Commentary on Kerr and Godfrey-Smith

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The main thesis of this paper (KGS for short) is that many 'multilevel' evolutionary processes can be modelled in two different ways:

- Contextual: fitnesses (expected number of offspring) are assigned to individuals, but depend on what other kinds of individual are present.
- Collective: fitnesses are assigned to groups, but depend on the Proportions of different kinds of individual comprising the group.

They show that, provided clear-cut groups exist, contextual and collective models can both be formulated, and are mathematically equivalent. They do not argue that one method or the other is *in general* superior, but that it may be illuminating to bear both models in mind, both in understanding particular cases, and in seeing analogies between processes.

I have a lot of sympathy with this view although, as explained below, I have some reservations. I agree that equivalent mathematical descriptions are often although not always possible. I also agree that it can sometimes be illuminating to have both models in mind, in two ways. First, a 'gestalt switch' between two models can be helpful. For example, the effect of genetic relatedness can be modelled either by ascribing an 'inclusive fitness' to individuals (Hamilton 1964), or, as sketched by Hamilton (1963) and made more explicit by Dawkins (1976), by a gene-centred approach: note that, in this example, the individual is the 'higher level' entity and the gene the 'lower level' one. I confess that in this case I find the gene-centred approach both mathematically simpler and causally more appropriate, but this may merely reflect the fact that I prefer microscopic to holistic models: Maxwell-Boltzmann to classical thermodynamics, and Dawkins to Price's equation.

But the value of having two types of model is most apparent when comparing different processes. KGS describe the analogy between the stable genetic polymorphism in a single-locus diploid system (the lower level 'units' are the alleles and the higher level 'group' the individual) and the mixed ESS in the Hawk-Dove game (the individual organisms are the lower level units; it is less clear what is the higher level 'group'). The recognition of

such analogies between levels is particularly helpful when thinking about the 'major transitions' in evolution (Maynard Smith and Szathmary 1995), for example the origin of cells, of eukaryotes, of multicellular organisms, of animal societies. In these transitions, entities which before the transition could reproduce on their own can only do so as part of a larger whole after the transition. The problem is to explain why selection between the lower-level entities for 'selfish' behavior does not disrupt the functioning of the higher level. It turns out that similar mechanisms (relatedness, synergy, policing) are often present at different levels, a fact that only becomes apparent if one sees the formal analogies.

However, I have reservations about the collective approach, which can best be explained in the context of the settlement of animal contests by signalling rather that escalated fighting. I first learnt about this when a zoology under-graduate in the 1940s by reading Konrad Lorennz. I remember that the behaviour was explained by Julian Huxley by saying that ritual evolved because escalated fighting would 'militate against the survival of the species'. Even as a student I knew that had to be wrong. However, I did not think seriously about the problem until 1970, when it was the stimulus for devel-oping evolutionary game theory (Maynard Smith and Price 1973). I saw this as an attempt to replace Huxley's 'group selection' account by an explana-tion in terms of 'individual selection'. Although animal contest behaviour is still not fully understood, all serious work on the topic is couched in game theoretic terms, in which fitnesses are ascribed to individuals with different behaviours, conditional on what others are doing. I have little sympathy, therefore, with the suggestion that the problem can be treated as an example of group selection. KGS could reply, reasonably, that Huxley's mistake was in his identification of the species as the appropriate 'group'. If the pair of contesting individuals is identified as the group, then a collective model is possible, formally equivalent to the game theoretic model. My difficulty with this is that, although formally possible, such a collective model would be causally inappropriate: I will return to this below.

As always, it is best to start with Darwin. His basic idea can be summar-ized as follows. Given a population of entities that can reproduce, that have heredity (like begets like), and that vary in ways that affect their chances of reproduction, then the population will evolve characteristics ensuring individual survival and reproduction. This can explain the astonishing adap-tedness of living organisms, which otherwise would call for the existence of a divine creator. Unfortunately, by the 1950s it had beconme common for biologists to explain the characteristics of organisms by saying that they contributed to the survival, not of the individual, but of the species, without realizing that such an explanation, although not necessarily wrong,

also requires an explanation of why individual selection does not disrupt the species adaptation. Huxley's remark is an example of such thinking: others that stimulated me at the time are Wynne-Edwards' (1962) explanation of social behaviour, and Darlington's (1939) of sex. This facile model of thinking had to be corrected before progress on these topics could be made. Williams (1966), provoked by other examples of 'group' thinking, played a crucial role. I do not share the view of Sober and Wilson (quoted with approval by KGS) that it was 'mistaken' to get rid of this mode of thought: it was essential to do so. But it could not be the end of the discussion, for several reasons. Sex can plausibly be seen as an adaptation enabling species to evolve, and between-species selection has probably been an important cause of its evolution, although certainly not the only one. Selection does sometimes operate between groups of organisms lower than species. Perhaps most important has been a recognition of the distinction between genes as 'replicators' and organisms as 'vehicles' (Dawkins 1982), and the discovery of 'selfish' genetic elements. These problems are today a central concern of evolutionary theorists: this would not be so if 'old-fashioned' group selection thinking, illustrated by Wynne-Edwards and Darlington, had not been banished.

Consider the following list of adaptations in the living world:

 i) The halteres of Diptera are sense organs needed to stabilize flight.

 ii) The behaviour of worker bees contributes to the productivity of the hive.

 iii) The members of a group of meerkats take it in turns to act as sentinels, thus reducing predation on the group.

 iv) Signals between funnel-web spiders fighting over webs reduces the likehihood of escalated fights that might injure both parties.

 v) In a forest composed of trees mainly of a single species, the morphology of individual trees helps them to compete for light.

How should we think about these examples? Would a pluralist approach be helpful? I do not find it easy to answer these questions, but I will try. The last question is perhaps the easiest. It cannot be treated by the 'collective' approach – or at least not by the one proposed by KGS – because there are no 'groups'. However, the morphology that would maximise the fitness of an individual tree is context-dependent: it depends on how many trees, of what kinds, are its neighbours. I include this example because I think there are many cases in which individual fitness is context-dependent, but there are no definable groups.

It is also easy to answer the first question, but a little harder to justify the answer. We know why flies have halteres: they are an adaptation for flight, and not context-dependent. Most physiological explanations are of this kind: the

heart is an 'individual' adaptation, although its optimal size may depend on the amount of conspecific competition. But an individual organism consists of millions of cells, and contains millions of potentially selfish genes. Why do we ignore these facts when thinking about halteres or hearts? Essentially because we treat intercellular and intragenomic conflict as problem in their own right, and assume that they have seen 'solved' when thinking about individual adaptations. I think this is OK, provided we occasionally remember what we are doing.

Questions ii) and iii), concerning bees and meerkats, do seem to me appropriate for a pluralist approach. In both cases, the hard question is why individual organisms behave cooperatively, anyway most of the time. In the case of bees, the answer is complex, involving at least three factors – the sterility of workers, genetic relatedness of workers and queen(s), and 'punishment'. There are many difficulties: for example, workers can lay unfertilized eggs that develop as males, but are 'punished' by other workers if they do so. Obviously, a simple model of the kind proposed by KGS is not adequate, but it is true that there is a 'group' – the colony – whose success contributes to the survival of the genes of the queen that founded it, and that there is room for conflict between the individuals within a hive.

Meerkats also live in clearly defined groups. Relatedness is probably unimportant, and I know of no evidence of the 'punishment' of individuals that do not take their turn as a sentinel. Probably the important factors are that individuals have a better chance of reproducing if they are members of a large group, and that acting as a sentinel may not be as expensive to the individual as might appear at first sight (Clutton-Brock et al. 1999).

I find that the hardest question to answer is the one I have spent most time thinking about – the contest behaviour of spiders, and of animals generally. The contextual approach is obvious, and is the one usually adopted in the form of game theory. Is a collective approach helpful? One can treat a pair of contesting individuals as a 'group', and calculate the 'fitness' of that group as the sum of the fitness, after the contest, of the two individuals, Thus, formally, one could apply the collective model proposed by KGS. But why would one want to?

Although a group of two fighting individuals can be used as an accounting device, it cannot be thought of as a 'cause' of anything. KGS quote Sober and Wilson as saying that 'only a multilevel description is faithful to the causal structure involved.' This seems to me precisely wrong. The cause of what happens is the behaviour of individuals (and, behind that, the genes that cause that behaviour): the fitness of a group is merely the arithmetical sum of the fitnesses of the individuals that compose it. I think that there *are* cases in which a group of individuals can be seen as part of the 'causal structure':

for example, a mated pair of birds both caring for the young may be able to achieve more (e.g. one guards the nest while the other collects food) than could two isolated individuals. But if a pair of individuals are fighting. I cannot see the 'group' of two as constituting a causally effective unit.

The fact that, in some cases, the same process can be described by two mathematically equivalent models, contextual and collective, might suggest that the debates about 'group selection' have been arguments about the use of words rather than about what the world is like. Certainly there has been much semantic confusion: the term 'group selection' has been used to mean everything from the existence of group-level adaptations (e.g. sex) arising by the selective survival of some groups and the extinction of others, to any case in which the fitness of individual organisms is in part determined during interaction with other members of the same species. But I think there are empirical questions as well: in particular, what processes were responsible for the evolution of higher-level entities – cells, organisms and societies?

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