental patterns in ecological communities, including species area relationships, species turnover, and the lognormal distribution of abundance. However, critics of this approach suggest that the assumption of ecological equivalency among similar species ignores the importance of functional traits in shaping an organism's fundamental/realized niche and its ultimate position within a complex, speciose community (McGill *et al.* 2006). Some have suggested that the niche and neutral approaches are two extremes at the end of a continuum and that community structure is not determined by either one of these processes alone (Leibold and McPeek 2006). Odonates can potentially be useful model organisms for addressing the importance of niche and neutral processes in community ecology. Some larval *Enallagma* damselflies appear to be ecological equivalents (McPeek and Brown 2000), and many larval odonate communities are comprised of species that differ very little in their morphological characteristics. Whereas most of the community-level studies with larval odonates have approached this issue from a niche standpoint, it will be important to examine how

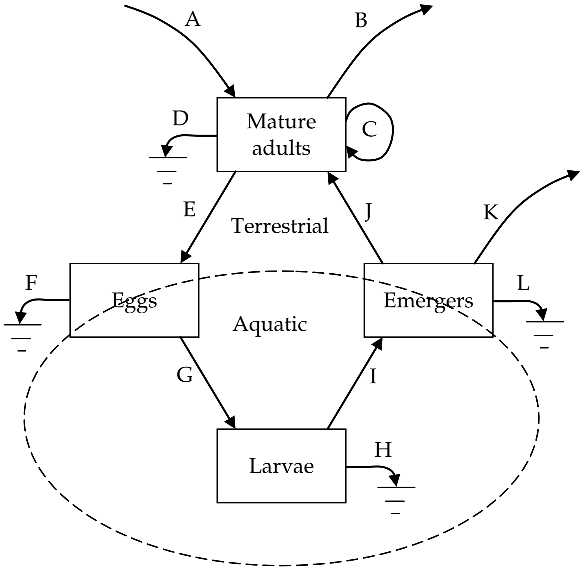

Figure 3.2 Odonate life stages and processes that determine local odonate community structure and dynamics. Arrows indicate dispersal (A, B, C, K), mortality (D, F, H, L), and life-stage transitions (E, G, I, J). The dispersal processes connect sites as a metacommunity at the landscape level, influencing, along with local emergence (J), the assemblage of mature adults at each site across the season; reproduction, oviposition, and hatching (E, F, G) strongly filter this distribution to produce the larval odonate community, further filtered by the risky aquatic environment (H) to produce a seasonal pattern of emergence (I). Emergers that neither disperse (K) nor die (L) close the loop to mature adults. The local odonate community may be well characterized by output from the aquatic system (i.e. the seasonal emergence pattern, strongly influenced by risk management) and by the seasonal pattern of mature adults (i.e. those with access to the site). Quantification of these two seasonal patterns across sites would greatly enhance our understanding of odonate communities.

neutral processes influence odonate communities. This approach may be particularly useful for communities that include many rare species, as some evidence suggests that neutral community models can effectively predict species abundance patterns for rare species in communities (Chave 2004). The neutral perspective has value but this does not necessarily mean that researchers should divert their attention from the traditional foci of community ecology. A potentially more fruitful approach to elucidating the factors that influence odonate community structure will be to consider both niche and neutral perspectives when examining patterns at the community level.

Perhaps the greatest challenge and opportunity for odonate community ecology is to determine the characteristics and implications of metacommunity structure. Almost all community ecology of odonates has focused on local communities, sometimes including comparisons of local communities, with little or no acknowledgement that these are connected by dispersal and other landscape features. Empirical difficulties are daunting, and yet it is the intersection of local and landscape processes

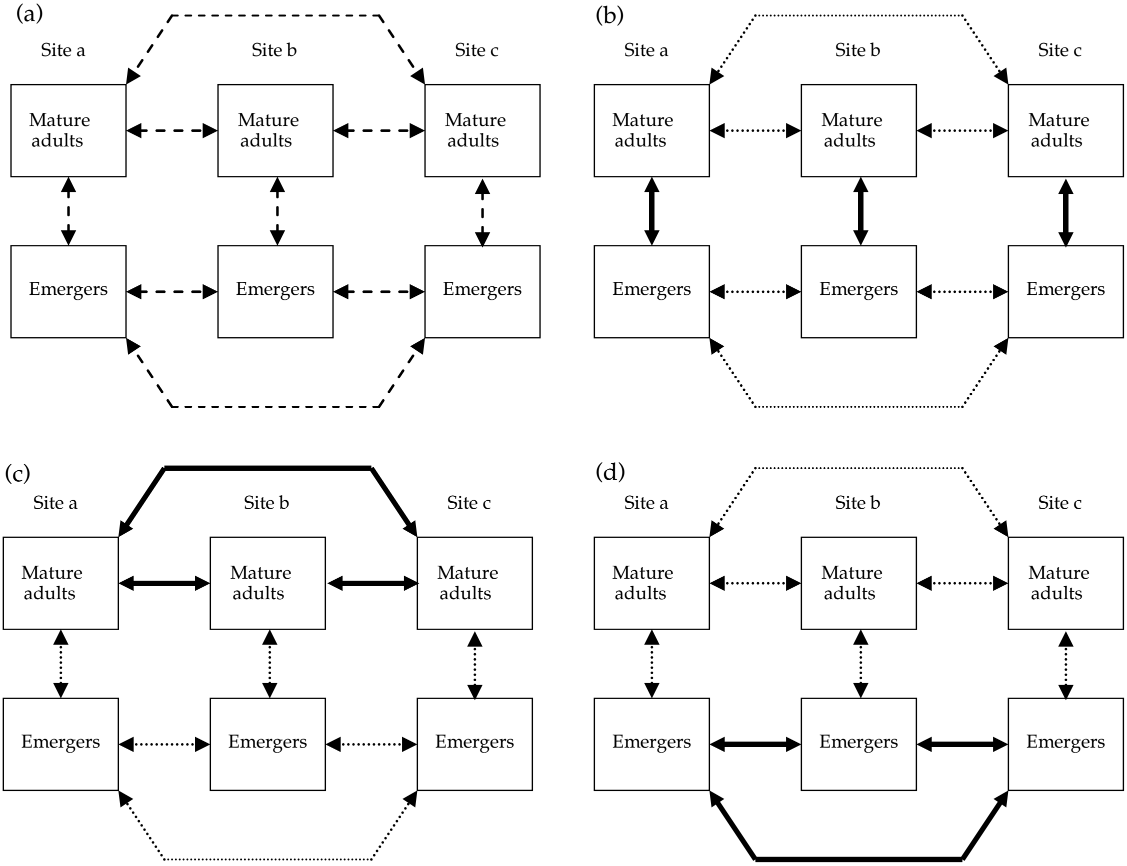

Figure 3.3 (a) Comparing seasonal patterns of mature adults and emergence across local odonate communites (e.g. sites a–c here) reflects the importance of processes that link emergers and mature adults within sites, mature adults between sites, and emergers between sites. (b) Here, mature adults at each site are tightly coupled with local emergence, and dispersal linkages and aquatic-system features fail to dominate, producing strong landscape heterogeneity. (c) When adults disperse sufficiently to homogenize the mature adults across sites, any divergence between sites is attributable to strong influences within the aquatic habitat, such as differences in hydroperiod or predation regime. (d) In some cases, when those dominant aquatic features are similar or identical across sites, it is filters acting between emergence and oviposition that account for between-site differences.

that shape anything we can really consider to be an odonate community.

The focus to date on site-specific larval assemblages and dynamics (Figure 3.2) has taught us much about 'aquatic odonate communities', though few studies examine directly the seasonal distribution of emergence as the community-level output from local aquatic systems. We also know something about 'terrestrial odonate communities' through studies of territoriality, mating, and oviposition in the context of multi-species assemblages; yet the seasonal distribution of mature adults as the indicator of access to the aquatic habitat is determined only rarely. Although much of the focus in odonate community ecology has addressed how larvae respond to risk, this may simply reflect the ease of working with this particular life-history stage and does not necessarily indicate that larval interactions have the greatest impact on odonate community structure. Furthermore, the relationship between the seasonal patterns of emergence and of mature adults across sites connected by dispersal (Figure 3.3) will contain an enormous amount of information about local compared with landscape processes, aquatic compared with terrestrial influences, and the role of predictable and unpredictable seasonal variation. Work in this area is severely lacking primarily because these types of studies are challenging from a logistical standpoint. Nonetheless, these studies are necessary to develop a more complete understanding of odonate communities.

Measuring the key rates (Figure 3.2) for at least some populations will enable the construction of models to show how seasonal patterns of emergence and mature adults across sites arise from the processes we observe. Comparisons with empirical data will highlight weaknesses in our understanding of this complex metacommunity. The potential for manipulating factors like predation regime, hydroperiod, and dispersal access may then enable predictions arising from models to be tested in natural or near-natural systems. This ambitious agenda should become more feasible as the need to consider communities across more realistic scales of space and time becomes ever more compelling.

The past 30 years have been an exciting period for the study of community ecology and odonates have played an important role in illuminating many of the features of fundamental ecological interactions. For many reasons odonates are excellent organisms with which to carry out experimental and comparative studies, and it is likely that they will continue to play a key role in the development of a more predictive theory of community ecology.

Acknowledgements

Portions of this chapter were written while PVS was on sabbatical at the University of Kentucky. We would like to thank the USDA NRI program for providing financial support and the Department of Biology at the University of Kentucky and Nicholas McLetchie for providing logistical support for his visit. The constructive comments of Volker Rudolf, Frank Johansson, and one anonymous reviewer greatly improved this chapter.

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CHAPTER 4

Life-history plasticity under time stress in damselfly larvae

Robby Stoks, Frank Johansson, and Marjan De Block

Overview

Time stress, such as imposed by seasonality, is a widespread and major selective force shaping life history in a wide variety of animal taxa. These insights were initially driven by theoretical models, and experimental empirical proof was lagging behind. Several crucial aspects of the models, like the role of behaviour and physiology in mediating life-history responses, long-term fitness costs, and the interactions between time stress and other stressors, have been explored almost exclusively using damselflies as model systems. Damselflies react to time stress imposed by seasonality by shortening their development time, and under certain conditions show an increased growth rate to avoid emerging at a smaller size. Increased foraging behaviour as well as an increased growth efficiency may underlie this accelerated life history. Both ecological and physiological costs of this accelerated life history have been shown: time-stressed larvae are less responsive to predators and hence suffer higher mortality by predation, and show larger mass loss during starvation and reduced investment in immune response and storage molecules. These life-history responses and costs may explain results from experimental field studies that time-stressed larvae suffer reduced lifetime mating success as adults. Future avenues of research include the implications of time stress at the community level. Further, the well-documented response to time stress in odonates may provide a good model system with which to study the macroevolution of life-history plasticity. Finally, predictive responses to global warming might become more precise if aspects of time stress are included.

4.1 Life-history plasticity

Life-history traits are traits closely linked to fitness and as a result have attracted much attention in both empirical and theoretical work (Roff 2002). Typically these traits show phenotypic plasticity where a given genotypic group expresses different values of these traits depending upon environmental conditions. Age and size at maturity are probably the most studied life-history traits as they are thought to be especially strongly linked to adult fitness (Roff 2002). Many studies showed these traits to be traded off against each other: a beneficial lower age at maturity typically comes at a cost of a smaller size at maturity, and vice versa. The resulting pattern in age and size at maturity stems from the relative rates of development and growth. For a long time, growth rate was thought to be maximized rather than optimized, which unavoidably results in the trade-off between age and size at maturity.

In the last two decades, it has become apparent that growth rate is not always maximized; that is, not all animals grow at their physiological maximum determined by food level and temperature (Nylin and Gotthard 1998). Instead, animals often optimize their growth rate, which has the potential to decouple the trade-off between age and size at maturity. Life-history theorists also started including adaptively flexible growth rates in their models (e.g., Rowe and Ludwig 1991; Werner and Anholt 1993; Abrams and Rowe 1996; Abrams *et al.* 1996a; Day and Rowe 2002). These models often show that the inclusion of flexible growth rates may change the predicted effects of various factors (e.g. predation risk) on life-history traits.

4.2 Time stress

One widespread environmental condition known to underlie life-history plasticity is time stress imposed by seasonality. Animals often face time stress in seasonal climates because they have to reach a certain stage before a certain time horizon (e.g. the onset of winter or pond drying). This is especially true for animals with a complex life cycle, with a discrete larval and adult stage often inhabiting a different habitat and where a discrete shift occurs during an abrupt ontogenetic transformation (metamorphosis) (Werner 1986). In line with predictions of theoretical models (Rowe and Ludwig 1991; Abrams *et al.* 1996a), animals under time stress typically speed up their development. As this shortens their growing period, they should ideally do this by also showing compensatory growth to keep size at metamorphosis as constant as possible (Abrams *et al.* 1996a). Many empirical studies indeed showed growth acceleration in time-stressed larvae (see Gotthard 2001 for an overview). However, this pattern is far from general and many studies did not find compensatory growth in response to time stress. Further, even in the presence of compensatory growth, animals typically show reduced size at metamorphosis (see below).

During their larval stage, animals are often not only confronted with time stress, but typically face several stressors simultaneously (Sih *et al.* 2004). These other environmental conditions, like food shortage and predation risk, may also shape optimal age and size at maturity, and life-history theory has made significant steps towards predicting how life-history transitions will be affected jointly by both time stress and biotic factors (Ludwig and Rowe 1990; Rowe and Ludwig 1991; Werner and Anholt 1993; Abrams and Rowe 1996; Abrams *et al.* 1996a). Empirical studies that have included time stress and at least one biotic factor have for a long time lagged behind the theory. So far, many studies have focused on time stress in damselflies (see Table 4.1).

4.3 Adaptive life-history response to time stress in damselflies

Damselflies have a typical complex life cycle and have been shown to be elegant model systems with which to study life-history plasticity to time stress. Like most other insects (Nylin and Gotthard 1998), they use photoperiod to assess the progress of the growing season, which allows elegant experimental manipulation of the perceived time stress. Moreover, and in contrast to, for example, butterfly larvae, their foraging behaviour can be scored easily, which opens the possibility to study the mechanisms underlying life-history plasticity. Further, their larval and adult ecology and the fitness implications of age and size at emergence in terms of survival and sexual selection are relatively well known (see Chapter 5 in this volume). As we will further illustrate, several crucial aspects of the life-history models dealing with time stress, like the role of behaviour and physiology in mediating life-history responses, long-term fitness costs, and interactions between time stress and other stressors, have been explored almost exclusively using damselflies as model systems.

Most studies on time stress in damselflies have looked at time stress associated with the progress of the growing season and this will be the main objective in our chapter. The pioneering work was done by Corbet (1956), Lutz (1968, 1974), and Norling (1984a, 1984b). These authors did not manipulate the progress of season in their experiments and the main focus was on development per se, with little focus on evolutionary ecology. A few studies have focused on pond drying (Table 4.1), and these studies have shown no or apparently non-adaptive responses. Fischer (1964) reported that the temporary-pond *Lestes dryas* and *Lestes virens* did not react to cues associated with pond drying. In a study where pond drying was mimicked by removing water from large tubs, *L. viridis* responded to pond drying with exactly the opposite life-history response as predicted by theory (Abrams *et al.* 1996a): larval development rate and growth rate were reduced (De Block and Stoks

Table 4.1 Overview of published studies in damselfly larvae reporting effects of time stress on life history (age, mass and size at emergence, and larval growth rate). When another stressor was also studied, the table indicates how this other stressor affected the response to time stress. Effects of time stress are coded as an increase (↑), decrease (↓), or no effect (=). When the other stressor did not affect the response to time stress, this is indicated as (0). Empty cells denote that the effect was not reported.

Species	Time stress	Other stressor?	Age	Mass	Growth rate	References
Calopteryx splendens	Date of F–2[a]	Food	↓ (0)	↓ (fatless) (0)		Plaistow and Siva-Jothy 1999
Enallagma cyathigerum	Photoperiod		↓	↓ (size =)	= (size ↑)	Strobbe and Stoks 2004
Lestes congener	Photoperiod		↓	↓		Johansson and Rowe 1999
Lestes sponsa	Photoperiod		↓		↑	Stoks *et al.* 2005
Lestes sponsa	Photoperiod	Predator	↓ (less with predator)	↓ (0)	↓ (0)	Johansson *et al.* 2001
	Photoperiod	Food	↓ (high food) ↑ (low food)	= (0) ↑ (0)	= (0) = (0)	
Lestes viridis	Pond drying		↑	=	↓	De Block and Stoks 2005b
	Hatch date		↓	=	↑	
Lestes viridis	Photoperiod	Food	↓ (0)	↓ (only early hatched) ↑ (only in late photoperiod)	↑ (only late hatched)	De Block and Stoks 2005a
	Hatch date		↓ (stronger at high food)	↑ (only at high food)	↑ (more late photoperiod) ↑ (more at high food)	
Lestes viridis	Photoperiod	Food	↓ (only at low food)			Rolff *et al.* 2004
Lestes viridis	Photoperiod	Food	↓ (stronger at high food)	↓ (0)	↑ (only at high food)	De Block and Stoks 2004a
Lestes viridis	Photoperiod		↓	↓	=	De Block and Stoks 2004c
	Hatch date (laboratory)		↓	↑	↑	
	Hatch date (field)		↓ (only in high-food pond)	↑ (only in high-food pond)	↑ (only in high-food pond)	
Lestes viridis	Photoperiod		↓	=	↑	De Block and Stoks 2004b
Lestes viridis	Photoperiod	Temperature	↓ (0)	↓ (not at highest temperature)	= (0)	De Block and Stoks 2003
Lestes viridis	Photoperiod	Predator	↓ (stronger with predator)	↓ (0)		Stoks *et al.* 2006a
	Hatch date		↓ (stronger with predator)	↑ (stronger with predator)		
Lestes viridis	Photoperiod		↓	↓ (when both time stresses combined)	↑	Stoks *et al.* 2006b
	Hatch date		↓		↑	

[a] With F–0 being the final instar.

2005b). This was probably due to deteriorating growth conditions when water levels dropped in the experimental rearing tubs.

Studies looking at the effects of time stress associated with seasonality mainly manipulated photoperiod, some used differences in egg-hatching date or in the date when animals entered a certain instar (Table 4.1). Most studies on time stress focused on *Lestes* damselfly larvae, with a majority on *L. viridis* (Figure 4.1). However, also in genera belonging to other families (Calopterygidae: *Calopteryx* and Coenagrionidae: *Enallagma*) adaptive life-history responses have been observed (Table 4.1). Most of the studies looking at effects of time stress on life-history traits were done under controlled laboratory conditions. However, similar adaptive responses have been shown under more natural conditions in outdoor experimental tubs (De Block and Stoks 2005b) and in field enclosures in ponds (De Block and Stoks 2004c) (Figure 4.2). The emerging pattern is that damselflies react to time stress imposed by seasonality by shortening their development time, and under certain conditions show an increased growth rate to avoid emerging at a smaller size (Figure 4.3). Deviations of the general pattern do, however, occur and were observed mainly in experiments where time stress was crossed with other stressors (Table 4.1). Such deviations and the conditions under which they occur may inform about environmental constraints

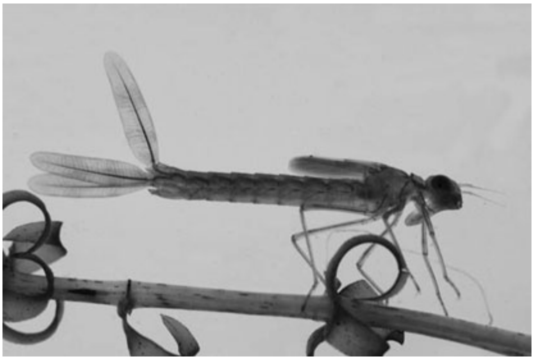

Figure 4.1 *Lestes viridis*, a univoltine species known to react strongly to time stress: close-up of a final instar larva. Photograph by Ine Swillen.

Figure 4.2 Overview of rearing methods to assess effects of time stress on life history: laboratory rearing experiment (left), outdoor tubs experiment (top right), and *in situ* enclosure experiment (bottom right).

that impede an optimal life-history response (see below).

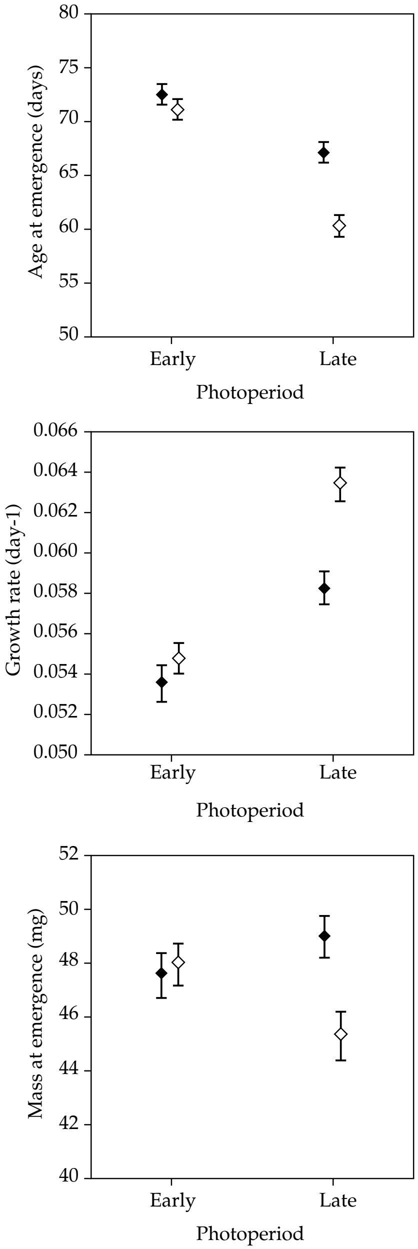

Figure 4.3 Life-history response in age, size, and growth rate to time stress associated with photoperiod and hatching date in the damselfly *Lestes viridis.* Black symbols denote larvae hatched early in the season; white symbols represent late-hatched larvae. Compared with larvae reared in the early photoperiod, larvae in the late photoperiod reduced age at emergence and increased growth rate, especially when late-hatched. In the late photoperiod, larvae emerged at a smaller mass, but only when late-hatched. Modified from Stoks *et al.* (2006b).

4.4 Constraints on an adaptive response to time stress

One reason that the expected response to time stress is not always observed is the presence of constraints, which can be environmental, intrinsic non-genetic, and intrinsic genetic. We here discuss some of the evidence obtained so far for these types of constraint.

4.4.1 Environmental constraints

With regard to environmental constraints, studies that looked at life-history responses to combined time and other stresses are especially informative. So far, time stress has been crossed with food level, temperature, and predation risk. A life-history response may only be possible under optimal energetic conditions, and therefore no adaptive response to time stress may be possible when food stress is present (Table 4.1). For example, *L. viridis* could only increase growth rate under time stress under high-food conditions but not with low food availability (De Block and Stoks 2004a). Similarly, in a reciprocal transplant experiment in two natural ponds, only in the pond with good growth conditions could animals under time stress accelerate development and growth rates (De Block and Stoks 2004c). A particularly striking finding was the later age at emergence under time stress in *Lestes sponsa* at low food, whereas the expected earlier emergence under time stress was found at high food (Johansson *et al.* 2001). This suggests that the larvae at low food were so limited in energy that they tried to delay emergence until the next year. Similar to food stress, an adaptive growth response may only be possible under optimal thermal conditions (Gotthard *et al.* 2000). The only study on this topic performed with damselflies so far could not confirm this: *L. viridis* larvae did not show a growth increase under time stress at any of the three experimental rearing temperatures (De Block and Stoks 2003). Potentially, other constraints were present that limited this response.

Another interacting environmental variable may be predator stress, as the optimal predicted responses to time stress and predator stress in terms of development and growth rates are in opposite directions: an acceleration under time stress and a deceleration under predator stress (Abrams and Rowe 1996; Abrams *et al.* 1996a). As expected, both stressors had opposing effects on the life history of *L. sponsa* larvae, with a trend for a smaller reduction in age at emergence under time stress when predatory fish cues were present (Johansson *et al.* 2001). In the only other study looking at the combined exposure to time stress and predator stress, however, the opposite pattern was found in *L. viridis* (Stoks *et al.* 2006a): larvae under predation risk showed a stronger reduction in age at emergence in response to time stress. Under predation risk emergence was considerably delayed, and this probably urged for a stronger life-history acceleration under time stress compared with the larvae reared without predation risk. The differences between the studies may reflect species differences in their willingness or ability to increase risk taking under time stress, where *L. viridis* may be prioritizing time stress above predator stress. In line with this, development times are considerably shorter in this species than in *L. sponsa*.

4.4.2 Intrinsic constraints

Developmental constraints may mean that under some conditions animals can no longer further accelerate their life history. For example, under time stress *L. viridis* reared on low food accelerated development whereas those on high food did not (Rolff *et al.* 2004). This was explained by the fact that animals on high food already had a short development time (*c.*60 days), so developmental constraints probably precluded larvae of shortening this period even more.

Genetic constraints that may impede the predicted optimal life-history response to time stress have also been demonstrated. For example, no genetic variation in plasticity in age at emergence to time stress was detected in *L. viridis* (De Block and Stoks 2003). Although an adaptive reduction in age under time stress was present, the reduction may have been larger if not genetically constrained. Positive genetic correlations between the same life-history variable across time-stress treatments have been reported for age at emergence and growth rate (based on mass) in the damselfly *Enallagma cyathigerum* (Strobbe and Stoks 2004). This means that selection to reduce age at emergence and increase growth rate under time stress probably also reduces age at emergence and increases growth rate in the absence of time stress. Although these changes would be beneficial under time stress, they may shift animals away from the optimal phenotype in the absence of time stress. For example, growing too fast may be costly in terms of starvation risk and predation (see below), and these costs may only be acceptable under time stress. Also genetic correlations between different traits in the same time stress treatment may constrain the evolution of an adaptive response to time stress. For example, age and mass at emergence were positively genetically correlated under time stress in *E. cyathigerum* (Strobbe and Stoks 2004). This reflects the well-known trade-off between the two life-history traits (Roff 2002). Under time stress, it seems imperative first to reduce development time, and in the presence of this genetic trade-off this inevitably results in the cost of emerging with a reduced mass. Interestingly, the above-mentioned genetic constraints were only present for growth rate based on mass and mass at emergence, and not for growth rate based on size and size at emergence. In line with a scenario of genetic constraints, larvae under time stress did show the expected increase in growth rate in size and avoided emerging at a smaller size, but did not show an increase in growth based on mass and emerged at a smaller mass (Strobbe and Stoks 2004).

4.5 Mechanistic basis of the life-history response to time stress

The life-history response to time stress seems to have an important behavioural and physiological component. Several studies on damselflies have so far jointly quantified a life-historical and behavioural response to time stress. Three of these studies (Johansson and Rowe 1999; Johansson *et al.* 2001; Stoks *et al.* 2005) showed the expected increase in activity under time stress manipulated through photoperiod. Despite this increase in activity, the Johansson and Rowe study showed that larvae with similar growth rate differed in development rate. This suggests that the increased activity, which may translate into a higher growth rate, does not necessarily result in faster development. One study (De Block and Stoks 2003) could not detect an effect of time stress on activity. However, in this study general movements were scored in the absence of food, which may not accurately reflect foraging activity.

Stoks *et al.* (2005) demonstrated a physiological mechanism underlying the life-history response to time stress. They evaluated growth efficiency; that is, the efficiency with which ingested food is transformed into body mass. Under time stress, *L. sponsa* larvae could speed up growth rate not only by ingesting more food but also partly physiologically by converting more ingested food into body mass. The latter was not due to a higher efficiency of assimilating ingested food as this efficiency decreased, probably because of a reduced gut passage time associated with the higher activity levels. Instead the increased growth efficiency was due to an increased efficiency to convert assimilated food into body mass. This suggests that larvae under time stress increase their energy allocation towards growth rate, away from other energy-demanding processes (see below).

4.6 Fitness implications of responding to time stress

Optimality models typically consider only size and timing of the life-history transition to be optimized, because these are assumed to tightly couple stressors during the larval stage with adult fitness (overview in Day and Rowe 2002). Both age and size at maturity have indeed been shown to be important for fitness (reviewed in Nylin and Gotthard 1998; Blanckenhorn 2000). The typical response to time stress in damselflies, and most other animals—namely an earlier metamorphosis at a smaller size—has direct fitness implications. A lower age at metamorphosis should be beneficial under time stress associated with seasonality and pond drying. For example, earlier emerging females may have better oviposition sites; also, in species with eggs without diapause, the offspring of these females will hatch earlier and therefore have a size advantage, making them less vulnerable than later-hatched offspring in terms of cannibalism (Thompson 1997; Anholt 1994). A later emergence, however, does not necessarily translate into fitness costs (Anholt 1991; De Block and Stoks 2005a). A smaller size at metamorphosis has been shown to be disadvantageous in terms of both sexual and fecundity selection in damselflies (Sokolovska *et al.* 2000; but see also Thompson and Fincke 2002).

Two studies explicitly exploring the link between larval stressors and adult fitness showed that effects of larval stressors on survival in two *Rana* frogs (Altwegg and Reyer 2003), and on survival and mating success after attaining reproductive maturity in the damselfly *Enallagma boreale* (Anholt 1991), could be explained completely through size and timing of the life-history transition. In another study where larvae of the damselfly *L. viridis* were exposed to time stress and food stress, age and size at emergence did also explain variation in adult survival and lifetime mating success (De Block and Stoks 2005a). However, the larval stressors still also explained part of the variation in adult fitness, with lifetime mating success being lower in adults that experienced time stress or food stress as larvae (Figure 4.4). In other words, the two life-history variables typically included in optimality models (e.g. Rowe and Ludwig 1991; Abrams *et al.* 1996a), size and timing of the life-history transition, did not completely account for effects of time stress and nutritional stress on fitness. This indicates that the predictive value of traits such as age and size at maturity might be restricted. These results indicate that larvae may be optimizing not only these life-history variables but also other unmeasured variables, like investment in immune response and investment in energy storage. These unmeasured variables are very likely independent targets of selection, even potentially traded off against each other. Current life-history optimality models are only valid when larval stressors are completely captured by age and size at maturity. Therefore, these results strongly suggest that identifying variables that are under more direct selection and including them in optimality models is of primary importance to better understand and predict fitness effects of larval stressors and the evolution of life-history plasticity in response to stressors.

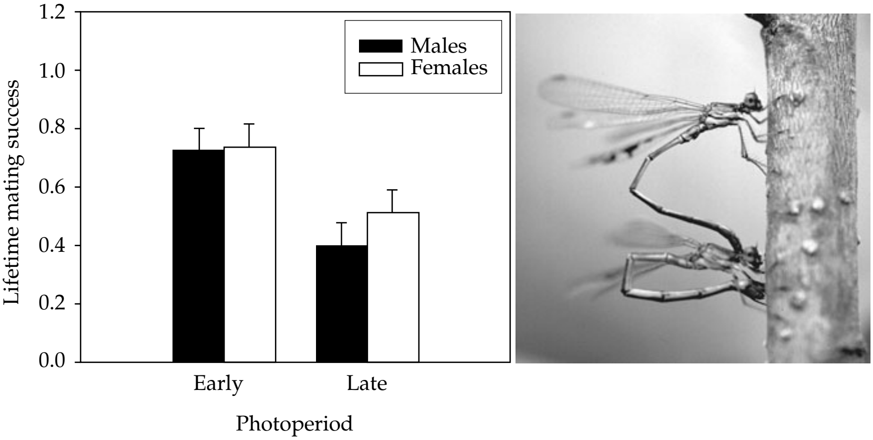

Figure 4.4 Effects of time stress on lifetime mating success of *Lestes viridis.* In both sexes, adults obtained from larvae reared in the late photoperiod had a lower lifetime mating success. The photograph shows a marked ovipositing couple reared as larvae under time stress and whose lifetime mating success was followed in a large insectary. Modified from De Block and Stoks (2005a).

4.6.1 Physiological costs

In a series of follow-up studies on the damselfly *L. viridis*, several physiological traits were identified that are good candidates to explain carry-over effects of larval stress into adult fitness. In the first study, where larvae accelerated development but not growth rate under time stress (Table 4.1), it was shown that both total fat content and activity of phenoloxidase (a key enzyme involved in insect immunity) were affected negatively and independently from age and size at emergence in freshly emerged adults that were reared as larvae under time stress (Rolff *et al.* 2004). Further studies also showed that increased growth rates induced by time stress may result in a lower investment in short-term (glycogen) and long-term (triglycerides) energy storage (Stoks *et al.* 2006b), and activity of phenoloxidase (and its precursor prophenoloxidase; Figure 4.5) (Stoks *et al.* 2006a). Both types of molecule have also been shown to be related to adult fitness in damselflies (Plaistow and Siva-Jothy 1996; Rolff and Siva-Jothy 2004), and as such they are likely to couple time stress with adult fitness. Unfortunately, studies directly demonstrating this assumed link between larval stressors and adult fitness are lacking so far. In the only other study looking at effects of time stress on investment in energy storage, no effect was found on size-corrected fat reserves in *Calopteryx splendens* (Plaistow and Siva-Jothy 1999). Time stress was, however, not manipulated here, and the date animals entered F−2 (with F−0 being the final instar) was used as a measure of the perceived time stress.

Other costs of a life-history response are likely to show up in the larval stage itself and as a result are also not captured by age and size at emergence. A well-known physiological cost of compensatory growth is a reduced ability to cope with starvation in the larval stage. Typically, faster-growing individuals lose more mass during a successive period of starvation than do slower-growing ones (Gotthard *et al.* 1994). Two physiological mechanisms have been hypothesized to underlie this (Gotthard 2001): (1) rapid growth may be associated with high metabolic rates, causing a faster depletion of energy reserves during starvation or (2) rapidly growing animals may allocate more resources to growth and less to energy storage that could be used during periods of food shortage. This type of physiological cost was detected in *L. viridis* that grew faster under time stress and proof was found for both mechanisms (Stoks *et al.* 2006b).

4.6.2 Predation risk

One likely ecological cost of time stress in the larval stage may be an increased risk of mortality by

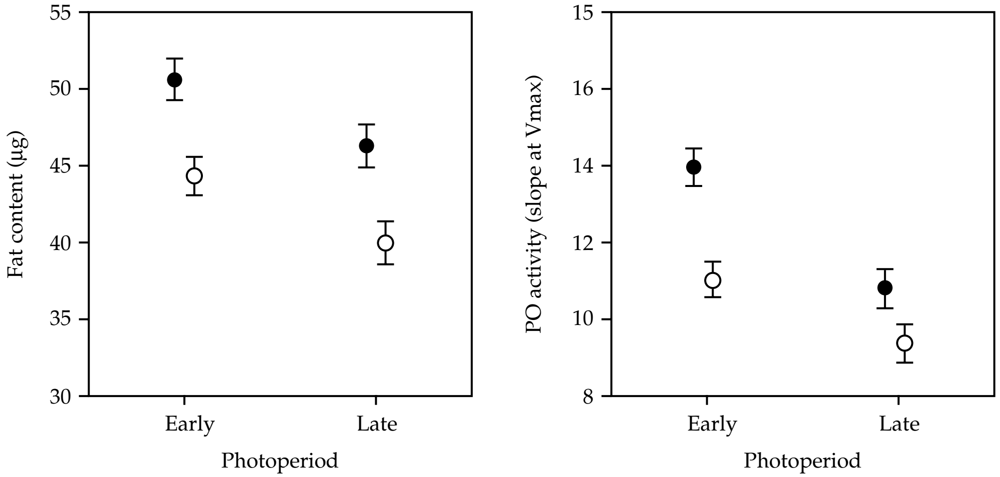

Figure 4.5 Physiological response in investment in energy storage (fat content) and investment in immune response (activity of phenoloxidase, PO) to time stress. Black circles denote larvae hatched early in the season; white circles represent late-hatched larvae. Compared with larvae reared at the early photoperiod, larvae at the late photoperiod emerged with a lower fat content and a lower PO activity, especially when late-hatched larvae. Modified from Stoks *et al.* (2006a).

predation. Increased behavioural risk-taking under time stress has been predicted by several models (Rowe and Ludwig 1991; Werner and Anholt 1993; Abrams *et al.* 1996a), and may be a general pattern causing higher mortality. As discussed above three studies showed increased activity under time stress in damselfly larvae; moreover, two of these studies showed the expected higher behavioural risk-taking under predator stress. Johansson and Rowe (1999) kept *L. congener* larvae in groups and showed a higher activity in larvae under time stress, which resulted in a higher risk of cannibalism compared with the non-time-stressed larvae. Similarly, higher cannibalism under time stress has been shown in *L. viridis* (De Block and Stoks 2004a). Further, an increased risk by fish predation under time stress was shown in *L. sponsa* (Stoks *et al.* 2005). Under fish predation risk all larvae reduced foraging activity, but larvae under time stress less so, which resulted in higher mortality rates by fish predation. In another study on *L. sponsa*, foraging increased but only marginally so for higher risk-taking under time stress (Johansson *et al.* 2001). However, in the latter study foraging activity was compared of larvae that were never and continuously exposed to a perch. When applying a short period of exposure to predators more pronounced anti-predator responses are to be expected (Lima and Bednekoff 1999), making it more likely to see differences in anti-predator responses among time-stress treatments.

4.7 Conclusions and suggestions for future research

The emerging pattern is that time stress imposed by seasonality has a profound influence on damselfly life-history traits, and this largely in accordance with optimality models. This has considerable implications for studies on effects of other stressors on life-history plasticity, as time stress may interact with these stressors. Ignoring time stress may thereby cause inconsistent and apparently maladaptive patterns when interpreting larval life-history responses to other environmental variables. For example, larvae may not show the expected life-history deceleration under predation risk when they are time-stressed (Stoks *et al.* 2006a). Effects of larval time stress may bridge metamorphosis and may affect not only adult fitness but also adult life-history patterns. For example, adult sexual size dimorphism decreased with temperature in the absence of time stress, but increased with temperature under time stress in *L. viridis* (De Block and Stoks 2003). More general, time stress has been proven a good model stressor to evaluate general life-history theory. For example, using time stress it could be shown that life-history traits and physiological traits may be decoupled to a large extent (Rolff *et al.* 2004; Stoks *et al.* 2006a), and that age and size at emergence do not completely translate larval stressors into adult fitness (De Block and Stoks 2005a). More studies that focus on the connection between the juvenile and the adult stage are needed. Such studies should measure both life-history and physiological traits at metamorphosis and then quantify their relative contribution to adult fitness.

Ramifications of time stress may go further than the auto-ecological level and ultimately play at the community level. Time stress may make larvae more willing to take risk in the presence of predators (Johansson and Rowe 1999; Stoks *et al.* 2005), and thereby shift the trade-off between growth and mortality by predation towards higher growth and higher mortality by predation. Therefore, under time stress lethal effects of predators on the less responsive animals may become more important than non-lethal effects (decelerated development and growth). The presence of strong non-lethal effects can make food webs inherently unpredictable (Werner 1992; Abrams *et al.* 1996b). Factors like time stress that affect the relative importance of lethal and non-lethal effects in food webs are therefore of great interest (Altwegg 2002). Future research could manipulate time stress to shift the relative importance of direct and indirect effects and thereby study responses at the community level.

The well-documented response to time stress in damselfly larvae may also provide good study systems for the micro- and macroevolution of life-history plasticity and their potential links. We know very little about population differentiation in the response to time stress (but see De Block and Stoks 2004c), nor about intrapopulation differentiation in the life-history reaction norms to time stress (but see De Block and Stoks 2003; Strobbe and Stoks 2004). Such information should be very valuable these days when global warming is more prominent than ever. Global warming may result in considerable fitness decreases if organisms are not able to adaptively shift their photoperiodic response (Bradshaw and Holzapfel 2006). Since damselflies show strong responses to time stress, they might be excellent model organisms for further studies on whether organisms can adapt their photoperiodic response to global warming. Integrated studies at inter- and intrapopulation levels may prove rewarding in understanding microevolution of time-stress reaction norms. Moreover, studying these reaction norms in congeneric species with known phylogeny opens the exciting possibility to reconstructing the macroevolution of reaction norms, a largely enigmatic topic (Pigliucci 2001).

Acknowledgements

Many thanks to Wolf Blanckenhorn and Sören Nylin for constructive comments on this chapter. MDB is a postdoctoral researcher at the Fund for Scientific Research-Flanders (FWO). Throughout the years, our work on time stress has been supported by travel and research grants from FWO and the Research Fund of KULeuven (OT and GOA) to MDB and RS, and the Swedish Research Council to FJ. We dedicate this chapter to the late Philip S. Corbet for his inspiring, pioneering work on odonate life histories.

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CHAPTER 5

Ecological factors limiting the distributions and abundances of Odonata

Mark A. McPeek

Overview

Many ecological processes contribute to regulating the distributions and abundances of odonate species. In local populations, mortality imposed by predators (including cannibalism and predation by other odonates) on larvae appears to be the dominant factor limiting abundances of many odonate species, although lower growth rates due to food limitation and stress responses to the presence of predators also contribute to limiting population sizes in most species that have been studied. Little is known about such processes in the adult stage of the life cycle, but parasites have been shown to limit adult survival and fecundity. Predation also causes many species to segregate among different water bodies with different top predators in eastern North America: different assemblages of odonate species are found at ponds and lakes that support centrarchid fishes than at fishless ponds and lakes. However, this pattern of species segregation between fish and fishless water bodies is not apparent in other parts of the world. Stream-dwelling odonates also show analogous types of segregation to different types of stream (e.g. small creeks compared with large streams and rivers), but the ecological processes that enforce this segregation is not known. Many unanswered questions about the ecological regulation of odonates makes them a continually fascinating group for study.

5.1 Introduction

Every budding amateur odonatologist quickly learns the type of habitats to search if he or she wants to find a particular species. If one is after a *Calopteryx*, then a slow-flowing stream with woody structures is needed. If an *Epitheca* is sought, then one goes to a lake with good macrophyte beds. *Gomphus* can be found around sandy-bottomed waters. This predictability in species distributions results from the fact that different species have different ecological requirements to maintain population abundances greater than zero.

Although individuals of species can sometimes be found in places where they cannot sustain a population (e.g. migrant individuals passing through an area, or a so-called sink population that is only maintained at a site by continual immigration from nearby thriving populations), the distribution of a species in the environment is determined largely by the distribution of suitable habitats to maintain source populations (i.e. populations that can be maintained without continual immigration) (Pulliam 1988). Local abiotic factors such as the temperature and water chemistry as well as biotic factors such as the abundances of various food resources, predators, and parasites all affect the survival, growth, and fecundity individuals at a particular site. At some sites, local ecological conditions will allow a species to have an adequate combination of survival, growth, and fecundity to maintain a source population. However, at other sites, a subset of these factors will make it impossible for the species to maintain a source population. Thus, the factors that limit local abundances are also those that shape the distribution of a species on the local landscape.

In this chapter, I review recent experimental and observational studies of the environmental features that shape the distribution and abundances of odonates among various water bodies. First, I reiterate the basic life cycle of the typical odonate and explore the various ecological factors that have been identified to influence survival, growth, and fecundity in various life stages. Then I examine how these same factors may limit the distributions of species among various habitat types. The results of this review highlight the importance of the larval phase of the life cycle to local population regulation, but they also highlight the glaring gaps in our knowledge about many aspects of odonate ecology.

5.2 What factors regulate population abundances locally?

Local population abundance is the outcome the demographic processes that impinge on all life stages of a species. The odonate life cycle has three primary stages: eggs, larvae, and adults (Corbet 1999). Eggs are deposited into water bodies, and may either enter a diapause phase to pass through harsh environmental conditions (e.g. many *Lestes* species in temporary ponds have diapausing eggs to pass through periods of pond drying) or begin developing immediately. After hatching, individuals emerge as aquatic or semi-aquatic larvae. Individuals can remain as larvae for weeks (e.g. those occupying vernal ponds) to years (e.g. semivoltine species in permanent waters) depending on species. At the end of the larval phase, individuals metamorphose into aerial adults that may survive for a few days (e.g. most species) to months (e.g. those species that pass the dry season in tropical climes).

Local population abundances are determined by the component demographic rates of each of these life stages (McPeek and Peckarsky 1998). These component demographic rates are: mortality rates in all three stages, growth and development rates in the egg and larval stages, and fecundity rates as adults. For the most part, these demographic rates are determined by how the phenotypes of individuals in a stage interact with the ecological environment in which they find themselves, but size and energy reserves at the end of the larval phase may also have some influence on adult fecundity (i.e. carryover effects from larval to adult stage).

Local population abundances can be quite constant from generation to generation, suggesting strong population regulation (Crowley and Johnson 1992). Population regulation occurs when the component demographic rates change in a negative density-dependent fashion. Negative density dependence means that a per-capita demographic rate changes in a way that will slow the rate of overall population increase—less positive or more negative—as population size increases. Thus, negative density dependence implies that mortality rate increases or fecundity decreases with population size.

5.2.1 Eggs

Little is known about demographic rates in the egg stage. Eggs certainly may die or fail to develop because they are unfertilized, or development may be arrested. However, we know nearly nothing about causes or rates of egg mortality in the field. One study found that 22.6% of the eggs of *Lestes disjunctus*, a species that oviposits endophytically in plants above the water, failed to hatch (Duffy 1994). Eggs of the stream-dwelling *Calopteryx splendens* developed faster and had lower mortality when oviposited into faster-flowing water than those placed in slow-flowing water, because encrusting algae was less likely to overgrow the eggs in faster water (Siva-Jothy *et al.* 1995). Although egg parasites and predators are certainly prevalent in many insect groups, these sources of egg mortality seem to be rare among odonates (Fursov and Kostyukov 1987). In addition, the degree to which demographic processes acting in the egg stage are density dependent is also unknown.

5.2.2 Larvae

Because many species spend the majority of their life as larvae, the larval stage is a demographically critical phase of the life cycle for determining both distributions and abundances in water bodies in a local area. Moreover, larval mortality due to predation is the overriding demographic force shaping abundances for most species. The predominant larval predators are fish (Morin 1984; McPeek 1990b, 1998; Johnson *et al.* 1995, 1996; Johansson and Brodin 2003; Stoks and McPeek 2003b), other odonates, including intraguild predation and cannibalism (McPeek and Crowley 1987; Van Buskirk 1989; Wissinger 1992; Wissinger and McGrady 1993; Anholt 1994; Hopper *et al.* 1996; ClausWalker *et al.* 1997; Ryazanova and Mazokhin-Porshnyakov 1998; Crumrine 2005; Ilmonen and Suhonen 2006), and other aquatic insects (Della Bella *et al.* 2005; Magnusson and Williams 2006; Wissinger *et al.* 2006). The identities of the dominant predators depend on the types of water body inhabited by a species (see below). Field experimental results indicate that up to 80% of larval mortality is due to the dominant predator with which a species lives (McPeek 1990b, 1998; Johnson *et al.* 1995, 1996; Stoks and McPeek 2003b), and that larval mortality rate due to predation increases with increasing larval odonate density (McPeek 1998). Also, the intensity of predation will depend on the structural complexity of the physical environment (e.g. the type of macrophyte species present) in which this interaction takes place (Crowder and Cooper 1982; Dionne and Folt 1991; Rantala *et al.* 2004; Warfe and Barmuta 2004). Thus, predation on larvae is probably the primary factor regulating local abundances of many odonate species (McPeek and Peckarsky 1998).

Parasites are prevalent in odonates, and are possibly significant sources of larval mortality and hindrances to growth, although the demographic effects of parasites have been much better studied in the adult stage (see below). Some of the major parasites that infect odonates as larvae are nematodes (Moravec and Skorikova 1998) and microsporidians (Kalavati and Narasimhamurti 1978), among others.

Larval growth rates are also very sensitive to environmental conditions and often change in a negatively density-dependent manner. Odonate larvae are often food-limited (Johnson *et al.* 1987; McPeek 1998), meaning that food levels are less than those that could sustain maximal growth rates. This limitation can be due to lower productivity of the habitat overall, or because of resource competition with other groups in the food web (Johnson *et al.* 1987, 1995, 1996; Baker 1989; Martin *et al.* 1991). Although limited food availability often slows growth, food levels are rarely low enough for starvation to be a significant source of mortality.

Larval growth rates also decrease with increasing larval density, which is the hallmark of competition (Johnson *et al.* 1985; Pierce *et al.* 1985; Crowley *et al.* 1987; Anholt 1990; McPeek 1990b, 1998; Fincke 1992b; Van Buskirk 1992; Stoks and McPeek 2003b; Suutari *et al.* 2004). These decreases may be caused by resource limitation. The other major factor limiting larval growth is in fact the presence of mortality threats such as predators and cannibals. Many studies have shown that odonate larvae grow more slowly in the presence of conspecific cannibals and other predators (Crowley *et al.* 1988; Martin *et al.* 1991; Johansson 1996; Schaffner and Anholt 1998; Stoks and Johansson 2000; Johansson *et al.* 2001; McPeek *et al.* 2001; Stoks and McPeek 2003a, 2006; Brodin and Johansson 2004; McPeek 2004; Dmitriew and Rowe 2005; Stoks *et al.* 2005a, 2006b). Larvae generally respond behaviourally to the presence of mortality threats by reducing activity, which may then alter their short-term rate of food intake (Dixon and Baker 1988; McPeek 1990a; Johansson 1992, 1993; Ryazanova and Mazokhin-Porshnyakov 1993; Wiseman *et al.* 1993; Shaffer and Robinson 1996; ClausWalker *et al.* 1997; Koperski 1997; Elkin and Baker 2000; Hopper 2001; Suhling 2001; Trembath and Anholt 2001; Stoks *et al.* 2003; Brodin and Johansson 2004; Brodin *et al.* 2006; Crumrine 2006; Stoks and McPeek 2006; Wohlfahrt *et al.* 2006).

These non-lethal effects of mortality threats are usually thought to be causally related: reduced short-term feeding rates cause reduced growth. However, recent studies have shown that this relationship may be only fortuitous. A number of odonate species show strong stress responses to the presence of mortality threats that can account for most or all of these decreases in growth rate (McPeek *et al.* 2001; Stoks and McPeek 2003a, 2006; McPeek 2004; Stoks *et al.* 2005a). Larvae feed at slower rates in the presence of predators, but continue to eat for longer so that over the course of a day they consume the same total amount of food. However, they are physiologically less able to convert ingested food into their own biomass in the presence of mortality threats. These stress responses can reduce larval growth rates by more than 50% in some species, and the interspecific variation in growth rates in natural populations can be explained by interspecific differences in the levels of these responses (McPeek 2004). At present, the physiological basis for this stress response is unknown.

One must also remember that processes influencing growth rate will also indirectly affect the total mortality that a particular cohort experiences by altering the length of the larval period (McPeek and Peckarsky 1998). Processes that slow growth and development rates will expose larvae for longer to potential mortality sources: larvae will spend longer time in smaller size classes and will thus be more susceptible to both cannibals and predators (McPeek and Crowley 1987; Dixon and Baker 1988; Van Buskirk 1992; Wissinger 1992; ClausWalker *et al.* 1997; Crowley 2000; Peckarsky *et al.* 2001; Crumrine 2005). In fact at both intraspecific and interspecific levels, larval growth and survival differ among groups in ways that suggest strong trade-offs between these two fitness components (Anholt and Werner 1995; Johansson 1996; McPeek 1998; Elkin and Baker 2000; McPeek *et al.* 2001; Stoks and McPeek 2003b; McPeek 2004; Brodin and Johansson 2004; Stoks *et al.* 2005a, 2005b).

Ecological factors that decrease larval growth rates may be most critical for species that live in water bodies that may potentially dry completely during the larval period. The effects of pond drying have been studied extensively in amphibians (e.g. Semlitsch and Wilbur 1988; Leips *et al.* 2000), but much less is known about odonate responses to drying. Many odonate species inhabit water bodies that dry periodically. For example, larvae of the giant helicopter damselfly, *Megaloprepus coerulatus*, inhabit water-filled treeholes and must develop rapidly to metamorphose before the water dries (Fincke 1994). Also, many species have life-history adaptations to occupy temporary ponds that may dry (Stoks and McPeek 2003b). In such habitats, rapid growth is crucial.

5.2.3 Adults

Although previous work has elucidated much about the factors that influence mating success, we know comparatively little about the population processes that operate in the adult stage to affect population growth rates. Mortality rates of adults are quite high for most species, with most individuals living on average only a few days or weeks after they metamorphose into adults (Fincke 1982, 1986, 1994; Anholt 1991, 1997; Córdoba-Aguilar 1994; Bennett and Mill 1995b; Cordero 1995; Marden and Rowan 2000; Beukema 2002; Thompson and Fincke 2002). Also, because of the differences in breeding tactics of males and females, females sometimes have higher mortality rates than males (Bennett and Mill 1995b; Anholt 1997; Marden and Rowan 2000; Beukema 2002; Kery and Juillerat 2004; Córdoba-Aguilar *et al.* 2006). Females of most species spend considerable time away from water bodies to forage and presumably to reduce harassment by males, but at the expense of greater mortality (Anholt 1997; Marden and Rowan 2000; Anholt *et al.* 2001). In fact, the primary determinant of female lifetime fecundity is the number of times a female is able to return to the pond to oviposit (Fincke 1982, 1986; Bennett and Mill 1995a; Cordero *et al.* 1998).

Food limitation on females may play a substantial role in limiting population abundances. At emergence, odonate adults have substantially depleted stores of fat and tend to lose weight over the first few days of the adult period (Anholt *et al.* 1991; Anholt 1997; Marden and Rowan 2000). The gonadal tissue of odonates does not mature until they are adults, so the number of eggs a female has to lay depends primarily on the amount of food she eats as an adult (Richardson and Baker 1997). However, we know almost nothing about the degree to which female fecundity is limited by resource availability or by competition over those resources.

One interaction about which we do know a great deal is how various parasites influence adult survival and reproduction. Odonates are hosts for many parasites, both internal and external, and these parasites can be substantially detrimental to the adults they infect. For example, adults infected with gregarines have lower fat content, are poorer flyers, and sometimes are shown to survive more poorly (Åbro 1996; Siva-Jothy and Plaistow 1999; Siva-Jothy *et al.* 2001; Marden and Cobb 2004; Canales-Lazcano *et al.* 2005; Córdoba-Aguilar *et al.* 2006). Likewise, ectoparasitic mites (Acari) frequently also reduce survival and fecundity of adults (Åbro 1982; Forbes and Baker 1991; Leonard *et al.* 1999; Rolff 1999; Rolff *et al.* 2001).

These findings about mortality and fecundity in adults strongly suggest great opportunities for adult demographic processes to operate in a density-dependent manner. In particular, competition for resources and parasitism can be strongly density dependent in other species, and so may make similar contributions to population regulation in odonate populations. This should be a fruitful area for research into population regulation in the future.

5.3 What factors set the distributions of species among water bodies?

Odonates can be found associated with just about every type of freshwater habitat in nature. Most odonate species are relatively strong flyers, and all species as adults have at least the capacity to travel in the order of one to a few kilometres to move between water bodies. However, each type of water body has a characteristic species assemblage that can typically be found there. Surprisingly, we know very little about the ecological factors that limit species distributions to particular habitats. Although adult choice may play a proximate role in setting limits, species distributions are probably ultimately set by processes acting on the aquatic larval phase. Some ecological limits are probably set by physical requirements, some by structural features of the habitat, and some by species interactions.

Although most species are restricted to fully aquatic environments, a few species around the world can be found as larvae in upland habitats (e.g. a few *Megalagrion* species are found in wet leaf litter) where relative humidity is always high (Polhemus and Asquith 1996). The larvae of a number of species develop in small water-collection sites scattered throughout forests (e.g. water that collects in epiphytes and bromeliads, discarded fruit husks, or treeholes; Polhemus 1993; Fincke 1994; Polhemus and Asquith 1996; Englund 1999).

A number of the most threatened and endangered species in North America, including the only odonate species on the US Endangered Species List (*Somatochlora hineana*; http://ecos.fws.gov/tess_public/SpeciesReport.do?groups=I&listingType=L), are often associated with bogs and wetlands that tend to be more extreme in terms of some physical factor. For example, *S. hineana* is restricted to intermittent carbonate-rich wetlands that overlay dolomite bedrock (Zercher and Team 2001). *Williamsonia lintneri*, a species that is listed as threatened or endangered in a number of US states, is restricted to low-pH fens and bogs (Westfall and May 1999). The rarity of these physically extreme habitats contributes to the rarity of species occupying these types of habitats, and habitat destruction only exacerbates their difficulties.

One of the primary environmental features that demarcate habitat distributions is the difference between flowing and standing waters. Characteristic assemblages of species can be found all along the river continuum, from the seeps and springs at the head of first-order creeks up to large rivers (Dijkstra and Lempert 2003; Hofmann and Mason 2005; Salmah *et al.* 2006). Many of these taxa appear to require specific habitat features found only in a particular range along this continuum; for example, *Hetaerina* damselflies in low-order, fast-flowing, rocky-bottomed creeks; *Calopteryx* damselflies clinging to woody roots and stems; burrowing gomphids in sand and mud substrates; and climbing coenagrionids and libellulids in slower-moving waters with macrophytes and emergent vegetation. One of the major physical factors that may limit species distributions along the river continuum is oxygen availability, with species requiring more oxygen being limited to faster-flowing waters in lower-order streams, and those that can tolerate lower oxygen concentrations found in larger-order, slow-flowing areas (Buss *et al.* 2002; Apodaca and Chapman 2004; McCormick *et al.* 2004; Hofmann and Mason 2005). Many other physical and biological factors also change along the continuum (Vannote *et al.* 1980; Power 2006), which may all contribute to limiting the distributions of species. Although we have substantial observational evidence for the impacts of these factors on odonate distributions, almost no experimental tests have been conducted (e.g. Leipelt 2005).

We best understand the factors setting species distributions among standing water bodies along the gradient of pond permanence, from vernal ponds that dry each year to large lakes that contain water essentially permanently. A major demarcation along this gradient is the frequency with which a pond may dry: if a pond dries at sometime during the year, any larvae present at that time will die. Some groups possess life-history features that permit them to inhabit these temporary waters (e.g. the desiccation-resistant, diapausing eggs of many *Lestes* species; Sawchyn and Church 1973). As a result, species compositions are very different at ponds that do and do not routinely dry during a year (Stoks and McPeek 2003b; Della Bella *et al.* 2005; Magnusson and Williams 2006).

Predators play a significant role in limiting the distributions of species to particular parts of both the stream and pond gradients. Fish play a substantial role in limiting some species to smaller streams (Power 1992; Wiseman *et al.* 1993; Dijkstra and Lempert 2003). However, the clearest experimental demonstrations of habitat limitation by various predators come from work done along the pond permanence gradient in eastern North America. In eastern North America, sunfishes (primarily *Lepomis* species) exclude large, active dragonflies (e.g. *Anax*, *Aeshna*, and *Tramea* species) from ponds and lakes where these fish are found. These large, active dragonflies are relegated to ponds and lakes where fish cannot colonize (Crowder and Cooper 1982; Werner and McPeek 1994), and a set of smaller, less active dragonflies (e.g. *Basiaeschna*, *Celithemis*, *Epitheca*) that are less effective predators co-exist with these fishes (Crowley and Johnson 1982; Blois-Heulin *et al.* 1990; Johnson *et al.* 1995, 1996; McPeek 1998; Johansson *et al.* 2006). In areas of the world where fish taxa besides centrarchids dominate (e.g. western North America, Eurasia) this pattern of segregation between fish and dragonfly waters is much less clear (Johansson and Brodin 2003; Johansson and Suhling 2004; Johansson *et al.* 2006; R. Stoks and D.R. Paulson, personal communication; M.A. McPeek, personal observation).

Species in a number of other genera (e.g. *Enallagma*, *Lestes*) are forced to segregate between ponds and lakes with fish or with large dragonflies based on their susceptibilities to these two predators (Pierce *et al.* 1985; Blois-Heulin *et al.* 1990; McPeek 1990a, 1990b, 1998; Stoks and McPeek 2003a, 2006). In these segregating taxa, species that are found only with fish typically are moderately active and do not swim away from attacking predators, which are effective phenotypes against fish predators but ineffective against dragonfly predators. In contrast, species that are found only with large dragonflies in fishless waters are more active and swim away from attacking predators, which are effective tactics against dragonflies but not against fish (Pierce *et al.* 1985; McPeek 1990a; Stoks and McPeek 2003a).

Functional and evolutionary studies have shown that these behavioural differences among taxa found co-existing with different predators are the result of adaptive evolutionary responses to living with those predators (McPeek and Brown 2000; Stoks *et al.* 2003; Stoks and McPeek 2006). Moreover, lineages of *Enallagma* are also adapted to live with dragonflies in fishless waters by evolving morphological and biochemical features that make them faster swimmers (McPeek 1995, 1997, 1999, 2000; McPeek *et al.* 1996). Some dragonfly species that co-exist with fish have also evolved the ability to inducibly grow long spines to deter fish predation (Johansson and Samuelsson 1994; Westman *et al.* 2000; Johansson 2002; Johansson and Wahlstrom 2002; Hovmoller and Johansson 2004; Mikolajewski and Johansson 2004; Mikolajewski *et al.* 2006). Thus, predators have been powerful agents of natural selection in the evolutionary histories of odonates and remain significant sources of mortality enforcing habitat distributions today.

5.4 Future directions

As this review attests, odonates have been a prime taxon for study of the ecological and evolutionary regulation of distribution and abundance. Ecologists and evolutionary biologists around the world have made tremendous progress in demonstrating how various ecological factors influence the mortality, growth, and fecundity of specific odonate taxa. However, the gaps in our knowledge of these processes remain vast. In this final section, I would like to highlight what I see as critical gaps to be filled.

To me, our largest gap in understanding is the role that demographic factors operating in the adult stage of the life cycle play in determining local population abundances. As the above review demonstrates, we fairly well understand the forces shaping mortality and growth rates of larvae in many species of dragonflies and damselflies. In addition, although a number of factors (e.g. parasites, predators) influencing adult survival and fecundity have been identified, the quantitative impacts that these factors have on population growth and regulation are largely unmeasured. The main reason for this gap is logistical. Larvae are relatively easy to work with, but anyone who has ever tried to follow a female odonate away from a pond to watch where she spends her time will attest to the difficulty of quantifying the factors that influence adult demography. However, manipulative experiments that quantify the effects of factors shaping adult survival and fecundity are sorely needed to close the loop on population regulation through the full odonate life cycle.

Another glaring hole in our understanding are the processes that regulate the distributions of species across stream orders and habitats. Experiments over the past 20 years have clearly identified predators and hydroperiod as the main ecological factors limiting species distributions among ponds and lakes (see above). Whereas these same factors may play a substantial role across stream orders as well, almost no experimental studies have been done to isolate and identify the factors that shape odonate distributions among streams of various sizes and with various habitat structures.

A personal desire is to understand the differences between lake assemblages dominated by centrarchid fishes and those dominated by other taxa of fish predators. As mentioned above, the checkerboard pattern of species distributions that are found for many odonate taxa between centrarchid dominated and fishless waters in eastern North America is much less evident in areas outside the historical range of centrarchids. Mechanistically, all fish seem to forage on odonates in the same way, but the intensity of that predation appears to differ. The lack of a clear fish/fishless pattern of prey distributions in lakes dominated by non-centrarchid fishes suggests that the reduced predation intensity from fish in these lakes results in a substantially altered community structure. Experimental comparisons of lakes in areas dominated by centrarchids with lakes in areas dominated by other fish taxa may provide great insights about the overall patterning of the lake food webs.

Finally, as with most taxa, we know much less about taxa in the tropics than their non-tropical counterparts. Tantalizing work by a few have shown the potential richness of ecological interactions that abound in the tropical odonate fauna (Fincke 1992a, 1992b, 1994; Suhling *et al.* 2004, 2005). The periodicity of a long wet and dry seasons may have profound effects on the types of life histories and ecologies that develop in the tropics and may have forced taxa to evolve very different ecological solutions to such problems that are unknown to many temperate taxa.

Acknowledgements

I am grateful to Phil Crowley and Andreas Martens for thorough reviews of a previous draft of this chapter which greatly improved the presentation. This chapter was supported by NSF grant DEB-0516104.

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CHAPTER 6

Migration in Odonata: a case study of *Anax junius*

Michael L. May and John H. Matthews

Overview

Although migration by Odonata has been recognized for well over 100 years, the phenomenon is still poorly understood. We argue that it may provide substantial new insight into the patterns, mechanisms, and evolution of insect migration in general, for at least two reasons. First, as aquatic/aerial carnivores dragonflies can broaden our view of migratory insects, most of which are terrestrial herbivores, and of the selective pressures to which they respond as well as their consequent genetic, physiological, and behavioural adaptations. We expect this to help differentiate common characteristics of migrant animals in general from those particular to certain groups. Second, because they are large, diurnal insects, they lend themselves to some techniques of direct observation that are hard to achieve in most other insects. Our focus here is on the best-studied North American migrant, *Anax junius*, the common green darner. We first discuss the behavioural and ecological attributes of migration and provide a brief descriptive overview of evidence for its occurrence in Odonata. We then describe recent research on migration in *A. junius*. Large-scale patterns of movement and the influence of weather are briefly reviewed. Geographic analysis of genetic structure and stable and radiogenic isotope composition and use of newly developed radio-tracking techniques has shed new light on the nature of migration in this species. Developmental phenology indicates the existence of early (resident) and late (migrant) cohorts at most sites, but genetic analysis does not indicate genetic differentiation of these groups. Apparently environmental cues and physiological responses to photoperiod and temperature engender migratory behaviour. Successful radio-tracking of individual *A. junius* has revealed alternating periods of migration and energy replenishment and responses to wind and temperature similar to avian migration. Little is known of orientation mechanisms during migration, and this should be a fruitful area of future research. Also, additional observations of reproductive behaviour en route and estimates of relative reproductive success of migrants and non-migrants should provide more detailed information on selective advantages and disadvantages and the historical evolution of migratory behaviour.

6.1 Introduction

6.1.1 What is migration?

6.1.1.1 Behavioural and ecological definitions and attributes

Formulating a meaningful, operational, and comprehensive definition of migration has historically been difficult. Few, if any, insects undergo a round-trip, seasonal passage to and from geographically distant regions, as in many birds and large mammals. Alternative definitions tend to focus on either ecological or behavioural criteria. The former emphasize the consequences of migration: movement into spatially distinct habitats or communities, frequently associated with different phases of the life cycle of the migrant (Hack and Rubenstein 2001). Corbet (1999), for example, describes migration as 'spatial displacement that entails…leaving the habitat where emergence took place and moving to a new habitat where reproduction ensues'. Such definitions are heuristic in focusing on adaptive aspects of migration in the context of life history. Migration normally functions to move individuals and populations from an initially suitable habitat that deteriorates with time to an alternative and currently more favourable habitat. Indeed, migration through space may be likened to behaviours that effectively show migration through time, such as diapause or the development of drought-resistant life stages in odonates.

However, for many insects, the origin, ultimate destination, and fitness consequences of migration are not known in detail, so ecological definitions are often hard to apply rigorously in practice. Behavioural criteria, therefore, may be more suitable. Dingle (1996, 2006), following Kennedy (1985), suggests: 'Migratory behaviour is persistent and straightened-out movement effected by the animal's own locomotory exertions or by its active embarkation upon a vehicle. It depends on some temporary inhibition of station keeping responses but promotes their eventual disinhibition and recurrence'. In many instances these criteria are most easily recognized in organisms moving *en masse*, and observations of mass movements have been important in understanding migration in dragonflies (Russell *et al*. 1998; Corbet 1999) as well as other insects, but note that neither definition requires that individuals migrate in groups. Mass movement may simply be our own visual clue that migration is occurring in a given species.

6.1.1.2 Ecological, genetic, and evolutionary consequences

We tend to assume that spectacular events like mass migration must reflect adaptations for movement from the migrants' place of origin to their eventual destination, but this might not always be the case. Rabb and Stinner (1979) suggested that large-scale movements of some important crop pests represent accidental wind-borne transport followed by local increase on concentrated resources, from which, however, the migrants have little chance of returning before succumbing to the hazards of winter or of migration itself. A different non-adaptive scenario was suggested by Dumont and Hinnekint (1973) for a well-known European dragonfly migrant, *Libellula quadrimaculata*. They documented large migrations at long intervals (approximately 10 years), typically following very large mass emergences, probably synchronized by delays due to cold spring weather. They hypothesized that large migratory swarms may result from non-adaptive movements set off by optical interaction-synchronization (i.e. individuals that see others in flight are likely to start flying themselves) potentiated by internal irritation due to high trematode parasite loads. Corbet (1999) supposed that occupation by *Anax junius* of northern areas where larvae cannot overwinter may have originated by swarms of tropical origin flying on prevailing winds toward areas of abundant rainfall (and hence favourable breeding areas) but overshooting their intended destination. Some must have reproduced in northern ponds, but perhaps less successfully than further south. If such occurrences were frequent and lead to substantial fitness reduction, however, strong selection would ensue for either avoidance of movement into temperate areas or adaptation to the northern environment.

To the extent that it is adaptive, migration must allow either exploitation of an ephemeral resource and/or avoidance of periods of adverse environmental conditions. This is the case for seasonally migratory monarch butterflies (*Danaus plexippus*), which breed in the northern USA and southern Canada on abundant milkweed during summer, then migrate to specific refuges in Mexico and California where conditions are suitable for adult diapause. Many tropical insects, including dragonfly species such as *Hemianax* (=*Anax*) *ephippiger*, in response to crowding or drought, fly or are transported downwind toward the intertropical convergence zone (ITCZ), where reliable rains renew vegetation and aquatic habitats. In both cases, insects are able to occupy resource-rich habitats for a portion of their life cycle, or sometimes for several generations, then move to more suitable regions when the original situations deteriorate (Dingle 1996; Corbet 1999).

6.1.2 Migration in dragonflies

6.1.2.1 Historical observations

Mass flights of dragonflies have probably attracted attention for millennia, but the first written record, to our knowledge, was by Hermann Hagen (1861). Observations of dragonfly migrations in North America date back at least to the late nineteenth century (Calvert 1893), and movements along the east coast and parts of the midwest were recorded and mapped by Shannon in 1916. Although large swarms naturally attract attention and are the subject of the vast majority of anecdotal reports (e.g. Osburn 1916; Borror 1953; Cook 1991; Daigle 1991; Glotzhober 1991), migrants may often occur as scattered individuals or small groups. Shannon (1916), Bagg (1958), Dumont (1977), and Sprandel (2001) reported movements of this sort.

Beyond intermittent observations of dragonflies on the move, the role of migration in their life history soon excited interest. As early as 1929 Calvert raised the possibility of two emergence groups in populations of *A. junius*. Robert Trottier (1966, 1971), working on *A. junius* in southern Canada, found that near Montreal larvae probably did not overwinter at all, although they were regularly found during summer, whereas in southern Ontario both early-emerging and late-emerging cohorts existed. The former emerged from late June to mid-July and finished oviposition by mid-August. The latter, evidently offspring of mature adults that appeared in April or May before any evidence of emergence, developed rapidly during the summer and emerged in late August to September. Adults then disappeared, presumably having flown southward. These observations clearly imply that migrations are a normal part of the life cycle that permits colonization of northern areas. This idea is supported by reports of apparently annual movements described along the eastern seaboard by Shannon and on the northern shores of Lake Erie by Nisbet (1960), Walker (1958), and Corbet (1984). Trottier's data also raised the possibility that the separate emergence cohorts could be genetically distinct since the adult emergence seasons did not overlap. A similar pattern is observed on the west coast of North America (D.R. Paulson, personal communication).

6.1.2.2 Which dragonflies migrate?

Russell *et al.* (1998) listed 18 probable North American migrant Anisoptera, of which nine were regarded as 'core' species that engage in annual seasonal movements. Others were thought to be irruptively sporadic migrants or based on doubtful reports. Corbet (1999) listed about 40 Anisoptera and 10 Zygoptera (all but one of the latter *Ischnura* spp.) worldwide as well-documented migrants. The best-represented anisopteran genera are *Anax* (seven species listed by Corbet) and *Tramea* (nine species), but several others include frequent migrants, for example, *Sympetrum* (five species) and *Diplacodes* (four species, including "*Philonomon*" *luminans*). Except for *Hemicordulia*, the known species are either Aeshnidae or Libellulidae, most of which breed in lentic waters. Not surprisingly, migratory species characteristically inhabit ephemeral to semi-permanent ponds that dry up frequently or unpredictably and generally support few or no fish.

These surely are not exhaustive lists, and the number of known migrants is likely to increase substantially with more focused study. Moreover, 'migration' in general tends to be conflated with long-distance migration over large spatial scales, and not all implicated species may engage in migration over tens of kilometres. Given that caveat, migration appears to be an exceptional life-history strategy among Odonata in general. On the other hand, given the evidence (see below) that migration is a facultative response in *A. junius*, we cannot discount the possibility that a small minority of individuals of mostly non-migratory species may migrate. Such varying behaviour could evolve by small adjustments to environmental cues and might account for occasional reports of species such as *Pachydiplax longipennis* among mixed aggregations of migrants (Russell *et al.* 1998).

6.2 The evidence

6.2.1 Movement patterns: visual observations

The Atlantic coast of North America from Maine at least to New Jersey, and probably the entire Atlantic seaboard, is a major migratory route (Shannon 1916). Other major hypothesized pathways run along the north shores of Lakes Ontario and Erie and thence into Ohio, along Lake Michigan, and into central Illinois, and on a broad front from Minnesota into eastern Oklahoma. Large swarms have been noted as well along the coast of the Gulf of Mexico from

Florida to Texas, along with a few observations of movement over the Gulf far from land. Numerous records also exist of migrating dragonflies, principally *A. junius*, at hawk watches along mountain ridges in the eastern USA (K. Soltesz, personal communication; Matthews 2006).

A consequence of migratory behaviour, however, may be that many individuals, responding to the same cues for initiation, orientation, and arrestment of flight may aggregate at 'leading lines' such as lake- or seashores (Russell *et al.* 1998). Corbet (1999) pointed out that aggregation may, in fact, be adaptive when reproduction occurs en route or at the destination, but it is also possible that aggregation of *A. junius* is entirely or partly a consequence of a tendency to fly downwind but to avoid being forced over broad expanses of water. Similar behaviour may also account for large accumulations of dragonflies, especially *A. junius*, during the fall at southwardly directed peninsulas such as Point Pelee, Ontario (Corbet and Eda 1969) and Cape May, New Jersey (Russell *et al.* 1998). A number of accounts suggest that some of these may redirect their flight around the water barrier (Shannon 1916; Russell *et al.* 1998; Wikelski *et al.* 2006), but other may cross expanses of water or remain trapped until they perish with the onset of winter. *Sympetrum corruptum* congregates similarly along the Pacific coast of Washington and Oregon during periods of east winds in fall (D. Paulson, personal communication, based on numerous accounts on the Internet).

6.2.2 Weather and climate

Weather profoundly affects when and how migrants travel. Many insects, even strong fliers like migratory locusts that actively maintain a constant flight heading, nevertheless actually move mostly passively with prevailing winds. Dumont (1977, 1988) and Dumont and Desmet (1990) presented evidence that *Anax ephippiger* migrations are mainly of this type. Other tropical migrants like *Pantala flavescens* probably fall into the same category. Some of these may fly at great height (Corbet 1984). Even species that closely follow distinct routes may take advantage of favourable winds created by particular weather patterns, as migrating birds do. Bagg (1958) and Nisbet (1960) confirmed apparent correlations of *Anax* migratory flight in New England and along Lake Erie, respectively, with the passage, in early fall, of cold fronts that brought winds that could assist migration. Numerous dragonflies, some known to be migratory, arrived with a fall weather front on the coast of Nayarit, in western Mexico (Paulson 2002). Russell *et al.* (1998) documented additional instances of the association of mass movements southward with the passage of cold fronts and of the arrival of spring migrants with southerly flows of warm air, but they noted that in some instances the relation of flights to frontal activity is not clear. One possible explanation is that migrating *Anax* may move beyond frontal systems that initiate aggregated flight, especially as cold fronts slow or stall in southern latitudes. Nevertheless, there has as yet been no strict quantification of a correlation of migration with weather fronts. Only very recently did Wikelski *et al.* (2006) quantitatively document that individual southbound migrant *A. junius* do fly with light northerly winds (see below).

6.2.3 Reproduction and refueling

The physical and physiological condition of migrants may be indicative of the adaptive function of migration. Many insect migrants are pre-reproductive, with females often pre-vitellogenic; this presumably assures that when they reach a favourable destination they retain maximum reproductive capacity (Johnson 1969; Dingle 1996). Migrating Odonata, too, are often described as teneral or 'fresh', but numerous exceptions are known (Corbet 1999). Many but not all of these occur during what Corbet has distinguished from migration as 'seasonal refuge flights'; these would be considered migratory under our behavioural definition. Corbet (1984) found that the great majority of apparent migrant species in Uganda and in Ontario, except *Sympetrum vicinum*, were pre-reproductive and laden with fat. Odonates that accumulate fat stores, as indicated by preserved specimens that are detectably greasy, are typically those of migratory genera such as *Anax*, *Pantala*, and *Tramea* (Paulson 1998).

Among *A. junius*, and perhaps other species, along the Atlantic seaboard of North America,

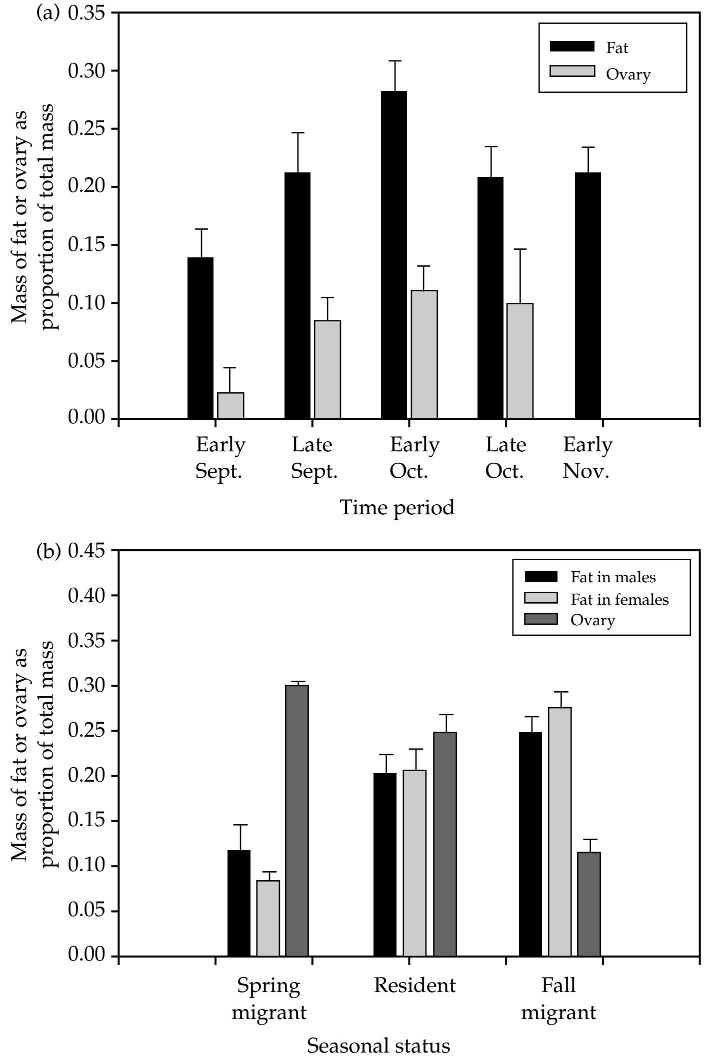

Figure 6.1 (a) Change with time in fat content and ovary mass as a proportion of body mass in fall migrant *A. junius*. Fat content increases markedly from early September to mid-October, then decreases slightly, suggesting progressive fat accumulation during early fall, possibly followed by reduction as migrants from farther north are collected later. Ovary size increases, then stabilizes, as the proportion of mature females increases with time; no females were collected in November, when remaining migrants are very few. (b) Change in fat content and ovary mass as a proportion of body mass with seasonal status in *A. junius* in New Jersey. Fat content is lowest in putative spring migrants and highest in putative fall migrants while ovary size is high in spring migrants and residents but lower in fall migrants. These patterns are expected if the former have already migrated a long distance and are mature while the latter are still accumulating fat and include many immature individuals.

evidence suggests that sexual maturity and fat stores increase progressively as the season advances, so that by mid-October most individuals are mature (Figure 6.1a). We have also seen pairs in tandem among migrants in early September. It appears likely that individuals initiate migration soon after emergence but mature en route.

Most migrants, regardless of taxon, accumulate, and, when possible, replenish, energy stores before or during migration (Dingle 1996). Fat content in *A. junius* is higher than in most dragonflies (<10%; Anholt *et al.* 1991; M.L. May, unpublished results) even among presumed non-migrants, although there is a trend towards still higher fat stores in fall migrants (Figure 6.1b). Notably, spring migrants in New Jersey have much less fat, as expected if they were near the end of their migratory journey. Likewise, the ovary size of spring migrants appears to be about as large as in non-migrants, whereas in fall migrants the mean is significantly less, although maximum values are similar. This would be expected if spring females were freshly mature whereas fall females included a mixture of mature and immature individuals. From radio-tracking data on individual *A. junius* (see below), substantial time during fall migration apparently is spent during days with little southward advance that are thought to be devoted to feeding.

6.2.4 The scale and adaptive basis of *Anax junius* movement

The study of why a species migrates requires a description of the movement itself; the latter is a prerequisite for untangling the former. Molecular techniques have a long history as a means of describing the geographic component of populations across generations. However, odonates are a group with few such applications to date. Species with relatively limited vagility have proven amenable to molecular approaches (Watts *et al.* 2004, 2007), whereas attempts to discern major patterns of movement in odonates suspected of high rates of long-distance movement have had little or no resolution, even on a multi-continental scale (e.g. Artiss 2004).

The first significant attempt to understand the scope of *A. junius* movement used a single mitochondrial locus, with samples of adults and a few larvae taken over a multi-year period from eastern Canada to Hawaii (Freeland *et al.* 2003). A nested clade analysis of haplotypes (Templeton 2004) showed a spiderlike pattern, with about half of all individuals falling into one of two near-identical haplotypes, with other lineages radiating out from this core. No significant spatial pattern was found that was related to this haplotype network, and Freeland *et al.* (2003) concluded that high rates of movement were blurring the ability to resolve population structure.

Several confounding issues may have reduced the effective power of this analysis. The collection site of adults potentially capable of moving hundreds or thousands of kilometres may not be a very meaningful predictor of their natal pond. Indeed, without additional information, a population structure study based on adults may not be able to explain geographic clustering. In a currently unpublished study Matthews, Mynhardt, and Cognato focused on a single 500-km transect of larvae from eastern Texas to northern Arkansas, collecting enough individuals at each site over a narrow temporal window to make both intra- and inter-site comparisons based on the sample mitochondrial DNA (mtDNA) locus (J.H. Matthews, G. Mynhardt, and A. Cognato, unpublished results). Even with this data-set, however, no population structure was evident. Indeed, the additional larvae only contributed a few new haplotypes, and the resulting haplotype network was very similar to that of Freeland *et al.* (2003), with no significant geographic patterning.

Similar patterns have been seen with other species in which many individuals migrate or disperse long distances, such as European eels (*Anguilla anguilla*). Early studies using coarse mitochondrial and allozyme approaches found no geographic patterns in species such as *A. anguilla* and monarch butterflies (*Danaus plexippus*), leading to the presumption that such vagile species were panmictic (Brower and Jeansonne 2004). Development of multilocus techniques using neutral markers such as nuclear microsatellite DNA has markedly improved molecular approaches to address such questions, finally applying a tool suitable to the task at hand. Thus, nine microsatellite loci were able to parse the high gene-flow rates of *A. anguilla*, estimating the Fst value (a standard measure of inter-population gene flow; Wright 1951) to be as low as 0.0002 (Wirth and Bernatchez 2001), nearing the theoretical limits of Fst. Microsatellite loci have recently been developed for *A. junius* (Matthews *et al.* 2007a), significantly increasing their value as a model for insect migration. Clearly, without developing markers for monarch butterflies that have a similar degree of resolution to microsatellite loci, we cannot make comparable inferences about gene flow and population differentiation.

Biomolecular studies of movement analyse *intrinsic* proxy markers in individuals (Webster *et al.* 2002). Mark–release–recapture methods epitomize *acquired* proxy markers, but new methods of studying naturally acquired markers have been developed since the early 1990s. The application of stable and radiogenic isotopic ratios to movement studies assumes that an environmental source such as prey items or ambient water contains recoverable information about the origin or path of movement. Most such studies have focused on birds, although stable isotopes have proven highly effective at measuring the scale of continental movement by monarch butterflies and distinguishing separate migration routes (e.g. Dockx *et al.* 2004).

A handful of studies have gone further and combined molecular genetic and isotopic ratio techniques to the same set of individuals, generating synergies between analytical techniques with high power over large regions for much less effort than required for direct tracking of individuals via telemetry or large-scale banding networks (e.g. Chamberlain *et al.* 1997; Clegg *et al.* 2003). As with isotopic ratio studies, these few multi-method studies have focused overwhelmingly on birds.

By applying two isotopic ratio techniques with microsatellite-based population genetics to a set of 180 adult *A. junius* collected during a 6-week window in the fall of 2005, Matthews (2007c) was able to demonstrate continental-scale movement by individual adults, some of which traveled over 2800 km before capture. Moreover, these distances were measured as net north–south distances traveled—displacement—rather than, as might be generated by telemetry studies, the length of the actual route followed. Mean southbound movement before collection was over 900 km. Although collection sites were all near coastal areas between 45 and 19°N latitude, more than 80% of individuals originated between 36 and 49°N, with more than 95% of individuals showing isotopic evidence of southbound movement. Genetic and radiogenic isotopic ratio evidence indicated that individuals at each collection site were 'mixed swarms', originating from multiple latitudes, parent populations, and largely inland sites although collection often occurred in or within sight of tidal wetlands.

Genetic data also indicated that near-panmictic conditions prevail, with continental-scale Fst values in the order of 0.04 for this group. Traditional population genetic estimates of spatial organization (e.g. a Mantel test) showed no isolation by distance. Bayesian population clustering of individuals into 'populations' based on microsatellite patterns (Pritchard 2000) again found no geographic pattern among southbound migrants. Moreover, a large study of the population structure of some 500 individuals, including 300 larvae, found an Fst value of 0.02 over the same spatial scale, a pattern also found when focusing only on the subset of larvae, at continental, regional, and single-pond scales (Matthews 2007d). That is, populations in single ponds contain a nearly random sample of the gene pool within eastern North America. Together, these data suggest (1) that the mixed swarms reflect largely random-origin assortments of individuals, (2) that these individuals are mating and ovipositing during large-scale movement, and (3) that mating and ovipositing are probably occurring multiple times for each individual en route. Eastern North America may reasonably be described as a single population.

Thus, *A. junius* population structure is shallow. In addition to the isotopic evidence mentioned above, a northern spring movement is also implied by the uniformity of genetic diversity across North America. Repeated major southbound movements, would eventually result in the gradual loss of genetic diversity over most of the northern part of the range (as in Hanski *et al.* 2004) unless compensated by an influx of alleles from elsewhere. When coupled with a northbound movement, however, especially if by a different generation of individuals, both genetic diversity and spatial homogeneity would be maintained. Moreover, since reproduction and ovipositing are coupled during the movement, long-distance displacement in *A. junius* is not made in a pre-reproductive/teneral adult stage seen in many migrant lepidopterans. This pattern generally goes against the 'classic' views of insect migration summarized in Dingle (1996), in which large-scale movement precedes or follows reproduction, focusing physiological resources on movement and reproduction in series rather than contemporaneously. In fact, the coupling of migration and reproduction may make *A. junius* migration a novel form of large-scale movement.

The combination of reproduction and long-distance movement suggests that whereas *A. junius* flight can safely be described as migration (Dingle 1996), this migration is not to a specific locality. Rather, movement is almost certainly from habitats declining in seasonal quality to more southern habitats with better average quality (but with a substantial variance in quality), suggesting migration as ecological movement, occurring at a landscape scale. The genetic evidence in particular suggests that *A. junius* movement spreads reproductive risk across multiple water bodies, minimizing threats from predation, intra- and inter-specific competition, and droughts. Given that *A. junius* larvae are most abundant in shallow, largely lentic wetlands that are often ephemeral and susceptible to even small shifts in precipitation on a regional scale, a bet-hedging strategy seems singularly appropriate as an adaptive basis for large-scale movement. Indeed, a large body of theoretical literature on dispersal polymorphisms would predict such patterns (e.g. Roff 1994). In a more speculative vein, the patterns and basis of *A. junius* migration may be representative of many taxa with a relatively non-dispersive aquatic larval stage and a highly vagile reproductive adult stage, such as many aquatic insects and amphibians.

6.2.5 The evolutionary ecology of dispersal phenology and phenotype

Although Calvert (1929) and Walker (1958) made scattered observations suggesting the presence of more than one emergence group, Trottier (1971) first clearly described distinct but sympatric spring-emerging and fall-emerging cohorts of *A. junius* in Caledon, Ontario. The spring-emerging group has been referred to as residents or non-migrants, and the fall-emerging group is normally described as migrants.

Resident larvae take up to 1 year between oviposition and emergence, with a diapause or quiescent period during the winter months. Thus, development proceeds through part of the fall before stopping or slowing and begins again the following late winter or spring. The migrant larvae develop over a much shorter period spanning only a few months between late spring and late summer or early fall (Figure 6.2). These patterns have been tracked at several sites (summarized in Corbet 1999), including one locality as far south as 30°N latitude (although at least one site at 42°N apparently lacked bimodal emergence; M.L. May, unpublished results). Generally, the spring cohort emerges earlier and the fall cohort later with decreasing latitude (J.H. Matthews, unpublished results). Moreover, ponds with bimodal size distributions have been

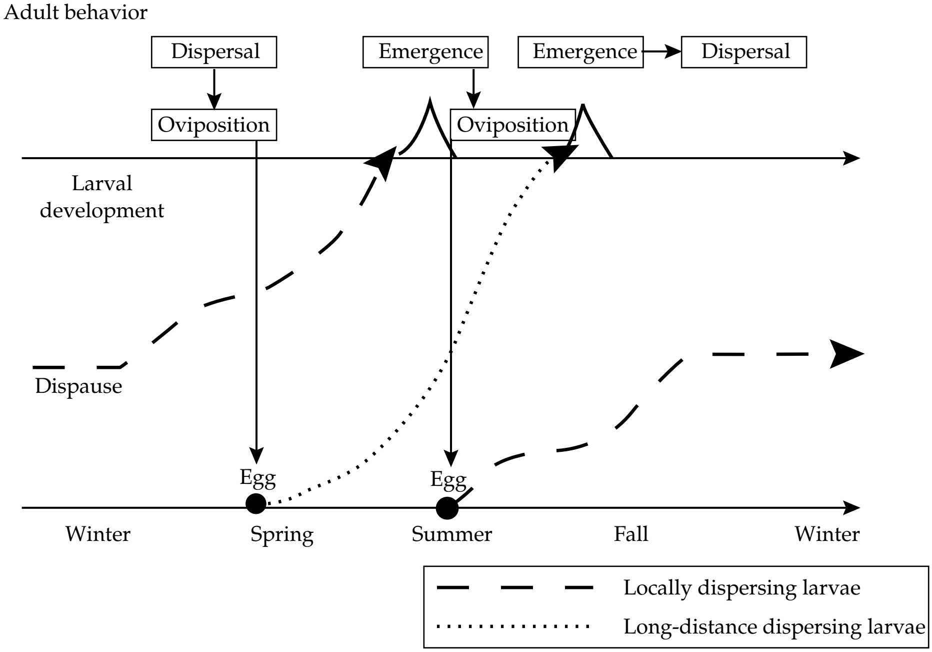

Figure 6.2 Generalized larval life-history tracks for *A. junius*. 'Migrant' fall-emergent larvae are shown with a dotted line (long-distance-dispersing larvae). 'Resident' or 'non-migrant' spring-emergent larvae are shown with a dashed line (locally dispersing larvae). Note that residents complete their life cycle in just under 1 year, undergo winter diapause, and are active as mature adults before emergence of migrants. The latter complete development in 4–6 months without diapause. Both patterns have been observed between latitudes 45 and 19°N in eastern North America, but the clear separation of adult flight seasons is not always evident. After Trottier (1971).

seen as far south as 19°N latitude (J.H. Matthews, unpublished results). Another distinct emergence 'bump' well before most spring-emergers mature has also been observed in a few instances (Wissinger 1988), suggesting that some larvae 'destined' for a fall emergence entered a temperature-triggered quiescent state until the following spring, perhaps as a result of early cold-water temperatures, a pattern also seen in *Anax imperator* in Europe (Corbet 1957).

Debate about the major spring- and fall-emergence groups has centred on two points. First, how are these emergence phenologies maintained over large spatial scales? Second, what is the adaptive strategy maintaining this bimodal strategy?

The basis for determining emergence (and thus dispersal) phenology and phenotype is arrived at more easily. Direct and indirect evidence discussed above suggests that fall-emergers migrate south and spring-emergers migrate north, although only limited estimates of the scale of north-bound movement are available currently (Matthews 2007c). Thus, the traditional terms resident and migrant for describing these groups are misleading and inaccurate. Moreover, since at least the time of Trottier (1971), these groups have been described as separate 'populations', even when referring to individuals belonging to different cohorts in the same pond. Assuming that 'population' implies measurably restricted gene flow between these groups, the work of Freeland *et al.* (2003), Matthews (2007d), and Matthews (2007e) suggests that these cohorts are not different populations. Indeed, Matthews (2007d) measured multilocus gene flow between spring- and fall-emergers within and between 500 adult and larval samples collected over 27° of latitude across eastern North America, finding Fst values in the order of approximately 0.02 between all categories, without regard to geographical structuring. Although based on a much coarser means of genetic resolution via a nested clade analysis, Freeland *et al.* (2003) found a similar pattern, leading them to attribute variation in emergence phenology to phenotypic plasticity rather than a genetically determined phenotype. Conceivably, a maternal effect could also be involved.

Phenotypic plasticity is widespread in nature and has been identified in a handful of odonate species (e.g. Hopper 2001; De Block and Stoks 2003). For any particular plastic trait, a particular phenotype—whether one of several qualitative alternatives (e.g. phenotype A or B) or a point on a continuum of possibilities (e.g. phenotypic expression ranging from 1 to 10)—is cued by some environmental trigger. *A. junius* presumably follow the qualitative model with two alternative states. Trottier (1971) found that the rate of development of late-instar larvae could be manipulated across a wide range of values by ambient temperature, but he also found that spring- and fall-emerging larvae showed different categories of responses to temperature. A similar pattern was found by Corbet (1957) with *A. imperator*. Moreover, Calvert (1929, 1934) found that an *A. junius* larva bound for spring emergence entered diapause when raised from an egg indoors where it was exposed to relatively constant room-temperature conditions rather than the harshness of a Pennsylvania winter. All of these leads suggest that emergence phenology is determined early in development and that temperature has little or no cueing effect for phenotype, even if temperature can play a role in determining relative rates of development within phenotypic states. Corbet (2003) suggested that aeshnids at intermediate to high latitudes may regulate emergence phenology via photoperiod. Given the especially wide latitudinal range of *A. junius*, photoperiod would be a very reasonable and reliable cue for dispersal phenotype.

Matthews (2007e) tested this hypothesis with split-sibling groups of *A. junius* exposed to constant, increasing, and decreasing photoperiod from the egg in an environmental chamber. The increasing photoperiod treatment group (corresponding to the fall-emerging larvae, with eggs laid between the spring equinox and summer solstice) developed significantly ($P < 0.001$) more rapidly than the equinoctial constant (light/dark period of 12 h:12 h) and decreasing photoperiod (the latter corresponding to eggs laid between the summer solstice and fall equinox) groups. These results suggest that there is little if any maternal effect on emergence phenology, but they do not rule out the possibility of a gene × environment effect, which might reflect significant lineage differences in plasticity. Indeed, several families did show significant differences in their responses.

In essence, any individual egg could develop along the slow spring-emergence pathway or the fast fall-emergence route based on the photoperiod experienced by the egg or a very early instar. This result fits neatly with the genetic data (Matthews 2007d) showing no significant differences between spring-emerging and fall-emerging larvae. Temperature may modulate the rate of development within the limits set by photoperiod and, presumably, determine the direction of adult migration as well. This model also implies that the small emergence bump noted by Wissinger (1988) may reflect mismatches between temperature modulation and photoperiod cues, leading a few individuals to develop rapidly before ambient temperatures triggered diapause, halting development in the final or near-final instar.

Although not tested experimentally, no evidence indicates an effect of larval crowding on migratory predilections, as is well known in locusts (reviewed by Dingle 1996). For example, no effect on development or evidence to suggest early migration has been observed in populations in which the early-emerging cohort is much larger than the late-emerging larvae (M.L. May, unpublished results).

The second issue mentioned above regarding the adaptive basis of emergence phenology and phenotype is much harder to test. The key question here is, why maintain two and only two cohorts? One theory is based on the observation that there appears to be a latitudinal relationship between the climate-normal timing of rain and emergence phenology across eastern North America (Matthews 2007a, 2007b). This relationship suggests that long-distance migration may be timed in the fall to arrive when the largest number of suitable habitats are available; for example, lake and wetland water levels in south Florida generally peak in October and, at least in larger lakes, remain high until February (Abtew *et al.* 2006), consistent with arrival of probable northern migrants and timing of local emergence (Paulson 1999). Northern movement is in turn set to coincide with the coincidence of appropriate temperatures for larval development with high spring water levels. In a closely related hypothesis, northern fall-emerging larvae ('migrants') may be habitat generalists, capable of reaching adulthood in both shallow (ephemeral) and deep (more permanent) water bodies, with northern spring-emerging larvae ('residents') acting as habitat specialists for permanent water bodies (Matthews 2004). Several theorists predict just such a system for the evolution of movement polymorphisms (Roff 1994). However, these adaptive explanations remain to be tested.

6.2.6 Behaviour en route

6.2.6.1 Orientation

Migratory monarch butterflies are known to use time-compensated sun-compass orientation (Mouritson and Frost 2002), and other butterflies may be able to use magnetic orientation (Srygley *et al.* 2006). Nothing, however, is known with certainty about mechanisms of long-distance orientation in dragonflies. Typical routes of aggregated migrants follow obvious landmarks for much of their length, and several writers, especially Shannon (1916) and Dumont and Hinnekint (1973), have emphasized the importance of visual landmarks in orienting migration. On the other hand, as already noted, accumulation along leading lines need involve no more than downwind flight and avoidance of open water. Furthermore, dragonflies may sometimes pass over long stretches of water, such as Delaware Bay or Lake Erie (Corbet 1984; Root 1912), or featureless plains without obvious landmarks. Corbet (1984), reporting on movements of *A. ephippiger*, a well-documented Old World migrant, on the plains of East Africa, suggested that their strikingly constant flight heading was due to sun-compass orientation.

We suggest that landmarks are probably used at least as secondary aids to navigation as suggested above but note that for consistent southerly movement along a coastline, for example, some mechanism of choosing one of two directions must exist. Likewise, it appears that individual *Anax* can distinguish northerly from southerly winds (see below). Certainly sun-compass orientation is possible given the known capabilities of other insects. On the other hand if, as we suppose, a specific narrow destination is not necessary for *A. junius*, it is possible that positive phototaxis toward the sun or the brighter southern sky in fall might suffice for southward orientation. If so, this might again be a useful model for other insects with similar migratory strategy. Of interest would be to determine whether orientation in spring is based only on reversal of the response to similar cues as during fall and, in any case, how this intergenerational change is mediated. Also unresolved is whether some other odonate species might have more stringent navigational requirements (e.g. *A. ephippiger*, which may depend on finding desert oases; Dumont and Desmet 1990) and species that sometimes migrate at night (Feng *et al.* 2006).

6.2.6.2 Flight patterns

Virtually nothing is known about individual decision rules and trajectories of migratory insects, because it is very difficult to follow such small organisms over vast distances. Recently, however, Wikelski *et al.* (2006) were able to attach micro-radio transmitters to 14 *A. junius* and follow them during fall migration for up to 12 days. Although the presence of the transmitters may have affected behaviour, individuals migrated up to 140 km per day, and two were observed foraging apparently normally.

These observations provide unique insight into individual behaviour. *A. junius* alternated distinct stopover periods with active migration and on average migrated about every 3 days. The average advance of 13 migrating individuals was approximately 60 km (12 km/day), but daily movement ranges (Figure 6.3a) exhibited a trimodal distribution: short-range and omni-directional and medium or long-range and directional. Average direction was within a few degrees of due south. Dragonflies only migrated when wind speeds were low, independent of wind direction, although winds on days when the dragonflies migrated were, on average, more northerly than on non-migratory days, thus indicating, as suggested above, that *A. junius* have at least a rudimentary directional sense. They did not seem to compensate strongly for wind drift as individual migration paths only differed by approximately 20° on average from wind direction (Figure 6.3b). Thus flight paths often zig-zagged on consecutive days. Daily high temperatures did not differ significantly between migrating and non-migrating days, but a migrating day always succeeded a night that was colder than the previous night, whereas non-migrating days had on average warmer nights leading up to them. This behaviour makes sense if migrating after a decrease in night-time temperatures ensures that individuals ordinarily migrate when cold, northerly winds aid their southward migration.

Three individuals changed their migration route by more than 120° when hitting an ocean barrier (e.g. the Delaware Bay), clearly reorienting in response to landmarks. Two actually flew out over the bay for about 5 km, then turned north to spend the night on the New Jersey side, about 30 km north of the capture point; 2–4 days later they crossed the upper end of the bay, as shown in Figure 6.4. Such behaviour mirrors that of numerous songbirds and small hawks upon reaching this same spot during fall migration (e.g. Wiedner *et al.* 1992).

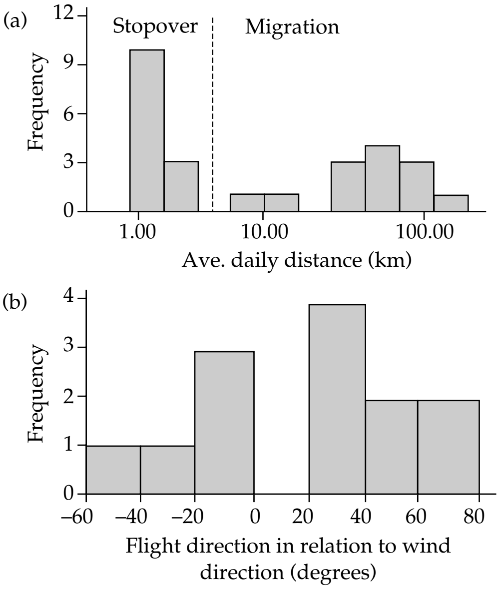

Figure 6.3 (a) Daily movement of radio-tagged *A. junius*; movements greater than 5 km were assumed to represent migration whereas shorter movements were thought to occur during periods when the dragonflies forage to replenish energy stores and are thus relatively sedentary. (b) Flight direction relative to wind direction of radio-tagged *A. junius*; zero deviation represents due south. Note that the modal direction is quite close to south and that none of the movement vectors deviated more than 90° from south. Both from Wikelski *et al.* (2006).

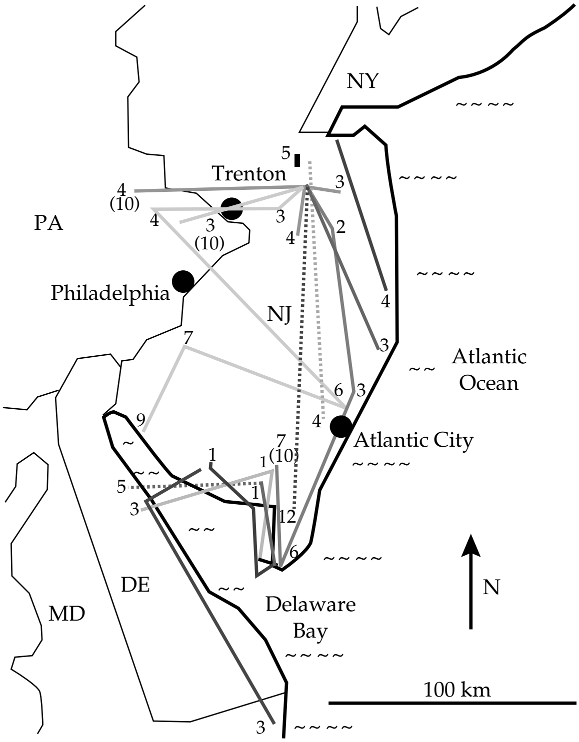

Figure 6.4 Flight tracks of 13 radio-tagged *A. junius* in Fall 2005 in New Jersey. Each line represents a separate individual; numbers depict days since tagging, numbers in parentheses show maximum number of days individuals were tracked, broken lines indicate uncertainty about which day individuals conducted their migratory flight. Note that four individuals changed direction near the coastline of Delaware Bay, apparently avoiding flying far over water. One individual (black line) initially flew over Delaware Bay for about 5 km, then turned north and stopped for the night about 25 km north; it was re-found on day 3 in Maryland and is assumed to have crossed the bay well north of its capture point. From Wikelski *et al.* (2006).

6.3 Comparisons with other airborne migrants: what can dragonflies teach us?

A. junius differs in several respects from most better-known animal migrants. Unlike birds and mammals, they do not provide parental care beyond oviposition and both sexes are able to reproduce at intervals shorter than the duration of migration throughout most of their adult lives. Unlike migratory insects that have been closely studied heretofore, they apparently do not exhibit an oogenesis flight syndrome, although we cannot discount the possibility that maturation might be somewhat slowed during migration. As already noted, many southbound migrants are evidently reproductively mature. Tandem linkage is seen from southern Ontario southward (J.H. Matthews and M.L. May, independent personal observations), and one of us (JHM) observed oviposition by apparent migrants throughout Atlantic and Gulf coastal regions in the USA in September and in Veracruz state, Mexico, as late as mid October. Thus direct observation establishes that oviposition occurs during southward flight, although strong indirect and anecdotal evidence also indicates that much reproduction occurs at or near the southern terminus of migration (Paulson 1999; D.R. Paulson, personal communication; J.H. Matthews, personal observation). In fact, *A. junius* is incapable of adult diapause as far as we know (unlike some tropical Anisoptera, including probable migrants; Corbet 1999). *A. junius* are generalized predators at all life stages, so adults can obtain food widely as long as flying insects are available, unlike specialized plant feeders such as monarch butterflies or *Oncopeltus* bugs, and larvae can develop in frequently encountered, but unstable, aquatic habitats. Moreover, the aquatic larval habitat provides a refuge from thermal extremes. These characteristics, coupled with high adult mobility, allow *Anax* to reproduce in a succession of sites as it moves progressively southward. Repeated oviposition both spreads risk to offspring from drought and predation and allows adults to employ a bet-hedging strategy against cumulative mortality risks during migration. We expect that other organisms with low parental care costs and generalized and reasonably abundant energy resources, especially other aquatic insects in unstable lentic habitats, may employ similar strategies.

On the other hand, individual migratory behaviours and decision rules are strikingly similar to those proposed for songbirds, and may represent a general migration strategy for directional long-distance travel of self-propelled aerial organisms (Wikelski *et al*. 2006). These studies should be replicated and extended, both geographically and to include spring migration, but they can provide independent confirmation of movement patterns inferred from stable isotope markers as well as more details about behaviour, possibly including reproductive behaviour and success. In any event, they highlight characteristics that are likely to be shared very widely among migrants across taxa because of pervasive effects of limitations on energy stores in small, flying organisms and the consequent needs to replenish internal supplies and take advantage of external power sources; that is, favourable winds.

Acknowledgements

Our sincere thanks to the many people who have helped and encouraged us during this work, including those, too numerous to mention individually, who sent observations of dragonfly migrations. MLM especially acknowledges Bob Barber, Joanna Freeland, Bob Russell, and Ken Soltesz for earlier collaboration and Martin Wikelski and Dave Moskowitz for introducing him to the art and science of radio-tracking. Funded in part by New Jersey Agricultural Experimentation Project 08190, supported by State and U.S. Hatch Act Funds to MLM.

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CHAPTER 7

The use of dragonflies in the assessment and monitoring of aquatic habitats

Beat Oertli

Overview

Aquatic resources are under particular threat today, and therefore the management of aquatic habitats and of their watersheds requires the development of comprehensive assessment and monitoring methods. Biological methods are now widely used, and many include Odonata, in association with other groups or even taken singly. Odonata constitute a valuable tool for various types of assessment and monitoring, such as the measure of biodiversity, the appraisal of water-body health or integrity (including water quality and ecosystem function), the monitoring of management or restoration practices, and the detection and prediction of the biological impact of climate warming. Furthermore, sampled through standardized methodologies, they have already provided excellent data-sets for hypothesis testing in ecology or evolution. However, some types of assessment show that the use of Odonata as a single group can have limitations which can be avoided if other complementary biological groups are also used. For efficient sampling of Odonata, a method should focus on the three stages: larvae, exuviae, and adults. Since this approach may be too expensive, most existing methods only use one stage. In applied issues, the adult stages of Odonata are surveyed at a low cost, and are therefore useful for rapid assessments; they can be used for preliminary screening, for example when identifying local hotspots of diversity or, on the contrary, of degraded sites. Existing methodologies are highly numerous, particularly in applied studies. The development of unified standardized procedures would be beneficial, as it would enable spatial and temporal comparisons.

7.1 Introduction: bioassessment and biomonitoring in freshwaters

Aquatic resources are essential to human life and activities. Although water pollution has existed for many centuries, these resources are particularly under threat today because human impacts have diversified and intensified. For these reasons, the management of aquatic habitats and their watersheds has been applied widely. The invertebrates is one of the main groups of bioindicators used in biological assessment and monitoring. Nevertheless, our knowledge of biomonitoring still varies widely between geographic regions and different types of water body. Temperate countries are clearly leading in the development and application of assessment and monitoring methods. Furthermore, running waters are much more studied than lakes, wetlands, and ponds around the world.

The objectives of freshwater bioassessment and the procedures to carry it out are schematized in Figure 7.1. Until now, these have focused mainly on (1) the magnitude or value of biodiversity, (2) the degree of integrity or health of a water body or a region (e.g. water quality, ecosystem structure and function), (3) the success of restoration

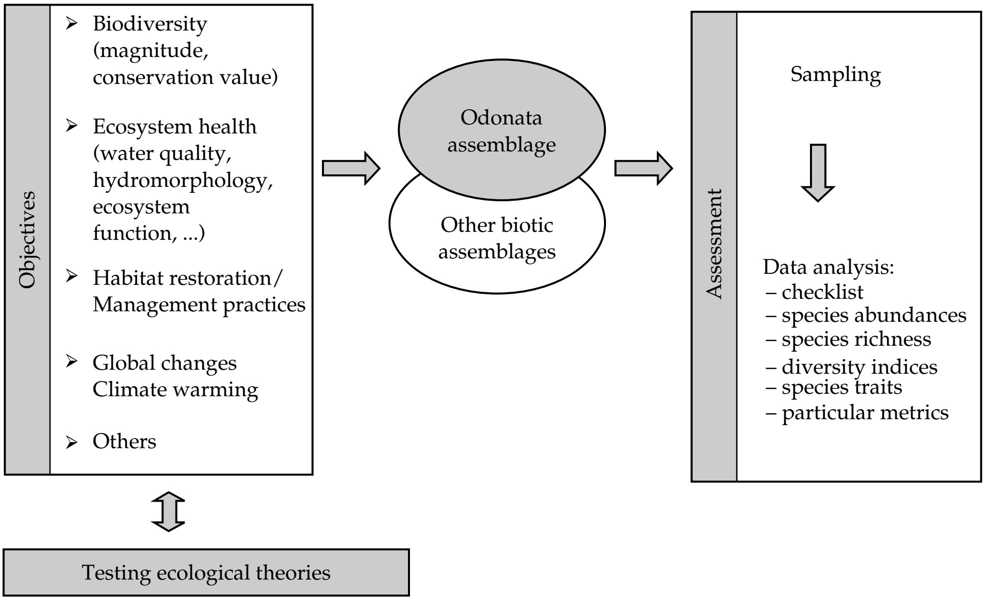


Figure 7.1 Procedure for freshwater bioassessment using Odonata and examples of objectives.

or management practices, (4) the effects of global changes (i.e. hydrological perturbations and climate warming), and (5) other factors such as the impact of species introductions (e.g. invasive species). These issues, addressed by managers (in conjunction with the scientific community), are also closely related to more fundamental ecological and evolutionary theories, which can be tested with such data-sets. These theories, in turn, can also provide guidelines for management plans.

An assessment can take place at different spatial scales, from local (water body, network, nature reserve) to regional (watershed, other area with political or biogeographical limits). Bioassessments are conducted with a selected indicator group (e.g. plants, plankton, invertebrates, dragonflies, fish, birds) or several together. Each bioassessment has its own objective and this has to be clearly identified, so that (1) biotic group(s), (2) type of data to be recorded (species inventory, species richness, species abundance, diversity index, conservation value, and other metrics), and (3) sampling scheme are chosen correctly. The results of the assessment are then used for analysis and final evaluation.

Biomonitoring is essentially a time series of bioassessments. Its objective is usually to describe biotic changes (richness, community composition, abundance, etc.) in relation to, for example, perturbation or management measures.

7.2 Rationale behind bioindication and species traits of dragonflies

To be useful for bioassessment (or for monitoring), species or groups of species have to provide some answer to the question underpinning the assessment. Invertebrates are usually good bioindicators and dragonflies are in many cases well suited for the following reasons:

- they constitute a keystone, umbrella, and flagship group;
- they are representative of wetlands, lake shorelines, ponds, or running waters but, nevertheless, are not the most diversified insect order in fresh waters;
- they are reasonably diverse and have a well-established taxonomic framework; even when taxonomic literature on Odonata is not available anywhere in the world, it is better known than for other macroinvertebrate groups;
- they have diverse life stages; indeed, they use aquatic habitats as larvae and terrestrial areas as

adults; nevertheless, functionally they are not very diversified, all species being predaceous;
- several species are stenotopic, and require specialized habitat conditions;
- they are geographically widespread, although they are missing at high altitude;
- they are particularly well accessible and amenable to quantitative sampling by standard techniques;
- they are likely to generate political sympathy and support;
- they are already well studied and as a result there is a substantial body of ecological knowledge on many species (e.g. ecological traits, conservation value), although this still has to be achieved for many tropical species.

The advantages of using Odonata as bioindicators have already been often highlighted and this is supported by a large base of scientific evidence. As several species are stenotopic, a given assemblage reflects the effects of environmental variables, for example the presence of vegetation (emerged, submerged, or floating), current velocity, hydroperiod, ambient temperature, water oxygen concentration, the chemical characteristic of the water (e.g. pH, conductivity, pollutant concentrations; reviewed extensively by Corbet 1999). Databases on species traits are already available to water managers (e.g. Moog 2002 for Europe).

7.3 What is assessed and monitored? With or without dragonflies?

7.3.1 Biodiversity

Measuring biodiversity in itself often constitutes the central objective of an assessment. Furthermore, as biodiversity value is generally recognized as an indicator of ecosystem health and integrity, it is also used as a metric in other assessment objectives. Therefore, most assessment and monitoring programmes record taxa richness, at local (water body or network) or regional (watershed, biogeographical region, political area) levels. The most investigated groups in fresh waters are plants, mammals, birds, fish, and reptiles/amphibians. In terms of invertebrates, Odonata is often one of the most used groups, especially for wetlands and small water bodies. Indeed, investigating the adult stages is both technically easy and cost-effective (see Section 7.4).

At national or international levels, red lists are drawn up on the basis of species distributions and of their temporal trends (increasing or decreasing). Monitoring programmes are therefore conducted for Odonata in many regions of the world, where they are more or less well coordinated, depending on countries, and involve mostly volunteers (see also Chapter 8 in this volume).

At the local scale, assessment of odonate diversity is mostly made through species inventories, which need to be exhaustive if the aim is also to include the less-abundant species. If exhaustive sampling is not a requisite, an index of diversity reduces survey costs. Such indices are particularly appropriate for conducting a preliminary screening on multiple sites, before studying the 'hotspots' in more detail.

Odonata by themselves can sometimes be relatively good indicators of global biodiversity, but this is not always the case. A correlation between species richness of dragonfly larvae and of vascular plants was highlighted in Scandinavian small lakes (Sahlen and Ekestubbe 2001). Furthermore, Briers and Biggs (2003) suggest that the richness of the Odonata family Coenagrionidae shows the best performance for indicating the overall pond invertebrate community richness. However, macroinvertebrate richness is not necessarily correlated with the diversity shown in other groups (bacteria, ciliates, phytoplankton, zooplankton, fish, and water plants), as demonstrated for shallow lakes of Western Europe (Declerck *et al.* 2005). Moreover, odonate diversity is sometimes poorly correlated with that of other groups. For example, in Swiss ponds, species richness of adult Odonata was poorly correlated ($0.38 < R^2 < 0.56$) with those of aquatic plants, Gastropoda, Coleoptera, and Amphibia, even if the relations were significant ($P<0.001$; Oertli *et al.* 2002). In the assessment of backwaters in the Sâone floodplain (France) (Godreau *et al.* 1999), adult Odonata richness was correlated with that of aquatic Coleoptera, but was not with that of aquatic plants, Trichoptera, and Mollusca (B. Oertli, unpublished results). In backwaters of the Danube floodplain, adult odonate richness was not correlated with amphibian richness (Tockner *et al.* 1999). In UK ditches, the conservation value of invertebrate assemblages showed no correlation between rankings of larval Odonata, aquatic Coleoptera, and Mollusca (Painter 1999). At the regional scale (gamma diversity), areas rich in Odonata species (hotspots) frequently do not coincide with those from other taxa (Prendergast 1993). In conclusion, for a coherent approach to global biodiversity assessment, it is always preferable to use some complementary group(s) in addition to Odonata.

Most assessments of Odonata diversity aim to identify species-rich sites, these being considered 'the best sites' (where conservation efforts should be directed). However, low species richness does not necessarily reflect degradation. Indeed, some endangered stenotopic species are found only in species-poor systems, like bogs. Therefore, in assessment procedures, it is always important to score not only species richness, but also the degree of threat to the species.

In the assessment of biodiversity, the social value should be given a high importance. Indeed, Odonata are especially useful as they have a high cultural and aesthetic value (Chapter 8). For small water bodies, they are used regularly for engaging the public, along with two other flagship groups, aquatic plants and amphibians.

7.3.2 Ecosystem health

7.3.2.1 Water quality

Assessment of water quality is carried out through the use of a wide range of physical, chemical, or biological variables. It is now often also coupled with the quality of the aquatic habitats.

For running waters, aquatic macroinvertebrate assemblages are widely used as bioindicators, particularly through biotic indices that give a unique score for a site. Odonata larvae usually contribute to this unique score. Their use is nevertheless generally low in running waters. Three types of approach can be distinguished, as follows.

1. Odonata are used, together with other macroinvertebrates, in assessment systems comparing observed communities with reference communities [e.g. the River Invertebrate Prediction and Classification System (RIVPACS) and the Australian River Assessment System (AusRivAs)].

2. Odonata can be included in the calculation of a metric in association with other taxa (see Table 7.1). Odonata are never used as a single group. In most cases, the life stage used is larvae. For example, Odonata can contribute to macroinvertebrate community richness score (total number of taxa), as in many biotic indices or rapid bioassessment, but are rarely chosen as a single indicator taxon. They can also contribute to an average score of pollution sensitivity.

3. Odonata can simply be ignored (e.g. in most metrics presented in Hering *et al.* 2004).

For lakes, water quality is less frequently investigated with aquatic macroinvertebrate assemblages, and other groups are more often used (e.g. plankton, fishes). The use of macroinvertebrates (and potentially Odonata) should, however, increase in the future, especially in Europe where the Water Framework Directive of 2000 includes them in the biotic variables that have to be used to assess the ecological status of European lakes. For ponds and wetlands, the use of macroinvertebrates (and Odonata) is much more widespread, especially for accessing their biological integrity. Odonata is here frequently solicited, and is a component of many metrics (see Table 7.1).

In the assessment of water quality, there are relatively few methods which use Odonata (i.e. Table 7.1), and this is probably because of (1) their low diversity (compared to other macroinvertebrate groups) and (2) the moderate sensitivity of Odonata larvae to organic pollution (Carchini and Rota 1985). Indeed, the diversity of Odonata is only a minor part of the whole macroinvertebrate assemblage and, for example in running waters of Europe, represent less than 2% of the total diversity (Schmidt-Kloiber *et al.* 2006). Furthermore, Odonata are globally clearly less sensitive to organic pollution than most Ephemeroptera, Plecoptera, and Trichoptera species (known as EPT taxa) (see Moog 2002). Nevertheless, larvae are absent in heavily polluted waters (e.g. Corbet 1999); as larvae need oxygen for respiration, they cannot survive in anoxic conditions. The level of sensitivity is also variable among Odonata species; for example European *Cordulegaster boltonii* and *Coenagrion mercuriale* are associated with relative nutrient-poor streams, whereas *Calopteryx splendens* tolerates a much larger gradient of nutrient concentrations.

Even if their sensitivity is weak, it is undoubtedly still enough for Odonata to be used in assessment of water quality. Moore (1997) reported that a count of dragonflies provided a quick, and therefore low-cost, indication of the health or richness of a lake or river. Therefore, rapid bioassessment of ecosystem health should pay more attention to these benefits, especially for habitats where the potential species pool of Odonata is important. For example, in a first screening process, the classification of sites in relation to Odonata abundance and diversity will be efficient for a relatively low cost. This could even be conducted with adult stages. With adults, assessment of odonates is quicker than for the other sensitive EPT taxa, because they are more easily observed and identified in the field. From Table 7.1 it appears that biological monitoring of water quality rarely integrates study of the adult stage of Odonata; but it would gain from doing so, and therefore methodologies should be developed in this direction (nevertheless see Section 7.4.1 about the pros and cons of using larvae/exuviae/adults).

Beside the trophic status of water (and organic pollution), many assessments are also concerned with providing information on particular pollutants. These include heavy metals, organo-metallic compounds, chemical elements causing acidification, and pharmaceutical products (including hormones and antibiotics). Pollutants not only affect species survival or growth rate, but also induce deformations and alteration in symmetry. In these cases, Odonata are a good biomonitoring tool. For example, levels of fluctuating asymmetry in cell patterns in adult wings were increased when larvae where exposed to pesticides (Hardersen and Wratten 1998). However, Odonata have to be present in sufficient numbers in a water body to allow for their investigation; frequently other target organisms, like Ephemeroptera, Diptera, or Trichoptera, will be more numerous and easier to sample.

In conclusion, Odonata are never used as a single group for the assessment of water quality; they are mostly integrated as part of macroinvertebrate assemblages. This position is probably justified, first because of their lower species diversity in comparison with some other groups, and second because of their resistance to pollution compared to other groups. Nevertheless, the actual sensitivity of Odonata to pollution remains largely under studied. More information would allow using Odonata in rapid assessments, and possibly using adult stages, especially for approaches that involve the screening of many sites.

7.3.2.2 Ecosystem function

Odonata have complex habitat and microhabitat requirements that differ according to individual species (see details in Corbet 1999). This is particularly obvious when comparing assemblages from water bodies with different functions. This bioindication property of Odonata is well exploited for the assessment of backwaters in dynamic floodplains, and has been described for larvae in the rivers Rhône and Ain (Castella 1987) and for adults, exuviae and larvae in the River Danube (Chwala and Waringer 1996; Tockner *et al.* 1999). In terms of species richness (local or regional), the highest values for Odonata occurred in the para- and plesiopotamal channels (neither connected to the main channel, nor totally isolated) of the floodplain of the Danube (Tockner *et al.* 1999). Furthermore rivers with moderate disturbance have higher species richness than rivers with high disturbance (Stewart and Samways 1998). Longitudinal specificities also exist along the main channel (Rehfeldt 1986), with clear distinction between the fauna of small streams and large rivers, as shown on the River Kiewa (Australia) (Hawking and New 1999) or on rivers in the Upper Guinean forest (Dijkstra and Lempert 2003). A standardized scheme for assessing the ecological status of floodplain areas using Odonata (adults, larvae, and exuviae) was developed and tested at local level in Austria (Chovanec *et al.* 2004): the Odonata Habitat Index (OHI).

Hydrological aspects can also be surveyed with Odonata. Temporary water bodies have different species assemblages from those of permanent ones, and habitats with different hydrological parameters can be well discriminated by their dragonfly assemblages, as demonstrated for example for

Table 7.1 The use of Odonata in metrics to assess the health of freshwater ecosystems.

Water-body type	Type or name of the biotic index	Main assessment objective	Geographical location	Odonata life stage/ identification level	Metrics using Odonata	References
Various (running and stagnant)	Pollution-sensitivity index (or also various biotic indexes)	Water quality	Various	Larvae/family	Average pollution-sensitivity index of the macroinvertebrate community (including Odonata)	Various, e.g. Armitage *et al.* 1983 for the Average Score per Taxon (ASPT)
Streams	AQEM assessment method	Organic pollution	Mountainous areas of Central Europe	Larvae/species	One metric (among six): EPTCBO richness	Hering *et al.* 2004
Streams	AQEM assessment method	General degradation	Southern Apennines, Italy	Larvae/genus	One metric (among 15): abundance in *Cordulegaster* (Odonata) and *Dinocras* (Plecoptera)	Hering *et al.* 2004
Streams	IBE	Water quality	Italy	Larvae/genus	Biotic index of the macroinvertebrate community (the number of Odonata genus contributes to overall taxonomic richness)	Ghetti 1997
River	Biotic index SIGNAL	Water quality	Australia	Larvae/family	Average pollution sensitivity index of the macroinvertebrate community (including Odonata)	Chessman 1995
Large rivers	Multimetric index	Water quality	Missouri, US	Larvae/species	Two metrics (among 15): – EPOT richness – percentage EPOT	Poulton *et al.* 2003
River/floodplain systems	Floodplain Index	Ecological status	Austria	Adults/species	The Floodplain Index uses species' habitats preferences of five indicator groups (MoTOAF)	Chovanec *et al.* 2005
Ponds	Multimetric index PSYM	Biological integrity	Britain	Larvae/family	One metrics (among six metrics): MO richness	Pond Action 2002

Ponds	Multimetric index	Eutrophication	Switzerland	Adults/species or family	Three metrics (among four): COGA species richness; MO family-level richness; family-level richness of macroinvertebrate (including Odonata)	Menetrey *et al.* 2005
Ponds	Pond Macroinvertebrate Integrity Index	Water quality	Italy (mountains)	Larvae/genus	One metric (among seven metrics used in the integrity index): percentage of total richness composed by EOT	Solimini *et al.* 2008
Wetlands	Wetland Index of Biological Integrity (WIBI)	Biological integrity	Minesotta, USA	Larvae/genus	Two metrics (among 10 metrics used in the WIBI score): ETSD richness in pollution-sensitive groups: number of ET taxa and presence of S and D; Odonata richness	Gernes and Helgen 1999
Wetlands	NEFWIBP Invertebrate community index	Ecological integrity	New England, USA	Larvae/family	Three metrics (among 13 metrics used in the community index): EOT richness; EOT/Chironomidae ratio; other Odonates/Coenagrionidae ratio	Hicks 1997
Wetlands	Various indices	Biological integrity	USA	Mainly larvae/–	Various metrics	US Environmental Protection Agency 2002

A, Amphibian; B, Bivalvia; C, Coleoptera; D, dragonflies; E, Ephemeroptera; F, Fish; G, Gastropoda; M, Megaloptera; Mo, Mollusca; O, Odonata; P, Plecoptera; S, Sphaeriidae; T, Trichoptera; AQEM, Integrated Assessment System for the Ecological Quality of Streams and Rivers throughout Europe using Benthic Macroinvertebrates; IBE, *Indice Biotico Esteso*; NEFWIBP, New England Freshwater Wetlands Invertebrate Biomonitoring Protocol; PYSM, Predictive System for Multimetrics.

freshwater habitats in Western Namibia (Suhling *et al.* 2006).

7.3.3 Management practices and habitat restoration

The twenty-first century is, in many regions of the world, the century of 'turning back the clock', with a multitude of restoration and management schemes. To measure the success of such practices, and particularly the short- and long-term impact on biocoenosis, assessment and monitoring programmes are necessary. Nevertheless, such programmes are often missing, because all funds available are used in the restoration scheme itself, and monitoring is considered to be a time-consuming and unnecessary stage. When restoration or management success is evaluated, most studies include a measure of diversity. Therefore, biodiversity assessments are often carried out, and Odonata are frequently represented. In specific cases, individual Odonata species can also act as indicators of success of management measures.

The creation of new water bodies, such as ponds, is a frequent restoration measure which already benefits Odonata in the short term (e.g. Moore 1991). Such practice is also useful by its contribution to regional network restoration.

The drainage of ponds or lakes is another management tool sometimes used (1) as a necessary step during fish farming for harvesting fish or/and for the removal of nutrient-rich sediments, and (2) for restoration, reducing fish densities and promoting the growth and diversity of macrophytes, amphibians, or birds. Indeed, the impact on biodiversity of such drainage is often assessed with macrophytes, zooplankton, or birds. However, macroinvertebrates are also good indicators (Van de Meutter *et al.* 2006) and the adult stages of Odonata may constitute a good tool, but this has yet to be investigated.

The extensive artificialization of lake shorelines reduces the native littoral vegetation in quantity and quality. As larval Odonata seem to be indicators of littoral and shoreline habitat integrity, particularly for emergent and floating macrophyte species (Butler and deMaynadier 2008), they could be used for the monitoring of lake shores where restoration measures are planned, to assess management success. This can also apply to running waters; for example, along the River Tisza (Hungary), Odonata communities are indicators of degradation of the littoral marsh zone caused by sports fishing activity (Muller *et al.* 2003).

In wetlands, the effects of some classical management practices can be measured through the assessment of Odonata species assemblages. For example, water bodies with different water levels will also have different Odonata communities (Johansson and Suhling 2004), and the impact of grazers (e.g. cattle) can be measured through the abundance or diversity of larval or adult Odonata (Foote and Hornung 2005). In the case of management of ditches and especially their mechanical cleaning, adult and larval Odonata are valuable indicators of (1) the age of excavation and (2) the stage of plant development (marginal, submerged, and floating) (Painter 1998). In combination with other aquatic macroinvertebrates, Odonata larvae can also be used to assess the impact of rewetting measures carried out for the conservation and restoration of raised bogs (Van Duinen *et al.* 2003).

The success of the restoration of river floodplain function, or of individual backwaters, can also be well described with invertebrates, including Odonata, as already described (see the above section on ecosystem function). Restoration also addresses management practices in issues of water quality (see above section on water quality). For example, adult or larval Odonata can be used to assess artificial neutralization in cases of acidification (D'Amico *et al.* 2004). At a regional scale, tropical forest burning is a management practice that impacts biodiversity including Odonata. The diversity and community composition of Odonata, used in conjunction with butterflies, were reliable indicators in Indonesia (Cleary *et al.* 2004).

All these examples demonstrate that for freshwater, measuring the success of restoration or management schemes can be carried out using Odonata (larvae, adults). Indeed, the specificity of species to habitat (and microhabitat) conditions make them a suitable group for detecting change. Furthermore, as active colonizers, they appear rapidly at new sites. However, it is always an advantage to accompany them with other complementary groups.

Many restoration programmes choose indicator or flagship species to engage people, and to explain the way in which public money is used. In this sense, the social attractiveness of Odonata is a real opportunity (see also Chapter 8).

7.3.4 Global changes

Global changes will have drastic consequences for the geographical distribution of species; range shifts have already been reported for various taxonomic groups, including Odonata (e.g. Ott 2001). Various species traits are also likely to be modified in response to warmer temperatures, as for example growth rate, fertility, and duration of the life cycle. Although some recent investigations have been devoted to Odonata (e.g. Ott 2001; Hickling *et al.* 2005; Hassall *et al.* 2007), they are probably still being largely underused as indicators of changing climate conditions. In the same way that butterflies have been used for grassland, Odonata are suitable for models assessing the effect of climate warming, particularly for wetlands. The reasons for this are that (1) they are active dispersers, (2) many species are univoltine (in tropical or temperate species) and can therefore colonize new wetlands each year, (3) temporal species distribution is well monitored (mainly through volunteers), and (4) they are likely to attract people's attention.

Changes in geographical distribution of Odonata species in Europe show an extension to the north for southern species (Ott 2001). At the same time, the range of cold stenothermic species will be decreased in boreal and mountain areas. Their altitudinal distribution will logically shift upwards; ultimately, the possible consequence of these processes for these cold stenothermic species is local extinction, and replacement by eurythermic species. For example, the two boreo-alpine species *Aeshna caerula* and *Somatochlora alpestris* are associated in the Alps with altitude (mainly above 1200 m above sea level); warming would lead to their extinction from the Alps, and will confine them to boreal areas north of the treeline. Similar changes will occur elsewhere in the world and affect species confined to high altitude. To assess the shift in the geographical distribution of species, extensive data collection, coordination, and centralization are needed. This could be achieved by, for example, national biodiversity centres or fauna data banks.

For most species, life-cycle characteristics will also change with a warming climate, and these can therefore be monitored as a fingerprint of global warming, especially if a large set of species is considered together. Warming will lead to an earlier emergence in the season (e.g. Hassall *et al.* 2007), resulting in more rapid larval development and a shorter larval life period. Univoltine species may become multivoltine, and partivoltine species may become monovoltine.

The response to climate warming will also take place at community level. Local or regional species diversity is likely to increase with higher temperature. At the regional scale, the type of altitudinal gradient described for regional species richness by Samways (1989) will shift upwards; the same type of change is likely to be observed in all areas of the world with mountains. On the local scale, species richness will particularly increase in mountain regions. In Switzerland, models showed that for a mountain pond, an increase in mean annual air temperature of 5°C could potentially double or even triple odonate species richness (Oertli 2008). Only long-term monitoring will track such biotic changes. Long temporal series of observations are the best data for assessing variation related to climate change, and the Odonata, because of their relative facility of observation, are therefore a very good choice of study model.

7.3.5 Testing theories in ecology and evolution

Assessment and monitoring of Odonata are frequently motivated by applied issues, often related to management, as shown by the range of examples reported previously. Assessment and monitoring can also be motivated by fundamental research in ecology or evolution. Applied and fundamental researches are also often linked, and if sampling was standardized, the results could be used for both research and management. Through standardized assessments, Odonata can be used efficiently for ecological research and for testing ecological theory, as illustrated in the other chapters of this book. In another example, dragonfly species richness was used to confirm the intermediate-disturbance hypothesis for rivers (Stewart and Samways 1998). Odonata data were also used to test the island biogeography theory (pond size and species richness) (Oertli *et al.* 2002). Food-web interactions can also be investigated with Odonata as predators (McPeek 1998). In landscape ecology, Odonata are used as models for testing dispersal, for example in a patchy environment (Angélibert and Giani 2003), among structurally dissimilar habitat types (Pither and Taylor 1998) or along corridors (Stettmer 1996). Furthermore the role of local or regional processes in structuring the communities can also be explored (McCauley 2007). Pond organisms (and therefore Odonata) offer a large potential for testing theories in ecology, evolutionary biology, and conservation biology (De Meester *et al.* 2005).

7.4 Methods of assessment and monitoring

There are two successive steps to assessing Odonata communities, at a local or regional scale (see Figure 7.1): sampling and data analysis. The data gathered through sampling include various descriptors of the communities (species lists, semi-quantitative data, indices of diversity, and other metrics) depending on the assessment objective. Measures are also sometimes focused on an individual species of conservation interest. Basic knowledge of assessment and monitoring methods is presented in numerous textbooks and underlines the necessity to record data in a standardized way, with a precise sampling protocol. For sampling of Odonata, unfortunately there is currently too little literature available on standardized methods; no comprehensive textbook exists that is comparable with those for, for example, amphibians or butterflies. Descriptions of methods are scattered in various publications or in the grey literature. A review of methods and the building of a core standardized protocol would be greatly beneficial for future assessment and monitoring.

7.4.1 Usefulness of dragonflies: larvae, exuviae, or adults?

In theory, without taking into consideration financial limitations, it would be recommended to sample all three life stages: larvae, exuviae (from last instar larvae), and adults. Such an approach can be conducted or adapted from standardized protocols, such as that proposed in Europe by Schmidt (1985). If it is feasible to sample only one of the three life stages (often for economic reasons), it is recommended to prioritize exuviae, then larvae and only lastly the adults. The presence of exuviae on the shore is undoubtedly the best indicator of the association of a species with a water body. It demonstrates that the species was present at all stages of the life cycle, including reproduction and egg laying. Furthermore, if using standardized methods, exuvia collection provides a reliable estimate of population density and is therefore an exceptional monitoring tool for species of conservation interest (see the case study developed for the endangered North American species *Somatochlora hineana* by Foster and Soluk 2004). Nevertheless, repeated searching is required (sometimes in a hostile and inaccessible environment), which is time-consuming. Another inconvenience is the level of identification skills required: it takes real expertise and, in addition, identification keys for exuviae are not always available.

When studying larvae, one often faces the same taxonomic problem, further exacerbated when larvae are not well developed. Furthermore, larvae have to be sorted from sampled material, a procedure that is very time consuming. Sampling sessions have also often to be repeated according to species phenology so as to collect last-instar stages for all the species present.

The study of adults is motivated principally by financial reasons: sampling and identification is much less expensive. The sampling of adults can be easily performed and the species assemblage at a site can be identified rapidly (see Section 7.4.2.3). Therefore, the sampling efforts can be usefully directed to assess a larger number of water bodies at regional scales instead of intensifying the sampling in fewer sites. Another feature of adults which encourages their study is that they are popular with local communities. This social aspect is not negligible, as it sometimes helps to justify management or restoration measures. However, the studies on the adult stages of Odonata often receive criticism. Migration events from neighbouring water bodies are common, especially in networks. Therefore, when recording an adult assemblage, these allochthonous species generate background noise. In most cases, because its magnitude does not prevent identification of the main trends, this noise can be coped with.

7.4.2 Sampling dragonflies

7.4.2.1 Exhaustive surveys

Conducting an exhaustive survey of Odonata is often the first goal for a wetland manager, at a local or regional scale. The aim is to obtain a complete inventory of the species present (sometimes also recording their abundances), including species of conservation interest. Because species inventories of adult stages impose fewer procedural constraints, they can easily be produced by informed volunteers, amateurs, and hobbyists. Such surveys have proliferated, and the grey literature (partly available on the Internet) abounds with such lists. Most nature reserves have probably already conducted inventories of odonate species. However, the absence of standardization is probably a common trend for most of these studies. Methods are abundant, and in fact there may be nearly as many methods as species lists, because each observer conducts the sampling in their own way.

7.4.2.1.1 Checking exhaustive sampling: species-accumulation curves and real-richness estimators

As the aim of exhaustive sampling is to record all species present, it is important to assess whether sampling was really exhaustive. The best control method is to use species-accumulation curves and real-richness estimators (see examples in Box 7.1).

If the sampling was exhaustive enough, accumulation curves will show an inflexion and later a plateau. For adults, such a plateau is reached only if the sampling site is isolated. If there is a connection with other sites, then the accumulation curve is likely to still increase slightly, until potentially reaching the regional richness (including all allochthonous species) (see Box 7.1).

A complementary (but not alternative) method to accumulation curves is the use of estimators of real richness. Richness measured from a non-exhaustive sampling programme is affected by the sampling effort: as the sample number increases, the number of sampled individuals consequently rises, and the number of species will also rise. This sampling bias can be reduced by means of real-richness estimators like Jackknife or Chao, now easily calculated with simple software. Furthermore, these estimators can be used to compare species richness scores obtained from different sampling strategies. A requisite for the use of some of these estimators is that the observed species list represents at least 50% of real richness. The required data for the calculation of Chao 1 estimator are a species list with species abundances, and for Jackknife 1 or Chao 2 estimators, presence/absence data in replicates (samples, quadrats, days). An example at the local scale (a ditch) is presented in Box 7.1. The same estimators can also be used for assessing the regional species richness.

The use of estimators should come with a word of warning: the estimated species richness will only match the habitats and the season sampled. For example, if only sunny shore segments have been surveyed, an estimator will not be able to account for species that live exclusively in the shadow or far from the shore. In the same way, if the sampling is done during the summer, the estimation will not predict how much species are flying during spring or autumn.

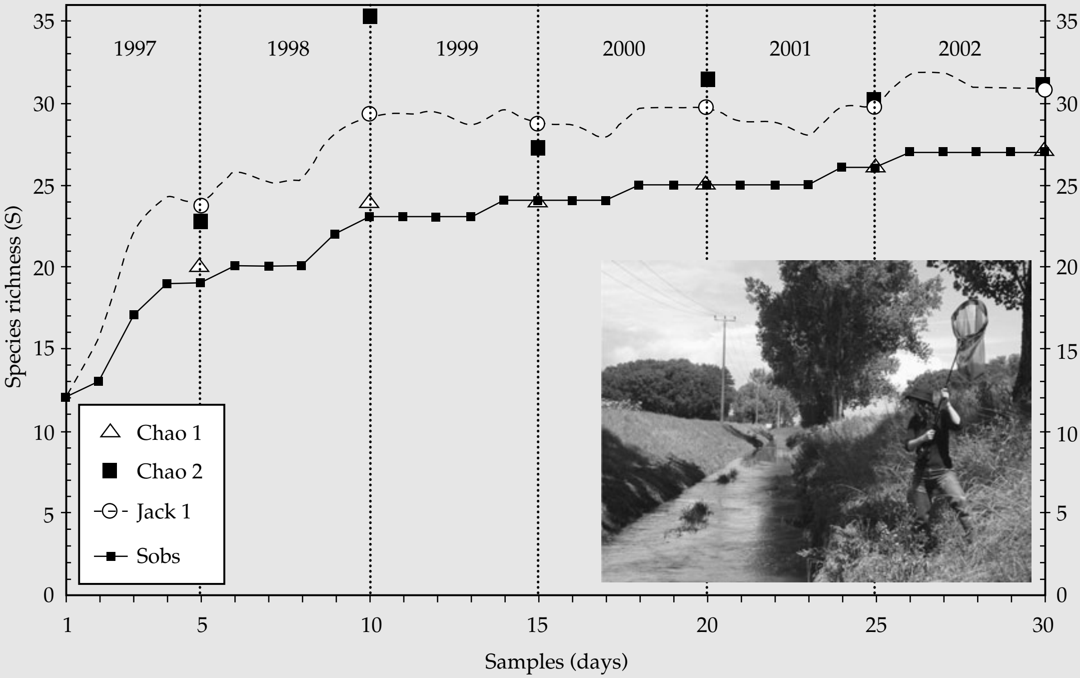
The use of estimations of real richness is very attractive for assessment and monitoring. Indeed, if correctly used, they offer the possibility of carrying out comparisons at local (e.g. time series, multiple sites) or regional (e.g. different biogeographical regions) scales.

7.4.2.1.2 Representative species assemblages

Species richness alone is only one type of information. If the Odonata community is used for bioindication, then the species assemblage has to be taken into consideration. Probably the most comprehensive sampling protocol published, which aimed to construct a ‘representative spectrum of Odonata species’ was presented by Schmidt (1985). It is based on semi-quantitative observations of larvae, exuviae, and adults, made over 2–3 years (see an application in Chovanec *et al.* 2004). A representative spectrum of Odonata species is useful for most of the objectives presented in Figure 7.1; it is also

Box 7.1 Species-accumulation curves and real-richness estimation

Shown is an example of a species-accumulation curve (30 sampling days) for a 6-year inventory conducted with adult Odonata on a 1.5-km long ditch ("Seymaz", Geneva Canton, Switzerland). The estimations of real richness (Jackknife 1, Chao 1, Chao 2) are also indicated for the end of each year. The curve of observed richness (Sobs) bends after the second year and reaches 27 species at the 30th sample day. The real richness estimators show a stabilization after just 2 years (Jackknife 1) or 4 years (Chao 1 and Chao 2), and finally reach values between 27 (Chao 1) and 31 (Chao 2 and Jackknife 1). This shows that the sampling effort was therefore satisfactory, although a few new species could still potentially be observed at the site. As other sites (ponds, wetlands) are present in the surrounding area, the curve presents a continuous slight increase, due to visits of allochthonous species. On a much longer timescale, this increase could potentially reach the regional richness level (regional richness was assessed for the Geneva Canton at 52 species, i.e. Angélibert *et al.* 2006). Therefore, a further step would be to present the same curves showing only data for autochthonous species. Data from Oertli (2002).



particularly well suited to conducting classification or ordination of water bodies.

7.4.2.2 Non-exhaustive surveys

Depending on the type of ecological study, exhaustive surveys are not necessarily useful, and it is often enough to perform sub-sampling to give an index that is representative of odonate diversity. This procedure is much less expensive, and so more effort can be devoted to replication (spatial or temporal). Standardization is also easier to implement here than for species inventories. Therefore, ecological research often uses such an approach, with a strong emphasis on standardization.

Rapid bioassessment protocols are an example of non-exhaustive surveys. They aim to be efficient, effective, low in cost, and easy to use. For aquatic invertebrates, a comprehensive review of rapid assessment approaches is provided by Resh and Jackson (1993). Odonates (especially adults) show the required characteristics and therefore can make a very beneficial contribution to such protocols. At the regional scale, rapid bioassessment of Odonata is already used for biodiversity assessment, for example in the African Freshwater Biodiversity Assessment. Rapid bioassessment are also particularly useful for screening to identify local diversity hotspots or degraded sites.

7.4.2.3 Sampling methods

The sampling of the adult stages of Odonata can be conducted easily, and in most cases it only requires a net and pair of binoculars. A species assemblage can be identified quickly, as the populations usually have a high number of individuals in a given water body; species with only a few individuals, or only one specimen, are an exception. This may concern adults of territorial species with a large territory (e.g *Anax* and *Cordulegaster* males). A quick examination of methods shows that there are two types of sampling units for surveying the adult stages of Odonata:

- transect survey as used for butterflies; that is, fixed travel routes along a section of the bank (e.g. Brooks 1993; De Marmels 1998; Cleary *et al.* 2004);
- quadrangular or rectangular survey plot (e.g. Stewart and Samways 1998; Oertli *et al.* 2005).

Typically, all species flying or perching in the sampling area are counted. The sources of bias or errors during the survey of a water body are numerous, especially for the non-specialist. In planning a standardized protocol, and in particular the number and timing of surveys, it is important to consider the phenologies of targeted species and their ecology (habitat association, diurnal activity).

To sample the larval stage, most methods developed for sampling aquatic macroinvertebrate assemblages (in particular for measuring biotic indices) are useful, and they usually have a standardized protocol (see in Elliott and Tullett 1993). The kick-net and the Surber-net samplings are techniques frequently used in streams, and artificial substrates in non-wadable streams or in lakes. For ponds or wetlands, a sweep pond-net is the most common sampling tool; different types exist, which vary in their size, the shape of the opening, and the mesh size. To collect exuviae, the vegetation or substrate near the water has to be searched (e.g. Foster and Soluk 2004). Such sampling can be completed by collecting teneral adults by using traps during emergence.

The use of replicates (survey plots of a fixed area) for sampling Odonata (adults, larvae, or exuviae) is particularly recommended, as it allows conduction of statistical analyses using means and standard deviations, simple non-parametric tests (e.g. Mann–Whitney U or Wilcoxon tests), accumulation curves, and real-richness estimators.

7.4.3 Assessment of the dragonfly community

Odonate assemblages can be analysed directly, for example as an attempt to carry out classification or ordination analyses and to investigate the relationship between assemblage patterns and environmental variables (e.g. Juen *et al.* 2007). The composition of a community can also be compared with predicted assemblages from reference conditions.

In a multimetric approach, the Odonata species list can be used to produce various metrics:

- species-richness measures, such as mean sample richness, total number of species, number of autochthonous species, number of species of conservation interest, and β diversity;
- conservation value (see examples of scoring in Painter 1999; Oertli *et al.* 2002; Van Duinen *et al.* 2003);
- diversity indices, such as Shannon, Margalef, or Simpson;
- other metrics, related for example to phenology, behaviour, water quality or habitat health (e.g. Table 7.1), reproduction, or habitat association.

These metrics have to be chosen before planning the monitoring/assessment, because they are linked directly to the study objective. Furthermore, the selected metrics will dictate the sampling strategy to use.

The next step after calculating the metrics is to conduct an assessment. For the evaluation of the quality of a given water body, or for a measure of its degradation, reference conditions can be used as a baseline. For example, for each measured parameter (species richness or other metrics) one can calculate the ratio of the observed value to that of the reference conditions. An example of this is the assessment system adopted in Europe for the Water Framework Directive of 2000. A major advantage of the Water Framework Directive is that assessment is based on a comparison between a status quo and a 'water-body-type-specific' reference state. This has a major implication for the role of 'species richness' in assessment procedures. For example, an impounded running water (with originally two autochthonous rheophilic odonate species) might show a species richness of 15 limnophilic species after rehabilitation of the inshore structures. Although species richness has increased the ecological status of the water body it has decreased significantly due to the loss of the autochthonous dragonfly fauna.

7.5 Conclusion: suggestions for future research

This review presents evidence that Odonata can constitute a very valuable tool in the assessment and monitoring of freshwater bodies. Furthermore, when sampled through standardized methodologies, they provide excellent data-sets for hypothesis testing in ecology or evolution.

For applied issues, adult stages of Odonata can be surveyed at a low cost. Additionally, as many species of Odonata are stenotypic, assemblages will always give accurate indication about habitat or microhabitat conditions. The good ratio of *quality of gained information* over *monetary price of the study* constitutes undoubtedly the greatest advantage of using Odonata assessment. Therefore, this group can often be used for preliminary screening, before investigating selected sites in more detail.

Their value as a tool nevertheless depends on the field investigated. For example, Odonata have limitations for water-quality assessment if they are used as a single group; a combination with other groups tends to give a more reliable diagnosis. The most promising use of Odonata is probably for biodiversity assessment. This is enhanced by the high value of Odonata to society, and they are recognized as an excellent flagship group (see also Chapter 8). Nevertheless, for biodiversity assessments, the use of complementary groups is advantageous to increase the accuracy of the analysis. Another particularly suitable application of Odonata monitoring is the assessment of habitat changes, related to perturbations or management measures. In particular climate change can be assessed by using Odonata at the local and regional scales; Odonata are still probably underexploited for this purpose.

In applied studies, existing methods are much too diverse and often lack standardization. Future research should focus to the development of unified standardized procedures. This would be particularly useful for conducting comparisons (e.g. across continents), and would help in testing ecological theories.

The use of Odonata in bioassessment could also be improved through more extensive use of metrics, based on Odonata as a single group or in a combination with other groups. The use of databases of ecological or biological species traits should offer the opportunity to identify a large variety of new metrics. The ecological information in these databases can still be improved, particularly with the help of national or international centres which could easily conduct statistical analyses of biological data (e.g. geographical species distribution, duration of life cycle).

Acknowledgements

I am grateful to Jane O'Rourke, Anita Weatherby, and Pascale Nicolet for improvements to the English version of this chapter. Comments from Sandrine Angélibert, Nicola Indermuehle, and two anonymous referees helped to improve an earlier draft of the manuscript. Thanks to Michael de la Harpe for his efforts in producing Box 7.1. Surveys presented in the box were funded by the Canton of Geneva (Département du territoire, Domaine nature et paysage) and Pro Natura Geneva.

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CHAPTER 8

Dragonflies as focal organisms in contemporary conservation biology

Michael J. Samways

Overview

Fresh water ecosystems worldwide are highly threatened, with the biodiversity crisis in these systems being exceptionally severe. Dragonflies are among the most significant organisms in the systems that are under threat, and are therefore important focal organisms in contemporary conservation biology. Their role is as top predator for other invertebrates, as well being food themselves for vertebrates. At the outset of a conservation exercise, we must be clear as to whether a species is at its geographical range margin or at the centre, as this makes a difference as to how we go about the conservation. Threats to odonates are many and synergistic, with global climate change also beginning to impact on them, although not necessarily adversely for some species. Worldwide, assessments are being made of dragonfly conservation status. In this respect, they are one of the highest-profile invertebrates in conservation awareness, planning and action. During the process of conservation, it is becoming increasingly important to be clear on how we value the subjects of that conservation. Dragonflies are highly valued as they are iconic, have aesthetic value, and are sensitive indicators of landscape change. They are both important subjects in their own right and also important role players in overall biodiversity conservation. In view of their charisma and their role in ecosystems, they will continue to play an important role in conservation circles for the foreseeable future.

8.1 Introduction

Fresh water is essential for a whole range of human activities. Indeed, it has driven the rise and fall of civilizations over the last 15000 years, and prior to that determined where and how humans moved and migrated across landscapes (Fagan 2004). Yet we share this critical resource with a wide range of organisms. Indeed, we share it with a disproportionate species richness in comparison with other ecosystems. This is borne out when we consider that fresh water makes up only about 0.01% of the world's surface free-flowing water (and about 0.8% of the Earth's surface), while about 100000 out of 1.3 million so far scientifically described species (8%) live in it (Naiman *et al.* 2006). This means that fresh water is a massive 10 times richer in species than the world average.

Of the world's ecosystems, fresh waters are under the most pressure (Postel and Richter 2003; Millenium Ecosystem Assessment 2005), and inevitably the threats to freshwater biodiversity are particularly severe (Dudgeon *et al.* 2006). Evidence is accumulating that over 20% of freshwater species are currently threatened or extinct, with indications from North America that extinction rates are four to five times higher than in terrestrial systems (Ricciardi and Rasmussen 1999).

Dragonflies are among those casualties, and as they are arguably the most conspicuous of all freshwater invertebrates, it is inevitable that they are playing a major role in contemporary conservation biology. On the one hand, they are significant conservation subjects per se, while on the other, they are excellent indicators of environmental quality.

Increasingly, they are also being used as indicators of success, or not, of conservation activities. In this chapter, I explore where this important insect group is shaping conservation biology thinking, and in turn, where conservation activities are making positive strides in the conservation of dragonfly species.

8.2 Utilitarian and intrinsic value of dragonflies

In conservation management, we must begin by asking on what values we are basing our conservation action (Rolston 1994). The approach to values adopted by most conservation policy makers is that of utilitarian or instrumental value. This approach posits that nature is there for our benefit and for us to use. Utilitarianism may be consumptive (we physically consume it) or non-consumptive (we utilize it to satisfy our cultural, aesthetic, educational, or scientific needs without using it up). We rarely consume dragonflies, although dragonfly larvae and adults are eaten in some low-economic income cultures.

On the non-consumptive side, dragonflies have featured strongly in many cultures. Traditional East Asian art has often featured dragonflies. Japan even has parks dedicated to dragonflies (Primack *et al.* 2000). Dragonfly viewing trails and artificial ponds are now becoming more commonplace (Suh and Samways 2005; Niba and Samways 2006) and books are being published on where to go to view dragonflies (Hill and Twist 1998), in addition to the surge in dragonfly field guides worldwide. Such field guides are an essential first step for increasing awareness (Pearson and Shetterly 2006). Dragonflies also regularly feature as motifs on fabrics, and for jewelry and household items, illustrating forcibly that there is a sector of society which appreciates dragonflies enough to purchase these goods. D'Aguilar *et al.* (1986) give an interesting illustration of a South American Indian wearing a damselfly wing through the septum of the nose.

These non-consumptive, utilitarian, cultural, and aesthetic values generally bear little relationship to the conservation of rare species, although they nevertheless respect the rights of individuals (Rolston 1994). Arguably however, dragonflies do have very important indirect utilitarian value in that they are one invertebrate taxon to which the public can relate, and thus dragonflies have an important ambassadorial function.

Parks, ponds, and trails, besides providing enormous cultural value, also lend themselves to education, so introducing the young to animals to which they might otherwise not be directly exposed. But we must remember that the dragonfly species in these largely artificial water bodies are mostly widespread generalists. This means that visitors to such retreats are not seeing a segment of species that are of immediate conservation concern (Samways 2007). Exposure to these threatened species then only comes about with hiking trails to and within the habitats where the species occur. Then, to recognize them, a field guide is essential.

Some reserves have been set up specifically for dragonfly species, or at least for certain dragonflies which are high on the conservation agenda. *Hemiphlebia mirabilis*, an Australian endemic of great phylogenetic interest, yet highly threatened, has been given special and specific attention in Wilson's Promontory, southern Victoria (Sant and New 1988).

Intrinsic value recognizes that every form of life has its worth, regardless of its value to humans. Although the utilitarian approach has held sway in most conservation circles for a long time, there is now a swing towards consideration of intrinsic value. Sometimes though, this conservation for conservation's sake is still tinged with utilitarianism, as in the precautionary principle (Fauna and Flora International 2006), which declares that we conserve as much as possible (compositionally, structurally, and functionally) in case there might be adverse consequences should we not do so. Dragonflies per se have not featured in this debate. This is because the task at hand has been maintenance of ecological integrity and ecosystem function without teasing out isolated taxa which would otherwise stand in ecologically meaningless isolation.

There is one area where intrinsic value does play a role in dragonfly and other species conservation, and that is in connection with the Red List. The point is that the Red List gives equal attention to all and every species, whether deer, dugong, or dragonfly.

This is very significant because the Red List has enormous currency in global conservation trend analysis and conservation planning. Dragonflies feature strongly on the Red List, partly because there are indeed many species which are threatened but also because dragonfly conservationists have been highly active with this iconic taxon.

8.3 Threats

The various threats to dragonflies are those generally applicable to many other freshwater invertebrates. Among those threats is habitat loss. In reality, this is a broad term, which although used often to describe a threat, when unpacked, relates to a whole host of possible impacts. Dragonflies have illustrated this point. Among the impacts is canalization, where the natural river system, with its naturally porous margins, is converted into an unforgiving concrete-bounded channel, often with fast-moving water, and rarely suitable for any odonates, except the occasional tolerant generalist (Ott 1995). Canalization also has a strong impact on fluvial dynamics, negatively affecting the diversity of backwaters on floodplains (Davies and Day 1998).

Other engineering activities also impact on odonates. Bridges can affect their dispersal (Schutte *et al.* 1997), whereas dams affect water flow and change the odonate assemblage from lotic to lentic (Steytler and Samways 1995). As dams often disturb both the aquatic and riparian community, inevitably the odonate assemblage changes from one with specialists to one with widespread generalists. Similarly, artificial ponds, while increasing the area of occupancy, do so generally only for the widespread generalists (Samways 1989), with colonization of new ponds not following any particular ecological assembly rules, but instead according to the presence of suitable microhabitats (Osborn and Samways 1996).

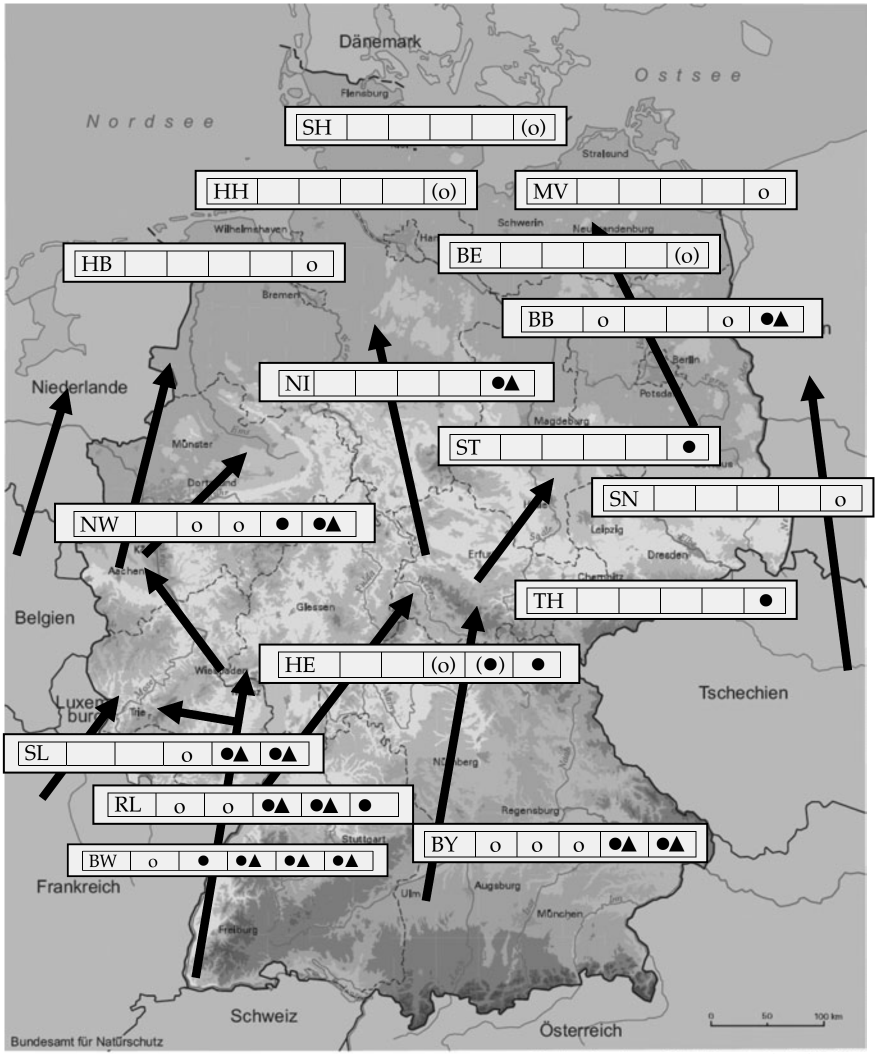
Various types of pollution can also have an impact on dragonflies (Ott 1995; Corbet 1999), but rarely has it been possible to associate a particular odonate population decline with a specific pollutant. Zgomba *et al.* (1986), however, showed that dragonfly populations can decline as a result of impact by the biopesticide *Bacillus thuringiensis israelensis*, which is used against mosquitoes. One of the reasons why there have been few correlations between specific pollutants and demonstrable dragonfly population decline is that pollutants generally pulse, and, after an infusion, may well be washed downstream and no longer detectable, but nevertheless leave a swathe of 'mysterious' mortality in their wake. On the other hand, where pollution is persistent and insidious, it can have an ongoing ameliorating effect on the local dragonfly assemblage. The species that are particularly affected are the narrow-range endemics, as in the small streams on Mayotte island, which are subject to continuous detergent input (Samways 2003b).

Alien organisms have become a major concern for conservation worldwide (Mooney and Hobbs 2000). Alien fish, for example, can have cascading effects on various other biota and even on neighbouring ecosystems through impact on dragonfly larvae (Knight *et al.* 2005). Surprisingly, fish removal rarely has been factored into conservation plans specifically for dragonfly conservation, despite the fact that alien fish can eliminate certain naïve damselflies of running waters on islands (Englund 1999; Englund and Polhemus 2001).

Invasive alien trees have had an enormous impact on South African endemic (and other) dragonflies (Samways and Taylor 2004), with 11 out of the current 12 Red-Listed species in South Africa being threatened by alien trees (Samways 2006a). The impact of these alien trees is seen in reverse when the trees are removed, with extraordinarily fast recovery of even the rarest of specialists (Samways *et al.* 2005). The key threat from the trees is shade, which has a direct impact on the odonates, but also an indirect one through shading out of perch sites and oviposition sites for some of the species (Samways 2006b). Of great concern are synergistic effects, with, for example, the alien trees triggering bank erosion as indigenous plant cover is lost.

Physical loss of habitat, whether from draining of wetlands or conversion of land for agricultural or urban development, is a worldwide phenomenon. Whereas there is loss of temperate forest that is impacting on temperate dragonflies (Sahlén 2006), it is tropical forest loss and the impact on tropical species that is of greatest concern (Bedjanič 2004; Dijkstra and Clausnitzer 2006; Orr 2006; Paulson 2006), principally because the wet tropics are so rich in narrow-range species, and yet such extensive deforestation is taking place. A corollary is that the actual level of severity of the tropical biodiversity crisis is still uncertain (Laurance 2007). Yet dragonflies are indicating that there are probably many extinctions taking place, and we certainly cannot be complacent.

In conservation circles there has been some optimism that certain focal species may be surviving in landscape fragments, but a cautionary note comes from Tilman *et al.* (1994) who point out that remnant fragments may incur an extinction debt as ecological relaxation starts to unfold. This is the process whereby species are lost from fragments over time



Quelle: Bundesamt für Naturschutz (BfN), 2006

Figure 8.1 Geographic range expansion of the scarlet darter *Crocothemis erythraea* in Germany, with speculated distribution routes denoted by arrows. The abbreviations represent various Federal States. Open circles, observations of single individuals; closed circles, established populations; closed triangles, increasing area of occupancy/extent of occurrence; parentheses represent speculated expansion. The first subdivision of the bar represents prior to 1970; the second, 1971–1979, the third 1980–1989, the fourth, 1990–1999, the fifth, 2000–2006. From Ott (2007) with permission of Scientific Publishers.

as various stochastic environmental factors, such as drought and fire, as well as genetic effects, such as inbreeding depression and genetic bottlenecks, impact on the population refugia over time. Such impacts may well be synergistic, and, of particular concern, interactive with global climate change, thus hastening the process of biotic attrition, as is occurring in British butterflies (Warren *et al.* 2001).

Global climate change has been implicated in geographical range expansion of dragonflies in both Germany (Ott 2007) and Japan (Aoki 1997). In Germany, *Crocothemis erythraea* has gone from being a rare species a few decades ago to a common one today, with its expansion being facilitated by using gravel pits as stepping-stone habitats (Figure 8.1). Hassall *et al.* (2007) have shown for British dragonflies that there have been significant advances in phenology, with a mean advance of the assemblage of 1.51 days per decade, which is equivalent to 3.08 days per degree rise in temperature. These examples show that certain species are highly responsive to global climate change, but this does not by any means suggest that all odonate species will respond positively to climate change. Species which are spatially confined in highly fragmented landscapes (Thompson and Watts 2006) and those that are confined to mountain peaks (Dijkstra *et al.* 2007; Samways 2008a) are highly susceptible.

8.4 Marginality and dragonfly conservation biology

Conservation at geographical range margins is a challenging topic (Gärdenfors 2001), with dragonflies having been at the forefront of the debate. Extinction comes about through loss of populations, until finally the last individual dies. Some species are widespread and generally common (i.e. have a large extent of occurrence and area of occupancy). Populations may be lost well within the geographical range. Usually, however, it is marginal populations that are most at risk (Lawton 1993; Samways 2003a).

The corduliid *Oxygastra curtisii*, for example, used to occur in Britain (and indeed it was described from there) but was last recorded in Hampshire in 1951. While scarce and localized in northern and central Europe, its stronghold is in the western Mediterranean, where it appears to be comparatively safe (Askew 1988; Dijkstra and Lewington 2006).

Marginal populations may not necessarily be in optimal habitat, which becomes critical when weather conditions are unusually adverse. At the centre of their geographical range the comparative weather extremes may have less impact, simply because the species has been selected over long periods of time to survive those various extremes. At the edge of the range, the weather extremes may be of an intensity that the species has rarely or never had to deal with in the past, and is thus ill-equipped to survive such extremes. This is seen in South Africa, where species push south from farther north in Africa, only to be pushed back, and occasionally driven farther south, by extreme droughts or floods (Samways 2008b).

Marginal and isolated populations are also genetically cut off from the main metapopulation. This is seen in isolated British populations of the damselfly *Coenagrion mercuriale*, which suffers from allele frequencies rapidly drifting apart from the closest neighbouring population (Thompson and Watts 2006).

Furthermore, when threats are synergistic, and, in addition, populations are isolated, there is greater risk of population extinction as landscape fragmentation increases. This situation is aggravated when there is climate change (Figure 8.2) (Travis 2003). This background is conceptually important for odonate conservation biology, especially from a global perspective. Some species may be very rare at their range margins and in one political entity or another (country, province, state, county, municipality) and be declared 'threatened' and in need of conservation action. Yet often the species is common elsewhere and not necessarily threatened from a global perspective. This is the case for *O. curtisii*, which is protected by law in Germany (Ott *et al.* 2007), and *C. mercuriale* in Britain (Thompson and Watts 2006), while both are protected under Annex 2 of the Bern Convention.

In contrast to nationally rare and threatened species, there are those that are threatened globally. These are normally those with a small geographical range (extent of occurrence) coupled with a small area of occupancy, and often associated with specialized habitats. Should these species be lost from

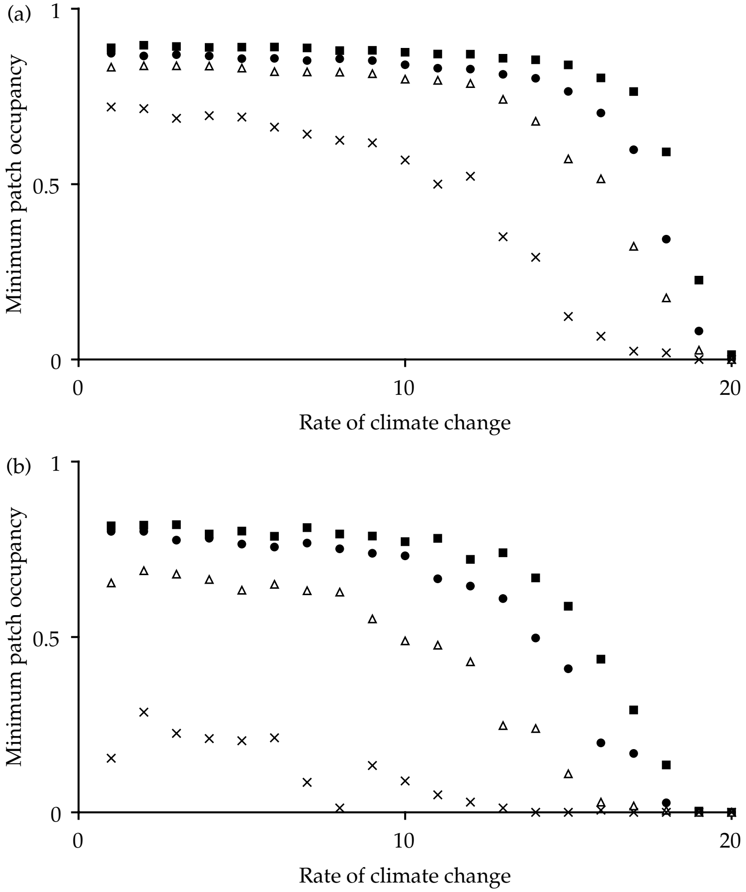


Figure 8.2 A computer model showing that habitat loss reduces the ability of a species to survive climate change as a generalist (a) and as a specialist (b) species. The squares show the results for no habitat loss, circles with 20% loss, triangles with 40% and crosses 60%. Increased fragmentation has a particularly severe effect on a specialist species in the event of climate change. From Travis (2003) with permission of the Royal Society.

the local area, then they are lost to the world. In conservation biology, such species (or sub-species, i.e. evolutionarily significant units) are described as irreplaceable. Often these narrow-range species are also habitat specialists, which is normally the very reason for their rarity. They are also particularly vulnerable to the adverse impacts of global climate change (Figure 8.3).

8.5 Biodiversity assessment

Dragonflies, being conspicuous invertebrates, have featured strongly in biodiversity assessments at various spatial scales from municipal to national. The products have mostly been 'red books', 'red data books', and 'red lists', and, with assessments of other, concordant taxa, have enabled conservation planners to identify the geographical areas where there is sensitive and significant fauna. At the global scale, there is only one Red List®, or to give it its full title, the IUCN Red List of Threatened Species™ (Baillie *et al.* 2004; IUCN 2006). Underpinning the Red List is a database, known as the Species Information Service (SIS). In the case of dragonflies, data are entered on to the SIS through the World Conservation Union/Species Survival Commission (IUCN/SSC) Odonata Specialist Group (SG). Species that are

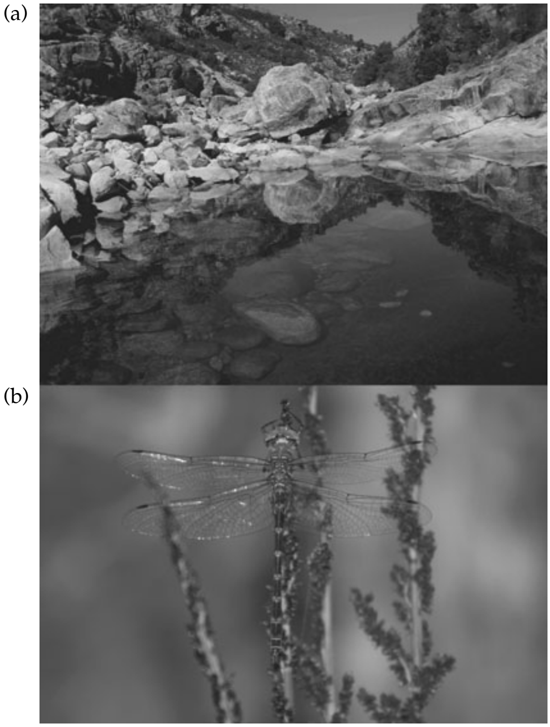


Figure 8.3 Some unusual, even unique, habitats can occur on mountain peaks. (a) Pictured here is the source of a stream (Witrivier) in the Western Cape, South Africa, and home to the recently discovered and very rare habitat specialist, the rustic presba *Syncordulia serendipitor* (b). Of real concern is that only a minor change in habitat conditions, such as climate change, might result in the demise of this species.

threatened globally (which includes the threat categories of Vulnerable, Endangered, and Critically Endangered; IUCN 2001) tend to have a great deal of currency and often play a role in conservation planning and action. They may be the sole focal taxon, or be included in a range of taxa being conserved in a particular area.

Species are assessed locally by a designated individual known as an Assessor (through the Odonata SG). The Odonata SG then acts as a Red List Authority, thus authenticating (technically termed evaluating) those assessments. The information is then passed on to the IUCN Red List Office in Cambridge, UK, for entry on the SIS database. This Red-Listing process is largely an *ad hoc* process depending almost entirely on the activity of dedicated and much valued volunteers (who nevertheless may be professional odonatologists). Discussions of the process and considerations with regards to dragonflies have been outlined in Samways (2002) and Samways and Grant (2007). An overview of the conservation status of dragonflies across the world has been given in the volume edited by Clausnitzer and Jödicke (2004).

Large-scale assessments feed into this Red List process, and significant among them is the African Freshwater Biodiversity Assessment being undertaken by the IUCN. Dragonfly data, along with those of freshwater crabs, molluscs, and fish, across Africa are being collated into the SIS database. In turn, this database is also the forum for the Global Dragonfly Assessment (GDA), which is a bold initiative to collate data on all dragonflies worldwide. It is being spearheaded by the IUCN Species Programme, the IUCN/SSC Invertebrate Conservation Sub-Committee, as well as the Odonata SG, and is bringing together a consortium of individuals and institutions. With the data gathered, there will then be an overall picture of conservation trends of dragonflies worldwide. Of significance here is that it is the first global assessment of any invertebrate group.

The Red List is an authoritative document that is proving to have considerable conservation planning value worldwide (Baillie *et al.* 2004; Rodrigues *et al.* 2006). However, dragonflies have barely featured so far in the trend analyses given in these papers, but will do so in the future, particularly with completion of the Global Dragonfly Assessment. Additionally, dragonflies are also featuring in another IUCN/SSC initiative, the Sampled Red List Index, which aims to select a sample of the world fauna from a wide variety of taxa, dragonflies included, and to assess changes in population levels of these focal taxa over time, especially relative changes in environmental conditions. In conclusion, as dragonflies are such a conspicuous and scientifically tractable taxon (i.e. they have high iconic value), yet also tied to the scarce resource of fresh water, they are inevitably going to play a major role in the new assessments worldwide, and alongside such well-known groups as amphibians, birds, and mammals.

8.6 Systematic conservation planning

The issue of values as discussed above is largely about why we should do conservation. The next question is what should we conserve? At first glance, this would seem to be intuitively obvious: dragonflies and their habitats (Moore 1997). Yet it is not quite as simple as that. This is because there are many other taxa (and their habitats) which are perceived by other conservation champions as also important. Mammals and birds are among those organisms which are charismatic enough to galvanize conservation action easily. Even among the invertebrate ranks there are also taxa which command attention because they are both adored and threatened. Among them are the butterflies. In Britain, the organization Butterfly Conservation has a staggering 14 000 members, whereas the British Dragonfly Society, which covers all aspects of odonate biology, has only 1400 members, which nevertheless is still impressive.

This brings us to systematic conservation planning which has received considerable attention in recent years, and has been pioneered by Margules and Pressey (2000), among others. Dragonflies have at times played a key role in these planning exercises, as seen in the key paper by Prendergast *et al.* (1993). The picture which emerged is that there is not necessarily concordance between the various taxa, neither in temperate countries, as shown by Prendergast and his colleagues, nor in the tropics (Lawton *et al.* 1998).

The field of conservation has evolved considerably in recent years, with focus on a combination of species approaches (see the critique by Favreau *et al.* 2006) and landscape approaches (Margules and Pressey 2000). The process involved is one of prioritization, whereby ideal reserve areas are selected by an iterative process involving complementarity, which involves giving priority to most irreplaceable of faunas. What is emerging is that when such systematic planning exercises are undertaken, as much as 50% of the land surface should be conserved to maintain biodiversity at current levels (Reyers *et al.* 2002). The significance of this is that some hard decisions have to be made, which inevitably means that some form of landscape triage needs to be instigated (Samways 1999). Besides undertaking prioritization, there still has to be some selection of reserve areas based on feasible goals.

Dragonflies will continue to play an important role in systematic conservation planning. Besides being highly iconic, they are also sensitive indicators of landscape change (Samways and Taylor 2004). Consequently, they are the grist of some important databases currently being developed, especially through the Global Dragonfly Assessment mentioned above.

8.7 Conservation management

Having discussed the why and what of dragonfly conservation biology, let us now move on to the how, which is conservation management. There are essentially two levels (discussed in Samways 2005): that of the landscape and that of the species, known as the coarse and fine filters respectively. At the landscape scale (and larger), dragonflies are part of the management activity. In other words, the landscape is conserved to conserve biodiversity in general. Dragonflies may be part of the planning process and they may also be one of the target groups of organisms for conservation. This is not surprising because they are hardly likely to be excluded, as with any other taxon. The issue though, is that such landscape management does not focus specifically on any one taxon but on compositional, structural, and functional biodiversity in its entirety. Indeed, dragonflies are part of food webs in any particular ecosystem and even between ecosystems (Knight *et al.* 2005; Taylor 2006), as they are generally very vagile organisms. Many do of course need more than one ecosystem to become mature adults. Landscape approaches that incorporate dragonflies include the restoration of riparian corridors (Samways and Grant 2006; Samways 2006b), assisted by natural reforestation, as has taken place in Hong Kong, where over 40% of the land area is designated as a Country Park (Figure 8.4).

The landscape or coarse-filter approach is generally overlain by the species or fine-filter approach. Thus landscapes are conserved but it may still be necessary to provide particular management activities that hone in on the needs of particular, focal species. This is built into the Red Listing process in that the listing is not just about flagging threatened

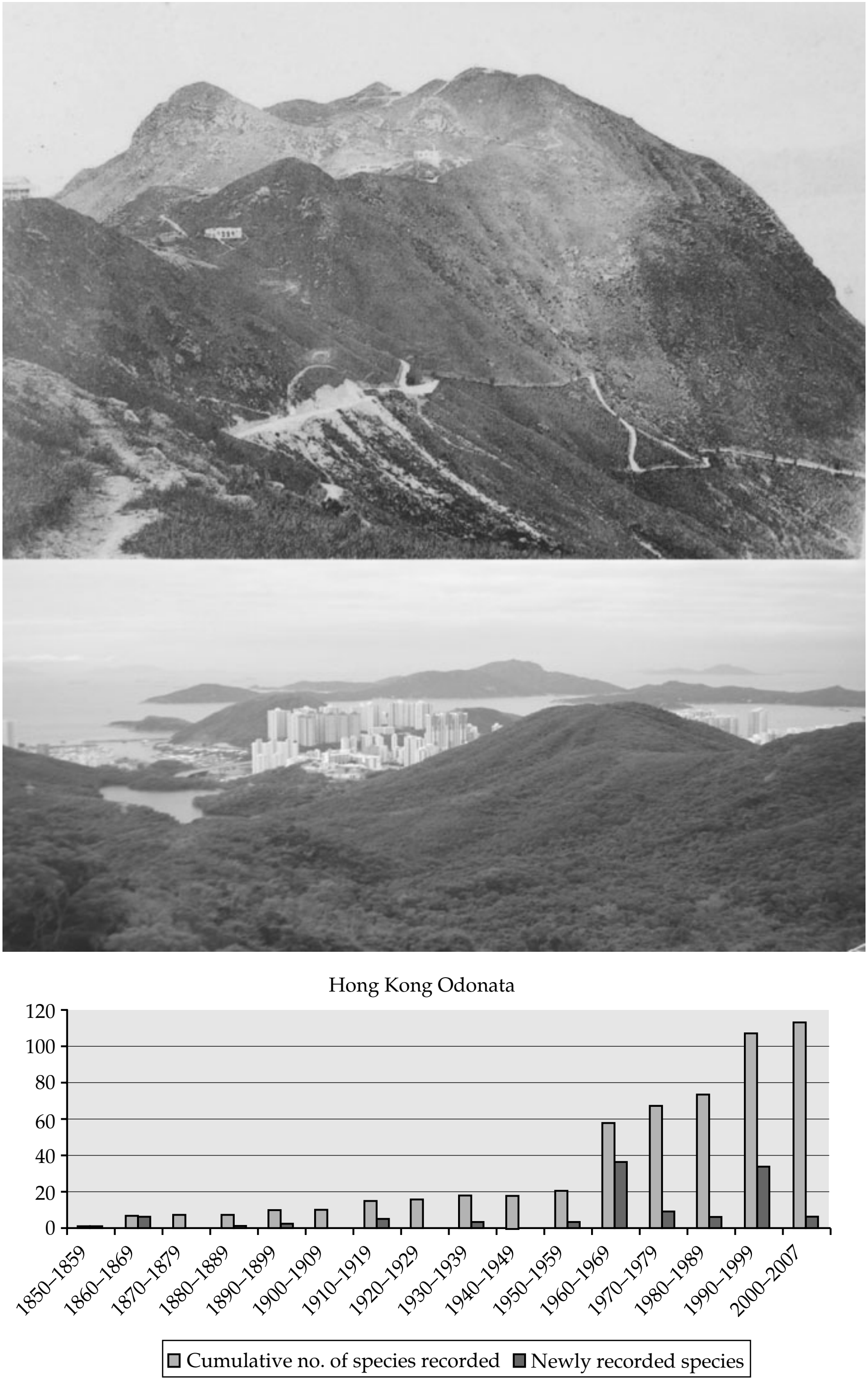


Figure 8.4 By 1870, Hong Kong had been extensively deforested (top), but, unlike many tropical areas, has undergone considerable assisted and natural reforestation, so that today it is largely green, with pockets of intense urbanization (middle). This re-greening has meant that many dragonfly species that presumably once were there, but went extinct locally due to deforestation, have been able to return to the area (bottom). Source and figure courtesy of Keith Wilson; presentation at the 17th International Symposium of Odonatology, Hong Kong, 2006.

species, but also making suggestions for their conservation, and indeed proliferation, which feeds into the 2010 targets.

Although dragonflies are featuring at the global level in this management process (through for example the Global Dragonfly Assessment), most real-life management takes place at the local level. Thus many countries have recovery plans. For British dragonflies, as well as other insects, this has been well articulated by Shirt (1987).

8.8 Conclusions

Dragonflies, being graceful and iconic, are high-profile insects. Being associated with a scarce resource, fresh water, and also largely sensitive to landscape and global climate change, they have featured strongly in contemporary conservation-biology thinking. They have also been instrumental in formulating conservation action, whether as participants or as the focal taxon. However, we must be fully aware they are part of food webs and generally cannot be separated out and put on a pedestal of their own: they are components of compositional and functional biodiversity. Nevertheless, because they are so high-profile, it is inevitable that there are several species-specific action plans across the globe dedicated to certain of their species. Of special significance is that they are one invertebrate taxon that is playing a major role in conservation at all spatial scales, and are likely to do so even more in the future.

Acknowledgements

I really do appreciate the insightful comments of Vincent Kalkman and an anonymous referee. The research was funded by the European Community within the FP6 Integrated Project ALARM (Assessing Large Scale Environmental Risks for Biodiversity with Tested Methods; GOCE-CT-2003-506675).

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CHAPTER 9

Valuing dragonflies as service providers

John P. Simaika and Michael J. Samways

Overview

Valuing the services provided by ecosystems and their components is emerging as a new, practical tool for conservation of biodiversity. One such framework for quantifying the components of biodiversity and their attributes that are important for the diversity of ecosystem services is the service providing unit (SPU). This framework, which is additive to other, current frameworks, provides a conceptual link between ecosystem services and the role of populations of different species in providing these services. Any particular SPU provides a given service at a given spatial or temporal scale. Service provision may benefit humanity either directly or indirectly. Dragonflies provide several ecosystem services to humanity at the population level. Their role as SPUs encompasses most of the 28 ecosystem services, directly or indirectly, as recognized by the Millennium Ecosystem Assessment, in the categories of provisioning, cultural, supporting, and regulating services. Odonates lend themselves well as SPUs, as they are well known taxonomically, conspicuous, and flagships of freshwater conservation. Dragonflies provide enormous cultural benefit to humans, as shown by much visual and literary art, and the many worldwide recreational parks, trails, and field guides dedicated to this taxon alone. Service provision by dragonflies sometimes can be quantified easily. We provide examples of this in pest control and riparian restoration. The latter has been a huge success for South African dragonflies, with the populations of many species, including Red Listed ones, stabilizing and even increasing. Indeed, dragonflies are now being widely used as habitat quality indicators. On the negative side, odonates may also have adverse effects on services, thereby reducing their value, as for example with pollination. The SPU concept, as a value metric, has considerable currency with dragonflies, and there is merit in investigating its application to other invertebrate taxa and ecosystems.

9.1 Introduction

Biodiversity is the diversity of genes, species, and ecosystems. Efforts to conserve biodiversity have increased substantially in recent years, as a reflection of the realization that our well-being depends not only on conserving, but also using, biodiversity wisely. To do so depends in part on how we value that biodiversity.

In its simplest form, biodiversity value may be divided into utilitarian value (of use to humans) and intrinsic value (not necessarily of use to humans). Although we focus here on dragonflies as an entity, they are essentially no different from any other group of organisms, in terms of their *intrinsic* value. Furthermore, we should bear in mind that dragonflies are not a finite ecological box, but rather they are components of ecosystems, interacting with many other organisms and responding to various abiotic variables (Knight *et al.* 2005).

In contrast to intrinsic value, although not mutually exclusive (Rolston 2000), is utilitarian value. This is the language of most biodiversity conservation initiatives, and is presently the most persuasive for policy-makers. The current approach requires that for biodiversity to be conserved, it must pay its way. This is not only an economic issue but also one of service provision (Millennium Ecosystem Assessment 2005; Bishop *et al.* 2007). The utilitarian standard set by the Millennium Ecosystem Assessment can be seen as providing the vital conceptual link between individual species and their contribution to the provision of ecosystem services. In addition, this link can also be translated into an economic measure. For example, Losey and Vaughan (2006) estimate that wild insects that control pests, pollinate flowers, bury dung, and provide nutrition for other wildlife are worth US$57 billion per year in the USA alone.

The European Union's Co-ordination Action Project RUBICODE (Rationalising Biodiversity Conservation in Dynamic Ecosystems; www.RUBICODE.net) is now exploring this predominantly utilitarian approach. The project's aim is to review and develop concepts of dynamic ecosystems and the services that they provide. Those components of biodiversity which provide specific services to society are being defined and evaluated to increase our understanding of the value of biodiversity services, as well as the cost of losing them. This will give decision-makers a more rational base and will help the understanding of the need for adequate conservation policies, which are essential to halting biodiversity loss.

Building on the Millennium Ecosystem Assessment (2005), a new approach is also being developed, which was first articulated by Luck *et al.* (2003). This novel approach uses the concept of service providing units (SPUs), which focuses on what biodiversity does for humanity, using quantifiable services. These levels may be the populations of single species but they may also be the populations of several species. The SPU concept identifies the important species populations for service provision, as well as the important attributes of those populations (size, temporal or spatial distribution, etc.). The reasoning behind this approach is that it translates threats to, and value of, biodiversity into tangible and quantifiable factors for use by policy-makers. As well as one or more species contributing to a service, they may also contribute to more than one service.

Conceptually there is also the converse of the SPU, where certain populations of certain species can reduce a service. Such populations are termed service antagonizing units (SAUs; see www.RUBICODE.net). These concepts can be illustrated with, for example, the service of pollination. The SPUs are the right pollinators in sufficient numbers to carry out the service; that is, pollination. Yet these pollinators may be subject to ameliorating factors such as infestation by the *Varroa* mite, a bee parasite, which, in sufficient numbers, may reduce provision of the service, and so are an SAU. When communities are considered, there is a whole host of species which can alter the dynamics of food webs (Memmot 2000). In the final analysis, the quantity and quality of the service provision depends on the sum of the SPUs minus that of the SAUs.

As research into service provision is just beginning, it is difficult to quantify accurately many of these services. Nevertheless, it is the aim of RUBICODE to build upon what is known to date. In keeping with the theme of this book, dragonflies as model organisms for ecological and evolutionary research, and because this taxon is being considered in contemporary SPU research, it is appropriate to review the topic.

9.2 Dragonflies and ecosystem services

As the Millennium Ecosystem Assessment (2005) is an authoritative document, it is a valuable platform from which to launch a discussion of the significance of dragonflies in service provision. The Millennium Ecosystem Assessment recognizes 28 ecosystem services to humans, in four distinct categories: provisioning, cultural, supporting, and regulating services. These services can be applied at the population level (Table 9.1). They could be considered of direct benefits to humans, and thus species or populations providing these services are SPUs. As dragonflies are top predators, only certain services are, by definition, applicable to them.

9.2.1 Positive contributions (service provision)

9.2.1.1 Provisioning services

Provisioning services are the products obtained from ecosystems (Millennium Ecosystem Assessment

Table 9.1 Ecosystem services provided, and diminished, by Odonata as service providers, or service antagonizers, at the population level. Parentheses denote indirect contributions.

Ecosystem service	Contribution by Odonata populations
Provisioning services	
Biochemicals and medicines	Traditional and Western medicine
Freshwater	(Monitoring ecosystem condition)
Genetic resources	Models for research and population dynamics
Ornamental resources	Preserved for display purposes
Production (food and fibre)	Food in some traditional societies
Cultural services	
Cultural diversity and heritage	Some cultures, especially in East Asia
Education and inspiration	Dragonfly trails or parks, and field guides
Knowledge system	Both professional and amateur odonatology
Recreation and aesthetic values	Dragonfly trails or parks, and field guides
Sense of place	Parks, field guides, festivals
Spiritual and religious values	Significant to past and present cultures
Supporting services	
Nutrient cycling	Top predator and wide disperser
Primary production	Not applicable
Production of atmospheric oxygen	Not applicable
Provision of habitat	For parasites; vector of these to poultry and humans
Soil formation and retention	Negligible; biomass small
Water cycling	Negligible; biomass small
Regulating services	
Climate regulation	(Sensitive indicator of global climate change)
Disease regulation	Negligible; biomass small
Erosion regulation	Negligible; biomass small
Herbivory	Not applicable
Invasion resistance	Some, for example, on introduced bee species
Natural hazard protection	Not applicable
Pest regulation	Mosquito control by augmentation
Pollination	Can severely lower value of service
Seed dispersal	Can inhibit seed production and plant dispersal
Water-flow regulation	(Important bioindicator)
Water purification and waste treatment	(Important indicator of habitat health)

2005). These include food, fibre, fuel, genetic resources, ornamental resources, freshwater, biochemicals, natural medicines, and pharmaceuticals (Table 9.1). As regards provisioning services, dragonflies play a role as a source for genetic resources, as research subjects in medical laboratories. For example, recent research by Schilder and Mardens (2006) on metabolic syndrome in the dragonfly *Libellula pulchella* may give clues to metabolic diseases such as diabetes and obesity in humans. Despite the obvious differences between humans and insects, advances from invertebrate biology have often led to a better understanding of mammalian biology. For example, the discovery and dissection of mechanisms regulating innate immunity pathways in mammals were based on knowledge gleaned from *Drosophila* (true flies). Schilder and Mardens (2006) hope that pathways involved in the development of metabolic abnormalities may be similarly homologous, which opens the way for the use of non-mammalian systems as an additional tool to study causes and treatments for metabolic diseases such as diabetes and obesity.

Dragonflies also have ornamental value. As with butterflies, they are often preserved for display in cabinets, although their main value is as motifs on household items.

Dragonflies are not a staple food (like rice) that nations depend on. Nevertheless, they are often enjoyed as a delicacy or as an ingredient in main dishes in a variety of cultures in Asia (e.g. China, Japan, India), Africa (including Madagascar), and the Americas (Mexico) (Corbet 2004). For example, on Bali, dragonflies are fried in coconut oil and served with vegetables (Hardwicke 1990).

Dragonflies are being used more extensively in genetic studies, particularly to elucidate aspects of their conservation. Thompson and Watts (2006), for example, using genetic studies, showed that for the European damselfly *Coenagrion mercuriale*, it was not habitat loss that is the main concern but limited movement, indicating that sites for conservation must be placed close together.

9.2.1.2 Cultural services

Cultural services are the non-material benefits that people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences, including cultural diversity, spiritual and religious values, knowledge systems, educational values, inspiration, aesthetic values, social relations, sense of place, cultural heritage values, recreation, and ecotourism (Table 9.1) (Millennium Ecosystem Assessment 2005). Dragonflies have cultural significance (Corbet 2004). For example, to the Navaho Indians, odonates symbolize pure water. Traditionally known as the 'invincible insect', the dragonfly was a favourite symbol of strength among Japanese warriors, and the old name for the island of Japan (Akitsushima) means 'dragonfly island' (Kritsky and Cherry 2000). Dragonflies are thought to possess medicinal properties and are used by practitioners of traditional medicine in China and Japan (Asahina 1974).

Along with butterflies, dragonflies arguably are the most significant in terms of recreational service. They are especially appreciated by the Japanese, where Odonata reserves or parks are well established, and new areas rehabilitated to help promote conservation awareness (Figure 9.1) (Primack *et al.* 2005). The recreational value of Odonata is also increasingly recognized by other developed nations, as the burgeoning number of field guides, associations, and websites would suggest (Lemelin 2008). Many parks worldwide feature dragonfly

Figure 9.1 Sophisticated infrastructure at the Nakamara Dragonfly Reserve in Japan, emphasizing the cultural significance of these insects in this region.

trails, not necessarily for threatened species, but rather for enjoyment of the insect subjects and to increase awareness (Niba and Samways 2006). In South Africa, for example, a dragonfly trail has been established (Suh and Samways 2001).

9.2.1.3 Supporting services

Supporting services are those that are necessary for the production of all other ecosystem services. They differ from the other services in that their impacts on humanity are often indirect or occur over a very long period of time, whereas changes in the other categories have relatively direct and short-term impacts on people (Millennium Ecosystem Assessment 2005). These services include soil formation, photosynthesis, primary production, and nutrient and water cycling (Table 9.1). Dragonflies contribute to nutrient cycling in that they are top predators in vertebrate-free habitats, both as larvae and adults. Dragonfly larvae prey on other insects including other odonates, fish fry and eggs, amphibian larvae, crustaceans, molluscs, flatworms, and leeches (Corbet 2004). Adults, like their immature counterparts, are also predators, feeding on a variety of insects including other dragonflies. For example, Pritchard (1964) reports that at least 79% of prey items available to Aeshnidae, and 90% to Libellulidae, are Diptera, followed by 58% and 20% Coleoptera, respectively. Pritchard also reports that large Aeshnidae consume Trichoptera and other Odonata. Overall, however, Diptera are the major prey of odonates (Corbet 2004). Dragonflies have very wide dispersal capability, and they introduce nutrients from aquatic ecosystems to terrestrial ecosystems. For example, there may be over 1.2 million individuals partaking in the large annual migration of *Anax junius* adults in North America (Russell *et al.* 1998). These migrations are now known to have great similarity with songbird migration strategies (Wikelski *et al.* 2006).

Both larval and adult dragonflies have associations with other organisms, which relates to the definition of supporting services in the Millennium Ecosystem Assessment. These supporting services have great variety and come from numerous taxa; thus only some are mentioned here briefly. Associations include, apart from predators, commensals, mutualists, pathogens, and parasites. On dragonfly larvae, the associated commensal organisms may include diatoms, rotifers, molluscs, and other insects. Water mites are commensal on larvae, but parasitic on adults (Corbet 2004). An interesting mutualism involves an alga and the damselfly larva, *Mecistogaster ornata*, whereby the larva provides substrate for the alga and postures itself to enhance the photosynthetic activity of the alga, increasing the oxygen concentration around its respiratory surfaces (Willey *et al.* 1970).

Parasites of larval and adult dragonflies include organisms from the Phyla Protozoa, Platyhelminthes, Aschelminthes, and Arthropoda. Of special interest are the trematodes, several species of which infest poultry and humans. These infestations are mediated by dragonflies, as described in Section 9.2.2. Adult dragonfly commensals are varied. These include pseudoscorpions, biting lice, wasps, milichiid flies, algae, and microorganisms. Dragonflies appear to be susceptible to some well-known fungal insect pathogens, including *Claviceps* and *Cordyceps* (Corbet 2004). By far the most conspicuous and prevalent parasites are the ectoparasitic water mites (Hydrachnida) (Smith 1988). Water mites are ubiquitous on dragonflies wherever there are eurythermic waters that are lentic or slow-flowing, and usually permanent, or temporary. Damselflies are parasitized more often than dragonflies (Smith 1988). Furthermore, common, widespread odonate species are more susceptible to mite infestation than sympatric rare and threatened ones, indicating the significance of species traits (Grant and Samways 2007b).

9.2.1.4 Regulating services

Regulating services are the benefits obtained from the regulation of ecosystem processes (Millennium Ecosystem Assessment 2005). They include regulation of air quality, climate regulation, water regulation, erosion regulation, water purification and waste treatment, disease regulation, pest regulation, pollination, and natural-hazard regulation. Dragonflies are only very minor components as drivers of climate regulation, as their total biomass is relatively small. However, they are highly responsive to climate change, in terms of both geographic range change (Aoki 1997; Ott 2007) and phenology (Hassall *et al.* 2007).

Being a top predator, dragonflies may have some impact on invasive organisms lower in the food chain, including honey bees in Florida (Wright 1944). Dragonflies also have potential in pest regulation. Both larval and adult dragonfly stages may be used in pest control. For example, as explained in more detail below (Section 9.3.1), an experiment in a village in Myanmar (Burma) demonstrated that larval odonates of *Crocothemis servilia* could be used to control larvae of *Aedes aegypti*, a vector of dengue fever (Sebastian *et al.* 1990). Another example for pest control comes from several Asian countries, where various species of damselflies breed in rice fields. The damselflies consume large numbers of stem borers and leafhoppers from among the leaves of rice plants. Dragonflies are among the most effective predators of rice pests, partly because their density among the rice plants increases as the growing season advances (Nakao *et al.* 1976). According to Yasumatsu (in Corbet 2004), in some rice fields where dragonflies occur, about 80% of farmers use no pesticides.

Dragonflies are increasingly used as bioindicators of freshwater health and ecological integrity (see Chapter 7 in this volume). They compare very favourably with benthic macroinvertebrates in general, and yet have the advantage that, as adults, they are more spatially explicit than the benthic macroinvertebrate assemblage as a whole (Smith *et al.* 2007).

Odonata may not provide a water purification or waste treatment service in the sense that they provide a filtration or significant long-term storage service of pollutants. However, as a faunal assemblage, they do store significant amounts of pollutants in their tissues, due to their long ontogenetic development (Peters 1988). Furthermore, different assemblages or species are sensitive to different types and gradients of chemical pollution (Rahmel and Ruf 1994). This makes them excellent indicators of ecosystem health (Clark and Samways 1996; Smith *et al.* 2007).

9.2.2 Negative contributions (service antagonism)

Whereas all the above relates to positive contributions (i.e. SPUs) by dragonflies, they can also have negative effects (i.e. be SAUs). For example, certain species attack bee colonies of apiaries, but also wild colonies and solitary pollinators. Wright (1944) reports that bee colonies of apiary yards along the Mississippi River in Louisiana were severely reduced by predation by large aeshnids. Reportedly, where normally 75–85% of queens would return to the yard after a nuptial flight, only 5% were doing so in the summer of 1941. Predation on worker bees was also severe. Predation on pollinators by some dragonflies, such as *Coryphaeschna ingens*, a species occurring in Florida, is so severe that it is locally known as the 'bee butcher'. Apparently this species has made queen rearing unprofitable and impracticable in parts of the south-eastern USA (Corbet 2004). The effect of predation on pollinators is measurable not only with domesticated populations for commercial use, but also with wild populations (Knight *et al.* 2005; discussed in greater detail in Section 9.3.2).

Dragonflies may serve as intermediate hosts of a number of parasites, including trematodes. This includes a fluke, *Prosthogonimus* sp., that causes severe inflammation in the oviducts of birds, production of abnormal eggs, and peritonitis that is normally fatal. The fluke also affects poultry. When found in eggs, a farmer's produce is ruined. Birds are usually infected in spring or early summer, and contract the parasites by eating larval or adult dragonflies. At least 13 orders of birds are known to be definitive hosts for *Prosthogonimus* sp. To prevent infection of stock by 'dragonfly disease', poultry farmers in eastern Europe keep their poultry away from water's edge when large numbers of dragonfly larvae emerge, and shut the birds away when large numbers of migrating adults appear (Street 1976). In south-east Asia, humans too, may be susceptible to trematode infection vectored by dragonflies. Humans are definitive hosts for two species, *Phaneropsolus bonnei* and *Prosthodendrium molenkampi*. People are infected with these trematodes by ingestion of larvae, which are eaten raw or ground up and added to other foods (Manning and Lertprasert 1973). Infection can be avoided by cooking the larvae before eating them.

9.3 Quantifying SPUs and SAUs

The value of the SPU lies in its identification and quantification of *changes* in population *levels*, and where these changes make a difference to service provision, whether positive or negative. Identification of quantitative links between components and service provision then become crucial for guiding the management of services. This is of importance to policy-makers and land managers as it facilitates specific rather than vague management guidelines. We now look at three examples, two positive and one negative, in more depth.

9.3.1 Dragonflies as SPUs in pest control

Certain dragonfly species and population levels have great potential in pest regulation, as demonstrated by a pilot study described in Sebastian *et al.* (1990). In an experiment in a village in Yangon, Myanmar, Sebastian *et al.* (1990) used larval odonates of *Crocothemis servilia* to control larvae of *A. aegypti*, a vector of dengue fever. The libellulid *C. servilia* lends itself well for the task in pest control, as it is a eurytopic species and easily reared in captivity from egg to adult. Gravid females of this multivoltine species are available throughout the year, ensuring a continuous supply of eggs for rearing. Also, the larvae of *C. servilia* survive well in large containers for several weeks on a low diet.

In their pilot study, Sebastian *et al.* (1990) established a treatment and control area. In the former, three to four dragonfly larvae were released into variously sized containers that the home-owners in the community used to collect water for drinking and other household usage. They found that at the first evaluation, half a month after the augmentative release, *A. aegypti* larval indices had fallen by 46–86%, and at the second evaluation, one full month after augmentative release, by 77–96%. The indices continued to fall to negligible levels as the experiment continued. These findings are consistent with earlier, preliminary results, that two half-grown libellulid larvae can kill virtually all mosquito larvae in a drum of 90-litre capacity in 4–9 days, depending on the number of mosquito larvae initially present (Figure 9.2) (Sebastian *et al.* 1990).

9.3.2 Dragonflies as SAUs in pollination

In the case where dragonflies may act as SAUs, this can also be quantified. Recently, Knight *et al.* (2005) investigated how predation affects trophic cascades, both directly and indirectly, across ecosystems. The researchers set up predation experiments on pollinators, using dragonflies. In their experimental

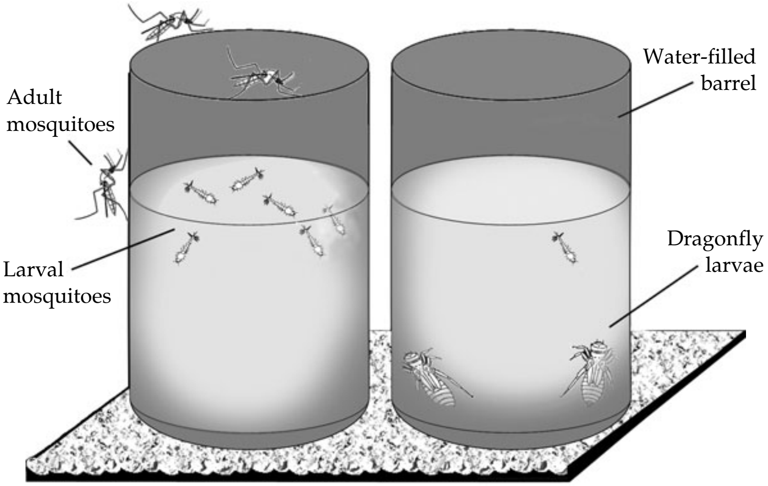


Figure 9.2 Stylized diagram illustrating the pest-control experiment by Sebastian *et al.* (1990) in a village in Yangon, Myanmar. Sebastian *et al.* (1990) used larval odonates of *Crocothemis servilia* to control larvae of *Aedes aegypti*, a vector of dengue fever. In the dragonfly-free barrel (left) mosquito larvae mature without predation pressure. However, with as few as two dragonfly larvae present, the mosquito population is severely decimated in as few as 4–9 days, depending on the initial number present in a 90-litre barrel.

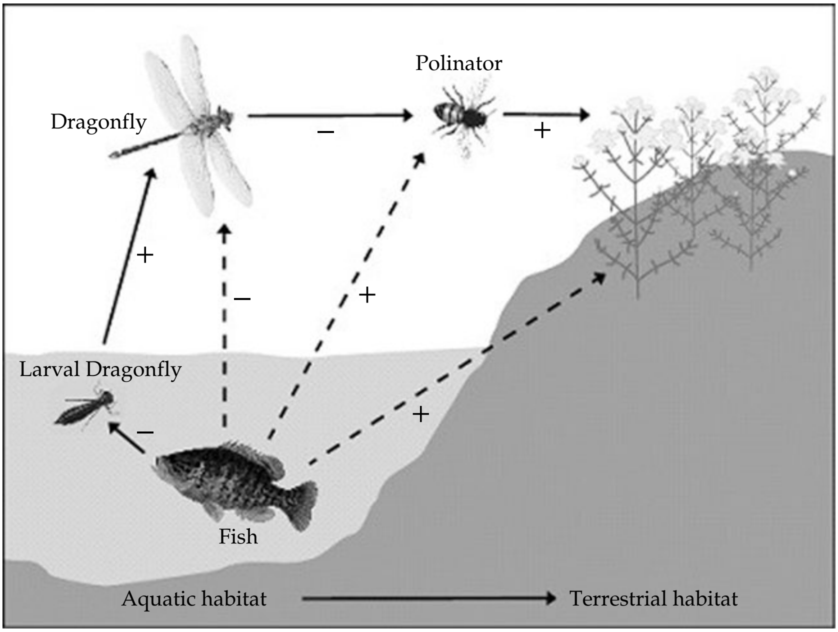


Figure 9.3 Trophic cascade in an ecosystem. In fish-free ponds, there are large dragonfly species of great abundance, whereas in fish ponds smaller species and fewer individuals are present. Dragonfly abundance has direct (negative) effects on pollinator visits on flowers. Thus dragonflies indirectly (negatively) affect pollination and thereby plant seed production. The presence of fish reduces pressure on pollinators by dragonfly predation, and thus indirectly, positively affects pollination and plant seed production and dispersal. Solid arrows, direct effects; dashed arrows, indirect effects; +, positve effect; −, negative effect. Redrawn from Knight *et al.* (2005).

set-up, they chose eight similar ponds, of which half had no fish, and the other half had fish present. This allowed them to test the hypotheses that fish would reduce larval and adult dragonfly abundance and that this would permit a higher abundance of insect pollinators, indirectly increasing the pollination and reproductive success of nearby terrestrial plants. They confirmed that adult and larval dragonfly abundances are much lower in fish ponds than in fish-free ponds. Also, dragonflies are small at ponds with fish, whereas medium-sized to large dragonflies frequent fish-free ponds. Pollinator visitation is lower at fish-free ponds, because dragonflies feed on the pollinators, and because the prey behaviourally avoids foraging near adult dragonflies. Knight *et al.* (2005) demonstrated this finding by using cages covered in a small mesh, large enough to let pollinators through, but not dragonflies. Empty cages served as the control, and the treatment cages contained dragonflies. Visits to flowers in the treatment cages were lower, and pollinators spent less time in these cages.

Knight *et al.* (2005) also investigated the effect of fish on dragonflies and whether the cascading effect on pollinator visits influenced plant reproductive output (Figure 9.3). Plants near fish-free ponds were more than twice as pollen-limited than plants near ponds with fish. The strong linkages between consumers in aquatic and terrestrial ecosystems are not an isolated occurrence, and could have been demonstrated with other aquatic or semi-aquatic predators revealing a similar trophic cascade into terrestrial ecosystems.

9.3.3 Dragonflies as SPUs for riparian restoration

Benthic macroinvertebrates have been widely used for monitoring freshwater condition, which includes riparian condition (e.g. Rosenberg and Resh 1993). Adult, aerial dragonflies are excellent surrogates of benthic macroinvertebrates, and are more sensitive at the small scale of several metres than the benthos, which responds principally to overall stream condition (Smith *et al.* 2007). Arguably, the adult dragonflies are also fairly good surrogates of stream biodiversity in general. This is especially significant bearing in mind that freshwater systems are among the most threatened of any in the world (Naiman *et al.* 2006).

Without detailed studies focusing on a particular species, it is generally difficult to assess population levels of invertebrates. This is because they are often small, cryptic, and seasonal, making even Red List assessments difficult without considerable resources and some detailed knowledge of their biology (Samways and Grant 2007). This is despite many insect taxa in particular being excellent indicators of environmental health (McGeoch 1998). Dragonflies are among those sensitive taxa. They are large and conspicuous and have a range of sensitivities from one species to the next. Whereas certain individual species may be good indicators of landscape change (Sahlén 2006; Smith *et al.* 2007), and even global climate change (Ott 2007), it is really the whole assemblage and the relative change in its species composition which signals best any change in environmental conditions. Thus, we propose here that the SPU is the dragonfly assemblage.

The quantitative level at which the SPU operates is the nominal; that is, species presence or absence. However, species differ qualitatively in their response traits to river restoration and thus each species is given a Dragonfly Biotic Index (DBI). This is based on the sum of three sub-indices: (1) the size of the species' geographical range, (2) risk of extinction, and (3) its sensitivity to habitat change. Each sub-index has a score of 0–3, resulting in widespread and common habitat generalists scoring 0, and threatened, endemic habitat specialists scoring as much as 9. The scores relative to geographical distribution, threat level, and sensitivity are given in Table 9.2.

By far the greatest threat to South African dragonflies is from invasive alien trees, which block out sunlight and cause general deterioration of the river bank (Samways and Taylor 2004). Invasion is a key threat (Samways 2006), and lifting it results in an immediate recovery of even the rarest and most sensitive of endemics (Samways *et al.* 2005).

There has been ongoing and massive nationwide restoration of rivers in South Africa, known as the Working for Water Programme (Richardson and van Wilgen 2004). Its prime target has been the restoration of hydrology and to provide jobs. Biodiversity recovery was not originally high on the agenda, but as it turns out from the dragonfly studies, biodiversity has benefited enormously from this restoration activity. This is important, as South Africa has biodiversity hotspots (Myers *et al.* 2000). Although it was known that dragonflies are sensitive indicators for the success of this restoration programme at the local level (e.g. Clark and Samways 1996; Smith *et al.* 2007), it became clear after studies were done at larger spatial scales (e.g. Stewart and Samways 1998) that the use of dragonflies as SPUs could also be undertaken at the national scale (Grant and Samways 2007a). Thus we have a SPU that is easy to use and effective on

Table 9.2 Typical Dragonfly Biotic Index (DBI) scores for African dragonfly species. The DBI ranges from 0 to 9. It is based on the three sub-indices relating to geographical distribution, level of threat, and sensitivity to habitat change, with particular reference to invasive alien riparian trees. The DBI is the sum of the scores for the three sub-indices. A common, widespread, not-threatened, and highly tolerant (of disturbance) species would score 0 (0+0+0), whereas a highly range-restricted, threatened, and sensitive species would score 9 (3+3+3).

Score	Sub-index…	Distribution	Threat	Sensitivity
0		Southern African, and common in South Africa	Not threatened	Not sensitive; may even benefit from habitat change due to alien plants
1		Southern African, but rare in South Africa	Near threatened	Low sensitivity to habitat change from alien plants
2		National endemic in three or more provinces	Vulnerable	Medium sensitivity to habitat change from alien plants
3		Endemic, but to only one or two provinces	Endangered or critically endangered	Extremely sensitive to habitat change from alien plants

Table 9.3 Biodiversity recovery at Disa Stream, Table Mountain, as measured by the Dragonfly Biotic Index (DBI) before and after removal of invasive alien plants.

Before		**After**	
Species	DBI	Species	DBI
Stream Hawker	4	Conspicuous Malachite	7
Cape Julia Skimmer	4	Marbled Malachite	8
Little Scarlet	3	Sooty Threadtail	7
Red-veined Dropwing	0	Palmiet Sprite	7
Navy Dropwing	0	Friendly Hawker	3
		Stream Hawker	4
		Mahogany Presba	8
		Cape Julia Skimmer	4
		Little Scarlet	3
		Red-veined Dropwing	0
		Navy Dropwing	0
Total DBI	11	Total DBI	51

Table 9.4 Biodiversity recovery at DuToit's River, Franschhoek Pass, as measured by the Dragonfly Biotic Index (DBI) before and after removal of invasive alien plants.

Before		**After**	
Species	DBI	Species	DBI
Sooty Threadtail	7	White Malachite	7
Mountain Sprite	4	Ceres Streamjack	9
Orange Emperor	2	Sooty Threadtail	7
Boulder Hooktail	2	Mountain Sprite	4
Cape Julia Skimmer	4	Mauve Bluet	9
Red-veined Darter	0	Stream Hawker	4
Navy Dropwing	0	Orange Emperor	2
		Boulder Hooktail	2
		Gilded Presba	8
		Mahogany Presba	8
		Yellow Presba	7
		Cape Julia Skimmer	4
		Red-veined Darter	0
		Navy Dropwing	0
		Jaunty Dropwing	1
Total DBI	19	Total DBI	72

Table 9.5 Biodiversity recovery at White River, Bainskloof Pass, as measured by the Dragonfly Biotic Index (DBI) before and after removal of invasive alien plants.

Before		**After**	
Species	DBI	Species	DBI
Sooty Threadtail	7	Conspicuous Malachite	7
Mountain Sprite	4	White Malachite	7
Stream Hawker	4	Marbled Malachite	8
Orange Emperor	2	Sooty Threadtail	7
Boulder Hooktail	2	Mountain Sprite	4
Cape Julia Skimmer	4	Palmiet Sprite	7
Red-veined Darter	0	Stream Hawker	4
		Orange Emperor	2
		Common Thorntail	2
		Cape Thorntail	8
		Boulder Hooktail	2
		Rustic Presba	8
		Mahogany Presba	8
		Yellow Presba	7
		Cape Julia Skimmer	4
		Red-veined Darter	0
Total DBI	23	Total DBI	85

multiple scales. Naturally, there are differences in the 'players' (particular species), yet the principle is the same wherever the SPU is applied. This emphasizes that whereas the SPU approach focuses on function and the services provided, it is essential also to recognize ecological integrity; that is, species' identity and where they live (what Lockwood (2001) calls a sense of place).

Using the DBI is effective and easy, and all it requires is close-focus binoculars for species recognition. It can be applied to various streams and rivers. The service value can be calculated as the ratio of the sum of the DBIs after alien clearance to that before. For example, where the sum of the DBIs after clearance is 50, yet before it was 25, then the biotic recovery is 2. Translated into a percentage Biodiversity Recovery Score (BRS), this is 200%.

The great advantage of this BRS is that very high scores come out for streams which had previously lost their narrow-range and sensitive specialists, and have now been restored as a result of removal of the alien trees. Examples are given in Tables 9.3, 9.4, 9.5, and 9.6. The DBIs of the species used in the examples are given in Table 9.7. The massive BRS (464%) for Disa Stream on Table Mountain (Table 9.3) and the very high values for DuToit's River at Franschhoek Pass (379%; Table 9.4), and White River in Bainskloof Pass (370%; Table 9.5) are because these stretches of flowing water are in the centre of the Cape Floristic Region biodiversity

Table 9.6 Biodiversity recovery at Levuvhu River, Soutspansberg, as measured by the Dragonfly Biotic Index (DBI) before and after removal of invasive alien plants.

Before		**After**	
Species	DBI	Species	DBI
Dancing Jewel	1	Dancing Jewel	1
Goldtail	5	Common Threadtail	3
Common Threadtail	3	Painted Sprite	2
Painted Sprite	2	Kersten's Sprite	1
Kersten's Sprite	1	Slate Sprite	2
Swamp Bluet	1	Swamp Bluet	1
Boulder Hooktail	2	Orange Emperor	2
Two-striped Skimmer	2	Common Tigertail	1
Eastern Julia Skimmer	0	Boulder Hooktail	2
Portia Widow	1	Two-striped Skimmer	2
Round-hook Dropwing	0	Eastern Julia Skimmer	0
Riffle-and-reed Dropwing	3	Black-tailed Skimmer	1
Jaunty Dropwing	1	Portia Widow	1
		Broad Scarlet	0
		Little Scarlet	3
		Red-veined Darter	0
		Denim Dropwing	3
		Navy Dropwing	0
		Kirby's Dropwing	1
		Riffle-and-reed Dropwing	3
Total DBI	22	Total DBI	29

hotspot. This contrasts with the situation on the Levuvhu River in the Soutpansberg where there is only one national endemic species (albeit a sensitive one) and the BRS is comparatively low (132%; Table 9.6). The significant recovery of the Disa Stream is represented in Figure 9.4.

9.4 Critique of the SPU/SAU concept with respect to dragonflies

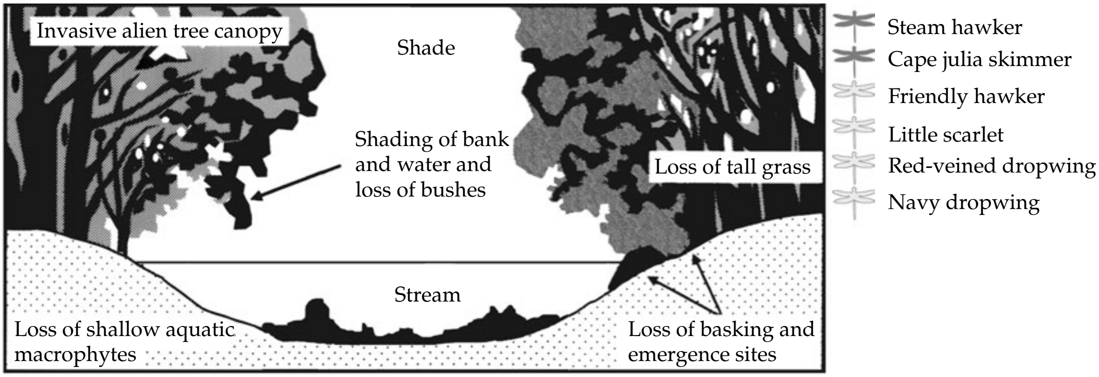
SPUs are essentially a way of quantifying service provision. As regards dragonflies, we may then ask whether the *quantity* of dragonflies matters to humankind. Furthermore, we may also ask whether the dragonflies contribute to the SPU concept.

There is no doubt that dragonflies play an enormous cultural role, but this is largely associated with their presence or absence, rather than their population levels. Yet in an era of rapidly declining

Table 9.7 Odonata species and their sub-indices reflecting the species geographical distribution (G), its extinction threat (T), and its sensitivity to habitat change (S). Each of the three sub-indices are on a scale of 0–3, and the sum of these three scores is the Dragonfly Biotic Index (DBI). Only those species featured in the examples given in this chapter are listed here.

Common name	**G**	**T**	**S**	**DBI**
Black-tailed Skimmer	0	0	1	1
Boulder Hooktail	0	0	2	2
Broad Scarlet	0	0	0	0
Cape Julia Skimmer	3	0	1	4
Cape Thorntail	3	2	3	8
Ceres Streamjack	3	3	3	9
Common Thorntail	0	0	2	2
Common Threadtail	0	0	3	3
Common Tigertail	0	0	1	1
Conspicuous Malachite	3	1	3	7
Dancing Jewel	0	0	1	1
Denim Dropwing	1	0	2	3
Eastern Julia Skimmer	0	0	0	0
Friendly Hawker	2	0	1	3
Gilded Presba	3	2	3	8
Gloldtail	2	0	3	5
Jaunty Dropwing	0	0	1	1
Kersten's Sprite	0	0	1	1
Kirby's Dropwing	0	0	1	1
Little Scarlet	1	0	2	3
Mahogany Presba	3	2	3	8
Marbled Malachite	3	2	3	8
Mauve Bluet	3	3	3	9
Mountain Sprite	2	0	2	4
Navy Dropwing	0	0	0	0
Orange Emperor	0	0	2	2
Painted Sprite	0	0	2	2
Palmiet Sprite	3	1	3	7
Portia Widow	0	0	1	1
Red-veined Darter	0	0	0	0
Red-veined Dropwing	0	0	0	0
Riffle-and-reed Dropwing	1	0	2	3
Round-hook Dropwing	0	0	0	0
Rustic Presba	3	2	3	8
Slate Sprite	0	0	2	2
Sooty Threadtail	3	1	3	7
Stream Hawker	2	0	2	4
Swamp Bluet	0	0	1	1
Two-striped Skimmer	0	0	2	2
White Malachite	3	1	3	7
Yellow Presba	2	2	3	7

(a) Invaded habitat



(b) Recovered habitat

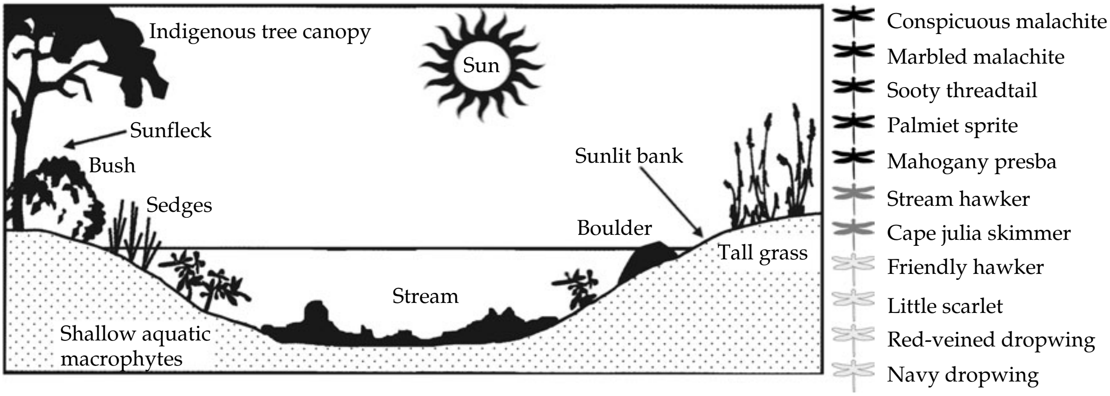


Figure 9.4 Dragonfly habitat invaded by alien trees (a) and recovery in rehabilitated habitat (b). In (a), the invasive alien tree canopy shades out the variety of indigenous grasses and bushes. This adversely alters the habitat structure, and also decreases the solar energy that adult dragonflies depend on. In recovered habitat (b), solar energy now penetrates indigenous tree canopy and allows grasses and bushes to grow. The indigenous habitat structures and increased solar energy now provide the habitat needed by rare, endemic habitat specialists and increase the diversity of the dragonfly assemblage. Stylized dragonflies represent the Dragonfly Biotic Index (DBI) as follows: extreme habitat generalists, DBI 0–3 (light grey); habitat generalists, DBI 4–6 (dark grey); habitat specialists, DBI 7–9 (black). Redrawn from Samways (2006).

biodiversity, presence also means healthy and robust populations (Bridle and Vines 2007). The presence of a population that is facing an extinction debt (Tilman *et al.* 1994) would be a population of concern.

At this point, we need to bring in the concept of intrinsic value. The reason for this inclusion is that arguably so long as the public at large is engaged with dragonflies, *any* dragonflies, that is enough to satisfy the cultural value. In such a case, only the real aficionados would be concerned whether or not it is a rare and threatened species. This is driven home when we consider theme parks that feature dragonflies. Normally the species to which the public are exposed are the common and widespread ones. Although this is good for being in touch with nature, it is doing little for the seriously threatened species to which the public is not normally exposed. We do not wish to see the 'extinction of experience', where people miss out to an increasing extent on their contact with nature, but there is a question of *quality* rather than *quantity* at stake here, where such parks should be instigated alongside conservation management of the threatened species at other locations (Samways 2007).

The three detailed examples given in this chapter give very different angles to service provision. The control of mosquitoes involves the deliberate introduction of dragonflies in particular quantities in artificial water bodies (Sebastian *et al.* 1990). Arguably this is not really what the SPU concept is about, as it is an artificial situation. Yet this might well be a representative example, as dragonflies are known to eat mosquitoes in natural ecosystems. Furthermore, it is common knowledge among odonatologists that many dragonfly species can be reared on mosquito larvae. The point that is brought home here is the possible consequences of *withdrawal* of a service (i.e. where dragonfly populations have been lost). This example illustrates that there is likely to be a huge amount of service provision in natural ecosystems that simply has not yet been quantified.

The example of dragonflies reducing pollinators (Knight *et al.* 2005) is very distinctly negative and, again, quantifiable. Interestingly, the fish that fed on the dragonflies were alien. Thus there is a situation here where an alien is improving a service provision. This is of course a violation of a sense of place (Lockwood 2001). Furthermore, this situation may well have other consequences such as loss of other macrobenthos. Alternatively, the plants benefiting from the increased predation of dragonflies by fish could, at least theoretically, increase in population level and in doing so impact on other, sympatric species of plants. What is clear from this example is that there are many possible ramifications when one starts to probe the changes in level of service provision.

The third example, very different from the other two, operates at the level of the assemblage. Dragonflies are clearly excellent indicators of riparian restoration where invasive alien trees are being removed. Yet the most sensitive species are the rare and threatened ones that occur in the global biodiversity hotspot, the Cape Floristic Region. Many of the species which have recovered following alien tree removal are localized Red-Listed endemics. Again, the presence or absence of species is intimately related to population levels. Red Listing is, after all, about population levels. Whereas in many insect species the population size, in terms of number of individuals, is difficult to measure, the Red-Listing process also works on measures of population size based on the extent of occurrence and area of occupancy (IUCN 2001). Thus the service is definitely quantifiable but in this case it uses both the number of species and the identity of particular species.

In summary, what the SPU/SAU concept does, as highlighted by these dragonfly examples, is enable focus on quantifiable aspects that would otherwise be overlooked. These examples show that service provision depends on the *quantity* of the components, whether individuals in a population or species in an assemblage. It also depends on strategic delivery of the services: populations and species must have the right traits, and be in the right area at the right time in sufficient density. This is not to ignore the overall service that the host ecosystem also provides, which must always be borne in mind when focusing on ecology, rather than on the artificial compartment of a single taxon, such as the dragonflies.

9.5 Conclusions

The SPU/SAU concept is new and challenging. What it does above all is to enable us to think of nature's service provision in quantitative terms. It enables the construction of hypotheses about the role that *numbers* of individuals of particular species, at strategic or significant places or times, play in determining the *quality* of that provision. We can hypothesize that if the system is modified by a *certain* amount, that the *level* of provision will be altered accordingly and presumably predictably. Translated into human well-being, this means possible changes in quality of life.

Acknowledgements

We would like to thank Richard Harrington and Paula Harrison for critical comment. This work was supported by the RUBICODE Coordination Action Project (Rationalising Biodiversity Conservation in Dynamic Ecosystems) funded under the Sixth Framework Programme of the European Commission (contract no. 036890).

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SECTION II

Studies in evolution

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CHAPTER 10

Evolution of morphological defences

Frank Johansson and Dirk Johannes Mikolajewski

Overview

Many organisms express morphological traits such as spines or armour as protection against predators. Understanding the ecology and evolution of these morphological defences helps to understand and protect the diversity of animal and plant forms. Among odonates, several dragonfly larvae express lateral and dorsal abdominal spines. In the most spectacular case the presence of cues from predatory fish induce longer spines in one species. Studies within and among species have shown that large spines reduce predation risk, so we suggest that larger spines in many cases are adaptations to reduce predation risk by fish. Interestingly, one form of costs of morphological defence seems to be associated with a higher predation risk by invertebrate predators, as long-spined larvae have a higher probability of being caught by these small predators. Dragonflies also use anti-predator behaviours to reduce predation risk. Studies on the relationship between morphological defence and behavioural defence have revealed that either a positive correlation between traits (trait cospecialization) or negative correlation between traits (traits compensation) occurs within species. We suggest that the inconsistent relationship between both traits is related to the differences in predation risk among different environments. The difference in vulnerability to different predators has the potential to affect temporal and spatial variation in the morphology of dragonfly larvae, and may ultimately result in speciation. A phylogeny suggests that larval spines in the genus *Leucorrhinia* represent the ancestral stage, and that species with spineless larvae have evolved twice within this clade. Future focus on the joint evolution of correlated traits such as morphology and behaviour and their plasticity might be fruitful for a better understanding of the development of animal diversity, and dragonflies are good model organisms for testing this.

10.1 Introduction

A fundamental approach in understanding the complex biological diversity on our planet is to study the interactions of individuals and their environment. Such studies try to understand how the environmental effects affect an individual's fitness and drive adaptive radiation and diversification of life (Schluter 2000; Kassen *et al.* 2004). One interaction that has the potential to affect organism diversity is the interaction between predators and their prey (Sih 1987; Vamosi 2005).

To avoid and repel predators prey species evolved a plethora of traits such as behavioural modifications, camouflage, morphological attributes, chemical weapons, plastic growth, and flexible development (Edmunds 1974; Lima and Dill 1990; Tollrian and Harvell 1999). Species and individuals differ in the characteristics and expression of these defensive traits, and it is well known that predation selects for the observed variation in appearance and expression of the traits (e.g. Trussel 1996; Vamosi and Schluter 2004). The challenge is to understand how interactions between predators and prey have shaped the variation we observe. The interaction between predators and defensive traits also has the potential to influence at the level of species diversity. For example, in a study on sticklebacks, Vamosi and Schluter (2004), suggested that the presence of predators might cause the morphological divergence of species in sympatry and that this process was facilitated through morphological defence. In contrast, Buckling and Rainey (2002) and Meyer and Kassen (2007) showed that predators reduced morphological diversity of bacteria in sympatric *Pseudomonas flouresence*. Thus, the presence of predators has the potential to decrease or increase diversification.

Variation in morphological defence can be found at many different levels; among individuals, populations, and species. For example, the wide variety of shell structure among marine snail species is believed to be a response through an increased predation from shell-destroying predators (Vermeij 1977). Similarly, within-species variation in morphological defence is also high, but in most cases the variation is less compared with between-species variation. One example of within-species variation involves the threespine stickleback complex, where distinct morphological forms occur and these forms differ in armour such as spines and lateral plates (Colosimo *et al.* 2005). These stickleback populations represent genetic population differentiation. However, there are also examples of phenotypic plasticity in the amount of morphological defence within species. Several gastropods show phenotypic variation in thickness and structure of the shell and this defensive morphology is induced by crab predators (Appleton and Palmer 1988; Trussel 1996). Because morphological defence structures vary both within and between species it is relevant to ask several questions concerning this variation.

Dragonfly larvae are excellent model organisms that not only have provided answers to some of these questions, but also have the potential to provide answers to some unanswered questions concerning morphological defence. Dragonfly larvae spend a large part of their total life span in aquatic habitats before they emerge and these habitats are inhabited by many different kinds of predators. The growth and development performance in the aquatic life stage does affect time and size at emergence which are important fitness components of dragonflies (Sokolowska *et al.* 2000; De Block and Stoks 2005). We should therefore expect adaptations in morphology and behaviour in the larval stage that balance the trade-off between avoiding predation and growing and developing at an optimal rate.

Larvae of some dragonfly species (Anisoptera), in contrast to damselfly larvae, express prominent abdominal spines (Corbet 1999). These spines have been shown to be important anti-predator structures (Mikolajewski and Johansson 2004; Mikolajewski and Rolff 2004). Our main focus will be on the spines in the genus *Leucorrhinia*, because it is one of the most thoroughly investigated morphological anti-predator traits in dragonflies. Another well-studied anti-predator trait is the three leaf-like lamellae that are present in damselflies. We will, however, touch on this subject briefly because it is the major topic in another chapter (see Chapter 5 in this volume). In each section below we will first give a brief background to the topic in focus, and then we will use dragonflies to illuminate our current understanding and future progress on the ecology and evolution of morphological defence. We will use dragonfly larvae as examples to answer the following questions with regard to morphological defence. (1) Is the morphological trait adaptive; that is, does it enhance survival? (2) Is there genetic variation in the phenotypic plasticity for morphological defence? (3) What are the costs of morphological defence? (4) Is there a relationship between morphological defence and anti-predator behaviour? (5) What does the phylogenetic pattern with respect to morphological defence look like? Answering questions 1–4 is interesting because they will tell ecologists how intra- and interspecific variation in ecological forces creates diversity that can be seen at larger scales, such as the pattern looked for in question 5.

10.2 Fixed morphological defences

In some species, anti-predator defences are more or less fixed; that is, individuals do not differ very much in their trait expression and traits are not affected or induced by the presence of predators. These fixed traits are probably the results of an evolutionary response to permanent coexistence with potential predators (Sih 1987). However, the effectiveness and mode of operation of these traits have been studied in detail in a handful of organisms but only rarely in aquatic insects. Two important

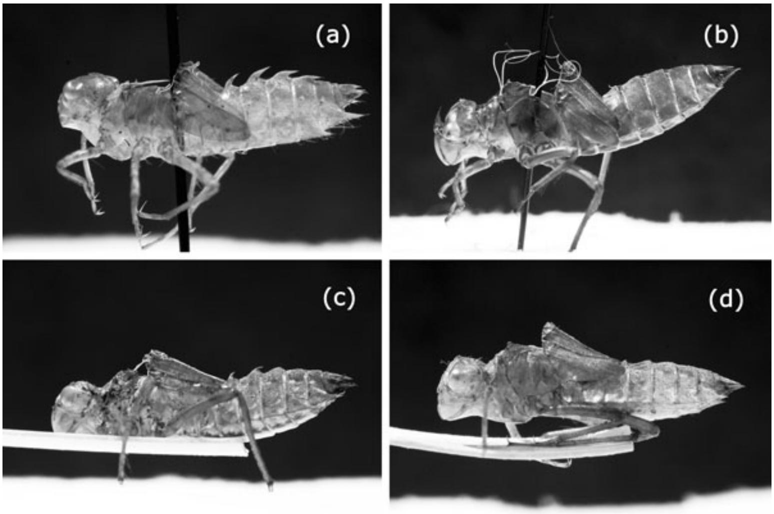

Figure 10.1 Exuviae (cast skins of larvae) showing variation in spine length between and within species of *Leucorrhinia*. (a) Long-spined species, *Leucorrhinia frigida*; (b) short-spined species, *Leucorrhinia rubicunda*; (c) *Leucorrhinia dubia* from lake with fish (note the long dorsal spines on the abdomen); (d) *L. dubia* from lake without fish (note the absence of dorsal spines on the abdomen).

questions to ask about these fixed morphological defences are, does it work, and is it an adaptation to predation risk? To prove the adaptiveness of traits, it must be shown that they increase fitness, for example by enhancing survival. There are several ways of showing this (Reznick and Travis 1996) and we will highlight two approaches with dragonflies as examples, using between-species comparison and manipulation.

For the between-species comparisons it is important to compare species that are closely related. Comparing species that are not closely related increases the probability that some other traits that are not the morphological defence per se could cause the observed difference in predator vulnerability. Larvae of the dragonfly genus *Leucorrhinia* show considerable variation in spine length on the abdomen (Figures 10.1a and b), and these spines are suggested to be an anti-predator adaptation (Mikolajewski and Johansson 2004). Mikolajewski and Johansson (2004) compared survival probability between the larvae of three species that differ in abdominal spine length and found that species with long spines had a higher survival probability when attacked by a fish predator. Hence, long spines provided protection. Interestingly, the spines provided protection only when larvae were attacked from behind. Attacks from behind are probably common because larvae detected by fish predators swim away from the fish.

The between-species comparisons have the problem that species might differ in other characters that also may affect the escape probability. A more direct estimate of the adaptive value of morphological defence is to manipulate the morphological character itself. Mikolajewski and Rolff (2004) used this approach when they manipulated the abdominal spines of the dragonfly larvae *Leucorrhinia caudalis*. They fed a predatory fish with larvae of two kinds: (1) larvae with intact spines and (2) larvae with either all lateral or all abdominal spines cut off. The results showed very convincingly that spines provide protection against predation because larvae with spines intact had a 4-fold higher survival probability when attacked from behind (Figure 10.2a). In addition, by manipulation of the spines other confounding variables such as anti-predator behaviour were excluded. In both studies survival was estimated as larvae rejected by the fish spitting them out. Larvae that were spat out always survived. Under natural conditions rejected larvae probably have a high chance of survival because they escape by swimming into the vegetation or to the bottom (see

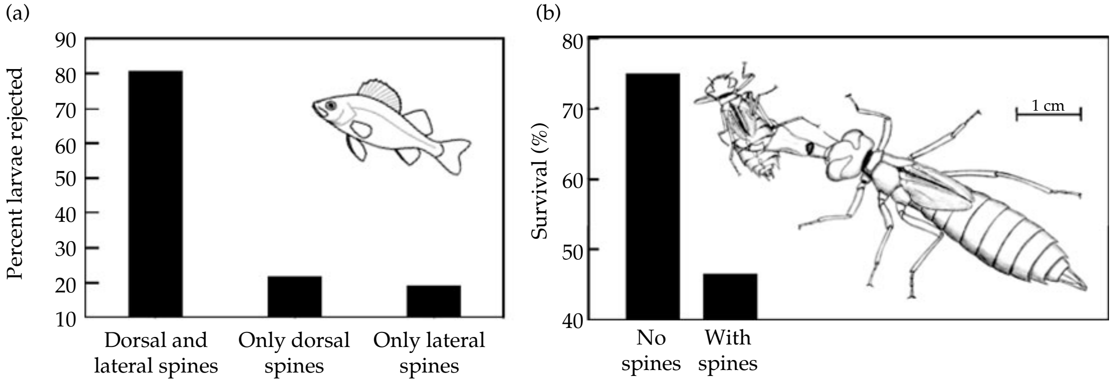

Figure 10.2 (a) The percentage of larvae rejected by perch preying on *Lecorrhinia caudalis* larvae with intact spines (dorsal and lateral spines) and spines cut off (only dorsal spines and only lateral spines). Larvae with spines intact have a higher probability of survival. (b) The percentage of larvae surviving when preyed upon by the invertebrate predator *Aeschna cyanea*. Larvae with spines cut off (no spines) have a higher survival probability than larvae with intact spines (with spines). Modified from Mikolajewsi and Rolff (2004) and Mikolajewski *et al.* (2006).

references in Corbet 1999). In conclusion, spines are adaptive with regard to reduced predation risk. The between-species comparison and the within-species manipulation showed that spines provided protection against attacking fish predators.

10.3 Predator-induced morphological defence

Fixed morphological traits may carry a cost. Such a cost could be the pure cost of production of the character. It could also be an environmental cost if the character interferes with other biotic or abiotic factors. Because predation risk may vary spatially or temporally, morphological defence might not always be beneficial. One way to avoid cost is to produce the morphological defence only in the presence of the predator. The ability to express different trait values in response to environmental condition is termed phenotypic plasticity. Phenotypically plastic morphological defence has been shown in a great variety of organisms (Tollrian and Harvell 1999), but only one example is known in dragonflies.

One prerequisite for the existence of inducible morphological defence is that predation risk should be variable (Tollrian and Harvell 1999). Fish commonly prey on dragonfly larvae (Frost and Smyly 1952; Rask 1986; Butler 1989) and fish presence is variable for two reasons: first, drought and freezing of waters can eliminate fish populations for some time, with subsequent re-colonization (Tonn and Magnusson 1982); second, adult dragonflies disperse from their native lake and may end up depositing eggs in lakes with or without fish, independent of their origin with regard to fish abundance from their native lake (Pajunen 1962; McPeek 1989). A recent mechanistic study suggests that damselflies of the genus *Enallagma* cannot recognize fish cues in waters (McGuffin *et al*. 2006). Hence, dragonflies encounter temporal and spatial variation in fish predator abundance. Dragonflies should therefore be an excellent system to study predator-induced defence, and we should expect the larvae to show phenotypic plasticity in morphological defence.

A second prerequisite for the existence of inducible morphological defence is that a reliable cue should be present (Tollrian and Harvell 1999). In a field study, Johansson and Samuelsson (1994) showed that larvae of *Leucorrhinia dubia* from lakes with fish had significantly larger abdominal spines than larvae from lakes without fish (Figures 10.1c and d). Two subsequent laboratory studies suggested that the presence of fish is the cue that induces longer spines in lakes with fish. When *L. dubia* larvae was given visual and chemical cues from fish simultaneously in the laboratory, longer spines were induced compared to in the absence of fish (Arnqvist and Johansson 1998; Johansson 2002). Hence, a reliable cue seems to be present.

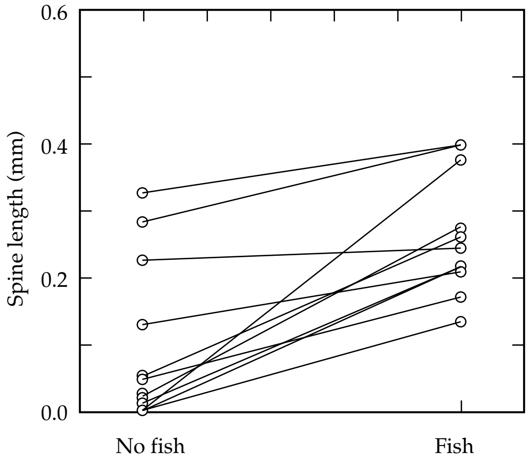

Figure 10.3 Reaction norms of dorsal spine length to fish treatment (fish absent or present). Each line represents one family where one half of the offspring were raised with and one half without fish respectively. The figure shows reaction norms for dorsal spine on segment 7. The dorsal spines on the other segments show a similar pattern of reaction norms. Modified from Johansson (2002).

The induction of longer spines has also been performed at the scale of whole lakes. In a 7-year study Johansson and Wahlström (2002) showed that spine length of *L. dubia* larvae decreased in two lakes after the authors had removed the fish.

Two interesting patterns became evident in the laboratory study on spine induction by fish (Johansson 2002). First, families differed with regards to spine length (Figure 10.3). Thus, there is genetic variation in spine length and hence, a potential for selection towards longer or shorter spines given that selection pressure changes. Second, there was significant interaction between genotype (family) and environment (fish present/absent). A significant genotype × environment interaction suggests a potential for the evolution of phenotypic plasticity in spine length. Hence, if spatial or temporal variations in predation risk increases or decreases in a geographical area, there is a potential for phenotypic plasticity in spine length to track these changes by becoming more or less plastic respectively. Genetic variation in the degree of plasticity has been found in other systems as well but how selection acts on this variation is not well known (Pigliucci 2005).

In summary, the study on *L. dubia* larvae plasticity has shown that (1) chemical and/or visual cues by predatory fish induce longer spines in these larvae, (2) there exists genetic variation for spine length as well as for plasticity in spine length, (3) lakes with fish have larvae with longer spines, and (4) the spines are probably adaptive because longer spines provide protection from attacking fish predators.

10.4 Costs

The benefits of morphological defensive attributes in animals and plants in general, and the benefits of abdominal spines in the few dragonfly species investigated so far, show that these attributes provide protection from attacking predators. Because not all species or individuals within a species show morphological defence, theory suggests that some costs are associated with the defence (Tollrian and Harvell 1999). It should however be remembered that absence of morphological defence also could be an effect of developmental and/or phylogenetic constraints.

10.4.1 Costs for a fixed defence

Four main types of cost have been suggested for a fixed response (Tollrian and Harvell 1999). Allocation or production costs result from the energy and material that is used to form and maintain the character. Self-damage costs are costs from using, storing, or producing the character that could harm the organism itself. Typically, such costs could be chemical defence produced by animals. Opportunity costs are referred to as costs that do not allow organisms to develop or behave optimally once the defence is present. Finally, there are environmental costs that depend on the environment in which the organism is living, such that a character might be beneficial in one environment but imply a cost in another environment.

One of the few examples of biotic environmental costs has been found in dragonfly larvae. As discussed above, the spines of larval *L. caudalis* provide protection against fish predators. On the other hand, it has been suggested that spines make prey organisms more vulnerable to invertebrate predators (Reimchen 1980). By feeding larvae with intact or cut-off spines to the invertebrate predator *Aeshna cyanea*, Mikolajewski *et al.* (2006) demonstrated that survival of larvae with spines cut off was higher than that of larvae with intact spines (Figure 10.2b). Hence, the presence of spines incurred a cost in terms of survival from the attacking invertebrate predator. Lakes without fish usually have a high abundance of invertebrate predators (Mallory *et al.* 1994), so Mikolajewski *et al.* (2006) suggested invertebrate predators may select for the lack of spines in environments without fish. In contrast, in lakes with fish, fish predators are likely the main predators on large invertebrates including dragonfly larvae, and therefore fish select for longer spines in these lakes. In conclusion, one cost for a fixed defence is that it is a disadvantage against another set of predators. Whether these costs occur in other organisms or systems is currently not well studied. A similar variation in divergent selection has been suggested on a temporal scale for a stickleback system. Reimchen and Nosil (2002) found evidence for increased spine number during winter and decreased spine number during summer in stickleback populations. They attributed this pattern to predation pressure from gape-limited avian piscivores and odonate predators respectively. No experimental evidence is currently available to support this relationship.

10.4.2 Costs for an inducible defence

Whereas organisms with induced defence also have the four costs associated with the fixed defence there is an additional cost involved for the induced defence, the cost of being plastic itself. True costs of plasticity are costs that organisms which are able to show phenotypic plasticity have; that is, costs higher than or lower than those incurred by individuals with a fixed phenotype (Scheiner and Berrigan 1998). DeWitt *et al.* (1998) defined five such costs: maintenance, production, information acquisition, developmental instability, and genetics. Most focus has been on production costs, which are costs of plasticity if the costs of producing the morphological trait are greater for plastic genotypes than for fixed genotypes producing the same phenotype. Costs of plasticity have been notoriously hard to find (Pigliucci 2005). Few studies have tried to estimate plasticity costs of morphological defence, and evidence received thus far has been scant (Scheiner and Berrigan 1998; Relyea 2002). As far as we know, no studies have tried to estimate costs of morphological defences in dragonflies. We can only agree with Pigliucci (2005), who states that research on costs of plasticity should become a major area for future enquiry. In our opinion, dragonflies might not currently be the best system for this enquiry for several reasons. First, generation time is fairly long; second, full-sib analysis with the appropriate level of replication and considerations of maternal effects are difficult to perform; third, ideally, plasticity studies should be performed on organisms where it is possible to study the cost in a plastic genotype that does not express the trait under consideration. Such studies have to be performed on known mutated individuals or gene-manipulated individuals, and none of those are currently available in dragonflies.

Production costs estimate the cost of producing the character when it is not necessary. Johansson (2002) estimated whether or not production costs in *Leucorrhinia dubia* are incurred in terms of a longer developmental time or smaller size for larvae with induced longer spines. He did not find any evidence for production costs. Neither was there a correlation between spine length and larval size in larvae from natural lakes (Johansson and Samuelsson 1994). However, production costs could be associated with other traits not measured in these studies.

10.5 Anti-predator behaviour and morphological defences

To avoid predation, animals not only show morphological adaptations, they also exhibit behavioural adjustments in response to predation risk. Typically such behavioural adjustments involve reduced activity, increased refuge use, and selection of less profitable prey (Lima 1998; Lima and Dill 1990). Many animals show morphological as well as behavioural anti-predator adaptations, so it is interesting to explore how these two traits are related. Dragonfly larvae are well suited for examining this relationship because morphological and behavioural responses to predators have been well investigated.

Four possible functional relationships between behavioural and morphological anti-predator traits have been suggested (DeWitt *et al.* 1999): (1) trait co-dependence, when for example, the behavioural trait is dependent on certain morphology to work efficiently, (2) trait complementation, when two traits are independent but must be combined to work efficiently, (3) trait co-specialization, when prey use both types of defence simultaneously (a positive relationship), and (4) trait compensation, when for example, prey with poor morphological defences show strong anti-predator behaviour (a negative relationship).

Mikolajewski and Johansson (2004) examined these functional relationships in the larvae of a suite of three species of *Leucorrhinia*. Results showed no consistency among species with regard to functional relationship. *Leucorrhinia albifrons*, the species with the longest spines showed stronger anti-predator behaviour than the species with intermediate spine length (*Leucorrhinia dubia*), which suggests trait co-specialization (a positive relationship). In contrast, *Leucorrhinia rubicunda*, the species with the shortest spines, also showed stronger anti-predator behaviour than the intermediate spined *L. dubia*, which suggest trait compensation (a negative relationship). We suggest that these patterns in relationship between morphology and behaviour are related to each species' preference of lake type with regard to presence and absence of fish (Johansson and Brodin 2003). For example, *L. albifrons* is common in lakes with fish and therefore showed strong behavioural as well as morphological anti-predator adaptations (co-specialization). In contrast *L. rubicunda* is rare in fish lakes and common in fishless lakes and therefore showed trait compensation.

Anti-predator behaviour and morphological defence has also been studied in damselfly larvae. These larvae have three leaf-like appendages that function as respiration organs. But the appendages can also be autotomized when grasped by a predator, and hence function as an escape defence. Stoks (1999) showed that larvae with autotomized lamellae showed stronger anti-predator behaviour than larvae with intact lamellae. Hence, this supports the trait-compensation mechanism because larvae with better morphological defence (intact lamellae) foraged in a more risky way.

In summary, whether trait compensation or trait co-specialization occurs in the system of organisms studied, is probably a function of variation in predation risk. In a species that always coexists with predators we should expect trait co-specialization because both traits should be beneficial. In contrast, if predation risk is more variable we should expect trait compensation because these organisms need to save the costs of either morphological defence or behavioural defence. The dragonfly-larvae system should be excellent for examining these ideas because species differ in morphological and behavioural anti-predator traits and abundance with regard to fish presence and absence.

10.6 Macroevolution

Interspecific differences in morphological traits that function as anti-predator traits suggest that predators have the potential to affect selection and, given enough time, speciation events (Vamosi 2005). We will exemplify this with two case studies. Studies on the damselfly genus *Enallagma* in North America suggest that predators have been important agents of diversifying selection in this system. Typically larvae of one group of *Enallagma* species can be found in lakes with fish and another group of *Enallagma* species exists in lakes without fish that are dominated by dragonfly predators. Although the morphology of larvae is similar within each species group, the species within a group are not closely related (McPeek 1995). Instead, predation pressure seems to have shaped the difference between the groups and similarities within the groups. The shape and size of the caudal lamellae of the larvae has been shown to be an important pre-contact predator avoidance trait because the lamellae are used for swimming away from dragonfly predators. Field experiments have shown that dragonfly predators impose selection on lamellae size and shape to increase swimming performance (McPeek 1997). A phylogeny on *Enallagma* showed that speciation events with shifts from fish lakes to fishless lakes are associated with corresponding changes in lamellae shapes (McPeek 1995; McPeek *et al.* 1996).

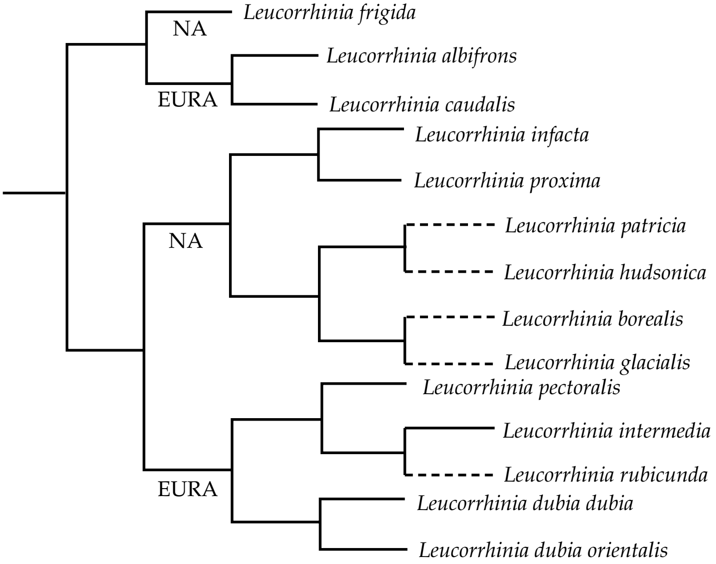

Figure 10.4 Phylogeny of the genus *Leucorrhinia* based on ITS1, 5.8S, and ITS2 ribosomal DNA sequences. The tree is modified from Hovmöller and Johansson (2004). Dashed lines denote species without dorsal spines and the abbreviations NA and EURA denote North American and Eurasian clades respectively.

Hence, shape and size changes of the lamellae seem to have facilitated habitat shift and diversification in this group.

The genus *Leucorrhinia* consists of 14 species, of which nine have prominent dorsal abdominal spines and five lack or have very small spines. It is interesting to explore the phylogenetic relationship among species with and without spines because the spines provide protection from fish predators and are disadvantageous against invertebrate predators. A phylogeny of the group based on ribosomal DNA sequences (Figure 10.4) showed that abdominal spines are the ancestral trait and that spines have been lost twice, independently; once in the North American clade and once in the Eurasian clade (Hovmöller and Johansson 2004). In contrast to the *Enallagma* system, no study between the association of spines and abundance with regard to fish presence/absence in habitats has been performed in this group. It is therefore premature to suggest that morphological defence has made a large contribution to speciation events in *Leucorrhinia*.

10.7 Outlook

The focus of this chapter has been on very few species, with the reasoning that morphological defence is not well studied in dragonfly larvae. Yet, dragonfly larvae have been useful as a model system in understanding and answering general questions on morphological defences, but many unanswered questions remain. There is large variation in spine length at many different taxonomical levels, so it would be interesting to examine the relationship between perceived predation risk and habit choice, spine status, and behaviour. We suggest that species with longer spines should be more common in systems with fish and that these species should show strong anti-predator behaviour towards their predators. However, some species with very prominent spines rarely occur with fish (Figure 10.5). We therefore suggest that spines might be adaptations to other factors as well. Phylogenetic constraints could also explain some of the cases where we do not have a good explanation for the presence or absence of spines in relation to predation risk. Manipulative experiments in combination with a phylogenetic approach, as has been used successfully for the *Enallagma* system (see Chapter 5) should be a fruitful approach to explore the evolution of abdominal spines.

Published studies on morphological defence have a strong focus on defence on mature individuals. However, an organism may go through several ontogenetic stages, which might include niche shifts with regard to predation risk. For example,

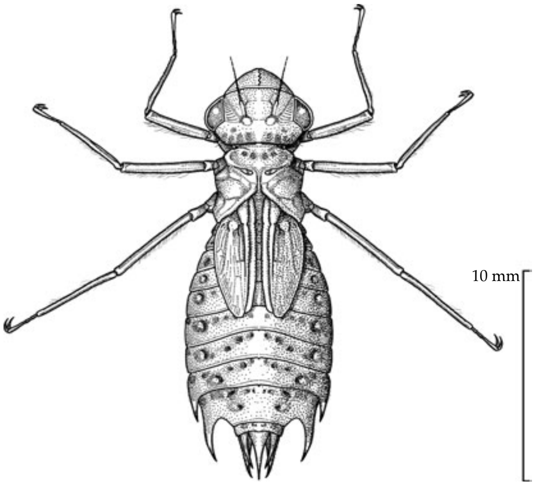

Figure 10.5 *Pantala flavescens* larva. The larvae of this species rarely occur with fish but they still show prominent lateral spines, although dorsal spines are lacking. Drawing by Ole Mueller.

although small larvae might be at risk from one guild of predators large larvae might be at risk from a different kind of predator. This shift might call for different morphological defences during ontogeny because a defence that works effectively early in life might be disadvantages later in life. Arnqvist and Johansson (1998) examined abdominal spine length in dragonfly larvae of *L. dubia* and found that spine length showed an ontogenetic acceleration in environments with fish. This suggests that the importance of spine length increases as larvae grow. A speculative interpretation is that spines are not a great advantage early during ontogeny in these larvae. More work is certainly needed in the area of ontogenetic reaction norms of morphological defence.

Our focus on morphological defence has centred on abdominal spines, but there might be other morphological anti-predator characters on dragonfly larvae as well. For example, some *Somatochlora* larvae have well-developed protuberances ('horns') on the back of the head early during ontogeny, but the function of these horns is, as far as we know, unexplored. Another example of morphological defence is the ability of damselfly larvae to autotomize their caudal lamellae to escape predation (Stoks 1998, 1999).

Information about the genetic mechanisms behind loss or gain of abdominal spines among or within species might provide more clues on the adaptation of these spines. In sticklebacks it has been shown that a single gene is responsible for the parallel loss and gain of spine formation that has occurred independently in populations around the world (Colosimo *et al*. 2005). By using the same approach for dragonfly larvae an increased understanding could be gained of how new animal forms evolve.

Acknowledgements

Thanks to Martin Lind, Robby Stoks, Jukka Sohonen, and one anonymous reviewer for valuable comments on previous drafts of this chapter. Thanks also to Pär Byström and Axel Conrad for drawing the animals in Figures 10.2a and 10.2b respectively.

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CHAPTER 11

Interspecific interactions and premating reproductive isolation

Katja Tynkkynen, Janne S. Kotiaho, and Erik I. Svensson

Overview

Interspecific interactions have several evolutionary consequences: for example, two species may compete, hybridize, or behave aggressively towards each other, or there may be predator–prey interactions. One consequence of these interactions is the evolution of premating reproductive isolation between the two species. The most obvious interspecific interaction, which has an effect on reproductive isolation, is the avoidance of hybridization, or, in other words, the reinforcement process. The theory of reinforcement states that when hybridization is maladaptive, selection pressure causes a divergence in female mate preference and/or in male secondary sexual characters. It is often assumed that, ultimately, females are responsible for hybridization because they are the choosier sex and their co-operation is needed for successful copulations. Despite this view, it is possible that males, rather than females, are responsible for hybridization, especially in species in which males can force copulations. In addition to the avoidance of maladaptive hybridization, other interspecific interactions, such as aggression or predation, may also have an effect on premating reproductive isolation. For example, if interspecific aggression is directed towards males with the most exaggerated sexual characters because of the similarity of these characters between the two species, natural selection for sexual character divergence may arise. Just like the reinforcement process, this process may lead to a strengthening of premating reproductive isolation. In this chapter, we will review the effect of interspecific interactions on premating reproductive isolation. As examples we will mostly use the studies conducted on *Calopteryx* damselflies.

11.1 Introduction

In nature, there are several kinds of interaction between species. Species can be involved in predator–prey interactions (including parasites; Zuk and Kolluru 1998; Kotiaho 2001; Svensson and Friberg 2007), they may compete or defend territories against each other (e.g. Nomakuchi and Higashi 1996; Genner *et al.* 1999; Adams 2004; Tynkkynen *et al.* 2006), and two species can hybridize (see Mallet 2005). Interactions between species can have evolutionary consequences, influencing reproductive isolation (Box 11.1) and speciation events. For example, competition over resources can cause divergent selection on ecological or behavioural traits, strengthening premating isolation between the two incipient species (see Coyne and Orr 2004 for a review of speciation).

Although there are several factors which may affect reproductive isolation, we will here concentrate on two questions. First, how can interspecific interactions, especially hybridization, aggression, and predation, affect premating reproductive isolation? Second, is reproductive isolation a direct target of selection or does it evolve as a correlated response to selection on other traits? We will mainly use *Calopteryx* damselflies as a model species, which have been under intensive study concerning our study questions.

Box 11.1 Reproductive isolation

Reproductive isolation can arise from several reproductive barriers, which may work before or after mating. Pre-mating barriers include factors that prevent the occurrence of mating, whereas post-mating reproductive barriers include factors that, after mating, prevent the formation of offspring, or that cause the hybrid offspring to be unviable or sterile (Coyne and Orr 2004).

In this chapter, we concentrate on pre-mating reproductive isolation. Pre-mating reproductive isolation can be classified as caused by several factors (see Coyne and Orr 2004 for more detailed description). First, there may be sexual isolation (also called behavioural isolation), in which reproductive isolation is based on behavioural differences between two species, or mate-recognition ability of individuals (for an example case, see Box 11.2). Second is ecological isolation, which means that gene flow between species is impeded because of a divergence in habitat or timing of reproduction. Finally, mechanical isolation occurs when reproductive structures are incompatible, thus preventing normal copulation (Coyne and Orr 2004).

11.2 Causes and evolutionary consequences of hybridization in animals

Hybridization means crossing of genetically distinguishable groups or taxa, leading to the production of viable hybrids (*sensu* Mallet 2005). Hybridization is a surprisingly prevalent phenomenon in nature: at least 25% of plant species and 10% of animal species hybridize (Mallet 2005). In animals, hybridization is mostly observed in conspicuous and intensively studied taxa such as birds (Grant and Grant 1992), mammals (see Coyne and Orr 2004), *Drosophila* (Coyne and Orr 1989; Mallet 2005), and butterflies (Mallet 2005). In odonates, some suspected and verified hybrids have been observed (e.g. Asahina 1974; Bick and Bick 1981; Corbet 1999; Monetti *et al.* 2002; Sánchez-Guillén *et al.* 2005). However, odonate hybrids may be more common than reported, since precopulative tandems and matings between heterospecifics are commonly observed in nature (Corbet 1999).

11.2.1 Why do animals hybridize?

A pair of species can hybridize only if they occur in sympatry (at the same place), and if they have incomplete pre- and postmating isolation barriers. In animals, the ultimate causes of hybridization can roughly be divided into two groups: either there is incomplete mate-recognition ability (e.g. Sætre *et al.* 1997a; Randler 2002) or hybridization is the result of adaptive decision-making (Nuechterlein and Buitron 1998; Wirtz 1999; Veen *et al.* 2001).

Hybridization can be caused by incomplete mate-recognition ability, if, for example, behavioural isolation between the two species is incomplete. Such is the case for instance, when the two species have occurred in allopatry (at separate places), and then subsequently become sympatric. Here, the mate-recognition ability that evolved in allopatry may be poorly adapted to discriminating heterospecifics. It is also possible that two or more closely related species occur in sympatry without hybridization, but after some environmental change, they start to hybridize (Rhymer and Simberloff 1996; Seehausen *et al.* 1997a; Lamont *et al.* 2003; Box 11.2).

Hybridization is not always maladaptive. For example, when an individual is unable to find a conspecific mate, it may do better by breeding with a heterospecific than not at all. This adaptive explanation for hybridization requires that the hybridizing individual gains some fitness return, meaning that hybrids can have reduced, but non-zero fitness (Grant and Grant 1992; Nuechterlein and Buitron 1998; Sætre *et al.* 1999; Wirtz 1999; Veen *et al.* 2001; Randler 2002). However, the two origins for hybridization, incomplete mate-recognition ability and adaptive decision-making, are not mutually exclusive, since both may occur at the same time within a sympatric population (Sætre *et al.* 1997a; Veen *et al.* 2001).

Box 11.2 An example of the relaxation of pre-mating reproductive isolation

In Lake Victoria are at least 500 endemic haplochromine cichlid fish species (Seehausen *et al.* 1997b). In these cichlid species, male coloration is an important factor in sexual selection, and works as a pre-mating isolating barrier between species (Seehausen *et al.* 1997a; Seehausen and van Alphen 1998). Females of the cichlid species are able to recognize conspecific males based on their coloration in clear water conditions. However, recent anthropogenic disturbance has increased the water turbidity and the coloration of the males is not easy for the females to observe. This has caused matings between heterospecifics that result in viable and fertile hybrids (Seehausen *et al.* 1997a). Thus, the relaxation of pre-mating reproductive isolation due to anthropogenic environmental change has resulted in formation of hybrid swarms, and may have lead to species extinctions through introgression (Seehausen *et al.* 1997a).

11.2.2 Consequences of hybridization

Hybridization leads to different outcomes depending on the viability and fertility of the hybrid individuals. If hybrid fitness is not reduced, or if it is even higher than that of parents (a phenomenon known as heterosis), the mechanisms to avoid hybridization are not strong or are missing, and the gene pool of the two species may eventually fuse (see, for example, Coyne and Orr 2004; Taylor *et al.* 2006). In such a case, if one species is less abundant than the other, the fusion of the gene pools may lead to extinction of the less-abundant species (or the sympatric population) (e.g. Liou and Price 1994; Rhymer and Simberloff 1996; Levin 2004). In the example of the Lake Victoria cichlid fishes (Box 11.2), relaxation of premating reproductive isolation had resulted in extinctions though introgression (Seehausen *et al.* 1997a).

When species hybridize there is often a catastrophic reduction in fitness, and thus selection to avoid interspecific matings is likely to be very strong. As a consequence, the mate preferences and the sexual characters of a pair of potentially hybridizing species may diverge. This process is referred to as reinforcement because it should reinforce premating reproductive isolation of the species (e.g. Dobzhansky 1951; Howard 1993; Sætre *et al.* 1997a; Rundle and Schluter 1998; Noor 1999; Higgie *et al.* 2000). As a result of reinforcement, the probability of copulation between heterospecifics, and thus the occurrence of hybrids in the wild, is reduced. The divergence of reproductively isolating traits between allopatric and sympatric populations of two species is referred to as reproductive character displacement (*sensu* Howard 1993; see Butlin 1987 for a different definition of the concepts). The pattern may also be observed across sympatric populations, in which the divergence of isolation traits depends on the relative abundance of the sympatric species (Howard 1993; Noor 1999; Tynkkynen *et al.* 2004). It should also be taken into account, that in addition to hybridization, matings between heterospecifics without production of hybrids may cause selection for reproductive isolation, if mating or courtship itself has a negative effect on fitness (see Chapman *et al.* 1998; Kotiaho *et al.* 1998; Kotiaho 2001).

When premating isolation has been reinforced such that matings between heterospecifics are not prevalent, the selection to further enhance the premating isolation may relax. It is possible, however, that sexual selection develops along with the reinforcement process, and that its role increases when reinforcement proceeds (Liou and Price 1994; Coyne and Orr 2004; Mallet 2005). When sexual traits or female mate preferences are shaped by reinforcement (i.e. by natural selection), a genetic correlation will be formed between male sex traits and female mate preference (Lande 1981; see also Liou and Price 1994; Coyne and Orr 2004). Similar patterns to reinforcement may also be caused by forces other than avoidance of maladaptive hybridization. For example, ecological factors and the associated selection pressures may cause premating reproductive isolation, which arises as a byproduct to divergent natural selection on different populations (e.g. Noor 1999; Coyne and Orr 2004; Mullen and Andrés 2007; see also Servedio 2001). One such ecological factor is interspecific aggression; an example of which is described later in this chapter.

11.2.3 Male coercion behaviour: can it lead to hybridization in odonates?

In general, females are thought to be choosy and it seems that female cooperation is frequently needed for a successful copulation. Therefore, it has been proposed that it is the females who are mainly responsible for hybridization (Sætre *et al.* 1997b; Wirtz 1999; Randler 2002). However, in some cases, males can coerce females to copulation, and thus male choosiness should not be neglected (e.g. Cordero 1999; Cordero and Andrés 2002). If females are indeed the choosier sex, it may be too costly for males to evolve to be choosy, since mating opportunies with conspecific females may also be missed (Parker 1983; Sætre *et al.* 1997b; Parker and Partridge 1998; Wirtz 1999). Nevertheless, it is likely that males will also be selected to display some discrimination of conspecifics, especially if the costs of reproduction activities are high (Wirtz 1999).

In some species of odonates, males are able to grasp a female and form the precopulatory tandem, and the females may have little option but to mate (Oppenheimer and Waage 1987; Cordero and Andrés 2002). This is the case in *Calopteryx* damselflies: when the anal appendages of the male grab the female neck to produce the tandem position, the pair usually proceeds with copulation (Oppenheimer and Waage 1987). Moreover, in most odonates it is unclear whether female mate choice even occurs (see Fincke 1997; Fincke *et al.* 1997; but see Córdoba-Aguilar 2006). The role of female mate choice seems to be more clear in calopterygid damselflies, in which males have conspicuously pigmented wings, and in which males court females by performing a flight display (Fincke *et al.* 1997; Siva-Jothy 1999; Córdoba-Aguilar 2002). However, since even in these species males can force females to mate (Cordero 1999; Cordero and Andrés 2002), it is thus still unclear who is, in fact, in control of the onset of mating.

Interestingly, in his classical studies, Waage (1975, 1979) suggested that character displacement observed in wing pigmentation of *Calopteryx maculata* and *Calopteryx aquabilis* is caused by avoidance of maladaptive hybridization by males rather than females. Although hybrids were not found, Waage (1975) observed copulations between heterospecifics followed by oviposition. Males of *C. maculata* had better mate-discrimination ability in sympatric populations than in allopatric ones, indicating occurrence of reinforcement. The selection for better mate discrimination may also have caused reproductive character displacement on female wing transparency; that is, on the trait in which males base their species recognition (Waage 1975, 1979). It is particularly interesting that in this case reproductive character displacement was observed in female characteristics and in male mate discrimination (Waage 1975, 1979), because in most other studies of reproductive character displacement it is the male secondary sexual characters or female mate-discrimination ability that has been investigated (e.g. Howard 1993; Sætre *et al.* 1997a; Rundle and Schluter 1998; Noor 1999; Higgie *et al.* 2000). It should be noted, however, that the suggestion of reinforcement made by Waage (1975) was challenged recently by the suggestion that reproductive character displacement may have arisen from selection caused by interference between mate-recognition signals rather than reinforcement (Mullen and Andrés 2007).

The role of females and males in reproductive isolation has been studied in detail in *Calopteryx splendens* and *Calopteryx virgo*. Hybrids between these two species occur in nature in low prevalence (less than 1% of adult individuals), but matings between heterospecifics are frequent (Svensson *et al.* 2007; K. Tynkkynen, J.S. Kotiaho, M. Luojumäki, and J. Suhonen, unpublished results). The discrepancy between number of observed matings and hybrids, and the pronounced genetic distance between the two species (Misof *et al.* 2000; Weekers *et al.* 2001), suggests that hybridization is likely to be maladaptive.

Females of these species mate assortatively and use male wing coloration as a visual cue in species recognition (Svensson *et al.* 2007). *C. splendens* males have melanized wing spots in their wings covering

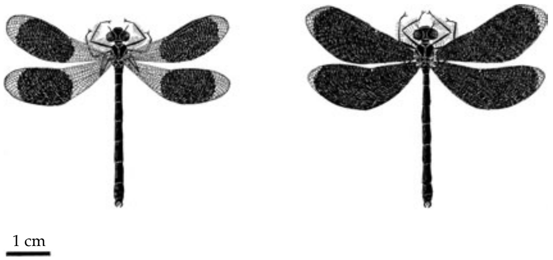

Figure 11.1 Males of *Calopteryx splendens* (left) and *Calopteryx virgo* (right). Artwork provided kindly by the artist Kaisa J. Raatikainen.

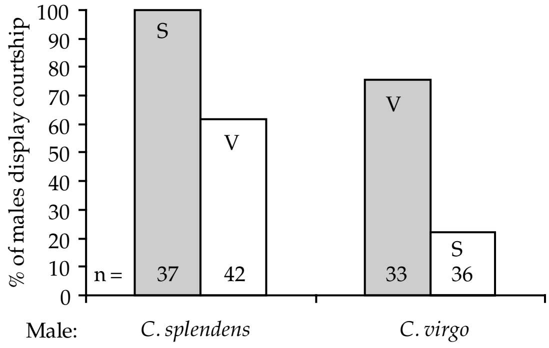

Figure 11.2 Percentage of males displaying courtship to conspecific (grey bars) or heterospecific (white bars) females. S indicates *C. splendens* and V means *C. virgo* females (Tynkkynen *et al.*, 2008). Reproduced with permission from Elsevier.

about 30–70% of wing area, and *C. virgo* have almost completely pigmented wings (Figure 11.1). As the extent of the wing pigmentation of *C. splendens* males was manipulated to resemble that of *C. virgo*, *C. virgo* females became more willing to copulate with *C. splendens* males, and at the same time the willingness of *C. splendens* females decreased (Svensson *et al.* 2007). Thus, there is strong sexual premating reproductive isolation between the two species (Svensson *et al.* 2007).

There is also a difference between *C. splendens* and *C. virgo* males in courting activity towards conspecific and heterospecific females (Tynkkynen *et al.* 2008; Figure 11.2). In central Finland, it was found that when heterospecific females were presented to territorial males of both species in field experiments, *C. splendens* courted as many as 62% of the females, whereas *C. virgo* courted only 22% of the females (Figure 11.2). This suggests, that in contrast to females, among which the sexual premating reproductive isolation was strong (Svensson *et al.* 2007), the premating isolation in *C. splendens* males was incomplete. The same asymmetrical discrimination between males of the two species was verified independently in a study in southern Sweden, where it was found that *C. splendens* males copulate with heterospecific females in the field more often than do *C. virgo* males (Svensson *et al.* 2007). In contrast, *C. virgo* males were apparently more discriminatory towards heterospecific members of the opposite sex than females in both species and *C. splendens* males (Svensson *et al.* 2007). Thus, in the genus *Calopteryx*, a consideration of male mating behaviours and male mate choice, not just female mate choice, is crucial to understand the causes of hybridization. It is possible that eagerly courting *C. splendens* males are able to force *C. virgo* females to copulate (see Cordero 1999; Cordero and Andrés 2002), and *C. virgo* females yield to mating since it may be costly for them to resist persistent harassment from *C. splendens* males. The elevated species-recognition ability and choosiness of *C. virgo* males (Svensson *et al.* 2007; Tynkkynen *et al.* 2008) may be due to the sex- and species-specific costs of matings: *C. virgo* males have an elevated predation risk from birds, presumably because of their more conspicuous, entirely dark wings (Svensson and Friberg 2007).

11.3 Interspecific aggression

11.3.1 Causes for interspecific aggression

There are at least two causes of interspecific aggression: it can result from interspecific interference competition over resources or from mistaken species recognition. The first is probably more common, as documented by published studies (e.g. Nomakuchi and Higashi 1996; Genner *et al.* 1999; Adams 2004).

Aggressive behaviour related to territorial defence can mistakenly be directed towards heterospecific individuals due to their phenotypic similarity (Murray 1981; Nishikawa 1987; Alatalo *et al.* 1994; Tynkkynen *et al.* 2004). For example, interspecific

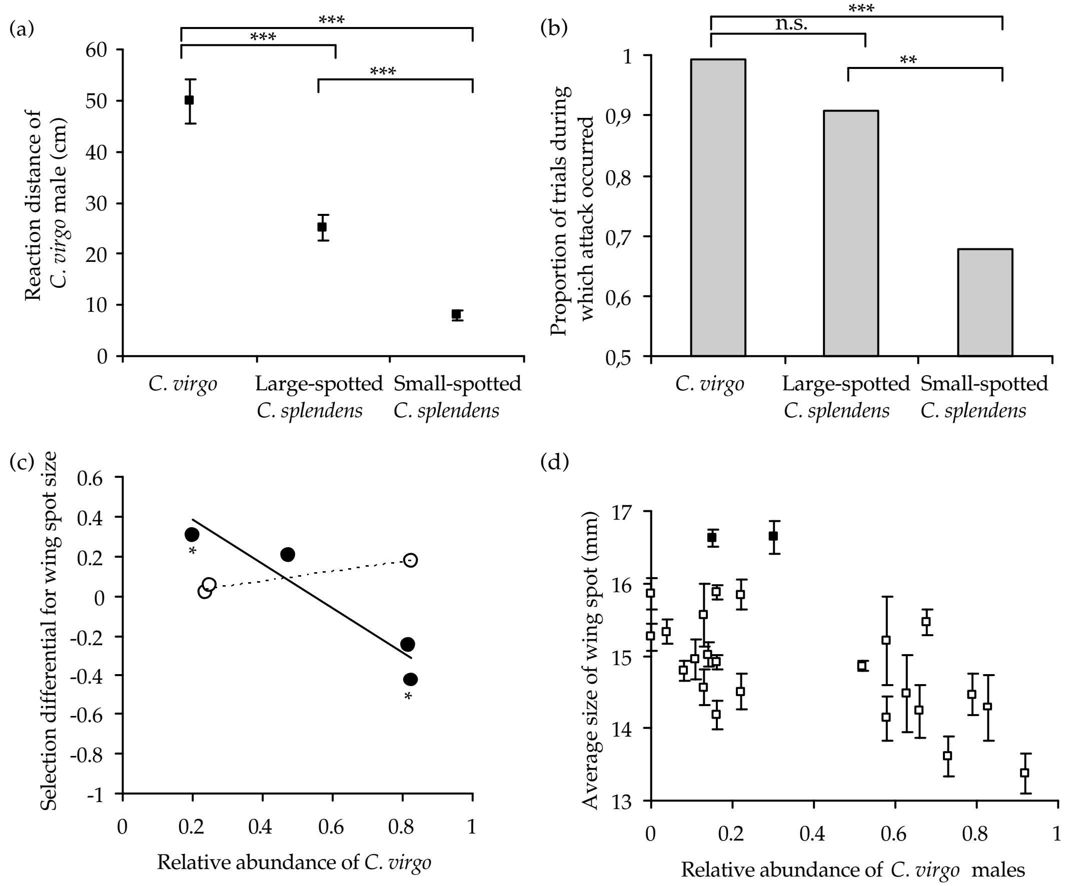

Figure 11.3 Interspecific aggression and character displacement in *C. splendens* and *C. virgo* males. (a, b) Results from the experiment in which aggressiveness of territorial *C. virgo* males was determined towards *C. virgo*, and *C. splendens* males with large and small wing spots. Reaction distance (a) and aggressiveness of reactions (b) were observed. Aggressiveness of reactions is indicated by proportions of trials in which attack occurred (Tynkkynen *et al.* 2004). NS, not significant; $^{**}P<0.01$, $^{***}P<0.001$. (c) Standardized selection differentials (measures of directional selection) on wing-spot size of *C. splendens* males in relation to relative abundance of *C. virgo* males. Filled circles indicate natural populations (controls), and open circles populations in which the relative abundance of *C. virgo* is reduced. There is significant interaction between the control and treatment (ANCOVA, $F_{1,3}=17.05$, $P=0.026$; Tynkkynen *et al.* 2005). For individual selection differentials, $^{*}P<0.05$. (d) Character displacement in wing-spot size of *C. splendens* males. The spot size decreases as relative abundance of *C. virgo* males (number of *C. virgo* males divided by the total number of both species) increases. The two populations indicated by filled circles are geographically distant, eastern populations (Tynkkynen *et al.* 2004). Reproduced with permission from Blackwell Publishing.

aggression occurs between males of *C. virgo* and *C. splendens*, and the aggression seems to be at least partially based on mistaken species recognition (although there may also be a component of interference competition over territories or oviposition sites) (Tynkkynen *et al.* 2004, 2006). *C. virgo* males react from greater distance to large-spotted *C. splendens* males, but they are also more aggressive towards large-spotted than small-spotted *C. splendens* (Figures 11.1 and 11.3a and b). Thus, it seems that, at least partially, interspecific aggression between *C. virgo* and *C. splendens* is based on mistaken species recognition. This is because if the behaviour was due to interference competition, *C. virgo* males should be equally aggressive towards large-spotted and small-spotted *C. splendens* males, whereas reaction distance could still vary, if the large-spotted *C. splendens* males are more detectable.

11.3.2 Consequences of interspecific aggression on premating reproductive isolation

Interspecific aggression may have an effect on premating reproductive isolation of closely related sympatric species at least in two ways. First, interspecific interference competition may cause ecological reproductive barriers to emerge. In other words, there may be shifts in habitat use or behavioural adaptations to avoid contacts with the heterospecific individuals. Such avoidance may lead into strengthening premating reproductive isolation (see Coyne and Orr 2004; Adams 2004). Second, interspecific aggression due to mistaken species recognition may have an effect on male sexual characters, which in turn may affect premating reproductive isolation through female mate choice or through interspecific male–male competition (e.g. Tynkkynen *et al.* 2004, 2005). Regardless of the origin of the aggression, interspecific aggression can reduce the fitness of the target. For example, interspecific aggression may force individuals of subdominant species to less preferred habitats or territories (Alatalo *et al.* 1994; Nomakuchi and Higashi 1996; Martin and Martin 2001; Melville 2002), it may reduce attractiveness of males to females when males are the targets of excessive interspecific harassment, or it may reduce the survival of individuals through injuries or depletion of energy reserves (e.g. Eccard and Ylönen 2002; Tynkkynen *et al.* 2005; Figure 11.3c). In addition, energetically demanding fighting with heterospecifics may reduce territory-holding potential and thus decrease territorial life span, which in turn can reduce reproductive success (Tynkkynen *et al.* 2006).

As an example, interspecific aggression from *C. virgo* towards large-spotted *C. splendens* males could have caused character displacement to the wing spot of *C. splendens* males such that wing-spot size decreases with increasing relative abundance of *C. virgo* males (Tynkkynen *et al.* 2004; Figure 11.3d). If the similarity between the males of the two species decreases, it may facilitate female mate recognition. In addition, it may cause a genetic correlation between a male sexual character and female mate preference (see Lande 1981). A genetic correlation may arise if males with a certain wing-spot size avoid interspecific aggression, but have sufficiently large spots to appeal to females, giving these males an advantage in both natural and sexual selection. If this process occurs, it may enhance premating reproductive isolation between the species. Thus, it seems likely that interspecific aggression has a role in creating premating reproductive isolation between the two *Calopteryx* species (Mullen and Andrés 2007; Tynkkynen *et al.* 2008).

11.4 A role for predation in the evolution of premating isolation

An influential review on laboratory selection experiments in *Drosophila* concluded that reproductive isolation between populations may often evolve as a correlated response to divergent natural selection between different environments (Rice and Hostert 1993). If two populations are inhabiting different environments and have different ecologies, they will become reproductively isolated from each other, given sufficient time, even if some gene flow connects the populations (Rice and Hostert 1993). This is the so-called byproduct model of speciation, which has been advocated by many workers since Ernst Mayr and in which there is no particular need to invoke any direct or indirect fitness benefits to males or for females to choose their own conspecifics as mates (Coyne and Orr 2004). There is very strong empirical support for this byproduct model of speciation, which is valid for both allopatric and sympatric scenarios (Endler 1977; Hendry *et al.* 2000; Hendry 2001; Svensson *et al.* 2006).

Given the strong evidence for the byproduct model of speciation, it follows that investigators should focus on ecologically important traits between species or incipient species, and estimate the form and direction of natural or sexual selection on the same traits. Interspecific differences in wing coloration in *Calopteryx* damselflies are particularly interesting in this context since they function as a species-recognition mechanisms in both males and in females (see above). If natural or sexual selection on such wing colour differs between populations, divergent selection could cause sexual isolation and speciation as a correlated response. Interestingly, the extent of wing melanization and darkness of the wing patches

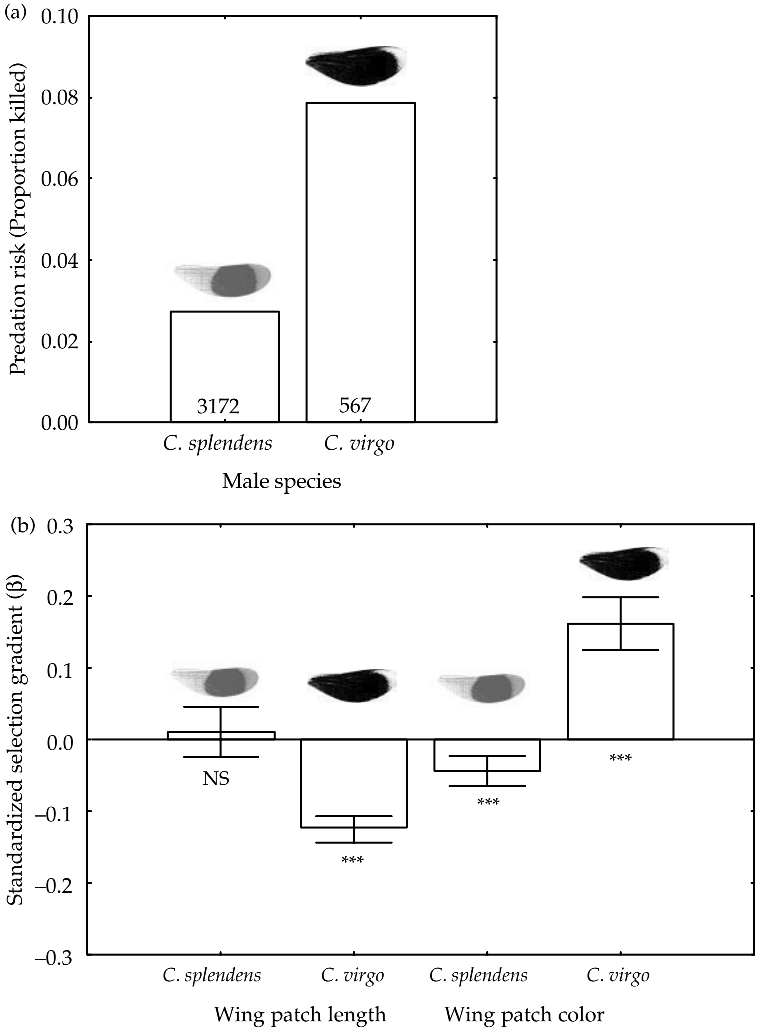

Figure 11.4 (a) Species-specific predation by *Motacilla alba* on *C. splendens* and *C. virgo* males. Male *C. virgo* suffered a 2.9-times-higher predation risk from wagtails than did male *C. splendens* and this difference was highly significant (99.9% confidence interval, 1.54–4.82; $P<0.001$). Sample sizes (total no. of live and dead males) for each species are also provided in graph. Wings of the two different species inserted in graph for comparison. Note the almost entirely melanized wings in *C. virgo*, compared with *C. splendens* males. (b) Directional selection gradients (β) on wing coloration of *C. splendens* and *C. virgo*. Selection gradients on wings were estimated from morphological measurements of predated individuals and these wings were compared with measurements of live males captured at the same time and at the same locality (see Svensson *et al.* 2007). The selection gradients for all traits differed significantly between species ($P<0.001$, in all cases). Estimated means ± 95% confidence intervals are shown in figure. NS, not significant; ***$P<0.001$. Reproduced with permission from Chicago University Press.

has a strong effect on predation risk by white wagtails (*Motacilla alba*) at a sympatric locality of *C. splendens* and *C. virgo* in southern Sweden (Figure 11.4) (Svensson and Friberg 2007). *C. virgo*, which has entirely dark wings (Figure 11.1), and is thus presumably more visible to avian predators, had an almost three-times-higher predation risk than sympatric *C. splendens* males (Figure 11.4a). Moreover, both wing-spot size and the intensity of wing-spot darkness were subject to natural selection, although the selection pressures differed between the two species (Figure 11.4b). Predation selected for a reduced extent of wing melanization but darker spots in *C. virgo*, whereas selection on the smaller wing spot in *C. splendens* was not as pronounced (Figure 11.4b). Taken together, these data indicate that predator-mediated selection acts on wing melanization and hence such selection could potentially interfere with both the character-displacement process between these two species and may indirectly also affect the development of reproductive isolation between populations or species. More generally, the evolution of reproductive isolation between incipient species is thought to be facilitated if the species-recognition characters are subject to direct selection, as in this case, rather than if the species-recognition characters are only 'arbitrary' signalling traits that are only subject to indirect selection (Felsenstein 1981; Dieckmann and Doebeli 1999).

11.5 Sexual isolation as a result of direct or indirect selection on female mate preferences, or a correlated response to divergent sexual selection?

Natural selection on the melanized wing spots in the genus *Calopteryx* could have caused sexual isolation (see Box 11.1) in this genus, irrespective of whether natural selection was caused by male interspecific interactions (Tynkkynen *et al.* 2004, 2005, 2006) or by avian predation (Svensson and Friberg 2007). However, studies on sexual isolation should preferably also be performed at lower taxonomic levels than species; that is, between conspecific populations. Such studies are still rare, relative to the numerous laboratory studies on *Drosophila* (Rice and Hostert 1993; Coyne and Orr 2004). Ideally, such studies should be performed not only between allopatric populations experiencing little or no gene flow, but between parapatric populations with varying degree of gene flow (Hendry *et al.* 2000; Hendry 2001), combined with simultaneous estimation of natural and/or sexual selection regimes in the different populations (Svensson *et al.* 2006). Sexual isolation could evolve between such parapatric populations, even in the presence of gene flow, provided that natural and/or sexual selection is strong enough to overcome the homogenizing effects of gene flow (Smith *et al.* 1997; Hendry *et al.* 2002; Svensson *et al.* 2006). Most previous studies in this area have focused on the role of divergent natural selection and the associated effects on the development of reproductive isolation (Nosil *et al.* 2002, 2003; Nosil 2004). However, divergent sexual selection can also cause sexual isolation as a correlated response, although the empirical evidence for this is much more limited (Lande 1981; McPeek and Brown 2000; Svensson *et al.* 2006).

Svensson *et al.* (2004) have studied divergent sexual selection and sexual isolation within conspecific populations of *C. splendens* in southern Sweden. These populations are connected by varying degrees of gene flow, as revealed by analysis of molecular population divergence using amplified-fragment length polymorphism (AFLP) markers (Svensson *et al.* 2004). The average neutral molecular population divergence between 12 populations (pairwise F_{st}) ranges from close to zero to approximately 0.13 (Svensson *et al.* 2004), implying strong to moderate gene flow and varying degrees of parapatry between these populations. In spite of ongoing gene flow, sexual isolation has apparently evolved since in six out of seven populations, experimental 'immigrant' males presented to local females in the field have lower courtship success than local males (Figure 11.5a). We also confirmed, in a reciprocal transplant experiment between two of our most intensively studied populations experiencing more or less full gene flow ($F_{st} \approx 0$), that local females to a large extent preferred their own local males, rather than immigrant males (Figure 11.5b). The average courtship success of immigrant males was about 0.85 compared with local males; that is, a selection coefficient of −0.15 against immigrant males (Svensson *et al.* 2006). The average courtship success of male categories in this study was estimated from the average female responses to tethered males, measured on an 11-degree scale that takes into account all the distinct precopulatory behaviours in *Calopteryx* (Svensson *et al.* 2006). Such a strong selection coefficient against immigrant males could be the result of either strong direct selection against females mating with immigrant males; for example, because of physical injury or increased predation risk, a possibility that we consider unlikely.

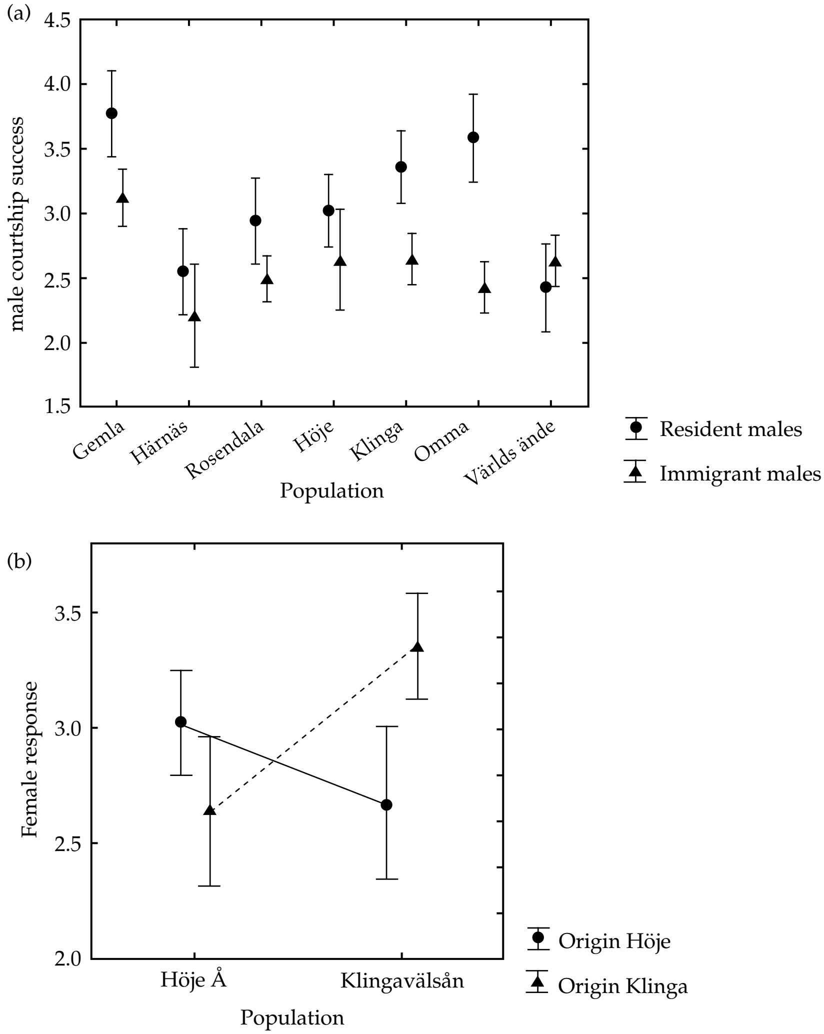

Figure 11.5 (a) Differences (means ± 95% confidence interval) in male courtship success (measured by monitoring female response; *y* axis) between resident males and experimental 'immigrant' males in seven different populations of *C. splendens.* Female courtship response towards residents and immigrants was quantified on a nominal scale using well-described and distinct precopulatory behaviors (Svensson *et al.* 2006). Each male was presented to several different females in tethering experiments in the field, and the average female response was used as a measure of male courtship success. (b) A sexually selected fitness trade-off between two damselfly populations differing in morphology and ecology. Resident males have higher courtship success towards females than experimental immigrant males, resulting in a significant phenotype × origin population interaction (Svensson *et al.* 2006). Reproduced with permission from Blackwell Publishing.

Another possibly more likely explanation is that sexual isolation has arisen as a correlated response to strong divergent selection between these populations. Sexual selection is clearly divergent between these populations (Svensson *et al.* 2006), so there is a clear potential for premating isolation to develop as a purely correlated response, exactly as predicted by the byproduct models of speciation (Coyne and Orr 2004). Such byproduct models of speciation predict that sexual isolation will arise as a result of either divergent natural selection (Rice and Hostert 1993) or divergent sexual selection (Svensson *et al.* 2006), both which may play a role in odonate divergence (Svensson and Friberg

2007; Svensson *et al.* 2006). Another possibility may of course be that females are rejecting immigrant males because of indirect fitness costs, for example if offspring from such interpopulation matings have lower survival. However, we consider this possibility unlikely given the fairly pronounced gene flow between these populations (Svensson *et al.* 2004), and indirect fitness costs and benefits are also considered to be a relatively weak force in the evolution of mate preferences (Kirkpatrick and Barton 1997; Møller and Alatalo 1999; Arnqvist and Kirkpatrick 2005; Orteiza *et al.* 2005). The reason why premating isolation between the populations on the female side has not more efficiently reduced gene flow between the same populations could be due to male coercive mating behaviour (see above). If immigrant males are able to overcome discriminating local females by obtaining enforced copulations, such male mating behaviour would constrain population divergence by increasing gene flow in spite of emergent sexual isolation among females (see Parker and Partridge 1998).

11.6 Conclusions and suggestions for future research

The possibility that males, rather than females, are primarily responsible for hybridization, opens up new perspectives in future studies of hybridization and reproductive character displacement. For example, almost all studies on reinforcement and reproductive character displacement assume intrinsically that females are performing active mate choice and thus are responsible for hybridization. However, if males are driving the hybridization, it may lead to unexpected patterns. For example, there may be character displacement in secondary sexual characters of the males, but it may be caused by factors other than reinforcement of female mate preferences.

One alternative mechanism for reinforcement and patterns of reproductive character displacement is interference of the mate-recognition signals of the two species. For example, a female may have problems to distinguishing signals of her own species, increasing the costs of mate searching. This may cause similar selection on female mate preference and male sexual characters as does avoidance of maladaptive hybridization (see Noor 1999; Coyne and Orr 2004; Mullen and Andrés 2007). We suggest that interspecific aggression originating from mistaken species recognition may form an unrecognized form of interspecific interference, which may explain reinforcement of premating isolation (see also Mullen and Andrés 2007). In contrast to increasing the costs for females, mistaken species recognition between males may cause selection on males for better species recognition or divergence in their sexual characters. If male sexual characters and female mate preference are genetically correlated (Lande 1981), interspecific aggression may drive population divergence in male traits, cause a correlated response in female preferences and, as a result, produce a pattern similar to the one predicted by classical reinforcement theory (see Alatalo *et al.* 1994; Tynkkynen *et al.* 2004, 2005, 2006).

The melanized wings in *Calopteryx* are unique in their multifarious and pleiotropic effects on suites of adaptive functions such as their links to male immunological condition (Rantala *et al.* 2000; Siva-Jothy 2000), their effect on predation risk (Svensson and Friberg 2007), their importance in male–male interspecific interactions (Tynkkynen 2004, 2005, 2006), and their role in female choice and intraspecific sexual selection (Siva-Jothy 1999; Svensson *et al.* 2004). In addition to all these documented links to adaptive functions, wing pigmentation also functions as a sexual isolation mechanism between species (Svensson *et al.* 2007). The adaptive and multiple functions of melanized wings in combination with their role in mediating sexual isolation make these an excellent illustration of so-called 'magig-trait' models in speciation research (Gavrilets 2004). Future work in the genus *Calopteryx* should aim to clarify whether and how these wing pigmentations have influenced speciation rates in a broader phylogenetic context and the relative importance of natural and sexual selection in speciation processes in this and other odonate groups (Svensson *et al.* 2006). The relative simplicity by which these wing pigmentations can be measured and experimentally manipulated in natural populations should make *Calopteryx* damselflies excellent model organisms in future speciation research.

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CHAPTER 12

Lifetime reproductive success and sexual selection theory

Walter D. Koenig

Overview

Odonates exhibit a variety of characteristics that make them suitable for studies quantifying reproductive success achieved by a cohort of individuals during their lifetimes. Such studies yield the best available measures of fitness and have been thought to be critically important in understanding the strength and patterns of selection acting on natural populations, including the importance of sexual selection. Here I summarize 23 studies of lifetime reproductive success (LRS) conducted on odonates since the 1980s. Such studies have focused on a variety of characters but have generally found that survivorship, in many cases strongly influenced by random environmental factors, is more important than mating efficiency in determining LRS. Furthermore, selection on virtually all characters, including body size, varies considerably not only from species to species but from population to population depending on factors such as density, sex ratio, and community composition. By themselves, LRS studies have largely failed to fulfil the promise of quantifying the relative importance of natural and sexual selection. LRS studies have been most successful when focused on specific traits and when complemented by experimental manipulations of those traits. Progress in understanding the current actions of natural and sexual selection is thus most likely to involve a combination of long-term, LRS work combined with experimental and comparative approaches. Such integrative studies will be necessary to address challenges of odonate systems, including incorporating the larval stage in fitness studies, performing parentage analyses to determine realized fitness, and considering the potential role of non-breeding behaviours such as foraging efficiency.

12.1 Introduction

Odonates make outstanding subjects for behavioural and evolutionary studies because they are often abundant, relatively easy to catch and mark, readily observed, and geographically widespread yet generally concentrated on and near water sources. Besides these logistical features, communities of odonates are often diverse, populations frequently exhibit intriguing morphological and behavioural polymorphisms, and adults are almost universally colourful and fun to observe. Given these traits, it is not surprising that this otherwise relatively modest order has been the subject of an inordinate amount of research in behavioural and evolutionary ecology. Here I review studies of lifetime reproductive success (LRS) in this taxon with the goals of summarizing the contributions these studies have made to our understanding of natural and sexual selection and identifying some areas in which progress remains to be made.

12.2 Historical background

Odonates have been the subject of detailed ecological studies, often involving marked individuals, since at least the 1930s (Borror 1934), with numerous such studies being conducted by the 1950s

(Corbet 1952; Moore 1952, 1954; Jacobs 1955). The focus of this work was frequently behavioural, often involving issues such as territoriality, mating behaviour, mate-guarding, and dispersal. By the 1970s, mating systems had started to attract widespread attention and became the focus of several notable longitudinal studies of odonates (Parr and Palmer 1971; Campanella and Wolf 1974; Johnson 1975; Campanella 1977).

The idea that LRS provides the best measure of fitness that can realistically be gathered was well established by the time of these latter studies (Cavalli-Sforza and Bodmer 1961). However, for many years LRS appears to have been primarily of interest to workers studying laboratory mice and domesticated livestock, and it was not until the University of Chicago's evolutionary biology group published a seminal series of papers on measuring natural and sexual selection (Wade 1979; Wade and Arnold 1980; Lande and Arnold 1983; Arnold and Wade 1984a, 1984b) that interest in quantifying LRS became a goal that field workers took seriously. These papers inspired a flurry of studies explicitly attempting to quantify lifetime reproduction (Clutton-Brock 1988a), of which those involving odonates played a prominent role. Although determining exactly what constitutes a study quantifying LRS is to some extent arbitrary, at least 23 such studies involving 20 different species of odonates (13 of damselflies and seven of dragonflies) have been published, starting with Ola Fincke's work on *Enallagma* (Fincke 1982) and peaking in the late 1980s (Table 12.1).

Although the stated goals of studies measuring LRS vary widely, two are most frequently repeated. First is to measure selection on particular phenotypic characters, often while attempting to control for confounding factors (Box 12.1). The second is to measure the opportunity for selection (Box 12.2), defined as the relative variance exhibited by fitness or a particular fitness component such as survivorship or mating efficiency (Arnold and Wade 1984a, 1984b), often in the hope of distinguishing the importance of natural and sexual selection or of testing Trivers's (1972) hypothesis that the intensity of selection on the limited sex should be greater as investment in reproduction between the sexes becomes more unequal.

How successful have studies of lifetime reproductive success been in achieving these goals? It is fair to say that their success has been limited. If nothing else, this is illustrated by the numbers: of the 23 studies listed in Table 12.1, nine were published in the 1980s in the wake of the Arnold/Wade/Lande papers, nine came out in the 1990s, and thus far five have been published since 2000. Thus, although studies of LRS continue to be conducted, there has been no explosion of field studies quantifying LRS since the early 1980s. Furthermore, there have been no recent follow-ups to the two main edited books published on the subject (Clutton-Brock 1988a; Newton 1990), the latter of which is no longer even in print. Although it is more difficult to expand this conclusion to other taxa, I believe that LRS studies in general no longer generate the kind of excitement they did in the 1980s following the publication of the Arnold/Wade/Lande papers on measuring selection.

What went wrong? Two main difficulties would appear to be paramount. The first is primarily logistic: despite the considerable effort required to gather LRS data, results are invariably prone to seasonal effects and biases that can only be addressed by conducting controlled studies under artificial conditions. For example, Michiels and Dhondt (1991), who conducted their LRS study in a large enclosure, were specifically attempting to reduce the potentially confounding effects of covariation on observed selection parameters and minimize the potential bias introduced by the typically large proportion of individuals—often on the order of 50% or more (Koenig and Albano 1987; McVey 1988; Beirinckx *et al.* 2006)—that disappear immediately after marking and release in odonate studies. Similarly, studies by Van Gossum *et al.* (1999, 2001, 2005) of female dimorphism in *Ischnura elegans* were conducted under artificial conditions to explicitly investigate this phenomenon while controlling for the potentially confounding effects of density, sex ratio, and morph frequency in ways that could not be accomplished in the field. Clearly LRS data are no panacea for the biases inherent in other less intensive investigations, and indeed run the risk of providing less satisfying results than carefully designed (and potentially less time-intensive)

Table 12.1 Studies of lifetime reproductive success in odonates.

Species	Opportunity for selection: survivorship predominant?	Selection		References
		Body size	Other	
Zygoptera (damselflies)				
Enallagma hageni (non-territorial)	MM, FF: yes	MM: correlation between body size and LMS NS but apparent stabilizing selection FF: NS	MM: no seasonal effect, LMS decreased with age FF: no seasonal effects; no differences between androchromes and heterochromes	Fincke 1982, 1986, 1988
Enallagma boreale (non-territorial)	MM, FF: yes	MM: smaller had lower survival to maturity but higher mating success FF: NS	MM: later favoured in 1 year, NS in 1 year FF: earlier favoured in 1 year, later in 1 year	Anholt 1991
Enallagma boreale (non-territorial)			FF: no difference in LMS between androchromes and heterochromes	Fincke 1994
Coenagrion puella (non-territorial)	MM, FF: yes	MM: stabilizing; declines seasonally FF: large females produce smaller clutches but live longer	MM: mating success declined with age FF: no differences in LRS between androchromes and heterochromes; lifetime egg production largely determined by chance	Banks and Thompson 1985, 1987; Thompson 1990
Coenagrion puella (non-territorial)		MM: larger MM had higher LMS	MM: more symmetrical MM had higher LMS	Harvey and Walsh 1993
Coenagrion mercuriale (non-territorial)		MM, FF: directional and stabilizing selection NS	MM, FF: highly constrained by poor weather conditions; age and season NS	Purse and Thompson 2005
Ischnura gemina (non-territorial)			No significant difference in OS between MM and FF	Hafernik and Garrison 1986
Ischnura elegans (non-territorial)	MM: yes; main correlate of LMS was lifespan	MM: body length not correlated with LMS, although possible slight advantage to smaller MM	MM: LMS declined seasonally	Cordero *et al.* 1997
Ischnura elegans (enclosure study; non-territorial)			FF: androchromes achieve fewer ovipositions at high density	Van Gossum *et al.* 2005
Ischnura graellsii (non-territorial)	MM: yes	MM: LMS greater in larger MM in one of two populations FF: NS	MM: more symmetrical MM had higher LMS but result weak and NS; MM that moved around more had higher LMS	Cordero Rivera *et al.* 2002
Argia chelata (territorial)			MM: mating efficiency independent of age	Hamilton and Montgomerie 1989

Table 12.1 (*Continued*)

Species	Opportunity for selection: survivorship predominant?	Selection		References
		Body size	Other	
Cercion lindeni (territorial)		MM: no significant effect	MM: no significant effect of fluctuating asymmetry	Carchini *et al.* 2005
Lestes sponsa (non-territorial)	MM: no; mating efficiency explained 71% of variation in LMS compared with 20% for survivorship	MM: stabilizing selection		Stoks 2000
Hetaerina americana (territorial)		MM: selection for larger body size	MM: selection for larger dark wing spot via MM competition confirmed experimentally	Grether 1996a, 1996b
Ceriagrion tenellum (non-territorial)	MM, FF: yes (calculated from data on unparasitized individuals)		MM: water-mite parasitism adversely affected LMS in 1 year FF: no effect of water mite parasitism on LMS	Andrés and Cordero 1998
Mnais pruinosa (territorial)			MM: no difference in LRS between orange-winged territorial and clear-winged non-territorial MM	Tsubaki *et al.* 1997
Anisoptera (dragonflies)				
Erythemis simplicicollis (territorial)	MM, FF: no, but still large		MM: age effects apparently NS; satellites achieved lower daily MS, lived shorter	McVey 1988
Libellula luctuosa (territorial)		MM: significant directional or stabilizing selection for larger body size, depending on the character	MM: significant directional selection for larger wing patches; satellites smaller	Moore 1990
Plathemis lydia (territorial)	MM, FF: yes	MM, FF: NS; declined seasonally	MM, FF: seasonal decline in LRS	Koenig and Albano 1987
Nannophya pygmaea (territorial)		MM: larger had higher LMS due to greater longevity and higher competitive ability	MM: weather factors very important	Tsubaki and Ono 1987
Sympetrum rubicundulum (territorial)		MM: no effect of body size on survival or MS; declined seasonally	MM: no effect of emergence date on survival or LMS	Van Buskirk 1987
Sympetrum danae (enclosure study; non-territorial)	MM, FF: OS for survivorship greater than OS for daily mating success	MM: larger MM had higher LMS FF: no effect of body size	MM: larger MM searched for mates more actively	Michiels and Dhondt 1991
Orthetrum japonicum (territorial)	MM: apparently low due to short reproductive period	MM: varied among episodes but in general NS		Kasayu *et al.* 1997

FF, females; LMS, lifetime mating success; LRS, lifetime reproductive success; MM, males; NS, not significant; OS, opportunity for selection.

Box 12.1 Measuring selection on phenotypic characters

Selection takes place when the distribution of phenotypes changes. Although traditionally measured as the *evolutionary response to selection* from one generation to the next, such changes can also be measured within a generation by quantifying the means, variances, and covariances of phenotypic distributions at different stages of the life cycle, thus sidestepping the issue of inheritance (Arnold and Wade 1984a).

Within a generation, selection can be measured by determining the statistical relationship between fitness and the phenotypic character or characters of interest. Since characters rarely act by themselves, multivariate techniques are frequently desirable to separate the effects of potentially confounding factors.

To measure *directional selection*, multiple regression can be used to determine the *selection gradient* associated with a particular character. Analyses to detect and measure *stabilizing selection*, *disruptive selection*, or other complex relationships between a character and its fitness effects require more elaborate methods such as quadratic regression (Lande and Arnold 1983) or the estimation of non-parametric fitness functions (Schluter 1988).

Box 12.2 Opportunity for selection

In order for selection, and thus evolution, to take place, there must be variation in fitness. Furthermore, variance in fitness sets an upper bound on the rate of evolution in both mean fitness and all phenotypic traits. Thus, the greater the variance in fitness, the stronger the force of selection (Shuster and Wade 2003).

Fitness variance has been called the index of total selection and the intensity of selection, but is now generally referred to as the opportunity for selection, defined as $I = V_{\mathrm{w}}/W^2$, where W and V_{w} are the mean and variance of fitness, respectively (Crow 1958). Because the opportunity for selection is expressed as a variance it is possible to quantify it in different subsets of a population or in separate stages of the life cycle by relatively straightforward analysis of variance methods (Arnold and Wade 1984a). For example, Koenig and Albano (1987), in a study of *Plathemis lydia*, partitioned male LRS (measured as estimated number of eggs fertilized) into six multiplicative ‘episodes’ of selection, including days alive, proportion of days alive present at the breeding pond, hours per day at the breeding pond, matings per hour present, ovipositions per mating, and eggs fertilized per oviposition.

Knowledge of inheritance or phenotype are not prerequisites for measuring I, since the opportunity for selection is measured with respect to fitness or a particular component of fitness independent of phenotypic characters. In contrast, a *selection gradient* is a regression of relative fitness on a particular character, requiring knowledge within a generation of the mean, variance, and covariance of the phenotypic distribution, whereas the *evolutionary response to selection* involves changes in phenotype across generations and thus involves both phenotypic distributions and inheritance (Arnold and Wade 1984a).

experimental manipulations focusing on a particular ecological or evolutionary issue.

The second shortcoming of LRS studies is theoretical: it was soon realized that it was not going to be as easy to distinguish natural and sexual selection (Box 12.3) as hoped initially, nor was it likely that the opportunity for selection was going to provide data that would necessarily illuminate the intricacies of selection in natural populations. No small part of the excitement generated by the early theoretical papers was the elegance and simplicity of measuring sexual selection as ‘the variance in numbers of mates’ (Wade and Arnold 1980) and thus being able to quantify, from data readily

Box 12.3 Natural and sexual selection

Natural selection occurs when certain traits or genes are more successful than others, thereby becoming more common in successive generations as individuals with those traits reproduce and leave more descendants than those with alternative traits or genes.

Darwin (1871) defined sexual selection as that form of natural selection specifically related to '. . . the advantage which certain individuals have over others of the same sex and species in exclusive relation to reproduction.' Darwin further divided sexual selection into *intrasexual selection*, typically thought of as male–male competition, and *intersexual selection*, typically female choice (although male choice occurs in some species as well).

Intra- and intersexual selection are often interrelated, and thus difficult to distinguish. For example, whereas female *Hetaerina americana* appear to choose males with large wing spots they are in fact choosing favourable oviposition sites dominated by males successful in male–male competitive interactions (Grether 1996b). Distinguishing between natural and sexual selection can also be difficult, since non-reproductive traits can be important to reproduction. An example would be in the case where females prefer older males, in which case the sexually selected trait (age) is explicitly the product of greater success at characteristics increasing male survivorship.

In general, distinguishing between natural and sexual selection is often least ambiguous and most interesting when they counteract each other, as in the extraordinary tails of male peacocks *Pavo cristatus* (Petrie *et al.* 1991, Petrie and Halliday 1994) and the calls of the Tùngara frog *Physalaemus pustulosus* (Ryan *et al.* 1990).

acquired in the field, the relative importance of sexual and natural selection (Arnold and Wade 1984b). It all seemed so simple, and indeed it was not long before it was realized that things were generally far more complex than implied by this definition. For example, random effects were likely to complicate the situation in ways that could be highly misleading (Houck *et al.* 1985; Sutherland 1985, 1987). Equally disturbing, variance in mating success was clearly not necessarily entirely, or even primarily, the result of sexual selection under many realistic circumstances, as such differences could readily be the result of behaviours or other factors unrelated to either intrasexual competition or mate choice (Koenig and Albano 1986) (Box 12.2). Alas, the goal of clearly and cleanly measuring natural and sexual selection remained elusive, despite a growing series of LRS studies.

An additional difficulty spanning both the empirical and theoretical realms involved the interpretation of the opportunity for selection of a particularly component of reproduction (Arnold and Wade 1984a, 1984b). This technique is elegant in principal, allowing workers to quantify the relative importance of different behaviours contributing to natural and sexual selection and, just as importantly, revealing potential trade-offs between different life-history stages or components of fitness. However, attempts to apply these techniques to field situations can result in a high proportion of uninterpretable covariance terms severely reducing the value of the analyses (Koenig and Albano 1987).

More seriously, measuring the opportunity for selection tells us little, if anything, about the strength of selection per se, much less the adaptations that have evolved due to selection (Grafen 1988). For example, consider the basic question of whether the wing spot of male rubyspot damselflies (*Hetaerina americana*) is the subject of sexual selection rather than due to sexual differences in foraging behaviour (Hafernik and Garrison 1986) or sexual recognition (Waage 1975, 1979a; De Marchi 1990). Although variance in LRS among males is necessary for selection to be occurring, no amount of LRS data quantifying the opportunity for selection can answer this question. Instead, Grether (1996a, 1996b) used a combination of selection analyses with LRS data and experimental phenotype manipulations to confirm that this character is indeed subject to sexual selection involving male–male competition for territories favoured as oviposition sites by females rather than female choice. This result was elaborated on further by Contreras-Garduño *et al.* (2006), who used experimental implants to investigate the relationship between territoriality, wing-spot pigmentation, immune response, and fat reserves in this species.

It is this failure to directly involve the phenotype, perhaps more than anything else, which has led to the decline of the Arnold/Wade/Lande techniques of partitioning selection and their emphasis on opportunity for selection. Whether a recent attempt to re-energize this approach (Shuster and Wade 2003) will succeed remains to be seen.

Although some of the analytical techniques and ideas that inspired many of the LRS studies to be discussed here have not necessarily stood the test of time, this is not to say that the studies themselves have not been valuable or that they failed to illuminate important features concerning the ecology and behaviour of odonates. What have these studies taught us and what approaches should workers take in the future?

12.3 Selection and the opportunity for selection

12.3.1 Opportunity for selection

As mentioned above, a goal of many early LRS studies was to test the predictions that the opportunity for selection should be greater as investment in reproduction between the sexes becomes more unequal (Fincke 1986, 1997) and that it should be greater in polygynous and promiscuous systems than in monogamous species (Clutton-Brock 1988b). Unfortunately, these predictions proved difficult to address because, as demonstrated by Sutherland (1985, 1987), differences in the opportunity for selection between males and females can emerge even when there is random mating assuming there are differences in encounter rates between the sexes. Since LRS studies in general have not attempted to control for such effects, it remains questionable as to whether observed differences in the opportunity for selection between the sexes or between species are meaningful. Other indices of sexual selection, such as the maximum daily mating rate (Johansson *et al.* 2005) or sexual dichromatism or dimorphism in size (Anholt *et al.* 1991; Fincke *et al.* 1997), will perhaps prove more successful in testing these predictions of sexual selection theory.

One conclusion concerning fitness variance that can be drawn from the studies summarized in Table 12.1 is that a greater proportion of the opportunity for selection is due to differences in survivorship than to episodes of fitness potentially related to sexual selection. Of the 11 studies for which information on the relative opportunity for selection of survivorship could be determined, eight (73%) indicated that survivorship is a major, if not the primary, contributor to variance in LRS, often for both males and females. For two of the remaining studies variance in survival was important but not predominant, while in only one (*Orthetrum japonicum*; Kasayu *et al.* 1997) was variance in survivorship notably low, a result attributed to the short duration of this species' reproductive period. In general, however, these studies indicate that variance in survivorship, in turn determined largely by stochastic factors (Cordero 1995; Thompson 1997), is often the predominant source of differences in LRS in odonates. This suggests that the opportunity for sexual selection is generally less important than the opportunity for natural selection in this taxon.

12.3.2 Selection on body size

The results of LRS studies investigating the relationship between fitness and body size encompass almost every possible outcome (Table 12.2). For males, 29% of studies found that selection favoured larger body size, often because of greater competitive ability. Three studies (18%) found evidence for stabilizing selection whereas one found little or no selection for body size overall, but did find evidence for trade-offs in the sense that smaller males had higher mating success but lived a shorter period of time than larger males. Nearly half of all studies found no significant selection on male body size. There were no obvious differences between territorial and non-territorial species.

For females, one study found evidence of trade-offs between different components of lifetime

Table 12.2 Summary of selection on body size based on odonate LRS studies. Studies finding varying results depending on year, population, or character are divided in half.

Selection on body size	Territorial species	Non-territorial species	All species
Males			
Favours larger males	3.5 (44%)	1.5 (17%)	5 (29%)
Stabilizing	0.5 (6%)	2.5 (28%)	3 (18%)
Trade-offs, overall NS	0	1 (11%)	1 (11%)
NS	4 (50%)	4 (44%)	8 (47%)
Total	8	9	17
Females			
Trade-offs, overall NS	0	1 (17%)	1 (14%)
NS	1 (100%)	5 (83%)	6 (86%)
Total	1	6	7

NS, not significant.

reproduction whereas six found no significant selection on body size. Thus, although apparently clear selection for larger body size has been found in some cases (see Chapter 13 in this volume), LRS studies do not support the hypothesis of Sokolovska *et al.* (2000), based on a meta-analysis, that there are general fitness benefits to large size in odonates, a conclusion questioned previously by Thompson and Fincke (2002).

12.3.3 Selection on other characters

Beyond body size, LRS studies have focused on a variety of characters, including seasonality, age, and weather (Table 12.3). Four characters that have been of particular interest are behavioural and morphological sex-limited polymorphisms, parasitism, sexually dimorphic wing patches on males, and fluctuating asymmetry. The first of these categories includes at least one study of a male dimorphism (Tsubaki *et al.* 1997) but otherwise generally focus on the fairly common phenomenon of colour dimorphisms in female zygopterans whereby some mimic males (androchromes) while others are the 'normal' female phenotype (heterochromes). This phenomenon is discussed at length elsewhere (see Chapter 17). Of the studies summarized in Table 12.1, however, three yielded no significant differences between the LRS of androchromes and heterochromes, while one indicated that androchromes were less successful, at least at high densities (Van Gossum *et al.* 2005). These studies suggest that colour dimorphisms in female zygopterans are maintained by opposing patterns of selective pressures favouring one or the other morph under constantly changing conditions.

The potential effects of parasitism by water mites, first discussed in studies of *Enallagma ebrium* by Forbes (1991) and Forbes and Baker (1991), was studied more recently using lifetime mating success in *Ceriagrion tenellum* by Andrés and Cordero (1998), who found no effect of parasitism on lifetime mating success of females and a negative effect in only one of 2 years on males. Given the key role that parasitism is believed to play in sexual selection (Hamilton and Zuk 1982), more studies investigating mites and other odonate parasites using LRS data are desirable to complement the many recent advances in this area discussed in Chapter 14.

The third character, sexually dimorphic wing patches on males, is of particular importance because it is a character that is unambiguously a product of sexual selection, generally via male–male competition, although an experimental study by Siva-Jothy (1999) provides evidence for active female choice of male wing-spot heterogeneity in *Calopteryx splendens*. Such wing patches have been the focus of two LRS studies, including Grether's (1996a, 1996b) work in which he confirmed experimentally that male–male competition selected for

Table 12.3 Targets of selection other than body size measured by LRS studies in male odonates. Numbers indicate the number of studies with a given result.

Character	Relationship of character to reproductive success		
	Increases	Decreases	No significant effect
Seasonality	1 of 2 years in one study (Anholt 1991)	2 (Koenig and Albano 1987; Cordero *et al.* 1997)	3+1 of 2 years in a fourth study (Van Buskirk 1987; Fincke 1988; Anholt 1991; Purse and Thompson 2005)
Increased age		2 (Fincke 1988; Banks and Thompson 1985, 1987)	3 (McVey 1988; Hamilton and Montgomerie 1989; Purse and Thompson 2005)
Increased mobility	2 (Michiels and Dhondt 1991; Cordero Rivera *et al.* 2002)		
Larger wing spot	2 (Grether 1996a, 1996b; Moore 1990)		
Wing-colour dimorphism			1 (Tsubaki *et al.* 1997)
Increased parasitism		1 of 2 years (Andrés and Cordero 1998)	1 of 2 years (Andrés and Cordero 1998)
Satellite behaviour		2 (McVey 1988; Moore 1990)	
Greater symmetry	1 (Harvey and Walsh 1993)		2 (Cordero-Rivera *et al.* 2002; Carchini *et al.* 2005)

larger, dark wing spots in *Hetaerina americana*. A similar result demonstrating directional selection for larger wing patches in males of the dragonfly *Libellula luctuosa* was found by Moore (1990) using multivariate statistical analyses. These are apparently the only two studies measuring LRS thus far that reach a conclusion countering the general perception that relatively little of the variance in odonate reproduction is attributable to phenotypic variance (Fincke *et al.* 1997).

Finally, three of the LRS studies in Table 12.1 focused on testing the hypothesis that fluctuating asymmetry is an index of developmental instability and ultimately of genetic quality (Møller and Swaddle 1997). Of these, two found no significant differences in LRS of males related to asymmetry while one found that more symmetrical males had higher lifetime mating success (Harvey and Walsh 1993). Thus, as with most of the other characters investigated in the context of LRS studies in odonates, results are mixed and indicate wide variation among species and/or studies depending on factors such as density, sex ratio, and weather that are generally not controlled or, in field studies, controllable.

12.4 The role of LRS studies

What conclusions can be drawn from these LRS studies and how should workers allocate their efforts in the future? One main conclusion is that selection in many odonates is sensitive to population factors such as density, sex ratio, and (when morphs are present) frequency, as well as external factors such as weather and community composition, including populations of predators, competitors, and prey, all of which can potentially shift on a day-to-day basis. The variable importance of such factors, which is tantamount to fluctuating or oscillating selection within and across generations, makes it difficult to determine the overall importance of natural or sexual selection on morphological characters except under the particular conditions present at the time of a study. Whether the long-term consequences of such variable selection regimes is essentially stabilizing, as suggested for Darwin's finches (Grant *et al.* 1976), is an intriguing possibility but remains to be determined.

One apparent exception is with respect to the importance of survivorship, which in general appears to be a more important contributor to overall variance in LRS than factors influencing mating success. Although this conclusion is most likely to hold for insects and other invertebrates whose small size makes them subject to the vagaries of environmental conditions, survivorship has been found to correlate with LRS in many vertebrate species as well (Clutton-Brock 1988b).

With respect to specific traits, odonates have evolved a variety of intriguing sexual behaviours, from sperm removal and displacement by males (Waage 1979b) to alternative mating strategies by both sexes, demonstrating unambiguously that sexual selection has played an important role in odonate evolution. However, given the varying evolutionary landscape against which these factors find themselves, it is perhaps not surprising, at least in retrospect, that LRS studies have not proved consistently to be an effective means of determining the current importance of such traits on fitness. Rather, such evidence has tended to come from comparative studies of conspecific populations (Cordero Rivera *et al.* 2004; Svensson and Gosden 2007) and experimental manipulations investigating key questions such as the role that male wing spots play in female choice (Siva-Jothy 1999), male–male competition (Grether 1996a, 1996b), and conspicuousness to prey (Grether and Grey 1996), as well as the fitness consequences of parasites (see Chapter 14) and female polymorphisms (see Chapter 17). If one's goal is to test whether, say, symmetry is a potential target of female choice, or whether community composition influences male–male competition, it would be prudent to design an experiment to test these specific questions rather than trust that the answers will emerge from an observational LRS study involving the measurement of fitness among males within a population.

Nonetheless, there is a key role to be played by LRS studies in understanding the evolutionary agents important to odonates, as well as other species. Although a controlled experiment involving phenotype manipulations may be the most efficient way to test whether female choice based on, for example, male wing spots may be occurring, almost by definition longitudinal studies measuring survivorship as well as mating success—in other words LRS—are necessary to test whether wing spots potentially entail fitness costs via increased depredation, decreased foraging success, or other factors. Given that selection ultimately acts on the LRS of individuals rather than on their success at a particular stage of the life cycle, there will always be good reasons to measure LRS rather than restrict one's focus on a particular component of fitness. The optimal approach, given the complexities and potential biases inherent in different kinds of studies, is to combine long-term LRS studies with experimental work to address key questions such as the importance of sexual selection (Clutton-Brock 1988b, Grether 1996a).

12.5 Future challenges

In conjunction with other kinds of studies, LRS data can and should continue to contribute key insights into our understanding of odonate life-history evolution. At least three basic features of such systems remain to be incorporated into LRS studies. First and most obvious is the larval stage. Indeed, all of the studies listed in Table 12.1 are restricted to adults despite work indicating that larval ecology plays a potentially critical role in adult fitness (Buskirk and Sherman 1985; Conrad 1992; Fincke 1992; De Block and Stoks 2005; see also Chapter 3). As with other taxa in which major life-history transformations occur, the challenges of linking larval and adult phases in the field are considerable. Doing so, however, will be necessary to achieve the goal of understanding selection in such taxa.

A second major fitness character that has been largely ignored is parentage, a factor particularly important given the potential for trade-offs between mating efficiency, mate-guarding, and paternity of eggs. Thus far, only one odonate study has incorporated modern molecular methods to determine how paternity affects estimates of fitness. Studying a treehole-breeding damselfly, Fincke and Hadrys (2001) found that both female fecundity and male fertilization success were poor predictors of realized fitness measured by the number of offspring surviving to adulthood. Clearly both consideration of larval survivorship and more complete analysis of parentage are needed before we will be able to accurately understand the forces of selection acting in odonate populations. Fortunately, continuing advances in molecular biology make the potential for conducting such studies in the future bright.

A third key fitness character largely absent from the odonate literature is foraging behaviour. Foraging generally takes place away from breeding sites and so it has rarely been addressed, despite at least one study demonstrating potential trade-offs between a sexually selected character (wing spots) and foraging efficiency (Grether and Grey 1996). Integrating such non-breeding behaviours into LRS studies will be necessary if we are to understand the relative importance of natural and sexual selection. Such integration will be challenging, but appears within reach, especially given continuing advances in technology that have already successfully tracked migrating dragonflies over large distances (Wikelski *et al.* 2006).

Acknowledgements

I thank S. Albano, E. Deinert, A. Peters, M. Peterson, and R. Stanford for field assistance and J. Alcock, O. Fincke, and J. Waage for collegial help understanding odonate biology. I am particularly indebted to the reviewers for their comments and to Alex Córdoba-Aguilar for his encouragement.

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CHAPTER 13

Fitness landscapes, mortality schedules, and mating systems

Bradley R. Anholt

Overview

When males and females have differing mortality schedules, the population sex ratio becomes biased towards the sex with the lower mortality rate. It is possible to predict which sex has the higher mortality rate based on the relationship between reproductive success and body mass. If reproductive success increases with mass, then individuals are predicted to take greater risks to achieve it. The balance between these two competing life-history traits is when the marginal increase in fitness from reproduction is equal to the marginal loss due to mortality. In odonates the relationship between mass and reproductive success depends on sex and mating system. Females that acquire more resources prior to reproduction will be able to produce more eggs. This is true in both territorial and non-territorial mating systems. For males, reproductive success increases with mass much more steeply in a territorial than a non-territorial mating system. Thus, at reproductive maturity we find that in non-territorial mating systems females are often twice as heavy as males, whereas in territorial systems the mass of males and females are more similar with males in some cases exceeding females. These differences in mass gain translate to differences in mortality rates. Where females gain more mass than males prior to reproductive maturity they also have higher mortality rates than males. This necessarily leads to differences in population sex ratios at sexual maturity. These differences in population sex ratios have implications for the viability of different mating systems. When the population sex ratio is heavily male-biased, and this is then magnified at the mating site by differences in the frequency of reproductive activity between males and females, this selects for contact guarding because competition for mates is intense and males are unlikely to get a second chance to mate in their lifetime. This means that territorial behaviour is not feasible. If the population sex-ratio is female-biased, intrusion pressure is low and a territory holding male may have the opportunity to mate more than once in a day, making territoriality a viable mating system. Although consistent with empirical data, these hypotheses have not been subjected to experimental testing. In principle, odonates provide an ideal system where manipulations could be done in large enclosures or even natural systems.

13.1 Introduction

The evolutionary fitness of an individual can be mapped on to a conceptual landscape where the coordinates are measured in phenotype space and the height of the landscape is fitness (Wright 1932). Selection will tend to move the average population phenotype uphill towards a local maximum. The shape of the landscape is highly contingent on the local environmental conditions so that the phenotype with highest fitness may differ between hot or cold, or wet or dry years. It will depend on what other predators, competitors, and disease agents might be present. It will also depend on the abundance of conspecifics, with some phenotypes favoured at low density and others at high density.

Different species will have different fitness landscapes as will genetically determined morphs of a single species. This difference also applies to males and females of the same species.

One indication of these differing fitness landscapes for male and female odonates is their sexual size dimorphism. Females are typically larger (Johansson *et al.* 2005; see Chapter 18 in this volume) and heavier than males at sexual maturity (Anholt *et al.* 1991), but this difference declines with the size of the species (Johansson *et al.* 2005). However, this difference is confounded by taxonomy and mating system (Anholt *et al.* 1991; Johansson *et al.* 2005). With important exceptions, small species tend to be zygopterans with non-territorial mating systems whereas large species are anisopterans with territorial mating systems.

This chapter examines the features of the fitness landscape for male and female odonates, the determinants of that landscape, and the potential consequences. Where appropriate I point out areas where we lack data, and make specific suggestions for studies and appropriate analyses.

13.2 Fitness of sexually mature adults

Odonates complete their reproduction in a single flying season, so the number of fertilized eggs is a reasonable estimate of fitness. There is some evidence of timing effects on the probability of survival of those eggs. Larvae hatching from eggs laid late in the season can be subject to cannibalism by larvae produced earlier (Anholt 1994; Padeffke and Suhling 2003). They can also be subject to higher mortality rates because they take more risks to reach metamorphosis by the end of the season. Usually, estimates are made of components of fitness such as longevity, clutch size, or number of clutches. Provided these estimates are uncorrelated with each other, then other things being equal, these measures will be correlated with fitness. However, it is entirely possible that clutch size, for example, is negatively correlated with longevity. A cost of reproduction is expected on theoretical grounds (Williams 1966) but its demonstration is fraught with difficulty. Regardless, as soon as there is a statistical relationship between fitness components (significant or otherwise) then accurate estimates are far more complicated. A recent advance in measuring fitness in sequential episodes of selection provides a means to solve these difficulties (Geyer *et al.* 2007). It remains to be seen whether these can be successfully applied to species as vagile as odonates where recapture success (independent of survival) will always be less than 100%.

13.2.1 Females

Sexually mature females that have garnered more resources have a fecundity advantage because they can produce more eggs (Richardson and Baker 1997). The skeletal size of a female is determined in the larval phase and must set some upper limit to clutch size. However, it is not clear how often this upper limit is reached (Banks and Thompson 1987) because females frequently gather fewer resources than they can use (Anholt 1992; Richardson and Baker 1997). In the cases where females have been shown to produce larger clutches at larger body sizes, *Plathemis lydia* (Libellulidae) and *Pyrrhosoma nymphula* (Coenagrionidae) (Koenig and Albano 1987; Gribbin and Thompson 1990), then we should also be able to detect a relationship between skeletal size and foraging success, or skeletal size and allocation patterns. Marden and Rowan (2000) report that heavier individuals of *Libellula pulchella* (Libellulidae) have higher future foraging success, but their study does not account for the probability of recapture.

The number of clutches oviposited by a female, or its correlate, lifespan, is often associated with larger body size or mass: this is the case for *Enallagma ebrium*, *Ischnura graellsii*, *Coenagrion puella* (Coenagrionidae) (Gribbin and Thompson 1990; Cordero 1991; Leung and Forbes 1997), *Lestes viridis* (Lestidae) (DeBlock and Stoks 2005), and *Lestes pulchella* (Marden and Rowan 2000). However, this is by no means universal, as for *Enallagma hageni*, *Enallagma boreale* (Coenagrionidae), *Lestes congener*, *Lestes disjunctus* (Lestidae), *Sympetrum pallipes*, *Sympetrum danae*, and *P. lydia* (Libellulidae) (Koenig and Albano 1987; Fincke 1988; Michiels and Dhondt 1989; Anholt 1991; Smith 2004).

Although we have many studies that examine foraging and survival of larvae under manipulated conditions, and some on the consequences for adults (e.g. Anholt 1991; Stoks 2000; DeBlock and Stoks 2005), we have not invested any effort into measuring foraging effort of adults under different resource regimes. Our understanding is limited to the inferences we can draw based on adult survivorship and mass gain. We have few direct observations and no experiments. Replicated enclosures for adults, such as those used by DeBlock and Stoks (2005), with food and predator manipulations, remain to be attempted.

13.2.2 Males

Reproductive success tends to increase with body size in males (reviewed in Sokolovska *et al.* 2000 but see Thompson and Fincke 2002 for discussion). The effect is strongest in species where males are larger than females (e.g. *Megaloprepus coerulatus*; Fincke *et al.* 1997), or in strongly territorial mating systems (e.g. *Mnais pruinosa costalis*, Calopterygidae; Plaistow and Tsubaki 2000). The effect of body size on mating success is weaker in non-territorial species (Sokolovska *et al.* 2000), with evidence for balancing selection (*C. puella*, *E. hageni*, *Lestes sponsa*; Banks and Thompson 1985; Fincke 1988; Stoks 2000), and sometimes smaller males have higher mating success (*E. boreale*, *Ischnura elegans*, Coenagrionidae; Anholt 1991; Carchini *et al.* 2000). In the polymorphic damselfly *Mnais costalis* (Calopterygidae) mating success increases with body size for orange-winged territorial males but is unrelated to body size in clear-winged non-territorial males (Plaistow and Tsubaki 2000).

Males spend more time at the breeding site than females, so they may suffer higher mortality there. In one case, higher mortality due to bird predation was associated with larger size (*Calopteryx splendens* wings, Calopterygidae; Svensson and Friberg 2007). We rarely have measures of mortality away from the study site where predators such as spiders are more cryptic. Large enclosures as used by DeBlock and Stoks (2005) and advocated by Cordero and Stoks (Chapter 2) may be necessary to make these measurements. It would be worthwhile comparing adults captured by orb-weaving spiders with the population at large to see whether they are exerting directional selection on mass, wing loading, or other measures of phenotype as Svensson and Friberg (2007) have done at the breeding site.

13.2.3 Males and females

Where modern mark–recapture methods that account for differences in recapture have been used to estimate survival rates (White and Burnham 1999; see Chapter 2), most studies find no difference in survival of mature adults: for example, *L. disjunctus* (Anholt 1997; Smith 2004), *L. congener* (Smith 2004), *C. puella* (Anholt *et al.* 2001), *S. pallipes* (Smith 2004), and *Orthetrum coerulescens* (Libellulidae) (Kéry and Juillerat 2004). One striking exception is *I. elegans*, where males have much higher survival rates than females (Anholt *et al.* 2001).

13.3 Mass gain and survival of adults before sexual maturity

Most research on adult odonates has been on sexually mature individuals. However, the time between emergence and sexual maturity sets the stage for reproduction. Males and females are nearly the same mass at emergence (Anholt *et al.* 1991), although males of the strongly territorial *M. coerulatus* (Pseudostigmatidae) are both heavier and larger than females at emergence (Fincke 1984).

Females emerge without eggs, and forage actively to gain the resources required for reproduction, often doubling their mass in only 1–2 weeks (Anholt *et al.* 1991). Both males and females of territorial *Calopteryx* increase flight-muscle mass and energy stores between emergence and sexual maturity (Marden *et al.* 1998). In non-territorial coenagrionids, mass gain by males is minimal (Anholt *et al.* 1991). Correlated with this mass gain is mortality. The sex that gains more mass typically has higher mortality rates, as shown for *E. boreale*, *L. disjunctus*, and *L. congener* (Anholt 1991, 1997; Smith 2004). Stoks (2001) inferred higher mortality of *L. sponsa* females due to higher foraging intensity in his cage and field study to account for changes in population sex ratio. Higher mortality rate of more actively foraging individuals is also supported when examined within a single sex. Heavy, newly emerged *E. boreale* males tend to lose mass after emergence whereas light males tend to gain mass. At the same time, heavy males have lower mortality than light males (Anholt 1991).

Where mass gain is more similar, so are mortality rates (e.g. *S. pallipes*; Smith 2004). Kéry and Juillerat (2004) report similar adult mortality rates of males and females both before and after sexual maturity for *O. coerulescens*, with no bias in sex ratio. Given that *O. coerulescens* has a territorial mating system (Kéry and Juillerat 2004), I expect that mass gain of males and females is more similar than in non-territorial coenagrionids. The genetic determination of *Mnais* male morphs (Tsubaki 2003) argues that the higher mating rates of territorial males are balanced by higher mortality rates of the territorial morph, because the system must be an evolutionarily stable strategy to persist (Maynard Smith 1974). Higher mortality rates do not appear to prevail once sexually mature (Tsubaki *et al.* 1997). Territorial males gain more mass compared with non-territorial males prior to sexual maturity (Plaistow and Tsubaki 2000) when the higher mortality is expected to occur.

It seems likely that the primary source of this mortality between emergence and sexual maturity is predation, but little direct field evidence exists. Tenerals can be under such severe energetic stress that they may starve to death (Marden *et al.* 1998), which would also contribute to their risk of predation (Anholt and Werner 1995). An additional possibility is endogenous oxidative stress (Barja 2002) associated with growth.

13.4 Mass gain and survival of larvae

What is most remarkable about the contribution of larvae to the sexual size dimorphism of adult odonates is that it is so small. The larval life history lasts for months or years, whereas the time after emergence but prior to sexual maturity is measured in days or weeks. Even though larvae increase their mass by three to five orders of magnitude from egg to emergence, in most cases the difference in mass between males and females at emergence is either non-existent (Anholt *et al.* 1991) or small. For example, Mikolajewski *et al.* (2007) found that under most experimental conditions, male *L. depressa* were 2–3% heavier than females at emergence. However, in the few days after emergence and prior to sexual maturity, stark differences become apparent. Mature adult female lestids often weigh 100% more than males (Anholt *et al.* 2001). Why so small a difference before maturity and so large a difference afterward? Skeletal size is fully determined by the larval life history, but mass gain can occur as larvae or as adults.

Larval odonates are clearly flexible in their foraging decisions, behaving in ways that are consistent with balancing evolutionary costs and benefits (Schaffner and Anholt 1999). Experimental manipulations have demonstrated further that male and female larvae balance costs and benefits in different ways (Mikolajewski *et al.* 2005).

The ratio of growth rate and mortality rate is at the centre of substantive theory developed originally by Gilliam (Werner and Gilliam 1984) and then applied to organisms with complex life histories (Werner 1986) to predict the timing of life-history switches. This theory predicts that the timing of metamorphosis should occur when the ratio of growth rate and mortality rate becomes lower in the alternate habitat. Seasonal constraints can modify these ideal predictions but the general patterns still apply (Ludwig and Rowe 1990). Usually, the life-history switch is presented as a function of attained body size, but it can also be due to changes in the quality of the habitats. Whereas elegant experiments have demonstrated that odonate larvae are sensitive to seasonal constraints consistent with theory (Johansson and Rowe 1999; see Chapter 4), no one has attempted the challenge of testing whether the timing of metamorphosis is consistent with theoretical predictions based on maximizing expected fitness over the entire life history, and whether the predictions for males and females are the same. In the absence of clear theory, experiments seem premature. One approach would be to develop state space models (Mangel and Clark 1988; Houston and McNamara 1999) that incorporate sex-specific fitness returns with mass gain, mortality, and growth increments due to behavioural choices, and constrain reproduction to occurring in realistic situations (i.e. when both sexes are present).

13.5 Sexual size dimorphism, sex ratio, and mating system

Changes in sex ratio that occur because of mortality associated with differences in foraging effort have consequences for other aspects of a species' life history. When sexually mature females are more common than males, the average male can expect more than one mating in a lifetime. Under these circumstances, defending an oviposition territory and being available to mate with newly arrived females will lead to higher fitness than contact mate-guarding. For this to be true, the expectation of future fertilizations has to exceed the expected loss to other males remating a previously mated female. This will depend on the sex ratio at the breeding site (operational sex ratio), which in turn depends on the ratio of sexually mature males and females and the time they spend at the breeding site. But clearly, when male mortality rates exceed those of females the probability of polygyny increases.

When females are rarer than males, the average male will obtain less than one mating in its lifetime. Assuming that males mate completely at random, males that are currently mating can expect less than one mating in the future. Given that there are many more unmated males than females in the population (because there are more males and those males spend more time at the breeding site), and that odonates have elaborated structures for the removal of previously stored sperm (Waage 1979), guarding a female until she oviposits will be a strategy that maximizes fitness. When male densities are very high, territoriality in almost any form becomes impossible because of intruder pressure (Schoener 1983) and we expect to see contact guarding (Cordero 1999).

Under this view, the benefit of large male size associated with a territorial mating system reinforces that mating system because males will suffer additional mortality in gaining the resources to achieve that size. Similarly, in non-territorial coenagrionids where males usually have higher survival rates than females, the operational sex ratio will always be highly skewed towards males and it will be very difficult to maintain territoriality.

Here again, large enclosures, where sex ratio and absolute abundance of mature males can be manipulated, seem to be the only reasonable way to approach these questions. The most difficult part may be in choosing the right set of species. They must be large enough that they clearly exhibit territoriality, but small enough that they are abundant and can be maintained in cages.

13.6 Discussion

The covariance of relative fitness with body size is pervasive across the Odonata. It is not always detected, and the direction and shape of that covariance is rarely consistent. However, given modest sample sizes of hundreds of individuals, selection of some type is almost always detected. In spite of this pervasive selection, the phenotype continues to maintain variation, which is often explained as being a balance between mutation and selection (Haldane 1937). Most new mutations are deleterious and move individuals away from the optimum while selection eliminates variation as it moves the population towards the optimum. A shifting in shape of the fitness landscape because of changes in the environment from season to season slows the rate of approach to the long-term optimum and reduces the rate of loss of variation from the population. Genetic correlations among characters also constrain the rate of evolution towards the optimum (Schluter 1996). Correlations that are in a different direction than the direction of maximum slope of the fitness landscape will slow the approach to the optimum phenotype.

Whereas I (along with almost everyone else) have focused on behavioural adjustments affecting growth and mortality rates, there are alternatives. McPeek (2004) and Stoks *et al.* (2005) have demonstrated differences among species that implicate digestion and allocation while the results of Mikolajewski *et al.* (2007) also suggest that these differences exist between sexes. An additional axis differentiating males and females is allocation to immune function (Joop *et al.* 2006). To make further progress on the question of sexual size dimorphism and its life-history causes and effects, we need to better integrate these diverse trade-offs.

Genetic covariance of characters that are expressed in both males and females also affect the maintenance of variation. If large fathers tend to have large daughters and small mothers tend to have small sons, then it will be very difficult for both sons and daughters to be at their fitness maxima simultaneously (Lande 1980). Estimating these covariances will require artificial breeding programmes (e.g. Van Gossum *et al.* 2003), but the required sample sizes are breathtaking (Klein 1974). A first approximation might be available by using the phenotype variance–covariance matrix as suggested by Cheverud (1988) but the correspondence between phenotypic and genotypic matrices remains controversial (McGuigan and Blows 2007).

Finally, it is worth remembering that size is a condition-dependent character. Much of the variation we see is due to the environment experienced by individuals. Even if we had dragonfly clones in the environment, they would end up different sizes by virtue of the chance events that place more food in the way of one individual or another. Selection still acts on this variation.

The size of odonates makes them nearly perfect subjects for estimating fitness landscapes. They are small enough that they are abundant, but large enough that they can be observed readily in a natural setting. They are captured, measured, and given unique marks easily. Much of the early work (including my own) that used marked animals suffers from the assumption of constant probability of recapture. Fortunately, the statisticians have been hard at work, and modern theory is being rapidly elaborated so that sophisticated measures of survival as a function of phenotype can now be made. Repeating earlier studies with the benefit of hindsight and new measurement tools including image analysis and portable microbalances, along with powerful analytical tools, will shed new light on ecology and evolution generally, and of the Odonata specifically.

Acknowledgements

I am extremely grateful to the Department of Animal Ecology, University of Sheffield and the Centre for Ecology and Conservation Biology, University of Exeter in Cornwall for being such gracious hosts during the preparation of this work. Comments on drafts of the chapter by Alex Córdoba-Aguilar, Frank Johansson, Dirk Mikolajewski, and Stuart Plaistow greatly improved a previous version. Financial support was provided by a Conviron fellowship at the University of Sheffield, and the University of Exeter. This research was also supported by a Discovery grant from NSERC Canada, and the Canada Research Chairs programme.

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CHAPTER 14

Testing hypotheses about parasite-mediated selection using odonate hosts

Mark R. Forbes and Tonia Robb

Overview

Parasites are thought to play a role(s) in the evolution of host traits. Evidence for their roles comes from studies examining parasite-mediated selection. Odonates are model insects and water mites and gregarine protozoans are model parasites for such investigations. These parasites can exert fitness costs on their dragonfly hosts, such as reduced survivorship, and affect signals and possibly also mating success of males, but more experimental work is needed. Resistance against ectoparasitic mites is governed by the parasite–host association being considered and by temperature following host emergence, but not by host gender. Other work suggests that host gender and age influence immunological responses to bacterial and artificial challenges. Recent evidence with dragonflies suggests that the likelihood of demonstrating parasite-mediated selection might depend on whether or not the parasite species being considered is a generalist parasite. Ideas also are emerging on how prey species should deal with co-occurring threats from multiple enemies such as predators and parasites. Here again, dragonflies and their parasites should provide tests of developing theory.

14.1 Parasitism and parasite-mediated selection: an introduction

Parasitism is widespread in nature. It is defined as two organisms interacting where one species, the parasite, benefits at the expense of another, the host. However, this definition does not capture the diversity of parasite–host associations. There are, for example, situations in which a parasite attacks a host species, but does not appear to exploit it effectively (Lajeunesse and Forbes 2002). The study of dragonfly-parasite associations has provided such examples (Forbes *et al.* 2002). Researchers also have tested or informed recent hypotheses on how hosts should respond to parasitism and how parasites are designed to overcome host defences, using dragonflies and their parasites. We review these studies, but first identify general considerations of parasite-mediated selection (PMS).

PMS occurs when parasites reduce the lifetime reproductive success of their hosts. Parasitism is thought to be a major driving force in the evolution of mechanical, behavioural, or physiological resistance, and also more subtle traits such as the ability to alter reproductive output once parasitized. Researchers often take a host-centred view of parasitism (e.g. how much reproductive output is depressed by parasitic infections). We continue with this tradition. However, it is also important to understand the natural history of dragonfly parasites (Box 14.1), because changes in host reproduction or behaviour might be understood best from the perspective of the parasite. Our approach in this chapter encompasses evolutionary and

Box 14.1 Relevant natural history of the common parasites attacking dragonflies

Three main groups of dragonfly parasites have been studied extensively: water mites, gregarine protozoans, and trematodes (see review by Corbet 1999).

Water mites

There are two main families of water mites that attack dragonflies (Smith 1988). One includes the sub-genus *Arrenurus*, which are found commonly on coenagrionid and lestid damselflies and libellulid dragonflies. The generalized life cycle of *Arrenurus* mites is as follows: adult females lay eggs that hatch into swimming larvae, and these larvae seek out and attach to, but are not parasitic on, larval damselflies and dragonflies that are nearing their final or penultimate instar (e.g. Leung *et al.* 1999). When the damselfly or dragonfly emerges, the larval mites abandon the cast exoskeleton and scramble on to the newly forming imago. There, they pierce the host's exoskeleton, usually from a position on the venter of the thorax or abdomen and more rarely the wing veins (Figure 14.1). Upon attachment, they secrete a mucopolyssacharide feeding tube (Figure 14.2a; Smith 1988). This feeding tube delivers food to the larval mites derived from external digestion of host tissues and haemolymph. After a period of time and as the damselfly or dragonfly nears sexual maturity, the mites complete engorging (or have engorged sufficiently). Some mites, however, encounter host resistance as melanotic encapsulation of the feeding tube as it forms (Figure 14.2b). Those mites often die. Successful mites drop off the adult host as it nears (or is over) water. The mite then develops through two quiescent nymphal stages that are punctuated by periods of being an active predator on aquatic microcrustacea (e.g. ostracods and daphnids). Limits to viability of larval Arrenurid mites have not been examined generally. However, mites that spend long times searching for hosts are less likely to engorge successfully than are larval mites with shorter host search times (Robb and Forbes 2005a).

A second family of water mites that are parasites of damselflies and dragonflies is represented by the genus *Limnochares*. Here, eggs hatch into larvae that climb upon emergent vegetation where they quest for perching dragonflies. Unlike *Arrenurus* mites that synchronize their parasitism with emergence of the host, *Limnochares americana* water mites are capable of accumulating on hosts over time and often show vastly different stages of engorgement on a single host. These mites are more likely to encounter territorial males perching over water than females foraging away from the water's edge (Lajeunesse *et al.* 2004). With few exceptions, *Arrenurus* mites tend not to show sex bias in patterns of infestation of damselflies or dragonflies (e.g. Robb and Forbes 2006b).

Gregarine protozoans

Infection by gregarines is also common for damselfly or dragonfly species worldwide. Gregarine infection can be confined to the midgut of the dragonfly adult, although infections of dragonfly larvae are common (Åbro 1974). Following Åbro (1971, 1974), hosts ingest gregarine spores adhering to legs of prey such as small Diptera. Spores are filled with *sporozoites* that develop into the trophozoite, the gregarine feeding stage. In the midgut, trophozoites attach to the epithelium, further developing into *gamonts*, which eventually mate and form cysts, which contain the infective sporozoites and are eventually voided with the host's faeces. Intensity of gregarine infections can be highly variable (e.g. 0–900 gregarines were found in samples of *Enallagma cyathigerum*; Åbro 1974). It has been suggested that gregarines damage the insect by blocking the gut and via secondary bacterial infections, thought to be visible as brown spots on the abdomen (Åbro 1971); this suggestion has not been tested formally. Notwithstanding, researchers have observed fitness costs associated with gregarine infection (Table 14.1). Cytotoxic responses during the prophenoloxidase cascade in the midgut epithelium are thought to be an immune defence against gregarines (Siva-Jothy *et al.* 2001).

continues

Box 14.1 (*continued*)

Trematodes

Haematoloechus spp. trematodes are dragonfly parasites that use snails as first intermediate hosts and frogs as definitive hosts (Snyder and Janovy 1996). Eggs pass in frog faeces, hatch into miracidia, and infect the snail. Following asexual amplification and development into cercaria, snails shed cercaria. Cercaria swim actively, searching for dragonfly larva and, depending on the parasite, encyst either in the branchial basket or through an intersegmental membrane. These trematodes complete their life cycles when the infected dragonfly is ingested by a frog. Other trematode life cycles involving dragonflies as intermediate hosts are detailed in Corbet (1999).

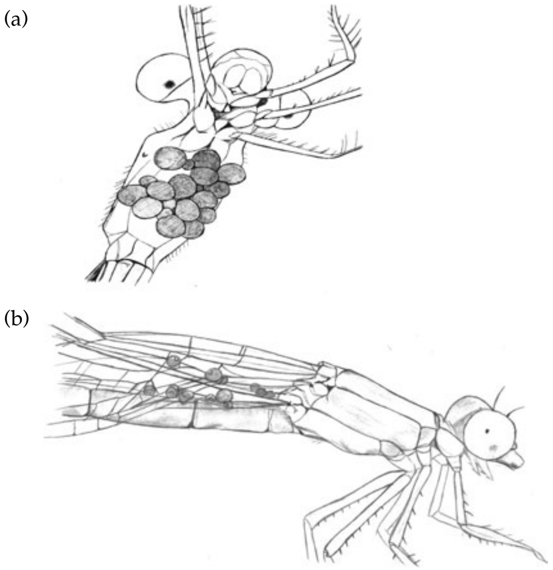

Figure 14.1 (a) Ventral view of thorax of *Lestes forcipatus* damselfly sketched with engorging *Arrenurus planus* larval mites. The mites are seen as a grape-like cluster of individuals and are coloured deep red in life. Some mites are near to fully engorged (≈1 mm in diameter) whereas others are only partially engorged and probably the recipients of immune responses shown in this species. (b) A sketch of an unidentified damselfly with larval water mites engorging on the wing veins. Photograph from which the sketch was drawn was taken in Bannerghatta, India by Saleem Hameed.

behavioural ecology, wherein the bulk of research on dragonfly–parasite associations is found. Dragonflies and also parasites of dragonflies are amenable to study, although there are gaps in our knowledge of parasite biology that need to be acknowledged and corrected.

14.2 The importance of observational and experimental approaches

Many studies of PMS are directed at demonstrating whether it exists, and is common in nature. Many more observational than experimental studies have been done. Parasites appear associated with reduced longevity and depressed reproduction of their damselfly hosts, although exceptions exist (Table 14.1). Measures of parasite **prevalence** or **intensity** often covary with other factors thought to influence host fitness: the most obvious are time of season and host condition. For example, parasitism by larval water mites (*Arrenurus* spp.) is high early in the season and declines later on (Forbes and Baker 1991). For temperate damselflies, reductions in size at emergence with advancing season have been documented (e.g. Johansson and Rowe 1999). Furthermore, mites are either lost or gained with host age, depending on the mite–dragonfly associations examined (Smith and Cook 1991).

Using experiments, researchers hope to determine whether reductions in host fitness associated with parasites are actually caused by parasites. However, observational studies also are important. Patterns of parasitism observed are thought to result from selection acting on the parasite. Timing of breeding is likely under directional selection in dragonflies (see Anholt 1991) and parasitic mites might have evolved timing of larval activity to exploit this availability of their hosts (Rolff *et al.* 2001). Observational studies inform hypotheses on the relative importance of host life history to parasites, and the importance of parasites to host fitness and host populations.

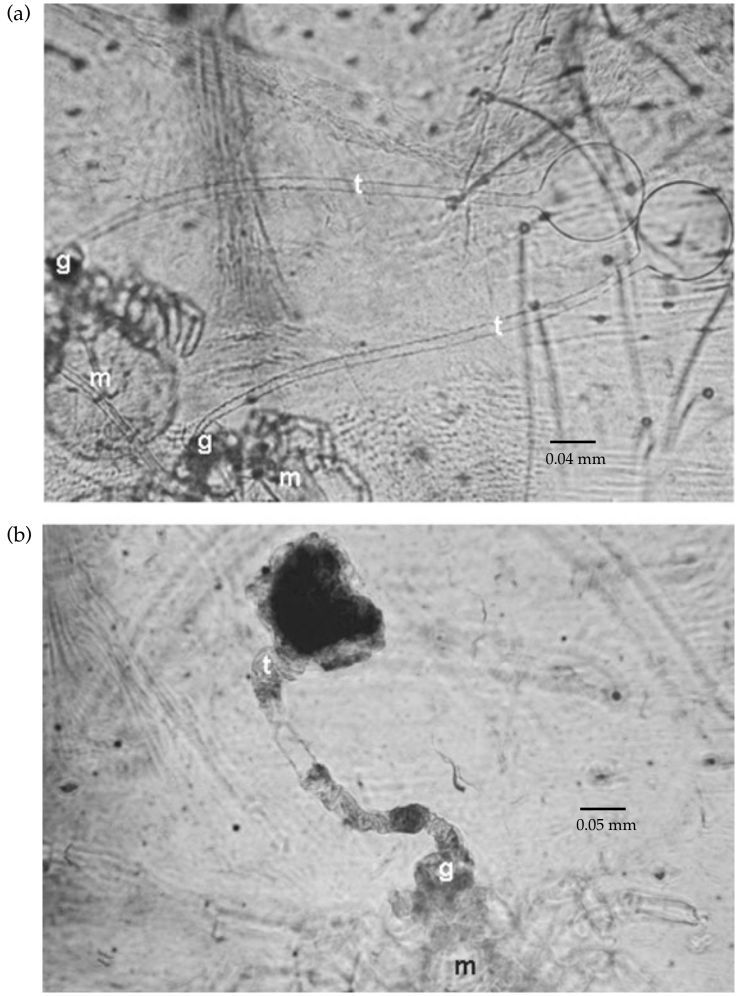

Figure 14.2 Digital photographs illustrating (a) feeding tubes of an engorging *Arrenurus planus* mite in the thoracic tissue of the host *Lestes forcipatus* and (b) the melanotic encapsulation response by *L. forcipatus* to an *A. planus* feeding tube. Visible in the preparation are the mites (m) still attached to the cuticle, and the attachment point of the mite or gnathostome (g) where the feeding tube (t) begins. Scale bars are indicated in each panel.

14.3 Proxies for host fitness: a cautionary note

Parasitism should reduce host condition and thereby depress fitness. However, reduced condition might also elevate parasitism. Nutritional stress results in elevated parasitism because less time is spent grooming by food-deprived hosts (Leung *et al.* 2001). Thus, heightened parasitism and reduced condition might co-occur and interact in nature. In a similar vein, researchers have expected inverse relations between fluctuating asymmetry (sometimes called FA) and individual fitness. In the damselfly, *Coenagrion puella*, males that were more symmetrical (presumably in better condition) averaged higher lifetime mating success than less symmetrical males (Harvey and Walsh 1993). The evidence for a general relation between fluctuating asymmetry and parasitism, however, is far from convincing (Table 14.1). One study showed that damselflies emerging with more parasitic mites had higher wing asymmetry than damselflies emerging with fewer mites (Bonn *et al.* 1996). Mites were either responsible for the greater asymmetry, or individuals with a greater propensity to become asymmetrical were more susceptible to mites. Researchers often have to examine proxies of host fitness, especially in studies involving destructive sampling to assay parasite presence or numbers.

However, such proxies have to be viewed with caution when trying to infer causal mechanisms. Notwithstanding, such studies are very important as they inform how often parasitism covaries with metrics of host condition in samples.

14.4 Parasite-mediated natural selection

PMS is seen as the driving force for certain host traits (such as immune and signal traits; see below). We first address parasitism–longevity and parasitism–fecundity relationships in damselflies and dragonflies to see how often fitness costs of parasitism are documented.

The work on parasitism and longevity of host dragonflies is reasonably conclusive. In all experimental studies, increasing levels of parasitism were associated with reduction in longevity, although the magnitude of this reduction often depended on the age class or gender of the host being considered (Table 14.1). In the observational studies, a reduction, increase, or no change in host longevity associated with parasite burden was reported. Such variable reports are expected. For example, gregarines are expected to be more numerous in well-fed hosts because they are transmitted trophically. Longevity was actually greater in *Enallagma boreale* with heavy natural infestations of *Haploryhnchus* spp. compared with conspecifics that had lower burdens (Hecker *et al.* 2002).

To date, three observational studies (no experiments have been done) suggest that parasitism is associated with reduced clutch size of females (Table 14.1). A question that remains, however, is how important clutch size is to lifetime reproductive success of female dragonflies (see Fincke 1988). Parasitized females might forgo further investment in a clutch because the actual number of eggs per clutch is less important than the number of clutches to her eventual lifetime reproductive success. One useful approach would be to examine whether experimentally parasitized females show eggs resorption and whether resorption is under control of the parasite or the host, or both. In a related study, Rolff (1999) demonstrated that female *Coenagrion puella* that were heavily parasitized by larval mites produced larger first-instar larvae than lightly parasitized or unparasitized females (after correcting for female size): this relation was not found for 10 females that had their mites removed.

14.5 Parasite-mediated sexual selection

Researchers have attempted to determine whether heavily parasitized males are less competitive than lightly parasitized or unparasitized males for access to mates. There has been no study where males were experimentally parasitized or not and examined for their relative ability to secure mating, although the effect of experimental parasitism on expression of traits known to be important in female mate choice has been examined (Siva-Jothy 2000). Gregarines and mites are not expected to interfere with the actual ability to mate. For example, there have been no documented cases of mites attaching near to the intromittent organ of males and thus interfering with sperm translocation or copulation. Rolff *et al.* (2001) showed that experimental mite parasitism did not affect ejaculate volume in male *C. puella*. There is also no evidence that mites on the abdomen of males interfere with their ability to clasp females. Females should, however, easily see such mites when in the tandem or wheel position. It would be intriguing if females mated to mite-parasitized males differed in the numbers of eggs oviposited or likelihood of re-mating from those mated to unparasitized males. Forbes (1991) found that heavily parasitized males were less likely to be found mating with females compared with males lightly parasitized by mites. Contrary to expectation, heavily and lightly parasitized males did not differ in the number or duration of flights.

All other studies on relations between male mating success and parasitism have been observational. In three of the four cases, there was some support for a reduced male mating success with (increased) parasitism (Table 14.1). When certain proxies for male reproductive success (e.g. territorial ability, wing pigmentation) were examined in relation to parasitism, there was again support for parasite-mediated sexual selection (Table 14.1).

Perhaps the best evidence that parasites might have a role in sexual selection of dragonflies comes

Table 14.1 Studies examining the associated fitness or proxies of fitness costs of infection to dragonfly hosts. The host, parasite (in some cases the parasite was only identified to family or genus level), and the findings of each study are indicated. We also indicate whether the study approach was observational (O), experimental (E), or both.

Host	Parasite	Study findings	References
Longevity			
Ischnura posita	Water mite	Based on recapture success, the degree of parasitism was associated with reduced longevity in females but not males (O).	Robinson 1983
Enallagma ebrium	*Arrenurus* sp.	The degree of parasitism in males was associated with reduced longevity (O).	Forbes and Baker 1991
Enallagma ebrium	*Arrenurus magnicaudatus*	Mite load was not associated with longevity (O).	Forbes and Leung 1995
Enallagma ebrium	*Arrenurus* sp.	The degree of parasitism was associated with reduced longevity for newly emerged but not mature individuals (O).	Leung and Forbes 1997
Ceriagrion tenellum	*Arrenurus* sp.	Based on recapture success, the degree of parasitism was not associated with reduced longevity (O).	Andres and Cordero 1998
Enallagma ebrium	*Limnochares americana*	High (but not low) numbers of mites significantly reduced longevity (E).	Léonard *et al.* 1999
Coenagrion puella	*Arrenurus cuspidator*	Mite abundance was negatively correlated with longevity but there were sex differences in survival parasitism relationships (E).	Braune and Rolff 2001
Enallagma boreale	*Hoplorhynchus* spp.	Parasite burden was positively correlated with longevity (O).	Hecker *et al.* 2002
Calopteryx haemorrhoidalis	Gregarine	A heavy parasite burden was associated with reduced female survival (O).	Córdoba-Aguilar *et al.* 2003
Sympetrum obtrusum	*Arrenurus planus*	Based on recapture success a heavy parasite burden was associated with reduced longevity (or increased dispersal) for males but not females (O).	Forbes *et al.* 2004
Mnais costalis	*Hoplorhynchus polyhamatus*	Parasite abundance was negatively correlated with longevity only under low feeding rates (E).	Tsubaki and Hooper 2004
Enallagma praevarum	Gregarine	Parasite number was negatively correlated with longevity (O).	Canales-Lazcano *et al.* 2005
Fecundity			
Enallagma ebrium	*Arrenurus* sp.	Degree of parasitism was associated with reduced fecundity (O).	Forbes and Baker 1991
Calopteryx haemorrhoidalis	Gregarine	Heavily parasitized females produced fewer eggs (O).	Córdoba-Aguilar *et al.* 2003
Coenagrion puella	*Arrenurus cuspidator*	Heavily parasitized females produced fewer eggs. Offspring size related inversely to numbers of eggs produced (O/E).	Rolff 1999
Enallagma praevarum	Gregarine	The degree of parasitism was negatively correlated with egg number (O).	Canales-Lazcano *et al.* 2005
Mating success			
Enallagma ebrium	*Arrenurus* spp. and *Limnochares americana*	A heavy parasite burden for males was associated with a reduced success in competition for females (O).	Forbes 1991
Coenagrion mercuriale	Water mite	A heavy parasite burden for males was associated with more attacks from other males and being less likely to form tandems (females were less likely to accept mite-infested males) (O).	Rehfeldt 1995
Ceriagrion tenellum	*Arrenurus* sp.	A heavy parasite burden was associated with decreased flight and mate searching efficiency; parasitism was not related to female mating success (O).	Andres and Cordero 1998
Coenagrion puella	*Arrenurus cuspidator*	There was no correlation between degree of parasitism and mating success for males (O).	Rolff *et al.* 2000
Calopteryx haemorrhoidalis	Gregarine	A heavy parasite burden was associated with reduced female mating success and length of mate-guarding (O).	Córdoba-Aguilar *et al.* 2003

Proxies			
Body size or condition			
Enallagma cyanthigerum	*Arrenurus* spp.	The formation of the mite feeding tube is associated with host-tissue destruction and cellular breakdown (O).	Åbro 1984
Calopteryx splendens xanthostoma	Gregarine	There was a negative relationship between gregarine burden and the ability to store fat in pre-reproductive males only (O/E).	Siva-Jothy and Plaistow 1999
Coenagrion puella	*Arrenurus cuspidator*	The degree of parasitism was negatively correlated to fat content in males (O).	Rolff *et al.* 2000
Libellula pulchella	*Haplorhynchus* sp.	Parasitism was associated with lower fat content (measured as a percentage of dry mass) (O).	Marden and Cobb 2004
Enallagma praevarum	Gregarine	There was no relationship between parasitism and fat content (O).	Canales-Lazcano *et al.* 2005
Fluctuating asymmetry			
Coenagrion puella	*Arrenurus* sp.	Fluctuating asymmetry of forewing length and the number of mites on both males and females was correlated (O).	Bonn *et al.* 1996
Coenagrion resolutum	*Arrenurus* sp.	Study suggests that individuals with high fluctuating asymmetry and that are heavily parasitized may suffer greater mortality (O).	Forbes *et al.* 1997
Sympetrum obtrusum	*Arrenurus planus*	No relationship between wing cell asymmetry and parasitism (O).	Forbes *et al.* 2004
Flight ability			
Coenagrion mercuriale	Water mite	A heavy parasite burden for males was associated with less frequent and shorter flights (O).	Rehfeldt 1995
Nahalennia speciosa	*Arrenurus* sp.	A heavy parasite burden was associated with shorter escape flights (O).	Reinhardt 1996
Coenagrion puella	Water mite	Parasitism may be related to male ability to disperse (O).	Conrad *et al.* 2002
Signal/territorial ability			
Calopteryx splendens xanthostoma	Gregarine	The degree of parasitism was positively correlated with male wing-pigment heterogeneity (males with darker pigment had fewer gregarines; degree of pigmentation is associated with territorial disputes and female choice) (O/E).	Siva-Jothy 2000
Calopteryx haemorrhoidalis	Gregarine	The degree of parasitism was negatively correlated with male wing pigmentation, as above (O).	Córdoba-Aguilar 2002
Libellula pulchella	*Haplorhynchus* sp.	Parasitism was associated with an inability to maintain a territory (O).	Marden and Cobb 2004

from work on how signalling and immune ability of hosts are related. These studies concern whether secondary sexual traits signal male quality and potentially the ability to resist to parasites. In *Calopteryx splendens xanthostoma*, parasitized males were less likely to accumulate fat important to winning territory disputes, wing pigmentation of males reflected the ability to withstand parasites, and finally females used wing pigmentation in mating decisions (Siva-Jothy 1999, 2000; Siva-Jothy and Plaistow 1999). Similar findings by Rantala *et al.* (2000) and Koskimaki *et al.* (2004) further support the finding that maintenance and induction of immune traits is costly to males and that limited resources are traded off between immunity and sexually selected traits. For male calopterygid damselflies, the limiting resources are probably substrates of the prophenoloxidase cascade, such as tyrosine involved in melanin deposition in the wings (Hooper *et al.* 1999) and immune responses (Siva-Jothy 2000).

Recent work, based on large samples, has shown the degree of secondary sexual traits related to metrics of immune system function for territorial males of *Hetaerina americana* (Contreras-Garduño *et al.* 2006). The authors further suggested that the links between fat content (higher in males with more pigment) and immune ability (higher in territorial males that have more pigment) have been selected indirectly through male–male competitive interactions. In this same species, territorial males with larger spots showed stronger phenoloxidase and hydrolytic enzymic activity than non-territorial, smaller-spotted males, following challenge with a nylon implant (Contreras-Garduño *et al.* 2007; Figure 14.3). Additionally, territorial males survive

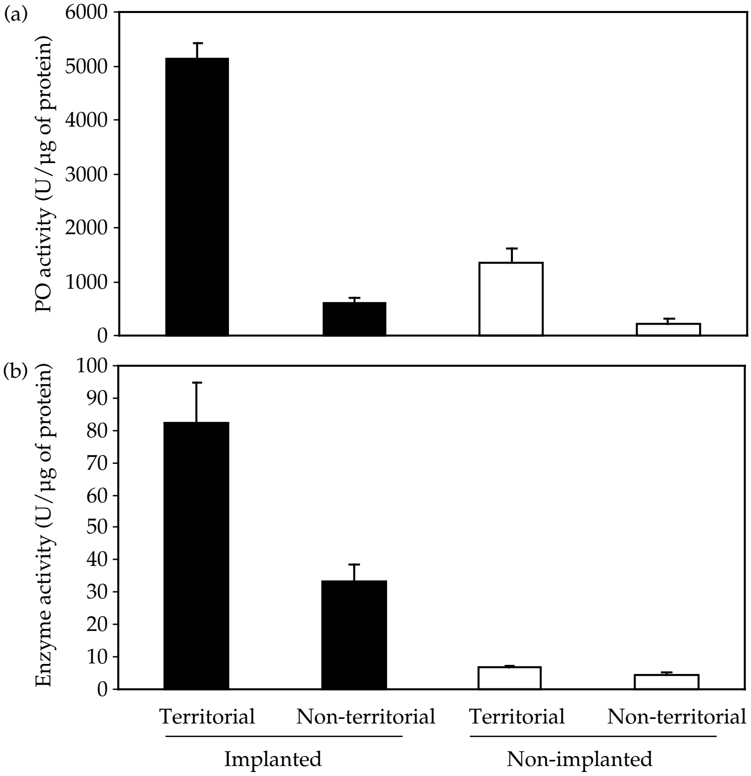

Figure 14.3 Territorial males in *Hetaerina americana* are known to have larger wing spots than non-territorial males but they also show greater activity of enzymes associated with immunity (a, phenoloxidase; b, hydrolytic enzymes) in comparison with non-territorial males, following a nylon implant. Although not shown, territorial males also survived better than non-territorial males following challenge with the implant. Redrawn from Contreras-Garduño *et al.* (2007). PO, phenoloxidase; U, enzyme units.

better following this challenge than do non-territorial males.

One issue that remains to be explored is the degree to which such signalling–immunity relationships are confined to Calopterygids; that is, why does such signalling appear to been seen only in one family of odonates, whereas the parasites and presumably their effects are widespread?

14.6 Parasitism and host behaviour

The behaviour of dragonflies is well catalogued and yet the effect of parasites on dragonfly behaviour is not well studied, except in the context of effects of parasites on measures of territoriality of males (Marden and Cobb 2004). Of particular interest is the potential to test hypotheses on adaptive manipulation of hosts by parasites using dragonflies. One of the main problems in demonstrating adaptive manipulation by the parasite is describing changes in behaviour of parasitized hosts as parasite-induced.

Although mites are not expected to manipulate their host, they also are not expected to interfere with reproductive activity, which occurs at or near the rendezvous site. Returning to water is of paramount importance for continuation of the mite's life cycle. A more productive avenue of research might involve trematode–dragonfly associations. We have reported what is known about the life cycle of *Haematoloechus* spp. trematodes. It is possible that these species actually interfere with oxgyen uptake of their dragonfly larval hosts (because cercariae encyst in the branchial basket, following from work of Synder and Janovy 1996). We might therefore expect parasitized hosts to be found in well-oxygenated areas, perhaps near to the water's surface, which might make these dragonflies more susceptible to sit-and-wait frog predators. Many other examples of putative manipulation of hosts by parasites invoke much more complex interactions with the host's nervous systems that are not easily amenable to study.

More work is also needed on anti-parasite behaviour. Of particular interest will be the extent to which larval dragonflies use specific or generalized behavioural responses to threats from different species of larval mites and also trematode cercariae and how the degree of response relates to the likelihood of successful parasitism. Dragonflies are well suited to studies determining the effectiveness of grooming and other responses as anti-parasite defences (Leung *et al.* 2001).

14.7 Parasitism and host traits

Here we address hypotheses on among- and within-species variation in resistance and immunity. A fundamental tenet of life-history theory is the concept of the allocation of time, energy, and resources to competing demands, often considered as trade-offs (Roff 1992). Researchers have suggested parasitism as a cost of high reproductive effort. Work by Smith and Cook (1991) has shown that as male *Leucorhinnia frigida* age, they become more parasitized by larval *Limnochares americana* mites. Males that are successful in holding territories are expected to be more exposed to larval mites. Here, mite parasitism is probably best viewed as a cost of engaging in territorial behaviour.

Measuring costs of parasites (and selection imposed by parasites) is difficult because of the simultaneous costs of immune responses and because the confounding effects of host condition plague such measures. Investment in immune traits should relate to the probability of becoming parasitized and the costs of parasitism. Recent work on orthopteran and coleopteran insects suggests that the probability of being parasitized by directly transmitted parasites should increase with increasing population density (Wilson *et al.* 2002). Here, we see that investment in immunity relates to population density and is associated with darker cuticular melanism. It is possible to use prevalence as a gross surrogate of likelihood of parasitism (e.g. Forbes *et al.* 2002). The problem here, of course, is that prevalence already incorporates investment in parasite avoidance. Work by Yourth *et al.* (2001) showed that prevalence was not related to resistance to *Arrenurus planus* mites (Yourth *et al.* 2002). In brief, an early-emerging species showed no resistance. Furthermore, within one species with a relatively long emergence period, early-emerging individuals were less resistant that those that emerged later. Using experimental infections, Robb and Forbes (2005b) showed that temperature-related changes in immune investment could explain seasonal changes in resistance.

Researchers are now interested in testing several related hypotheses explaining resistance variation within host species. In brief, defence against parasitism is advantageous and, therefore, there should be selection for increased investment in defence albeit at a cost to expression of other traits. In partial support of this idea, the encapsulation response of males and females of the damselfly *Matrona basilaris japonica* has been found to be reduced with reproductive effort (i.e. oviposition and copulation) (Siva-Jothy *et al.* 1998). Tests of this life-history hypothesis also take the form of inducing an immune trait and then measuring some fitness trait such as survival (e.g. Moret and Schmid-Hempel 2000). Trade-offs between immunity and other fitness traits are not always evident, especially when phenotypic trade-offs are measured. There are examples where trade-offs occur only under particular conditions (Moret and Schmid-Hempel 2000) or at a particular life stage of the host (Robb and Forbes 2006a). In the latter example, the effect of induced immunity on longevity of *Enallagma boreale* was related to host age and the type of immune trait induced.

The divergence of male and female reproductive strategies is thought to have resulted in evolved sex differences in immune function (Rolff 2002). Researchers have found some support for female dragonflies having heightened immune traits (Rolff 2001; Córdoba-Aguilar *et al.* 2006; Robb and Forbes 2006a). However, there are few examples (even in the general insect literature) where a consistent sex difference in resistance against parasites is evident (McKean and Nunney 2001). One reason that females were thought to require higher immunity was because longevity was seen as more important to their fitness than longevity was to a male's fitness. This assumption can be evaluated with studies on lifetime reproductive success of dragonflies (see Chapter 12 in this volume) and has been challenged generally (Stoehr and Kokko 2006). Another argument is that, even if males invest little in immunity, they should still advertise their genetically based resistance to parasites to prospective mates. Such signalling of resistance appears to exist, as mentioned above.

Thus there are reasons to question whether female biases in immunity should be observed often in odonates. Nonetheless, it would still be instructive to assess whether variation in egg production (and, presumably, 'egg tanning') relates to variation in resistance observed for females. Additionally, studies on immunity in species showing female-limited polymorphism, such as the study by Joop *et al.* (2006), will be instructive, especially for those species where one female morph appears patterned and coloured almost exactly like the conspecific male (see Chapter 17).

14.8 Diffuse co-evolution and effective parasitism

Co-evolution is said to occur when there is reciprocal evolutionary change by interacting species, such that a change in traits of one species can best be explained by the selection imposed by another. For example, the host species might evolve an ability to recognize and respond to a parasite, which then is countered by the parasite evolving an ability to evade the host's recognition or immune response. Such interactions might become diffused and less likely to invoke change when a single host species interacts with many parasite species, or vice versa. Therefore, when exploring patterns of parasite success or host resistance, it is also important to consider multiple host species and multiple enemies. For example, Forbes *et al.* (1999) were interested in whether mites engorged better on some species of hosts than on others. They compared two species of dragonfly, the cherry-faced and white-faced meadowhawks (*Sympetrum internum* and *Sympetrum obtrusum* respectively). Both species are similarly attacked by mites and have similar intensities of mite infestations. However, 100% of female cherry-faced meadowhawks had one or more dead mites. Similarly, 87% of male cherry-faced meadowhawks had just dead mites. Yet most white-faced males and females had fully-engorged mites. Upon closer examination, the authors found that neither species showed resistance to the mite that was typical of other dragonfly species (see above). In the white-faced meadowhawk, feeding tubes were fully formed and sphere-shaped. In the cherry-faced meadowhawk, feeding tubes did not exist or look collapsed, but there were no visible signs of resistance such as melanotic encapsulation

(Figure 14.2). Interestingly, the susceptible species accounted for nearly 90% of all dragonflies captured. Perhaps by tracking the white-faced meadowhawk in evolutionary time, the mite pays a cost of being incapable of exploiting another species effectively. Much more work needs to be done on taking a parasite-centred view in asking whether parasites that are well adapted to certain host species also do poorly on others. Lajeunesse *et al.* (2004) also showed recently that an abundant species (*Leucorhinnia frigida*) was susceptible to a generalist parasite, whereas a rare host (*Nannothemis bella*) was relatively resistant.

Another view of diffuse co-evolution considers multiple enemies. Damselfly larvae groom when faced with mites, but this grooming makes them more susceptible to attack from, and being killed by, sunfish predators (Baker and Smith 1997). When damselflies are faced with both fish and mites, they continue to groom despite the threat of predation. Baker and Smith (1997) collected their damselfly larvae from a fishless site and thus might have included subjects 'primed' to respond to mites in their experiments. Another possibility is that host larvae cannot easily shut down their grooming behaviour when they first initiate it (i.e. it follows fixed action patterns). This might explain Baker and Smith's (1997) results in so far as mites were presented to larval damselflies before they were exposed to fish predators. To address this problem, Rutherford *et al.* (2007) examined whether damselflies show behavioural personalities and experimentally altered the order of exposure to threats from mites and fish. Their larval damselflies were collected from a site that had both fish predators and mites. They demonstrated that personalities existed, but these personalities could not easily explain Baker and Smith's (1997) results. In brief, they found the same result as Baker and Smith (1997) and that the actual degree of response did not differ between treatments where mites were used as a threat first and instances where fish were used as the threat first.

14.9 Conclusions

PMS appears to be occurring in many damselfly and dragonfly species. However, the effect of parasites on population genetics of their hosts tends not to be investigated. Notwithstanding, it is possible to assess whether parasites might account for within- and among-species variation in diverse life-history and immune traits and signalling ability, given their observable fitness effects in contemporary populations. So far, studies of parasite–dragonfly associations have been used to test ideas about adaptive host responses to parasitism, evolution of epigamic characters and signalling ability, and more generally, likelihood of being adapted to certain species. Arguably, some of the strongest advances in the latter two areas have been made with studies on odonate hosts and additional critical studies are still possible because of the wealth of information on dragonfly territorial and mating activities and how these might be influenced by parasites. There also appear to be good reasons to expect trematodes to alter behaviour of their odonate hosts in ways that make them more susceptible to frog predation. Other recent hypotheses on how hosts should respond to multiple enemies can be tested using dragonfly larvae and their enemies – at the very least we will learn how effective and general putative anti-parasite behaviours are in larval odonates.

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CHAPTER 15

Cryptic female choice and sexual conflict

Alex Córdoba-Aguilar and Adolfo Cordero-Rivera

Overview

Current knowledge of post-copulatory sexual selection in odonates has provided dubious results as to whether females exert choice of males or male competition overrides female reproductive decisions. We suggest some lines of research for future studies aimed at supporting or rejecting cryptic female choice and sexual conflict perspectives in odonates. These include (1) the copula invitation that males carry out during tandem but previous to genital engagement, (2) copulation duration, (3) male post-copulatory displays preceding and during oviposition, (4) genitalic diversity across populations in the same species, (5) genitalic complexity at the multi-species level, and (6) the balance in female benefits of mating with 'attractive' males and the costs to evade superfluous matings. We provide predictions and, where possible, methodological ideas to disentangle both cryptic female choice and sexual conflict possibilities for each of these lines of research.

15.1 Introduction

One area where odonates have been more studied intensively is sexual selection (Cordero Rivera 2002) and perhaps the most striking and ground-breaking discoveries of sexual phenomena in the Animal Kingdom are related to the copulatory interactions between the sexes in this group (e.g. Waage 1979). In this chapter we focus on this aspect. Although a more comprehensive review was written recently (Córdoba-Aguilar *et al*. 2003), including many ideas derived from the theories of sperm competition, we here concentrate more on lines of research where ideas of cryptic female choice (Box 15.1) and sexual conflict (Box 15.2) can be explored, while sperm-competition theories (Box 15.1) are discussed when they are relevant.

15.2 Sexual selection and its action on odonates

Sexual selection supposes a competition among individuals to leave more offspring (Darwin 1888) and takes place at all instances during the interaction between the sexes, which broadly includes pre-, syn-, and post-mating interactions. Several chapters in this book devote their attention to the pre-mating instance (e.g. Chapters 11, 12, and 16 in this volume), including the recent interesting case of female polymorphism due to sexual conflict (see Chapter 17). Here we mostly concentrate on the interactions that occur during and after copulation.

Sexual selection has been traditionally assumed to take place via two processes. One process is male–male competition by which males compete among each other to have access to females. In the context of syn- and post-copulatory sexual selection, this competition must be interpreted as access to eggs, because sperm has already been transferred to females. This is particularly the case for insects, in which mating is not synonymous with fertilization because females have the ability to store sperm for relatively long periods (Parker 1970). The second process is female choice. Again, in the

Box 15.1 Sperm competition and cryptic female choice

Two forces of sexual selection act during and after copulation. On one hand, when the spermatozoa of two or more males are found in the female genitalia, they may compete to fertilize the female's ova. This is called sperm competition, a powerful selective force that has shaped male morphology, physiology, and behaviour, to reduce the risk and/or win in this competition (Parker 1970). On the other hand, females may also play a role. According to Eberhard (1996), who extended the view of Thornhill (1984), females may be able to choose males during and after copulation by using a variety of mechanisms. Since many mechanisms may remain obscure to the observer's eye (as several occur inside the female), the choice was called cryptic. According to this, males should 'entice' females to use their sperm via courtship. This may take different forms which explain the extended and otherwise enigmatic behavioural patterns that the male performs during and after copulation.

Box 15.2 Sexual conflict

At the heart of the sexual interaction, males and females do not share similar reproductive interests, as male reproductive success is predicted to increase more rapidly than female reproductive success with the number of mates. Although this fundamental principle applies to all species that undergo sexual reproduction and was advanced by Parker (1979) as a conflict between the evolutionary interests of the two sexes, it has gained importance in recent years (Arnqvist and Rowe 2005). The consequence of this is that females may be 'persuaded' continuously to mate to levels that are not optimal for them in terms of fitness, or male reproductive opportunities may be limited due, to, for example, female choice. The definition of sexual conflict, however, not only includes processes occurring prior to mating, but in general involves any trait the optimal value of which differs between the sexes (Tregenza *et al.* 2006).

context of syn- and post-copulatory sexual selection this must be interpreted as female mechanisms (morphologically, physiologically, or behaviourally based) favouring some sperm over others, a process also known as cryptic female choice (Thornhill 1984; Eberhard 1996). This change in interpretation is meaningful for insects as females of most species can mate with more than one male before fertilization and, also, because females have the ability to delay fertilization. However, about a decade ago this traditional view of sexual selection underwent a major re-interpretation: the evolution of characters traditionally assumed to be affected by male–male competition and female choice is alternatively explained by sexual conflict and this includes any sexual interaction (Arnqvist and Rowe 2005; Tregenza *et al*. 2006). Although currently sexual selection theory is undergoing major changes due to this interpretation, whether the traditional view or the new philosophical emphasis should be applied is still a matter of controversy (e.g. Kokko *et al*. 2006). In this chapter, we apply both philosophical explanations. Our aim, as Fincke (1997) asserted and discussed nearly a decade ago, is to reach a 'conflict resolution' to the difference in reproductive interests between the sexes in this order.

15.3 Why odonates?

One first reason to use odonates to test sexual selection ideas is that these animals are tremendously easy to observe as they occur at places where animals are very conspicuous. Mating pairs are visually tractable in these conditions, particularly calopterygids, coenagrionids, and libellulids. Second, matings occur in large numbers due either to high rates of female mating or the high population densities at which several of these species occur. Third, despite the negative effect of handling for marking on recapture probability (see Chapter 2), marked animals show some site fidelity. Fourth, the relatively large size of both sexes allows fairly easy sperm quantification and dissection of genitalia and, in many cases, direct inspection of the copulatory process (Miller and Miller 1981).

15.4 Copulatory interactions: outlining some instances of cryptic female choice and sexual conflict

15.4.1 Pre- and syn-copulatory interactions

Prior to copulation, a male has to grab the female. For this males use their paired appendages located at the end of the abdomen to grasp the female mesostigmal plates located in the female neck (zygopterans) or head (anisopterans). It seems that a sort of recognition occurs in non-territorial species (Robertson and Paterson 1982) as, unlike territorial species with male courtship displays, females do not necessarily accept the copula 'invitation' once they are grabbed. This invitation takes place when the male bends his abdomen, trying to draw the female to him, producing a series of pre-copulatory genital touches, only if the female is sexually responsive (Robertson and Tennessen 1984). Actually the female can refuse to mate and spend hours being held by the male (Cordero *et al.* 1992). Some field observations suggest this is a potential instance where sexual selection is occurring.

In one species whose males are non-territorial, *Enallagma praevarum*, males that are ejected once are more likely to be rejected again during the copula invitation with different females (79 out of 85 cases), whereas those males whose invitation was accepted by a first female were more likely to be accepted by a second, different female (48 out of 56 cases; Córdoba-Aguilar, unpub. data). One sexual-selection interpretation for this is that a sort of female choice is taking place. This discrimination may be based on the male's ability of persuasion related to the male's ability for sensory stimulation (e.g. Eberhard 1996). If this is the case, one may expect that males vary either in the morphology of their abdominal appendages or in the behaviour they produce when inviting the female to mate. It may also be that males can persuading unwilling females to mate. This sexual-conflict perspective supposes that females which are not ready to mate will accept an invitation anyway because, possibly, the cost of resistance is higher than the cost of acceptance, a case of convenience polyandry (*sensu* Thornhill and Alcock 1983; for an example in odonates see Cordero Rivera and Andrés 2002). These two alternative perspectives are one promising instance for future research. In any case, if the female accepts a mate, she carries out the 'genital touch', when the genitalia of both sexes simply touch each other (Robertson and Tennessen 1984). This is followed by the transfer of sperm from the male primary genitalia (at the end of the abdomen), where sperm is produced, to the secondary genitalia (in the first segments) where the intromittent genitalia are. This sort of female response to the male invitation does not occur in species in which there is an overt pre-copulatory courtship, presumably because females in these latter species have already accepted an invitation to mate and, actually, as soon as the female is grabbed, the male transfers his sperm (Corbet 1999).

Copulation (the intromission of male genitalia to the vagina) takes place in two stages (Miller and Miller 1981; Miller 1987a). During stage I the male carries out a series of abdominal movements which are linked to genital movements aimed to remove sperm from previous matings, although a stimulatory function is also likely (see below). This stage appears highly variable and it may even last for hours (Uhía and Cordero Rivera 2005). The movements perceived by the observer include a series of rhythmic abdominal flexions of both sexes. The stage II is when the male transfers his sperm and is fairly constant in duration and movements within and among species (Uhía and Cordero Rivera 2005).

Copulation duration has been reported in many observational and experimental studies, in both the field and laboratory (Table 15.1). Soon it became apparent that odonates could be classified in three groups according to this variable (Corbet 1962).

Table 15.1 Variation in copulation duration (min) in selected odonate species.

Family	Species	Variation in copulation duration (min)					Factors influencing copulation duration	References
		Mating system	Min	Max	Mean±SE	*N*		
Calopterygidae	*Calopteryx haemorrhoidalis*	T	0.9	2.8	Courtship, 1.9±0.1	73	Time of day (–); temperature (–)	Cordero 1999; Cordero-Rivera and Andrés 2002
					Forced, 1.7±0.1	40	Density and type of copulation interact	
	Calopteryx maculata	T	0.5	5	1.7	90		Waage 1973
	Mnais p. pruinosa	T			T, 1.3±0.26	199	Type of male	Siva-Jothy and Tsubaki 1989
					S, 2.5±1.02	65		
	Mnais p. costalis	T			T, 1.0±0.06	33	Type of male	Watanabe and Taguchi 1990
					S, 1.4±0.08	97		
Chlorocyphidae	*Libellago aurantiaca*	T	1.6	2.2	1.9	13		Orr 1996
	Libellago hyalina	T	1.9	2.5	2.2	22		
	Libellago semiopaca	T	1.1	2.1	1.4	52		
	Rhinocypha aurofulgens	T	0.9	2.1	1.4	12		
Megapodagrionidae	*Paraphlebia quinta*	T			T, 15.5±4.7	23	Type of male	González-Soriano and Córdoba-Aguilar 2003
					S, 40.0±12.5	13		
Coenagrionidae	*Argia vivida*	T	4	49	31.3±4.8	11	Time of day (–)	Conrad and Pritchard 1990
	Ceriagrion tenellum	N	30	180	V, 56.4±2.6	17	Time of day (–); male disturbance (+)	Andrés and Cordero-Rivera 2000
					M, 126.4±9.2	39	Female mating status (+)	
	Coenagrion mercuriale	N	14.2	45	23.1±1	22	Time of day (–); temperature (–)	Purse and Thompson 2003
	Coenagrion scitulum	N	13.6	141.2	51.6±7.7	17	Time of day (–); male disturbance (+)	Cordero *et al.* 1995
	Enallagma cyathigerum	N	25.3	75.1	V, 33.2±2.0	8	Female mating status	Uhía and Cordero-Rivera 2005
					M, 49.5±6.0	8		
	Ischnura elegans	N	25	456	Laboratory, 86.8±4.7	70	Female mating status (+)	Miller 1987a; Cooper *et al.* 1996
					Field, 324±25.0	13		
	Ischnura gemina	N			43.6±2.0	190		Hafernik and Garrison 1986
	Ischnura graellsii	N	38	329	High density, 189.2±8.4	95	Time of day (–); male disturbance (+)	Cordero 1989; Cordero 1990

					Low density 133.7±13.6	33	Female mating status (+)	
	Ischnura pumilio	N		306	79.7±8.2	51	Time of day (–)	Cordero-Rivera and Andrés 1999
	Ischnura ramburi	N	90	400	202±114	11	Time of day (–)	Robertson 1985
	Ischnura senegalensis	N	93	433	395.3±11.6	12	Time of day (–); female mating status has no influence, but sample size is very low	Sawada 1995; Sawada 1999
	Ischnura verticalis	N			43.5±2.0	14		Fincke 1987
	Mortonagrion selenion	N	69.3	190	152.1±8.3	18	Time of day (–)	Naraoka 2005
	Nehalennia speciosa	N	25.6	267	136.0±41.3	6	Time of day (–)	Naraoka 1996
	Pseudagrion pilidorsum	T	4.1	50.3	17.4±1.8	29		Matsubara and Hironaka 2005
Lestidae	*Lestes barbarus*	N	4.7	19.5	V, 8.8±0.9	12	Female mating status (+)	Uhía and Cordero-Rivera 2005
					M, 12.4±1.6	12		
	Lestes virens	N	3.8	23.7	V, 12.2±2.2	13	Female mating status (+)	Uhía and Cordero-Rivera 2005
					M, 13.6±1.8	13		
	Lestes viridis	T	3.1	66.2	V, 9.1±1.3	16	Female mating status (+)	Uhía and Cordero-Rivera 2005
					M, 19.6±2.0	16		
	Sympecma paedisca	N	7.9	24.6	15.8±5.6	13		Naraoka 1997
Platycnemididae	*Platycnemis acutipennis*	N	9.9	96.8	V, 27.9±2.2	17	Female mating status (+)	Uhía and Cordero-Rivera 2005
					M, 66.0±4.9	17		
	Platycnemis latipes	N	20.5	163.7	V, 30.9±1.8	19	Time of day (–); female mating status (+)	Uhía and Cordero-Rivera 2005
					M, 71.4±6.2	19		
Pseudostigmatidae	*Megaloprepus coerulatus*	T	52	108	79.8±8.9	6		Fincke 1984
Protoneuridae	*Nososticta kalumburu*	T	11.5	21	15.4±0.9	10		Thompson 1990
Libellulidae	*Celithemis elisa*	T			4.6±0.2	14		Waage 1986
	Crocothemis erythraea	T			0.12±0.06	44		Siva-Jothy 1988
	Erythemis simplicicollis	T			0.3±0.01	207		Waage 1986
	Notiothemis robertsi	T	0.37	8.7	2.9±0.4	18		Clausnitzer 1997
	Orthetrum cancellatum	T			T, 0.35±0.23	30	Type and age of male (–)	Siva-Jothy 1987
					S, 14.9±2.4	21		

Table 15.1 (*Continued*)

Family	Species	Variation in copulation duration (min)					Factors influencing copulation duration	References
		Mating system	Min	Max	Mean±SE	*N*		
	Orthetrum chrysostigma	T	1	64	T, 3.2±5.5 S, 28.3±23.3	21	Type of male	Miller 1983
	Pachydiplax longipennis	T		2	1980, 0.4±0.01	312		Sherman 1983
					1981, 0.7±0.05	88		
	Perithemis tenera	T	0.25	0.33	0.29	623	Temperature (–); male disturbance (+)	Jacobs 1955
	Plathemis lydia	T	0.05	0.25	0.05	200	Male disturbance (+)	Jacobs 1955
	Sympetrum danae	N	6	62.9	23.2±12.7	187	Time of day (–); temperature (–); copulation number for male (–)	Michiels 1992
	Sympetrum frequens	N			14.7±6.7	18	Temperature (–)	Ishizawa 1998
	Sympetrum parvulum	N	0.8	14.5	T, 3.4±2.5	85	Type of male	Naraoka 2001
			2.1	32.5	S, 7.7±5.8	46		
	Sympetrum vicinum	N	3.3	12.3	5.8	19		McMillan 1996

M, mated females; N, non-territorial; S, satellite males; T, territorial; V, virgin females.

Some taxa, notably Libellulidae, copulate on the wing, and many are able to perform this process in less than 10 s. A second group has short copulations, ranging from 1 to 5 min, and this characterizes the Calopterygidae and the Chlorocyphidae (Table 15.1). Finally, there is a third group that copulates for very long periods, the record being *Ischnura elegans* in France, with 7 h 36 min (Miller 1987a).

Given the evident negative effects that such long matings could have for both male and female fitness, for example increasing predation risk (Daly 1978), there should be strong selective pressures to favour its evolution and maintenance. One of the first manipulative experiments performed to study the adaptive value of long copulations in odonates maintained males of *Ischnura graellsii* at low and high density in insectaries (Cordero 1990). Copulation duration was strongly affected by time of day, so that copulations starting early lasted for longer. It was also affected by population density, with longer copulations at high density, and also by female mating status, with virgin females being involved in shorter copulations. This phenomenon was therefore interpreted as a mechanism of 'in-copula' guarding, selected for by sperm competition: males increased their paternity by temporarily sequestering females until the moment of oviposition.

The existence of long copulations and a huge variation among and within species in copulation duration (Table 15.1) makes this order an ideal model system to test current ideas about post-copulatory sexual selection (Uhía and Cordero Rivera 2005). The theories of sperm competition and cryptic female choice, and consequently the sexual conflict that is behind all sexual interactions, can be tested by comparing their predictions with manipulative experiments. If prolonged copulations are the result of sperm competition, we can predict that males should prolong copulation when the risk of sperm competition increases. Also, copulation should last longer if this maximizes sperm displacement. For instance, if sperm removal needs a long time (e.g. Siva-Jothy 1987), then males should prolong copulation with mated females compared with virgins. Nevertheless, given that males cannot engage in copulation and simultaneously perform other activities like searching for more females or defend their territory, there should be an optimal copulation duration taking these trade-offs into account. On the other hand, if prolonged copulation evolved via cryptic female choice (Eberhard 1996), specifically as a means of copulatory courtship (Eberhard 1994), we can predict that copulation should be longer with females that have more opportunities to be selective (e.g. comparing virgin with mated females, copulation should be longer with mated females). Finally, the existence of a conflict between the sexes, in this case for how long copulation lasts, predicts that copulation duration should be explained by the fitness benefits achieved by the sex that controls copulatory activities. If males control copulation, then the male perspective should suffice to explain variation in its duration. If females control when copulation ends, then the female perspective would better predict copulation duration. Further, if conflicts over copulation duration are important selective agents (Arnqvist and Rowe 2005), then we can expect re-mating frequency per clutch to be higher for females of species with short copulations, assuming that costs of re-mating are low in these species (see for instance Cordero Rivera and Andrés 2002), while in species with very long copulations (notably *Ischnura*), females should rarely re-mate (see also Fincke 1997).

Andrés and Cordero Rivera (2000) tested male and female views to explain the variation in copulation duration (30–180 min) in the damselfly *Ceriagrion tenellum* under controlled laboratory conditions. Their results indicated several important points: (1) males control copulation duration (see also Miller 1987a), (2) males are able to detect and quantify the amount of sperm stored by the female from previous matings (i.e. males 'know' whether a female is virgin or not), (3) females have two sperm-storage organs, but only one is accessible to male genitalia, and sperm removal from this organ takes just 10 min (Figure 15.1), and (4) by experimental lengthening of some copulations, a positive relationship between copulation duration and male paternity success was found. Although in Andrés and Cordero Rivera (2000) no specific predictions from the sexual-conflict hypothesis have been tested, results were in complete agreement with the hypothesis of cryptic female choice, and only agreed partially with

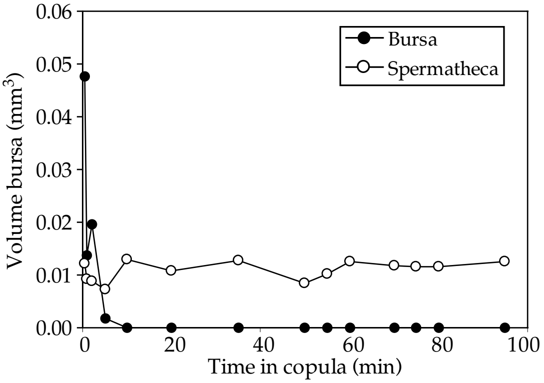

Figure 15.1 The relationship between copulation duration and the volume of sperm stored in the sperm-storage organs of female *Ceriagrion tenellum*, whose second copulation was interrupted at different times. Note that males remove all the sperm from the bursa in 5–10 min, but no change in sperm volume in the spermatheca was detected. Males of this species maintain copulation for a mean of 126 min with mated females. Source: Andrés and Cordero-Rivera (2000).

the sperm-competition predictions, because sperm removal was accomplished in a few minutes, but copulation could last for hours.

This example highlights the difficulty of separating male and female contributions to the variation in copulation duration, and also stresses the fact that both perspectives are to be taken into account. As is clear from Table 15.1, time of day has a strong negative effect on copulation duration in the majority of species that perform medium-to-long copulations. This is associated with time constraints (Andrés and Cordero Rivera 2000), and can be interpreted from a male perspective if copulations serve to guard the female until the time of day when oviposition takes place. The positive effect of male disturbance (correlated with population density) on copulation duration is another example of a sperm-competition effect, expected if males act as a sort of nuptial plug. Female mating status (mated or virgin) also has a widespread effect, detected for species with long copulations. Both sperm-competition and cryptic-female-choice hypotheses predict this effect, but based on different assumptions (Andrés and Cordero Rivera 2000). If sperm removal is associated to copulation duration, then males should prolong copulation with mated females compared with virgins. This is clearly not the case for many zygopterans (Uhía and Cordero Rivera 2005). The only alternative explanation is that males are 'obliged' to perform long copulations with mated females, precisely because these females are in a position to perform 'sperm selection'. Mated females are therefore being courted by prolonging copulation, and this should increase paternity success of males able to perform these long copulations, as Andrés and Cordero Rivera (2000) found.

15.4.2 Genitalic evolution

This has been relatively well studied in Odonata, particularly in groups such as the calopterygids and ischnurans, and, to a minor extent, the libelullids and aeshnids. Waage's discovery that *Calopteryx maculata* males, prior to sperm transfer to the female, remove the female's stored sperm by using specialized penis structures, is a central issue in ideas of sperm competition (Waage 1979). This was followed by fine descriptions of similar processes in other odonates (Miller and Miller 1981; Miller 1987b). Since then our knowledge, based on morphological and functional evidence, has revealed a complex and dynamic co-evolution between the sexes in which the female ability to store sperm from previous mates is the cornerstone for such processes (Córdoba-Aguilar *et al*. 2003). Males have responded to such pressure by evolving adaptations aimed to have access to a rival's stored sperm from previous matings.

In general, the male intromittent genitalia in Zygoptera have an aedeagus which ends distally with what is known as the penis head (Figure 15.2). In the Anisoptera, both parts are more complex, being composed of many other small segments and structures (Figure 15.2). On the other hand, females of most odonates have two sperm-storage organs: the bursa copulatrix and the spermatheca (Figure 15.2). Genital evolution has been studied in more detail in calopterygids (reviewed in Córdoba-Aguilar and Cordero Rivera 2005). Males have developed two types of adaptation to have access to the female's stored sperm. One is via sperm removal during which males use specialized spines present on the penis head to trap the sperm masses and bring them to the outside (e.g. Waage

Figure 15.2 Distal male genitalia in Odonata: (a) *Ischnura graellsii*, a polygamous zygopteran species, (b) *Ischnura hastata*, a monandrous species, and (c) *Macromia splendens*, an anisopteran. (d) Female genitalia in the zygopteran *Calopteryx splendens*, showing the paired spermathecae and the bursa, full of sperm.

1979). This mechanism allows removing bursal sperm and, in some species, spermathecal sperm (Figure 15.1). The second mechanism is via sensory stimulation of the female fertilization-related structures. During copulation and using aedeagal movements, males stimulate the vagina where a number of sensilla are embedded. These structures have presumably evolved in a context not related to sexual selection, as they are used during fertilization and egg laying (Córdoba-Aguilar 2002). The sensory stimulation mechanism takes advantage of this principle to induce the female to eject sperm (Córdoba-Aguilar 1999, 2000).

It has been uncovered that these mechanisms and the morphology behind them show tremendous variation among species and among populations of the same species (Cordero Rivera *et al*. 2004). This evidence has been used to build evolutionary scenarios consistent with the sexual co-evolution hypothesis. For example, the number of sensillae among calopterygids vary with *Calopteryx haemorrhoidalis asturica* females, the species whose males use the sensory stimulation mechanism having the fewest number. The hypothesis to explain this reduction was that females possibly, once the ability for sensory stimulation evolved, experienced a reduction in sensillum number to make sperm ejection more difficult. This was tested experimentally by producing aedeagal-based vaginal stimulation in females of two species: *C. h. asturica*, the species where sensory stimulation is present, and *Calopteryx splendens xanthostoma*, a species in which sensory stimulation apparently has not evolved. The experimental results were in the predicted direction, with females of *C. s. xanthostoma* ejecting more sperm than those of *C. h. asturica*, presumably because, having more sensilla, the former species will eject more sperm (Córdoba-Aguilar 2005). Using a within-species population comparison, genital morphology and sperm-displacement function were compared in four species of calopterygids. The results showed differences in both mechanisms of sperm displacement and the morphological traits associated to these functions. These differences were related to the different male ability exhibited in distinct populations, to have access to the stored sperm. The underlying explanation was that these populations were undergoing a process of differentiation within each population (i.e. allopatry) due to post-copulatory sexual selection acting on these traits (Cordero Rivera *et al.* 2004). Again, as with the example of sensilla reduction, the case can be understood on the basis of sexual co-evolution in which the stored sperm is at the centre of the co-evolution. Similar approaches should be taken not only to see whether these co-evolutionary patterns are taking place but also to investigate whether these differences are also present at the genetic level. It may be, for example, that if genitalic traits are condition-dependent, the differences are only phenotypic.

If allopatric evolution is somehow responsible for population differentiation, it may be hypothesized that genital evolution is also responsible for species differentiation (Eberhard 1985) and, hence, species diversity. One way this can be done is by comparing the extent of variation in genital morphology in particular taxa (i.e. families) and contrast it with the number of species within each taxon. A straightforward prediction is that more variable genital morphology should be found in more speciose taxa. It would be interesting to include both sexes in the comparison measurements to see whether the same applies to both and also to evaluate which sex is evolving more rapidly. In particular, the latter can shed some light as to whether a process of cryptic female choice or sexual conflict is governing genitalic evolution in odonates. Under the scenario of cryptic female choice one would expect that rates of genitalic evolutionary change should be higher in females, or similar to males, as females would be continuously screening males by evolving new genital ‘puzzles’ for males to solve. Sexual conflict, on the other hand, should be led by males as, according to theoretical expectations (Arnqvist and Rowe 2005), the selective pressure on males is higher than on females, making males ahead in the co-evolutionary interaction.

As we have asserted repeatedly in different papers that the underlying question here is what motivates this co-evolution (e.g. Córdoba-Aguilar *et al.* 2003). We understand that the centre of the conflict is the stored sperm and that it is advantageous for the male to displace this sperm. This force of sperm competition is easy to understand and predict. Actually all genital adaptations seem aimed to directly displace sperm, which makes one think that odonates are somehow predisposed to sperm displacement. This is because, unlike females of other insect orders, odonate females have sperm-storage organs that seem to be of relatively easy access to the male genitalia. Whether this is favoured by females themselves (to promote sperm competition), males, or both is unknown. Interestingly, from the two monandrous species that have been studied (Robinson and Allgeyer 1996), males still have genitalia similar to those of species whose males empty sperm-storage organs (Figure 15.2), which suggests that the ability to displace sperm is favoured in males, or that these species evolved from polyandrous species. No doubt sperm-competition mechanisms via sexual conflict are a prevailing force in odonate genitalic evolution, but is not clear to what extent this has been shaped by females too.

Eberhard (1996) put forward the idea that after mating, females may still be exercising choice of mates. This remained a controversial issue in Odonata and, actually, it was a sort of common belief that females could not do this (see e.g. Fincke 1997). These ideas suppose that females have little option to decide whether to accept a mate, not to say actually choosing a mate. This claim is based on the assumption that males always occupy the oviposition sites and that females have to mate to be allowed use of these sites. This supposition should, however, not be considered a prerequisite to not evolving female choice as several studies in animals with similar biology and female choosiness have shown (see references in Córdoba-Aguilar 2006). Two sources of evidence in Odonata suggest that females may indeed exercise cryptic choice. One is that the sensory-stimulation ability of males may be used by females to bias paternity (for an example see Andrés and Cordero Rivera 2000). However, this can be explained on the grounds that males are exploiting a female sensory bias and, therefore, females again have little choice but to mate. This logic can be applied to any sensory channel that females use in making a choice. However, a second strand of evidence that seems more sound is the pattern of sperm ejection after copulation that was described recently (Córdoba-Aguilar 2006). A detailed study in three non-territorial odonate species has found that pairs of females that mated with the same male consistently ejected similar amounts of sperm after mating and laid a similar number of eggs (Córdoba-Aguilar 2006). This consistency is compatible with the idea that females are exerting some sort of choice which does not seem forced by males. The fact that the reduction in sperm was also considerable shows that the penalization for males is high in the long term too. What are the traits likely to be assessed by females? Two possible traits are the abdominal appendages which males use to grab females and the male precopulatory behaviour. In species in which females gain no information prior to mating, as occurs in non-territorial species, and females are grabbed without any courtship, males may simply 'invite' the female to mate once she has been grabbed and this could create the scenario for female screening of males, as we have suggested.

15.4.3 Post-copulatory interactions

After copulation, males of many species remain close to the female or even in contact with her by holding her with the abdominal appendages. Males of calopterygid species perform a series of courtship displays at each female movement, the function of which has not been elucidated. These displays take place with the male facing the female and the male opening his wings in front of her at each change of perching site, which includes landing on the water current. One possible function is that males signal water current to females, because eggs undergo high mortality in microhabitats with low current (e.g. Siva-Jothy *et al*. 1995). Nevertheless, some species lay eggs in a total absence of current, but still maintain this display, like *C. h. haemorrhoidalis* (Cordero 1999), which suggests other functions for this behaviour. The possibility of courtship still remains as the male flying displays do not only take place on the water. This possibility of courtship is not remote as females of at least one calopterygid species have the ability to use sperm of different males (Siva-Jothy and Hooper 1995, 1996). In other species in which males remain in contact a similar rationale can be applied by which males can continue to persuade the female to use their sperm. This contrasts with the traditional view put forward by Waage (1984) that the function of this behaviour is to reduce the probability of other males taking the female.

15.5 Conclusion: odonates as model insects for post-copulatory studies of sexual selection

Reinhardt (2005) indicates that the status of the Odonata as a model taxon for studying the evolution and diversity of reproductive behaviours has declined relative to crickets and *Drosophila*. He suggests that this is because data on ejaculate size, sperm number, and the duration of sperm storage are scarce in this order. We hope that this book will contribute to reversing the trend and increasing the number of model systems used to study post-copulatory sexual selection. Scientific knowledge should produce general patterns, but these patterns are unlikely to be reached if only a tiny proportion of existing life histories are studied. Odonates might contribute to increasing 'scientific diversity' and add a further level to the study of biodiversity.

Acknowledgements

We thank K. Vahed and R. Stoks for their comments. Part of ACR's research described here was financed by grants from the Spanish Ministry of Education and Science (Grants PB97-0379, BOS2001-3642 and CGL2005-00122). Raúl Iván Martínez Becerril provided logistic help to ACA.

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CHAPTER 16

Territoriality in odonates

**Jukka Suhonen, Markus J. Rantala,
and Johanna Honkavaara**

Overview

Within odonates, male mating patterns range from active mate search to long-term territorial defence of oviposition sites. In territorial species, males may use three mating tactics or strategies that may be determined environmentally or genetically: territoriality, non-territoriality, or reversible switches between the two. The tactic exhibited by a male in any given case is determined by the cost/benefit ratio of territorial and non-territorial behaviours. The main benefit of territoriality is increased access to females; costs may accumulate due, for example, to predation, injuries, and/or energy loss due to territorial contests. The density of both males and females, as well as the sex ratio at breeding sites, contribute to the costs and benefits of each tactic. Interspecific aggression by heterospecific males may also influence the profitability of these tactics.

16.1 Introduction

Territory can be defined as a fixed part of a species' range where an individual has priority of access over conspecifics to one or more resources in short supply, achieved through social interactions that vary in intensity (Kaufmann 1983). Territorial behaviour over mating sites is very common in animal mating systems. The fact that it has evolved numerous times independently (Andersson 1994) suggests general benefits from this behaviour, which may compensate the costs of fighting for mating opportunities. Given this, it is predictable that natural selection will favour male territoriality and traits that facilitate successful territory defence. In general, male mating success increases with territory size and quality as well as with the quality of the male himself (Andersson 1994). Male–male contests have received much empirical and theoretical attention (see recent reviews by Kemp and Wiklund 2001; Kokko *et al.* 2006; Briffa and Sneddon 2007). Theoretical studies have typically modelled the evolution of fighting strategies, such as motivation, whereas most empirical studies have recorded various phenotypic correlates of contest outcome (Table 16.1) (Kokko *et al.* 2006; Briffa and Sneddon 2007).

According to Corbet (1999), Kaufmann's (1983) definition of territoriality is applicable to most examples of agonistic resource defence common in both the Zygoptera and Anisoptera. The presence and strength of territoriality vary at the level of both the species and the individual (Corbet 1999); for example, site fidelity (length of time that males occupy the same site) may vary between species from less than a minute to more than a month. Within species, males may also exhibit both inter- and intra-individual variation in mating tactics (for more details see Section 16.2). The degree and type of competition for matings profitable for odonate males is determined by the distribution and abundance of conspecific males and females (Fincke *et al.* 1997; Corbet 1999). However, more detailed interspecific comparative analyses would give

Table 16.1 Correlates of contest outcome success in male odonate territorial disputes.

Species	Description of interaction	Source
Age		
Calopteryx maculata	Winners younger than losers, territorial males younger than non-territorial ones	Forsyth and Montgomerie 1987; Fitzstephens and Getty 2000
Calopteryx splendens xanthostoma	No difference between winners and losers	Plaistow and Siva-Jothy 1996
Hetaerina americana	No difference between mating tactics	Raihani *et al.* 2008
Libellula pulchella	No difference between territorial and non-territorial males	Marden and Cobb 2004
Libellula quadrimaculata	No difference between territorial and non-territorial males	Convey 1989
Nannophya pygmaea	Winners younger than losers	Tsubaki and Ono 1987
Perithemis tenera	Winners younger than losers	Switzer 2004
Body size		
C. maculata	No difference between winners and losers	Marden and Waage 1990
C. splendens	No difference in wing length between territorial and non-territorial males	Tynkkynen *et al.* 2006
C. splendens xanthostoma	No difference in dry fatless body mass between territorial and non-territorial males	Plaistow and Siva-Jothy 1996
Calopteryx virgo	No difference in fresh body mass between winners and losers	Koskimäki *et al.* 2004
Erythemis vesiculosa	No difference in wing size between territorial and non-territorial males	Córdoba-Aguilar and Méndez 2006
H. americana	No difference in body size between territorial and non-territorial males, but in one study territorial males were larger than non-territorial ones	Grether 1996; Serrano-Meneses *et al.* 2007; Raihani *et al.* 2008
Hetaerina miniata	No difference in body size between territorial and non-territorial males	Lefevre and Muehter 2004
L. quadrimaculata	Non-territorial males had longer wings than territorial ones	Convey 1989
Megaloprepus coerulatus	Territorial males larger than non-territorial ones	Fincke 1984
Mnais costalis	Mature territorial orange-winged males had higher dry body mass than mature non-territorial clear-winged males	Plaistow and Tsubaki 2000
N. pygmaea	No difference in body size between territorial and non-territorial males	Tsubaki and Ono 1987
Orthetrum chrysostigma	Territorial males larger than non-territorial ones	Miller 1983
P. tenera	No difference in wing length between winners and losers	Switzer 2004
Pyrrhosoma nymphula	No difference in fresh body mass between winners and losers	Gribbin and Thompson 1991
Sexual ornaments		
Calopteryx haemorrhoidalis	Territorial males had more wing pigmentation than non-territorial ones	Córdoba-Aguilar 2002
C. maculata	Territorial males bluer than non-territorial males	Fitzstephens and Getty 2000
C. splendens	No difference in wing spot size between territorial and non-territorial males	Tynkkynen *et al.* 2006
C. splendens xanthostoma	Territorial males had less wing pigmentation heterogeneity and larger wing spot size than non-territorial males	Siva-Jothy 1999

H. americana	Territorial males had larger wing-spot size and higher wing pigmentation than non-territorial males, but one study did not find differences in wing pigmentation between mating strategies	Grether 1996 ; Contreras-Garduño *et al.* 2006, 2007 ; Raihani *et al.* 2008
Hetaerina titia	Territorial males had more black pigmentation in the anterior wings than non-territorial males; no such difference was found in the posterior wings, or the red pigmentation part of either wing pair	Córdoba-Aguilar *et al.* 2007
Fat content		
C. splendens xanthostoma	Winner males had larger fat reserves than loser males	Plaistow and Siva-Jothy 1996
C. maculata	Winner males had larger fat reserves than loser males	Marden and Waage 1990; Marden and Rollins 1994
C. virgo	Winner males had larger fat reserves than loser males	Koskimäki *et al.* 2004
H. americana	Territorial males had larger fat reserves than non-territorial males	Contreras-Garduño *et al.* 2006; Serrano-Meneses *et al.* 2007; Raihani et al. 2008
H. titia	Territorial males had larger fat reserves than non-territorial males	Córdoba-Aguilar *et al.* 2007
Flight muscle mass		
C. splendens xanthostoma	No difference between winners and losers	Plaistow and Siva-Jothy 1996
C. maculata	No difference between winners and losers	Marden and Waage 1990
Plathemis lydia	The most successful males have the highest mass	Marden 1989
H. americana	No difference between territorial and non-territorial males, but switchers had the lowest mass	Serrano-Meneses *et al.* 2007; Raihani *et al.* 2008
M. costalis	Territorial orange-winged males have greater mass than non-territorial clear-winged males	Plaistow and Tsubaki 2000
Muscle power output		
C. maculata	No difference between winners and losers	Marden and Waage 1990
L. pulchella	No difference between territorial and non-territorial males, but the most successful males had the highest output and spent more time defending territories	Marden and Cobb 2004
Immunocompetence		
C. virgo	Winner males had higher encapsulation rate than loser males	Koskimäki *et al.* 2004
E. vesiculosa	Territorial males had a higher encapsulation rate than non-territorial males	Córdoba-Aguilar and Méndez 2006
H. americana	Territorial males exhibited higher phenoloxidase and hydrolytic enzymatic activity with and without immune challenge than non-territorial males	Contreras-Garduño *et al.* 2007
H. titia	Territorial males had a higher encapsulation rate than non-territorial males	Córdoba-Aguilar *et al.* 2007
Hemocyte density		
C. virgo	No difference between winners and losers	Koskimäki *et al.* 2004
Parasite load		
L. pulchella	Territorial males had fewer gregarine parasites than non-territorial ones	Marden and Cobb 2004
M. costalis	Territorial orange-winged males had higher parasite abundance than non-territorial clear-winged males	Tsubaki and Hooper 2004

further insight into the underlying factors contributing to this variation.

Following emergence the sexually immature individual has very scanty lipidic reserves, which are important for male territorial contest and female egg production (e.g. Marden and Waage 1990). During the teneral stage, the immature odonate builds up a large gain in body mass and energy reserves (Kirkton and Schultz 2001). Once sexual maturity is reached, males spend most of their time at reproductive sites awaiting females. Females, in contrast, visit these sites only briefly, primarily to mate and oviposit. Thus the sex ratio at breeding sites is typically highly male-biased. In territorial species females prefer to mate with territorial males; in concert with the male-biased sex ratio this often results in a highly skewed mating pattern, with only a few males achieving most of the matings (Plaistow and Siva-Jothy 1996; see Chapter 12 in this volume).

In this chapter we discuss various mating strategies and tactics and address the cost/benefit-ratio of odonate male territorial behaviour. In addition, we consider the effects of intra- and interspecific interactions on territorial behaviour. We also suggest some ideas for further research.

16.2 Mating strategies and tactics in territorial odonates

Alternative mating strategies and tactics evolve because ecological and social environments often favour more than one phenotype (Gross 1996). In territorial odonate species, adult males may use three different mating strategies or tactics, which may be determined genetically (Tsubaki 2003) (Box 16.1) or conditionally: territoriality, non-territoriality, or switching between the two (Corbet 1999; Switzer 2004; Raihani *et al.* 2008) (Box 16.2). Males that exhibit the territorial tactic defend sites that females may or may not use for oviposition (Fincke 1997; Corbet 1999; Raihani *et al.* 2008). However, only some males are able to secure a territory; males unable to do so—that is, non-territorial individuals—use alternative mating tactics, such as sneaking and wandering (Gross 1996).

The reproductive behaviour of individual males—the mating tactic exhibited—varies during the flying season (e.g. Corbet 1999; Raihani *et al.* 2008). Much of the variation among males in territorial behaviour seems to be caused by energetic constraints (in the form of muscular fat reserves) contributing to their fighting ability or so-called resource-holding potential (RHP; for more details see Section 16.4) (e.g. Marden 1989). Recent studies have found that several male traits, such as muscular fat reserves, immunocompetence, intestinal parasite load, and wing pigmentation, were correlated with contest outcome (Table 16.1). These findings suggest that only males in good condition are able to occupy and defend territories. Generalizations are difficult, however, since so far only a few damselfly and only one dragonfly species have been studied closely. Furthermore, the ability to occupy

Box 16.1 Genetically based mating strategies in odonates: a case study

Genetically based mating strategies (Gross 1996) have been well studied in the genus *Mnais* (see review in Córdoba-Aguilar and Cordero-Rivera 2005), with two morphological and behavioural genetically based morphs (Tsubaki 2003). Studies have shown that the smaller, hyaline winged, non-territorial morph lives longer than the larger territorial morph with pigmented wings (Tsubaki *et al.* 1997; Tsubaki and Hooper 2004). This difference in longevity between morphs is possibly a consequence of gregarine parasite pressure (Tsubaki and Hooper 2004), the cost of producing wing pigmentation (Hooper *et al.* 1999), and amount of energy reserves (fat) consumed during contests (Nomakuchi *et al.* 1984; Watanabe and Taguchi 1990; Tsubaki *et al.* 1997). Estimates of lifetime reproductive success indicate that both morphs achieve similar fertilization success; this explains the effectiveness and maintenance of both the territorial and the non-territorial morph (Tsubaki *et al.* 1997).

Box 16.2 Condition-based non-territorial mating tactics in territorial odonates

In territorial odonate species, non-territorial males use three alternative mating tactics, based on conditions (environmental and/or physiological): sneaker, wanderer, and switcher. Sneaker males wait near a breeding territory and try to intercept arriving females; wandering males search actively for females around possible breeding places (behaviour similar to scrambling); switcher males exhibit reversible switches between territorial and non-territorial behaviours several times over their lifespan (Raihani *et al.* 2008). Both sneaker and wanderer males use a tactic whereby they make the best of a bad situation, and typically have low mating success. Several studies, however, have found that males applying a mixed strategy (i.e. territoriality, followed after displacement from the territory by sneaking or wandering) had higher life-time mating success than males using a purely territorial strategy (Forsyth and Montgomerie 1987; Wolf and Waltz 1993).

and defend a territory changes with age. Young but sexually mature males are still accumulating fat; middle-aged males usually have the highest fat content, while old males often have depleted fat reserves and therefore reduced competitive ability. Moreover, older males tend to lose territorial fights when faced by younger males, although this is not always the case (Table 16.1). Males that have exhausted their energy reserves lose territorial fights and are prone to adopt a non-territorial tactic (Plaistow and Siva-Jothy 1996). Interestingly, the fat load of switchers has been found to be higher than that of non-territorial males but lower than that of territorial males (Raihani *et al.* 2008). Switchers may not be capable of uninterrupted territorial defence, and therefore adopt a partially territorial tactic split up into sequential periods. They may on the other hand be better at regaining energy reserves compared with territorial males, who cannot return to territoriality once they are displaced. The discovery of the switching tactic has provided an interesting opportunity to study for instance the effect of phenotypic variation in physiological traits on the cost/benefit ratio of territorial behaviour (Raihani *et al.* 2008).

Male mating strategy may also have a genetic basis (see review in Córdoba-Aguilar and Cordero-Rivera 2005). In the *Mnais* genus, males have two different morphological and behavioural genetically based forms (Tsubaki 2003) (Box 16.1). The smaller, non-territorial morph has hyaline wings, while the larger, territorial one bears pigmented wings (Watanabe and Taguchi 1990). The genetic polymorphism of *Mnais* seems to be explained by an autosomal, single locus, with two alleles of complete dominance (Tsubaki 2003). *Mnais* is the only proven case of genetically determined mating strategy in odonates.

Interestingly, some species of the New World genus *Paraphlebia*, such as *Paraphlebia quinta* and *Paraphlebia zoe*, have both territorial black-winged and non-territorial hyaline-winged males (González-Soriano and Córdoba-Aguilar 2003). Furthermore, within several species of an Old World group, malachites (Synlestidae: *Chlorolestes*), there are both clear-winged and coloured, banded-winged males. The proportion of banded males in the population varies seasonally and between species (Taborton and Taborton 2005). Banded winged males have been observed to be sexually more attractive to females; they defend their territory aggressively and chase away clear-winged males (Samways 2006). In addition, some *Clorolestes* species have only clear-winged males. It is not yet clear whether polymorphism in *Paraphlebia* and malachites is a genetically determined trait, similarly to *Mnais*. More detailed studies are also needed to verify that territorial behaviour is strictly morph-specific, although unpublished information on *Paraphlebia* indicates that when the territorial male is not present, the non-territorial is able to defend a territory (E. González-Soriano and A. Córdoba-Aguilar, personal observations). It may be worth determining the ecological factors related to variation in the proportion of banded males within and between populations, and to the lack of banded males in some *Clorolestes* species.

16.3 Benefits and costs of territoriality

16.3.1 Benefits

Both males and females derive benefits from territoriality. For males, the main benefit of defending a territory is increased access to females. Mating success in territorial individuals has been found to be considerably higher than in non-territorial ones except for the genetically polymorphic *Mnais* species (Table 16.2). However, there is huge interspecific variation in relative mating success between territorial and non-territorial males. In *Calopteryx splendens xanthostoma*, for instance, the mating success of territorial males was about a thousand times that of non-territorial males (Plaistow and Siva- Jothy 1996), whereas in *Hetaerina americana* mating success did not differ between mating tactics (Raihani *et al.* 2008).

For females, male territorial behaviour may provide both direct and indirect benefits (Table 16.2). One direct benefit seems to be that the high quality of a territory may be associated with high egg-hatching success and offspring survival. Another direct benefit for females is that mating with a territory owner reduces harassment during copulation or oviposition. Likewise, the risk of predation for the female herself and/or her offspring may be lower in a high-quality territory (Table 16.2). On the other hand, one cost may be that mating with highly successful males may reduce the rate of egg fertilization (Jacobs 1955), possibly because mating males allocate fewer sperm to each particular copulation when mating repeatedly over a relatively short time. Mating with a successful male may also increase the risk of sexually transmitted diseases, which are common in insects (see Knell and Webberley 2004).

In species with intense agonistic competition for mates, females may use correlates of RHP as measures of male quality; thus traits associated with

Table 16.2 Benefits of territorial behaviour for males and females.

Species	Description of breeding success	Source
Male benefit: mating success		
Calopteryx maculata	Daily copulation rate higher in territorial than non-territorial males	Forsyth and Montgomerie 1987
Calopteryx splendens xanthostoma	Copulation rate higher in territorial than non-territorial males	Plaistow and Siva-Jothy 1996
Hetaerina americana	Mating rate higher in territorial than non-territorial males, but one study did not find differences between territorial, switcher, and non-territorial males	Grether 1996; Serrano-Meneses *et al.* 2007; Raihani *et al.* 2008
Hetaerina cruentata	Mating success higher in territorial than non-territorial males	Córdoba-Aguilar 1995
Mnais costalis	Daily mating success higher in territorial orange-winged males than non-territorial clear-winged males, but lifetime reproductive success is the same	Tsubaki *et al.* 1997
Nannophya pygmaea	Mating success higher in territorial than non-territorial males	Tsubaki and Ono 1986
Pyrrhosoma nymphula	No difference in number of matings between territorial and non-territorial males	Gribbin and Thompson 1991
Female benefit		
Calopteryx aequabilis	Large vegetation patch	Meek and Herman 1991
Calopteryx amata	Large vegetation patch	Meek and Herman 1991
Calopteryx maculate	Large vegetation patch	Waage 1987; Meek and Herman 1991
Paltothemis lineatipes	Large vegetation patch	Alcock 1990
Pyrrhosoma nymphula	Large vegetation patch and lower risk of predation	Rehfeldt 1990
C. splendens xanthostoma	Egg-hatching success	Siva-Jothy *et al.* 1995
Plathemis lydia	Low risk of male harassment during copulation and oviposition	Koenig 1990; McMillan 1991

RHP may increase male attractiveness for potential mates (Briffa and Sneddon 2007). One indirect benefit for females may be that the male's ability to occupy and defend a territory may be an indicator of 'good genes' (the hypothesis that females derive indirect benefits from mating with males with conspicuous, costly traits; Andersson 1994). These traits reflect broad genetic quality, which increases the viability of offspring (Andersson 1994). There is some indirect evidence to support this hypothesis: territorial males have been found to have fewer parasites and stronger immune defence than non-territorial males (Table 16.1). So far, however, there is no direct evidence from odonate studies for the good genes or so-called sexy sons that females might receive by preferring territorial males. Indirect benefits might be studied in territorial *H. americana*, which has no obvious direct benefits arising from the properties of the territory. In this species, the males do not defend oviposition sites. Instead, the couple leaves the territory for a communal site, where a number of females gather to lay their eggs (Raihani *et al.* 2008). Such studies should of course control for the possibility that territorial males may provide superior protection from male harassment during oviposition.

16.3.2 Costs

Since odonates lack all obvious traits traditionally associated with animal aggression, such as horns and spines, their fights can be better described as wars of attrition, in which the male that endures longer is usually the winner. Sometimes these fights can last for several hours (e.g. Waage 1988; Marden and Waage 1990; Marden and Rollins 1994; Koskimäki *et al.* 2004). The evolution of contest behaviour in Odonata is therefore interesting; persistence must carry some cost, since otherwise contests would never be settled. Odonate wars of attrition are therefore expected to be costly on logical grounds, and indeed this assumption underlies all present attempts to understand their occurrence. Here we review the possible costs (see also Kemp and Wiklund 2001; Briffa and Sneddon 2007) that can be incurred by an individual male in defending a site: intrinsic costs, such as energetic and other physiological costs and injury cost, and circumstantial costs, such as opportunity cost and predation cost.

16.3.2.1 Energetic and other physiological costs

Agonistic behaviours, such as competition over mating opportunities, are expected to be demanding to perform; this leads to physiological costs, such as depletion of energy reserves or changes in endocrine status (Briffa and Sneddon 2007). Odonate contests are thought to constitute an excellent system for testing whether wars of attrition are energetically costly. This prediction is supported by experimental studies with territorial odonates that compete via prolonged aerial contests; the winners are mostly middle-aged males in possession of greater fat reserves (Table 16.1). Despite the apparent cost of territorial behaviour, no study has tested energy consumption by non-territorial animals in searching for mates.

Another possible physiological cost of male–male contest and reproduction may be reduced immune function against parasites and pathogens (Contreras-Garduño *et al.* 2006). This is supported by three lines of evidence: (1) contest winners have stronger immune defence and more fat reserves than losers, (2) fat reserves are positively correlated with the strength of immune defence (e.g. Koskimäki *et al.* 2004), and (3) losing males have reduced immune ability compared with other non-territorial males (Contreras-Garduño *et al.* 2006; Table 16.1). The energy metabolism of both territorial and non-territorial males may also be affected negatively by parasites. Gregarines are intestinal parasites that, once ingested, aggregate and attach to the posterior gut region of the adult; they then develop and reproduce, presumably by using the host's ingested food (Corbet 1999; Siva-Jothy and Plaistow 1999; see Chapter 14 for biological data of gregarines infecting odonates). Gregarine infection apparently has massive metabolic consequences, including the inability of the flight muscles to oxidize fatty acids, resulting in reduced muscle performance and lipid accumulation in the thorax (Schilder and Marden 2006). A study conducted with a territorial dragonfly species, *Libellula pulchella*, found that in a population with high gregarine incidence and intensity most parasitized males remained non-territorial, whereas males with no parasites were territorial

(Marden and Cobb 2004). Territory holders showed a positive relationship between muscle power and fat content, whereas no such relationship was found in parasitized males. This suggests that territorial males were able to adjust the energy consumption of their flight muscles with their rate of energy mobilization (Marden and Cobb 2004). Gregarine infection, and the resulting compromised ability to optimally activate energy reserves, may be especially detrimental to territorial males utilizing their fat reserves during patrol and contest flights. Non-territorial males may be better able to compensate for metabolic disorders by spending less time in search of mates or in challenging territorial owners. This issue could be addressed by exposing both territorial and non-territorial males to similar numbers of parasites and then examining the gain in energy reserves after controlling for feeding rates.

16.3.2.2 Injury cost

In Odonata, physical contact occurs occasionally in both intra- and interspecific fights (e.g. Corbet 1999). This contact often seems closer to an accidental collision than to a clear physical attack. In any case, such escalated contests may lead to permanent injury, such as wing and leg damage or even death (reviewed by Corbet 1999). Despite this, it is not unusual to see males successfully defending territories with a broken or even missing wing (M.J. Rantala, personal observation). Although injuries may inflict a cost on fighting males, their importance remains unknown. This could be addressed experimentally by artificially damaging or even removing the wings and then studying the costs in terms of territorial defence.

16.3.2.3 Opportunity cost

Perhaps the simplest and most obvious cost of engaging in a war of attrition is the loss of time and energy that could be otherwise devoted to mate location (Waage 1988; Kemp and Wiklund 2001; Tynkkynen *et al.* 2006) or feeding. Another potential opportunity cost is loss of a mate; a non-territorial male may capture a female that has arrived in a territory while the territory owner is currently engaged in a contest. This opportunity cost could affect both combatants equally.

16.3.2.4 Predation cost

Predation by birds (reviewed by Corbet 1999; Svensson and Friberg 2007), spiders (Rehfeldt 1992), and other dragonflies causes substantial mortality in odonate adults. Since territorial odonates engage in conspicuous circling contests, predation by visual predators may be more likely. On the other hand, predators do not have to be active (attracted to the contesting odonates), but may be passive, for example when the fighting activity renders males more easily predatable. Related to this, Rehfeldt (1992) found that territorial *Calopteryx haemorrhoidalis* males were more likely to be caught in webs of orb-weaving spiders than non-territorial males; this occurred chiefly at noon, when territorial disputes were most frequent. It might be worthwhile experimentally exploring differences between territorial and non-territorial males in predation rates, using both visual predators and orb-weaving spiders. Moreover, temporal and spatial variation in predation pressure may not only be local (see Svensson and Friberg 2007) but also geographical, resulting in possible variation in selection pressure on mating tactics.

16.4 Intra- and interspecific factors of interest

16.4.1 Asymmetry in resource-holding potential

The idea that male–male contests may be energetically costly came originally from studies on butterflies, such as the classic empirical test by Davies (1978) of the uncorrelated asymmetry hypothesis. Inter-individual differences in various traits are likely to influence the ability of each individual to withstand physiological costs. Contests can be asymmetrical with respect to costs and benefits for contestant males that differ in both energy reserves and RHP. If high enough, these costs may constrain the intensity of agonistic behaviour and affect strategic decisions during fights. Thus asymmetries in fighting ability (i.e. RHP) will greatly influence the form and outcome of a contest (Briffa and Sneddon 2007).

Theoretical and empirical analyses have demonstrated that owners win most territorial contests when challenged by rivals (reviewed in Kokko *et al.* 2006). In odonates, a territorial male often displays considerable day-to-day site fidelity to his territory (e.g. Switzer 1997; Corbet 1999), and the territory owner wins the majority of fights with challenging males (e.g. Waage 1988; Switzer 2004). A prior residency advantage was documented in non-escalated contests (e.g. Waage 1988; Switzer 2004); escalated fights were most common when both opponents became residents in the same territory, with highly valued contested resources (Waage 1988). The most common explanations invoked for the resident's advantage are that either individuals are following an arbitrary convention, such as 'the resident always wins', or that asymmetries favouring the resident already exist in terms of either RHP or resource value (Switzer 2004; Kokko *et al.* 2006). Evidence supporting a strong prior-residence effect is most often found in the case of three scenarios (see review in Kokko *et al.* 2006): (1) when individuals are more or less matched in size, (2) when individuals with high RHP tend to accumulate as residents, and (3) when residence allows a higher RHP (e.g. a sunspot where an insect resident is warmed, facilitating flight; Stutt and Willmer 1998). Recent studies in Odonata have indicated asymmetries in the physical and physiological characteristics of contestants which may correlate with RHP; these include age, ornament size, fat reserves, and immunocompetence, but seldom body size, flight muscle mass, or muscle power output (Table 16.1). Physiological studies, for example on the processing rate of metabolic waste products and energy reserves, would increase our knowledge of factors contributing to contest outcome.

16.4.2 Density at breeding sites

One fundamental question in ecology is how individual fitness is affected by increasing population density (Kokko and Rankin 2006). Population density has been suggested to influence mating success via male–male competition and female choice (Kokko and Rankin 2006). The effect of male density on territorial behaviour has been well documented in many odonates (see review in Corbet 1999), indicating that territorial males may adjust their behaviour in relation to male density. For example, in *Plathemis lydia* male mating success has been found to be at its highest at intermediate territory sizes. However, optimal territory size decreases with increasing conspecific density (Koenig 1990). Given that at high male densities both localization and site attachment become stronger, greater time wastage and energy expenditure evidently occur because a significant proportion of time is spent in flight (Corbet 1999). Under high-density conditions territorial behaviour may be not profitable at all, leading to a reduction in mating success (e.g. Koenig 1990). In some species territorial males have been found to share the same territory with as many as eight males (e.g. Koenig 1990; Corbet 1999). Such an extreme situation may lead to a breakdown in territoriality (Corbet 1999). For example, the usual logic—that a non-territorial mating tactic produces extremely low mating success compared with a territorial one (Table 16.2)—may be less extreme under high-density conditions (Kokko and Rankin 2006), a situation that awaits further testing. Thus it is possible that males that are not able to occupy or defend territories may benefit from increased male density. On the other hand, at high population densities males may need to invest less in courtship and mating, as females, to avoid sexual harassment due to the high number of approaching males, become less selective. Under high population densities, territorial defence becomes so energetically unprofitable that males may gain more by changing their mating tactics from territoriality to non-territoriality (Cordero 1999; Kokko and Rankin 2006). Furthermore, under these conditions mated males would be expected to guard their mates more intensively, whereas solitary males would try to achieve tandem forcibly (Cordero 1999).

In contrast to males, the effects of population density on female behaviour and reproductive success are poorly known. It has been suggested that odonate females appear not to mate indiscriminately (e.g. Fincke 1997; Siva-Jothy 1999; Córdoba-Aguilar 2000) except when male densities are extremely high (e.g. Cordero 1999), where it has been admitted that females mate according to a tactic of convenience polyandry to reduce energetic costs due to male harassment (Thornhill and Alcock 1983; Cordero-Rivera and Andrés 2002). At high densities, multiple matings and resistance to mating attempts may induce costs due to the waste of time that could otherwise be used for foraging and consequently egg development. Even laying eggs may be difficult, as males frequently interrupt ovipositing females (Cordero-Rivera and Andrés 2002). Thus variation in male density may modify female reproductive success and therefore also female behaviour. For example, to avoid excessive matings or harassment females may avoid breeding sites with a high male density, which might further affect the sex ratio at such sites.

Finally, most studies of density effects have been carried out only on a single population and have recorded density variation during one breeding season only. In the future, empirical studies should take into account possible between-year and between-population variation in both male and female density, to see how this variation affects male mating success, the ratio of males implementing non-territorial and territorial mating tactics, and the transition frequency between these tactics.

16.4.3 Sex ratio at breeding sites

Changes in the sex ratio can affect the intensity of competition for mates (see review in Kvarnemo and Ahnesjö 1996), and thus bear different costs and benefits for territorial behaviour. Thus changes in the sex ratio at breeding sites may modify the ratio of males exhibiting different mating tactics; if, for instance, females become very abundant in relation to males, it may be more profitable for territorial males to change to non-territorial tactics.

In territorial odonate species, males typically outnumber females at the site of oviposition (e.g. Corbet 1999). The contrary situation—male scarcity at the site of reproduction and female territorial behaviour—is extremely rare in odonates (Corbet 1999) and in fact only a few species exhibit a female-biased sex ratio in the field (Donnelly 1990; Cordero-Rivera *et al.* 2005; Van Gossum *et al.* 2007). Experimental work has shown that the removal of males in a natural population of *Perithemis tenera* caused females to start showing territorial behaviour (Jacobs 1955). In some species of the *Nesobasis* genus, found in the archipelago of Fiji, males are exceedingly rare in natural populations and sometimes only females have been found (Donnelly 1990; Van Gossum *et al.* 2007). It has been suggested (Donnelly 1990) that territorial behaviour in females may have arisen as a consequence of this rarity of the opposite sex. However, a recent study could not corroborate female territoriality in these species (Van Gossum *et al.* 2007).

Interestingly, in a female-biased species *Neobasis heteroneura* males still actively defended territories at the water (Van Gossum *et al.* 2007). In this species, however, the sex ratio varies highly between populations, and in *Neobasis* it also varies between species from male-biased to female-biased. It might therefore be interesting to investigate whether males of *N. heteroneura*, and of other species of the same genus, exhibit different mating tactics, and, if so, to determine whether the ratio between non-territorial and territorial male mating tactics varies in relation to the sex ratio. Current research on the *Neobasis* genus (H. Van Gossum, personal communication) aims to discovering whether infection with male-killing parasites, such as *Wolbachia*, could be related to the observed variation in the sex ratio.

16.4.4 Interspecific aggression

Interspecific aggression is a common behaviour in territorial odonates (reviewed by Corbet 1999). Although Tynkkynen *et al.* discuss this issue in relation to the evolution of character displacement and species isolation in Chapter 11, here we focus on the effects of interspecific aggression on territorial behaviour.

It has been shown that this kind of interaction leads to spatial partitioning (Rehfeldt and Hadrys 1988) or even to the exclusion of one species from certain water areas (Moore 1964). The fact that experimentally induced vacant territories were quickly occupied by heterospecific males (Moore 1964; Tynkkynen *et al.* 2006) suggests that the presence or absence of a particular species in breeding places may depend on interspecific aggression (Moore 1964). In general, larger species have better territory-holding ability than smaller species (Moore 1964; Tynkkynen *et al.* 2004). Aggression between species, however, seems to be weaker than aggression within species (Singer 1989; De Marchi 1990;

Nomakuchi and Higashi 1996; Schultz and Switzer 2001; Tynkkynen *et al.* 2004, 2006), and in fact territorial males have been found to react to approaching conspecific males at greater distances than to heterospecific males (e.g. Singer 1989; Tynkkynen *et al.* 2004). Conspecific *Calopteryx* males, for instance, never share the same territory, whereas heterospecific males often do so (De Marchi 1990; Tynkkynen *et al.* 2006). One consequence of this is that interspecific interaction may affect breeding behaviour. For example, interspecific harassment of ovipositing tandems and females, as well as interspecific tandems and copulations, frequently occur, although hybrid individuals have very seldom been documented (but see De Marchi 1990; Tynkkynen *et al.*, 2008).

Interspecific aggression is usually interpreted as resulting from interspecific interference competition over resources or from a mistake in species recognition (e.g. Murray 1981). For instance, some species responded equally to both conspecific and heterospecific intruders (e.g. Singer 1989). This may be due to the visual difficulty of rapidly and accurately identifying intruder males, whereas the advantage of a quick response could lead to a high probability of winning a possible ensuing battle (Singer 1989). More support for the mistaken-identity hypothesis comes from field observations between anisopterans and other insect groups (Schultz and Switzer 2001), and field experiments with closely related zygopteran species (Tynkkynen *et al.* 2004). In fact, most documented encounters have been found between species that resembled each other in size (Moore 1964; Singer 1989; Tynkkynen *et al.* 2004), thorax colour pattern (Moore 1964), and/or wing pigmentation (Tynkkynen *et al.* 2004). A field study in the eastern amberwing dragonfly (*Perithemis tenera*) found more similarity in the physical and behavioural characteristics of amberwings and other heterospecific insects, such as the butterfly *Anacyloxypha numitor* and horseflies (*Tabanus* spp.), which they commonly pursue, than in those of *P. tenera* and dragonfly heterospecifics (Schultz and Switzer 2001). This finding supports the mistaken-identity hypothesis (Schultz and Switzer 2001). The horsefly and anisopteran characteristics correspond to the cues that the male *P. tenera* may use to identify conspecifics; the relative rarity of intrusions by these two species probably made it more costly to discriminate and pursue only conspecifics than to engage in some mistaken pursuits (Schultz and Switzer 2001). More support for the mistaken species recognition hypothesis comes from a field experiment with *Calopteryx virgo* and *Calopteryx splendens*, where the former were more aggressive towards large-spotted *C. splendens* males, which were phenotypically more similar to *C. virgo* males, than toward small-spotted individuals (Tynkkynen *et al.* 2004).

Finally, differences in competitive ability among species that share the same place are expected to produce evolutionary responses, such as niche shift or character divergence (e.g. Murray 1981). There is evidence that niche shift has occurred in odonates (Moore 1964; Rehfeldt and Hadrys 1988). In addition, interspecific aggression has apparently had evolutionary consequences for wing pigmentation (e.g. Tynkkynen *et al.* 2005). Evidence for character displacement exists in *Calopteryx splendens*, whose male wing-spot size is negatively correlated with the relative abundance of sympatric *C. virgo* males across populations (Tynkkynen *et al.* 2004). In a similar manner, the wing pigmentation of *Calopteryx aequabilis* females decreased with an increasing relative abundance of sympatric *Calopteryx maculata* (Waage 1975, 1979). Moreover, *C. maculata* males are better able to discriminate between conspecific and heterospecific *C. aequabilis* females (Waage 1979). Wing-pigmentation pattern displacement is evidently recent relative to species divergence (Mullen and Andrés 2007).

Acknowledgements

We are grateful to Alex Córdoba-Aguilar for inviting us to write this review. Thanks also to Alex Córdoba-Aguilar, John Loehr, and Jim Marden for helpful comments and for checking the language of a previous draft of this chapter. The language of this draft was checked by Ellen Valle. All authors were funded by the Academy of Finland. We also thank the Section of Ecology of the Department of Biology at the University of Turku for providing us with a fruitful research environment.

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CHAPTER 17

The evolution of sex-limited colour polymorphism

Hans Van Gossum, Tom N. Sherratt, and Adolfo Cordero-Rivera

Overview

Species that exhibit colour polymorphism, the simultaneous occurrence of two or more discrete phenotypes with a genetic basis, are ideal for studying the microevolutionary forces that maintain genetic variation in nature. One very intriguing type of genetically determined polymorphism is the co-existence of several discrete morphs within only the male, or within only the female, sex. These morphs typically differ in body coloration and sometimes behaviour, with one morph often resembling the opposite sex. In males, this resemblance often allows access to receptive females, whereas in females the polymorphism appears related to avoiding excessive male sexual harassment. One might wonder why natural selection does not simply give rise to a single best male and female type for each species. Odonates are good candidate species to address this type of question because sex-limited polymorphism is widespread within the group, facilitating hypothesis testing through comparative analyses. Odonates are also widely distributed geographically and they are convenient to work with from a methodological perspective because they can be studied over their lifetime on an individual basis under either natural or artificial conditions. The phenomenon of sex-limited polymorphisms provides an important opportunity to test contemporary ideas relating to sexual selection and sexual conflict, and the diversity of polymorphisms that have arisen in odonates clearly offers one of the best natural systems for among-species comparative research.

17.1 The wheres and whys of intraspecific discrete colour variation

Variation in colour between individuals that has a genetic basis is widespread in nature, with multiple examples found in vertebrates, invertebrates, and plants (e.g. Maynard Smith 1998). Such variation is considered a polymorphism when two or more distinct and genetically determined morphs co-exist at the same time in a single interbreeding population, the least abundant of which is present in numbers too great to be due solely to recurrent mutation (Ford 1957). As Fisher (1930) argued, the existence of a permanent polymorphism often implies a selective balance (frequency-dependent selection) between the two (or more) alternative morphs, each enjoying a selective advantage when rare but also suffering some disadvantage when common. General explanations for these and other polymorphisms therefore include frequency-dependent selection, but also heterosis (where the heterozygote is fitter than either homozygote) and variable morph fitnesses in space or time. Clearly, polymorphisms are attractive model systems to explore how natural selection can work to maintain diversity. Among the two most widely known cases are the so-called massive polymorphisms seen in the land snail *Cepaea nemoralis* (e.g. Jones *et al.* 1977) and industrial melanism with light and dark morphs in the peppered moth *Biston betularia* (e.g. Majerus 2005).

Intriguingly, there are examples where the occurrence of colour polymorphism is restricted to just to one sex, with examples seen in a wide variety of taxonomic groups including reptiles (Shine *et al.* 2001), birds (Galeotti *et al.* 2003), and insects (Forsyth and Alcock 1990). Instances of female-limited polymorphism are generally considered to have evolved in response to excessive male sexual harassment, sometimes in combination with selection to resemble unpalatable heterospecifics (Beccaloni 1997). Species with alternative male morphs often include a territorial fighter male and a 'sneaky' male that resembles the conspecific female in behaviour and phenotype and that succeeds in intercepting females for mating at the borders of territorial male's territory (Gross 1996).

These examples illustrate that, rather than selection giving rise to a single best male and female type for each species, it has instead resulted in multi-modal phenotypic diversity. An important question is how and why selection favours the co-existence of multiple morphs. To address this question it is preferable to study taxonomic groups that are both widespread and convenient to work with from a methodological perspective. A wide geographical distribution not only allows easy access to specimens, but also provides sufficient variation in biotic and abiotic conditions (e.g. density, temperature) to explore environmental influences on morph frequency. Likewise, it is useful to select a study group for which several species show the trait while others do not, thereby facilitating comparative analyses.

17.2 Generality of polymorphic species within different animal taxa

In most animal taxa, the occurrence of male- or female-limited colour polymorphisms is restricted to a few cases (see Box 17.1); for example, in birds, 25 species have been reported to show sex-limited polymorphism (Galeotti *et al.* 2003). In copepods, sex-limited polymorphism has so far been reported in only a single species (Fava 1986). Arguably, sex-limited polymorphism is only truly common (i.e. many species throughout an entire order) among female odonates (e.g. Fincke *et al.* 2005) (see Box 17.1). Indeed, female-limited polymorphism is observed for species of both Anisoptera and Zygoptera and has been described for more than 100 species (Fincke *et al.* 2005).

The presence of female-limited polymorphism within groups of closely related species allows us to explore associations between polymorphism and life-history traits, thereby contributing to understanding the evolution of sex-limited polymorphism in general. Robinson and Allgeyer (1996), for example, tested whether female colour polymorphism was correlated with mating-system traits for North American representatives of the genus *Ischnura*. Based on this work it was suggested that evolution from a polyandrous to a monandrous mating system was accompanied with a change in character state from polymorphic to monomorphic species. Unfortunately, a phylogeny for the genus was unavailable at the time, preventing the authors from placing the data in the proper historic context. Meanwhile, species-level-based phylogenies and higher-level relationships between odonates have been explored more intensively (e.g. Brown *et al.* 2000; Rehn 2003). Now that robust phylogenies are available it may become possible to ask whether the current presence of polymorphism results from a common ancestor or rather is the consequence of convergent evolution. Given the simple genetic system underlying polymorphism (see the next section), it is not unreasonable to suppose that recurrent mutation can facilitate the repeated evolution of this character in different species. However, we note that the presence of polymorphisms may itself create challenges for reconstructing phylogenies if polymorphy is a transient state in the process of speciation (Wiens 1999).

17.3 The genetic basis of polymorphism

For natural or sexual selection to operate on a trait it has to be heritable in some way. Simple Mendelian inheritance patterns have been found to underpin sex-limited polymorphism (e.g. Shuster and Wade 1991). Thus, in odonate species with male- or female-limited polymorphism, the proportions of colour morphs in the progeny are consistent with morph type being controlled at an autosomal locus that has sex-restricted expression, with the number

Box 17.1 How common is sex-limited polymorphism in animals?

Three component questions are as follows.

1. In which animal taxa do we observe sex-limited polymorphism?

Co-existence of either multiple male or multiple female morphs is seen in most vertebrate phyla (such as birds, reptiles, and fish), in insects (such as dragonflies, butterflies, and beetles), and in crustaceans.

2. Are sex-limited polymorphisms equally common across animal taxa?

No, there is only example of a taxon in which sex-limited polymorphism is seen in over 100 species (Fincke *et al.* 2005).

3. Are male and female limited polymorphisms equally common?

In birds 23 species show female-limited polymorphism, whereas two species show male-limited polymorphism (Galeotti *et al.* 2003). In odonates female-limited polymorphism is observed for species of both Anisoptera and Zygoptera and has been described for more than 100 species (Fincke *et al.* 2005). By contrast, male-limited polymorphisms are relatively more rare, with examples reported in only a few families of odonates, including the Calopterygidae (e.g. Plaistow and Tsubaki 2000), the Megapodagrionidae (González-Soriano and Córdoba-Aguilar 2005), the Coenagrionidae (Polhemus and Asquith 1996), and the Amphipterygidae (Stewart 1980).

of alleles involved equal to the number of morphs (female polymorphism, Andrés and Cordero 1999; male polymorphism, Tsubaki 2003). In the case of female-limited polymorphism it has been possible to evaluate inheritance for several species. Interestingly these species appear to differ in their hierarchy of dominance and recessiveness (see Andrés and Cordero 1999).

Over the past decade it has been possible to test for the effect of selection by comparing the rates of differentiation between the colour locus and a set of molecular markers assumed to be neutral (see Lynch and Walsh 1998). Two contrasting alternatives are possible. Negative (pro-apostatic) frequency-dependent selection may create a situation where most populations have reached equilibrium in morph frequencies; under these conditions population differentiation in morph frequencies would be expected to be significantly lower than population differentiation in neutral loci as was shown through relating differentiation based on randomly amplified polymorphic DNA (RAPD) markers (assumed to be neutral) with the degree of differentiation based on colour alleles (Andrés *et al.* 2000, 2002). Alternatively, each female morph may exploit a slightly different ecological niche, and differences among populations may then reflect local adaptation to differing environmental conditions. Under this scenario, population differentiation in morph frequencies is expected to be significantly greater than population differentiation for neutral loci, which was indicated for a damselfly species using microsatellites (Wong *et al.* 2003).

The development of new molecular techniques that produce codominant markers, such as microsatellites, opens the door for fine-scale analysis of population differentiation and genotyping (e.g. Thompson and Watts 2006). Future advances might be made through mapping the genes involved in the expression of polymorphism, which may be particularly revealing given that there is variation across odonate species in terms of whether the polymorphism includes body colour only, or also includes body patterning or behavioural differences. It is quite possible that several genes are involved and phenomena such as pleiotropy or linkage disequilibrium may be relevant. Exploring this will allow for more powerful tests of evolutionary hypotheses on the maintenance of sex-limited colour polymorphism.

17.4 Male-limited polymorphisms: fighter males and sneaky males

As seen in other animal taxa (Gross 1996), male-limited polymorphism in odonates includes a territorial fighter male and a so-called sneaky male that resembles the conspecific female, allowing it to remain at the edge of the fighter male's territory, apparently not being recognized as a male by the territorial male while intercepting females on their way to the territorial male (e.g. Plaistow and Tsubaki 2000). Females in these species are monomorphic (Tsubaki 2003). The mating strategy of territorial males guarantees higher daily mating rates, but non-territorial males live longer and have lower costs to develop and maintain their phenotype (Plaistow and Tsubaki 2000). Despite territorial and non-territorial male morphs having contrasting life histories, lifetime reproductive success appears similar for both morphs (Tsubaki *et al.* 1997), which is what one would expect if the polymorphism were in some form of equilibrium. Although these studies support the general contention (see Gross 1996) that a territorial and a sneaky male co-exist, examples in odonates are few, not geographically widespread and no more amenable to study than examples in other animal taxa. It is noteworthy, however, that some males of Coenagrionid Hawaiian damselflies are also polymorphic (in body coloration), yet territoriality does not occur in these species (Polhemus and Asquith 1996). Therefore, different explanations may be applicable to the occurrence of male-limited polymorphism in different damselfly taxa.

17.5 Female-limited polymorphism and male sexual harassment

In cases where female limited polymorphism arises in odonates, one female morph typically resembles the male (the androchrome), while the alternative morph (or morphs) does not (the gynochrome). This polymorphism is generally assumed to have arisen as a consequence of negative frequency-dependent (pro-apostatic) selection, in which the fitness of a given morph is higher than any alternative morph when it is relatively rare in a population. Most contemporary theories have assumed that the primary selective force generating this frequency-dependent selection is the differential harassment of female morphs by conspecific males (see Box 17.2). Male harassment is believed to affect female fitness in several ways: in particular, repeated attention by males can upset individual female time and energy budgets, and it may bring an increased likelihood of physical damage (Robertson 1985; Sirot and Brockmann 2001). Nevertheless, evidence that male harassment does reduce female fitness in damselflies is currently limited. Sirot and Brockmann (2001) indicated costs of sexual interactions to androchromes but not to gynochromes in an experimental setting only including male harassment (i.e. predation and other factors were excluded). Less directly, Svensson *et al.* (2005) applied a population-genetic model in combination with measures of female morph fecundity and field estimates on morph frequencies to support the contention that frequency- and density-dependent male harassment may drive the maintenance of female-limited polymorphism. In more recent work Gosden and Svensson (2007) show in natural populations that female morphs differ in their fecundity tolerance to matings and mating attempts.

Intuitively, if a female were seeking to avoid harassment then one might expect that it would pay more to look like something that is unprofitable to attack, rather than something which simply looked different. Mimicry is well known to generate frequency-dependent selection; indeed, the classical Batesian polymorphisms are generally explained by the diminishing effectiveness of mimicry as morph frequency increases (e.g. Ruxton *et al.* 2004). Given the morphological similarity to males and the occasional behavioural resemblance of androchromes to males (see for example Forbes *et al.* 1997; Van Gossum *et al.* 2001a), it is not surprising that male mimicry has been invoked repeatedly as the primary source of frequency dependence. Indeed, spectral reflectances have confirmed that androchromes more closely resemble males than gynochromes (Fincke *et al.* 2007). The reasoning is simple: when androchromes are rare compared with males then they suffer less male harassment compared with gynochromes; conversely once androchromes increase in relative abundance compared with males it will become profitable for males

Box 17.2 A summary of recent explanations for female-limited polymorphism and the nature of the underlying selective forces

Theory	Frequency-dependent benefit to androchromes when rare	Frequency-dependent cost to androchromes when common	Frequency-independent cost to androchromes	Comments	Reference
Interspecific mimicry and predation	Lower harassment by heterospecific males due to male mimicry	High rate of interspecific matings, which reduce fertility	Higher predation due to higher behavioural and morphological conspicuousness		Johnson 1975
Intraspecific mimicry and predation	Lower harassment by conspecific males due to male mimicry	Breakdown of mimetic advantage when androchromes are common	Higher predation due to higher behavioural and morphological conspicuousness		Robertson 1985
Intraspecific mimicry and mate recognition	Lower male harassment due to male mimicry when populations are at high density	Androchromes are selected against when populations are low density because they are not recognized as potential mates and risk zero matings		A density-dependent theory assuming temporally varying selection; however, the nature of the frequency-dependent selection cannot in itself promote polymorphism	Hinnekint 1987
Learned mate recognition	Lower probability of male harassment on encounter	Higher probability of male harassment on encounter		Males must learn to recognize conspecific females; precise equilibrium depends on differential conspicuousness	Miller and Fincke 1999; Fincke 2004
Intraspecific mimicry and harassment	Lower probability of male harassment on encounter due to mimicry	Breakdown of mimetic advantage when androchromes are common	Higher probability of encounter by conspecific males due to higher conspicuousness		Sherratt 2001

to attempt to distinguish male-like females from males (Robertson 1985), and the benefits of male mimicry are consequently reduced (Sherratt 2001). Note that androchromes do not have to be indistinguishable from males to benefit from male mimicry: no Batesian mimic would ever pass this test. All that is required is that androchromes gain some form of fitness advantage from rarity over alternative forms through their similarity to males.

Nevertheless, there is an alternative set of hypotheses, which simply assume that males have to learn to recognize the female types: this explanation has been dubbed the learned mate-recognition hypothesis (LMR for short; Miller and Fincke 1999). Many predators exhibit a frequency-dependent preference for attacking the more common form of prey in an environment, and it is quite possible that mate-searching males exhibit an analogous response.

The reasons for this 'switching' (Murdoch 1969) are varied (see Sherratt and Harvey 1993 for review). In particular, in his classic posthumous paper, Tinbergen (1960) argued that through chance encounters with cryptic prey, predators (in the current case, male damselflies) may only gradually learn to recognize those stimuli that enable them to differentiate prey types from their surroundings (in the current case, unsuitable mates). This learning to recognize cryptic prey can readily generate higher attack rates on the more common morph, leading to polymorphisms (see for example Bond and Kamil 2002).

To distinguish between hypotheses on male mimicry and LMR (see Box 17.2) we need to study several populations of the same species over a wide range of androchrome frequencies, including contrasting populations where androchromes are the minority and the majority female morph. Male mate-choice experiments have indicated that male preference in *Ischnura elegans* correlates positively with female morph frequency (Van Gossum *et al.* 1999); that is, the more common a female morph the more it will be preferred by the male (Figure 17.1a). This positive frequency-dependent selection, when costly in terms of fitness for the more common morph, will then result in negative frequency-dependent selection, thereby supporting LMR predictions. In contrast, a review of female mating frequencies in natural populations of the same species, over a range of androchrome frequencies (8–90%), indicated that androchrome females consistently mate less often

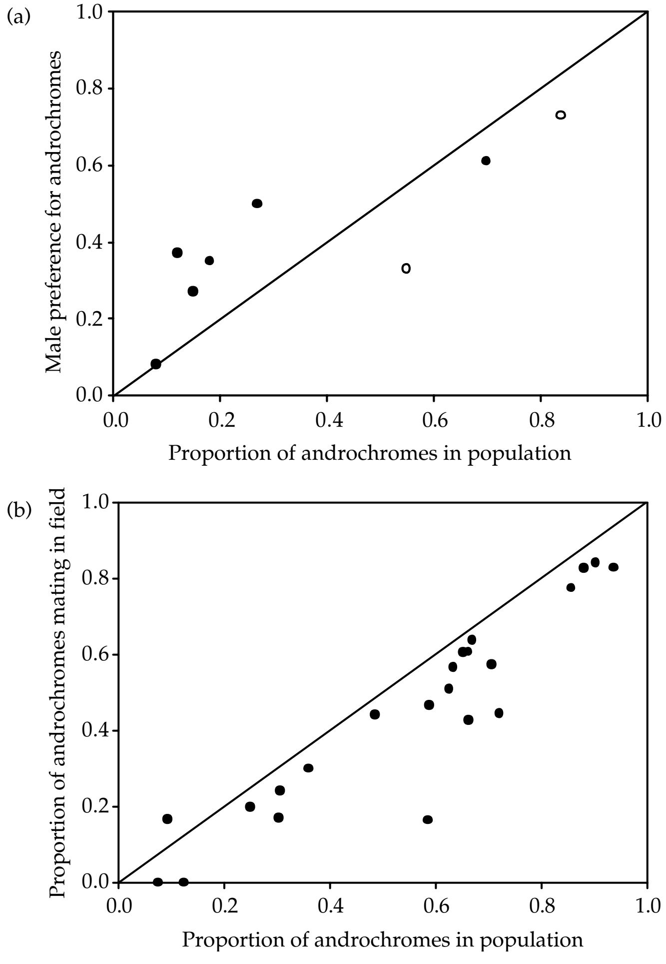

Figure 17.1 (a) Relationship between the proportion of androchrome females in a population (androchromes/all females) and male preference for the androchrome female in an experimental setting. Filled circles refer to binary choice experiments where males were offered the choice between an androchrome and a gynochrome female; open circles refer to trials where males were confronted with only androchromes and male sexual interest for this female morphs was scored. (b) Relationship between the proportion of androchrome females in a population (androchromes/all females) and the proportion of androchrome females found mating in the field. Data for these graphs were derived from Cordero and Andrés (1996); Van Gossum *et al.* (1999, 2001b); Cordero-Rivera and Sánchez-Guillén (2007).

than expected from their population frequency, with no element of frequency dependence based on relative frequencies of females (Cordero-Rivera and Sánchez-Guillén 2007) (Figure 17.1b). These contrasting results offer insight into the difficulty to test predictions on male mimicry or LMR. One likely explanation is that choice experiments measure mainly male preference (i.e. exclude most female behaviour), whereas field surveys are the combined result of male preference, morph conspicuousness, and female avoidance of male harassment.

In many damselflies, males search continuously for females, but females are not passive objects of male attention. It seems that morphs may sometimes differ in their response to male attention and also more generally in their behavioural patterns. For example, androchrome female *I. elegans* are more aggressive towards approaching males than gynochromes (Van Gossum *et al.* 2001a). Also, androchromes of *I. elegans* use more open habitat and fly less than gynochromes, which reside more within vegetation and fly longer distances (Van Gossum *et al.* 2001a). Female morphs therefore not only have contrasting coloration, but also show different behaviour. Consequently, manipulative experiments in which female behaviour is excluded or restricted may not adequately provide insights in the interaction between males and females in the field. It is interesting, in this context, that where sexual interactions among free-ranging individuals in natural populations have been studied, contrary to LMR predictions, it was found that the rarer morph (gynochrome) was more likely to receive male harassment (e.g. Sirot *et al.* 2003). Clearly, more studies following male–female interactions over a range of androchrome frequencies are needed.

17.6 Conspicuous or cryptic morphs: risks of being eaten?

As we have seen, sex-limited morphs have different phenotypes, and this appears relevant in the context of sexual selection. Two further questions are relevant: (1) do morphs differ in phenotypic traits other than colour, pattern or behaviour and (2) do phenotypic differences between morphs have additional consequences beyond those relating to reproductive success? At least for examples where polymorphism is not restricted to only one sex, it has been shown that different colour morphs may differ in traits as diverse as development, fecundity and disease resistance (e.g. Svensson *et al.* 2002; True 2003). Where morphs differ in other traits, then selection on these traits potentially can result in a correlated response in morph frequencies. Furthermore, if morphs differ not only with respect to reproductive success, but are differentially affected by other selective pressures, these may help explain how polymorphism is maintained. Although a variety of mechanisms are possible, the possibility of differential predation on the morphs has been discussed most frequently (see Box 17.2). For example, it is interesting that examples of Batesian mimicry and related polymorphisms are sometimes restricted only to females and one leading explanation is that females of these species are more exposed to predators than males (Stamps and Gon 1983; Ruxton *et al.* 2004).

It has been argued (e.g. Robertson 1985), but not formally shown, that both territorial males and male-like females in odonates are more conspicuous than the alternative morph and as a consequence are more prone to predation by visual hunters such as birds and dragonflies (see Box 17.2). To start addressing this question information is required on morph spectra, backgrounds, environmental light conditions, and also predator visual sensitivities. This research remains to be done.

Clearly if androchromes do suffer higher predation then this source of mortality could offset any benefit that androchromes would have in avoiding male harassment (e.g. Robertson 1985). Little is known, but where female morphs have been compared for mature daily survivorship using capture–mark–recapture data, female morphs did not differ (e.g. Fincke 1994; Cordero *et al.* 1998). Also, if predators preferentially attack conspicuous individuals, then males (and androchromes) should have lower survival rate than gynochrome females (all else being equal), yet males tend to have higher survival rates than females in the Coenagrionidae, one of the most polymorphic groups of damselflies (see Chapter 2 in this volume). Further, it appears that gynochromes, possibly as a consequence of behaviour, were far more likely to end up and die in spider webs than androchromes (Van Gossum *et al.*

2004). In addition, birds are important predators on newly emerged odonates that have difficulty flying, but these immature damselflies frequently do not show their mature coloration. Together, empirical support for predators favouring the relatively more conspicuous morph remains absent.

17.7 Conclusion and future avenues of research

The wide distribution of female-limited polymorphisms in odonates provides researchers with the opportunity to evaluate the validity, and generality, of proposed hypotheses for certain species by applying it to others with rather different life histories. Furthermore, given that several of these odonate species are widespread and common, research can be conducted in contrasting environments. However, one disadvantage of using odonates to study polymorphisms is (within insects at least) the relatively long generation time, making laboratory based multi-generational studies extremely laborious. Field experiments in which the relative densities of androchromes and gynochromes are manipulated are also challenging because of the typically high abundance of species and their ability to disperse, so that, in a few hours, populations can return to the pre-treatment density (Moore 1962). Experiments in which artificial enclosures are used offer one potential solution (see for example Van Gossum *et al.* 2005) and in the future we may see more of this type of experiment. With female-limited polymorphism so common among odonates and phylogenies appearing regularly in the literature, phylogenetically controlled analyses of the correlates of sex-limited polymorphism will also be forthcoming.

Several aspects of female-limited polymorphism in odonates deserve future attention. Most research has focused on selection acting on mature individuals; however, selection may also act on immature individuals or even on the much longer-lasting (in terms of time) larval stages (e.g. Abbott and Svensson 2007). This sort of research may be accelerated if the genes involved in the polymorphism could be better characterized, leading to diagnostic tests of morph identity at any stage in the life cycle. There are also several key gaps when it comes to researching mature adults. For example, there is a continued need for more detailed studies on the behaviour and success of female morphs in populations where androchromes are the majority female morph, since the main contending explanations are best distinguished under these conditions. It is also important to note that different morphs may differ in microhabitat use (e.g. Van Gossum *et al.* 2001a) and microhabitat use may relate to thermoregulation (e.g. Watanabe 1991), so more work is needed to elucidate the role of temperature in mediating morph frequency. As seen in vertebrates (e.g. Miles *et al.* 2007) morphs may differ in endocrine levels, which shape behaviour, physiology, and performance, and this research angle also remains unexplored in studying female-limited polymorphism in odonates.

Finally, we note that polymorphism is not only of interest in its own right, but may represent be a transient stage in sympatric speciation, particularly where assortative mating arises (Gray and McKinnon 2007). The case of the dragonflies *Palpopleura lucia* and *Palpopleura portia*, for more than 200 years considered two forms of the same species (see for example Tarboton and Tarboton 2002), but recently identified as good species using molecular techniques (Mitchell and Samways 2005), is a possible example of a colour polymorphism that predates speciation.

Acknowledgements

We thank Gerrit Joop and two anonymous referees for comments on an earlier version of the manuscript. ACR was supported by research grants from the Spanish Ministry of Education and Science (grants PB97-0379, BOS2001-3642, and CGL2005-00122). HVG is a postdoctoral fellow with the Fund for Scientific Research-Flanders (FWO).

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CHAPTER 18

Sexual size dimorphism: patterns and processes

Martín Alejandro Serrano-Meneses, Alex Córdoba-Aguilar, and Tamás Székely

Overview

Sexual differences in body size (sexual size dimorphism; SSD) are widespread among animals. Odonates exhibit variation in SSD that ranges from species in which females are the larger sex to species in which males are larger. The distribution of SSD in body length centres around monomorphism in Anisoptera, whereas body lengths of most Zygoptera are male-biased. We provide an overview of three major functional hypotheses of SSD: sexual selection, fecundity selection, and differential niche utilization. Evidence suggests that sexual selection acts mainly on males, whereas fecundity selection appears to influence female body size. Interestingly, the influence of sexual selection on body size depends on the agility of males, since sexual selection favours large size in males relative to females in non-agile territorial species, whereas in agile territorial and non-territorial species alike sexual selection favours small size, presumably because agility – and thus being small – is particularly important in such species. Fecundity selection appears to favour larger size in females via increased fecundity and longevity. We argue that these studies, however, were limited in that they focused on few hypotheses and used relatively crude data. Further tests are essential, in particular of viability selection, differential niche utilization, and fecundity selection. We conclude that odonatologists should continue collecting data on the ecology, behaviour, and life history of damselflies and dragonflies, since many species, especially the tropical ones, have not been studied in detail. These data, coupled with robust phylogenetic hypotheses, will allow us to tackle evolutionary questions, including the processes generating and maintaining SSD. Studies are also needed to understand the development of SSD throughout different life-history stages, and to reveal the genetic architecture of both body size and SSD.

18.1 Introduction

> So again, male dragon-flies (Libellulidae) are sometimes sensibly larger, and never smaller, than the females....
>
> Charles Darwin (1871, p. 321)

Differences in male and female body size (termed sexual size dimorphism; SSD) are common in many animals. Some of these differences are extreme. For example, male northern elephant seals (*Mirounga angustirostris*) are up to five times heavier than females (Andersson 1994), whereas blanket octopus (*Tremoctopus violaceus*) females may be 40 000 times heavier than males (Norman *et al.* 2002). Females are usually the larger sex (female-biased SSD) in many fish, spiders, and marine invertebrates, whereas males are typically the larger sex (male-biased SSD) in most birds and mammals (Blanckenhorn 2000; Blanckenhorn *et al.* 2007; Fairbairn *et al.* 2007).

This immense variation in SSD inspired several hypotheses that are aimed at explaining the variation in size across animal species ever since Darwin's (1871) seminal exposure of SSD (reviewed by Andersson 1994; Blanckenhorn 2005; Fairbairn *et al.* 2007). Darwin's original ideas on the evolution of SSD still form the foundation of modern research; nevertheless, their explanatory power, in a particular species or across a range of organisms, have remained controversial (Fairbairn *et al.* 2007).

Body size usually correlates with a number of physiological and fitness traits, and mating advantages (Blanckenhorn 2000, 2005; Fairbairn *et al.* 2007). Males and females are genetically nearly identical, yet they sometimes exhibit extreme differences in size. Therefore, since SSD affects and is affected by animal life histories, behaviour, development, and ecology, the understanding of the processes that cause SSD in animals provides a unique research opportunity to understand how evolution works (Fairbairn *et al.* 2007). That is, the study of SSD provides visible and testable evidence of the effect of natural and sexual selection and their capabilities to cause differentiation between the sexes, even under the influence of strong developmental and/or genetic constraints (reviewed by Blanckenhorn 2000, 2005; Fairbairn *et al.* 2007).

To date, most research on SSD has centred around two main issues (Fairbairn *et al.* 2007). First, it has addressed the adaptive significance (or functionality) of SSD; that is, researchers aim to explain the selective forces that shape and maintain the differences in body size between males and females, given that body size is typically correlated with reproductive success in both sexes (usually through mating success in males and fecundity in females). Second, it aims to explain the extent to which conflict within and between the genes that determines body size in both males and females constrains the evolution of SSD (Fairbairn *et al.* 2007). It is noteworthy that a vast majority of

Box 18.1 The phylogenetic comparative approach

The comparative analysis of traits (Harvey and Pagel 1991) has become a major research method in biology. Evolutionary biologists use comparative methods extensively to explore (1) whether patterns exist across a wide range of taxa, (2) the timing and mode of evolution, and (3) hypotheses that do not lend themselves to an experimental approach (Bennett and Owens 2002).

The comparative approach has been applied to evolutionary biology to address two major processes in the evolution of traits within and across species (see examples in Pagel 1999 and Martins 2000). First, comparative methods have been used to reconstruct the evolution of one or many traits by adopting an evolutionary model such as maximum parsimony or maximum likelihood. This enables researchers to determine whether transitions in trait values or states occur, and to determine whether there exist any differences in the direction and frequency of these transitions when compared with a suitable null model.

The second major use of the comparative approach is to explore relationships between traits across species. Straightforward cross-species analyses (which usually employ species as data units) and analysis methods, such as least-squares regression or multiple regression, are not appropriate. The reason is that species (data units) are not independent from each other since closely related taxa are more likely to share a trait than more distantly related taxa due to common ancestry. Phylogenetically independent contrasts (Felsenstein 1985) or generalized least squares (Martins and Hansen 1997; Pagel 1997) are two of several methods proposed to deal with the statistical non-independence of species.

For details of phylogenetic comparative methods see reviews by Harvey and Pagel (1991), Freckleton *et al.* (2002), and Blomberg *et al.* (2003). Appropriate software is available for most of these methods (e.g. CAIC, COMPARE, CONTINUOUS, and DISCRETE), and their manuals provide detailed examples. For further explanations of how to access and use such software see the websites of Joe Felsenstein (http://evolution.genetics.washington.edu/phylip/software.html), Emilia Martins (http://www.indiana.edu/~martinsl/index_files/programs.html), and the Evolutionary Biology Group at the University of Oxford (http://evolve.zoo.ox.ac.uk/software.html).

research has concentrated on a few selected species among birds, mammals, reptiles, insects, and spiders. Curiously, the patterns of SSD and their possible causes in odonates have rarely been investigated. For instance, less than a handful of studies have investigated SSD in odonates using modern comparative approaches (Box 18.1), and there is a general lack of field- and laboratory-based studies. We genuinely believe, therefore, that SSD in the Odonata constitutes a relatively new and promising avenue of research that can take advantage of the wide variety of habitats, morphology, development, feeding behaviour, and mating strategies of this aerial insect taxon to expand understanding of the adaptive and genetic processes that may select for different body sizes of males and females.

In this chapter we review SSD patterns in odonates, partly using unpublished results, and integrate comparative analyses with single-species studies to evaluate the possible processes that shape their patterns of SSD.

18.2 Measuring SSD in odonates

There are several ways of measuring SSD (Lovich and Gibbons 1992; Fairbairn 2007a), and here we use $\log_{10}$(male body size) – $\log_{10}$(female body size); thus positive values indicate male-biased SSD, whereas negative values indicate female-biased SSD. Log-transformed data are commonly used to calculate SSD. Differences between male and female size expressed as a logarithm have statistical properties that are preferable to those of ratios because the latter are not symmetrical and therefore violate the assumptions of certain statistical tests.

The rigid, fixed exoskeleton of odonates makes it a convenient morphological measure for estimating body size. For instance, wing length is commonly used as a measure of body size (Corbet 1999). Different morphological traits may exhibit different directions of SSD (e.g. Fairbairn 2007b; Székely *et al.* 2007), thus it is useful to calculate several measures of SSD including body length, wing length, and head width. Note that body mass is a less-desirable measure of size since it varies with age and body condition (Anholt *et al.* 1991; see Strobbe and Stoks 2004 for further limitations of body mass). Among anisopterans, for example, SSD in both body length and head width tend to be symmetrical around zero; that is, monomorphic (Wilcoxon one-sample tests with test median = 0 in all cases; W = 1159, $P = 0.3028$; W = 787, $P = 0.8900$, respectively; Fig. 18.1a), whereas wing lengths tend to be female-biased (W = 473, $P = 0.0004$; Fig. 18.1a). In zygopterans body-length SSD is male-biased (W = 1808, $P = 0.0009$; Figure 18.1b), head-width SSD is symmetric around zero (W = 717.5, $P = 0.1022$; Fig. 18.1b), and wing lengths are female-biased (W = 191, $P = 0.0001$; Figure 18.1b). The direction of SSD may also vary within a single species: in the calopterygid *Hetaerina americana*, for instance, body length, head width, and body mass are male-biased, whereas wing length is female-biased (Serrano-Meneses *et al.* 2007a).

Although no single measure of SSD is ideal for estimating body size, here we use body length as the main proxy variable for body size.

18.3 Patterns of SSD in odonates

18.3.1 Adults

Odonata exhibit both male-biased (e.g. *Orthemis ferruginea*, *H. americana*) and female-biased SSD (e.g. *Dromogomphus spinosus*, *Enallagma antennatum*), sometimes within a single genus (e.g. *Libellula*; Serrano-Meneses *et al.* in press). Note that the latter fact appeared to escape the attention of Charles Darwin; this is unusual, given Darwin's outstanding knowledge of natural history. At the family level, males are larger on average than females, for instance, in Calopterygidae (Wilcoxon one-sample tests, W = 648, $P = 0.0001$; Figure 18.2) whereas females are larger in Coenagrionidae (W = 84, $P = 0.034$; Figure 18.2). A range of SSD values may be observed within a single family (e.g. Gomphidae; W = 49, $P = 0.839$; Figure 18.2).

18.3.2 Larvae

Adult SSD may simply be a consequence of size dimorphism already existing during early development. Alternatively, SSD in adults may result from sexually monomorphic larvae. These alternatives were tested by rearing seven species of Odonata (*Anax imperator*, *Cercion lindeni*, *Cordulegaster boltonii*,

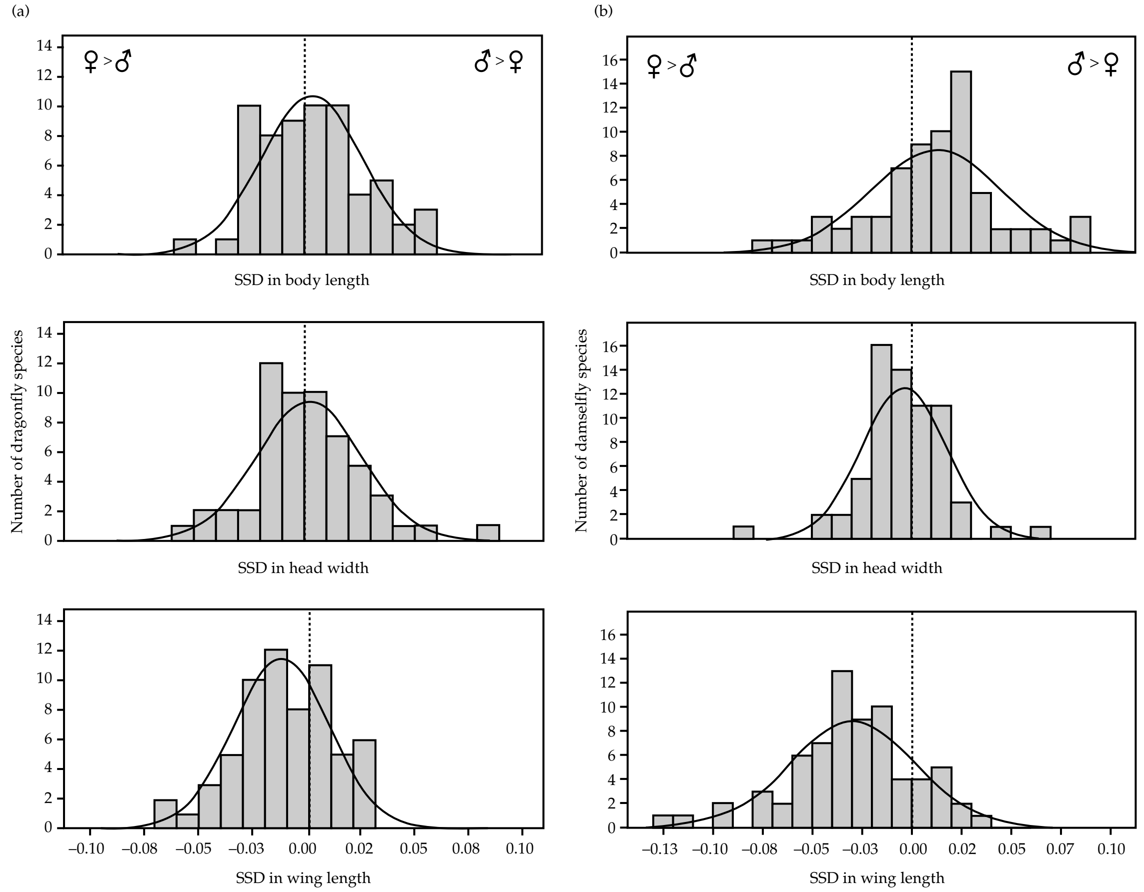

Figure 18.1 Distribution of SSD in body length, head width, and wing length in (a) Anisoptera and (b) Zygoptera. The dotted vertical line represents monomorphism. Bars represent number of species. SSD was calculated as $\log_{10}$(male size) – $\log_{10}$(female size).

Ischnura graellsii, *Onychogomphus uncatus*, *Oxygastra curtisii*, and *Platycnemis acutipennis*) in the laboratory (Serrano-Meneses *et al.* 2007b). The degree and direction of SSD were measured and compared in both larvae and adults using the same individuals. The study revealed somehow unexpected results: the larval and adult SSD were consistent in *A. imperator*, *Ce. lindeni*, *Co. boltonii*, *I. graellsii*, and *Ox. curtisii*, whereas in *On. uncatus* dimorphic adults emerged from monomorphic larvae, and larval SSD disappeared in adult *P. acutipennis*. Serrano-Meneses *et al.* (2007b) suggested that (1) developmental pathways affecting growth and metamorphosis and, ultimately, adult sizes can differ among closely related odonates and (2) the selective pressures driving SSD can differ in larvae and adults within a single species.

18.4 The adaptive significance of SSD

18.4.1 Functional hypotheses of SSD

Three major functional hypotheses have been advanced to explain the selective processes separating the sizes of the sexes: sexual selection, differential niche utilization (or ecological division of resources), and fecundity selection (reviewed by Blanckenhorn 2005; Fairbairn *et al.* 2007). These hypotheses are usually tested on fully grown animals using the evolutionary comparative (see

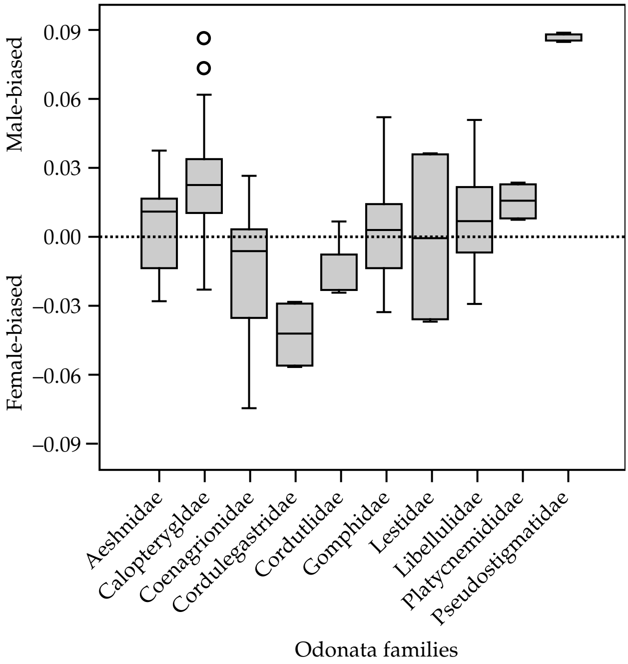

Figure 18.2 SSD in body length of Odonata families (median, upper and lower quartiles; open circles are extremes). The dotted line indicates monomorphism. The number of species in each family is 7, 36, 25, 2, 4, 13, 2, 35, 2, and 2, from left to right. See Appendix 18.1 for the data-set.

Box 18.1) and/or behavioural ecology approach, whereas the development of body size throughout the ontogeny of individuals is investigated rarely (Badyaev 2002; Blanckenhorn *et al.* 2007; Fairbairn *et al.* 2007).

Darwin (1871) proposed that SSD was largely due to fecundity selection favouring large female size, and/or sexual selection favouring large male size. These ideas are supported by a number of studies (reviewed by Andersson 1994; Blanckenhorn 2000, 2005; Fairbairn *et al.* 2007). However, directional fecundity and sexual selection are unlikely to be the only selective pressures shaping SSD, because body size is likely to be additionally influenced and/or constrained by viability selection (reviewed by Shine 1989; Blanckenhorn 2000) and genetic correlations, as is the case for many other morphological traits (e.g. Temeles *et al.* 2000; Fairbairn 2007b). The interplay between different selective pressures acting on males and females will ultimately determine SSD within a species, assuming that the underlying genetic correlations between males and females are low so that the sexes may achieve their respected optima.

In the following sections we overview functional hypotheses of SSD and highlight the strengths and weaknesses of the studies that have produced supporting data for each hypothesis.

18.4.2 Sexual selection

Darwin (1871) proposed that certain individuals have reproductive advantages over other individuals of the same sex. Thus, when competition between individuals of the same sex (usually the males) is more intense than between the individuals of the other sex, sexual selection will drive the size of the more competitive sex towards its optimum (Fairbairn *et al.* 2007). There are two ways in which sexual selection may influence SSD, since the optimum size of the competing sex may depend on whether sheer power or agility is prized in male-male competition or in the choice of females (Jehl and Murray 1986; Székely *et al.* 2007). On the one hand, sexual selection is expected to favour large males relative to females (i.e. male-biased SSD) when sheer bulk increases the chances of winning, since the power of a blow increases with muscle size (Lindenfors *et al.* 2007). Sexual selection may also favour large male body size in species in which males compete intensely for females (Lindenfors *et al.* 2007; Székely *et al.* 2007), which would be the case for species with polygynous mating systems (Owens and Hartley 1998). This is because large males are able to endure competition for longer than small males, and are preferred by females (for instance, if these males offer better resources to females). Large size may additionally enable males to coerce females and induce them to mate (reviewed by Andersson 1994). On the other hand, sexual selection will favour small male size relative to females (i.e. female-biased SSD) if agility and manouverability enhance the males' success in aerial combats (Andersson and Norberg 1981). Small male size may be reinforced by female preference for small, agile males (Hakkarainen *et al.* 1996; Blomqvist *et al.* 1997).

In odonates, it is generally believed that sexual selection favours large size in males of territorial species (see also Chapter 16 in this volume). For instance, in a seminal study, Anholt *et al.* (1991) analysed the patterns of mass gain in several odonate species (see also Chapter 13) and showed that females were usually heavier than males; however, in territorial species this difference was less apparent or even opposite. From this study it can be concluded that the intensity of sexual selection, by way of territoriality, favours larger-than-average male size (with respect to female size) in territorial odonates. Further support for this hypothesis was generated by Sokolovska *et al.* (2000) and Johansson *et al.* (2005). Sokolovska *et al.* (2000) used meta-analysis to investigate the relationship between body-size and fitness components in odonates and found that large size increases male fitness (e.g. longevity, mating rate, lifetime mating success, and territorial defence) in territorial species. Their results also suggest that in non-territorial males large size significantly affects longevity and lifetime mating success. Johansson *et al.* (2005) for the first time investigated the relationship between body size and the extent of SSD (Rensch's rule; see Box 18.2) in Odonata using a phylogenetic comparative method (Box 18.1). They concluded that odonates exhibit the full scope of Rensch's rule, and suggested that it can be explained by sexual selection favouring large male size in territorial species.

These studies, however, have a number of limitations. Thompson and Fincke (2002) highlighted the methodological problems in terms of sampling and statistical methods of the study by Sokolovska *et al.* (2000). They further criticized Sokolovska *et al.* for failing to test the role of stabilizing selection

Box 18.2 Rensch's rule

Across subspecies of a species, or species of a taxon, males and females often show a puzzling relationship between SSD and body size: SSD increases with body size in species in which males are larger than females, and it decreases with body size in species in which females are larger than males (Rensch 1950; Fairbairn 1997; Figure 18.3).

This pattern is exhibited by a wide range of animal taxa including mammals, birds, reptiles, and insects (Abouheif and Fairbairn 1997; Colwell 2000; Blanckenhorn *et al.* 2007; Székely *et al.* 2007). A number of hypotheses have been proposed to explain Rensch's rule for specific taxa (reviewed by Reiss 1986; Webster 1992), although it is generally agreed that sexual selection acting on male size is likely to account for the observed allometric pattern (Abouheif and Fairbairn 1997; Székely *et al.* 2004). On the one hand, sexual selection is likely to promote increases in male size that will be followed by lesser increases in female size due to the genetic correlation between the sexes, explaining the greater extent of SSD in large species. On the other hand, sexual selection may also favour small male size and hence its reduction over time, followed by lesser decreases in female size. Therefore, male body size is assumed to change more rapidly than female size over evolutionary time, not least also because female size may be constrained by fecundity selection (Abouheif and Fairbairn 1997).

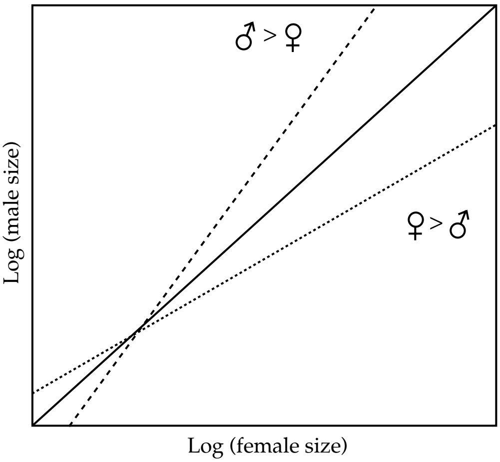

Figure 18.3 Rensch's rule when $\log_{10}$(male size) is plotted against $\log_{10}$(female size). The solid line represents isometry (size of males = size of females). The dotted line represents an allometric relationship in which female size varies more among species than male size, and therefore its regression slope (β) is less than 1. The dashed line represents an allometric relationship in which male size varies more among species than female size and therefore $\beta > 1$. Deviations of these lines from the 1:1 line illustrate the degree of SSD. When $\beta > 1$ SSD declines as size increases for female-biased species, but increases with size for male-biased species, as predicted by Rensch's rule. If $\beta < 1$, the pattern of allometry is reversed, and is inconsistent with the Rensch's rule (adapted from Fairbairn 1997).

on body size. Under stabilizing selection fitness is not a linear function of size; therefore the benefits of large body size would be balanced by the benefits of small size, which would favour intermediate body size. Second, the study by Johansson *et al.* (2005) was limited because they did not test functional hypotheses of SSD and also failed to investigate the link between sexual selection and Rensch's rule. Furthermore, the prediction that male-biased SSD is generally favoured in territorial species is not always met (reviewed by Fincke *et al.* 1997): although certain territorial species exhibit male-biased SSD (e.g. *H. americana*, *Megaloprepus coerulatus*; Serrano-Meneses *et al.* 2007a; Fincke 1984, respectively), many others do not (e.g. *L. quadrimaculata*, *Plathemis lydia*; Convey 1989; Koenig and Albano 1987, respectively).

In a recent study, Serrano-Meneses *et al.* (in press) used phylogenetic comparative methods (Box 18.1) (1) to test whether sexual selection (in the form of territoriality, non-territoriality, and male agility) is related to the degree and direction of SSD, (2) to expand on work by Johansson *et al.* (2005) in terms of the number of species for testing allometry consistent with Rensch's rule, and (3) to test whether sexual selection influences Rensch's rule. First, Serrano-Meneses *et al.* (in press) showed that male-biased SSD increases with territoriality only in Zygoptera whereas non-agile territorial Odonata exhibit male-biased SSD and agile territorial odonates exhibit monomorphism and female-biased SSD in some cases (Figure 18.4). In contrast, neither territoriality nor male agility are related to SSD in non-territorial odonates. Second, similar to Johansson *et al.* (2005), Serrano-Meneses *et al.* (in press) found that Rensch's rule is exhibited by odonates. However, Anisoptera showed an allometry not consistent with Rensch's rule (Figure 18.5a), whereas Zygoptera showed the full scope of Rensch's rule (Figure 18.5b). Finally, Serrano-Meneses *et al.* (in press) showed that the mating system (territoriality or non-territoriality) contributes to Rensch's rule in Odonata and Zygoptera. Note, however, that the mating system is not the sole selective pressure that influences Rensch's rule (see below).

These results suggest why previous studies came to different conclusions on the effects of sexual selection on SSD (e.g. Fincke *et al.* 1997; Sokolovska *et al.* 2000; Johansson *et al.* 2005). Thus, the expected relationship between territoriality and male-biased SSD is only exhibited by Zygoptera, but not by Anisoptera. This is consistent with single-species studies of SSD in Zygoptera. On the one hand, large males are more successful in territory acquisition and defence in *H. americana*, *M. coerulatus*, *Mnais pruinosa*, and *Paraphlebia quinta* (Serrano-Meneses *et al.* 2007a; Fincke 1984; Tsubaki *et al.* 1997; González-Soriano and Córdoba-Aguilar 2003, respectively). On the other hand, intermediate and small male sizes are usually favoured in non-territorial males, for instance in *Coenagrion puella*, *Enallagma boreale*, *Enallagma hageni*, *Ischnura elegans*, and *Lestes sponsa* (Banks and Thompson 1985; Anholt 1991; Fincke 1982; Cordero *et al.* 1997; Stoks 2000, respectively). Interestingly, in Stok's (2000) study, stabilizing selection on male size is suggested to result from

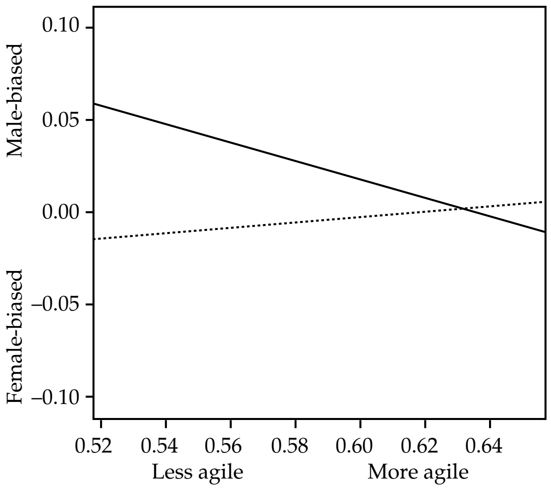

Figure 18.4 The predicted relationship of SSD in Odonata in relation to male agility in non-territorial (dashed line) and territorial (solid line) species. Mating system (territoriality and non-territoriality) and male agility (estimated from wing shape) were used as estimates of the intensity of sexual selection (after Serrano-Meneses *et al.*, in press).

sexual selection alone favouring small male size (see below).

Serrano-Meneses *et al.* (in press) suggest that small male size may be advantageous for males of certain territorial anisopteran species, because (1) it may enhance male agility and (2) it may be energetically more efficient for males that compete, defend territories, mate mostly on the wing, and search actively for females. First, if male–male competition requires high speed and/or complicated manoeuvres (e.g. zig-zag flying, hovering) then these males would benefit from smaller or intermediate sizes. Second, small males may have lower flying costs per unit time compared with large males. This would enable small males to allocate more time for searching potential mates rather than foraging (the 'Ghiselin–Reiss small male hypothesis'; Blanckenhorn *et al.* 1995). This could explain why small and intermediate-sized males are more successful in some territorial anisopterans (e.g. *L. luctuosa*, *L. quadrimaculata*, *P. lydia*, *Sympetrum rubicundulum*; Moore 1990; Convey 1989; Koenig and Albano 1987; Van Buskirk 1987, respectively). Therefore, sexual selection may not only favour large male size but also small male size in territorial and non-territorial odonates. This process may explain why anisopterans do not show a clear relationship between increasing territoriality and male-biased SSD, although it is likely that other selective pressures are involved. For example, many migratory species fall into this suborder (Corbet 1999).

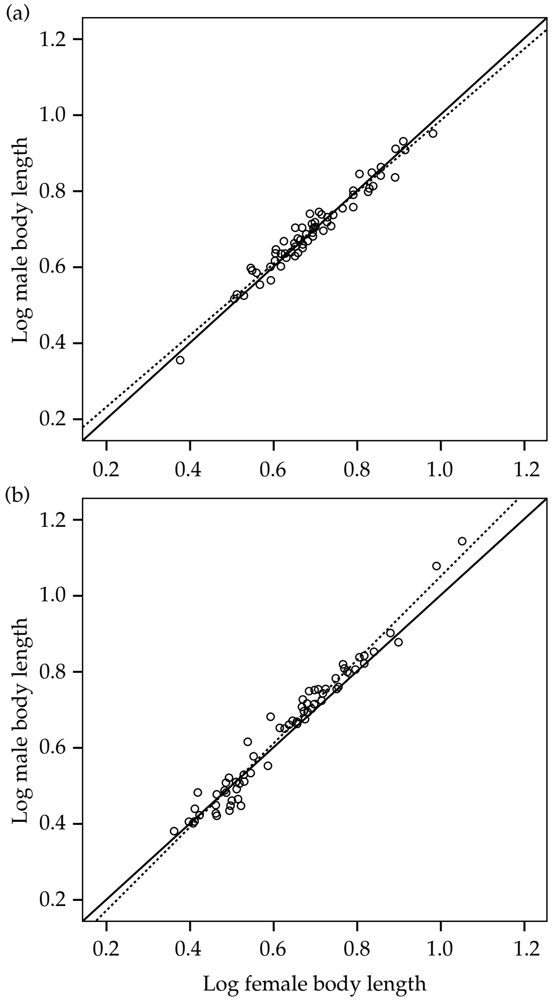

Figure 18.5 Log$_{10}$(male body length) on log$_{10}$(female body length) in (a) Anisoptera and (b) Zygoptera. Solid lines indicate the isometric relationship, and dashed lines represent the fitted relationship using major axis regression (MA). The sexes scale isometrically in Anisoptera, as indicated by an MA slope not significantly different from unity ($\beta = 0.963$; 95% confidence interval, 0.912 – 1.016), whereas the Zygoptera exhibit Rensch's rule ($\beta = 1.115$; 95% confidence interval, 1.068 – 1.165).

18.4.3 Fecundity selection

Fecundity selection is likely to occur if large females achieve higher reproductive success through higher capacity for producing and laying eggs (Honěk 1993). Consistent with fecundity selection, studies of spiders, insects, and ectothermic vertebrates (fish, frogs) demonstrated positive relationships between body size and fecundity (Fairbairn *et al.* 2007). Fecundity selection may also favour large females if they provide better parental care that enhances offspring survival (e.g. in mammals and birds that have only few offspring; Ralls 1976; Wauters and Dhondt 1995).

Only few studies have explored the direct relationship between female body size and fecundity in Odonata. Using an optimization model, Crowley and Johansson (2002) showed that large body size increases female fecundity (see also Crowley 2000). This theoretical prediction was supported by empirical studies: for instance *Coen. puella*, *I. graellsii*, *P. lydia*, and *Pyrrhosoma nymphula* (Banks and Thompson 1987; Cordero 1991; Koenig and Albano 1987; Gribbin and Thompson 1990, respectively) have all shown that female fecundity generally increases with female body size.

However, Fincke and Hadrys (2002) showed that in female *M. coerulatus* clutch size correlates positively with female body size but their number of surviving offspring does not. Furthermore, Strobbe and Stoks (2004) found no relationship between female size (mass, head width, abdomen length, and wing size) and clutch traits (egg number, mean egg size, and mean hatching date) in *Enallagma cyathigerum*. Similarly, female body size and the number and size of eggs within the abdomen showed a non-significant relationship in *H. americana* (Serrano-Meneses *et al.* 2007a).

In summary, although fecundity selection is expected to be a major process selecting for large body size in females, the results of theoretical and empirical studies are conflicting. More studies are needed to validate the generality of this hypothesis.

18.4.4 Differential niche utilization

Selection may act on body sizes of males and females simultaneously to avoid competition with each other, or to enhance foraging efficiency when resources are scarce (Selander 1966; Shine 1989). Thus specialization in the exploitation of resources is expected to lead to morphological divergence (Temeles *et al.* 2000). In odonates, to our knowledge, virtually nothing is known regarding sex-specific use of habitats or exploitation of resources. Although it is known that adult males and females often differ in habitats (Corbet 1999), it is not known whether they differ in feeding habits and whether such differences relate to SSD. Adult body size is achieved through an extended pre-adult period in which environmental, developmental, and activity factors interact and determine adult body size. Thus our understanding of the processes that select for adult SSD will benefit from data on differential use of resources between the sexes during the larval stage.

We are aware of only one study that has produced such data. Fincke (1992) showed that large territorial males of *M. coerulatus* control large water-filled tree holes, oviposition sites that are rich in resources. These large oviposition sites produced the largest males, compared with the smaller oviposition sites controlled by smaller males. This effect, however, was only significant for male, but not female body size. Fincke (1992) argued that males emerging from large tree holes may already be genetically predisposed to develop large body sizes so that the high availability of resources in such oviposition sites may maximize the expression of body size. Note that Fincke's (1992) proposition refers to sexual selection rather than natural selection on male size, since the emergence of large male offspring depends to some extent on the ability of large males to control large oviposition sites.

In other taxa, much research has concentrated on how differences in sex-specific development and larval activity (which increases with higher resource availability) determine adult SSD (e.g. Blanckenhorn *et al.* 2007). For species with fixed developmental times, adult SSD is expected to be achieved through sex differences in growth rates mediated by larval activity (Crowley 2000; Crowley and Johansson 2002). However, in odonates empirical tests are inconsistent with this prediction. For instance, Johansson and Rowe (1999) found no sex-specific differences in growth rate in *Lestes congener*, and Johansson *et al.* (2001) found no sex-specific differences in developmental times or activity in *L. sponsa*. For species with flexible development, adult SSD is assumed to be achieved through differences in developmental times. Consistent with this, Mikolajewski *et al.* (2007) showed that male-biased SSD in *Libellula depressa* was achieved through males developing for longer than females rather than by sex-specific differences in activity. In contrast, in *Ischnura verticalis* males developed faster than females and were more active than females in laboratory conditions (Baker *et al.* 1992).

These discrepancies between theoretical expectations and empirical studies highlight the need for further empirical studies. In addition, the results may depend on the measure of body size. Strobbe and Stoks (2004) have shown that when the larvae of *E. cyathigerum* are subjected to a developmental-time constraint, both larval development and growth rate accelerate. Nevertheless, whereas head width remained constant at emergence despite the shorter development time, indicating faster growth, body mass did not, resulting in individuals with lower body mass at emergence. Low body mass at emergence may not necessarily be a problem since odonates can augment body mass during the teneral stage (Corbet 1999).

18.5 Adaptation and genetics of SSD

Most studies on SSD in odonates have focused on the adaptive significance of SSD and little attention has been drawn to the possible genetic constraints of SSD posed by genes that affect both male and female fitness. By considering both adaptive and genetic influences, theory predicts that when SSD reaches its evolutionary equilibrium, stabilizing selection should maintain the optimum size of each sex (Lande 1980; Fairbairn 2007b). However, genetic conflict between the sexes may cause an evolutionary lag in the attainment of SSD, resulting in opposite directional selection on males and females (Lande 1980; Fairbairn *et al.* 2007). In a series of studies in water striders, *Aquarius remigis*, Fairbairn *et al.* (2007b) revealed that primarily fecundity selection in females and sexual selection in males drives the adaptive divergence in body size between the sexes, and the mean overall sizes of the sexes were found to be close to their selective optima. This suggests that the respective sizes of the sexes are at equilibrium. Despite the expectation that the estimated high genetic correlations between the sexes should constrain the evolution of SSD, it appears that the genetic structure of both males and females have evolved in response to sexually antagonistic selection, thus enabling the sexes to respond adaptively to differential selective pressures. Ideally a similar approach, which requires the estimation of net adult fitness and genetic correlations between the sexes, should be applied to odonates to determine the influence of genetic constraints on SSD.

18.6 Conclusions and future directions

We have shown that odonates show a range of SSD including female-biased and male-biased SSD. This pattern, however, depends somewhat on the morphological trait measured. An evaluation of the published studies on odonate SSD shows that odonates exhibit Rensch's rule only in the Zygoptera but not in the Anisoptera. Although sexual selection seems to provide some explanatory power to Rensch's rule, it is not the sole selective process shaping the allometric pattern. Other hypotheses, such as female fecundity, sex-differential use of niches, or sex-specific differences in growth rates (e.g. Blanckenhorn *et al.* 2007) should be used to investigate the proximate causes of Rensch's rule.

In non-agile territorial odonates, sexual selection is related to evolutionary increases in male-biased SSD, but in agile territorial odonates sexual selection is correlated with evolutionary increases in female-biased SSD. The need for more agility in males, as occurs in many avian taxa (e.g. Székely *et al.* 2007), may have selected for small male size. We propose that selection for agility may be more necessary in non-territorial Zygoptera and generally in both territorial and non-territorial Anisoptera. This may explain why no relationship exists between territoriality and SSD in Anisoptera: territorial and non-territorial species can benefit from small male size, although this requires further evidence.

Note, however, that the above process is presumed to act only on males. This assumption may not be fully correct, because females may also compete over mates. This implies that the same processes proposed to influence male size can in principle influence female body size. Although the evidence demonstrating the advantages of large male size in sexual selection is overwhelming (Fairbairn *et al.* 2007), only a few studies have shown that sexual selection may favour large female size, and no study has found sexual selection favouring small size in females (reviewed by Blanckenhorn 2005).

We identify six areas where advances should be made in the near future in odonate research. First, the selective pressures affecting SSD in the larva stage are largely unknown, even though theory predicts that time and environmental constraints should cause plasticity in the development of odonates, and supporting empirical evidence that this occurs sex-specifically is scarce. Second, phylogenetic comparative methods are excellent tools for revealing macroevolutionary patterns, but they are limited in that they rely on events that took place in the past, and most of these methods are correlational. Therefore, the results of phylogenetic comparative methods should be, when possible, assessed empirically and experimentally to broaden the understanding of the processes behind the extant patterns of SSD. Third, the patterns of selection on male size in those species where males occur as territorial and non-territorial morphs have not been investigated thoroughly. Such male dimorphism is thought to be determined genetically (Tsubaki *et al.* 1997) and driven by a trade-off between reproductive advantages and longevity, underpinned by differences in energy expenditure between the morphs (Plaistow and Tsubaki 2000). Although it is known that large size is associated with mating success in territorial males and that it confers no mating advantages to non-territorial males, no study has measured the selection acting on male size in such species. Studies concentrating on the selection acting on the body size of both morphs may shed light on the opportunities for body-size diversification in species with high levels of sexual selection. Fourth, SSD is expected to evolve in response to selection associated with the differential reproductive roles of males and females (Fairbairn 2007b); nevertheless, whether body size is correlated genetically between the sexes and whether these genetic correlations constrain the evolution of SSD is virtually unknown in odonates. Adopting a quantitative genetic approach in the study of SSD in odonates will allow us to assess the relative strength of selections acting on adults and larvae, and predict how populations should change in the future given the genetic correlations and heritabilities of traits. Fifth, there is a prevalent, simplistic view in behavioural ecology that large size is always better. Thompson and Fincke (2002) have criticized this view by arguing that if large size provided fitness benefits to all taxa, animal lineages would show the tendency to increase in size over time. According to Thompson and Fincke (2002) stabilizing selection may be more common in nature than is thought. The development of large size and adult size itself is expected to be penalized or regulated by natural selection (Blanckenhorn 2000); however, there is a documented phyletic size increase over time (Cope's rule; Cope 1896; Kingsolver and Pfenning 2004) even when this increase in size accelerates the rates of extinction. There are of course, exceptions to this rule; in such taxa, selection for decreased developmental time may halt the selection for increased size, whereas in taxa that exhibit Cope's rule, selection for increased size may predominate over selection for decreased developmental time (Kingsolver and Pfenning 2004). More research is needed to determine whether overall selection on large size compared with selection on developmental time is variable across taxa and whether this variation is likely to influence Cope's rule (Kingsolver and Pfenning 2004).

Finally, we encourage fellow odonatologists to find species and populations with new and puzzling breeding systems because, ultimately, much of what we know is driven by curiosity in natural history.

Acknowledgements

We would like to thank Wolf U. Blanckenhorn for his comments, which greatly improved an earlier version of this chapter. We are greatful to David Goodger (Odonata collection, Natural History Museum, London, England) and Enrique González-Soriano (Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico), for allowing M.A.S.-M. to measure specimens of the Odonata collections. M.A.S.-M. and T.S. would like to thank A.C.-A. for his effort in editing this volume and for inviting this contribution. M.A.S.-M. was supported by CONACyT, Mexico (Apoyos integrales para la formación de Doctores en Ciencia, 58784).

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Appendix 18.1 Data used in the study and references

Male and female body size is shown as the mean body length, head width, and wing length (in cm) of at least three individuals per sex.

Species	Body length (cm)		Head width (cm)		Wing length (cm)		References
	Male	Female	Male	Female	Male	Female	
Aeshna grandis	7.039	6.857	0.996	0.993	4.801	4.783	3, 5
Anaciaeschna isosceles	6.417	6.745	0.991	0.952	4.328	4.474	3, 5
Anax imperator	6.927	7.194			4.908	4.839	1, 5
Anotogaster sieboldii	8.976	9.596	1.232	1.377	5.475	6.330	3, 5
Archineura hetaerinoides	7.556	7.964	0.784	0.876	4.693	5.284	3, 5
Archineura incarnata	8.013	7.617	0.845	0.842	4.675	5.186	3, 5
Argia plana	3.420	3.510			1.980	2.460	3, 5
Argia sedula	3.320	3.120			1.880	1.980	3, 5
Arigomphus cornutus	4.845	4.757	0.727	0.783	2.828	2.950	3, 5
Atrocalopteryx atrata	6.294	5.985	0.612	0.621	4.024	4.211	3, 5
Boyeria irene	6.309	6.153			4.127	4.320	4, 5
Brachyton pratense	5.470	5.520			3.290	3.430	4, 5
Caliaeschna microstigma	6.298	6.714	0.959	1.005	4.701	5.099	3, 5
Caliphaea confusa	4.462	4.228	0.516	0.514	2.917	3.039	3, 5
Calopteryx aequabilis	5.092	4.677	0.567	0.554	3.292	3.259	3, 5
Calopteryx amata	5.537	5.238	0.583	0.602	3.689	3.913	3, 5
Calopteryx cornelia	7.135	6.968	0.726	0.737	4.536	5.061	3, 5
Calopteryx exul	5.184	4.983	0.564	0.583	3.007	3.178	3, 5
Calopteryx haemorrhoidalis	4.980	4.717			2.981	3.250	3, 5
Calopteryx intermedia persica	4.659	4.544	0.559	0.550	2.728	3.136	3, 5
Calopteryx japonica	5.749	5.710	0.628	0.628	3.592	3.984	3, 5
Calopteryx maculata	5.204	4.766	0.554	0.564	3.101	3.164	3, 5
Calopteryx orientalis	4.599	4.548	0.555	0.567	2.988	3.240	3, 5
Calopteryx splendens	4.557	4.339	0.537	0.553	2.865	3.108	3, 5
Calopteryx syriaca	5.049	4.898	0.559	0.575	3.043	3.326	3, 5
Calopteryx virgo	4.679	4.431	0.523	0.536	2.894	3.181	3, 5
Calopteryx xanthostoma	4.640	4.527	0.571	0.555	2.858	3.265	3, 5
Celithemis eponina	3.838	3.627	0.628	0.597	3.423	3.262	3, 5
Chlorocypha curta	3.034	2.627	0.468	0.460	2.196	2.374	3, 5
Chlorogomphus brunneus	8.150	7.805	1.092	1.079	5.088	5.410	3, 5
Coeliccia loogali	4.913	4.823	0.502	0.512	2.728	2.751	3, 5
Cordulegaster boltonii	6.855	7.785			4.090	4.588	4, 5
Crocothemis erythraea	3.898	3.536	0.644	0.608	3.104	2.898	1, 5
Dromogomphus spinosus	5.732	6.183	0.723	0.764	3.530	3.820	3, 5
Echo modesta	5.682	5.323	0.653	0.629	4.003	3.842	3, 5
Enallagma antennatum	2.721	3.132	0.355	0.367	1.515	1.813	3, 5
Enallagma aspersum	2.808	3.148	0.360	0.397	1.656	1.783	3, 5
Enallagma boreale	3.100	3.265	0.416	0.428	1.917	2.048	3, 5
Enallagma carunculatum	3.229	3.244	0.404	0.395	1.817	1.872	3, 5
Enallagma civile	3.210	3.065	0.380	0.380	1.960	1.910	2, 5
Enallagma clausum	3.198	3.295	0.389	0.389	1.931	2.096	3, 5
Enallagma cyathigerum	3.035	3.075	0.410	0.395	2.050	2.050	2, 5
Enallagma divagans	2.890	3.174	0.321	0.326	1.746	1.976	3, 5
Enallagma doubledayi	2.916	3.281	0.391	0.418	1.688	2.018	3, 5
Enallagma ebrium	3.001	2.914	0.388	0.348	1.657	1.670	3, 5
Enallagma exsulans	3.245	3.400	0.365	0.350	1.900	2.210	2, 3, 5
Enallagma geminatum	2.540	2.570	0.340	0.355	1.405	1.589	3, 5
Enallagma hageni	2.807	2.902	0.383	0.361	1.686	1.748	3, 5

Species	Body length (cm)		Head width (cm)		Wing length (cm)		References
	Male	Female	Male	Female	Male	Female	
Enallagma praevarum	3.075	3.050			1.800	1.850	3, 5
Erythemis simplicicollis	4.350	4.410	0.665	0.685	3.185	3.395	2, 5
Euphaea impar	5.323	4.707	0.679	0.701	3.701	3.552	3, 5
Gomphus exilis	4.142	4.008	0.600	0.604	2.387	2.462	3, 5
Gomphus externus	5.236	5.334	0.706	0.719	3.204	3.169	3, 5
Gomphus graslini	4.662	4.805	0.693	0.716	3.034	3.153	3, 5
Hagenius brevistylus	8.116	8.210	0.978	1.015	5.194	5.608	3, 5
Hetaerina americana	4.113	3.470	0.502	0.483	2.490	2.503	5
Hetaerina titia	4.801	3.935	0.510	0.496	2.756	2.624	3, 5
Iridictyon myersi	6.578	5.871	0.612	0.605	3.799	3.896	3, 5
Ischnura cervula	2.651	2.915	0.331	0.347	1.462	1.722	3, 5
Ischnura demorsa	2.545	2.505	0.310	0.320	1.485	1.555	2, 5
Ischnura denticollis	2.745	2.590	0.355	0.345	1.680	1.665	2, 5
Ischnura erratica	3.372	3.382	0.429	0.414	1.884	2.065	3, 5
Ischnura perparva	2.646	2.652	0.351	0.355	1.289	1.617	3, 5
Ischnura posita	2.400	2.310	0.340	0.290	1.280	1.340	2, 5
Ischnura ramburii	2.805	3.330	0.340	0.410	1.535	2.040	2, 5
Ischnura verticalis	2.677	2.902	0.343	0.365	1.273	1.655	3, 5
Ladona deplanata	3.290	3.209	0.612	0.616	2.732	2.755	3, 5
Ladona depressa	4.589	4.479	0.790	0.793	3.551	3.744	3, 5
Ladona exusta	3.355	3.379	0.604	0.586	2.876	2.908	3, 5
Ladona fulva	4.320	4.029	0.786	0.723	3.701	3.461	3, 5
Ladona julia	4.004	3.927	0.696	0.699	3.323	3.408	3, 5
Lestes disjunctus	3.563	3.873	0.463	0.501	2.056	2.291	3, 5
Lestes viridis	4.484	4.127	0.527	0.535	2.528	2.681	1, 5
Libellula auripennis	5.210	5.001	0.797	0.788	4.071	4.051	3, 5
Libellula comanche	4.907	4.946	0.789	0.776	4.216	3.963	2, 3, 5
Libellula composita	4.410	4.032	0.740	0.683	3.290	3.244	3, 5
Libellula croceipennis	5.490	4.880	0.970	0.880	3.925	4.350	2, 5
Libellula cyanea	4.300	4.161	0.682	0.703	3.490	3.560	3, 5
Libellula flavida	4.478	4.663	0.697	0.766	3.589	3.764	3, 5
Libellula foliata	4.566	4.576	0.774	0.760	4.017	3.888	3, 5
Libellula forensis	4.648	4.224	0.854	0.751	3.792	3.634	2, 5
Libellula herculea	5.110	5.470	0.860	0.925	4.335	5.005	2, 5
Libellula incesta	5.088	5.027	0.772	0.782	4.074	4.225	3, 5
Libellula luctuosa	4.555	4.690	0.820	0.840	4.210	4.460	2, 5
Libellula needhami	5.394	5.333	0.819	0.793	4.069	4.097	2, 3, 5
Libellula nodistica	4.740	4.560	0.840	0.770	3.865	3.82	2, 5
Libellula pulchella	5.061	4.970	0.836	0.831	4.237	4.067	3, 5
Libellula quadrimaculata	4.207	4.275	0.775	0.744	3.379	3.409	1, 5
Libellula saturata	5.480	5.170	0.905	0.875	4.330	4.425	2, 5
Libellula semifasciata	4.305	4.230	0.732	0.751	3.545	3.525	3, 5
Libellula vibrans	5.692	5.838	0.863	0.901	4.464	4.923	3, 5
Lindenia tetraphylla	7.000	6.400			3.900	4.000	4, 5
Macromia amphigena	7.300	7.185	1.022	1.030	4.768	4.967	3, 5
Macromia splendens	6.498	6.869	0.868	0.983	4.397	4.773	1, 5
Matrona basilaris	6.620	6.580	0.640	0.660	4.073	4.613	3, 5
Matrona nigripectus	6.394	6.265	0.616	0.619	3.886	4.281	3, 5

Species	Body length (cm)		Head width (cm)		Wing length (cm)		References
	Male	Female	Male	Female	Male	Female	
Matronoides cyaneipennis	6.424	5.910	0.684	0.681	3.822	4.040	3, 5
Megaloprepus caerulatus	12.000	9.850			6.720	6.140	3, 5
Mnais pruinosa	5.651	5.008	0.621	0.612	3.814	3.592	3, 5
Neurobasis chinensis	5.700	5.668	0.558	0.573	3.296	3.643	3, 5
Onychogomphus forcipatus	5.052	4.482			2.892	2.957	4, 5
Onychogomphus uncatus	5.187	4.931			2.984	3.194	4, 5
Ophiogomphus severus	4.844	4.762	0.730	0.742	3.061	3.219	3, 5
Orthemis ferruginea	5.060	4.665	0.795	0.750	4.265	4.175	2, 5
Orthetrum cancellatum	4.693	4.629	0.734	0.692	3.803	3.622	1, 5
Oxygastra curtisii	4.257	4.485	0.677	0.699	3.330	3.330	1, 5
Pachydiplax longipennis	3.953	3.512	0.631	0.600	3.105	3.122	3, 5
Perithemis tenera	2.270	2.380	0.475	0.490	1.750	1.845	2, 5
Phaon iridipennis	6.861	6.415	0.651	0.645	3.902	4.167	3, 5
Phenes raptor	8.536	8.109	1.176	1.204	5.872	5.738	3, 5
Philogenia cassandra	4.741	4.744	0.554	0.583	3.200	3.392	3, 5
Phyllogomphoides albrighti	6.205	6.157	0.825	0.819	3.733	3.694	3, 5
Platycnemis pennipes	3.766	3.574	0.493	0.468	2.160	2.110	3, 5
Pseudostigma aberrans	13.900	11.350			6.750	6.550	3, 5
Rhionaeschna californica	5.564	5.110	0.778	0.645	3.678	3.643	2, 5
Sapho bicolor	6.059	5.638	0.711	0.705	3.529	3.843	3, 5
Sapho ciliata	6.025	5.642	0.699	0.729	3.641	3.952	3, 5
Sapho gloriosa	6.941	6.578	0.828	0.819	4.297	4.399	3, 5
Somatochlora metallica	4.974	5.250	0.773	0.804	3.600	3.812	3, 5
Stylogomphus albistylus	3.681	3.918	0.535	0.543	2.136	2.434	3, 5
Stylurus amnicola	4.780	4.947	0.705	0.730	3.122	3.348	3, 5
Sympetrum corruptum	4.007	4.137	0.686	0.673	3.065	3.180	3, 5
Sympetrum illotum	3.59	3.687	0.644	0.640	3.040	2.882	3, 5
Sympetrum vulgatum	3.371	3.249			2.445	2.443	4, 5
Telebasis salva	2.513	2.547	0.352	0.362	1.362	1.396	3, 5
Tramea lacerata	4.903	4.912	0.636	0.612	4.218	4.388	2, 5
Tramea onusta	4.347	4.564	0.776	0.794	3.970	4.217	3, 5
Umma longistigma	5.666	5.127	0.657	0.649	3.506	3.611	3, 5
Umma saphirina	5.329	5.182	0.624	0.635	3.520	3.796	3, 5
Vestalis amoena	5.616	4.865	0.560	0.541	3.481	3.429	3, 5
Vestalis gracilis	6.249	6.062	0.585	0.590	3.736	4.064	3, 5
Vestalis lugens	5.155	4.988	0.533	0.557	3.332	3.62	3, 5
Vestalis smaragdina	5.300	5.203	0.565	0.580	3.425	3.878	3, 5

Sources: 1, M. Azpilicueta-Amorín, unpublished results; 2, Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico; 3, Odonata collection, Natural History Museum, London, England; 4, Ocharán (1987); (5) Serrano-Meneses *et al.* (in press).

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CHAPTER 19

Dragonfly flight performance: a model system for biomechanics, physiological genetics, and animal competitive behaviour

James H. Marden

Overview

Adult dragonflies are heavily dependent on their flight muscles and flight ability for nearly all of their adult activities. Here I review research that has used dragonflies as model organisms to examine mechanisms that underlie variation in flight performance within and between species, molecular mechanisms by which muscle performance is adjusted within individuals, and how these physiological traits affect territorial and mating success. These results provide fundamental new knowledge that informs the theoretical bases of a number of fields: biomechanics of animal locomotion, physiological genetics, and game theory approaches to animal contests. Broadly based conclusions that cross the boundaries of these disparate fields demonstrate the payoff for performing integrative research.

19.1 Introduction

Adult dragonflies are extreme among insects in the degree to which their success depends on a single phenotype: flight ability. Dragonflies use their flight speed and manoeuvrability to capture prey, defend territories, copulate, and defend ovipositing females from abduction by rival males. This dominant role of a single, albeit complex phenotype makes dragonflies ideal for examining how physiological performance affects fitness in a free-living species.

These features of dragonflies have made them prominent subjects in research aimed at determining why animals display a wide range of variation in flight ability. Certain birds and insects are ponderous fliers that have difficulty becoming airborne and maneuvering around even stationary obstacles, whereas other species are capable of impressive aerial manoeuvres and complex interactions with other fliers. What causes these marked differences between species, in the sense of both proximate mechanisms and ultimate ecological and fitness factors? In addition, what causes variation in flight performance within species, and what are the fitness consequences thereof?

Here I present a brief overview showing how dragonfly studies have informed these types of questions. I place this work in the context of theoretical underpinnings of three disparate fields: biomechanics of animal locomotion, physiological genetics, and game-theory approaches to animal contests. There is no real synthesis of these three different perspectives—what we have learned from dragonflies does not unite biomechanics, physiological genetics, and game theory from a theoretical perspective—but it does inform each of these areas individually, and there are clear threads of connection that have helped shape hypotheses, experiments, and interpretation of results across these disparate fields. Ultimately this review reveals the rewards of performing integrative research.

19.2 What is flight performance?

Why are some animal species strong fliers and others weak fliers? This is a complicated question because there is no simple and universally applicable definition of what constitutes flight performance. One can refer to maximum speed, or ability to fly over a wide range of speeds, or the ability to change directions over a short distance; these are at least in part related to the mechanics and morphology of wings, as is described elegantly in Chapter 20 in this volume. In my own work I have chosen to take the approach of examining one fundamental and quantifiable aspect of flight performance—net force output against gravity—to allow comparative studies.

19.3 Theories underlying flight performance

As recently as the mid-1980s there was only one theory that directly addressed variables that should affect this type of performance across all types of flying animals. It was a scaling argument that involved body size and allometry of muscle power (Pennycuick 1969, 1972) based on seemingly well-supported knowledge of muscle biomechanics. Pennycuick used the scaling of muscle contractile force, shortening distance, and contraction frequency to predict the scaling of avian power output (although the theory applies equally well to insects and bats). Forces generated by muscles depend primarily on their cross-sectional area, which scales as mass$^{2/3}$ ($M^{2/3}$) in similarly shaped muscles. The distance that a muscle contracts tends to be a scale-invariant fraction of its resting length, therefore shortening distance scales as length^1 or mass$^{1/3}$. Muscle work output is the product of force ($M^{2/3}$ scaling) and distance ($M^{1/3}$ scaling), and should be scale-invariant ($M^{2/3} \times M^{1/3} = M^1$). Hence, power output (force × distance × time^{-1}) should scale according to wingbeat frequency, which in all types of flying animals scales as approximately $M^{-1/3}$ or $M^{-1/6}$ (Greenewalt 1962, 1975). Thus, according to this theory, animals should show a steady decline in mass-specific muscle power output as they increase in size and decrease in wingbeat frequency, whereas the power requirement for flight scales somewhere between M^1 and $M^{7/6}$ (Pennycuick 1968; Ellington 1991).

Measurements of the load-lifting capacity of flying animals (Marden 1987), power estimates based on those data (Marden 1990; Ellington 1991), and direct empirical measurements of the scaling of muscle power output of bird (Askew *et al.* 2001) and insect flight muscles (Schilder and Marden 2004) have overturned this theory. These results all show that power output from animal flight muscles scales in the range of M^1 to $M^{7/6}$, which is the same as the estimated scaling of power required for flight. Thus, adverse scaling of muscle power output is not an explanatory factor for variation in animal flight ability, but that leaves both the original question unanswered—what causes variation in flight ability among species?—and raises the new question of why a theory based on seemingly fundamental tenets of muscle biomechanics was wrong about the scaling of muscle power. Studies with dragonflies have provided compelling answers for both of these questions.

19.4 Mechanical determinants of flight performance

Dragonfly basalar muscles (Figure 19.1a) can be isolated mechanically and attached to external measurement devices; this has allowed detailed studies of the scaling of muscle performance (Schilder and Marden 2004). To understand this work, it is necessary to first consider how lever systems function. The basalar muscle in the dragonfly thorax and its anatomical connections are readily understood in terms of simple lever arrangements that conserve torque. Ignoring friction,

$$F_1 d_1 = F_2 d_2$$

In this equation for conservation of torque, F_1 is muscle force output, d_1 is the length of the internal lever arm between the muscle-attachment point and the fulcrum (hinge) of the forewing base, d_2 is the distance from the wing base to the point on the wing

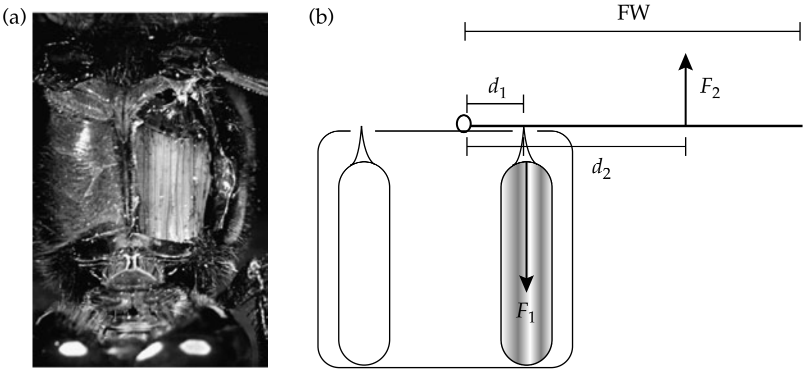

Figure 19.1 (a) Basalar muscle of a dragonfly that has been exposed by removal of a section of anterior thoracic exoskeleton and underlying air sacs. The base of the forewing, to which this muscle is attached, is visible at the upper right. The view is from above the head looking towards the posterior. (b) Diagram showing the anatomical arrangement of the basalar muscle and its anatomical connections to the forewing. F_1 is the mean net force output of the muscle undergoing sinusoidal contraction; d_1 is the distance between the muscle-attachment point and the forewing hinge; F_2 is the mean net aerodynamic force created by the beating wing at distance d_2 along the forewing (FW). Adapted from Schilder and Marden (2004).

where the mean aerodynamic force acts, and F_2 is the net aerodynamic force output (Figure 19.1b).

Using eight species of dragonfly across a broad range of sizes (0.1 – 1 g), we held the basalar muscle at constant length (isometric contraction) and found that tension during maximal tetanic stimulation scales as $M^{2/3}$, as expected for muscles in general and as was posed in Pennycuick's theory. However, it is important to consider that during locomotion, muscles tend to be stimulated by one or a few nerve impulses (not tetanically, which refers to trains of high-frequency action potentials), their length changes in a sinusoidal fashion, and they produce forces less than maximal isometric tetanus. Thus, both the magnitude and scaling of force output by muscles during locomotion could be quite different from isometric tetanus. Indeed, we found that the mean force output (F_1 in the torque equation) of dragonfly basalar muscles during realistic sinusoidal contraction scaled as $M^{0.83}$ [standard error (SE) = 0.09].

To determine the net force output of dragonfly flight muscles, we measured the maximum load that dragonflies can lift and found that it scales as $M^{1.04}$ (SE = 0.09) (Marden 1987; Schilder and Marden 2004); this provides the scaling of F_2 in the torque equation. What we needed next was an understanding of how muscle force output that scales as $M^{0.83}$ is converted by the lever mechanics to the approximately M^1 scaling of net lift force generated by whole dragonflies. To do this we examined the scaling of the other terms in the torque equation. The length of the external lever arm (d_2) is the distance between the wing fulcrum and the point at which the mean aerodynamic force acts upon the wing (calculated from the second moment of area of the forewing). This distance scaled as $M^{0.31}$ (SE = 0.03), which is very close to the expected scaling slope for dragonflies with geometrically similar wings. The internal lever arm length, d_1, which is the distance between the basalar muscle attachment point and the fulcrum of the forewing base, scaled as $M^{0.54}$ (SE = 0.04), a strong departure from the $M^{1/3}$ scaling for length dimensions of geometrically similar animals.

Putting these pieces together, we see that it is the combination of departures from expected scaling of the force output of flight muscles undergoing realistic contraction ($M^{0.83}$ rather than the predicted $M^{0.67}$) and the internal lever arm length ($M^{0.54}$ rather than the predicted $M^{0.33}$) that provides the answer for how the whole-motor force output scales nearly as unity ($M^{1.0}$). The key result is that the sum of the scaling exponents on the F_1d_1 side of the torque equation (0.83 + 0.54 = 1.37) comes very close to the sum of our estimates of the scaling exponents for the output side (F_2d_2) of the torque equation (1.04 + 0.31 = 1.35). On the wing side of the lever, aerodynamic power should scale as the sum of the scaling exponents for force ($M^{1.04}$ measured from loading experiments), distance ($M^{0.31}$ from wing dimensions), and frequency ($M^{-0.20}$ measured from high-speed video of wingbeat frequency), which yields $M^{1.15}$ and is in approximate agreement with the scaling of power output ($M^{1.24}$) that we measured directly from the muscle without any lever connections. Muscle strain (fractional shortening distance) and velocity must increase with size to accomplish this scaling, which is a departure from the traditional idea that muscle-shortening velocity and strain are relatively invariant.

Similar sets of mechanisms, perhaps commonly involving departures from geometric similarity of internal lever arm lengths and positive mass-scaling of power output, are likely to exist broadly among flying animals. There may, however, be taxonomic groups which, as they radiated and diverged in body size, did not evolve solutions to the inherently difficult problem of achieving M^1 scaling of flight performance so that their particular design series can only function over a limited size range. This may explain the small deviation away from M^1 scaling of flight performance in euglossine bees (Dillon and Dudley 2004). Phasianid birds are a more extreme example, as their take-off power scales with a mass exponent well below unity (Tobalske and Dial 2000).

In addition to revealing factors that allow different-sized fliers to maintain scale-invariant performance, these findings have significance for muscle systems in general. The assumption of $M^{2/3}$ scaling of muscle force (synonymous with the assumption of scale-invariant muscle stress for muscles of similar shape) permeates nearly all theoretical work on animal locomotion. For example, Hutchinson and Garcia (2002) made the very standard and seemingly safe assumption of scale-invariant muscle stress in a model that predicts running speeds of *Tyrannosaurus rex* dinosaurs; because of the extreme size of their subject species, this assumption affects their prediction profoundly.

19.5 Physiological determinants of flight performance

As explained above, flight performance does not vary across taxa in a systematic manner with body size, but M^1 scaling only describes a central tendency and leaves open the question of what causes the easily perceived variation in flight performance among weak and strong fliers. To the extent that performance depends on force output, the cause of this variation emerged with surprising clarity from experiments that measured maximum take-off load across birds, bats, and insects (Marden 1987). That study showed that all types of flying animals obtain nearly the same mass-specific net force output (60–80 N/kg) from their flight muscles (Figure 19.2). Greenewalt pointed out in 1962 that flight-muscle mass scales as M^1; again this refers to a central tendency, but it became widely mis-cited as an indication that the ratio of flight-muscle mass to body mass is constant among flying animals. That is far from correct, since some flying animals have just enough flight muscle to get airborne (about 15% of body mass) whereas other species, including dragonflies, have flight muscles that comprise up to about 60% of their body mass (Hartman 1961; Marden 1987). From Newtonian mechanics we know that acceleration equals force divided by mass. Because all flying animals obtain

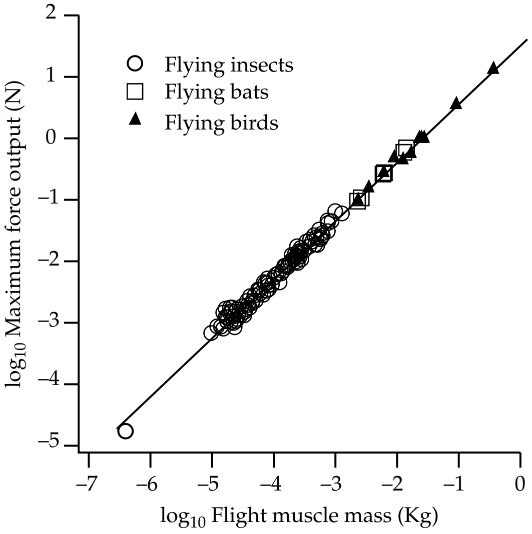

Figure 19.2 Maximum net force output as a function of total mass of the flight muscles in a wide variety of flying animals (Marden 1987; Marden *et al.* 1997). Force output scales as M^1 with surprisingly little variation around the mass-specific mean of approximately 60 N/kg.

nearly the same amount of force output per flight-muscle mass, their aerial acceleration (a key trait in predatory and competitive aerial interactions and in manoeuvrability) depends on the ratio of flight-muscle mass to total body mass, a trait known as flight-muscle ratio (FMR; but see also Chapter 20, where the effect of wing morphology and mechanics are discussed in relation to speed and manoeuvrability; clearly the wings and muscles work together to determine performance).

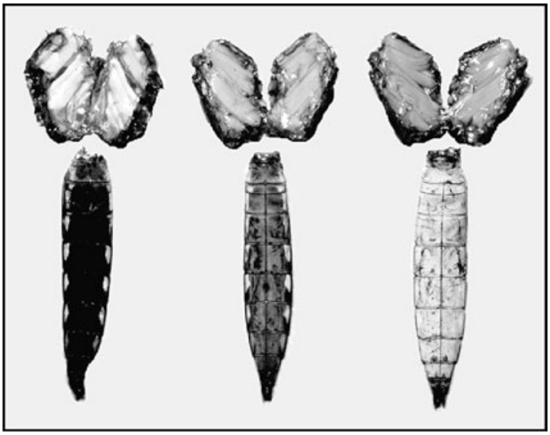

Figure 19.3 Split thorax and intact abdomen from three stages of maturation of adult male *Plathemis lydia* dragonflies. On the left is a newly emerged (teneral) individual; note the light colour of the muscles shaped as thin sheets and the visible gaps between muscles. The middle shows an individual that is near the mid-point of maturation as measured by mass. On the right is a fully mature male; note the darker colour of the muscle (due to more mitochondria and associated respiratory enzymes) and the degree to which the muscles have filled in nearly the entire thoracic cavity.

Identification of a trait that underlies a large portion of interspecific variation in flight performance (in the narrow sense of my operational definition of performance) stimulated the new question of how variation in FMR affects competitive ability within individual species. This question was first addressed in the dragonfly *Plathemis lydia*, a conspicuous and abundant libellulid species whose adults inhabit pond margins and adjacent early-successional habitats in the north-eastern USA. Early in this study it became apparent that newly emerged adults (tenerals) have body and thorax masses that are only about half that of mature adults (Figure 19.3); that is, there is substantial mass gain (hypertrophy) of the flight muscles during adult life in males, and to a lesser extent in females, along with remarkable increases in ovarian mass in females (Table 19.1; Marden 1989). The FMR of mature males reached as high as 0.6 (i.e. 60% of total body mass is flight muscle). Subsequent research showed that significant mass gain during the adult stage is not unique to libellulids, but rather is widespread, although generally less extreme, among odonates in general (Anholt *et al.* 1991; Plaistow and Tsubaki 2000).

The time course of mass gain over early adult life has been determined from mark–recapture studies of caged (Michiels and Dhondt 1989) and free-living (Marden and Rowan 2000) libellulid dragonflies. Fast-growing individuals are capable of gaining mass at a very high rate. For example, the most extreme growth rate in a sample of free-living *Libellula pulchella* dragonflies was 58 mg per day; this individual more than doubled its adult body

Table 19.1 Mean mass of body components of *Plathemis lydia* dragonflies of various sex, age, and behaviour categories (Marden 1989).

	N	**Mean mass (mg) (±SD)**			
		Total body	**Thorax**	**Abdomen**	**Ovaries**
Males					
Teneral	8	252 (±15)	115 (±6)	52 (±8)	
Adolescent/feeding	20	340 (±72)	178 (±50)	81 (±21)	
Territorial/mature	110	471 (±35)	281 (±20)	102 (±14)	
Females					
Teneral	8	229 (±16)	94 (±11)	50 (±4)	5 (±1)
Adolescent/feeding	16	477 (±147)	191 (±50)	202 (±93)	106 (±70)
Ovipositing/mature	9	571 (±60)	221 (±18)	260 (±39)	153 (±32)

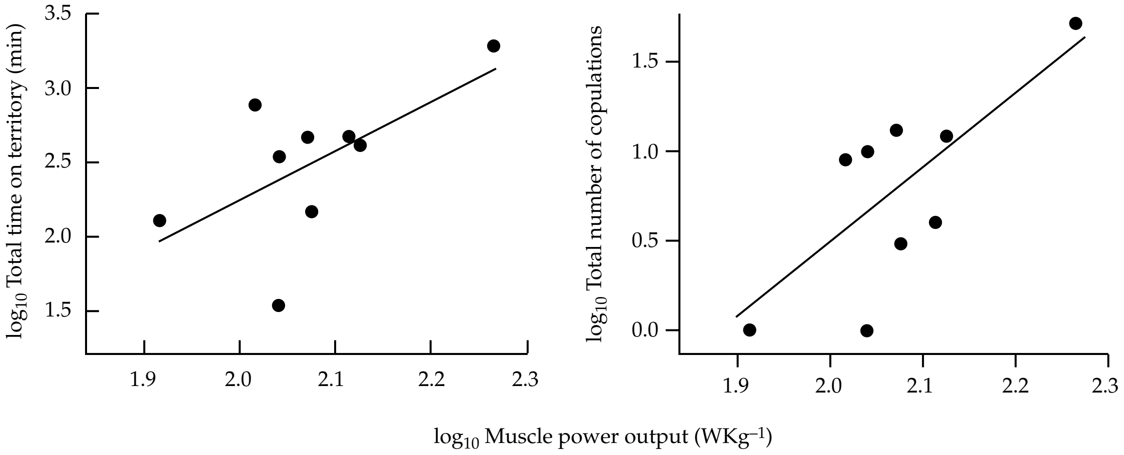

Figure 19.4 Time spent on territory and number of copulations for the entire lifetime of a sample of *Libellula pulchella* males in relation to their muscle power output (Marden and Cobb 2004).

mass during the first 5 days of adult life. Perhaps more importantly, the majority of new emergents in that study lost mass and quickly disappeared from the population. Thus, energy balance is a difficult challenge for newly emerged adults.

Energy balance may be especially tricky for the most flight-capable and aggressive males, judging by the results of feeding experiments in a damselfly with distinct male morphs (Plaistow and Tsubaki 2000). In that study, the non-territorial male morph attained normal mature mass and fat content when maintained on a low nutrition diet, whereas the territorial male morph gained a normal amount of flight muscle (double that of the non-territorial morph) but had lower fat than free-living territorial or non-territorial males.

Having undergone a 2–3 fold increase in their flight-muscle mass during early adult maturation, mature, territorial *P. lydia* males showed a significant positive relationship between FMR and territorial and mating success (Marden 1989). Among groups of competing males at a pond, the one with the highest FMR tended to have the highest mating success that day. Experimental attachment of small weights (27–57 mg; 6–13% of body mass) caused decreases in mating success, apparently due to inability of weight-loaded males to establish and defend high-quality territories. In another study, we have shown that long-term mating success of individual male *L. pulchella* dragonflies has a positive relationship with the power output of their flight muscles (Figure 19.4; Marden and Cobb 2004). This is a stronger result because all dragonflies received the same handling (capture for the purpose of wing marking with coloured powder), success was determined by more than just one day of competition, and there was a positive relationship between muscle power and time spent (i.e. effort, energy) on territorial defense, thereby indicating that variation in effort acts in parallel to variation in male quality. Thus, it appears to be generally true (see Chapter 16) that male libellulid dragonflies with higher flight performance achieve greater mating success.

19.6 Genetic determinants of flight performance

One of the primary goals of modern biology is to ‘find the genes that matter’ (Feder and Mitchell-Olds 2003). In this spirit, one can ask whether there are polymorphic genes that affect muscle contraction, flight performance, and mating success. The central dogma of molecular genetics originally included the one-gene/one-protein paradigm; that is, that a region of genomic DNA is transcribed to an invariant RNA that is translated to a protein. This turned out to be a vast oversimplification when it was discovered that the majority of eukaryote genes undergo alternative splicing, a process wherein alternative 5′ and 3′ splice sites and/or exon inclusion/skipping give rise to a variety of mRNAs from a single gene. This feature of RNA processing emerged in dragonfly studies when we discovered that a muscle regulatory protein, troponin T, is alternatively spliced in *L. pulchella* dragonflies to create different protein isoforms (Fitzhugh and Marden 1997; Marden *et al.* 1999, 2001), and that variation in the relative abundance of different splice forms is strongly correlated with how dragonfly muscle fibres are activated by calcium, and how much force and power they produce (Figure 19.5).

From high-speed video recordings of free-flying dragonflies, we found that there is a significant

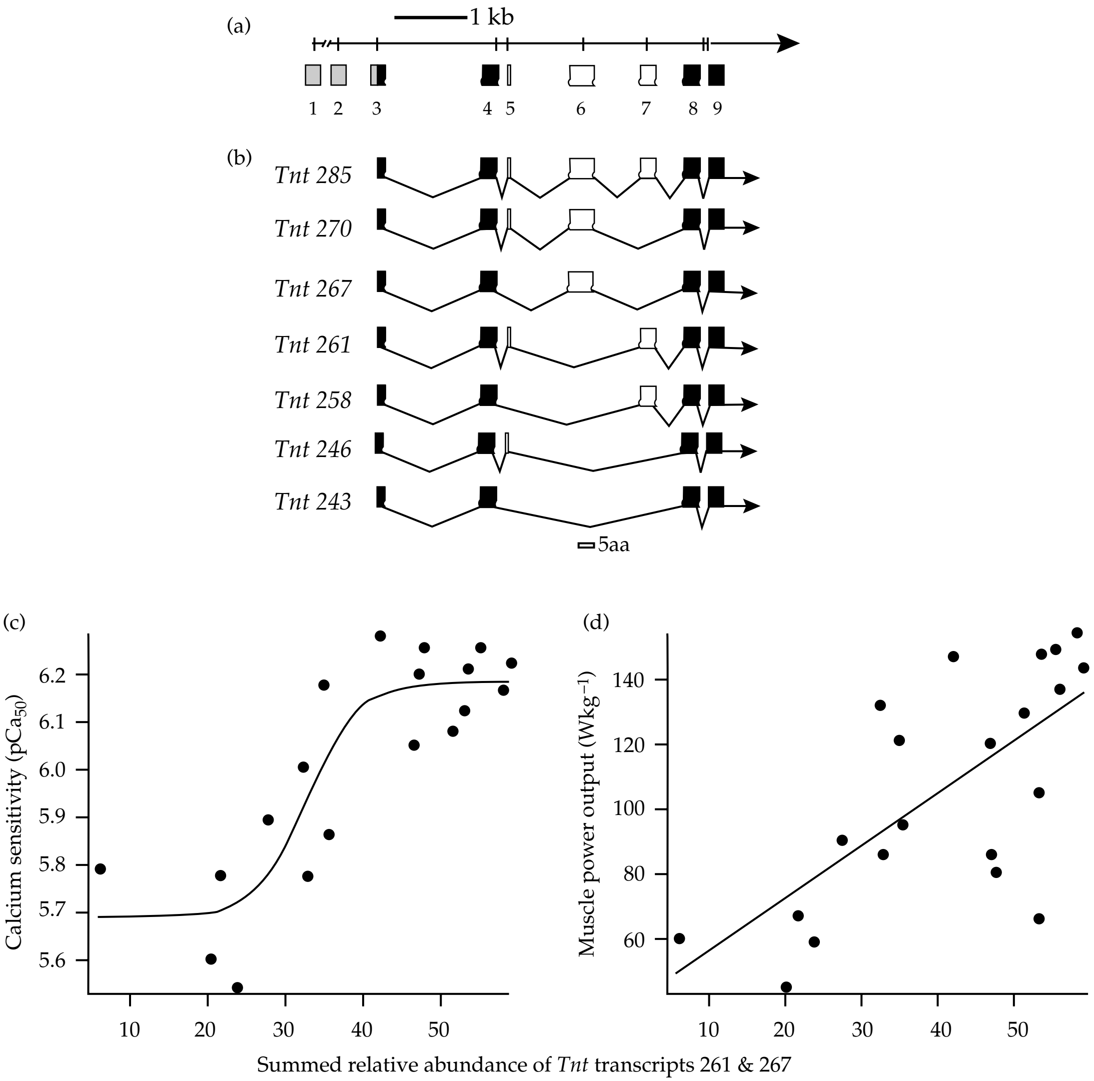

Figure 19.5 (a, b) Intron–exon structure and alternative splicing of exons near the 5′ end of the *troponin T* gene (*Tnt*) in *Libellula pulchella* dragonflies. Arrows represent additional constitutive exons (not shown) that extend to the 3′ end of the gene. aa, amino acids. (c, d) Relationship between the relative abundance (percentage of all *Tnt* transcripts) of two *Tnt* splice variants, the calcium sensitivity of skinned muscle-fibre activation, and the mechanical power output of intact flight muscle. Adapted from Marden *et al.* (2001).

correlation between the summed relative abundance of two particular troponin T transcripts (*Tnt 261* and *Tnt 267*; named according to length of the PCR product from primers on flanking constitutive exons) and wingstroke amplitude and frequency, the main kinematic variables that insects use to adjust aerodynamic force and power output (Wakeling and Ellington 1997a, 1997b). Dragonflies with greater wingbeat amplitude and frequency also had significantly higher rates of energy consumption during flight, as measured by the rate of CO_2 emission. These results suggest that alternative splicing of troponin T serves as a way to adjust energy conservation and flight performance, and this is probably the mechanism that underlies the positive relationship between *L. pulchella* muscle power and fat content (Marden and Cobb 2004). Although we have not yet been able to manipulate these variables experimentally, our working hypothesis is that dragonflies with ample energy reserves use troponin T splicing to adjust their consumption and performance upward, whereas those with low energy reserves down-regulate muscle contractility so that they are less energy-consumptive, albeit less powerful and less reproductively successful (i.e. making the best of a bad situation).

Measurements of muscle power and troponin T composition are destructive, and therefore we cannot determine how these variables change over time within an individual. All newly emerged adults have low muscle power and show the characteristic low-power pattern of troponin T splicing (Fitzhugh and Marden 1997), so phenotypic change must be occurring during maturation, but we do not yet know whether mature adults retain flexibility and can adjust muscle performance up or down over short time scales (i.e. over one or a few days), or if splicing patterns are established at a point during maturation and are fixed from that point onward.

19.7 Game theory and fitness consequences of flight performance

In this section I briefly discuss how knowledge of odonate performance physiology can inform studies of odonate territorial behaviour. Game-theory approaches to animal territorial contests have debated the importance of behavioural conventions (uncorrelated asymmetries, i.e. arbitrary differences between equally fit animals) and asymmetries in resource-holding potential (RHP) as determinants of the outcome of contests for territorial ownership (reviewed in Kokko *et al.* 2006; see also Chapter 16). In other words, are contests settled by the use of arbitrary rules or by real differences in ability? Hypotheses about uncorrelated asymmetries date back to the work of Davies (1978) and the other earliest applications of game theory to animal behaviour (Maynard Smith and Parker 1976; Maynard Smith 1982). The basic idea is that there can exist an evolutionarily stable strategy for contestants adopting a particular role in territorial encounters; the well-known hawk, dove, and bourgeois strategies. Kokko *et al.* (2006) recently solved an important theoretical problem for the evolution of behavioural roles based on purely uncorrelated asymmetries. Their theory differs from previous theory by incorporating frequency-dependent feedbacks created by the behaviour, and the fate of floaters that lack a territory and must overcome residents or keep floating and wait for an open territory to appear. Their theory shows that behaviours such as respect for residency (dove behaviour by a territorial intruder) can evolve even if contestants are physiologically equal, that RHP differences among contestants do not necessarily constitute evidence that contest settlement is not arbitrary, and that RHP asymmetries can reinforce arbitrary behavioural roles. This stands in contrast to the conclusion of Kemp and Wiklund (2004) that the use of arbitrary roles in contests may be rare or non-existent in the wild, and which is consistent with evidence from damselfly studies showing that male fat content strongly affects behavioural roles in territorial encounters (Plaistow and Siva-Jothy 1996).

Results from odonate studies cannot resolve this fundamental debate about how contests are settled, but can sharpen our understanding of the nature of RHP asymmetries and the quantitative degree to which rival males differ in condition during territorial encounters. Rather than reiterate the broad review presented in Chapter 16, I will simply present and comment on some results that are relevant to this discussion.

As described above, competing territorial male dragonflies vary in both FMR and muscle power output, and both of these variables have a positive relationship with territorial success (Marden 1989; Plaistow and Tsubaki 2000). In *P. lydia* the FMR variation is quite subtle, amounting to a difference of a few milligrams in muscle and non-muscle mass between the most and least successful males. In *L. pulchella*, asymmetries in muscle power output are much less subtle. Among nine males observed for lifetime territorial and reproductive success, muscle power output ranged from 80 to 180 W/kg (Marden and Cobb 2004). Clearly there should be a huge asymmetry in flight performance and aerial competitive ability between rivals this disparate in their muscle physiology, and indeed there are large differences in time spent defending territories and number of copulations attained by males across this range of muscle performance (Figure 19.4). In addition, male dragonflies infected with gregarine parasites completely loose their ability to metabolize lipids (Schilder and Marden 2006), which ordinarily would be a large component of the metabolic fuel consumed during periods of prolonged flying such as occurs when dragonflies defend territories. It is not yet known how gregarine infection and loss of lipid oxidation affects flight endurance, but at a pond where the gregarine infection rate was about 50% nearly all satellite males were infected and nearly all territorial males were uninfected (Marden and Cobb 2004). In the damselfly *Calopteryx maculata*, males that won prolonged, escalated territorial contests almost always had more fat than the losers (Marden and Waage 1990; Marden and Rollins 1994); this result has been replicated and elaborated in a number of studies of other damselflies (Plaistow and Siva-Jothy 1996; Koskimäki *et al.* 2004; Contreras-Garduño *et al.* 2006). Post-contest fat content in *Calopteryx maculata* varies over an approximate 10-fold range (0.4–5.0% of body mass), with the leanest males having almost no fat remaining.

These enormous quantitative and qualitative differences in physiological traits that affect RHP make one wonder how likely it is that there can be a strong role for uncorrelated asymmetries in these contests, particularly because a male that cannot metabolize fat, or that has almost no fat remaining, or that is facing an opponent with a 2-fold difference in muscle power output, is unlikely to be capable of carrying out all of the behaviours that can be observed in dragonfly contests (i.e. playing all of the roles). Even so, most escalated contests in *Calopteryx* occur when males, by chance, become co-resident on a single territory, and this has been confirmed experimentally by merging adjacent territories that consist of clumps of aquatic vegetation (Waage 1988). The vast majority of non-territorial floaters withdraw quickly from interactions with territorial residents, even though the territory holder must often be physiologically inferior given the variability of fat content in *Calopteryx*. Thus, even though there is dramatic variation in odonate physiological status that affects RHP, most encounters between males demonstrate a respect for ownership (but see the study by Plaistow and Siva-Jothy 1996, which showed that most passive non-territorial males were old and had very little fat, whereas younger, fat-rich males were much more aggressive). Whether respect for ownership as displayed in species such as *Calopteryx maculata* is evidence of the use of arbitrary behavioural roles (uncorrelated asymmetries) or reflects the time and energy cost for floaters to gain information about residents (i.e. it may be too costly to challenge owners indiscriminantly) remains an open question. One thing that we have learned from libellulid dragonflies and which to my knowledge has not been incorporated into theory, is that the best territories tend to be occupied by the most superior males. It might be interesting to model the consequences of RHP variation in settings where the rewards and costs for floaters challenging residents are greatest for those contests in which the chances of success are lowest. It may be generally true in animals that the territories most worth having are the ones where successful challenge is least likely.

19.8 Conclusion and outlook

Research on dragonflies has revealed a number of general features of biomechanics, molecular physiology, and behaviour, along with specific things about the nature of dragonflies. Fundamental new knowledge from dragonfly studies includes an understanding of what traits determine flight ability, how musculoskeletal lever systems are configured to maintain the required scaling of force and power output, how and why muscle power output is regulated at the molecular level within individuals, and how asymmetries in traits such as muscle power and energy affect competitive interactions. These findings have broad impact; for example, they have stimulated a new theory for scale effects across nearly all forms of animal locomotion (Bejan and Marden 2006) and were the first demonstration that alternative splicing is used to accomplish phenotypic plasticity of whole-organism-level phenotypes (as opposed to cellular or developmental phenotypes, where alternative splicing has been studied extensively). Plasticity of traits on the level of the whole organism based on alternatively spliced genes responding to environmental variables is likely to be widespread but to date is known from only a few plant and animal examples (Marden 2006). Workers in my laboratory are currently investigating the signalling pathways and regulatory mechanisms that allow dragonflies to phenotypically adjust their muscle power output, and the disruption of that signalling and associated development of obesity and metabolic syndrome in dragonflies infected by gregarine gut parasites. It is even possible that work in this area can contribute new findings and hypotheses relevant to the epidemic of metabolic disease and physical inactivity in humans (Schilder and Marden 2007). All of this is exciting and keeps us returning to the ponds where our favourite subject species can always be found on hot summer days.

Acknowledgements

I am deeply grateful to the National Science Foundation for funding this research over a period of almost two decades, most recently through grants IBN-0091040 and EF-0412651. The manuscript was improved by suggestions from M. Siva-Jothy and an anonymous reviewer.

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CHAPTER 20

Evolution, diversification, and mechanics of dragonfly wings

Robin J. Wootton and David J.S. Newman

Overview

The Odonatoptera (Odonata + Protodonata + Geroptera) provide an excellent opportunity to apply biomechanical principles and techniques in understanding the evolution of the wings and flight capabilities of a high-performance insect order. Wings of typical zygopteran and anisopteran planforms are present from the Carboniferous onwards and represent convergent adaptations, respectively, to controlled slow flight and to versatile flight over a wide range of speeds. Wide variation is found within the two basic types, and a wider array of wing plans is found in Permian and Mesozoic deposits. The wings are complex flexible aerofoils, whose deformations in flight are encoded in the distribution of rigid and compliant components within their structure. Scanning electron microscopy shows these to be influenced by the local relief, and by the form of the cross-veins and their junctions with the longitudinal veins. High-speed photography, manipulation, and simple physical models have clarified the functioning of the leading-edge spar and nodus, and of the basal complex—the arculus and the various forms of the discoidal cell—in the automatic control of wing attitude and shape in flight. Their evolution can be followed in the fossil record, and demonstrate adaptive improvements in association with improved flight skills, and perhaps with increasingly complex behaviour.

20.1 Introduction

20.1.1 The odonatoid flight system

Odonata combine spectacularly skilful flight with a unique and in many respects archaic morphology. Lineages leading to other taxa with complex, versatile flight, within Diptera, Hymenoptera, Lepidoptera, and Hemiptera, have undergone progressive alteration and simplification of the pterothoracic skeleton and musculature, concentrating most of the power production into the mesothorax, reducing the number of muscles, and modifying the fore and hindwings by coupling or reduction into a single pair of functional aerofoils, usually with relatively simple venation. In Odonata, by contrast, meso- and metathorax are almost equally developed, fore- and hindwings operate separately, and the flight musculature is rich and complex.

Odonatoptera (Odonata + Protodonata + Geroptera) were already present some 320 million years ago in the Namurian division of the Carboniferous (Brauckmann and Zessin 1989), and the three orders were already distinct by the Westphalian division that followed immediately (Riek and Kukalová-Peck 1984; Jarzembowski and Nel 2002). They therefore provide one of the longest and best-represented records of the evolutionary history of any extant insect superorder. As in most insect taxa, most of our knowledge from fossils relates to the wings; and the wings of Odonatoptera are particularly informative. Palaeopterous insects have limited substrate mobility; flight is their principal locomotory method, and their wings appear more tightly flight-adapted than do those of many other groups. Odonata wings may assist in thermoregulation, or be used in display, but it is reasonable to assume that most of their morphology is flight-related, and to seek to interpret evolutionary trends primarily in association with their functioning in flight.

20.1.2 Odonatoptera as a model system in wing evolutionary mechanics

Odonatoptera therefore provide an excellent opportunity to investigate the evolution of the wings of a major insect group in terms of their flight mechanics, and to evaluate several hypotheses relating to dragonflies in particular, to insect wings in general, and to wider evolutionary issues. The following are proposed.

1. Wing planform (projected shape) in Odonatoptera is correlated with flight strategy.
2. Planform convergence is widespread.
3. Structural detail is related primarily to the operation of wings as flexible 'smart' aerofoils.
4. The functions of major characters can usefully be investigated by simple physical models.
5. Anagenesis (evolutionary 'improvement') is widely recognizable.

20.1.3 The determinants of flight performance

Flight 'performance' has many components: speed, speed range, stamina, acceleration capacity, manoeuvrability (space needed to alter the flight path while flying at a fixed speed), agility (the rapidity with which the flight path can be altered), and overall versatility. The performance of an individual dragonfly will depend on a complex of interacting morphological and physiological variables. Available speeds will be influenced by wing loadings: in a range of dragonflies of similar shape but different sizes maximum speeds should theoretically vary as (wing loading)$^{0.5}$. Large bodies will favour high wing loadings, as will small wings; relatively large wings will reduce them. Relatively large flight muscles will increase available power, and hence speeds and accelerations. High mass, and hence inertia, will tend to reduce agility; mass centred close to the centre of aerodynamic force will enhance it. Relatively long wings will create larger turning moments and increase both manoeuvrability and agility, as will wings whose area is concentrated distally. Long abdomens will tend to reduce these, but will assist stability.

Wing planforms are part of this complex, and their relationship with flight performance is incompletely understood. Odonatoptera display a mosaic of wing shapes from the mid-Carboniferous onwards (Figure 20.1), and isopterous and anisopterous plans are evident from the first; but a huge range of wing outlines is evident within these two basic patterns, and intermediate and other shapes occur. The array of planforms in the Mesozoic is extraordinary (see Carpenter 1992), and many have no modern parallels.

Wootton (1991), Wootton and Kukalová-Peck (2000), and Wakeling (1997) have discussed some of these issues. Narrow-based, and particularly petiolate wings should be associated with relatively slow, habitual flight. The flapping velocities of points along the wing increase from the base to the tip. In hovering and at slow speeds the base has low velocity, and contributes little aerodynamic force, so that in slow insects the wing area should be centred further out along the span. At faster speeds, however, the base is moving at the forward speed of the body, the spanwise velocity gradient is less steep, and a broad wing base is practical and worthwhile, particularly on the hindwing; forewing breadth is limited by the presence of the hindwing. Broad-based wings should not preclude slow flight and hovering—many skilful hoverers in other orders have broad-based wings or wing couples—but they should allow flight over a wider speed range; the more so since they allow higher stroke frequency for a given surface area.

These predictions fit common experience. Extant Zygoptera with petiolate wings are typically slow fliers, whereas Anisoptera, when not hovering, tend to operate at higher speeds, permitted by their generally higher wing loadings. The situation for Zygoptera without petiolate wings is less clear. Most extant examples are Calopterygoidea; and these show a range of complex flight behaviours associated with courtship and often territorial display as well as prey capture. The literature includes many detailed accounts of behaviour, but only in *Calopteryx* has

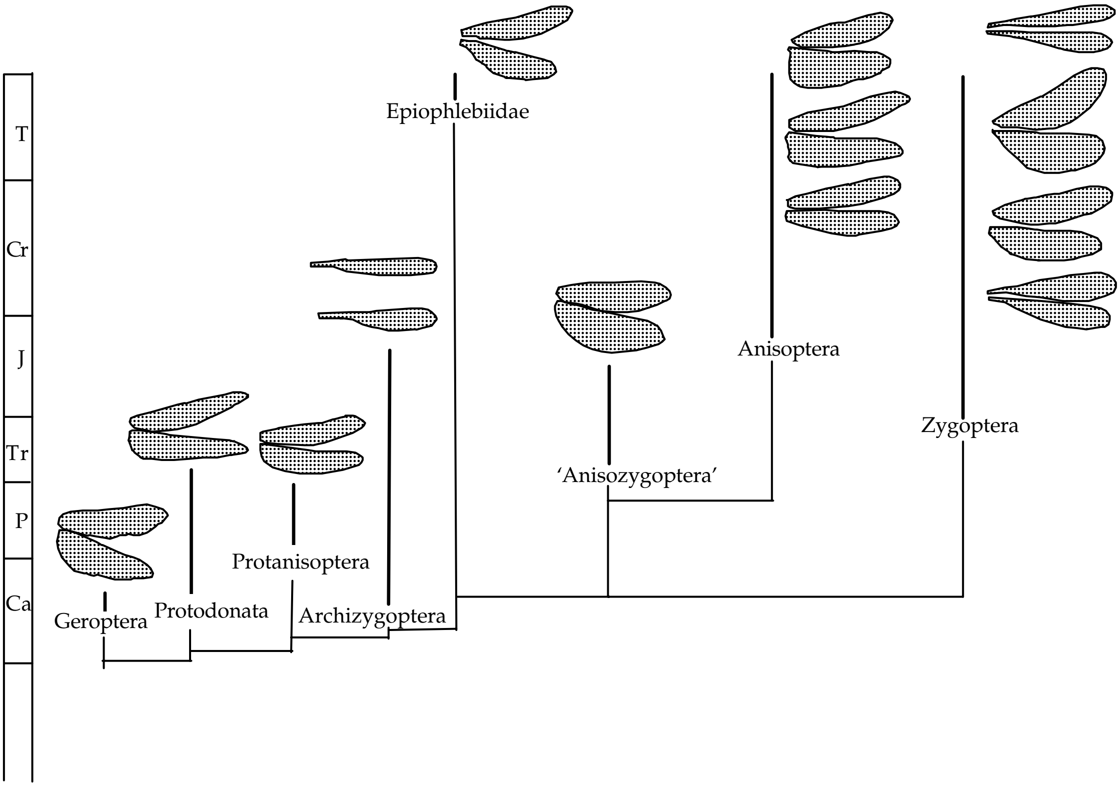

Figure 20.1 Simplified phylogenetic tree of Odonatoptera, showing representative planforms. T, Tertiary; Cr, Cretaceous; J, Jurassic; Tr, Triassic; P, Permian; Ca, Carboniferous.

flight been fully analysed (Newman 1982; Rüppell 1989; Wakeling and Ellington 1997a, 1997b, 1997c). With the forewings at least these typically use the 'clap and fling' mechanism for high lift (Weis-Fogh 1973; Ellington 1984a, 1984b) in which the left and right wings meet over most of their area at the top of the upstroke, and fling apart, leading edge first, into the downstroke, with the generation of large low-pressure vortices above each wing. Wakeling (1997) has suggested that the narrow wing base of Zygoptera assists this, as it maximizes the contact time of the trailing edge during the fling. This may be true of calopterygids, in which the wings are held together for a long period at the top of the stroke, but their flight is very different from coenagrionoids and and lestoids; *Pyrrhosoma* (Newman 1982), *Lestes*, and *Megaloprepus* (Rüppell 1989) do not routinely use clap and fling. We know less about flight in other calopterygoids, like Euphaeidae, with their rather Anisoptera-like wings, and the thick-bodied, narrow-winged Chlorocyphidae. In both cases wing loadings and hence available flight speeds should be high, and reports confirm this (Orr 1996; M. May, personal communication) but quantitative information is lacking. The widest range of wing plans is found in Anisoptera, particularly in Libelluloidea. Broader wings appear to be particularly associated with gliding and soaring (Ennos 1989; Wootton 1991; Wakeling 1997); the significance of other shapes needs more study.

We may not fully understand wing planforms, but we can reasonably assume that they are fit for purpose. Evolutionary changes in shape and proportion are relatively easily achieved, and this is reflected in the widespread convergence evident within Odonatoptera, as taxa whose wings differ fundamentally in detailed structure have radiated into parallel life styles.

20.2 Wing structural mechanics

20.2.1 Wings as smart aerofoils

Insect wings are unique in being flexible aerofoils with 'smart' properties, adapted to deform automatically and appropriately in response to the forces they receive (Wootton 1981, 1992, 2003). High-speed photographs and cine films show the deformations that the wings undergo in flight. Manipulation of fresh wings suggests how these may be brought about. A full engineering analysis is difficult, because the deformations are controlled by the distribution of elasticity around the wing, and this is highly non-linear, with major local differences in the properties of the cuticle and the dimensions and sections of the veins. Sophisticated numerical modelling is extremely time-consuming, even with major simplifications and assumptions, and has so far been of limited value. More has been achieved using simple physical and analytical models, which can be developed quickly to compare the operation of specific wing components, and checked against observed deformations in filmed and manipulated wings (Wootton *et al*. 2003).

The wings of Odonatoptera are particularly complex. In engineering terms they are space frames: three-dimensional frameworks of tension and compression members, the veins, supporting a membrane which itself in places has a structural, stiffening role (Newman and Wootton 1986). Some parts are built for rigidity; others are flexible, but in specific directions; and various internal automatic mechanisms also influence their functioning.

In investigating these, physical models have proved particularly useful. Dragonflies' use of relief to stiffen the wing makes it possible to model components as folded plates, using thin card, reinforced in places where applied forces cause the corrugations to buckle. Such buckling often indicates why the wings require particular stiffening at the corresponding sites; for example at the anterior end of the arculus, which in Zygoptera is usually aligned with a rigid antenodal cross-vein. The pleats themselves model the main veins and certain cross-veins. The compression stiffness of the card mimics the minor cross-veins, which act in the wing as compression struts.

Results from models of this kind can be checked against the behaviour of appropriately loaded actual wings, and are strong indicators of real function, and of the significance of observed adaptations and trends. They have been used to interpret the arculus of Diptera and Zygoptera (Ennos 1988; Wootton 1991); the hypertriangle/triangle complex in Anisoptera (Newman 1982; Wootton 1991), and an analogous basal complex in Carboniferous geropterid Odonatoptera (Wootton *et al*. 1998). We apply them here to examine and compare a wider range of Odonata, and to investigate the significance of some familiar structures and trends.

It is clear from an abundance of high-speed photographs and cine films that:

1. wings of Odonata remain straight in flight, without significant bending across the span;
2. the wings twist extensively between the upstroke and the downstroke, particularly around stroke reversal, and in the morphological upstroke;
3. distal regions of the wings, even in narrow-winged Zygoptera, develop a cambered section during the downstroke, which flattens and often becomes reversed in the upstroke.

All these have mechanical implications in flight, and much of the detailed structure of the wings can be interpreted with reference to them.

20.2.2 Maintaining rigidity: corrugation, cross-vein design, and section control

Figure 20.2 shows a forewing of *Calopteryx virgo* (Calopterygidae) and the wings of *Orthetrum cancellatum* (Libellulidae), illustrating the longitudinal veins and other structures specifically mentioned below. For clarity, most cross- and intercalary veins are omitted.

In flapping flight it is important that wing mass, and hence inertia, should be minimized. The metabolic cost of overcoming wing inertia is probably low, but the wings experience significant bending moments, particularly as they accelerate and decelerate at stroke-reversal, and insects tend to resist these by using high relief, rather than bulk, for rigidity. Odonata make particular use of corrugation, extended to the wing margins by intercalary veins between the main branches.

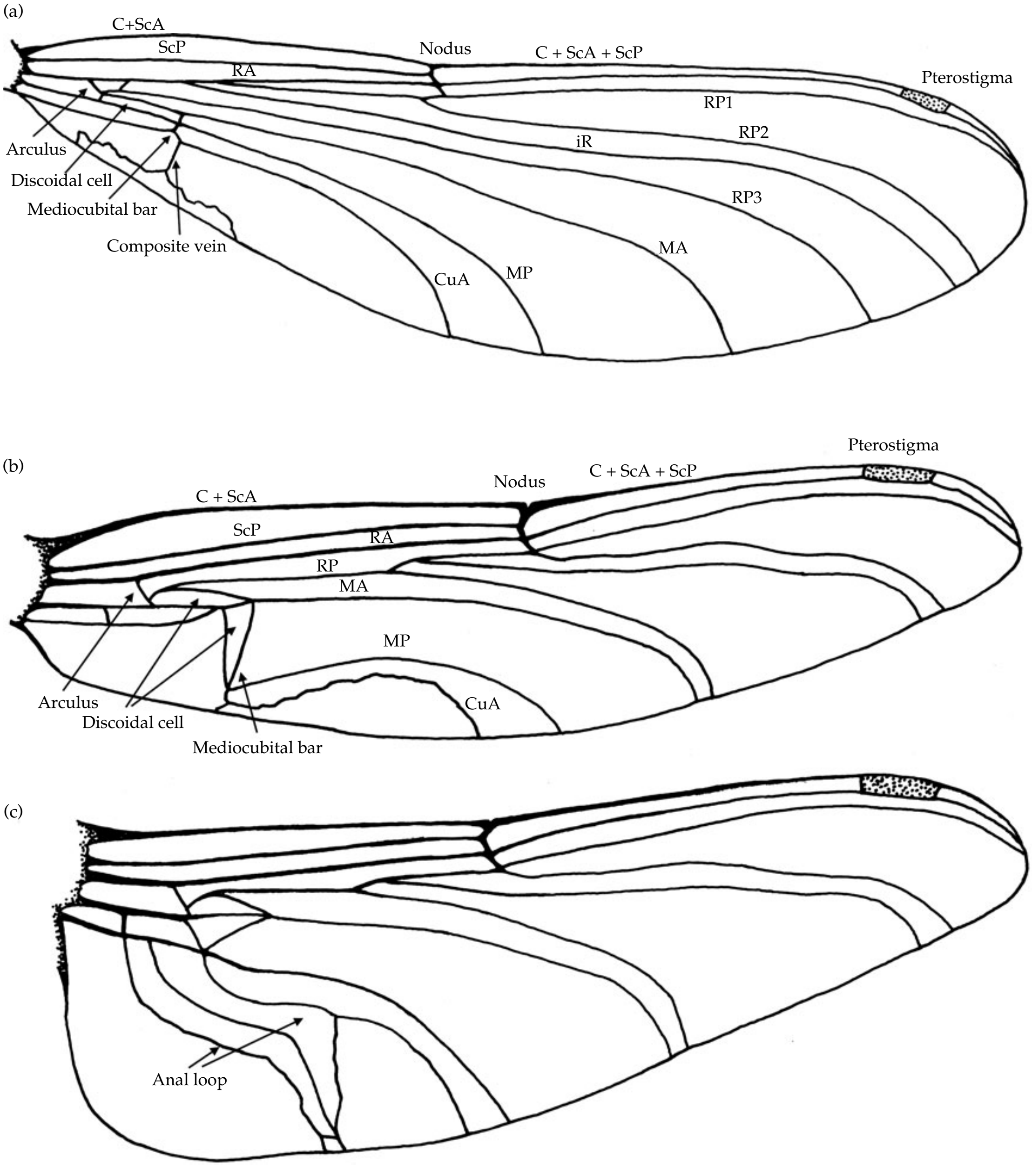

Figure 20.2 Wings of *Calopteryx virgo* (a) and *Orthetrum cancellatum* (b, c), showing longitudinal veins and selected other details. Nomenclature follows Rehn (2003), modified from Riek and Kukalová-Peck (1984).

The clearest adaptations for rigidity are at the base where the bending moments are greatest. Proximally to the nodus the three most anterior veins form a lattice girder, with a V-shaped cross-section, linked by strong bracket-like cross-veins—the primary antenodals—acting as compression-resistant struts (Figure 20.3a). In Calopterygidae and Libellulidae most of the antenodal cross-veins have this form, and their height increases, with the bending moments, towards

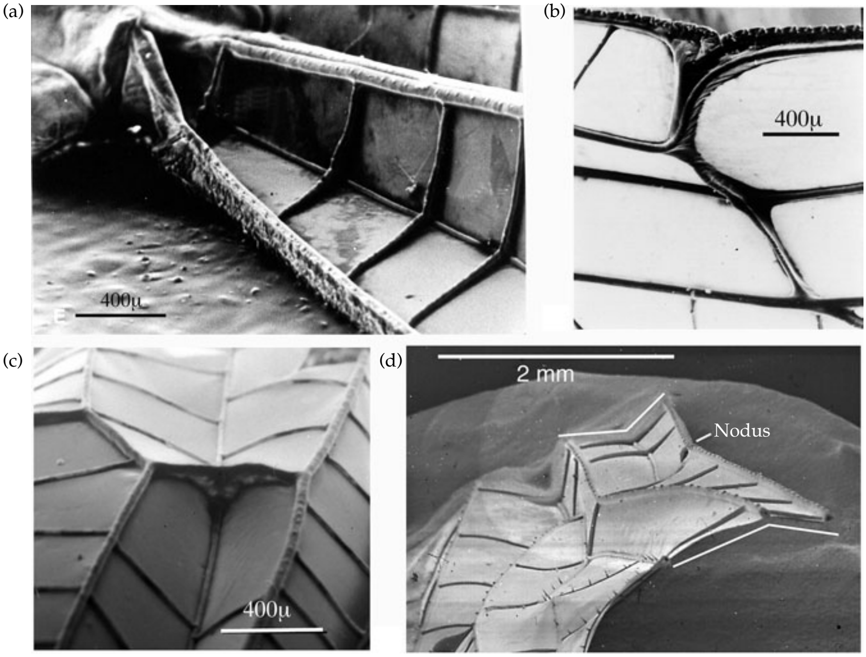

Figure 20.3 Wing details. (a) *Calopteryx splendens* forewing, antenodal cross-veins. (b) *Aeshna cyanea* forewing, ventral view of nodus, showing the high-relief subnodal bracket. (c) *C. splendens* forewing, mediocubital bar. (d) *A. cyanea* forewing, scanning electron micrograph, with view along leading edge towards the base, showing inversion of the cross-section at the nodus. (a–c) From Newman (1982); (d) original.

the base. In *Aeshna*, and probably generally, rigidity is enhanced by the membrane itself, acting as a 'stressed skin' to stiffen the structure (Newman 1982; Newman and Wootton 1986).

In Odonata proper, a high-relief cross-vein spans across C + ScA, ScP, RA, and RP at the nodus, terminating the rigid antenodal component of the leading-edge spar (Figure 20.3b); and in many forms another, the 'mediocubital bar', links across MA, MP, and CuA at the distal end of the discoidal cell (Figure 20.3c).

The depth of the corrugation diminishes towards the tip and the posterior margin. This is the area where camber develops and changes in flight. The wing must still resist bending, and a cambered section provides extra flexural rigidity; but for the camber to develop and invert, the wing must have some flexibility along axes parallel to the longitudinal veins. Corrugation allows this, provided that the cross-veins are themselves flexible, either throughout or at their junctions with the longitudinal veins. Odonata adopt the latter solution. Scanning electron microscopy reveals a range of flexible cross-vein endings in the deformable part of the wings of coenagrionids, calopterygids, aeshnids, and libellulids (Newman 1982; and Figure 20.4). Those shown in Figures 20.4d and e, found in many places in *Calopteryx* wings, are particularly interesting. The attachment is a flexible band of membrane which allows the cross-vein end to rotate slightly around the axis of the longitudinal vein. The horn-like structures on the upper and lower sides appear to act as stops, by pressing against the sides of the longitudinal veins and limiting the extent of this rotation. Gorb (1999) has found the elastic protein resilin in some flexible joints in Zygoptera.

Specialization of different areas for support and deformability is nearly universal in orthodox insect wings, and is an important part of the flight process (Wootton 1981, 1992). In Odonata the structure of the cross-veins is clearly crucial in determining both the degree of local rigidity, and the extent and direction in which the flexible areas deform.

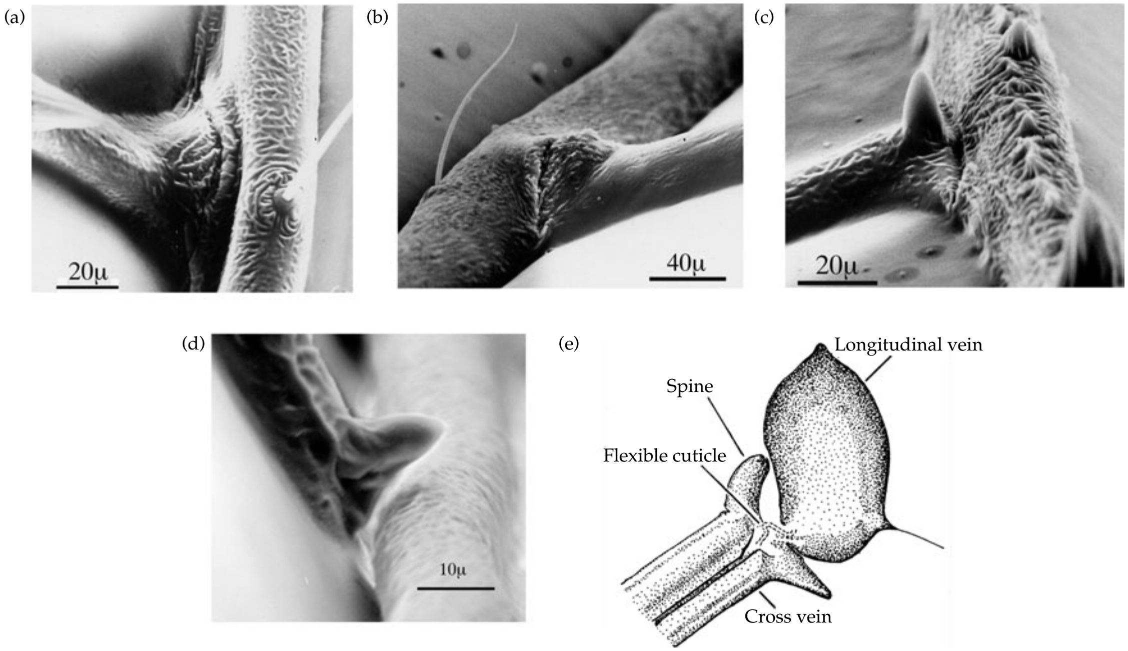

Figure 20.4 Flexible cross-vein junctions. (a, b) *Aeshna cyanea* forewing; (a) ra–rp, with RP, ventral view; (b) mp–cua, with MP, dorsal view. (c) *A. cyanea* hindwing, cross-vein on MP, ventral view. (d) *Calopteryx splendens*, cross-vein with RP1, dorsal view. (e) *C. splendens*, diagrammatic cross-section of a typical flexible junction. From Newman (1982).

20.2.3 Wing twisting: the leading-edge spar and the nodus

Wing twisting is important, particularly in animals that fly slowly and hover. Most insects use a technique known as 'normal hovering' (Weis-Fogh 1973) in which the stroke plane is nearly horizontal, and the wing twists extensively between the two half-strokes, generating weight-supporting force on both. Altering the stroke plane changes the direction in which the air is driven downwards, so that the insect can hover, helicopter-like, or fly forwards at a range of speeds, or briefly backwards or sideways. This mode of flight may be characteristic of all Zygoptera, although accounts of few species have been published: *Pyrrhosoma nymphula* and *Enallagma cyathigerum* (Coenagrionidae) (Newman 1982), *Platycnemis pennipes* (Platycnemididae), *Mecistogaster ornata*, *Mecistogaster linearis*, and *Megaloprepus coerulatus* (Pseudostigmatidae), *Lestes viridis* (Lestidae) (Rüppell 1989), and *Calopteryx splendens* and *C. virgo* (Calopterygidae) (Newman 1982; Rüppell 1989; Wakeling and Ellington 1997b). The anisozygopteran *Epiophlebia* also flies this way Rüppell and Hilfert 1993).

Unlike most insects, where moving the stroke plane towards the horizontal requires the body to be inclined towards the vertical, the back-tilted terga of Zygoptera allow a nearly horizontal stroke plane to be maintained while the body too is fairly close to the horizontal, although these insects are capable of altering the angle between the stroke plane and the body axis (Pfau 1986, 1991), which gives them some flexibility in body position at any speed. Pseudostigmatidae in particular tend to fly slowly and to hover with the body at a steep angle (Rüppell 1989). *Epiophlebia* also does this (Rüppell and Hilfert 1993).

Anisoptera have more limited wing-twisting capability. The terga are less tilted; they have less capacity to alter the angle between the stroke plane and the body; and they typically hover with an oblique stroke plane, generating most of their useful aerodynamic force on the downstroke. However, some at least are capable of typical normal hovering. We have film of *Cordulegaster boltoni* hovering in a flight enclosure with a horizontal stroke plane and body tilted 45–50° to the horizontal (Newman 1982). To what extent this happens in nature is unclear.

The need for the wings to twist has been crucial in the evolution of dragonfly flight. Some twisting is brought about actively, by relative movement of the costal and radioanal plates (Neville 1960; Pfau 1986, 1991), but far more is passive, elastic torsion within the wings' span, driven by inertial and aerodynamic forces, both of which are centred behind the wings' torsional axis (Norberg 1972; Newman 1982; Wootton 1991). Twist increases along the span, so that, for a given torque, longer wings will twist further than otherwise comparable short wings; but odonate wing torsion has subtle extra features.

First, the wing needs to twist most in the upstroke when, in Zygoptera at least, it is nearly inverted, with the ventral surface uppermost. This means that the wing has to be more resistant to leading-edge-down (pronatory) twisting than to leading-edge-up (supinatory) twisting. This asymmetry is achieved in many insects by an arched section, either of the whole wing, or of its anterior supporting spar (Wootton 1993; Ennos 1995). A thin cambered plate is far more resistant to bending when loaded from the concave side. Moreover, if the load is applied behind the torsional axis, the plate will undergo combined bending and torsion; and the asymmetry in the bending component of this process ensures that the plate twists easily when loaded from the convex side, but much less from the concave.

In the dragonfly wing, the camber of the leading edge spar inverts at the nodus, and its torsional properties abruptly change. The rigid antenodal component resists both bending and torsion; but at the nodus ScP ends as a free vein, and the postnodal spar has a shallow, inverted V section, with slender cross-veins (Figure 20.3d). Manipulation of fresh wings shows this to have the typical torsional asymmetry described above, and it is this above all that allows significant supinatory inertial twisting in the distal area of the wing. The effect can readily be reproduced in simple physical models.

The role of the nodus is clear: it is both a reinforcement and a shock absorber, coping with combined torsion and bending stress concentrations at the junction of the rigid concave antenodal and the torsionally compliant postnodal spars. These concentrations must have imposed strong selection pressure in the development of the nodus, which combines a stress-absorbing strip of soft cuticle with a strong, three-dimensional crossbar across the entire spar between the costal margin and RP1. The position of the nodus along the span varies between taxa, and almost certainly determines the amount of passive twist that the wings undergo in flight (Wootton 1991). In Anisoptera, where twist is limited, the nodus generally lies between 47 and 60% of the forewing's length from the base, and between 40 and 46% in the hindwing. Comparable figures for a range of Calopterygoidea are between 36 and 47% for both wings, with Euphaeidae providing the higher values; for Coenagrionidae and Lestidae the value is between 29 and 37%; but for the extremely twisty Pseudostigmatidae it is 15–20%. This parameter may be prove one of the more useful in relating flight behaviour to wing form.

20.2.4 Pitch regulation and trailing-edge depression: the pterostigma, curved veins, and the basal complex

Norberg (1972) first drew attention to a potential problem with wings, like those of dragonflies, with strong anterior support and flexible trailing edges. Unchecked, they would tend to swing into the airflow and flutter like flags; useless aerodynamically, and possibly damaging. By measuring the mass distribution across the width of *Aeshna* wings he demonstrated that the pterostigma could check this by acting as a counterweight in front of the wing's torsional axis, shifting the centre of mass towards the axis, and regulating the pitching of the wing. How far this principle can be extended to pterostigmata in general is yet to be tested, but it is probably widely true in Odonata, and proves to be only one of a battery of internal mechanisms operating to hold down the trailing edge in flight and maintain a cambered section and an effective angle of attack.

Ennos (1988), using both physical and analytical models, showed that wing torsion and camber can

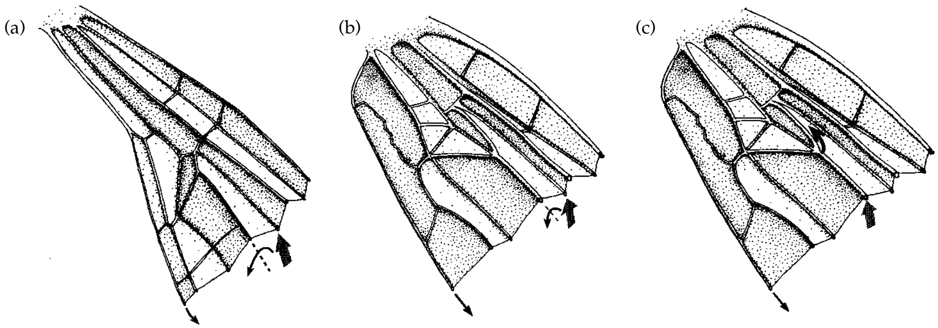

Figure 20.5 Functioning of basal complexes in depressing the trailing edge. Diagrammatic. (a) Coenagrionid; upward pressure on RP twists MA and the discoidal cell. (b, c) Aeshnid, showing separately the effects of upward pressure; (b) on RP; (c) on MA.

be connected. In wings like those of most Diptera and Odonata, in which the leading-edge spar is relatively straight but allows some twist, and from which a series of parallel veins, linked by cross-veins, run posterodistally to the trailing edge, passive wing torsion within the span automatically creates a cambered section. Narrow-winged Zygoptera provide nearly perfect examples of this kind of wing, and high-speed photographs of *Enallagma* (Dalton 1975, 1982) clearly demonstrate the effect. Further, Ennos (1988) showed analytically that if the posterodistally running veins are curved, like those of most broader winged Odonata, wing torsion tends to twist the veins along their length, so that the trailing edge will be depressed below the plane of the unloaded wing. Newman (1982) had earlier demonstrated that corrugated sheets with stiffened curved ridges and troughs, like the wings of *Calopteryx* and many other broad-winged Odonata, cannot be compressed flat; any pressure on the surface tends to force them into a cambered section. Again this tends to lower the trailing edge; and Wootton (1991) showed that in Calopterygoidea the broader the wing, the greater the vein curvature. However, the maintenance of an effective section by holding down the trailing edge is principally the responsibility of the basal complex of high-relief structures, comprising the arculus, the discoidal cell and its derivatives, and the mediocubital bar. In flight the aerodynamic force will be centred in the deformable area, within the part of the wing supported by the branches of RP. Applying pressure to this area in wings of freshly killed individuals shows the nature of the resulting deformations; and we have been able to simulate these in models of thin card (Figure 20.6), and to investigate the mechanisms involved (Newman 1982; Wootton 1991; Wootton *et al.* 1998).

These methods indicate how the basal complex functions in a wide range of Odonata. In Coenagrionoidea (Figures 20.5a and 20.6a) the mechanism is essentially that described by Ennos (1989) in Diptera. Pressure from below raises RP, which is attached to the rigid arculus. This flattens the concave pleat in which RP lies, and rotates MA about its length. As MA also arises from the arculus, part of which forms the base of the discoidal cell, the latter twists, approximately around the axis shown. The mediocubital bar, comprising the strong oblique vein forming the distal margin of the cell and the cross-vein that continues its line to CuA, is levered downward, and the trailing edge is depressed.

Similar mechanisms appear to operate in other coenagrionoid and in lestoid Zygoptera, although there are structural differences. The shape of the discoidal cell, and its alignment relative to MA vary. In most Coenagrionidae, Platycnemididae, and Lestidae the cell is inclined posterodistally, and the line of MA forms an appreciable angle with the axis of rotation of the cell, so that any upward pressure on MA would contribute to the torque on the cell, and to trailing-edge depression. In Pseudostigmatidae the basal complex is very close to the base, and tiny relative to the rest of the wing, but the process probably still operates,

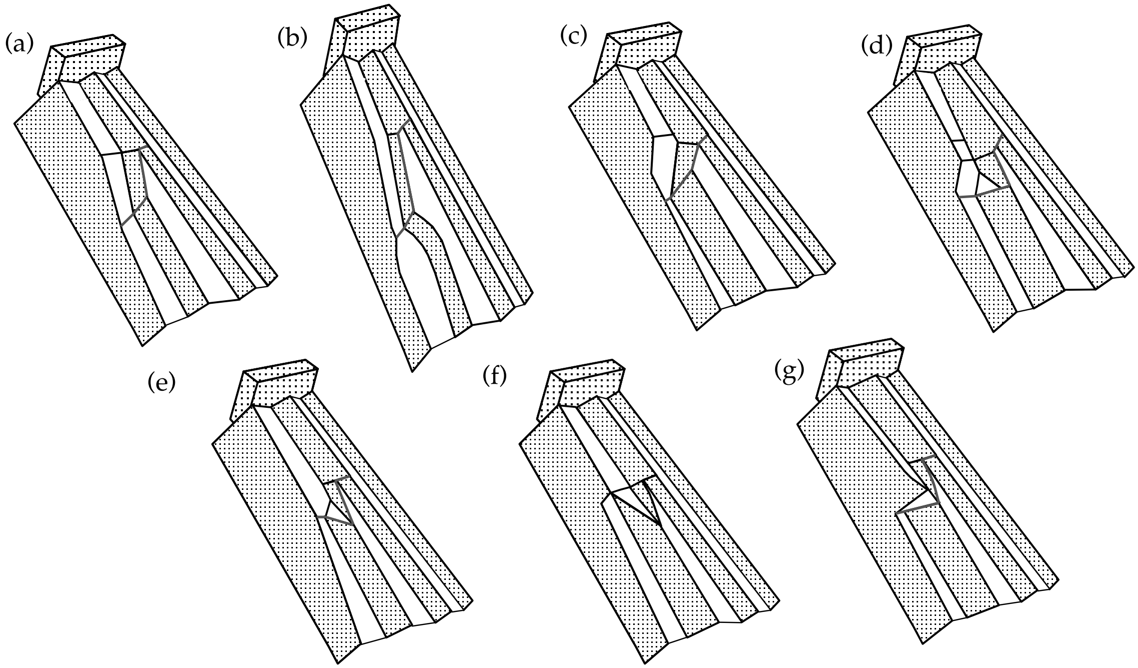

Figure 20.6 Diagrams of card models used in investigating trailing-edge depression mechanism; see explanation in the text. Some ridges representing homologous veins are shown as thicker lines. (a) Coenagrionid; (b) chlorocyphid; (c) *Heterophlebia* forewing; (d) *Heterophlebia* hindwing; (e) aeshnid; (f) libellulid hindwing; (g) libellulid forewing.

although this has not been investigated. In most Platystictidae and Polyneuridae, however, the discoidal cell is nearly rectangular, and MA continues in line with its anterior margin. The mechanism would probably still operate, but less effectively, and MA would not contribute to the process.

Calopterygoidea are more diverse. The discoidal cells are generally long, narrow, and rectangular, with the mediocubital bar short, transverse. and very stiff and strong (Figure 20.3c), although with shock-absorbing pliant cuticle directly below (Newman 1982). Models indicate that the mechanism still operates; raising RP rotates the discoidal cell along its length and depresses the trailing edge. In broad-winged calopterygids the force would be transmitted across the wide anal area by a high-relief composite vein that stiffens the area (Figure 20.2a), and the process would complement the camber-inducing mechanisms already described. In the usually narrow-winged Chlorocyphidae the discoidal cell is inclined more posterodistally, recalling the coenagrionid/lestid situation (Figure 20.6b). The adjacent part of MA is typically arched anteriorly, which probably increases its effectiveness in twisting the cell.

The situation in Anisoptera is very different, and the transition from the zygopteran condition can be followed with reference to *Epiophlebia* and to some fossil 'Anisozygoptera'. In the rather broader wing bases of *Epiophlebia* the discoidal cell has the typical irregular quadrangular form of coenagrionids and lestids, but is inclined more posteriorly. MA separates from the cell at a wider angle, and is more anteriorly situated in the wing. Its elevation would make a greater contribution to twisting the cell and to trailing-edge depression.

The Liassic *Heterophlebia buckmani* (Brodie) shows two more stages in the evolution of the anisopteran condition (Fraser 1957). Both wings have broader bases than *Epiophlebia*, and the hindwing is significantly broader than the fore. In the forewing the discoidal cell is again quadrangular, but is elongate, and sharply inclined posteriorly. MA separates nearer to the anterior apex. Its elevation in flight would tend to twist the cell along a nearly transverse axis, and modelling shows that this would strongly depress the posterior end; the anterior apex being fixed to the rigid arculus (Figure 20.6c).

The form of the discoidal cell is quite different in the hindwing, and is clearly transitional towards that of Anisoptera. The cell is now pentagonal; the anterior side is lengthened, the distal side is inclined anterodistally, and a new, concave vein crosses the cell, introducing relief to the structure and increasing its stiffness (Figure 20.6d). Raising the ridge representing MA in a model now tends to twist the cell across its breadth, forcing down the mediocubital bar, and lowering the trailing edge. Raising RP still tends to rotate the cell, as in Zygoptera, although along a different axis from the effect of MA. When both are raised together, as would be the case in flight now that MA is more anteriorly situated in the wing, the effects combine, and the depression is enhanced.

Within Anisoptera, further developments in the basal complex—the typical hypertriangle/triangle conformation, and its variations—can be seen as refinements in this mechanism, first described by Newman (1982) and developed by Wootton (1991) (Figures 20.5b and c). It works in all the types that we have modelled (Figures 20.6e–g). The basal complexes are similar in fore- and hindwings in all families apart from some Corduliidae, and most Libellulidae. Here they differ sharply. In the forewing the subtriangle is long, narrow, and transverse, extending almost to the margin, to lever down the trailing edge directly. The hindwing basal complex is small and broad, and its effect is extended across the anal area by the high-relief 'anal loop', recalling the composite vein in *Calopteryx*. Libellulidae are by far the most diverse of Anisoptera, and present fascinating, unsolved problems in relating wing morphology to flight behaviour.

20.3 Conclusions: evolution, divergence, convergence, and progress in odonatoid wing design

Figure 20.1 is a simplified phylogenetic scheme of Odonatoptera, following the conclusions of Rehn (2003), with some representative wing shapes for each taxon, on a time chart. Clearly today's two basic designs were already present in the Carboniferous: narrow-based, similar fore- and hindwings, and unequal wings with broader bases. The first seems to have persisted without interruption from Archizygoptera in the Palaeozoic through to the present day, although showing considerable diversity in detail. The 'anisopterous' design appears discontinuous, and shows convergence: Protodonata had 'anisopterous' wings, as had Permian Protanisoptera, but the true Anisoptera emerged from within the 'Anisozygoptera' assemblage in the Mesozoic. The latter, and the extant *Epiophlebia*, show an array of intermediate wing shapes; and some resemble the ancient Geroptera, the sister group of all other Odonatoptera. We can guess that the plans reflect broadly similar flight patterns: narrow, petiolate wings go with predominantly slow, manoeuvrable flight; broader-based, anisopterous wings are capable of strong flight over a wider range of speeds, with the larger species having higher maximum speeds. Intermediate forms were probably also intermediate in performance, as in many respects is *Epiophlebia* (Rüppell and Hilfert 1993).

Within these shape categories, right across the range, one can recognize and interpret certain trends in structural detail; reflecting both behavioural developments and a wider spectrum of flight techniques. Some relate to specific skills, particularly hovering and slow flight. Others point towards 'better engineering': improved designs for economy of materials, and greater strength to withstand the forces of flight and allow more powerful wing strokes. Across the board we see the differentiation of the leading-edge spar into rigid proximal and torsionally compliant distal components, facilitating upstroke twisting and hence slow flight and hovering. The giant meganeurid Protodonata, with a long ScP, were probably restricted to fairly fast flight, although some twisting may have been possible because the wings themselves were so long. Smaller protodonates—Paralogidae, Triadotypidae—had a shorter ScP, and the spar beyond had an inverted V section, allowing twisting and slower flight (Wootton and Kukalová-Peck 2000). In Triadotypidae (Nel *et al.* 2001), in the curi-

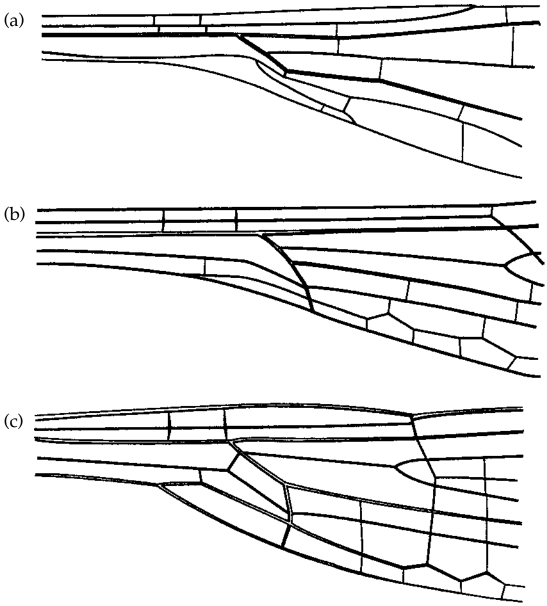

Figure 20.7 Wing bases, showing evolution of antenodal spar, nodus, and basal complex in damselfly-like forms. Semidiagrammatic. (a) Archizygopteran condition, based on *Progoneura venula* (Carpenter 1947), Lower Permian, Oklahoma. (b) *Permagrion/Hemiphlebia/Chorismagrion* forewing condition, based on *Hemiphlebia*, after Fraser (1957). (c) Coenagrionoid condition, based on *Platycnemis*.

ous *Lapeyria* (Nel *et al.* 1999), and in Archizygoptera and Protanisoptera, can be seen multiple beginnings of a true nodus; and in true Odonata the alignment and strengthening of some antenodal cross-veins, creating a rigid girder, strengthening the wing base and providing a firm anchorage for the basal complex.

The evolution of the basal complex is interesting. Physical models confirm that it serves to depress the trailing edge and maintain an effective wing profile in all Odonata, and suggest that an analogous arrangement of veins in Geroptera had the same role (Wootton *et al.* 1998). In Archizygoptera, however, the components of the complex are relatively unorganized (Figure 20.7a), and the development of the arculus and discoidal cell can be followed in the early fossil record. Many fossil forms and a few extant Zygoptera (most *Hemiphlebia* individuals, the forewings of *Chorismagrion*) lack the posterior component of the arculus, so that the discoidal cell is open (Figure 20.7b). Models indicate that the oblique mediocubital bar still acts in trailing-edge depression; but the cross-vein that completes the discoidal cell in most Odonata must provide extra rigidity to the complex and improve its effectiveness (Figure 20.7c).

Models also show how the development of the hypertriangle/triangle conformation allowed more effective recruitment of MA in trailing-edge depression in the broader-based wings of Anisoptera, via the intermediate conditions seen in the wings of some Jurassic 'anisozygopterous' types. They do not, however, allow us with any reliability to compare quantitatively the relative effectiveness of the various designs; these need proper engineering analysis.

Three directions for future research seem particularly worth following. All involve comparisons. We need quantitative information on the flight performance of a far wider range of Odonata, based on high-speed filming in the field, as in Rüppell (1989) and Rüppell and Hilfert (1993). Finite element analysis and optimization techniques could usefully be applied to compare the mechanics of selected wing components, like the basal complex, rather than entire wings; less time-consuming and more effective. Finally, there is a need for further morphometric analysis of wings and bodies of extant and extinct Odonatoptera, focusing on characters whose mechanics are understood, and related to known flight characteristics: distribution of body mass; wing loading; aspect ratio; the moments of mass and area, reflecting the distribution of these along the wing; and the relative lengths of the antenodal and postnodal components of the leading-edge spar.

Acknowledgements

We thank Richard Bomphrey, André Günther, Ed Jarzembowski, Bert Orr, Dennis Paulson, Georg Rüppell, and Jessica Ware, all of whom have increased our knowledge of dragonflies and their behaviour; and Michael May and Roland Ennos, whose comments have significantly improved this chapter.

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Glossary

aedeagus A heavily sclerotized male structure that is inserted into the vagina, used to transport sperm during copulation and to be transferred to the bursa copulatrix and spermatheca. In most insects it is a part or the primary genitalia, but in odonates it is a secondary genital element.

aerodynamic power The rate of work done on the air, created by mechanical power output of the flight muscles and transferred to the air by the lever system that includes the muscle connection to the wing, a fulcrum around which the wing rotates, and the wing itself.

allochthonous species Species not associated with the studied waterbody; that is, only adults are observed, not larvae or exuviae.

allometry The departure of geometric similarity or disproportionate change of a variable (not necessarily morphological) with body size. Allometry is detected statistically using the linear model $\log Y = \log a + b \log X$, in which the allometric exponent is estimated as the regression slope of logY on logX. Isometry, or geometric similarity occurs when the ratio of trait Y to trait X does not change with X, thus $Y/X = a$ and $b = 1$. In contrast, allometry occurs when $b \neq 1$. On the one hand, if $b > 1$, the ratio of trait Y increases faster than the ratio of trait X, and Y/X increases as X increases. This is termed positive allometry. On the other hand, negative allometry occurs if $b < 1$, and thus the ratio of trait Y increases more slowly than the ratio of trait X, and Y/X declines as X increases.

allopatry Describing the situation where populations of different species inhabit geographically separated areas.

allozymes Multiple forms of an enzyme, coded by different alleles of the same genetic locus, that differ in electrophoretic mobility.

alternative splicing This process occurs in the cell nucleus during gene expression; it is the variable inclusion or exclusion of particular exons (regions of gene sequence) from RNA prior to translation of the RNA into protein. The result is an increase in the diversity of protein products, and functions, of individual genes.

analytical model A mathematical model in which the solution to the equations used to describe changes in a system can be expressed as a mathematic analytic function.

andromorph A female exhibiting male coloration (and sometimes male pattern and behaviour) in a species in which females exhibit a colour polymorphism, as found in many damselflies. Also known as an androchrome or androgyne. Females in such species with 'normal' female coloration are known as heteromorphs.

anti-apostatic selection A type of frequency-dependent selection in which the more-common morph in a population is favoured by selection.

apparent competition Indirect interaction that may occur when two prey species have negative effects on the density of one another by increasing the abundance of a common predator.

arculus A transversely orientated composite vein near the wing base of most Odonata, formed from the common base of RP and M, and usually a short posterior crossvein.

area of occupancy The actual area on the ground that is occupied by the various populations of a species.

assembly rules A hypothetical concept which purports that certain species, once established at a habitat, can exclude others, or, alternatively, may not exclude the possibility of some establishment hierarchy.

assessment An ecological assessment is an evaluation or appraisal of both the biotic and abiotic components of the subject area.

autochthonous species Species associated with the studied waterbody (resident, breeding); that is, all live stages are observed (larvae, exuviae, adults).

balanced polymorphism Stable co-existence of two or more distinct types of individual, forms of a character, or different alleles of a gene in a population, with the proportion of each type being maintained by selection.

basal complex The functional unit comprising the arculus and the discoidal cell.

Bayesian population clustering A mathematical approach to analysing samples of known gene frequencies, normally with a Monte Carlo/Markov chain (MCMC) basis, to test hypotheses about population structure and gene flow. Bayesian clustering methods have proven to be a viable alternative to more traditional population-structure analysis techniques such as Mantel tests and Wright's F statistics.

bet-hedging A reproductive strategy to reduce, spread, or 'hedge' the risk of producing low-fitness offspring, such as mating with multiple partners, laying eggs in more than one site. Bet-hedging spreads risk of encountering an unfavourable environment over time or space.

Biodiversity Recovery Score (BRS) The cumulative Dragonfly Biotic Index (DBI) of all species, expressed as a percentage after a threat has been lifted relative to the cumulative DBI with the threat operational.

biomechanics The contribution of mechanical features to biological function.

C Costal vein. In most insects the anterior-most wing vein, which may have a multiple origin.

cascading effects A situation where a change in an ecological community may have knock-on effects, such that the structure of food webs are changed, either temporarily or permanently.

coarse filter A term used in conservation where whole landscapes are conserved as an umbrella for a wide range of species, interactions, and communities (*see also* fine filter).

co-evolution In the strict sense, co-evolution is defined as reciprocal evolutionary change between interacting species. In host parasite co-evolutionary interactions hosts can show specific memory to evade or minimize the effect of their parasitic organisms. In response to host selective pressures, parasites have evolved to avoid of host-recognition systems or particular host defences. In the case of diffuse co-evolution parasites or hosts or both are interacting with several species and the likelihood of identifiable reciprocal evolutionary change between any two species is thought to be less likely.

cohort A group or organisms of the same species and roughly the same age and size class; for example, a group of larvae that develop and transform within a given period of time.

compensatory growth Accelerated growth to compensate for a period of sub-optimal growth conditions (e.g. low food levels) or to deal with time constraints.

compositional biodiversity What biodiversity is made up of; the species in a given area.

concordant taxa (concordance) Different, specified taxa that occur together in the same, specified area.

constitutive exons Regions of gene sequence that are always incorporated into the mature mRNA of a gene. These are different from alternative exons, which during RNA processing can be included in the mature mRNA or removed by splicing.

convenience polyandry A behavioural tactic by which females mate multiply to reduce the cost of resisting mating attempts.

cost of reproduction The amount by which current reproduction reduces the expectation of future reproduction.

costs of phenotypic plasticity Costs that individuals which are able to show phenotypic plasticity have; that is, costs higher or lower than those costs incurred by individuals with a fixed response.

CuA Anterior cubital vein.

cultural service Non-material benefits obtained from ecosystems. These include spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences, including cultural diversity, spiritual and religious values, knowledge systems, educational values, inspiration, aesthetic values, social relations, sense of place, cultural heritage values, recreation, and ecotourism.

CuP Posterior cubital vein.

decision rules A description of alternative behavioural responses to particular environmental contingencies that initiate subsequent alternative patterns of behaviour; for example, initiation of flight leading to a migratory episode in response to a temperature decrease from one day to the next but not to stable or increasing temperature.

demographic rate The measures of survival, growth, and fecundity rates in a population.

density dependence The change in a per-capita demographic rate with population density.

developmental phenology Pattern of seasonal timing of developmental events in the individuals of a population.

diapause A seasonal period of physiological and often behavioural quiescence induced by specific environmental cues.

directional selection Selection that changes allele frequency in a constant direction. In a population, this type of selection acts on one extreme of the range of variation of a given trait and usually shifts the mean value of the trait to the opposite extreme of the range.

discoidal cell A cell near the wing base of most Odonata bounded by the arculus, MA, MP, and the mediocubital bar.

disinhibition Removal or cessation of response to an inhibitory stimulus.

dispersal polymorphisms Existence of two or more (often discrete) movement strategies in a single species or suite of species, such as separate migrant and resident phenotypes.

Dragonfly Biotic Index (DBI) A quantitative measure of the qualitative response of species to habitat traits. The index is based on the sum of three sub-indices: (1) the size of the species' geographical range, (2) the risk of extinction, and (3) sensitivity to habitat change.

ecological integrity The natural species composition of a specified area.

ecological relaxation The gradual loss of species from a community over time as a result of ecological disturbance around that community, as for example, when a patch of forest remains when the surrounding forest has been harvested.

ecosystem services Benefits that humans obtain from ecosystems that support, directly or indirectly, their survival and quality of life. These include provisioning, regulating, and cultural services.

endemic (endemism) A species that is confined to a specified geographical area, usually a relatively small area, for example an island, a forest, a mountain range, or a country (i.e. endemic to St Helena, endemic to Gabon).

environmental trigger An environmental change that elicits a change in the course of development of an organism.

ephemeral Brief in occurrence; in our context, usually referring to temporary water bodies that are likely to dry up within the course of a year.

eurytopic Species with a large range of tolerance to environmental factors, such as physicochemistry, habitat, etc.

evolutionarily significant units Sub-populations of species, sometimes termed sub-species, forms, or races, that are morphologically, and therefore genetically, distinct, and are given conservation status in their own right.

evolutionarily stable strategy A trait or strategy set for which there is no superior set.

exploitative competition A non-lethal indirect interaction that occurs when the fitness of some or all individuals is reduced through use of a shared resource.

extent of occurrence The overall geographic range of a species, as measured around all the marginal populations (see marginality).

extinction debt Survival of an ecological community in the short-term, but which, as it has become isolated, by landscape fragmentation for example, will inevitably lose species in the long term, especially when environmental conditions become adverse and when genetic viability is decreased.

exuvia Discarded exoskeleton that is left after a larva has moulted. Exuviae of the last larval instar are left behind on the shore when dragonflies emerge into the adult stage.

facultative A characteristic, trait, or phenotype that is expressed only under specific extrinsic conditions.

fall-emergers Larvae of *Anax junius* that emerge (metamorphose) to an adult stage in late summer or autumn.

fecundity rate The rate at which individuals produce offspring.

fine filter A term used in conservation where there is focus on one or several clearly targeted species; often overlays the coarse filter.

fitness component A character or trait (e.g. survival, fecundity, mating success) that contributes to fitness but is not a perfect predictor of fitness.

fitness landscape A graphical metaphor for the fitness of an individual as a function of its phenotype.

fitness The expected reproductive success of a group of individuals sharing a particular trait or set of traits. In general, selection is expected to favour individuals with relatively high fitness; that is, such individuals are expected to have higher lifetime reproductive success and leave more surviving offspring than individuals with relatively low fitness. A component of fitness is a distinct stage or aspect of lifetime reproductive success or total fitness such as viability (survivorship to sexual maturity), mating success (number of matings achieved), or fertility per mate (zygotes produced per mating). *See also* realized fitness.

flagship group Popular, charismatic organism group that serves as a symbol and rallying point to stimulate conservation awareness and action.

flight heading The horizontal orientation of the body of a flying animal.

flight muscle ratio Total mass of flight musculature in relation to total body mass.

fluctuating asymmetry Small, random deviations in symmetry in otherwise bilaterally symmetrical characters. Measures of fluctuating asymmetry are often used as an indicator of developmental instability and are predicted to be inversely associated with environmental stresses.

focal taxon (plural: focal taxa) The specified taxon of particular interest, and perhaps of particular conservation action.

food limitation The condition of a population having inadequate food available for all individuals in the population to survive and grow at their maximal rates (i.e. the rates when food is unlimited).

fragmented habitats Habitats which have been broken up into fragments, often isolating populations, thus reducing population viability and which may undergo ecological relaxation as the fragment becomes surrounded by adverse conditions.

frequency-dependent selection Selection occurring when the fitness of particular genotypes is related to their relative frequency in the population. For example, when rare, a particular genotype may be at a selective advantage compared with the other possible genotypes, but when it is common it may be at a selective disadvantage (pro-apostatic selection).

Fst Sewall Wright's fixation index compares genetic variability between and within populations, scaled from 0 (panmixia between 'populations') to 1 (complete genetic isolation between populations).

functional biodiversity The way biodiversity functions; the interactions between species relative to the functioning of a specific ecosystem.

gamont The gametocyte of the gregarine lifecycle; gametocytes encyst and form multiple gametes within the cyst. The fusion of gametes forms zygotes that mature into sporozoites.

genetic bottleneck Loss of genetic variation as a result of great reduction in number of individuals in a population, and which may have a great effect on its future viability.

genetic correlation Correlated variation in the breeding values of two or more traits. Genetic correlations are caused by the additive effects of overlapping sets of genes or genetic linkage.

genotype The underlying genetic make-up that gives rise to phenotype.

genotype-by-environment interaction Defined at the population level it means phenotypic effects that are due to the interaction between the environment and the genes. If reactions norm are non-parallel there is a genotype-by-environment interaction.

geometrically similar Objects or organisms that, over a size range, maintain constant ratios of the lengths of their body parts. In other words, they maintain the same shape as they vary in size. In geometrically similar animals, lengths scale as $M^{1/3}$.

gregarine parasites Protozoan parasites in the phylum Apicomoplexa that inhabit the gut and sometimes other tissues of a wide variety of invertebrates.

growth rate The rate at which individuals progress through their developmental stages.

gynochrome In female polymorphic species the female morph that least resembles the male in body coloration, pattern, or behaviour.

haplotype Originally a set of alleles of different genes on a single chromosome that are closely linked and usually inherited as a unit; now also commonly used to refer to a particular nucleotide sequence, from among several possibilities, found in an individual. Mitochondrial sequences are commonly compared as haplotypes.

haplotype network A diagram showing the haplotypes found in a population or group of populations, and the minimum number of nucleotide changes required to transform any one haplotype to another found within the group, which presumes some evolutionary relationship between haplotypes.

heteromorph A female exhibiting 'normal' female coloration in a species in which females exhibit a colour polymorphism. Also known as a heterochrome or gynochrome. Females in such species with male coloration are known as andromorphs.

heterosis Hybrid vigour; superiority of the heterotzygous genotype over both homotzygotic genotypes.

heuristic A technique or explanation that serves as an aid to understanding and problem-solving, especially by increasing the effectiveness of trial and error.

hybridization Crossing of genetically divergent individuals, leading production of hybrid offspring.

hydroperiod Temporal pattern of aquatic habitat availability.

iconic value The selection of certain species, that may be rare and/or glamorous, to illustrate a particular conservation principle.

immune trait Various physiological factors (e.g. phenoloxidase activity) that can be measured and are presumed to reflect ability to resist infection or mitigate the costs of parasitism.

immunity Baseline or elevated expression of immune traits in resisting infection.

inbreeding depression Loss of genetic viability when populations become very small and isolated from other populations of the same species.

infection The presence of a parasite or pathogen within the host. The cost of infection could be the detrimental effect to host tissue (biochemical or physical) as a result of interaction with a parasite or pathogen.

intensity The number of parasites in an infected host.

interference competition A non-lethal direct interaction that reduces the fitness of some or all individuals.

intersexual selection That part of sexual selection involving mate choice by the opposite sex. Typically refers to female choice, although male choice of females occurs in some species. Active female choice involves females choosing a mate based on direct assessment of one or more male phenotypic characters. Passive female choice refers to females choosing males indirectly on the basis of a character, such as territory quality, not directly part of the male phenotype but rather a character over which males may have competed among themselves for dominance.

interspecific variation Differences between species. This typically refers to differences in the mean value of a trait between two or more species.

Intertropical Convergence Zone (ITCZ) A region of low pressure that extends around the Earth in tropical regions, moving north and south slightly lagging the apparent seasonal movement of the sun and characterized by converging winds and enhanced rainfall; consequently, migrating insects that fly downwind in the vicinity of the ITCZ are likely to reach areas where water and food are seasonally available.

intraguild predation A mixed competition/predation interaction that occurs when species that interact as predator and prey also engage in exploitative competition for shared resources.

intrasexual selection That part of sexual selection involving competition among individuals of the same sex. Typically refers to male–male competition either directly for mating opportunities or indirectly via competition for territories or other resources important to females.

intraspecific mimicry (automimicry) Arises when the mimics and models are members of the same species. *See also* mimicry.

intraspecific variation Differences among individual organisms of the same species.

intrinsic value The worth of life, such as dragonflies, regardless of its value to humans.

irruptive Characterized by irregular population increases and/or movements that lead to large numbers of an animal occupying a region where it is ordinarily rare or absent. In migration ecology, irruptions are not necessarily signs of true migration events.

isometric contraction Contraction of a muscle that is held at constant length. For example, this is what your bicep muscle does when you attempt to lift something immovable.

isotopic ratio The ratio of alternative, naturally occurring forms of an element that differ in atomic mass due to differing numbers of neutrons in the nucleus. Modern mass spectrometers are much more accurate at measuring the relative amounts or ratios of isotopes of a given element in an object of interest than absolute quantities, so studies employing radiogenic and stable isotopes normally report the ratios of these isotopes. In many cases, these ratios are expressed in delta (δ) notation as a means of showing the ratio of the item of interest relative to some standard with a known ratio.

key threat The major threat to survival of populations, and even of a species, that, when lifted, results in the immediate increase in population levels.

keystone group An organism group that has a large effect on any aspect of ecosystem function (e.g. a structuring role in the food web).

landscape triage After systematic conservation planning, often there is the unfortunate fact that not all areas or all species will be able to be conserved, and the choice has to be made which of the areas would benefit most (i.e. where would conservation be most effective) given specific conservation management.

larval stage The immature aquatic stage of odonate development.

lattice girder A girder consisting of a lattice of tension and compression members.

leading lines Landscape features, such as coastlines or mountain ranges, that extend more or less linearly for some distance and can serve as landmarks that guide animal movements.

lentic Characteristic of still or slow-moving waters such as wetlands, lakes, cattle tanks, swamps, bogs, and ponds.

Liassic The lower division of the Jurassic period, between 208 and 178 million years ago.

life cycle The connected developmental stages through which an organism passes over the course of its life time.

life-history omnivory A change in the trophic level at which an organisms feeds as a function of size and/or developmental stage.

life-history track The temporal pattern of life-history changes exhibited by an organism. Some species exhibit more than one life-history pattern, often showing a suite of differences in the timing, order, and/or categories of life-history processes and states, such as diapause, dispersal, emergence, and reproduction. If these patterns are discrete rather than continuous, then the distinct life-history patterns may be referred to as life-history tracks.

longitudinal study A study following distinct or marked individuals through time.

MA Anterior median vein.

magnetic orientation Orientation mediated by detection of and response to force vectors within the Earth's magnetic field.

Mantel test In population genetics, a means of comparing geographic and genetic distance matrices representing pairwise relationships for individuals or populations within each matrix. A significant relationship suggests that genetic isolation has some association with distance.

marginality Describing populations at the edge of a species range, which may be isolated and thus vulnerable to attrition, and which may require particular conservation attention.

marking effect A significant change in behaviour after marking. Marked animals can become 'trap-shy' if they associate marking with an unpleasant experience, and might avoid areas where they have been marked. The opposite, 'trap-happiness', is commonly observed when traps are baited, and means that animals learn to associate traps with food or other rewards. A negative marking effect can also result from wing damage imposed during marking. These effects violate the assumptions of most mark–recapture methods, and have to be taken into account when data are analysed.

mass emergence Emergence of large numbers of adult insects within a very short period of time, so that exceptional numbers are evident near the emergence site.

mass movements Movement in a relatively short period of time of large numbers of individuals of a species, usually resulting in the movement being obvious to an observer.

mass-specific A quantity in relation to a mass. For example, muscle mass-specific power output relates mechanical power output of a muscle to the mass of that muscle (units, W/kg).

mate guarding The post-copulatory interaction when a male keeps himself either in contact with or a close distance from his recent female mate.

mating efficiency A measure of individual mating success per unit time spent attempting to mate. In contrast, mating success is often measured over a longer period of time that may include time when an individual may not be actively pursuing mating opportunities. Thus, say male dragonfly obtains a mating success of 10 matings during its lifetime. If it was present only a total of 5 h at ponds where mating potentially takes place during life, its mating efficiency would be $10/5=2$ matings h^{-1}.

maturation period The time elapsed between the emergence of the adult from its larval skin and the start of reproductive activities.

mediocubital bar A bar, often of high relief, formed by the distal margin of the discoidal cell and a cross-vein between MP and CuA.

metacommunity A collection of local communities that are linked by dispersal of multiple interacting species.

metapopulation A set of local populations connected by migrants. Some populations might act as sources (they receive a few immigrants, but produce a large number of emigrants) and others as sinks.

metric Biological variable (e.g. number of species or score based on sensitive taxon) that responds to human impact (e.g. eutrophication or habitat perturbation).

microsatellites Specific, relatively short nucleotide sequences consisting of tandem repeats of one to four nucleotides; because they are widely dispersed within the genome and have little or no functional effect, microsatellites are extremely variable among individuals and thus useful for genetic analysis of recent population interactions or evolutionary events. Primers designed to amplify microsatellite loci are an increasingly favoured means of studying fine-scaled population relationships, particularly when used with multiple microsatellite loci. Unlike mitochondrial loci, they are co-dominant (diploid) and not normally under selection and are thus more free to drift.

migrant An individual (or more generally a phenotype) that is migrating or will migrate at some stage of its life cycle; here, specifically an adult dragonfly that, as a normal part of its life cycle, moves a long distance from its place of emergence in order to reproduce; the term is often used in contrast to a resident strategy, phenotype, or individual.

migration Maintained directional movement that is not arrested by usually attractive cues and that typically has the effect of moving individuals from their place of origin to a relatively distant destination where they reproduce (see Chapter 6 for and extended discussion).

mimicry The resemblance in phenotype and/or behaviour of an organism (the mimic) to another organism (the model).

monandry A mating pattern by which a female mates with only one male in a single breeding season.

monitoring The collection and analysis of repeated observations or measurements to evaluate changes in condition.

monogyny A mating pattern by which a male mates with only one female in a single breeding season.

mortality schedule The expected probability of mortality rates for each age group.

MP Posterior median vein.

multivoltine Describing an organism that goes through two or more generations per year.

Namurian A division of the Carboniferous period, between 326 and 315 million years ago.

natural selection In general, a process by which successful traits or genes become more common in successive generations as individuals with those traits reproduce and leave more descendants than those with alternative traits or genes. When used in contrast to sexual selection, it refers specifically to traits that are not directly and in exclusive relation to reproduction, such as those facilitating survivorship, foraging, or interspecific competitiveness (see Box 12.3).

navigation Strictly, navigation is the orientation and movement from a known current position to a preset destination; more loosely, it is maintenance of a general direction of movement in the face of changing environmental cues and conditions that may tend to alter course.

nested clade analysis A coalescent method of analysing intra- or interspecific genetic data, such as mitochondrial haplotypes or allozymes, to infer the evolutionary relationship between individuals, populations, or species. For intraspecific nested clade analyses, these studies are often conducted to determine whether there is a spatial component within the 'nested' pattern of genetic data. Normally, these data are not codominant (diploid).

niche shift Restriction in the use of space because of intense interspecific competition and/or interspecific aggression, or predation by other species.

nodus A clearly marked structure in the leading edge of odonate wings, formed by the sharp deflection of ScP to meet C + ScA at the anterior margin, aligned with a strong cross-vein linking across ScP, RA and RP.

nuptial plug Usually a structure that is left obstructing the female vaginal entry; frequently produced by either the male or both sexes after copulation.

Odonatoptera Odonata plus the branches of the odonate stem: Protodonata and Geroptera.

oogenesis flight syndrome Migratory flight by reproductively immature individuals, particularly immature females. The term implies a trade-off or alternative life stage between migration and reproduction.

operational sex ratio The relative number of sexually active males and receptive females at the mating site.

opportunity for selection Variance in fitness among individuals either overall or in a particular fitness component such as survivorship or mating success. Also known as the index of selection or the intensity of selection. This value, defined as $I = V_w/W^2$ where W and V_w are the mean and variance of fitness, respectively, sets an upper bound on the rate of evolution (see Box 12.2).

optical interaction-synchronization The tendency of some animals to act as they see other animals, usually of the same species, acting; for example, to begin flying when seeing other individuals flying.

oviposition Deposition of eggs by a female insect, which in dragonflies typically takes the form of dropping eggs into water or inserting them into aquatic plants.

panmictic A population or entire species that exhibits no genetic differentiation from place to place owing to very rapid spread of alleles throughout the population. Theoretically, the concept that any given individual would have the same probability of mating with any other individual of the opposite sex. In practical terms, groups of individuals or populations described as panmictic have no detectable population structure and exhibit very high rates of gene flow.

parapatric populations Populations inhabiting geographically distinct areas that have a contact zone between them.

parasite load The relative numbers or impact of parasites on an individual animal.

parent population A population from which dispersing and/or migrating individuals originate.

petiolate wings Wings with a narrow, stalk-like base.

phenology The timing of life-history or other biological events, such as bud burst, adult metamorphosis, or feeding behaviour.

phenotype Any character or trait, (e.g. morphology, biochemistry, behaviour, life history) that can be measured on an individual.

phenotypic plasticity The expression of multiple phenotypes from a single genotype on the basis of some external cue; with odonates, these responses are often immature organisms that develop alternative morphological, physiological, or behavioural adult forms in response to environmental conditions experienced during development.

photoperiod The pattern of alternating light and dark, usually encompassing a 24-h cycle, that an animal experiences.

physiological genetics The molecular genetic mechanisms that underlie variation in physiological traits.

polyandry A mating pattern by which a female mates with more than one male in a single breeding season.

polygyny A mating pattern by which a male mates with more than one female in a single breeding season.

population regulation The action of ecological forces that tend to control the size of a population.

population structure The extent and pattern of genetic differentiation from place to place within a population or group of interacting populations (metapopulation).

population The individuals of a particular species within a defined area; it often, but not always, implies that genetic interchange is more likely within a population than between different populations.

postmating reproductive isolation The existence of a reproductive barrier that prevents or reduces gene flow between two populations after a mating has occurred. Such barriers include, for example, the inability of gametes to cause fertilization, and factors causing hybrid sterility or inviability.

potentiate To amplify the response to a primary stimulus by a secondary stimulus that may not, in itself, elicit an observable response.

power The product of force and distance (i.e. work), divided by time (SI unit, Watt or W).

precautionary principle The principle of conserving as much biodiversity (compositional, structural, and functional) as possible in case there may be adverse ecological consequences should we not do so.

predator-induced defence Phenotypically plastic traits that are only expressed in the presence of a potential predator.

premating reproductive isolation The existence of a reproductive barrier that prevents matings of individuals between populations; for example, behavioural or ecological differences between populations.

pre-reproductive An insect that has reached the adult (imago) stage but that has not yet become sexually receptive and/or whose gonads have not matured.

prevalence Percentage of individuals infected with one or more individuals of a particular parasite species or taxon.

pre-vitellogenic Developing oocytes of insects before they are provisioned with yolk; also the condition of the female until her first eggs are supplied with yolk.

primary genitalia In odonates, it refers to the genital organs, where sexual cells are produced and received in the case of females, and the appendages used to transfer sperm to the females. These appendages are absent in male odonates.

prioritization A process usually applied to species, and where ideal reserve areas are selected by an iterative process involving complementarity (where one area complements another in terms of its biotic composition), and which often gives high priority to the most irreplaceable biota (i.e. if they are lost from one area, they are lost forever).

pro-apostatic selection A type of frequency-dependent selection in which the rarer morph in a population is favoured by selection.

pro-phenoloxidase cascade Through a series of catalytic reactions, tyrosine and tyrosine derivatives are converted to melanin with phenoloxidase as the primary enzyme. Melanin is the major component of the defence reactions to larger parasites as it is often deposited around encapsulated objects (e.g. mite feeding tubes) and also serves as an anti-microbial compound.

provisioning service The products obtained from ecosystems. These include food, fibre, fuel, genetic resources, ornamental resources, freshwater, biochemicals, natural medicines, and pharmaceuticals.

RA Anterior radial vein.

radiogenic isotope An element derived from the radioactive decay of another element, as in the creation of ^{87}Sr from ^{87}Rb through β decay. Stable isotopes have negligible radioactivity, although they may be generated through radiogenic decay processes.

radio-tracking Monitoring the position and movement of an animal by receiving radio signals from a transmitter attached to the animal.

realized fitness The actual reproductive success of an individual or group of individuals under field conditions including all the various random and unpredictable factors that may make the lifetime reproductive success of an individual greater or less than the fitness of the group to which it belongs. Also used to denote the actual number of young parented by an individual as opposed to an estimate based on its mating success or other incomplete measure of fitness.

recovery planning A conservation-management activity that targets a particular species or set of species for enhancement of their population levels.

Red List The official Red List of Threatened Species™ produced by the IUCN (World Conservation Union).

regulating service Benefits obtained from regulation of ecosystem processes. They include air-quality regulation, climate regulation, water regulation, erosion regulation, water purification and waste treatment, disease regulation, pest regulation, pollination, and natural-hazard regulation.

reinforcement A process enhancing premating reproductive isolation through selection to avoid maladaptive hybridization. It may also occur when matings between heterospecifics reduces fitness otherwise, without production of hybrids. Can lead to a pattern known as reproductive character displacement.

reproductive character displacement A pattern created by reinforcement of premating reproductive isolation due to avoidance of maladaptive hybridization. Traditionally, it is divergence of isolating trait between allopatric and sympatric populations, but it can also be measured in sympatry in which the strength of isolations depends on relative abundances of the two species. *See also* reinforcement.

resident An individual (or phenotype), here an adult dragonfly, that does not migrate but remains in the general vicinity of its place of emergence; the term is often used in contrast to a migrant strategy, phenotype, or individual.

resistance, to a parasite One or more combined traits such as the host immune system, life-history traits, or behaviour that contribute to inhibiting the development and growth of a parasite and presumably do so at a cost that is less than the cost of infection.

riparian community The community of organisms along river banks.

risk enhancement The actual risk imposed by multiple predators is greater than the risk that would result from independent effects.

risk reduction The actual risk imposed by multiple predators is less than the risk that would result from independent effects.

RP Posterior radial vein.

Sampled Red List Index A long-term initiative of the IUCN (World Conservation Union) which focuses on the random selection of species (1500 in the case of Odonata) and periodic re-assessment of those species over time to gain insight into global trends in population levels and conservation status of those species over time; that is, a global trend analysis.

ScA Anterior subcostal vein.

scaling The quantitative relationship between a trait and body size. Scaling relationships often take the form of $Y = \mathrm{a}M\mathrm{b}$, where a is a constant, M is body mass, and b is an exponent describing the scaling relationship between a trait of interest, Y, and M. For similarly shaped animals, basic geometry dictates that lengths scale as $M^{1/3}$, areas scale as $M^{2/3}$, and volumes scale as M^{1}.

ScP Posterior subcostal vein.

search image A transitory filtering of external visual stimuli that enables animals to focus its attention on finding, for example, a prey item or a partner of a particular phenotype.

seasonal refuge flights Flights by adult dragonflies, usually pre-reproductive, away from their site of emergence to a region where they feed and mature over an extended period of time before eventually returning to suitable breeding sites.

secondary genitalia In male odonates, organs where sperm is stored momentarily before its transfer to the female genitalia. They do not develop from the sexual appendages, but from novel organs at the second and third abdominal segments.

sensillum (plural: sensilla) A sensory receptor usually embedded in the arthropod cuticle.

service-antagonizing unit (SAU) A single species or community responsible for the reduction of the benefits of an ecosystem service. It is the converse of the service-providing unit (SPU).

service-providing unit (SPU) The species or community and the attributes of their populations (size, temporal, spatial distribution) that contribute to an ecosystem service. A single species or community may benefit several services.

sex ratio The proportion of males in a given population. The primary sex ratio refers to the proportion of males at fertilization. This proportion can change if there is sex-biased mortality of embryos. The secondary sex ratio is the proportion of males among mature adults. When only the reproductive adults are counted at a given moment, then the proportion of males is known as the operational sex ratio.

sexual selection A form of natural selection specifically targeting characters in exclusive relation to reproduction (see Box 12.3). Often further subdivided into intrasexual selection, referring to male–male or female–female competition related to mating, and intersexual selection, referring to female (or male) choice of mates.

sexually antagonistic selection Selection that acts in opposing directions on sexually homologous traits and their underlying loci in males and females.

sink population A population that cannot be maintained without continual immigration.

sinusoidal contraction The sine-wave shape of the length/time relationship for a muscle involved in cyclical motion. Odonate flight muscles undergo sinusoidal contraction during flight.

size structure The distribution of body size among individuals in a population; often related directly to developmental stage.

source population A population that can be maintained without continual immigration.

spatial displacement Movement from on place to another.

sperm selection The phenomenon by which females would bias the use of a particular male's set of sperm for fertilization from a set or different males' sperm that are usually stored in the female sperm-storage organs.

sperm-storage organs Female structures specialized to receive and maintain sperm previous to fertilization. Usually there are two structures, a proximal bursa copulatrix and a distal spermatheca, which are linked to each other.

sporozoite The infective stage of the gregarine parasite (Apicomplexa). Gregarine sporozoites within a spore are ingested by the host and are released into the gut where they penetrate the midgut epithelial cells.

spring-emergers Larvae of *Anax junius* that emerge as adults in spring or early summer; such individuals have generally been considered non-migratory.

stabilizing selection Selection favouring an intermediate or average phenotype over more extreme phenotypes. The opposite of disruptive selection in which phenotypes more extreme than the mean are favoured.

stable isotope The alternative form of an element that differs in atomic weight with negligible radioactivity.

station-keeping responses Behavioural responses that tend to inhibit spatial displacement and thus keep an individual animal within a relatively small area.

stenotopic A species with a narrow range of tolerance to environmental factors, such as physicochemistry, habitat, etc.

stepping-stone habitats Habitats that are separated but not so far apart that individuals cannot move from one to the next, perhaps to eventually reach prime habitat.

strain The proportion of a muscle's contraction distance to the length of that muscle.

stress As used in engineering and biomechanics, this refers to the ratio of force to cross-sectional area.

stroke plane The average plane of the wing stroke, calculated by regression analysis of the wing-tip path.

structural biodiversity The structure of biodiversity; in terrestrial and freshwater systems this usually means the structure of the plant community.

struts Structural members primarily loaded in compression.

supporting service Services necessary for the production of all other ecosystem services. They differ from the other services in that their impacts on humanity are often indirect or occur over a very long period of time, whereas changes in the other categories have relatively direct and short-term impacts on people.

survival rate The rate at which individuals in a cohort die.

sympatry Describing the situation where populations of different species inhabit the same geographical area.

synergistic effects The additive or multiplicative effects of more than one adverse impact or threat to a population or species.

systematic conservation planning The systematic selection of high-priority conservation areas which should be given particular attention (*see also* prioritization).

tandem linkage A part of the mating behaviour of dragonflies in which the male grasps the female by the head with his terminal appendages (cerci and epiproct), either preparatory to copulation or to guard a female with which he has or will copulate; sometimes maintained for periods of hours, in flight or at rest.

teneral Term used to describe a newly emerged adult insect. The exoskeleton of teneral insects has not completely hardened and the colours are often different than those of more mature adults. In odonates, the teneral period also can be used to describe the first few days of adult life when the flight musculature and ovaries have not yet reached their mature mass. Reproductive behaviour (including territoriality) is either non-existent or greatly reduced in teneral odonates. The term adolescent has been used to describe the transitional stage between teneral and fully mature odonates.

tetanic stimulation Stimulation of a muscle by a series of electrical stimuli that occur so close together in time (milliseconds) that the muscle cannot relax between stimuli. Muscles stimulated in this fashion, while held at constant length (*see* isometric contraction), rapidly develop their maximal tension. Physiologists use this technique to measure the maximal force that can be exerted by a muscle. Odonate flight muscles do not operate in this fashion; rather they receive a single neural stimulus per contraction and except for behaviours such as struggling, they never develop maximal tension.

time constraints Constraints imposed by the need to reach a certain developmental stage before a certain deadline (e.g. onset of winter, pond drying).

time-compensated sun compass The ability to use the position of the sun to maintain a constant orientation or direction of movement, even as the azimuth direction of the sun moves during the course of a day.

torque The product of force and the distance between that forces and the fulcrum or pivot point around which a mechanical element (such as a wing) rotates.

trade-off A negative link between two traits that cannot be optimized simultaneously.

trend analyses (of species, often of conservation concern) changes in population levels over time, which may also include re-assessments of their conservation status.

umbrella group An organism group whose conservation is expected to profit to a large number of co-occurring groups.

univoltine Describing an organism that goes through one generation per year.

utilitarian value Of value to humans; may be consumptive (i.e. we consume the organisms) or non-consumptive (i.e. we use organisms but do not consume them; e.g. dragonfly watching).

vagility The property of moving readily from one place to another over an individual lifespan.

variance–covariance matrix A symmetrical square matrix with rows and columns representing all measured traits. The diagonal of the matrix is the variance of those traits, and the off-diagonals are the covariances. Variances and covariances can be measured directly on the phenotype or indirectly on the genotype.

viability The ability of organisms to develop and live normally.

war of attrition A fight between two males in which the winner is usually the male that endures longer and that is prepared to invest the greater amount of time and energy.

Westphalian A division of the Carboniferous period, between 315 and 306 million years ago.

wind drift The tendency for the actual movement trajectory of a flying animal (or machine) to depart from the intended heading owing to lateral wind movement; that is, being blown more-or-less off course.

wing loading The weight supported by unit area of wings; that is, total weight of the animal divided by the projected wing area.

wingbeat amplitude The arc of the beating wings. Higher wingbeat amplitude typically produces greater aerodynamic power output and thrust, particularly when combined with higher wingbeat frequency.

wingbeat frequency The number of wingbeats per second. Odonates typically have wingbeats in the range of 5–50 cycles/s (Hz).

work The product of force and distance moved (SI unit, Joules or J).

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