

COMMENT

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Altruism researchers must cooperate

Biologists studying the evolution of social behaviour are at loggerheads. The disputes — mainly over methods — are holding back the field, says **Samir Okasha**.

Last month, 30 leading evolutionary biologists met in Amsterdam to discuss a burgeoning controversy. The question of how altruistic behaviour can arise through natural selection, once regarded as settled, is again the subject of heated debate.

The question dividing biologists is the degree to which inclusive fitness theory, or kin selection, explains the evolution of altruism — in which an animal provides a benefit to another at a cost to itself. This theory, that natural selection can sometimes favour animals that behave altruistically towards relatives, has dominated empirical work on social behaviour since it was devised by W. D. Hamilton in the 1960s and 1970s¹. Yet some biologists are

now calling for a radical rethink, arguing that kin selection is theoretically problematic, and has insufficient empirical support, and that alternative models better account for the evolution of social behaviour². Others regard kin selection as solid, and the rethink as unnecessary and potentially retrograde.

Rival camps have emerged, each endorsing a different approach to social evolution. Heated exchanges have occurred at conferences, on blogs and in journals, and have even been reported in *The New York Times*. Biologists have accused each other of misunderstanding, of failing to cite previous studies appropriately, of making unwarranted claims to novelty and of perpetuating confusions. Yet

I contend that there is little to argue about.

Much of the current antagonism stems from the fact that different researchers are focusing on different aspects of the same phenomenon, and are using different methods. In allowing a plurality of approaches — a healthy thing in science — to descend into tribalism, biologists risk causing serious damage to the field of social evolution, and potentially to evolutionary biology in general.

DARWIN'S PUZZLE

Charles Darwin realised that altruism poses a special problem for his theory of evolution. He was particularly troubled by the sterile workers in colonies of social

D. PARKINS



Examples of favouring kin are widespread: Japanese macaques spend more time grooming their closer relatives and meerkats share feeding and guard duties.

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► insects, which devote their lives to helping a queen reproduce at the expense of having offspring themselves. One possible explanation, hinted at by Darwin, is that groups containing many altruists might out-compete groups containing fewer. This idea of ‘group selection’ fell out of favour in the 1960s when George Williams argued that it was unlikely to be a powerful evolutionary force compared to individual selection, and was not needed to explain empirical observations³.

Inclusive fitness theory, most biologists now believe, provides the solution to Darwin’s puzzle. Hamilton realised that a gene that causes an animal to behave altruistically can spread by natural selection as long as the beneficiaries are relatives, and so have a chance of carrying the same gene. In short, altruism can evolve if the cost to the actor is offset by sufficient benefit to sufficiently

closely related recipients. This means that animals should behave in ways that maximize not their personal fitness (or number of surviving offspring), but rather their inclusive fitness — a measure that also takes into account the offspring of their relatives.

“Many biologists regard kin selection theory as a resounding empirical success.”

Inclusive fitness theory predicts that animals should behave more altruistically towards kin than non-kin. This has been amply confirmed in diverse species, from microbes to primates⁴, leading many biologists to regard kin selection theory as a resounding empirical success. In many bird species, such as scrub jays and dunnocks, for example, breeding pairs receive aid from a non-breeding ‘helper’ bird, typically

a relative⁵. Similarly, rhesus and Japanese macaques are more likely to groom relatives than non-relatives, and to help them in disputes⁶.

Several biologists, however, have recently questioned the importance of kin selection in explaining social behaviour. Edward O. Wilson, famous for his empirical work on insect societies and once a forceful advocate of kin selection, now argues that kinship plays a minor part in the evolution of ant, bee, termite and other social insect colonies^{7–9}. More important, he says, are the ecological factors that make social living so successful. An easy-to-defend nest and a nearby food supply, for instance, may make it beneficial for animals to live in groups. Recently, Wilson, along with theoretical biologists Martin Nowak and Corina Tarnita, have argued that inclusive fitness theory rests on a number of assumptions that greatly limit its applicability — such as that natural selection is relatively weak². Still others argue that multi-level selection — a modern-day version of group selection — best explains the evolution of altruism (although many biologists remain suspicious of appeals to group, rather than individual, advantage).

The root of the problem is the existence of several different frameworks for modelling the evolution of social behaviour. These include numerous variants of kin selection theory; multi-level selection; evolutionary game theory; and an approach from quantitative genetics based on the notion of ‘indirect genetic effects’. The relationships between these frameworks are sometimes ambiguous, and biologists disagree about which is most fundamental and which most useful empirically (see ‘Coming to terms with social evolution’).

All this disagreement creates the impression of a field in massive disarray. In reality, many of the players involved are arguing at

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GLOSSARY

Coming to terms with social evolution

Altruism

Behaviour that is costly for an animal to perform but benefits others. Costs and benefits are measured in terms of reproductive success.

Inclusive fitness

A generalization of Darwinian fitness, which takes into account the effect of an individual’s actions on the reproductive success of their relatives, as well as on their own.

Kin selection theory

The idea that natural selection shapes individuals’ behaviour according to the effect it has on relatives.

Group selection

The idea that natural selection favours traits because they benefit whole groups, rather than individuals.

Multi-level selection theory

The idea, closely related to group selection, that natural selection can operate on more than one hierarchical level, for instance at the level of the individual, group or species.

Social evolution

Darwinian theory as applied to an animal’s social behaviour, that is behaviour affecting other individuals in the population.



Eciton burchelli army ant workers can form living bridges for other colony members to cross. Older moorhen chicks sometimes help feed their young siblings.

M. MOFFETT/MINDEN PICTURES/FLPA

cross purposes. Nowak and his colleagues, for instance, have developed a mathematical model that they claim provides a more direct way to calculate the evolutionary dynamics of a social trait such as altruism². However, they overlook the fact that inclusive fitness theory explains what organisms are trying to maximize. It is not just a tool for calculating when a social trait will evolve.

Likewise, in arguing that ecological factors, rather than kinship, are key to the evolution of social-insect colonies, Wilson is imposing a false dichotomy⁴. To fully understand how these colonies evolve, researchers need to consider ecological factors and relatedness. Whether they stress the importance of one over the other will depend on the question they are asking. For example, relatedness has proved crucial to understanding conflicts between the queen and her workers over the production of male versus female offspring in ants, bees and wasps. For questions about how tasks are allocated to the workers in an ant colony or why the size of colonies differs across species, ecological factors are probably more relevant.

Lastly, kin and multi-level selection are not alternative theories; they simply offer different takes on the question of how social behaviour evolved. Proponents of kin selection, for example, explain sterile workers in insect colonies by saying that the workers are helping the queen to reproduce, and thus boosting their own inclusive fitness. Proponents of multi-level selection argue that the workers are providing a benefit to the colony as a whole, thus making the colony fitter than other colonies. These explanations may seem different, but mathematical models show that they are in fact equivalent^{10–12}.

At the Amsterdam meeting, certain real disagreements did surface, but they were mostly over technical points and pitted against a background of broad agreement

over fundamentals. Most agreed that inclusive fitness theory has been extremely valuable for empirical biologists, but that it is not the only way to model social evolution.

BUILDING BRIDGES

Much of the current antagonism could easily be resolved — for example, by researchers situating their work clearly in relation to existing literature; using existing terminology, conceptual frameworks and taxonomic schemes unless there is good reason to invent new ones; and avoiding unjustified claims of novelty or of the superiority of one perspective over another.

It is strange that such basic good practice is being flouted. The existence of equivalent formulations of a theory, or of alternative modelling approaches, does not usually lead to rival camps in science. The Lagrangian and Hamiltonian formulations of classical mechanics, for example, or the wave and matrix formulations of quantum mechanics, tend to be useful for tackling different problems, and physicists switch freely between them.

History shows that, despite its enormous empirical success, evolutionary biology is peculiarly susceptible to controversy and infighting. This is particularly true of social evolution theory, in part because of its potential applications to human behaviour. In the 1970s and 1980s, for instance, left-wing scholars bitterly rejected biological explanations for phenomena such as religion and homosexuality, because they feared such explanations would be used to justify a continuation of existing inequalities.

Researchers should take stock before another overblown dispute does

serious damage to the field. Up-and-coming researchers are unlikely to be attracted to a discipline plagued by controversy. Moreover, if the experts cannot agree about what theoretical framework works best, the supply of research funding may eventually be threatened. Also worrying is the possibility that onlookers perceive the central question of social evolution theory — how altruism can evolve — as unresolved, even though it was answered decades ago. During the ‘sociobiology wars’ of the 1970s and 1980s, creationists proved adept at seizing on and exaggerating the differences in opinion between biologists for their own ends. It would be a disaster if the same were to happen again. ■ [SEE CORRESPONDENCE P.661](#)

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