



Altruism seems to be an intrinsic part of being human. But why?

3 A COMPLEX HISTORY

In the first part of the 20th century, the idea of group selection was accepted by most evolutionary biologists. In fact, it was embraced rather too eagerly and uncritically. Influenced by the lingering idea that nature was the creation of a benign god, many biologists thought that nature was adaptive at all levels - what is good for individuals must be good for groups, and so on. As a 1949 biology textbook put it: "The probability of survival of individual living things, or of populations, increases to the degree to which they harmoniously adjust themselves to each other and to their environment."

While some biologists realised that the evolution of prosocial traits would often be opposed by selection within groups, it was frequently assumed that group selection would usually prevail - a position that has come to be known as "naive group selectionism". It was typified by British zoologist Vero C. Wynne-Edwards, who in 1962 proposed that organisms evolve to regulate their population size to avoid overexploiting their resources.

When the idea of group selection came under scrutiny in the 1960s, naive group selection was rightly rejected. But the backlash did not stop there. Based on arguments about how plausible it is, rather than actual experiments and studies, a consensus formed that between-group selection is almost invariably weak compared with within-group selection. As evolutionary biologist George C. Williams put it in his highly influential book *Adaptation and Natural Selection*: "Group-related adaptations do not, in fact, exist."

This was a major change in thinking, and the rejection of group selection came to be regarded as a watershed in the history of evolutionary thought. For the ensuing decades, most evolutionary biologists interpreted social adaptations as forms of self-interest that could be explained without invoking group selection. In his 1982 book *The Extended Phenotype*, Richard Dawkins went so far as to compare efforts to revive group selection to the futile search for a perpetual motion machine.

Zoologist Richard Alexander went a step further, calling for a radical re-interpretation of morality. "I suspect that nearly all humans believe it is a normal part of the functioning of every human individual now and then to assist someone else in the realization of that person's own interests to the actual net expense of those of the altruist," he wrote in his 1987 book *The Biology of Moral Systems*. "What this greatest intellectual revolution of the century tells us is that, despite our intuitions, there is not a shred of evidence to support this view of beneficence, and a great deal of convincing theory suggests that any such view will eventually be judged false."

Yet the following decades saw a revival of group selection, which is firmly re-established. "Everyone agrees that group selection occurs," stated evolutionary biologist Andrew Gardner in 2008. What brought about such a remarkable change?

2 A SIMPLE SOLUTION

Darwin realised that the problem could be solved if there was selection at a group level, not just at an individual level.

If groups composed of individuals who behave in a more prosocial way outcompete groups of individuals who behave in a less prosocial way, then traits that are for the good of the group will evolve.

In short, natural selection between groups will counteract the costs of prosocial behaviour to individuals within groups. Or as Darwin put it: "...an advancement in the standard of morality will certainly give an immense advantage to one tribe over another. A tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to aid one another, and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection."

Darwin's insight was the starting point for the modern theory of multilevel selection. According

to this theory, biological systems are a nested hierarchy of units, from genes within individuals, individuals within groups, groups within a population and even clusters of groups.

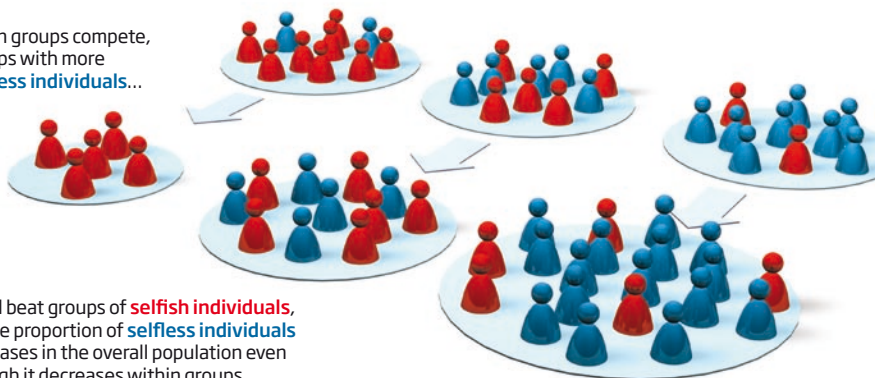
At every level, the traits that maximise relative fitness within a unit are unlikely to maximise the fitness of the unit as a whole. Genes that outcompete other genes within the same organism are unlikely to benefit the whole organism. Individuals that outcompete other individuals within their group are unlikely to benefit the group as a whole, and so on. The general rule is: "The evolution of adaptations at each level of the hierarchy requires a process of natural selection at that level and tends to be undermined by selection at lower levels."

When individuals within a group compete...

... **selfish individuals** will produce the most offspring and come to dominate the group



When groups compete, groups with more **selfless individuals**...



...will beat groups of **selfish individuals**, so the proportion of **selfless individuals** increases in the overall population even though it decreases within groups

RIGHT: YADUDEVIVANBERGER/EVOLVE ABOVE: IRENE LAXMI CORBIS

AN IDEA REJECTED

The theory of natural selection clearly explains how features such as the sharp teeth of the tiger, the thick fur of the polar bear and the camouflage of the moth evolved. When the ancestors of polar bears colonised the Arctic, for instance, those with thicker fur would have had a better chance of surviving and producing more offspring than those with thinner fur. Many social species, however, have traits that benefit others or the group as a whole, often to their own cost. It is much harder to see how such traits evolve. Darwin proposed that it was a result of the survival of the fittest groups, rather than the fittest individuals. Today, most evolutionary biologists think he was right, but group selection, as this idea is known, has a long and complicated history

“The idea of group selection was initially accepted too eagerly and uncritically”

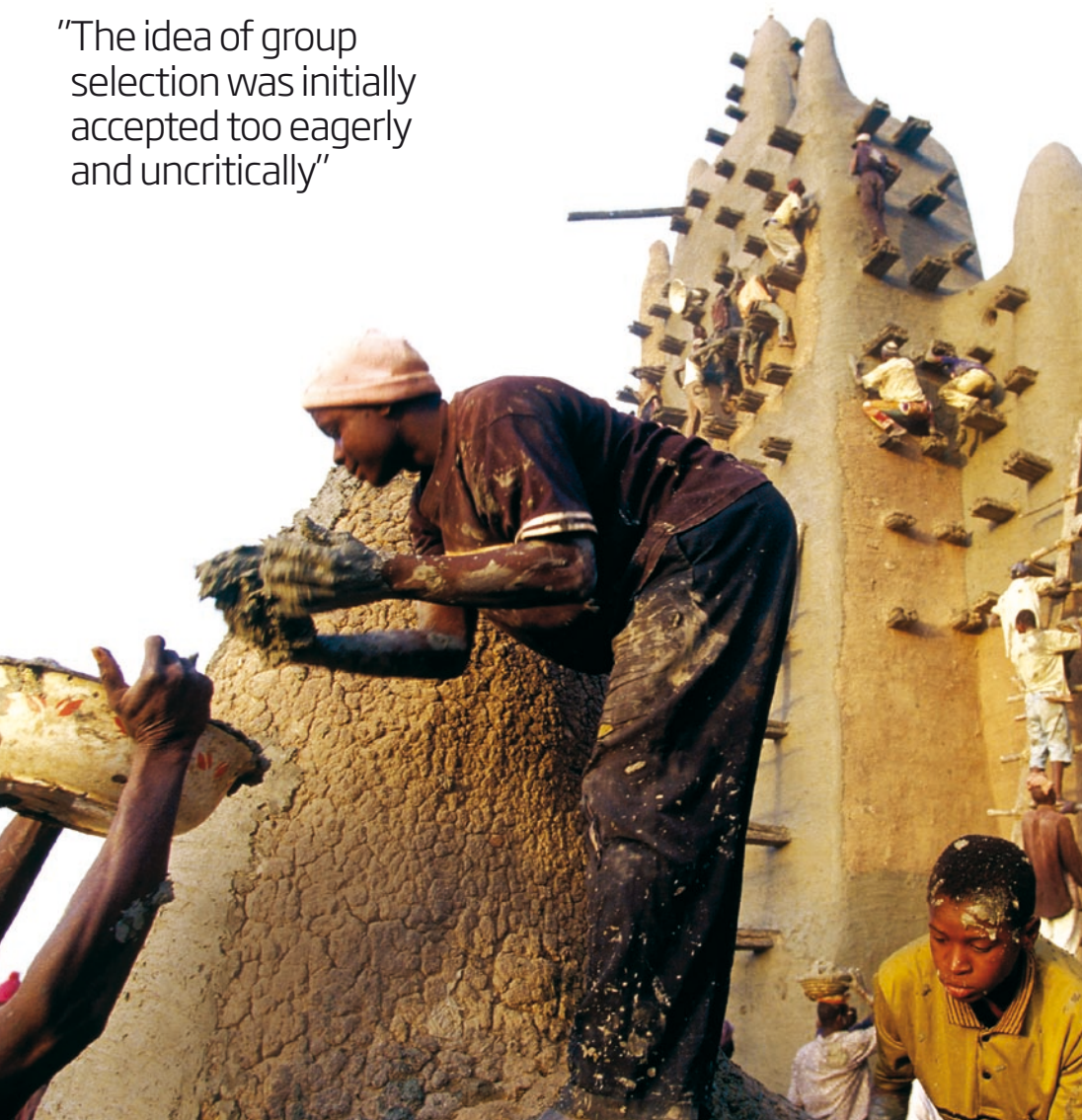
1 THE PROBLEM

Wolves share food with other members of the pack. Vervet monkeys make alarm calls that risk attracting a predator's attention to themselves. Bees sacrifice themselves to defend a hive. But why? It is hard to see how such traits evolve by natural selection because individuals that behave in these ways would seem to have far less chance of surviving and producing offspring than more selfish members of the same group.

Darwin himself was acutely aware that the suicidal sting of the honeybee and most of the virtues associated with human morality, such as bravery, honesty and charity, posed a severe challenge to his theory. “It must not be forgotten that... a high standard of morality gives but a slight or no advantage to each individual man and his children over other men of the same tribe,” he wrote in *The Descent of Man*.

The question, then, is how can traits that are oriented toward others or one's group as a whole - known as “prosocial” traits - evolve when they appear to reduce the relative fitness of individuals within groups?

Groups that can work together successfully will have an advantage over other groups



INCLUSIVE FITNESS, SELFISH GENES AND ALL THAT

The rejection of group selection in the 1960s meant biologists had to come up with alternative theories to explain the evolution of social adaptations. Several were put forward, including inclusive fitness theory - also known as kin selection - selfish gene theory and evolutionary game theory. In retrospect, all of these theories can be shown to invoke group selection after all.

William D. Hamilton, who came up with inclusive fitness theory in the 1960s, was among the first to realise this after encountering the work of theoretical biologist George Price in the 1970s. Hamilton's formula calculated when an altruistic gene evolves in the whole population but did not keep track of what happens in any particular group. In contrast, Price's formula divided evolution in the whole population into within and between-group components. When Hamilton viewed his own theory through the lens of Price's formulation, he saw that altruism is usually a disadvantage within groups and evolves only by virtue of between-group selection, exactly as Darwin envisioned.

This is true even when groups are composed of relatives. Group selection can occur only when there is variation among groups, and since groups of relatives are more likely to differ from each other than groups of unrelated individuals, relatedness increases the strength of between-group selection compared with within-group selection.

As Hamilton recalls his realisation: "Through a 'group-level' extension of [Price's] formula I now had a far better understanding of group selection and was possessed of a far better tool for all forms of selection acting at one level or at many than I had ever had before." Unfortunately, other biologists did not share this insight: while Hamilton's 1960s work was much cited, his revised formulation was largely ignored.

Recently, though, it has become clear that all evolutionary theories of social behaviour implicitly assume that social interactions take place in groups that are small compared with the population as a whole. Also, that the prosocial behaviours variously labelled "cooperation" or "altruism" are disadvantageous to individuals and evolve only by virtue of the differential contribution of groups to the total gene pool. In other words, each theory relies upon the simple logic of multilevel selection.

The reason that this was not obvious from the beginning is because these theories only tracked what evolves in the whole population without simultaneously tracking natural selection within single groups. It is impossible to evaluate whether group selection needs to be invoked without tracking natural selection at each relevant level of the biological hierarchy.

"A group can only evolve into a individual when between-group selection is the primary force"

MAJOR TRANSITIONS

Until the 1970s, evolution was thought to take place entirely on the basis of the accumulation of mutations over many generations. Then biologist Lynn Margulis proposed that complex cells did not evolve by small mutational steps from bacterial cells, but from symbiotic associations of different kinds of bacteria that became higher level organisms in their own right.

In the 1990s, evolutionary biologists John Maynard Smith and Eors Szathmari proposed that similar major transitions occurred throughout the history of life, including the evolution of the first cells, the advent of multicellular organisms and the development of social insect colonies (see diagram, right). They even suggested it could explain the origin of life, with groups of cooperating molecular reactions coming together to create the first life forms. The realisation that evolution takes place not only by small mutational steps but also by groups of organisms turning into higher-level organisms represents one of the most profound developments in evolutionary thought. Today's individuals are yesterday's groups.

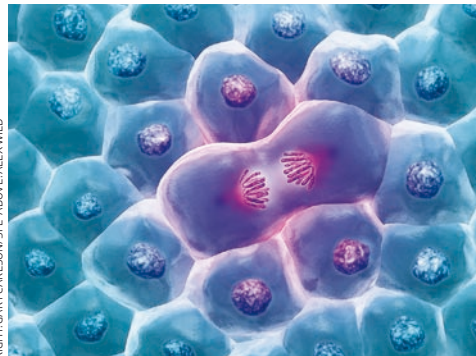
For a major evolutionary transition to occur, there has to be a shift in the balance between within-group

and between-group selection. A group can only turn into an individual when between-group selection is the primary evolutionary force, and this in turn can happen only when mechanisms evolve that suppress selection within groups. The rules of meiosis, for example, ensure that all genes on the chromosomes have an equal chance of being represented in the gametes. If genes can't succeed at the expense of each other, then the only way to succeed is collectively as a group.

Major evolutionary transitions are rare events in the history of life but they have momentous consequences, as the new super-organisms become ecologically dominant. Eusociality in insects only originated about a dozen times - including in ants, bees, wasps and termites - but insect colonies comprise well over half the biomass of all insects.

These transitions are never complete as selection within groups is only suppressed, not eliminated. Some genes do manage to bias the rules of meiosis in their favour. Increasingly, cancer is studied as an evolutionary process that takes place within individuals, causing some genes to succeed at the expense of others, with tragic results for the group as a whole.

When cells stop cooperating, cancer can result



RIGHT: CARY CARLSON/SPL. ABOVE: ALEX WILD

The revival of group selection is a result of better models and experimental studies showing it is indeed possible, as well as the realisation by biologists that today's individuals are yesterday's groups. In addition, it has become clear that the supposed alternative explanations for the evolution of prosocial behaviour are actually equivalent to group selection

THE EVIDENCE FOR GROUP SELECTION

The rejection of group selection was based on the claim that, in practice, selection within groups always beats selection between groups. However, recent studies have shown that traits can evolve on the strength of between-group selection, despite being disadvantageous for individuals within each group.

Take the water strider *Remigis aquarius*, an insect species that skates on the surface of quiet streams. Males vary greatly in their aggressiveness toward females, and lab studies by Omar Tonsi Eldakar and colleagues, including me, show that within any group,

aggressive males outcompete non-aggressive males for females.

However, the aggressive males also prevent females from feeding and can injure them, which results in a group with lots of aggressive males producing fewer offspring than groups with fewer aggressive males. Variation among groups is magnified by females fleeing groups containing lots of aggressive males and aggregating in groups with non-aggressive males. So our studies show that between-group selection is essential for maintaining non-aggressive males in the population (*Evolution*, vol 64, p 3183).

In another experiment, a team of microbiologists headed by Benjamin Kerr at the University of Washington in Seattle grew *E. coli* in wells on plates. They then infected some of them with a virus, and mimicked the natural spread of viruses by using robotic pipettes to transfer them between wells.

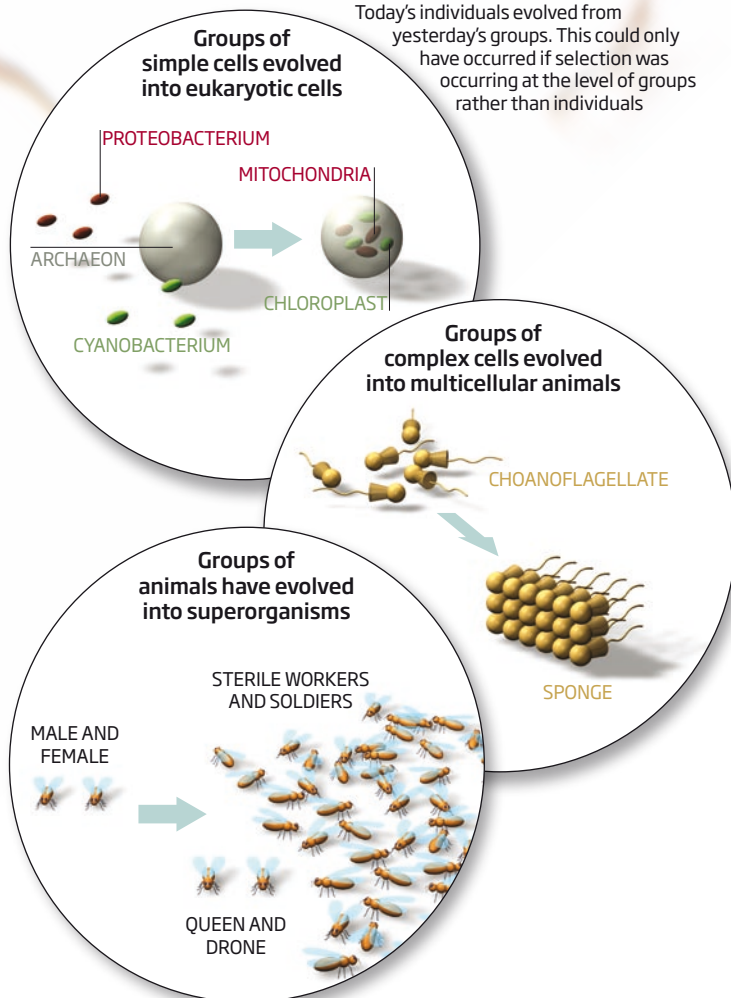
The team found that in some circumstances, a "prudent", slow-growing strain of the virus was more successful than a "rapacious", fast-growing strain. The rapacious strain often killed off all the bacteria in a well - and therefore itself - before it had a chance to spread. The prudent strain persisted for longer and so was more likely to get a chance to colonise other wells.

In this way, the prudent strain could remain in the population even though it was always outcompeted by the rapacious strain when both were present in a single well. In other words, it was only on the strength of between-group selection that the prudent strain survived (*Nature*, vol 442, p 75).

The conditions of this experiment closely resemble a scenario proposed by Vero C. Wynne-Edwards in the 1960s for the evolution of reproductive restraint in many species. Such restraints might not evolve in all species, but as this experiment shows, it is plausible that they can evolve in some species in some circumstances.

These two experiments involve very different spatial and temporal scales, but they embody the key problem and simple solution of group selection: the traits that benefit the whole group are not advantageous for individuals within the group and so require an additional layer of natural selection to evolve.

Today's individuals evolved from yesterday's groups. This could only have occurred if selection was occurring at the level of groups rather than individuals





The spread of cultural traits such as farming has reshaped the planet

CULTURAL GROUP SELECTION

Cultural evolution is a multilevel process, just like genetic evolution. Socially transmitted traits can spread because they benefit whole groups, or give individuals an advantage within groups, or because they act like parasites and do not benefit individuals or groups. Examples can be found at all levels but group-level selection appears to be an even stronger force for human cultural evolution than for human genetic evolution.

With genetic evolution, a mutant gene starts out at a low frequency within single groups. It takes many generations for a beneficial mutation to become common in a group and eventually in the total population. With cultural evolution, however, a new trait can become common within a group in less than a generation. Cultural variation between groups can even be maintained in the presence of migration, as long as individuals entering a group abandon their old customs and adopt the new ones. Finally, almost any trait can be established within groups by norms enforced by rewards and punishments. Group selection for norms that are stable within each group can be more powerful than group selection for traits that are selectively disadvantageous within groups.

Cultural group selection has resulted in the development of cooperative human societies several orders of magnitude larger than the pre-agricultural societies that existed only 15,000 years ago. Human history provides a detailed record of multilevel cultural evolution, including the expansion of the most cooperative and coordinated cultures and the collapse of cultures plagued by divisions. This dynamic might even explain the rise and fall of empires throughout human history, as ecologist Peter Turchin details in his 2005 book *War and Peace and War*.

Darwin's problem is encountered at every scale of human society: from the smallest group to the global village, the behaviours that maximise relative advantage within a social unit tend to undermine the welfare of the unit as a whole. Establishing prosociality at a large scale requires a process of selection at that scale - whether a raw process of variation and selection or a more deliberative process of selecting practices by intentional planning.



"Just like genetic traits, cultural traits can spread when they benefit groups"



A NEW VIEW OF HUMAN EVOLUTION

Our ability to cooperate closely with other group members and to suppress cheats means that selection at the group level rather than the individual level has been an exceptionally strong force during human evolution. It may have played a crucial role in shaping both our genes and our culture

THE HUMAN TRANSITION WAS A RARE AND MOMENTOUS EVENT

Converging lines of evidence suggest that human genetic evolution represents a major evolutionary transition and one which accounts for our uniqueness among primates. In most primates, members of a group cooperate to a degree, but there is also intense competition within groups for social dominance. In contrast, most extant hunter-gatherer societies are vigilantly egalitarian, suppressing individuals who try to benefit themselves at the expense of others. As we have seen, the suppression of within-group selection is the hallmark of a major transition.

Vigilant egalitarianism probably arose early in human evolution and was a precondition for the other attributes that make us so distinctive as a species.

This is an example of gene-culture co-evolution in which it is impossible to say which came first.

Our closest primate relatives are also highly intelligent but in a way that appears predicated on mistrust. In contrast, human intelligence appears to be based on trust among members of a group, making shared awareness and coordination of activities advantageous for so many generations that they are now instinctive in our species, as

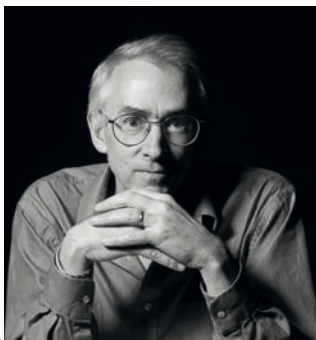
developmental psychologist Michael Tomasello has argued. Even dogs, which have been co-evolving with humans for tens of thousands of years, surpass most primates with respect to adaptations based on trust (*Science*, vol 298, p 1634).

As with other major evolutionary transitions, the human transition was a rare event that had momentous consequences. As the only primate super-organism, we have spread over the globe, occupied hundreds of ecological niches and displaced countless other species - for better or for worse. The human transition is also by no means complete. Within-group selection is only suppressed, not stopped, so constant vigilance is needed to maintain prosocial behaviour. Indeed, many aspects of human morality can be interpreted as the apparatus that evolved to make group selection a strong force in our species.

DAVID ROGERS/GETTY; BELOW RIGHT: IAN WALDE/GETTY

Punishing cheats is a key part of maintaining cooperation and keeping groups competitive





David Sloan Wilson

David Sloan Wilson is a professor of biology and anthropology at Binghamton University in New York state. He is best known for his work on multilevel selection, and has played a major role in reviving the idea of group selection after its dismissal in the 1960s.



A NEW CONSENSUS

Darwin's problem is an unavoidable fact of life for all species, including our own: prosocial adaptations usually put individuals at a disadvantage relative to other members of their group. The only way for them to evolve is if there is another layer to the process of natural selection. That layer is group selection. More prosocial groups robustly outcompete less prosocial groups, which means a prosocial trait's between-group advantage can make up for its disadvantage within groups. It's that simple.

If scientific history had taken a different path, multilevel selection could have become the theoretical foundation for studying the evolution of social behaviour, or sociobiology. Instead, after the 1960s biologists tried to explain all social adaptations as forms of self-interest. When an entire scientific discipline decides something is wrong, it is difficult to persuade people to reconsider their position.

Today, though, there is near-universal agreement among those familiar with the subject that the wholesale rejection of group selection was mistaken and that the so-called alternatives are nothing of the sort. Some, such as William Hamilton, reached this conclusion as early as the 1970s, but decades were required for others to follow suit. However, many people who do not directly study the subject, including many biologists, have got the impression that group selection was conclusively disproved and that nothing has changed since. As a result, there is widespread confusion.

It is probably not an accident that the

individualistic swing in evolutionary theory coincided with similar swings in economics, the human social sciences and western culture at large. While evolutionists were interpreting all social adaptations as varieties of self-interest, economists were explaining all human behaviour as individual utility maximisation, and British prime minister Margaret Thatcher was declaring that "there is no such thing as society – only individuals and families".

Science does not take place in a vacuum. Just as Darwin and his contemporaries were influenced by Victorian culture, we should be prepared to acknowledge – and correct for – the influence of a highly individualistic culture on the theories put forward during the second half of the 20th century.

The new consensus states definitively that the individual organism is not a privileged level of the biological hierarchy. The harmony and coordination associated with the word "organism" can exist at any level and individuals can lose these properties when selection takes place within them, such as when cancers evolve. Social groups can become organisms, and organisms are highly regulated social groups – not just figuratively but literally.

Group selection has been an exceptionally strong force in human genetic and cultural evolution. Accepting it at face value and exploring its consequences will have implications for all branches of the biological and human-related sciences, from the origin of life to the regulation of human society at large spatial and temporal scales.

RECOMMENDED READING

The Neighborhood Project: Using evolution to improve my city, one block at a time by David Sloan Wilson (Little, Brown, 2011)

Evolution for Everyone by David Sloan Wilson (Delta, 2007)

Why We Cooperate by Michael Tomasello (MIT Press, 2009)

Why Humans Cooperate: A cultural and evolutionary explanation by Joseph Henrich and Natalie Henrich (Oxford University Press, 2007)

The Price of Altruism: George Price and the search for the origins of kindness by Oren Harman (Norton, 2010)

Evolutionary Restraints: The contentious history of group selection by Mark Borrello (University of Chicago Press, 2010)

WEBSITES

David Sloan Wilson's blog
Scienceblogs.com/evolution

Evolution Institute blog
Evolution-institute.org

Evolution: This view of life
Thisviewoflife.com

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EVOLUTION OF SELFLESS BEHAVIOUR

David Sloan Wilson

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