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FOCUS

PROJECT

Conflict Resolution in Biological Systems

Scientific progress often comes through the identification of common principles of broad significance. One common principle is that the evolution of more complex biological units (e.g., genomes of many genes, multicellular organisms, societies, global human society) causes potential conflicts among sub-units (e.g., genes, individuals, countries). Complex biological units often have mechanisms that reduce conflicts among sub-units so that the higher-level unit can function more effectively. Conflicts arise because the interests of the sub-units are not identical and because resources are limited. General mechanisms for reducing conflicts include kinship to other group members and coercion (being prevented from acting in a way that is bad for the group).

The focus group members (Francis Ratnieks, Tom Wenseleers, Kevin Foster) are biologists who have studied conflicts and conflict resolution in insect societies (bees, wasps, ants), and also conflicts in multicellular slime molds and between symbiont organisms. They plan to write a book entitled "Conflict Resolution in Biological Systems", which will synthesise across all biological conflicts by determining common principles in conflict resolution. The book will focus on the following main levels of conflict: between individuals within animal societies; between symbiotic organisms of different species; and within organisms caused by self-promoting genes and intracellular symbionts. In addition, the book will discuss the degree to which these principles may be relevant to human society.

Recommended Reading

Ratnieks, F. L. W. "Reproductive Harmony via Mutual Policing by Workers in Eusocial Hymenoptera." *American Naturalist* 32: (1988): 217-236.

Ratnieks, F. L. W. and P. K. Visscher. "Worker Policing in the Honey Bee." *Nature* 342 (1989): 796-797.

Beekman, M. and F. L. W. Ratnieks. "Power and Reproduction in Insect Societies." *Philosophical Transactions of the Royal Society B* 258: (2003): 1741-1753.

These and other publications by Francis Ratnieks on conflicts in societies can be downloaded from www.shef.ac.uk/uni/projects/taplab/flwrpub.html.

COLLOQUIUM, 21.12.2004

Conflict Resolution in Insect Societies

A colony of honey bees, or indeed any social insect, is often considered a model of cooperation. The workers that are most easily observed, the foragers, busily collect nectar and pollen which they bring back to the nest to feed the colony. They cooperate directly with each other via their waggle dance by which a forager that has found a good

patch of flowers communicates the location to unemployed nestmate foragers. Within the nest many other cooperative activities are in evidence. Workers building and cleaning cells, nursing brood, and receiving nectar from foragers. In fact, the social life of an insect colony is basically one giant cooperative exercise dedicated to colony survival, growth, and reproduction.

One dramatic form of cooperation in a honey bee colony is stinging. A worker's sting is barbed, and detaches from her body when used, killing her. By detaching the sting's effectiveness is increased. The detached sting continues to pump venom, and also releases alarm pheromone which guides additional workers to the intruder. The remarkable thing is that the worker bee is designed to lay down her life for the good of the colony when she stings. This extreme altruism evolves because it improves the defence of the colony, which is the family of the self-sacrificing worker. By helping the colony, the self-sacrificing worker passes on more copies of her genes (via the drones and swarms made by her colony).

Cooperation in an insect colony is favoured by natural selection because the colony is a family. But like any family there can also be conflict. Conflict within families arises because family members are not genetically identical, as are the cells in your body, and this leads to family members having different interests. Despite the outward appearance of complete harmony, insect colonies are the scene of numerous conflicts. One important conflict concerns the production of males.

Worker bees, wasps, and ants are often referred to as sterile, but they are not. Each can lay viable eggs if her ovaries are activated. Because workers in most species cannot mate they can only lay unfertilized eggs. Due to the unusual sex-determination mechanism of bees, wasps and ants these eggs are male. Thus, the drones reared in the honey bee colony could, potentially, be the queen's sons or workers' sons because both the workers and the queen can lay male eggs.

Which is better for a worker-rearing workers' sons or rearing the queen's sons? To answer this question we have to consider the genetic relatedness of a worker to the males that could be reared in her colony. Genetic relatedness is a measure of the proportion of genes in common. Among the cells in your body relatedness is 1. The relatedness of a worker bee, wasp or ant to her mother queen's sons, her brothers, is 0.25. But the genetic relatedness to her own sons is 0.5. To a worker a son is worth twice as much as a brother because a son is twice as good at passing on her genes. This suggests, therefore, that workers should produce the males because sons are worth more than brothers. However, the picture changes dramatically when we consider the relatedness of workers to nephews-the sons of other workers. Honey bee queens mate with approximately 10 males so that the workers in a colony are mostly half sisters, with an average relatedness of 0.30. (If the queen only mated with one male then the workers would all be full sisters and be related by 0.75, whereas if every worker had a different father the workers would all be half sisters and be related by 0.25.) The relatedness of a worker to the sons of other workers is 0.30 divided by 2, or 0.15. Thus, even though each worker is more related to her own sons (0.5) than to the queen's sons (0.25), she is more related to the queen's sons than to other workers' sons (0.15). The consequence of this is that workers will be better off if they prevent each other from reproducing.

The theory, therefore, predicts that workers should stop each other from reproducing. Scientific theories must be tested against what actually happens in nature. In 1989 my colleague Kirk Visscher and I found that worker honey bees kill eggs laid by other workers. I named this mutual prevention of reproduction by workers "worker policing" in analogy to policing in human society. Worker policing of worker-laid eggs has since been found in many other species of social insects, with examples in bees, wasps, and ants. It is almost certainly widespread. (WSK Fellows Tom Wenseleers and Kevin Foster have discovered worker policing in 6 species of European wasps, getting stung many times in the process.)

Policing of worker-laid eggs resolves much of the potential conflict over male production. When we compare different species of wasp in which the effectiveness of policing varies, we find that the species with the most effective policing have the lowest proportion of workers who try to lay eggs. This is because there is no point in laying eggs if they will only be killed. The most extreme example is the honey bee in which fewer than one worker per thousand even tries to lay eggs.

Policing also resolves other reproductive conflicts in insect societies, including conflict over caste fate. Female larvae can develop into either a queen or a worker depending on how much food they receive. Because queens are normally larger than workers, the adult workers can prevent a larva from developing into a queen by giving it less

food. In this way the rearing of excess queens is prevented. In tropical American *Melipona* bees, queens are the same size as workers so that policing by food control is not possible. These bees produce large numbers of excess queens that are not needed.

The overall effect of policing in insect societies is to resolve the conflict that exists between individual interests and group interests in favour of the group. In insect societies this means that it consolidates the basic inequality that exists between the working individuals (workers) and the reproductive individuals (queen). However, the workers are not doing too badly out of this arrangement as they work to rear close relatives. Policing in human societies has been used to sustain inequalities and unpopular regimes, as shown by the negative connotation of the phrase "Police State". But a human police state in which policing is used to promote greater equality and justice is not an unattractive prospect.

EVENING COLLOQUIUM

16.03.2005

The Amazing Lives of Social Insects: Bees, Wasps and Ants

PUBLICATIONS FROM THE FELLOW LIBRARY

Ratnieks, Francis L. W. (Berlin, 2011)

Darwins special difficulty the evolution of neuter insects and current theory

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=1046032941>

Ratnieks, Francis L. W. (Chicago, Ill., 2006)

Comparative analysis of worker reproduction and policing in eusocial hymenoptera supports relatedness theory

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=1726537323>

Ratnieks, Francis L. W. (London [u.a.], 2006)

Enforced altruism in insect societies

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=1725917599>

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Ratnieks, Francis L. W. (Amsterdam [u.a.], 2006)

Kin selection is the key to altruism

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=1665053828>

Ratnieks, Francis L. W. (2006)

Conflict resolution in insect societies

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=1047209489>

Ratnieks, Francis L. W. (2005)

Working-class royalty : bees beat the caste system

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=772399301>

Ratnieks, Francis L. W. (2005)

A test of worker policing theory in an advanced eusocial wasp, *Vespula Rufa*

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=772398240>

Ratnieks, Francis L. W. (2005)

Policing insect societies

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=771340192>

Ratnieks, Francis L. W. (Amsterdam [u.a.], 2005)

A new eusocial vertebrate?

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=770485758>

Ratnieks, Francis L. W. (Düsseldorf, 2005)

Harmonie im Bienenstock? : wie Bienenvölker Gehorsam erzwingen ; Alexander Kluge im Gespräch mit Francis L. W. Ratnieks

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=669195812>

Prime Time - Spätausgabe

<https://kxp.k1oplus.de/DB=9.663/PPNSET?PPN=669195812>