



THE NEEDS OF THE MANY

The idea that natural selection acts on groups, as well as individuals, is a source of unending debate. **Marek Kohn** reports on what the two sides disagree about — and why it matters to them.

If biologists have learnt one thing about evolution over the past 40 years, it is that natural selection does not work for the good of the group. The defining insight of modern Darwinism is that selection ‘sees’ individuals and acts on them through the genes they embody. To imagine otherwise, generations of students have been warned, is to fall into a naive error definitively exposed as such in the mid-1960s.

Yet group selection — the idea that evolution can choose between groups, not just the individuals that make them up — has a higher profile today than at any time since its apparent banishment from mainstream evolutionary theory. And it gets better press, too. This is in part owing to the efforts of David Sloan Wilson, of Binghamton University in New York, who argues that the dismissal of group selection was a major historical error that needs to be rectified. And it does not hurt that he has been joined by Edward O. Wilson, the great naturalist and authority on social insects. They and many others have worked to reposition group selection within the broader theme of selection that acts simultaneously at multiple levels.

The remarkable feature of the debate is not that neither side has managed a conclusive victory; it is that they seem, from the outside, to agree on so much. “Everyone agrees that group



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selection occurs,” says Andy Gardner of the University of Edinburgh, UK. Yet Gardner and his colleagues Stuart West and Ashleigh Griffin have trenchantly criticized¹ David Sloan Wilson’s arguments on this subject — a critique to which David Sloan Wilson responded by initiating a lengthy debate in the community under the heading ‘If the theorists cannot agree...’

There is widespread agreement that group selection and kin selection — the post-1960s orthodoxy that identifies shared interests with shared genes — are formally equivalent. “If you’re talking about altruism, the mathematics that gives you kin selection is also the mathematics that if you slice it another way gives you group selection for altruism,” says Andrew Bourke, who studies social insects at the University of East Anglia, UK. To some researchers, this makes the choice between the two frameworks a matter of perspective. Others doubt that the idea of group selection adds much, if anything, to the understanding obtained from kin selection theory. And for theorists such as Gardner and his colleagues, debates about group selection are largely semantic.

But others see deeper conceptual disagreements, which, according to Samir Okasha, a professor of philosophy at the University of Bristol, UK, “stem from underlying theoretical assumptions about how we should ‘carve up’ nature”.

Okasha, who has written a well-regarded book on the subject², reels off a string of questions. How should a ‘group’ be defined? How should ‘altruism’ and ‘selfishness’ be defined? Does the ‘selfish-gene’ view of evolution conflict with the idea that units of selection can act at different hierarchical levels? Does group selection require that groups engage in a form of reproduction, as individuals do, or just that groups must have differing levels of productivity?

To clarify that last issue, Okasha distinguishes between two kinds of multi-level selection, known in the trade as MLS1 and MLS2. MLS1 focuses on how the division of a population into groups affects the frequencies of different types of individuals in the population. The classic example would be altruism: a population divided into groups may reward altruism more than an undifferentiated one would. MLS2 focuses on the frequencies of the groups themselves. The fittest groups in the MLS1 sense are those that contribute the most individuals to the next generation; the fittest groups in the MLS2 sense are those that contribute the most groups.

It is MLS1 that is implicated in the question at the heart of debates over levels of selection — how altruism can spread through a population. And it is MLS1 that can be taken as equivalent to kin selection. Interest in MLS2 processes has grown more recently, as the question of what levels of selection there are has become

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entwined with that of how those levels evolved; how the advent of multicellularity, say, created an 'organism' level above the level of the cell. In such major evolutionary transitions, smaller units are integrated into larger ones, be it replicating molecules into simple cells or organisms into societies. For a stable new class of entity to emerge, selfish tendencies among their constituent units had to be suppressed at the group level.

Establishing priorities

Charles Darwin saw that what was good for the group might not be good for the individual. In *The Descent of Man* (John Murray, 1871), he observed that "although a high standard of morality gives but a slight or no advantage to each individual man and his children over the other men of the same tribe", it would "certainly give an immense advantage to one tribe over another". However, by the 1960s, many naturalists and biologists had come to see the relationship between what is good for the individual and what is good for the group as unproblematic. They assumed that individuals would subordinate their own interests to those of the species.

Some, though, had doubts. And when the late naturalist Vero Wynne-Edwards argued explicitly that natural selection acted on groups and that individuals restrained their consumption and reproduction for the good of the community³, his book provoked a small but powerful backlash. An under-appreciated alternative model for the same phenomena had recently been proposed by the theorist Bill Hamilton, then at the London School of Economics. Hamilton argued that the spread of altruistic behaviour, which Wynne-Edwards assumed would be selected because of its benefits to the group at large, would in fact be determined by the degree to which altruists shared genes with

their beneficiaries. A quartet of the critics met in Oxford and coined the term 'kin selection' to distinguish Hamilton's theory from Wynne-Edwards's group selection.

Kin selection was easily and powerfully expressed in mathematics, and became the new orthodoxy, its ascendancy cemented in place by its forceful and compelling popularization in Richard Dawkins's *The Selfish Gene* (Oxford Univ. Press, 1976). Group selection might be possible in theory, these thinkers allowed, but it could be ignored in practice. As the theorist George C. Williams declared in his 1966 book *Adaptation and Natural Selection* (Princeton Univ. Press) — a rallying call against group selection that had great influence in America — "the higher levels of selection are impotent".

With the focus on altruism, disadvantageous by definition, the impotence of the higher levels seemed insurmountable. Evolutionary models developed by John Maynard Smith, the most junior member of the Oxford quartet, drove home the point that it would take just one selfish individual to spoil things for everybody. Cheats would inevitably multiply at the altruists' expense. Selection for characteristics that benefited a group at the expense of individuals would be opposed by selection within the group, and selection at that lower level would win.

In their recent writing on the subject⁴, Wilson and Wilson accept the first part of this proposition, but challenge the second. Sometimes selection between groups is weak and sometimes it is very strong, they argue; the balance between levels of selection should be evaluated case by case. Drawing on Darwin's original insight, they boiled down the principles underlying the altruism question to three short sentences. "Selfish-

ness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary."

Gardner, Griffin and West distinguish between the 'old' group selection of Wynne-Edwards and this 'new' version, embedded within a framework of multi-level selection⁴. David Sloan Wilson, however, just sees "one long argument" since the 1960s. Group selection was originally rejected on the grounds that it was implausible rather than on evidence it didn't happen, he says. But the evidence has changed. "It can now be accepted on the best of evidence," says Wilson, "not that it always happens, but it happens some of the time."

Wilson highlights experiments on microbes as being "totally definitive" in this regard — even if the experimenters don't always present their results that way. Benjamin Kerr, of the University of Washington in Seattle, and his colleagues have shown, for example, that "prudent"

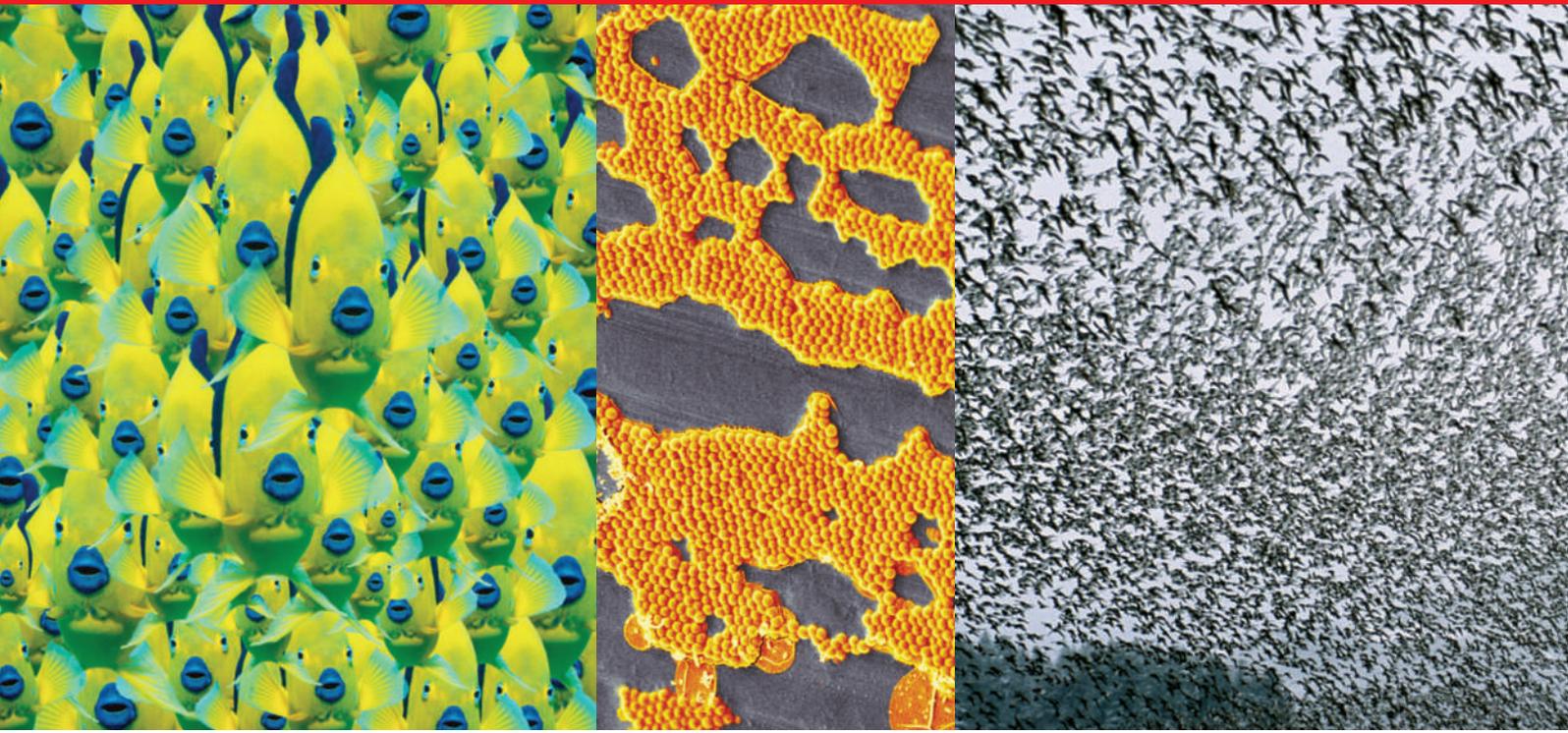
viruses, which do not over-exploit their bacterial hosts, prevail over "rapacious" ones when their ability to disperse and find new prey is restricted⁵. Wilson and Wilson say that the study "elegantly establishes the plausibility of Wynne-Edwards's hypothesis ... without citing Wynne-Edwards or the term group selection".

Kerr is happy to affirm the connection. Wynne-Edwards observed that groups would evolve to conserve their resources for the benefit of their descendants if those descendants lived in the same place — or as he put it, "fall heirs to the same ground". Kerr recalls that in 1964 Maynard Smith discussed the prospects for group selection on this basis using a model that involved imaginary mouse colonies in haystacks⁶. "Our experiment was similar in spirit to Maynard

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— Andy Gardner

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Smith's intent," says Kerr: "to elucidate the conditions favouring the type of restraint Wynne-Edwards wrote about." The intent is indeed similar in that the model and the experiment are attempts to put Wynne-Edwards's verbal arguments into a more rigorous form. But whereas Kerr feels that Wynne-Edwards had a point, Maynard Smith actually wanted to dispose of an argument he regarded as silly. The haystack model established the view that conditions permitting group selection were highly restrictive and unlikely to be encountered in real life.

David Sloan Wilson also points to a study⁷ by Paul Rainey and Katrina Rainey that looked at bacteria cooperating to form a mat on the surface of a liquid medium. The mat is made by mutants that produce larger than normal quantities of a sticky polymer, a trait called 'wrinkly spreader' (WS). Wilson and Rainey say that selection between groups maintains the WS trait, even though the individuals making the polymer incur costs that the other bacteria don't have to pay. But Rainey, who works at the New Zealand Institute of Advanced Study at Massey University in Auckland, says that this is not what the experiment showed. "In fact, given our experimental design, this possibility is more or less ruled out. Kin selection provides the simplest explanation for the evolutionary emergence of the WS type." After all, the fact that daughter cells are physically stuck to their progenitors tends to keep things in the family.

Paul Rainey does not dispute that kin selection is equivalent to multi-level selection of the MLS1 type. Indeed, he has described the emergence of the mats as "a triumph of selection acting at the higher level"⁸ He is quick to point out, however, that this is not group selection of the MLS2 type.

In Rainey's eyes, David Sloan Wilson does not provide an adequate solution to the problem that MLS2 selection needs groups to reproduce

as individuals. Wilson proposes that selection may act on groups identified by shared traits rather than kinship, and that such groups may be small and ephemeral. Rainey considers such models useful for explaining how cooperation is maintained, but doubts that they can account for adaptation at the level of the group, and is especially sceptical that they can explain the evolution of group-level adaptations during a major evolutionary transition such as the integration of cells into multicellular organisms. That requires an explanation for how selection shifts its focus from individuals within groups to groups themselves; from MLS1 to MLS2. Theorists have not paid much attention to this transition, Rainey says. "Samir Okasha refers to this as a grey area. I think it is a great black box!"

Rainey thinks that his mat work could help to open up that black box, and that the individuality groups need for MLS2 selection might develop in such systems. Cells that 'cheat' by enjoying the benefits of being in mats without contributing the chemical that holds them together may in fact have a role at a higher level. Because they can swim away and give rise to new colonies, they have the potential to act as a kind of germ line for colonies that otherwise cannot reproduce. If cheats can work like this they could give the mats the individuality that is needed if natural selection is going to operate at the colony level.

There is a problem here. For a cheat to found a colony, a fresh mutation is needed — WS has to be rediscovered. Rainey, though, is confident that selection can impose design on the process. From the outset, selection will work to optimize the rates at which cheaters arise — groups with too many fall apart. Rainey predicts that with this toe-hold in the process, evolution will

produce systems that can switch between mat forming and swimming stages by changing gene expression, not waiting for *de novo* mutation.

Rainey affirms that as natural selection favours the evolution of cheats whenever cooperation has a cost, selection will act on any population that contains cooperative types at both the individual and the group level. But he cautions that this should not make group selection the default explanation for the evolution of the higher level. His reservation echoes a complaint made by Bourke. "I don't like what I see as an almost systematic downplaying of the evidence in favour of kin selection," Bourke says. "There are lots of other people out there,

working on vertebrates right through to microbes, who find evidence for kin selection."

Bourke states the orthodox case firmly. "Everything is gene selection," he declares. When populations are structured into groups, either kin- or group-selection ideas may

need to be applied. "But it is still gene selection. What matters is the kind of trait being selected for, and the structure of the population it is in." If a group-level selection effect is seen, it will be because of relatedness — a nonrandom association of genes. "I don't see that labelling it group selection adds anything to that insight, which was essentially Hamilton's." Kerr, by contrast, regards kin selection and group selection not as alternative views but as potentially complementary perspectives. "Looking at the same system in different ways can often provide deeper understanding" he says.

Although semantic and conceptual confusion are in ample supply, on their own they don't sustain the controversies over group selection. Core beliefs are at stake, and powerful intuitions are at work.

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— David Sloan Wilson



From an orthodox point of view, group-selection ideas get in the way of an appreciation of the power of natural selection. Gardner says that in principle he is equally happy with kin selection and multi-level selection, but in practice he prefers to work with the former. It is closer to the basic theory of adaptation, connected through Hamilton to Ronald Fisher, one of the architects of the ‘modern synthesis’ that brought together population biology and evolutionary theory in the middle of last century⁹. It keeps the focus on the constantly striving individuals that populate Darwin’s vision.

And the idea of adaptation is to be treated with respect, not carelessly applied at the level of the group, where it doesn’t really work. “I guess the reason I fell in love with biology rather than, say, physics, is that you have this purely mechanical process — natural selection — that gives rise to purpose and function and the appearance of design in the living world,” Gardner says. “The adaptation of individual organisms is an amazing result, and nothing like it occurs elsewhere in the natural sciences. It should be treasured rather than abused.”

Avoiding the implications

Group-selection thinking is perceived by some as not just an abuse of natural selection but also a denial of it. Tellingly, Dawkins chose evolutionary theorist Robert Trivers’s version of this argument for his recent anthology¹⁰ of great science writing. Imagining that evolution works for the greater good looks like a way to avoid the radical implications of natural selection — like claiming that it has little effect, for instance, on the human mind.

For David Sloan Wilson, however, it is the individualistic perspective that betrays influences from outside science. “The concept that self-interest can be a grand explanatory principle seemed to become current in the middle

of the twentieth century, and what happened in evolutionary biology was part of that trend,” he says. “Now, against the background of individualism and self-interest, we have the proposition that our species is the primate equivalent of a beehive or a single organism — so what are the implications of that? That’s not science fiction; that is the growing consensus.”

And this human dimension is ultimately why group selection arouses passions. When Darwin considered selection at group levels, he thought of social insects and of humans. When Hamilton extended the equation derived by his collaborator George Price to accommodate group-selection processes, he combined the discussion with speculations about the adaptive value of warfare as a way for groups to compete — and encountered a reception similar to that of a cat who presents its owner with a half-dead mouse. But that was more than 30 years ago. Today the idea that warfare and altruism are two sides of the same coin — that competition between groups by way of warfare encourages altruism within groups — is widely discussed, as promulgated¹¹ by Samuel Bowles of the Santa Fe Institute in New Mexico.

Robert Boyd of the University of California, Los Angeles, and Peter Richerson at the University of California, Davis, have promoted the idea that selection between cultural groups can be highly effective in humans. Whereas genetic-group models are vulnerable to the fact that individuals can migrate from group to group, reducing the between-group variance on which selection works, cultural models have the advantage that human migrants can adopt the cultures of the groups to which they migrate. People intuitively recognize their species as ‘groupish’ and realize that models of group evolution can have implications for the understanding of human societies.

That is part of their attraction for Joel Peck,

whose modelling studies at the University of Sussex, UK, suggest that the conditions under which group selection could work might not be as restrictive as his late colleague Maynard Smith had implied. Underlying his interest in the life sciences, Peck says, is a desire to be involved in positive social change. “Group selection is one of the topics within evolutionary biology that is most directly about how societies change.” He notes that in the major transition that unified the ancestors of the mitochondrial and nuclear genome into the eukaryotic cell, the two ancestors’ interests were almost entirely united. As well as being fascinating in themselves, processes such as these “may give us hints about how to unify the interests of different human individuals, or groups of individuals”, he says.

Wilson suggests that in the light of group selection, the human species displays unity; Peck hopes that group selection may show humans how to achieve unity. Ultimately, their science is about the good of the species. ■

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See also pages 281 and 295, and online at www.nature.com/darwin.