LEVELS OF SELECTION

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1   INTRODUCTION

The generality of the theory of natural selection is both a virtue and, if not quite a vice, at least the source of much spilt ink, spirited discussion, and occasional despair. The theory of selection is general in that the conditions usually held to be necessary for natural selection to operate — that there be heritable variation the fitness of some trait within a population — is itself neutral about just what entities natural selection operates on. This kind of neutrality has provided evolutionary biologists with much room in which to develop the theory of natural selection, giving rise to "universal Darwinism" [Dawkins, 1983; Dennett, 1995], to both dualistic and integrative accounts of natural and cultural selection [Durham, 1991; Boyd and Richerson; 1985; 2004] and debate over the levels of selection. It is this final issue that will be our focus in what follows. Sections 2–5 will cover basic issues and views in this debate, while sections 6–8 will take up some more specialized topics that are of current debate: pluralism (section 6), the conception of groups (section 7), and evolutionary transitions (section 8).

   If the Darwinian theory of natural selection is neutral in the way the people have typically thought that it is, then there is a real question as to what the agents of natural selection are. What are the *units* on which natural selection acts? Darwin himself formulated his theory of natural selection with *organisms* in mind as the principal (and near exclusive) unit of selection. They were the bearers of the properties amongst which there was variation in a population, the raw material on which natural selection operates, and through their reproductive behavior were the source for the transmission of these traits across generations, and so important entities for inheritance. It is true that in several often quoted passages, Darwin also entertained the idea that *groups of organisms* could also serve these roles, but it is clear that Darwin appealed primarily to *individual selection* and only rarely to *group selection* as the mechanism through which patterns of descent with modification were established in the natural world.

2   FROM ORGANISMS TO GENES AND GROUPS

Such a view of natural selection was largely taken for granted by advocates of Darwin's theory until the Evolutionary Synthesis in the 1930s and 1940s. The

idea that natural selection acted at the level of the individual organism emerged from the Synthesis still a dominant view, but the seeds were sown during that time for developments within the biological sciences that fed views that have come to constitute the two chief challenges to this received view.

The first of these came from genetics, both in its experimental guise exemplified in "the fly room" established at Columbia University by Thomas Hunt Morgan, and in the development of theoretical population genetics that ranged from the mathematical modeling of Ronald Fisher [1930] and Sewall Wright [1929; 1931; see also 1968; 1969; 1977; 1978; 1980] to the broader applications of Theodosius Dobzhansky [1937]. This work introduced the gene as the principal agent of inheritance: it is genes that are inherited and that are causally responsible for the production of organismic traits. In a metaphor introduced in Erwin Schrödinger's *What is Life?* [1944] that has, since that time, come to dominate the scientific and popular conception of genetic agency, genes *code for* the fundamental products of inheritance. This cluster of developments thus formed the basis for a challenge to the role of the individual organism in the process of inheritance, a crucial part of the overall process of natural selection. The idea that natural selection operates *on genes*, although nascent in remarks in Fisher's *The Genetical Theory of Natural Selection* [1930], was developed in the late 1950s and early 1960s by George Williams [1966] and William D. Hamilton [1964], and received further extension and popularization in Richard Dawkins' first book, *The Selfish Gene* [1976].

The second development within the conglomeration of biological sciences associated with the Evolutionary Synthesis was centred disciplinarily in plant and animal ecology and institutionally at the University of Chicago. The Harvard entomologist William Morton Wheeler had introduced the term "superorganism" in his insightful and playful 1920 essay "The Termitodoxa, or Biology and Society", having earlier suggested conceiving of an insect colony as a higher-order organism in his "The Ant-Colony as an Organism" [1911]. This kind of view of at least some groups of organisms was already implicit in the work of the ecologist Frederic Clements on plant succession, who argued that plant-animal communities formed what he called *biomes*, which were more than simply the sum of the individual organisms that constituted them. Common to both the ecological and entomological works here was a physiological, organismic view of populations that came to occupy centre stage in the Chicago school of ecology, headed by Warder Clyde Allee and whose members included Alfred Emerson and Thomas Park. The conception of at least certain groups of organisms as themselves organism-like served as the basis for viewing such groups as the *beneficiaries* of natural selection, the entities that differentially survive as a result of the action of natural selection, as well as the *manifestors of adaptations*, the entities that come to bear adaptations through that process. This idea of group selection was a thread that ran through the Chicago school's *Principles of Animal Ecology* [1949] and received its now-classic expression in the work of the Scottish ornithologist V.C. Wynne-Edwards, *Animal Dispersion in Relation to Social Behavior* [1962].

So there have been challenges to the traditional Darwinian view of the level at

which selection acts from two fronts: from "the gene below", as well as from "the group above". Over the past 30 years, during which the philosophy of biology has emerged as a distinct sub-discipline within the philosophy of science, this debate has become increasingly sophisticated, in part due to interactions between philosophers and biologists. The question of the level(s) at which selection act has in fact become a staple in the diet of any healthy philosopher of biologist, a question answered in part via an appeal to a range of "isms" — pluralism, realism, reductionism, individualism, genocentrism — and methodologies — the drawing of distinctions (some of which I have already taken advantage of above), the reformulations of questions, the identification and questioning of taken-for-granted assumption — that are the signature of a philosophical presence.

3   GENES AND ORGANISMS: REPLICATORS, INTERACTORS, AND OTHER "UNITS"

Richard Dawkins has nicely captured one way in which the individual organism acts as a basin of attraction for evolutionary reflection:

> biologists interested in functional explanation usually assume that the appropriate unit for discussion is the individual organism. To us, 'conflict' usually means conflict between organisms, each striving to maximize its own individual 'fitness'. We recognize smaller units such as cells and genes, and larger units such as populations, societies and ecosystems, but there is no doubt that the individual body, as a discrete unit of action, exerts a powerful hold over the minds of zoologists, especially those interested in the adaptive significance of animal behaviour. [1982, 4]

One of Dawkins' own chief aims has been to break the hold that this image of adaptation, function, and natural selection has on biologists. He does this by making genes more focal in the range of evolutionary narratives that we tell about the biological world.

A simple, general distinction, introduced originally by Dawkins in *The Selfish Gene*, has been integral to the intuitive plausibility of the idea that natural selection operates typically at the level of the gene. This is the distinction between *replicators* and *vehicles*. A replicator is anything that can be reliably copied with a high degree of fidelity, while a vehicle is the entity in which a replicator is housed. Dawkins' claim was that genes are the primary replicators, and organisms the chief vehicles, in the process of evolution by natural selection.

The power of this distinction in motivating genic selection is threefold. First, as a general, functional distinction, it can be introduced neutrally and illustrated independently from the debate over the levels of selection. Second, the distinction allows us to probe any putative case of organismic or group selection by asking whether those entities serve as replicators or vehicles. Third, the asymmetry between functionally-active replicators and functionally-passive vehicles suggests

that it is the former which are the real agents or units of selection, and the latter that play some supplementary role in the process of selection.

David Hull [1980] generalized and tidied this distinction — in part to remove the above-mentioned asymmetry between replicators and vehicles — envisaging natural selection as composed of two processes, replication and *interaction*. These may (and Hull thinks, typically do) operate at distinct levels on distinct entities. Following Hull, a replicator is "an entity that passes on its structure directly in replication" and an interactor is "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential". Bypassing the apparent circularity in each of these definitions, they open the space for a two-part characterization of natural selection that has become common in the literature (e.g., [Brandon, 1987; Sterelny and Griffiths, 1999]). With these definitions in hand, Hull defines natural selection as "a process in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them" [1980, 318]

Following the standard Darwinian view, organisms are often taken for granted as the principal interactors in natural selection, and this has been central in thinking of them as the agents of selection. Although it is also common to dismiss the idea that sexually reproducing organisms are replicators, this idea deserves closer scrutiny. The reasons for rejecting organisms as replicators include appeals to facts about genetic recombination, the non-identity of parents and offspring at the phenotypic level, and the "indirectness" of the reproduction of organisms through sexual means (where directness is understood in terms of the notion of independence). These, in turn, serve as the basis for arguments that genes are special as agents in natural selection because they are permanent, or the only entities that are inherited across generations. But none of the basic appeals are very good reasons for denying that organisms are replicators, given the characterization of a replicator. Whether organisms are replicators turns largely on at how fine-grained a level we individuate structures, for there is a clear sense in which many phenotypic structures are passed on across generations, even "directly". If we individuate them relatively coarsely, many are transmitted through sexual reproduction and their genetic heritability is relatively high, but that is not strictly required by the definition of a replicator. Philosophers and biologists have been too quick to dismiss the idea that organisms themselves are replicators.

Elisabeth Lloyd [1992; 2001] has distinguished in addition two further issues that are sometimes built into the debate over the levels of selection, what she calls the *beneficiary* and the *manifestor of adaptation* questions. Beneficiaries of selection are those entities that end up being differentially represented in later generations as a result of natural selection. Lloyd plausibly considers species or lineages as putative beneficiaries of selection. Manifestors of adaptation are those entities that come to possess (or even lose) traits as a result of the action of natural selection. Organisms are readily conceived not only as interactors but also as beneficiaries — they are relatively easily counted, for example, and organisms with fitter traits are differentially represented in future generations — and as

manifestors of adaptations — their complex design was obvious before Darwin. Perhaps because of this, these distinct roles are sometimes not distinguished when considering other putative agents of selection, particularly groups. By invoking this additional distinction, Lloyd has turned the tables on the genic selectionist who appeals to the replicator/vehicle distinction to support his view. Just as proponents of traditional individual selection failed to recognize replicators as distinct from vehicles or interactors, so too do genic selectionists lump together genes as replicators, beneficiaries, and manifestors of adaptation in the process of natural selection. On Lloyd's view, there is not one but four questions about the unit of selection, and genic selectionists have concentrated on answering just one of these.

4   GROUP SELECTION AND INDIVIDUAL SELECTION

The most convincing articulation of *group selection* is one that is modeled on and builds on our intuitive views of individual selection. Just as there can be the natural selection of organisms within a population for some fitness-enhancing property — running speed, wing shape, color — so too can there be the natural selection of groups within a population of groups for some fitness-enhancing property. This selection of groups is group selection, just as the selection of individuals is individual selection.

We can build on this intuitive parallel by, in the first instance, being a little more precise about the conditions necessary for natural selection to occur. Following a seminal discussion of the units of selection by Richard Lewontin [1970], natural selection is often thought of as requiring that three things hold of the entities that it acts on. On the standard Darwinian view, these entities are individual organisms, and so on that view there must be:

(i)   variation in a population of organisms with respect to some phenotypic trait;

(ii)   a correlation between this variation and the fitness levels of organisms within the population; and

(iii) the heritability of this variation across generations.

There are analogs to Lewontin's three conditions for natural selection that take the group rather than the individual organism to be the relevant object of focus. These analogs are that there be:

(i′)   variation in a population of *groups* with respect to some phenotypic trait;

(ii′) a correlation between this variation and the fitness levels of *groups* within the population; and

(iii′) the heritability of this variation across generations.

The only difference between (i′)–(iii′) and (i)–(iii) is the occurrence of "groups" in place of "organisms" in the two places emphasized in (i′) and (ii′). The paradigm of laboratory or experimental group selection established by the geneticist Michael Wade [1977; 1978] is based on the satisfaction of (i′)–(iii′), much as the domestic breeding that Darwin appealed to in the opening chapter of the *Origin* was based on the satisfaction of (i)–(iii).

To ensure that this formal parallel is not superficial and misleading, it is crucial that we be able to make sense of notions that occur in each, such as fitness. An individual organism's fitness is its reproductive success, measured ultimately in terms of number of offspring that it produces. One can further distinguish between survivability and fertility as aspects of individual fitness that correspond, respectively, to the egg-adult and adult-egg halves of the life cycle, in order to attain a more fine-grained picture of where individual selection operates in particular cases, although since these have different mathematical representations, dividing fitness up in this way introduces some theoretical inelegance in modeling fitness dynamics. Individuals within the population are said to compete with one another to leave more offspring in future generations, although "competition" is used here in a "large and metaphorical sense", to use Darwin's own characterization of the idea of a struggle for existence. Whenever there is either differential survivability or fertility in a population of organisms, and finite use of resources, then there is competition, in this sense, between individuals in that population.

Group fitness can be understood in much the way that we understand an individual's fitness, namely, in terms of *its* reproductive success. As with individuals, in the case of groups we also have two types of reproductive success that correspond to organismic viability and fertility. A group's viability is its ability to endure over time, and it does this by replacing the individuals in it over as individuals die and others are born. A group's fertility is its ability to produce offspring. As with individuals, we might well view fertility as an index of the ultimate evolutionary currency, but in addition, there are two forms that currency can take.

First, groups can produce or recruit *more individuals than they lose*, and so grow in size. Second groups can produce *more groups* with the characteristics that they have as groups. Both of these involve producing (or recruiting) more individuals over time, but they are in principle independent means of increasing the fitness of the group such that groups with a given individual phenotypic or group trait successfully compete with groups without it, and thus come to replace those groups in the metapopulation. Thus, an individual-level phenotypic trait could increase its representation in the metapopulation via group selection in either of two ways. First, it could do so by the differential addition of individual organisms to existing groups — paradigmatically by one group increasing in size, or a competitor group having its size decreased. Second, it could increase its metapopulational representation by the differential addition of groups of individual organisms with that trait — paradigmatically through differential colonization and migration rates between groups.

As Okasha [in press] has recently pointed out, these two different kinds of group

fitness have been used in the literature in different ways. Proponents of trait group selection, such as Wilson [1975] for example, have been interested in a group-level mechanism that could explain the evolution of an individual-level trait, such as being an altruist. To show that altruism could evolve by group selection, Wilson uses the first measure of fitness, arguing that if groups with more altruists are fitter than groups with fewer altruists, altruism can increase in the global population. Proponents of species selection, such as Jablonski [1986; 1987], have focused on the second measure of fitness. Jablonski argued that species of mollusks with greater geographical dispersal evolved through the group selection of species, and his measure of this was the increased number of species of mollusks with that range, tying this to increased feeding opportunities.

5   THE PROBLEM OF ALTRUISM AND THE LEVELS OF SELECTION

Departures from the standard, individual-centred view of natural selection have their own motivations, as we have seen, but they also share one important motivation: the problem that altruism poses for the standard view. Group selection of the kind originally advocated was one response to the phenomenon of altruism, while genic selection arose as an alternative that was claimed both the avoid the problem that altruism posed for individual selection and to make appeals to group selection otiose. But what is the problem of altruism?

On the standard Darwinian view, populations of organisms evolve because the individuals in them have differential levels of fitness. As we have seen, those organisms can be said to compete with one another in a large and metaphorical sense for the survival of their offspring. In this same sense, organisms can be thought of as striving to maximize their fitness, i.e., their own survival and ultimately the survival of their progeny. Although organisms are often thought of as striving for their own survival, those that do so to the exclusion of producing viable offspring — say, either by producing no offspring at all or producing none that survive as fertile individuals — have a fitness of zero. Given that the fitness of any given organism is ultimately its expected number of offspring, any individual striving to maximize its fitness will be striving to maximize this number. Thus, it will act in ways that benefit at least some others, i.e., its progeny. But an individual's biological fitness places it in competition with other members of the population, and so individuals who reduce their own fitness in order to increase the fitness of others who are not progeny will reduce their representation in future generations.

Evolutionarily altruistic behavior is typically characterized as behavior that has just this property of reducing an individual's fitness while increasing the fitness of non-offspring in that individual's group. For example, Edward O. Wilson defined altruism as "self-destructive behavior performed for the benefit of others" in the glossary of his influential *Sociobiology: The New Synthesis*. But such behavior is merely an extreme form of a more general type of behavior that gives rise to the problem of altruism. This problem arises just when a behavior contributes relatively more to the fitness of non-offspring in the population than to the fitness

of the individual engaging in the behavior, and thus that decreases the *relative* fitness of the "altruistic" individual within the population. Because individual selection will diminish the relative fitness of individuals engaging in such behaviors from one generation to the next, it will select against them. If unchecked, it will drive them to extinction in the population. It is precisely such behaviors that give rise to the problem of altruism. Thus, these behaviors, which may or may not be "self-destructive" or "performed for the benefit of others", are altruistic, i.e., behaviors for which the problem of altruism arises. Behaviors that are self-sacrificial or that benefit others are merely as a special case. One advantage that this characterization of the problem of altruism has is that it makes it easier to dissociate altruism from self-sacrifice, a notion with a psychological caste that readily comes to mind in thinking of human altruism. The "sacrifice" involved in behaviors for which there is a problem of altruism is just that of the maximization of the number of one's viable offspring.

Given the individual as the agent or unit of selection, the existence of altruistic behaviors, so characterized, would be a puzzle, since individuals in a population who exemplify them will be less fit than those who do not. Thus, other things being equal, such individuals will leave fewer offspring in the next generation than do their competitors. From this perspective, being altruistic is a differential handicap, like being slow relative to others in a population, where greater speed allows one either to capture more prey or to escape more readily from predators. Such fitness-reducing behaviors may be the by-product of selective processes operating on other phenotypes but could not themselves evolve by individual selection.

The problem of altruism, then, is the conjunction of the standard Darwinian view of natural selection with the existence of evolutionary altruism. There are thus two ways to respond to the problem that could be said to represent solutions to the problem, rather than either an admission that the problem reveals the limits of the theory of natural selection (defeatism), or a denial that there is a problem at all for the standard Darwinian view to face (blind optimism).

The first is to deny the existence of evolutionary altruism. Given a range of often-cited cases — for example, sentinels in birds, caste specialization in social insects, "good Samaritan" behavior in humans — in which individuals help others or even sacrifice their lives for others — such a denial might be thought to lack credibility as a response to the problem of altruism. However, altruistic behavior is not simply helping or sacrificial behavior, but behavior that detracts from the relative fitness of the individual. So to demonstrate the existence of evolutionary altruism one cannot simply point to clear instances in which individuals help others or sacrifice themselves for the sake of others. For such behaviors might themselves be a way of maximizing individual fitness. This is the idea behind reciprocal altruism [Trivers, 1971]: individual's forego or limit their own direct reproductive opportunities in order to maximize their long-term fitness through gaining reciprocal benefits from those they benefit. Here individuals are still maximizing their own fitness, albeit indirectly. Hence these behaviors only appear to be evolutionarily altruistic. In effect, this response plays up the role of individual

fitness within evolutionary theory so that there is little or no room for evolutionary altruism. For it to solve the problem of altruism the net benefits to individuals engaged in "altruism" must be greater than the net benefits to those they help.

The second is to modify the standard Darwinian view so as to posit some other unit of selection, and then show how selection operating at that level could give rise to evolutionary altruism. Thus, proponents of group selection have pointed out that although individual selection acts so as to decrease the representation of altruists within a population, groups of altruistic individuals may have a higher level of fitness than non-altruistic groups [Sober and Wilson, 1994]. It follows that a process of group selection will act in a countervailing direction to that of individual selection, and thus altruists could survive as members of fitter groups. This version of the second response goes hand-in-hand with the idea that the traditional Darwinian view requires augmentation, and that there is a plurality of levels at which natural selection operates.

An alternative way to depart from the traditional Darwinian view is more radical in that it involves recasting the theory of natural selection (and thus fitness) in terms of the survival not of organisms but of the genes they contain. If genes are the agents of selection, then organisms can be altruistic if their behaviors maximize the fitness of genes that happen to be located within those organisms. Since not just progeny of a given organism but individuals related in other ways to it, such as siblings and cousins, bear a genetic relationship to that organism, altruism directed at those individuals may be a way of maximizing the fitness of that organism's genes. This is a common way of understanding Hamilton's [1964] kin selection theory (but see [Wilson and Sober, 1998, 66–67]). In effect, this view also denies the existence of evolutionary altruism, and thus implies that both conjuncts that constitute the problem of altruism are false.

There is an important asymmetry between genic and group selection that can be made more explicit by posing two questions:

(a)   Does the traditional Darwinian view provide us with a complete or exhaustive view of evolution by natural selection?, i.e., are there evolutionary phenomena that this conception of the agent of selection leaves out?

(b)   More radically, are the appearances here actually misleading?, i.e., are there other agents that are in general better candidates for the agent of selection than the organism?

Proponents of genic selection answer "Yes" to (b) because they think that genes are better candidates than organisms for the agent of selection. In part, this is because the gene's eye view of evolution provides a solution to the problem of altruism. Proponents of group selection, by contrast, answer "No" to (a) because they think that certain phenomena (e.g., altruism) require group selection. Thus, they hold that such a process must be added to individual selection to understand the complexity to the biological world. In fact, proponents of group selection are typically happy enough to embrace levels of selection smaller than the organism,

such as the gene, as part of an overarching *multilevel* approach to understanding natural selection [Wilson and Sober, 1994; Sober and Wilson, 1998].

6   PLURALISM AND REALISM

This way of thinking of the relationship between the problem of altruism and the debate over the levels of selection suggests the view, widely accepted in the literature, that there is fact of the matter about what *the* unit of selection is in at least some particular cases. If altruism really did evolve as a result of the action of natural selection, and the individual organism cannot be the unit on which it acted to produce that result, then genic and group selection are alternative accounts of how altruism evolved, alternatives that paint different pictures of biological reality. But some have denied that there is *always* a fact of the matter about what *the* unit of selection is, and others that there is a sense in which there is *never* (or rarely) such a fact of the matter. This dialectic raises issues of pluralism, realism, and reductionism into the debate over the levels of selection.

Realists about the level of selection hold that there is a fact of the matter, either in particular cases or in general, about what level selection operates at. They are like realists in other areas of science, holding that even if we have only limited evidence about what the underlying processes are that generate the phenomena we observe and measure, nonetheless there is an "in principle" fact of the matter here. The properties of electrons could not be reliably measured until into the 1920s, and the biochemical structure of genes was not known until the 1950s, but there was a fact regarding each of these matters that awaited our discovery. Likewise, even if it is hard for us to tell about whether, say, altruism evolves by genic or by group selection, either in a particular case or more generally, there is nonetheless a fact of the matter here. Those who deny this are *anti-realists* about the levels of selection.

The issue of realism is sometimes run together with, but is actually orthogonal to, the question of whether there is *a* level of selection, or whether there are multiple levels of selection. *Monists* hold the view that there is a single level of selection, either in a particular case or more generally, while *pluralists* deny this, hold that natural selection can and indeed does operate at different levels. In the case of altruism, a monist must view genic and group selection as exclusive alternatives to one another, such that at most one of these processes is causally responsible for the evolution of altruism. A pluralist, by contrast, could allow either that both genic and group selection act in a particular case to promote altruism, or that genic selection operates in some cases, group selection in other cases. Either way, there is no *single* level of selection that is responsible for the evolution of altruism, but a plurality of levels. According to pluralists, to ask the question "What is *the* level at which selection operates?" is to make a mistake insofar as this question invites monistic responses.

It is very natural to elide this pair of distinctions and (roughly speaking) equate monism with realism and pluralism with anti-realism, something encouraged by

the kind of sloganeering that has crept into the study of science. Monists/realists think there is One True Description of the world, a God's-eye view, whether or not we mere mortals can arrive at it, while pluralists/anti-realists think that "anything goes", that reality is socially constructed rather than discovery, that it's "different strokes for different folks" when it comes to our view of ontology. Although this is a mistake in general, I'll concern myself here with the kind of mistake it is when applied to debate over the levels of selection. Not only would such a collapse of the realism vs anti-realism and monism vs pluralism distinction gloss over a conceptual distinction, but it would serve only as a misleading caricature of the kinds of realism that are monistic, and the kinds of pluralism that are anti-realist. In addition, it would leave no room to characterize positions about the levels of selection that have been articulated and defended by some of the leading proponents in the field. In particular, there are varieties of positions that are properly characterized as *pluralistic realism*, and others that can be viewed as forms of *monistic anti-realism*. I will concentrate on pluralistic realism, which has gained much currency in recent years amongst both philosophers and biologists, but begin with monistic forms of realism.

The traditional Darwinian view is, for the most part, monistic about the level at which natural selection operates: the individual is the unit of selection (with the exception of occasional bouts of selection on tribes or groups). Genic selection has also often been viewed as a form of monistic realism in that it claims that it is the gene, rather than the individual organism, that is the *real* level at which natural selection occurs. This is a kind *genic fundamentalism* insofar as it views the gene as the fundamental unit of selection. On this view, genic selection might correlate with individual selection in a range of cases, and so models cast in terms of individual selection give the right answer in response to the question of what evolves in a particular case. But it is genic selection that constitutes the mechanism that generates the resulting distribution of traits that evolves. It is for this reason that genic selection is sometimes viewed as a *reductionist* view of the levels of selection.

There are at least two kinds of pluralistic realism, one of which retains strains of monism. The first is exemplified by the work of Elliott Sober and David Sloan Wilson, especially their *Unto Others* [1998]. In a series of publications they have articulated and defended a *multilevel view of selection*, which, as the name implies is a form of pluralism. On this view, one can begin with a question about the effects of natural selection at a given level (say, that of the organism), but then *frameshift* up (to groups) or down (to genes) to reformulate that very question. This multilevel view is a form of realism about the levels of selection insofar as it implies that there is a fact of the matter that determines the answer to each of these questions asked. In some cases, natural selection will operate at just a single level, at others it will operate at a different level, and in yet others it will operate at multiple levels at once. The last of these cases is most clearly pluralistic, but pluralism is also manifest in the multilevel framework by reflecting on the preceding two cases *together*, for together they imply that there is no overall, single level at

which selection operates. The strain of monism in the multilevel view comes out by considering cases in which just a single unit of selection is involved: although there is an overall pluralism, since this unit can vary across different cases, there is a *local monism*. I have elsewhere called this form of pluralism *unit pluralism* [R.A. Wilson, 2003] and *agent pluralism* [R.A. Wilson, 2005], since it is pluralistic about the units or agents of selection themselves.

A second form of pluralistic realism abandons monism altogether, holding that a plurality of units of selection is *always* present when natural selection operates. This is a view that is relatively undeveloped in the literature but one with which I have considerable sympathy. It is motivated by two considerations. The first is a view of the biological world as inherently complex, variable, and diverse. Even the oldest and, by some lights, the simplest organisms have many specialized parts, including parts that are specialized for replication and reproduction, and they nearly always interact with the rest of the world along with conspecifics and other group-mates. The second is a view of our categories and models for explaining this complexity, variability, and diversity: they are meager, simplifications that allow us to make certain kinds of predictions, but that never do full justice to the raw phenomena. Thus, we conceptualize the biological world in terms of distinct "levels", model how entities at each of those levels behave under certain conditions, and arrive at monistic or pluralistic views of the levels of selection. But this notion of levels is a kind of metaphor, one that carries with it limits and biases, and I have suggested that a metaphor that conformed better to the first point might be that of *entwinement* or *fusion* [R.A. Wilson, 2003] This form of pluralistic realism posits a significant mismatch between biological reality and our epistemic grip on that reality. Such a mismatch warrants viewing the monistic strain in the multilevel selection view as a reflection of our ignorance, rather than of the biological world itself. Thus, monism itself is the result of a kind of simplification of an inherently messy biological reality that metaphors like that of "levels" fail to do justice to.

A distinct form of pluralism from both of these is what I have elsewhere [R.A. Wilson, 2003; 2005, ch.10] called *model pluralism*, since it adopts a pluralistic view of our models of the biological world. This form of pluralism holds that various *prima facie* distinct models of natural selection, such as selfish gene theory and group selection theory, are actually non-competing accounts of one and the same reality. Model pluralists maintain that although there may be strategic or pragmatic advantage to using one rather than another model in a particular case, these models do not compete for, or share, the truth about the nature of natural selection.

Model pluralism has gained much currency in recent debates over the levels of selection. It has been defended by biologists, such as Lee Dugatkin and Hudson K. Reeve [1994) and Andrew Bourke and Nigel Franks [1995], and receives its crispest expression in the recent work of Benjamin Kerr and Peter Godfrey-Smith [2002]. Sober and Wilson have also embraced model pluralism, saying that inclusive fitness theory, selfish gene theory, and the theory of group selection that they propose are part of a "happy pluralistic family" of alternative perspectives on natural selection

that are "simply different ways of looking at the same world." [1998, 98]. When it is put in this way, model pluralism seems to imply a form of anti-realism about the levels of selection.

Model pluralism is motivated in part by the sense that participants in the debate over the levels of selection are "talking past one another", or that the debate is "just semantic". A core part of the support for model pluralism is the idea that there is an important sense in which the various models of natural selection *are equivalent* so that although there is a sense in which they carve up the world differently, this difference is underpinned by deeper affinity that these views share. Kerr and Godfrey-Smith, in particular, have shown how to translate key terms and equations between what they call the *individualist or contextual* models and what they call the *multilevel or collective* models. If these models are equivalent, then, model pluralists argue, it makes no sense to argue for one of the models rather than another as telling us how natural selection works, either in particular or in general. There are differences between these models, to be sure, but the choices between them are to be made on pragmatic grounds, rather than on the basis that one gets at what's really happening, while the other doesn't.

7   GROUPS AS CONTEXTS, GROUPS AS SUPERORGANISMS

Part of what separates proponents of genic and individual selection, on the one hand, from advocates of group selection, on the other, is their respective conceptions of the place of the structures of populations in the theory of evolution. We can distinguish three conceptions, each corresponding to a distinctive view of what appeals to group selection amount to.

The first is the conception of a group implicit in the early work on group selection associated with the Chicago school of ecology and people such as V.C. Wynne-Edwards. As the preceding discussion suggests, the conception of a group was very much that of an organism-like entity; groups, at least some of them, were *superorganisms* or sufficiently like organisms in the relevant respects to warrant treating them as organisms, and to treat their individual members as parts of that organism. That is why it seemed relatively unproblematic to shift the unit of selection from the individual to the group, since in effect this was simply to apply it to a different kind of individual.

The problem with this conception of a group, as Sterelny [1996] and others have pointed out, is that there are very few groups of organisms that can properly be viewed in this way: they are chiefly found in the social insects, which have a reproductive division of labour and feature sterile castes that don't reproduce at all or do so only under highly restricted conditions. Despite this *prima facie* problem, this conception of a group persists in several contemporary discussions. For example, Sterelny himself concedes that group selection can occur when there are superorganisms, and Wilson and Sober's multilevel view of selection, especially the version formulated in their [1994], seem to say much the same thing in employing their frameshifting model. Frameshifts "up" to the group, as well as "down" to

the gene, are justified just when those entities *function as individuals*. It is just that, unlike Sterelny, Sober and Wilson think that this is rather often the case.

Quite a different conception of groups lies at the core of the revival of group selection, however. This conception is of a group as a "sphere of influence", an aggregate of organisms that "share a common fate". Both of these phrases have been used by David Sloan Wilson [1975; 1983; 1997; 2002] and by Sober and Wilson [1994; 1998] in characterizing *trait groups*. On this view, a group is any aggregate of organisms whose evolutionary fates are tied together, no matter how temporarily or for what reason. In a striking example, Sober and Wilson consider a pair of crickets that find themselves sharing a leaf to cross a river as an example of a trait group, for whatever evolutionary outcome greets one will also greet the other.

Clearly, trait groups do not face the problem of rare instantiation that groups as superorganisms do; in fact, they might be thought to suffer from just the opposite problem, that of being a little too common. Consider clones of the myxoma virus located on a rabbit. It might be thought that all of those clones form a trait group, for if the rabbit dies they all die (they can't survive just on the carcass, or not for long). Yet clones that are located on lesions also form a trait group, since they have the same probability of being transmitted further by mosquito or flea vectors, which are attracted to lesions on an already infected rabbit. And since rabbits can transmit the virus to one another through direct contamination, clones located on rabbits within a hutch also constitute a trait group. This suggests that if there is any group selection in this example — an example well-known in the levels of selection literature in part because Richard Lewontin, in an influential paper [1970], claimed that it was an example whose details could *only* be explained by an appeal to group selection, a claim endorsed by Sober and Wilson [1998], amongst others — there is lots of it. That may be the right thing to say, but if so this in turn implies that there are many, many "levels" at which selection operates in at least a wide range of cases, and, to return to an earlier them, gives reason to question how accurately the metaphor of levels captures biological reality (see [R.A. Wilson, 2004]).

Both of these conceptions of groups make groups agents or units of selection. Those skeptical of how widespread group selection is in nature, particularly proponents of genic and individual selection, acknowledge that groups are often important in natural selection but claim that both traditional and neo-group selectionists are mistaken about the role that groups play. Rather than being agents of selection, groups serve as a part of the *context* in which genic and individual selection acts. In the myxoma case, natural selection is taken to select *individual clones* but to do so relative to the group environment they are in. Those on a given rabbit face common selection pressures, but they do so individually. Selection is always sensitive to an individual's environment: a dark moth will be selected for over its lighter variants in an environment in which the trees have been blackened through industrialization, but not in environments in which the bark of trees remains light-coloured. The insight of group selectionists, it is claimed, is to draw

explicit attention to *population structure* as a significant part of an organism's (or a gene's) environment. But this doesn't mean that groups themselves are agents of selection, any more than it means that the dark-coloured sub-group of the population of moths is selected through group selection.

This conception of groups as the contexts in which other kinds of entity, such as individuals and genes, are selected, plays a key role in model pluralism. For this forms one half of the two kinds of view — what Kerr and Godfrey-Smith call the *individualist/contextual* view as opposed to the *multilevel/collective* view of natural selection — that they claim are, in some sense, equivalent. But it also plays a role in conceptions of genic selection that accord the gene a fundamental status as a unit of selection, since it reinforces the divide introduced by the distinction between replicators and vehicles: genes have properties that make them suitable as agents of selection, while individuals and groups, even if occasionally manifesting such properties, are more usually conceptualized as playing a background, supplementary role to genic action.

A common complaint lodged against the contextualist conceptualization of groups [Brandon, 1987; Sober, 1984; Lloyd, 2001; 2005] is that it fails to reveal the causal dynamics that appeals to superorganisms and trait groups reveal. As it is sometimes put, accounts that focus on genes are accurate "bookkeeping devices" for what evolutionary outcomes develop, but they often do not reveal the *mechanisms* through which those outcomes are achieved. By providing detailed causal representations of both the contextualist and collective views of natural selection, Kerr and Godfrey-Smith [2002] have done much to reply to this kind of objection, though whether it is enough remains an issue subject to further debate [R.A. Wilson, 2003; Lloyd 2005].

8   TRANSITIONS IN EVOLUTIONARY HISTORY

The traditional Darwinian view of the levels of selection also gives rise to another question, one that has been informed by recent work on what John Maynard Smith and Eörs Szathmary [1995] have called the *major transitions* in evolution. The kind of individual organisms that we know and love best — multicellular, eukaryotic beasts like ourselves — emerged sometime during the 3.8–4 billion years during which there has been life on Earth. They are themselves a product of evolutionary processes, a kind of evolutionary achievement that represented a new type of biological organization. It is plausible, for many reasons, to think that multicellular organisms evolved from unicellular organisms, and that organisms with eukaryotic cells evolve from organisms with prokaryotic cells, with each of these evolutionary shifts constituting a major transition in evolution. More generally, one can consider the history of life as comprised of a series of such major transitions, starting with the simplest forms of living things at the origin of life, and ending (for now, at least) with the diverse collection of organisms that we see today. Many of today's organisms have many complex parts (including parts there were likely independently living organisms in the evolutionary past, such as mitochondria in

animal cells and chloroplasts in plant cells), many form integrated conspecific and inter-specific groups, and some manifest traits that we usually consider to be social or cultural.

If the major transitions in the history of life are a product of natural selection, then there is a obvious way in which the debate over the levels of selection is relevant to thinking about those transitions. For consider, say, the transition from unicellular to multicellular life, something that happened somewhere between one and two billion years ago. Since multicellular life is the product of this transition, natural selection cannot operate on *it*. Thus, if that process was one of individual selection, it must have been one that applied to existing kinds of organisms: unicellular organisms. But we can then raise just these same considerations about the relatively complex unicellular organisms that were the direct ancestors of the first multicellular organisms to arrive at the idea that the very first organisms must themselves have evolved *from something else*. If this is right, then the organism itself is an evolutionary achievement, and so natural selection cannot always have acted at the organismic level. The most plausible candidate for the earliest unit of selection is something like a simplified gene, a self-replicating sequence of DNA (or perhaps RNA), selection on which (somehow) gave rise to the first organism.

This perspective on the majors transitions of evolution has been taken up by Richard Michod [1999] and Samir Okasha [in press]. Here the debate over the levels of selection has not simply been applied to shed light on how to think about the major transitions; an understanding of the major transitions has also been viewed as offering support for specific views within that debate. In particular, much of the literature that conjoins these two issues adopts the view that at least some of the major transitions of evolution can be made sense of only (or best) by positing a process of genic (or gene-like) selection. This supports a version of the view that Dawkins expressed in several well-known passages in *The Selfish Gene*, which claimed that genes "ganged up" for form groups and (finally) us: we are the "lumbering robots" that are the evolutionary result of selfish genes acting in ways to further their own interests.

Although there is much here that is interesting, and some points that are clearly correct, I am more skeptical about some of the inferences drawn here and what is apparently presumed. Part of the reason for being cautious is the relative paucity of hard evidence to support a specific series of major transitions, and so for the necessarily speculative nature of many of the relevant empirical claims. But some of the caution issues from more purely philosophical, conceptual concerns. For example, although it is clear that multicellular, eukaryotic organisms are a relative recent evolutionary innovation, it is much less clear that the same is true of *organisms* per se. Minimally, the claim that genes or gene-like entities preceded organisms in the history of life, and so were the original or at least early units of selection, turns in part on what we think organisms are. My own view is that on the most plausible conception of an organism, according to which an organism is a living thing that forms part of a replicative lineage and has some kind of internal control and external freedom — what I have elsewhere called the *tripartite view of*

organisms (see [Wilson, 2005, ch.3]) — organisms likely appear very early in the
history of life, certainly within the first billion years of that history.

Likewise, the idea that Dawkins expresses mawkishly through his talk of "gang-
ing up" and "lumbering robots" requires closer scrutiny than it has received to
date. Suppose that we waive the preceding issue and grant that selfish replicators
of some kind predate organisms. Since there is more than just one such replica-
tor — in fact, the idea is that there are many of them — there is at least the
possibility that successful replicators are subject to natural selection *as a group*,
rather than individually. And since such replicators likely have some kind of in-
ternal complexity, with internal, specialized parts that perform specific functions,
it is also possible that natural selection could operate on *those parts*, and so only
derivatively on those replicators as entities that have those parts. Thus, we seem
to have just the kind of hierarchy of levels on which selection might operate that
we have in the contemporary debate over the levels of selection, except with selfish
replicators taking the place of organisms.

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