

Chapter 8

The Units and Levels of Selection

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1. Introduction

The “units of selection” question is one of the most fundamental in evolutionary biology. Though the debate it has generated is multifaceted and complex, the basic issue is straightforward. Consider a paradigmatic Darwinian explanation – of why the average running speed in a zebra population has increased over time, for example. The explanation might go as follows: “in the ancestral population, zebras varied with respect to running speed. Faster zebras were better at avoiding predators than slower ones, so on average left more offspring. And running speed was heritable – the offspring of fast zebras tended to be fast runners themselves. So over time, average running speed in the population increased.” In this explanation, the “unit of selection” is the individual organism. It is the differential survival and reproduction of *individual zebras* that causes the evolutionary change from one generation to the next. We could also express this by saying that natural selection “acts at the level of the individual organism.”

Traditional Darwinian theory treats the individual organism as the basic unit of selection. But in theory at least, there are other possibilities. For the principle of natural selection can be formulated wholly abstractly – it involves no essential reference to organisms or any other biological units. The principle tells us that if a population of entities vary in some respect, and if different variants leave different numbers of offspring, and if offspring entities resemble their parents, then over time the composition of the population will change, *ceteris paribus*. In Lewontin’s famous formulation, natural selection will operate on any entities that exhibit “heritable variation in fitness” (Lewontin, 1970). Entities at many levels of the biological hierarchy could satisfy these conditions – including genes, chromosomes, organelles, cells, multicellular organisms, colonies, groups and even whole species. Since each of these entities undergoes reproduction, or multiplication, the notion of fitness, and thus heritable variation in fitness, applies to each. The hierarchical nature of the biological world, combined with the abstractness of the principle of natural selection, means that there is a range of candidate units on which selection can act.

From this brief sketch, the units of selection question might seem purely empirical. Given the multiplicity of possible levels at which selection *can* act, surely it is just a matter of finding out the levels at which it *does* act? With enough empirical data, surely

the question can be conclusively answered? In fact matters are not quite so simple. As many authors have noted, the units of selection debate comprises a curious amalgam of empirical, theoretical, and conceptual questions, often not sharply distinguished from one another. (This is why philosophers of science have written so much about it.) The debate is of course responsible to empirical facts, but this cannot be all there is to it. For quite frequently, one finds authors in agreement about the basic biological facts in a given case but in disagreement about what the “true” unit of selection is. Disagreements of this sort are conceptual or philosophical in nature, rather than straightforwardly empirical.

A brief remark about terminology is needed. The expressions “units of selection” and “levels of selection” can both be found in the literature. Some authors treat these expressions as effective synonyms. On this usage, if the unit of selection is the individual organism, for example, then selection can be said to act at the organismic level. So it is possible to translate freely between talk of units and levels of selection. However, there is another usage, associated with the “replicator/interactor” view of evolution discussed below, which severs the close link between units and levels (e.g., Reeve & Keller, 1999). On this alternative usage, “unit of selection” refers to the replicators, typically genes, that transmit hereditary information across generations, while “level of selection” refers to the hierarchical level(s) at which there is variation in fitness. The former usage will be adopted here unless otherwise indicated.

2. Historical Remarks

The units of selection question traces back to Darwin himself. For the most part Darwin treated the individual organism as the unit of selection, but he recognized that not all biological phenomena could be interpreted as products of organism-level selection. Worker sterility in the social insect colonies was one such phenomenon, and it puzzled Darwin considerably. Sterile workers forgo reproduction, instead devoting their whole lives to assisting the reproductive efforts of the queen – by foraging for food, feeding the young, and protecting the colony. Such behavior does not benefit the workers themselves, so it is hard to see how it could evolve by selection at the organismic level. Worker sterility is a classic example of an *altruistic* trait: it reduces the fitness of the organism that expresses the trait but increases the fitness of others. (By an organism’s fitness we mean the expected number of offspring that it leaves; this quantity depends on the probability that the organism survives to reproductive age, and the reproductive success it will enjoy if it does survive.)

The problem of how altruistic traits can evolve is intimately linked to the units of selection question, historically and conceptually.

Darwin’s most explicit assault on the problem of altruism occurred in *The Descent of Man* (1871). Discussing the evolution of self-sacrificial behavior among early humans, Darwin wrote: “he who was ready to sacrifice his life, as many a savage has been, rather than betray his comrades, would often leave no offspring to inherit his noble nature” (1871, p.163). Darwin then argued that self-sacrificial behavior, though disadvantageous at the individual level, might be beneficial at the *group* level: “a tribe including many members who . . . were always ready to give aid to each other and sacrifice

themselves for the common good, would be victorious over most other tribes; and this would be natural selection” (1871, p.166). Darwin’s suggestion is that the behavior in question may have evolved by a process of between-group selection. Groups containing many altruists (self-sacrificers) might do better than groups containing fewer, even though *within* any group, altruists do less well than their selfish counterparts. So Darwin was open to the idea that at least sometimes, groups as well as individual organisms can function as units of selection.

August Weismann, the famous German evolutionist whose work on inheritance discredited Lamarckism, also saw that selection can operate at multiple hierarchical levels, as Gould (2002) has emphasized. While Darwin had toyed with the idea that selection could occur at levels above the organism, Weismann was interested in the possibility of sub-organismic levels of selection. His doctrine of “germinal selection” described a selection process between variant “determinants” (hypothetical hereditary particles) that occurred during the lifespan of a developing organism (Weismann, 1903). Though Weismann’s theory of development has not stood the test of time, his idea that selection can operate on variant units within the lifespan of a complex organism has endured. Selection between different cell lineages within multicellular organisms plays a major role in the vertebrate immune response, in neuronal development, and also, tragically, in carcinogenesis (Edelman, 1987; Czikó, 1995; Frank, 1996). This process is sometimes referred to as “somatic” or “developmental” selection.

The units of selection debate in its modern form owes much to G. C. Williams’ iconoclastic book *Adaptation and Natural Selection* (Williams, 1966). Williams’ stated aim was to bring some “discipline” to the study of adaptation. His concern was with a growing trend in biology, particularly among ecologists and ethologists, to think of adaptation in terms of “benefit to the species” rather than “benefit to the individual.” Thus for example Konrad Lorenz, the Nobel Prize-winning ethologist, would routinely explain an observed animal behavior by citing a benefit that the behavior confers on the species as a whole. If the Darwinian process one has in mind is ordinary organismic selection, this is a fallacious argument. For organismic selection produces adaptations that benefit *individual organisms*, and it is an open question whether such adaptations will on aggregate benefit any larger units (as both Fisher (1930) and Haldane (1932) had previously pointed out). Williams stressed that only a process of between-group selection would produce genuine group-level adaptations, and he regarded group selection as a weak evolutionary force, which would only rarely have significant effects. His main argument was that the generation time of groups is typically much longer than that of individual organisms, so the effects of group selection would be swamped by individual selection. The fragility of group selection as an evolutionary mechanism was also emphasized by Maynard Smith (1964).

As a result of Williams’ and Maynard Smith’s work, evolutionists in the 1960s and 70s increasingly came to see the importance of the units of selection question, and in particular to view the concept of group selection with great suspicion. This period also witnessed the rise of two crucial theoretical developments: the theory of kin selection, stemming from the seminal work of William Hamilton (1964) on the evolution of social behavior, and the “gene’s eye view of evolution,” stemming from the work of Hamilton and Williams and popularized by Dawkins (1976); see Section 3 below. Though no one

could doubt the importance of these new developments, they complicated the units of selection issue considerably, generating a certain amount of conceptual confusion and a proliferation of terminology. The relationships between “individual selection,” “kin selection,” “genetic selection,” “frequency-dependent selection,” “group selection,” and “species selection” were not always perspicuous; nor was it clear whether these types of selection were strict alternatives to each other at all. Unsurprisingly, it was at this stage that philosophers of science started to take a serious interest in the debate.

3. The Gene’s Eye View of Evolution

In *The Selfish Gene* (1976), Dawkins defends a gene-centric view of the evolutionary process. Ordinarily we think of natural selection as a competition between individual organisms, the winners surviving and reproducing, the losers dying. But Dawkins argues that organisms are mere epiphenomena of the evolutionary process – the real competition takes place between individual genes. Genes are engaged in a perpetual struggle to bequeath as many copies of themselves to future generations as possible, and organisms are simply “vehicles” that genes have built to assist them in this task. So the phenotypic adaptations we see all around us are not there because they benefit the organisms that display them, less still the groups or species to which the organisms belong. Rather, adaptations are there for the benefit of the underlying genes that produce them, Dawkins argues. Genes “program” their host organisms to express phenotypes – behavioral, morphological, and physiological – which help the organisms survive and reproduce, thus ensuring that copies of the genes will be found in future generations. The ultimate beneficiary of the evolutionary process, and thus the true unit of selection, is the individual gene, Dawkins claims.

This so-called “gene’s eye view of evolution” has its roots in the work of Hamilton (1964), mentioned above. Hamilton was concerned with the very problem Darwin had puzzled over – altruism. As we have seen, an animal that behaves altruistically will have lower fitness than its selfish counterparts, so altruism, and the genes which cause it, should be disfavored by natural selection. But Hamilton realized that if the altruistic behavior is directed at relatives, rather than at unrelated members of the population, then the situation is immediately changed. For relatives share genes, so there is a certain probability that the beneficiary of the altruistic act will *itself* carry the gene for altruism. So to determine whether the altruism-causing gene (and thus the altruistic behavior itself) will spread, we need to take into account not just the effects of the gene on the fitness of its bearer, but also on the fitness of the bearer’s relatives. Hamilton’s achievement was to express this insight in precise mathematical form. The condition required for the spread of an altruistic gene in a population, Hamilton showed, was $b/c > 1/r$, where c denotes the cost incurred by the altruist, b denotes the benefit enjoyed by the recipient, and r is the *coefficient of relatedness* between donor and recipient, which measures how closely related they are. This inequality is known as *Hamilton’s rule*; it tells us that altruism will be favored by natural selection so long as the cost to the altruist is offset by a sufficient amount of benefit to sufficiently closely related relatives, where the costs and benefits are measured in units of reproductive fitness. For obvious reasons, this idea came to be known as “kin selection.”

Hamilton's work revolutionized the way biologists study animal behavior. But what matters for the moment is the *way* Hamilton arrived at his idea. He did so by employing the gene's eye view of evolution. Hamilton realized that in trying to determine whether a given trait (e.g., altruism) will evolve, it is not enough to ask whether the trait benefits the individual organism that expresses it. The real test is whether the net effect of the trait leads the gene underlying the trait to increase or decrease in frequency; only that tells us whether the trait will spread. So to explain why a given trait has evolved, we need to show that the trait confers a selective advantage on the gene that causes the trait, rather than on the organism that expresses the trait. Looked at from this gene's eye view, the phenomenon of altruism makes perfect sense. Causing its host organism to behave altruistically to relatives is simply a strategy devised by a "selfish" gene to ensure its future propagation, and so long as the costs and benefits satisfy Hamilton's rule, the strategy will work.

The gene's eye view is a powerful heuristic for thinking about evolution, particularly where social behaviors are involved. Another phenomenon that looks anomalous from the traditional organismic viewpoint but makes sense from the gene's eye view is *intra-genomic conflict*. Usually the genes within a single organism behave cooperatively, because they have a common interest in ensuring the organism's survival and reproduction; that is why genes generally have phenotypic effects that benefit their host organism. But in some cases an individual gene can promote its own interests at the expense of the rest of the genome. Segregation-distorter (SD) genes, which violate the rules of Mendelian inheritance to secure a greater than 50 percent representation in the gametes of heterozygotes, are an example. SD genes often have adverse phenotypic effects on the organism itself, so from the organism's point of view, and from the point of view of all other genes in the genome, the SD gene is a liability. But from the gene's eye view, the behavior of the SD gene makes perfect sense – it has simply devised an unusual strategy for ensuring its transmission to future generations. Recent research has revealed intra-genomic conflict to be more common than was originally thought, and it constitutes one of the best arguments in favor of the gene's eye view of evolution (Pomiankowski, 1999; Hurst, Allan, & Bengtson, 1996; Burt & Trivers, 2006).

Dawkins offered another, quite different argument for treating the gene as the true unit of selection. (The argument had been hinted at, but not systematically articulated, by Williams.) Genes are what Dawkins calls *replicators*: entities which leave copies of themselves in subsequent generations. Thanks to the fidelity of DNA replication, the members of a gene lineage are usually perfect or near-perfect copies of one another. Entities such as organisms, colonies, and species also stand in ancestor–descendant relations, hence form lineages, but in no case does the fidelity of reproduction approach that found in gene lineages. This is especially true of sexually reproducing organisms, where offspring contain a mixture of genetic material from two parents. DNA replication is thus qualitatively different from organismic reproduction for Dawkins, for genes in existence today are descended unchanged or nearly unchanged from genes that existed hundreds of thousands ago; the same is obviously not true of whole organisms. Only genes have sufficient permanence to qualify as units of selection, Dawkins argues; organisms and their properties are mere temporary manifestations.

In the light of the gene's eye view of evolution, what becomes of the traditional units of selection debate? Prior to Dawkins, the debate had generally pitched group selection-

ists against organismic selectionists. But Dawkins (1976) argues that both are wrong, for the true unit of selection is the gene. This suggests that the claim “the gene is the unit of selection” is logically incompatible with the claim “the organism is the unit of selection” or “the group is the unit of selection.” G. C. Williams (1966) also contrasts genic selection with group selection, again implying that these are incompatible views of how evolution proceeds (1966, p.55).

However, in his later work Dawkins (1982) adopts a different line, arguing that genic selection is not really an alternative to traditional organismic selection at all. Rather, the gene’s eye view is simply a different *perspective* on the process of evolution that is heuristically valuable in certain contexts. So we can think of evolution either in the traditional way, in terms of selection between organisms, or in the gene’s eye way, in terms of selection between genes. There is no fact of the matter about which is right – both are valid perspectives on one and the same set of facts. Central to this argument is Dawkins’ distinction between replicators and vehicles, or replicators and interactors in the more widely used terminology of Hull (1981). As we have seen, genes are the paradigmatic replicators – they leave copies of themselves in future generations. However, natural selection does not operate on genes “directly” but only indirectly, via the effect the genes have on their host organisms. For it is whole organisms that survive, reproduce, and die, not individual genes. Organisms are thus interactors – entities that interact directly with their environment and are thus the direct target of selection. Both replicators and interactors are involved in the evolutionary process, according to Dawkins and Hull.

Dawkins and Hull argue that the expression “unit of selection,” as it occurred in the early discussions, was often ambiguous between replicators and interactors. Arguments about whether the gene or the organism is the unit of selection typically traded on this ambiguity (though not always – see below). In retrospect this was a bad question to ask, for it commits a category mistake, pitting a replicator against an interactor. (Similarly, Williams’ contrast between “genic selection” and “group selection” was a category mistake.) Arguments about whether the organism or the *group* is the unit of selection are different, however; this is a question about interactors, and does not commit a category mistake. It is an empirical question that can only be resolved by looking at the empirical facts, and may receive a different answer in different cases. So the Dawkins/Hull conceptualization permits a neat separation of the conceptual from the empirical aspects of the units of selection debate. “Group versus organism” is an empirical issue, but “organism versus gene” is not; rather, it is “an argument about what we ought to *mean* when we talk about a unit of natural selection,” in Dawkins’ words (1982, p.82).

This is a compelling analysis, but it raises certain questions. If the gene’s eye view is ultimately equivalent to the orthodox organismic view, what becomes of phenomena such as intra-genomic conflict and junk DNA, which *don’t* appear explicable in terms of advantage to the individual organism? The existence of such phenomena, which formed part of Dawkins’ original case for genic selection, sits badly with the idea that the gene’s eye view is merely a heuristic perspective, rather than an empirical thesis about the course of evolution. One response to this problem, favored by a number of commentators, is to allow that the gene is *sometimes* the unit of selection in the *same* sense as that in which the individual organism is the unit of selection, i.e., the unit of

interaction (Sober & Wilson, 1998; Reeve & Keller, 1999). On this view, if the genes within a single organism differ in fitness, as in cases of intra-genomic conflict, then “genic selection” takes place, but if, as is usually the case, the genes within any single organism have identical fitness, then all the selection must occur at a higher level, e.g., the organismic level, or the group level.

This means that we must sharply distinguish the *process* of genic selection, which is relatively infrequent, from the changes in gene frequency that are the *product* of selection at other hierarchical levels, which are ubiquitous (Okasha, 2004a, 2006). Organismic, kin, and group selection all will in general lead to changes in gene frequency; so a gene’s eye perspective is always going to be available on selection processes that occur at these levels. But in addition, there are selection processes that take place at the genic level itself – as in cases of intra-genomic conflict. The expression “genic selection” should be reserved for such processes. Thus we should not confuse the gene’s eye viewpoint, which is a heuristic tool for thinking about selection processes that may occur at many different hierarchical levels, with genic selection itself, which is a specific level of selection that is logically distinct from individual, kin, or group selection. Increasingly, this is how the label “genic selection” is in fact being used in the literature, e.g., by Maynard Smith and Szathmary (1995) and Okasha (2006).

In retrospect, it is clear that Dawkins’ arguments in *The Selfish Gene* failed to distinguish sharply enough between the units of selection and of inheritance. The distinction between selection and inheritance is conceptually straightforward: selection concerns which variants survive best/reproduce the most, while inheritance concerns the transmission of genotypic and phenotypic characters across generations. Thus quantitative geneticists typically distinguish selection itself from the evolutionary response to selection – where the latter depends on the heritability of the trait selected for. But Dawkins and Williams used facts about *inheritance*, e.g., that genes are faithfully replicated across generations while whole genotypes and organismic characters are not, to privilege the gene as the unit of *selection*. Had the distinction between selection and inheritance (or transmission) been kept clearly in mind, there probably would have been no need to introduce the terminology of replicators and interactors at all.

Indeed there are reasons for thinking that the replicator/interactor framework, though valuable for certain purposes, does not provide a fully general account of evolution by natural selection, despite what its advocates have thought (Griesemer, 2000). One such reason is that Lewontin’s “heritable variation in fitness” formulation arguably *does* provide a fully general account, and it involves no distinction between replicators and interactors, thus undermining the Dawkins/Hull idea that *any* selection process must involve entities of both these types. (Similarly, Maynard Smith’s (1988) abstract account of the conditions required for Darwinian evolution – multiplication, variation, and heredity – involves only one type of entity.) This suggests that the original Lewontin formulation of the units of selection question – “which are the entities that possess heritable variation in fitness?” – is superior to the replicator/interactor formulation (Okasha, 2006). Of course, rejecting the Dawkins/Hull framework as a *general* way of thinking about the units of selection does not mean abandoning the gene’s eye view of evolution; the latter has proved invaluable for understanding a whole host of evolutionary phenomena.

4. Group Selection and Kin Selection

The group selection question is one of the most intriguing, and polemical, chapters in the units of selection debate. As we saw in Section 2, group selection fell out of favor among evolutionary biologists in the 1960s, due mainly to the work of Williams and Maynard Smith. The essence of their argument was that group selection is a weak evolutionary force compared to individual selection, for the turnover of groups will generally be much slower than that of individuals, thus permitting individual selection to accumulate adaptations at a faster rate. Moreover, the phenomena which group selection had originally been invoked to explain, such as altruism, could be explained in other more parsimonious ways, they argued, such as kin selection or the evolutionary game theory of Maynard Smith and Price (1973). So not only was the hypothesis of group selection implausible, it was also explanatorily superfluous.

Something like this is probably still the majority view in evolutionary biology, but it has not gone unchallenged. D. S. Wilson has vigorously opposed the orthodox rejection of group selection for many years, both alone and in collaboration with Elliott Sober (Wilson, 1975, 1980, 1989; Sober & Wilson, 1998). Wilson argues that group selection was wrongly rejected by biologists in the 1960s and 1970s, and is in fact a potent evolutionary force after all. The early mathematical models, which purported to show the impotence of group selection, relied on unrealistic and maximally unfavorable assumptions, Wilson holds. More controversially, he claims that the supposed alternatives to group selection, such as kin selection and evolutionary game theory, are not in fact alternatives at all; rather, they are *versions* of group selection theory, but presented in a formal framework which tends to obscure this fact.

The precise relation between kin and group selection has long been a point of controversy. Some authors insist that these modes of selection are of a piece, while others see a sharp distinction between them (cf. Uyenoyama & Feldman, 1980). Hamilton's own views on the matter underwent an interesting evolution, as Sober and Wilson (1998) have documented. Initially Hamilton treated group selection with suspicion, but later he came round to the view that his own models for the evolution of altruism did actually involve a component of group selection after all (Hamilton, 1996). Despite this change of heart by Hamilton, many biologists continue to regard kin selection as an alternative to group selection, not an instance of it. The issue here is in partly terminological – must “group” mean group of unrelated organisms? – but it runs deeper than this. To focus the issue, let us recall the basic problem of altruism, then contrast Darwin's group selectionist solution with Hamilton's solution.

The basic problem is simply that in any group containing both altruists and selfish organisms, the latter will be at an advantage – they will enjoy the benefits of others' altruism but without incurring any of the costs. So within any one group the frequency of altruists will always decline. Darwin suggested that in a multi-group scenario the accounting may change, for groups containing many altruists, all engaged in mutual assistance, may out-reproduce groups containing predominantly selfish types; in this way, group selection in favor of altruism may counteract individual selection against. Hamilton suggested that if altruists preferentially direct their altruism towards

relatives, rather than towards unrelated members of the population, then altruism may spread, owing to the fact that relatives share genes.

Although Darwin and Hamilton may *seem* to have offered quite different solutions to the problem of altruism, there is actually a deep underlying commonality. In both cases, what permits the spread of altruism is that *the beneficiaries of altruistic actions have a better than random chance of being altruists themselves*; as Hamilton (1975) himself said, this is the “crucial requirement” for altruism to evolve. Darwin’s scenario, involving a population subdivided into groups, which differ in their frequencies of altruists, and Hamilton’s scenario, involving organisms which behave altruistically towards kin, are simply two different ways of satisfying this fundamental requirement. This is why Sober and Wilson (1998) maintain that kin-directed altruism, far from constituting an alternative to group selection, is actually group selection in disguise, an argument that Hamilton (1975) also endorsed.

Opponents of this argument point out that group selection, as traditionally conceived, involved discrete multi-generational groups reproductively isolated from other such groups, but kin-directed altruism may occur within a single population whether or not it contains such groups (Maynard Smith, 1976, 1998). However, Sober and Wilson (1998) reply that in the relevant sense of “group,” a group exists whenever a number of organisms interact in a way that affects their fitnesses, whether or not the group is reproductively isolated, spatially discrete, or multi-generational. So in the limit, two organisms that engage in a fitness-affecting interaction just once in their lifetime constitute a group. This concept was first developed by Wilson (1975) in his well-known “trait group” model for the evolution of altruism, in which the trait groups are simply temporary alliances of organisms that break up and re-form every generation. The transitory nature of these alliances in no way prevents them from qualifying as groups, Wilson insists, for groups must be defined by the criterion of fitness interaction.

The trait-group model and similar models of “intra-demic” selection have generated an interesting philosophical discussion. Sober and Wilson (1998) insist that these models involve a component of group selection, for the trait-groups exhibit differential productivity. Different trait-groups contribute different numbers of offspring to the subsequent generation, so there is selection between groups as well as selection within them. (This is why the trait-group models permit altruism to evolve.) However, other authors argue that these models involve only individual selection in a group-structured population (Maynard Smith, 1998). On this view, an organism’s trait-group is simply a part of its overall selective environment, so all the selection is at the level of the individual organism; the trait-groups are relevant only in that they partially determine individual fitnesses. Still others, including Dugatkin and Reeve (1994) and Sterelny and Griffiths (1998), have defended a pluralistic line. They argue that trait-group models *can* be construed as involving a component of group selection as per Sober and Wilson, but can equally be regarded as individual selection in a structured environment as per Maynard Smith. There is no fact of the matter as to which is right, according to these authors – we are faced with a choice of perspective, not empirical fact.

One notable contribution to this debate comes from Kerr and Godfrey-Smith (2002), who offer a sophisticated defense of pluralism. They construct a simple mathematical model of selection in a group-structured population and show that the model’s dynam-

ics can be fully described by two sets of parameter values, one of which ascribes fitness values only to individuals, the other of which ascribes fitnesses to groups *and* individuals. The former is called a “contextual” parameterization, for the fitness of an individual depends on its group context, while the latter is called a “multilevel” parameterization, for both individuals and groups are ascribed fitnesses. Kerr and Godfrey-Smith demonstrate that the two parameterizations are mathematically equivalent – each set of parameter values can be derived from the other. This does not *prove* that pluralism is the correct position – for it might be argued that only one of the parameterizations correctly captures the causal facts, even though the two are mathematically interchangeable, hence computationally equivalent. But Kerr and Godfrey-Smith certainly make a strong case for a pluralistic interpretation of the trait-group models.

It is obvious that the group selection controversy is partly fuelled by disagreement about what exactly the process of group selection amounts to. Damuth and Heisler (1988) argue that there are two distinct concepts of group selection (or multilevel selection more generally), which have often been conflated in the literature. The distinction hinges on the meaning of “group fitness” and its relation to organismic fitness. In group selection type 1 (GS1), the fitness of a group is defined as the *average fitness of its constituent organisms*, so there is a definitional relationship between group and organismic fitness. The fittest groups, in this sense, are the ones that contribute the most offspring organisms to the next generation of organisms (per capita). In group selection type 2 (GS2), the fitness of a group is defined as the expected number of offspring groups that it leaves, rather than the average fitness of its constituent organisms. The fittest groups, in this sense, are those that contribute the most offspring *groups* to the next generation of *groups*. Although in many situations the groups that are fittest by the GS1 criterion will also be fittest by the GS2 criterion, and vice versa, the two concepts are logically distinct. So there are two quite different things that “group selection” can mean.

The essence of the difference between GS1 and GS2 concerns the “focal” level, i.e., the level we are interested in. In GS1 the focal level is the individual organism, while in GS2 it is the group. This means that GS1 and GS2 have different explanatory targets. The former can explain the changing frequency of different types of *individual* in a group-structured population, while the latter can explain the changing frequency of different types of *group* in a metapopulation of groups. (Put differently, in GS1 we count individuals while in GS2 we count groups.) As Damuth and Heisler (1988) note, most of the literature on group selection has dealt with GS1: the aim has been to understand the evolution of an *individual* phenotype, often altruism, in a population subdivided into groups. So group fitness, in models for the evolution of altruism, has usually been defined as average organismic fitness. By contrast, the literature on species selection has had a GS2 focus: the aim has been to understand the changing frequency of different types of *species*, not their component organisms (see Section 5 below). So species fitness is usually defined as expected number of offspring species, rather than as average organismic fitness. It follows that species selection is *not* simply a higher-level analog of group selection, as the latter has traditionally been understood, for it is of a different logical type (Arnold & Fristrup, 1982; Okasha, 2001, 2006).

The GS1/GS2 distinction is relevant to the debate over pluralism and trait-group selection. As we saw above, Kerr and Godfrey-Smith (2002) argue for pluralism by showing the interdefinability of the multilevel and contextual parameterizations of their

model. However, this interdefinability result holds *only* in cases where group fitness is defined as average organismic fitness, i.e., GS1. If group fitness were defined in the GS2 way, as expected number of offspring groups, it would not be possible to switch between a multilevel and an individualist parameterization (Okasha, 2006). This means that group selection of the GS2 variety cannot be re-analyzed as organismic selection in a structured population. GS2 is thus an *irreducibly* group-level process, in one legitimate sense of the word “reducible.” This indicates a limitation on the types of selection process for which the pluralist thesis – that there is “no fact of the matter” about the true level of selection – will be tenable. One *might* take this to show that only GS2 is “real” group selection, as authors such as Vrba (1989) have argued, but this inference is not mandatory; it would have the unwelcome implication that much of the work purporting to be about group selection does not really deal with that topic at all.

The distinction between GS1 and GS2 goes a long way towards clarifying the group selection question, but certain outstanding issues remain. One such issue concerns causality. Virtually everybody agrees that the theory of natural selection is a causal theory – it aims to provide a causal-historical explanation for changes in gene/trait frequency over time. Therefore, where multiple levels of selection are in play, it follows that causes must be operating at more than one hierarchical level. Sober’s (1984) book contained a detailed attempt to use philosophical ideas about causality to address questions about the levels of selection. Recent work by Okasha (2004c, 2006) also addresses the issue of causality, though from a somewhat different angle. Most approaches to the levels of selection have addressed a purely *qualitative* question, namely, what are the level(s) of selection in a given situation? But this fails to address an important *quantitative* question, namely, given the levels of selection that are in play, what fraction of the total evolutionary change can be attributed to each? For example, suppose both group and organismic selection are in operation in a given situation. How do we tell how *much* of the resulting evolutionary change is due to selection at each level? Okasha (2004c) explores three different statistical techniques designed to address this question, and finds that they yield incompatible results – each decomposes the total change into different components, allegedly corresponding to distinct levels of selection. This raises an overarching philosophical issue: how do we choose between the techniques? Or is there perhaps “no fact of the matter” about which is correct? Focusing on the quantitative rather than just the qualitative question brings new conceptual problems to the fore.

5. Species Selection and Macroevolution

The concept of species selection was developed in the 1970s by Stanley (1975) and Eldredge and Gould (1972) as part of their attempt to “decouple” macroevolution from microevolution. The long-term evolutionary patterns revealed in the fossil record are not simply the cumulative upshot of the microevolutionary forces that adapt local populations to their environments, these authors argued. Phenomena such as the origins of new species and higher taxa, long-term phylogenetic trends, and the greater diversification of some clades compared to others need to be studied “at their own level,” not treated as incidental effects of microevolution. This requires us to recognize the

existence of autonomous macroevolutionary forces, of which species selection is a potential example.

The basic idea of species selection is that a selective force operates on whole species, analogous to but distinct from ordinary organismic selection, favoring those species that are fittest and disfavoring the least fit. Organismic death is analogous to species extinction, and organismic reproduction to speciation. So just as an organism's fitness is its expected number of offspring organisms, so a species' fitness is its expected number of offspring species. It is obvious that species vary in their characters, or traits. Some species are more geographically widespread than others, some are ecological generalists while others are specialists, some are more genetically diverse than others, some are composed of larger-bodied organisms than others, and so on. Conceivably, these species-level traits could affect fitness – either by affecting a species' probability of extinction or of speciation. If so, and if the traits in question are inherited by offspring species, then species selection could in theory have a significant effect on long-term evolutionary trends.

Most though not all biologists accept that species selection is possible, but there is substantial disagreement over its empirical significance. Additionally, there is disagreement about what exactly the concept of species selection amounts to, what type of evolutionary phenomena it is capable of explaining, and how the relation between species selection and lower-level selection should be understood. These conceptual issues require resolution before the empirical case for species selection can be adequately assessed.

In a series of publications, Elisabeth Vrba has argued that genuine species selection is extremely rare; most of the alleged examples involve only “species sorting,” she claims (Vrba, 1984a, 1984b, 1989). The idea behind Vrba's selection/sorting distinction is that even if differential extinction or speciation rates correlate with species-level characters, this does not necessarily mean that an autonomous higher-level selection process exists. The trend may instead be a by-product of lower-level causal forces, such as organismic selection. For example, if red and grey squirrels compete for the same resources and the former are driven to extinction, it would be inappropriate, intuitively, to attribute this to species selection. Grey squirrels had higher individual fitness than red ones, and as a consequence the latter all died, hence the species went extinct. But no causal forces were acting on the species *as units*. So the higher-level trend, i.e., the survival of the one species and the extinction of the other, is not the product of species selection. Rather, it is the by-product of selection at the *organismic* level, the effects of which “percolate up” the biological hierarchy. In Vrba's terms, this is a case of species sorting but not species selection.

Most biologists agree with Vrba that genuine species selection involves more than mere differential extinction/speciation, but there is disagreement over exactly what the missing ingredient is. Vrba herself argues that true species selection requires the existence of “emergent” species-level characters that causally influence species fitness. Emergent characters are usually contrasted with “aggregate” or “sum of the parts” characters such as “average height” or “average running speed” that are produced by combining measurements on individual organisms. Intuitively such characters are statistical artifacts rather than real species-level traits. Emergent characters, by contrast, are not mere statistical summations of organismic characters. Vrba cites

“characteristic population size, spatial and genetic separation between populations, and the nature of a species periphery” as possible examples of emergent characters of species (1984a, p.325). Genuine species selection only occurs, Vrba holds, where emergent properties lead to differences in species fitness.

The significance of the distinction between aggregate and emergent characters has proved controversial. One problem is that the distinction itself, while intuitively clear, is difficult to characterize in general terms; Vrba herself offers several non-equivalent characterizations. Another problem is that the emergent character requirement represents a substantial metaphysical thesis, which surely requires further explanation. For emergent characters of species, no less than aggregate ones, supervene on underlying organismic characters. Characters such as species range or spatial separation between populations are ultimately dependent on organismic characters and behaviors, e.g., dispersal distance. Vrba’s requirement implies that a genuine species-level causal process occurs only when species fitness is affected by emergent characters. But since aggregate and emergent characters are *both* determined by underlying organismic characters, some explanation of this alleged difference in causal potential is surely needed. Alternative approaches to distinguishing “real” species selection from its surrogates are explored by Williams (1992), Gould (2002), Gould and Lloyd (1999), Sterelny (1996), and Okasha (2006).

A quite different challenge to species selection comes from Damuth (1985), who argues that species are not the right *type* of entity to function as units of selection in the first place. Most species are divided into many partially isolated populations, each subject to different local conditions, Damuth stresses. So there are unlikely to be selection pressures acting on a whole species as a unit; rather, different populations within the species will be subject to different selection pressures. In short, species are not ecologically localized the way that individual organisms are, and thus not the sorts of thing to which Darwinian fitness can be ascribed. Damuth thus proposes to replace the concept of species selection with “avatar” selection. Avatars are local populations of species that are ecologically localized, hence capable of competing and interacting with local populations of other species. This move is required to preserve the analogy with organismic selection that motivated the idea of species selection in the first place, Damuth argues.

Even if the concept of species selection can overcome the conceptual and empirical challenges it faces, there is still a fundamental reason for regarding the species as a relatively unimportant unit of selection. For species are not functionally organized the way other paradigmatic units of selection, such as cells, organisms, and insect colonies, are. These entities exhibit a division of labor between their constituent parts, the hallmark of true functional organization. The different proteins in a cell, the different tissues and organs in an organism, and the different castes in an insect colony each perform distinct roles in the functioning of the larger entity. The same is not true of the organisms that make up a species. (For this reason, the species should probably not be thought of as a level of biological *organization* at all.) Though this disanalogy does not invalidate the concept of species selection altogether, if only because many rounds of cumulative selection are required to produce functionally integrated entities, it does suggest that species selection has been much less important than selection at lower hierarchical levels.

6. Multilevel Selection Theory and The Major Transitions in Evolution

The expression “multilevel selection theory” is increasingly common in the biological literature. The basic idea of this theory – that natural selection may operate simultaneously at more than one hierarchical level – is not new; indeed, it is implicit in the very earliest discussions of the levels of selection, including Darwin’s. What is new is the *use* to which multilevel selection is currently being put. Increasingly, biologists interested in explaining what Maynard Smith and Szathmary call the “major transitions in evolution” have made use of ideas from multilevel selection theory (Buss, 1987; Michod, 1997, 1999; Maynard Smith & Szathmary, 1995; Frank, 1997; Queller, 2000). The work of these authors extends the traditional units of selection question in an important new way.

The “major transitions in evolution” refer to the transitions from solitary replicators to networks of replicators enclosed within compartments, from independent genes to chromosomes, from prokaryotic cells to eukaryotic cells containing organelles, from unicellular to multicellular organisms, and from solitary organisms to colonies. Some of these transitions occurred in the distant evolutionary past, others much more recently. In each case a number of smaller units, originally capable of surviving and reproducing on their own, became aggregated into a single larger unit, thus generating a new level of biological organization. The challenge is to understand these transitions in Darwinian terms. Why was it advantageous for the lower-level units to sacrifice their individuality, cooperate with one another, and form themselves into a larger corporate body? And how could such an arrangement, once first evolved, be evolutionarily stable?

This is where multilevel selection enters the picture. As Buss, Michod, and Maynard Smith and Szathmary all stress, to understand the major transitions we need to know why lower-level selection did not disrupt the formation of the higher-level unit. In the transition to multicellularity, for example, we need to know why selection between competing cell lineages did not disrupt the integrity of the emerging multicellular organism. One possibility is that selection acted on the higher-level units themselves, leading them to evolve adaptations that minimize conflict and increase cooperation among their constituent parts. Thus in the case of multicellularity, Buss and Michod argue that early sequestration of the germ-line may be one such adaptation, for it reduces the probability that mutant cells, arising during ontogeny, will find their way into the next generation. Another idea is that passing the life cycle through a single-celled stage, as occurs in most animal and plant species, is an adaptation for minimizing within-organism conflict, for it increases the relatedness, hence decreases the competition, between the cells within an organism. These particular examples have both been contested, but the general idea that the major transitions involve an interaction between selection at different levels is very widely accepted.

Though still in their infancy, these theoretical developments suggest that the traditional way of posing the units of selection question was somewhat inadequate. For as Griesemer (2000) notes, the traditional formulations of the question, including Lewontin’s “heritable variation in fitness” formulation employed above, generally take the existence of the biological hierarchy for granted, as if hierarchical organization

were simply an exogenously given fact about the biotic world. But of course the biological hierarchy is *itself* the product of evolution – entities further up the hierarchy, such as multicellular organisms, have obviously not been there since the beginning of life on earth. The same is true of cells and chromosomes. So ideally, we would like an evolutionary theory which explains how the biological hierarchy came into existence, rather than treating it as a given. From this perspective, the units of selection question is not simply about identifying the hierarchical level(s) at which selection *now* acts, which is how it was traditionally conceived, but about identifying the mechanisms which led the hierarchy to evolve in the first place (Okasha, 2005).

This new “diachronic” perspective gives the units of selection question a renewed sense of urgency. Some biologists were inclined to dismiss the traditional debate as a storm in a teacup – arguing that in practice, selection on individual organisms is the only important selective force in evolution, whatever about other theoretical possibilities. But as Michod (1999) stresses, multicellular organisms did not come from nowhere, and a complete evolutionary theory must surely try to explain how they evolved, rather than simply taking their existence for granted. So levels of selection other than that of the individual organism *must* have existed in the past, whether or not they still operate today. From this expanded point of view, the argument that selection on individual organisms is “all that matters in practice” is clearly unsustainable. Moreover, this lends further weight to the view that group selection was prematurely dismissed in the 1960s. For multicellular organisms are themselves groups of cooperating cells, and chromosomes are groups of cooperating genes. Since multi-cellular organisms and chromosomes obviously have evolved, the efficacy of group selection cannot be denied (Michod, 1999; Sober & Wilson, 1998).

The attempt to understand the major transitions has thrown up a number of interesting questions. One concerns the extent to which the different transitions are thematically similar, and thus explicable in similar terms. For example, is the transition from unicellularity to multicellularity relevantly similar to the transition from solitary insects to eusocial insect colonies? If so, then can the theoretical principles needed to understand the former be extrapolated to the latter and vice versa? More generally still, can concepts such as kin selection and the gene’s eye view of evolution, originally developed to help explain social behavior in animals, shed light on the major transitions? Theorists take different stands on these questions. Most agree that the principle of kin selection is of fundamental importance at all hierarchical levels, especially in the evolution of multicellularity, though Buss (1987) accords much less explanatory weight to this principle than others. Maynard Smith and Szathmary (1995) explicitly advocate a Williams/Dawkins gene-centered approach to the major transitions, but Michod (1999) describes Dawkins’ gene-centric view of evolution as a “mistake” (p.139). These disagreements show that the application of multilevel selection theory to the major transitions raises substantial, and as yet unresolved, conceptual issues.

7. Conclusion

In some ways it is surprising that the units of selection question has engendered so much conceptual and foundational discussion, for the principle of natural selection is

essentially straightforward and can be formulated very simply. Nonetheless, as the forgoing survey has hopefully made clear, the myriad of conflicting opinions among evolutionary biologists about the units of selection are not the “ordinary” scientific disagreements of opinion that arise from lack of empirical data. Rather, they are disagreements about which concepts to employ, which questions to ask, and which explanatory strategies to pursue. It is hard to predict what direction the debate will take in the twenty-first century, though it is likely that the flurry of interest in the major evolutionary transitions will continue. It remains to be seen whether the ensuing biological discussions will provide as fertile a ground for philosophy of science as did the units of selection discussions of the twentieth century.

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