Murphy RC (1936) *Oceanic Birds of South America,* vols 1 and 2. Macmillan, New York: American Museum of Natural History.
Nelson JB (1978) *The Sulidae: Gannets and Boobies.* Oxford: Oxford University Press.
Pennycuick CJ (1989) *Bird Flight Performance. A Practical Calculation Manual.* Oxford: Oxford University Press.
Schneider DC, Hunt GL, Jr and Harrison NM (1986) Mass and energy transfer to seabirds in the southeastern Bering Sea. *Continental Shelf Research* 5: 241–257.
Warham J (1990) *The Petrels: Their Ecology and Breeding Systems.* London: Academic Press.
Warham J (1996) *The Behaviour, Population Biology and Physiology of the Petrels.* London: Academic Press.
Whittow GC and Rahn H (1984) *Seabird Energetics.* New York: Plenum Press.

SEABIRD POPULATION DYNAMICS

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The population biology of seabirds is characterized by delayed breeding, low reproductive rates, and long life spans. During the breeding season, the distribution of seabirds is clumped around breeding colonies, whereas when not breeding, birds are more dispersed. These population traits have important consequences for interactions between people and seabirds. The aggregation of large portions of the adult population of a species in colonies means that a single catastrophic event, such as an oil spill, can kill a large segment of the local breeding population. Although seabird populations can withstand the failure to produce young in one or even a few years without suffering severe population-level consequences, the loss of adults has an immediate and long-lasting impact on population dynamics. Even a small decrease in adult survival rates may cause population decline.

Seabirds breed in colonies on islands, cliffs, and other places where they are protected from attacks by terrestrial predators. Species that forage at large distances from their colonies usually choose locations for their colonies that are less vulnerable to incursions by predators than are the colonies of species that forage in the immediate vicinity of the colony. For the offshore species, the cost of increased travel to a more protected site may be minor compared with the benefit of freedom from unwanted visitors. In contrast, for species that need to forage close to their colonies, even a short increase in the distance traveled between colony and foraging site may mean that it is uneconomical to occupy a particular breeding site.

Colony size tends to vary with the distance that a species travels in search of food. Inshore-foraging seabirds may nest singly or in small groups, whereas species that forage far at sea may have colonies that are comprised of hundreds of thousands of pairs. Two hypotheses have been offered to explain this trend. One hypothesis focuses on the issue of food availability. If birds forage far from their colonies, there is a much greater area in which food may be encountered than if foraging is restricted to a small radius around the colony, and thus a larger size colony can be supported. This hypothesis assumes that seabird colony size is limited by food availability. For species that forage near their colonies, there is evidence that reproductive parameters sensitive to prey availability, such as chick growth rates and fledging success, vary negatively with colony size. Likewise, there is evidence that colony size and location may be sensitive to the size and location of neighboring colonies. Evidence that seabirds depress prey populations near their colonies is limited. The second hypothesis focuses on the role that colonies may play in the process of information acquisition by birds seeking prey. When birds forage far from their colony, there may be a need for large numbers of birds so that those flying out from the colony are able to observe successful returning foragers and thereby work their way to productive foraging areas using the stream of birds returning to the colony for guidance. The longer the distance from the colony, the greater the number of birds that are required to provide an unbroken stream of birds to guide the out-bound individuals. The evolution of a system of this sort is possible because each individual will benefit from information on food resources gained by being part of a large colony. Selection for large colony size will continue so long as the colony is not so large that food supplies are severely depressed.

Seabirds show considerable philopatry, with individuals often returning to the same colony, or even the same part of the colony from which they fledged. Once a nest site or territory is established, individuals and pairs may use the same site in subsequent years. Pairing tends to be for multiple seasons ('for life'), particularly when pairs are successful at raising young. Divorce does occur, and may be most frequent after failure to raise young. However, experience is important, including experience with a particular partner, so changing partners may result in a period of adjustment to a new partner and consequent lower reproductive success.

The philopatry of seabirds and their tendency to remain in the same part of a colony once they are established may have important implications for the genetic structure of seabird populations. Few data are presently available, but there is some evidence for closer genetic ties for individuals nesting in close proximity. If this is proven to be generally true, there would be important ramifications for understanding a genetic basis for the evolution of coloniality based on inclusive fitness and the reciprocal aid of relatives.

Thus far, there is scant information regarding the genetic distance between individuals in different colonies. The issue of whether colonies are discrete populations (stocks in fisheries parlance) or whether there is considerable exchange between colonies has important implications not only for the evolution of local variation, but also for the conservation and management of seabirds. Little information is available as to whether some colonies are net exporters of recruits (sources) and others net importers (sinks), or if when a colony is decreased in size by a catastrophe unrelated to food resources, it will be quickly replenished by recruits from other colonies.

Delay in the age at which breeding commences is a striking characteristic of seabird population biology. Most species do not begin breeding until they are in their third or fourth year, and some groups, such as the albatrosses, delay breeding until they are 10 or more years of age. Birds that commence breeding at a younger age than is usual for their species have reduced reproductive success in their first year of breeding when compared with individuals that wait to breed at an older age. Additionally, birds that commence breeding at an early age tend to have an elevated mortality rate in the first year of breeding. The delay in the commencement of breeding may be a reflection of the long period needed for young birds to acquire the skills for efficient foraging. Several studies have shown that sub-adult birds are less efficient foragers, and have a lower success rate in capturing prey than do adult birds foraging in the same area. Additionally, sub-adult birds may visit the colony where they will breed for one or more years before they make their first attempt at breeding. This time may be necessary for learning where prey is to be found in the vicinity of the colony. The delay of breeding is particularly great in the Procellariiform birds, and these birds forage over vast areas of the ocean. It may be particularly challenging for them to learn where prey may be most predictably located within the potentially huge foraging arena available to them. The delay in the commencement of breeding may also provide time for birds in newly forming pairs to learn each others behavioral rhythms so that they will be more effective parents, although evidence to test this hypothesis is lacking. Certainly, coordination between the members of a pair is an essential ingredient of successful reproduction.

Most species of marine birds lay small clutches of eggs, with typical clutch size being one or two eggs. There is a tendency for species that forage far from their colonies to have smaller clutches (one egg) than those which forage inshore near the colony (two or three eggs). Likewise, species that live and forage in areas of strong upwelling tend to have considerably larger clutch sizes (three or four eggs) than closely related species that forage in mid-ocean regions. Two factors may come into play here. First, birds that forage at great distances from their colonies may be unable to transport sufficient prey sufficiently quickly to raise more than one offspring. In many of these species, individual parents may visit the colony to provision their young at intervals from 1 to 10 days or more. In some species of Procellariiformes, adults alternate long and short foraging trips while provisioning their young. After short trips, chicks gain mass, but adults lose body mass, whereas, after long trips, adults have gained mass, although the chicks will have not benefited as greatly as after short trips. These results point to the constraints on the ability of these birds to raise larger broods.

Many species that forage close to their colonies (inshore-foraging species) raise larger broods than offshore-foraging species. Parent birds of the inshore-foraging species usually make multiple provisioning visits to the colony during a day. Although they may not be able to carry more food per trip than similar-sized species that forage offshore, the possibility of multiple trips allows sufficiently high rates of food delivery to permit supplying the needs of more than one offspring. Multiple-chick broods are common in pelicans, cormorants, gulls, and some species of terns, and are also found in the most-inshore-feeding alcids.

Species breeding in upwelling systems and subject to the boom or bust economy of an ecosystem with extreme interannual variation in productivity may be a special case. In these species, periodic declines in ecosystem production, as may occur in El Niño years off Peru or California, can result not only in reproductive failures, but also considerable mortality of adults. In these cases, the potential for high reproductive output in the years when prey is plentiful may be necessary to offset adult mortality rates that may be higher than is typical for most seabird species.

For the offshore-foraging species, annual fluctuations in reproductive output may be small, particularly when compared with inshore-foraging species. This low variability may be a reflection of the wide expanse of ocean over which they can search for food. For the inshore species, there may be many years in which no young are fledged and only a few years in which they are successful at fledging young. This interannual variation may reflect the dependence of inshore-foraging species on localized upwelling and other forms of physical forcing of prey patches, which may show considerable interannual variation in the amount of prey present. Thus, the 'good' years become disproportionately important for the success of the local population. Additionally, there is limited evidence that suggests that a few individuals within a seabird population may account for a large proportion of the young produced. The implications of these findings, if further work shows them to be generally true, will be considerable for management efforts toward the conservation of seabirds. Loss of the most productive individuals or disruption of breeding in one of the rare years in which food resources are sufficient to lead to strong production of young will have a disproportionate impact on population stability. However, identifying the most productive individuals, or predicting which years will be critical for good reproductive output will be a challenge.

The third component of seabird life histories that must accompany delayed commencement of reproduction and low rates of reproduction is an extended period of survival during which reproduction is possible. The life spans of seabirds are among the longest of any birds. Survival to the age of 20 years or more is probably common in most species, and the larger species of Procellariids are known to live in excess of 40 years. Knowledge of the actual life spans of seabirds is difficult to obtain, as most of the marking devices used until recently have had much shorter life spans than the birds whose life spans were being measured. The result is a considerable underestimate of the expected life spans of seabirds, and thus of their possible life time reproductive potential. Despite these problems, estimates of adult survival rates of 92–95% are the norm. Thus, even a small decrease in the rate of adult survival will have a proportionally large impact on mortality rates.

Survival of recently fledged young and juveniles is considerably lower than that of adults. The highest rates of mortality are most likely to occur in the first few months of independence, when young are learning to fend for themselves. Mortality is also high during the first winter, again probably due to experience. Possibly as many as 50% of fledglings fail to survive to their first spring. Survival rates for juveniles are higher, but there may be an increase in mortality as birds begin to enter the breeding population and encounter the aggression of neighbors and the increased energetic demands of caring for young.

There are conflicting hypotheses about what limits the size of seabird populations, although in most cases it is believed that food rather than predation or disease is the most likely limiting factor. Phillip Ashmole has argued that seabirds are likely to be most stressed for food during the breeding season, when large numbers of individuals are concentrated in the vicinity of breeding colonies. In contrast, during winter, seabirds are spread over vast reaches of ocean and are not tied to specific colonies and their associated foraging areas. During winter, seabirds should be free to move about and take advantage of prey, wherever it may be found. As discussed above, there is a modest suite of data that suggests that prey availability may limit colony size and reproductive output of breeding seabirds. There are even fewer data to test the hypothesis favored by David Lack, that seabird populations are limited by wintertime food supplies and survival rates. Few studies of seabirds have focused on winter ecology during winter conditions, although this is the time when 'wrecks' (masses of dead birds driven ashore) are most common. Marine birds are sensitive to ocean conditions, with foraging success being reduced during periods of high winds. It is likely that in winter, even if there is no change in the amount of prey present, prey may be harder to obtain. Additional information on winter food stress comes from species that perform transequatorial migrations, thus allowing them to winter in the summer of the opposite hemisphere. Even under these presumably benign conditions, Southern Hemisphere shearwaters wintering in the North Pacific Ocean and Bering Sea experience occasional episodes of mass mortality, apparently from starvation. There is increasing evidence that decreases in the productivity of the California Current system are causing declines in the numbers of both migrant shearwaters and locally breeding species. The question as to which is the most stressful season for seabirds remains to be resolved.

Because of the sensitivity of seabird population dynamics to changes in adult survival rates, any factor that increases adult mortality is potentially detrimental to the conservation of seabirds. Thus, the loss of adult birds in fishery bycatch is of great concern. Breeding adults caught in gill nets and/or on long lines result in the loss not only of the adult, but also the chick for which it was caring. The loss of a breeding adult may also result in lower subsequent reproductive output by the surviving parent because it will likely have lower reproductive success during the first year with a new partner. The group most vulnerable to bycatch on long lines appears to be the Procellariiformes, which make shallow dives to grab baited hooks as they enter or leave the water. These are amongst the longest-lived of seabirds, and the curtailment of their breeding lives has a severe impact on their populations. Indeed, the populations of many species of albatross are declining at an alarming rate. A second major threat to seabirds is the presence of introduced predators on the islands where the birds breed. Rats, cats, foxes, and even snakes kill both chicks and attending adults. Again, loss of adult breeding birds has the most potentially serious impact on the future stability of the population. Reduction of anthropogenic sources of adult mortality in seabirds must be one of the most urgent imperatives for conservation biologists and managers.

See also

Alcidae. Procellariiformes. Seabird Conservation. Seabird Reproductive Ecology. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions.

Further Reading

Ainley DG and Boekelheide RJ (1990) *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community*. Stanford, California: Stanford University Press.

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458–473.

Ashmole NP (1971) Seabird ecology and the marine environment. In: Farner DS and King JR (eds) *Avian Biology*, Vol. 1, pp. 224–286. New York: Academic Press.

Furness RW and Monaghan P (1987) *Seabird Ecology*. London: Blackie Books.

Gaston AJ and Jones IL (1998). *The Auks: Family Alcidae*. Oxford: Oxford University Press.

Hunt GL Jr (1980) Mate selection and mating systems in seabirds. In: Burger J, Olla BL and Winn HE (eds) *Behavior of Marine Animals*, Vol. 4, pp. 113–151. New York: Plenum Press.

Lack D (1966) *Population Studies of Birds*. Oxford: Clarendon Press.

Lack D (1968) *Ecological Adaptations for Breeding in Birds*. London: Chapman and Hall.

Nelson JB (1978) *The Sulidae: Gannets and Boobies*. Oxford: Oxford University Press.

Warham J (1990) *The Petrels: Their Ecology and Breeding Systems*. London: Academic Press.

Warham J (1996) *The Behaviour, Population Biology and Physiology of the Petrels*. London: Academic Press.

Williams TD (1995) *The Penguins*. Oxford: Oxford University Press.

Wittenberger JF and Hunt GL Jr (1985) The adaptive significance of coloniality in birds. In: Farner DS, King JF and Parkes KC. *Avian Biology*, Vol. VIII. Orlando, FL: Academic Press.

Wooller RD, Bradley JS, Skira IJ and Serventy DL (1989) Short-tailed shearwater. In: Newton I (ed.) *Lifetime Reproduction in Birds*. London: Academic Press.

SEABIRD REPRODUCTIVE ECOLOGY

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Introduction

Finding the food necessary to produce and raise offspring is a fundamental problem that animals face. The oceans, despite being a productive and rich environment, rarely provide a steady or reliable source of food; instead, feeding opportunities are patchily distributed in both time and space. As a consequence, seabirds, from 20 g least petrels (*Halocyptena microsoma*) up to 37 kg emperor penguins (*Aptenodytes patagonicus*), have had their life history strategies shaped by the need to cope with this ebb and flow of resources.

The British ornithologist David Lack published two landmark books in 1954 and 1968 that influenced the way that we think about reproduction in birds. Lack hypothesized that the clutch size of birds has evolved so that it represents the maximum number of chicks that can be reared. His logic suggested that food is most constraining when parents have chicks (i.e., the period when they need to both feed themselves and provide enough food for their chicks to grow) and this must inevitably limit how many chicks parents can care for adequately. It