Survival of
the selfless

Pitching in boosts the success of the entire community

"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... an advancement in the standard of morality will certainly give an immense advantage to one tribe over another."

In this famous passage from *The Descent of Man*, published in 1871, Charles Darwin perceived a fundamental problem of social life, and a possible solution. The problem is that for a society to function, its members must perform services for each other. Yet members who behave "for the good of the group" often put themselves at a disadvantage compared with more selfish members of the same group. If so, then how can altruism and other prosocial behaviours evolve?

The solution, according to Darwin, is that groups containing mostly altruists have a decisive advantage over groups containing mostly selfish individuals, even if selfish individuals have the advantage over altruists within each group.

Darwin's insight would seem to provide the basis for understanding the evolution of social behaviour, a field known as sociobiology. That's not what happened, however, as anyone familiar with the subject knows. During the 1960s evolutionary biologists, while agreeing with Darwin's logic, decided that between-group selection – the evolutionary force favouring altruism – is almost invariably weak compared with within-group selection, the evolutionary force favouring selfishness. As George C. Williams put it in his 1966 book *Adaptation and Natural Selection*, "group-related adaptations do not, in fact, exist".

The consensus that formed in the 1960s turned group selection into a pariah concept, taught primarily as an example of how not to think. Interpreting behaviours as "for the good of the group" was said to be just plain wrong. Inclusive fitness theory (also called kin selection), evolutionary game theory and selfish gene theory were all developed to explain the evolution of apparently altruistic behaviours in individualistic terms, without invoking group selection.

This received history is still taught in many textbooks and popular accounts of evolution, but a closer look reveals a field in disarray. In modern sociobiological literature it is possible to find the following contradictory positions: nothing has changed since the 1960s; group selection is an important evolutionary force after all; there is a new concept of group selection that bears little relationship to the old version; and no mention of group selection, as if the idea never existed.

We think that sociobiology's theoretical foundation can be as clear today as it appeared to be on the basis of the 1960s consensus, but only if we revisit the pivotal events of that period. Why was group selection rejected so decisively? Do the arguments against group selection remain valid after 40 years of subsequent research? What are the consequences of acknowledging that group selection might be a significant evolutionary force after all?

To begin with the third question, the consequences of regarding evolution as a multilevel process, with higher-level selection often overriding lower-level selection, are profound. The 1960s consensus was essentially a denial of the concept of society as an organism. It claimed traits can evolve for the good of the individual, but not for the good of the group. Turning individuals into a privileged level of the biological hierarchy was a momentous event in the history of evolutionary thought. If it was unwarranted, then its retraction is equally momentous.

Multilevel selection theory is relevant to any trait that affects the fitness of other individuals in addition to the individual possessing it, which includes but goes far beyond the stock example of altruism. The theory can help explain the origin and major transitions of life, the structure of animal societies and multi-species ecosystems, and human evolution – even including the rise and fall of empires and the nature of religion.

The case against group selection during the 1960s rested upon three arguments: it is theoretically implausible as a significant evolutionary force; there is no solid empirical evidence for it; and there are robust theoretical alternatives. All these arguments ▶

For half a century biologists have tied themselves in knots trying to explain how social traits like altruism evolve. The answer has been staring us in the face all along, say **David Sloan Wilson** and **Edward O. Wilson**

have failed in the face of subsequent research.

The first mathematical and computer models of multilevel selection made it seem that between-group selection could prevail against within-group selection only in very unlikely circumstances. Yet these early models were published before the desktop computing revolution, the study of complex interactions, and the appreciation of such things as social control and gene-culture coevolution. It should surprise no one that this initial assessment of group selection must be revised in the light of decades of further research.

For the greater good

For example, the early models assumed that genes code directly for behaviours. In such models, all the members of a group will behave in the same way only if they share the same gene. In reality, the relationships between genes and behaviour are far more complex. Behavioural variation between groups can be large even when genetic variation between them is small – for instance, when members within a group imitate each other or impose distinct social norms. This matters because the larger the difference between groups, the more likely group selection is to prevail, as later models show.

A model published in 2004 even confirms the plausibility of a hypothesis proposed by zoologist V. C. Wynne-Edwards in 1962; that animals might evolve to reduce their fertility to avoid overexploiting their resources (*Proceedings of the National Academy of Sciences*, vol 101, p 11019). In general, the latest models do not show that between-group selection always prevails against within-group selection, but they do show that between-group selection cannot be ignored.

Group selection might now be theoretically plausible, but does it actually happen? Numerous lines of empirical evidence suggest that the answer is yes. Virtually every multilevel selection experiment in the laboratory shows that between-group selection is a potent evolutionary force. Some of the best evidence comes from microbes, in part because they are such good systems for ecological and evolutionary research spanning many generations.

In one study last year, groups of bacteria and bacteria-infecting viruses were grown in 96 separate wells on plates. "Migration" between the groups was executed by a robot transferring small quantities of liquid

Ants cooperate en masse to benefit their colony, while individual lions risk death to defend their pride's territory

between wells according to prespecified schemes. Under biologically plausible migration schemes, "prudent" virus strains were able to outcompete more "rapacious" strains, despite their selective disadvantage within each group, as proposed by Wynne-Edwards and predicted by the 2004 model (*Nature*, vol 442, p 75).

Field studies are seldom as precise as lab experiments, yet they too provide convincing evidence for group selection. The following description of territorial defence in lions corresponds closely to Darwin's conjecture about human morality: "Female lions share a common resource, the territory; but only a proportion of females pay the full costs of territorial defence. If too few females accept the responsibilities of leadership, the territory will be lost. If enough females cooperate to defend the range, their territory is maintained, but their collective effort is vulnerable to abuse by their companions. Leaders do not gain additional benefits from leading, but they do provide an opportunity for laggards to gain a free ride" (*Science*, vol 269, p 1260). In this field study, extensive efforts to find a

and thus can only evolve by virtue of between-group selection. In other words, every major theoretical "alternative" to group selection includes Darwin's logic of multilevel selection within its own structure.

William Hamilton was one of the first to come to this realisation. In the 1960s, he developed the theory of inclusive fitness, or kin selection, which suggests that behaviours such as altruism arise because, by helping relatives survive and reproduce, individuals help their own genes in the bodies of others.

In the 1970s, Hamilton encountered the work of George Price, who had derived a formula for partitioning selection into its within and between-group components. When Hamilton related his inclusive fitness theory to Price's equation, he realised that altruistic traits are disadvantageous within every kin group and evolve only because kin groups with more altruists contribute more genes to the total gene pool. Hamilton's key insight about the importance of genetic relatedness remained valid, but his previous

selection in the total population. It is bizarre (in retrospect) to interpret this as an argument against group selection. Both Williams and Dawkins eventually acknowledged their error, but it is still common to find the "gene's-eye view" of evolution presented as a drop-dead argument against group selection.

The old arguments against group selection have all failed. It is theoretically plausible, it happens in reality, and the so-called alternatives actually include the logic of multilevel selection. Had this been known in the 1960s, sociobiology would have taken a very different direction. It is this branch point that must be revisited to put sociobiology back on a firm theoretical foundation.

Accepting multilevel selection has profound implications. It means we can no longer regard the individual as a privileged level of the biological hierarchy. Adaptations can potentially evolve at any level, from genes to ecosystems. Moreover, the balance between levels of selection is not fixed but can itself evolve – and when between-group selection

"Animals can even evolve lower fertility to avoid overexploiting resources"

within-group advantage for territorial defence failed, leaving between-group selection as the most likely alternative.

What about the other theories? Even though they were initially developed as alternatives to group selection, in retrospect they are nothing of the sort. All evolutionary models of social behaviour must make certain assumptions to remain biologically realistic. First, they must assume the existence of multiple groups, because social interactions almost invariably take place among small fractions of the total population. In n-person evolutionary game theory, for example, n refers to the size of the group within which social interactions occur.

Second, all models must identify the appropriate groups for any particular trait. This is because the fitness of an individual depends upon the others with whom it interacts, which must be appropriately specified to arrive at the right answer. If individuals interact in groups of five, then two-person game theory won't do.

Third, when fitnesses are compared within and among groups, the behaviours labelled cooperative or altruistic are almost invariably selectively disadvantageous within groups

interpretation of inclusive fitness theory as an alternative to group selection was wrong, as he freely acknowledged.

A similar realisation dawned for the concepts of selfish genes and extended phenotypes, which Richard Dawkins had developed as arguments against group selection. The concept of extended phenotypes is that genes can have effects that extend beyond the body of the individual, such as a beaver dam. Genes that cause beavers to build dams are still at a local disadvantage compared with genes in beavers in the same pond that don't build dams. So the concept of extended phenotypes does not solve the problem that Darwin identified, except through between-group selection.

The concept of genes as "replicators" and "the fundamental unit of selection" averages the fitness of genes across all contexts to predict what evolves in the total population. The whole point of multilevel selection theory, however, is to ask whether genes can evolve on the strength of between-group selection, despite a selective disadvantage within each group. When this happens, the gene favoured by between-group selection is more fit overall than the gene favoured by within-group

becomes sufficiently strong compared with within-group selection in a given population, a major transition occurs and the group becomes a higher-level organism in its own right.

Major transitions have occurred repeatedly during the history of life, perhaps beginning with the origin of life itself as groups of cooperating molecular reactions. Other examples include complex cells, which arose from groups of simpler cells, and multicellular organisms, which arose from groups of complex cells. Ironically, the rejection of group selection made it heresy to think of groups as being like organisms. Now it has emerged that the organisms of today are literally the groups of past ages.

The evolution of "eusocial" colonies like those of bees falls squarely within the paradigm of major transitions. These colonies were widely regarded as superorganisms until the rejection of group selection made this interpretation inadmissible. Kin selection then became the primary explanation for eusociality, as if this was an alternative to colony-level selection. Hamilton's original theory claimed that the extra-strong altruism exhibited by eusocial insects could be ▶

explained by the extra-high relatedness of workers and queens, due to the unusual system of reproduction in ants, bees and wasps (but which is not found in termites).

As the decades passed, it became clear that kin selection was not a denial of group selection. Most traits that increase colony fitness are not selectively advantageous within colonies and evolve only by between-colony selection. Some traits do evolve by within-colony selection, but these are forms of selfishness that decrease colony fitness. Moreover, relatedness is no longer considered the decisive factor in the evolution of eusociality. Many factors influence the balance between levels of selection, and eusociality can evolve with only modest genetic variation between groups.

Human evolution, too, has all the hallmarks of a major transition. Anyone who studies humans must acknowledge our groupish nature and the importance of between-group interactions. Explaining these obvious facts without invoking group selection involves needless contortions.

According to anthropologist Christopher Boehm, a key event in early human evolution was a form of enforced egalitarianism that made it difficult for some individuals to dominate others within their own group. Suppressing fitness differences within groups is the hallmark of a major evolutionary transition, enabling between-group selection to become the dominant evolutionary force. The human major transition was a rare event, but once accomplished, our ability to function as team players in coordinated groups enabled our species to achieve worldwide dominance, replacing other types of hominid and a

range of other species along the way.

A common scenario for human evolution begins with the evolution of sophisticated cognitive abilities, such as a "theory of mind", which in turn enabled widespread cooperation. However, a 2005 review suggests it would be more reasonable for the sequence to be reversed (*Behavioral and Brain Sciences*, vol 28, p 675). Our capacities for symbolic thought and communication are communal activities that probably came after a shift in the balance between levels of selection.

Only when we could trust our social partners to work toward shared goals could we rely upon them to share meaningful

"It's heresy to view groups as organisms, yet today's organisms are yesterday's groups"

information. Our ability to function as team players is reflected in anatomical features such as the whites of the human eye, which turn it into an organ of communication, and in basic cognitive skills such as the ability to point things out to others and to laugh in a group context, in addition to more advanced cognitive and cultural abilities.

Group selection is an important force in human evolution partly because cultural processes can create variation between groups, even when they are composed of large numbers of unrelated individuals. A new cultural "mutation" can quickly spread within a group, causing it to be very different from other groups and providing a decisive edge in direct or indirect between-group competition.

Group selection for genetic and cultural

traits can explain our groupish nature at face value. Of course, within-group selection has only been suppressed, not entirely eliminated. Thus multilevel selection, not group selection alone, provides a comprehensive framework for understanding human sociality.

These ideas might explain the broad sweep of recorded history in addition to the remote past. In his book *War and Peace and War: The rise and fall of empires*, biologist Peter Turchin argues that virtually all empires arose in areas where major ethnic groups came into contact with each other. Intense between-group conflict acted as a crucible for the cultural evolution of extremely cooperative societies, which then expanded at the expense of less cooperative societies to become major empires. Their very success was their undoing, however, as cultural evolution within such empires led to myriad forms of exploitation, free-riding and factionalism. Turchin has marshalled an impressive amount of evidence to support his thesis, with profound implications for understanding conflict and cooperation in modern human societies.

It is difficult to revisit an important decision that has been made and acted upon, but that is precisely what needs to be done in the case of the rejection of group selection in the 1960s. This is not a return to the sort of naive group selectionism that interprets all traits as "for the good of the group". On the contrary, modern multilevel selection theory affirms key parts of the 1960s consensus, including the idea that group-level adaptations require group-level selection and tend to be undermined by lower levels of selection. It is only the categorical rejection of group selection that must be reconsidered.

When Rabbi Hillel was asked to explain the Torah in the time that he could stand on one foot, he replied: "Do not do unto others that which is repugnant to you. Everything else is commentary." In closing, we offer this one-foot summary of sociobiology's new foundation: "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary." ●

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Groups of unrelated humpbacks hunt together