



How Does Social Behavior Evolve?

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Why do animals help others at the potential cost of their own survival and reproduction?



Social behavior consists of a set of interactions among individuals of the same **species**. A wide range of sociality occurs among animals. Some animals rarely if ever interact with one another, even when it comes to issues of parental care. Examples of relatively asocial animals include mosquitoes and polar bears. Highly social organisms live together in large groups, and often cooperate to conduct many tasks. Examples of **social groups** include packs of wolves and schools of **fish** (Figure 1). The most highly social animals form tightly knit colonies and include all ants and termites, some bees and wasps, and a few other organisms.

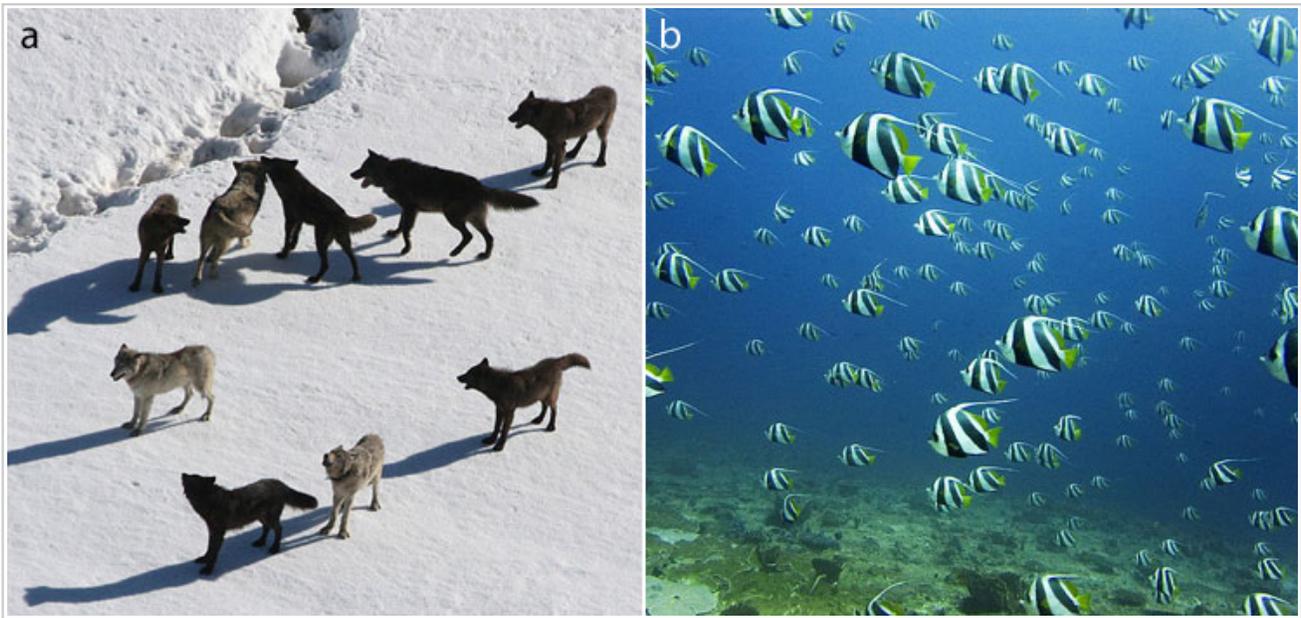


Figure 1: Social groups which have formed to improve the probability of survival and reproduction of individual members: pack of wolves (a) and school of fish (b)

Social Behavior is Adaptive

Many social behaviors of animals are **adaptive**, meaning that being social ultimately increases an animal's **fitness**— its lifetime **reproductive success**. One example of how social behavior is adaptive is aggregation against predators. This concept applies to caterpillars feeding together on a leaf, a herd of wildebeest, schools of fish, and flocks of birds.

A landscape filled with solitary wildebeest will offer easy pickings for large predators such as lions (Figure 2). If the wildebeests gather into a single group, then the risk of any single individual being eaten is reduced. In the circumstance of an attack by a predator, the odds of one individual being targeted are 100% for solitary individuals, 1% in a group of 100, and 0.1% in a group of 1000. Wildebeests do suffer social costs from aggregating in groups — grazing sites may not provide adequate food for every individual in the group, for example. However, it is not difficult to imagine that the costs of social aggregation are much smaller than the benefits of the defense against **predation**. This is a simple example of how the costs and benefits of social behavior may evolve and be maintained.



Figure 2: Wildebeests gathered into groups are more protected from predators than any solitary wildebeest.

Living in groups involves a balance of conflict and **cooperation**, which is mediated by the costs and benefits associated with living socially. When the benefits of living socially exceed the costs and risks of social life, scientists predict that social cooperation will be favored.

Altruism

The benefits of social life typically occur when one individual is the benefactor of an act of **altruism**. An **altruistic** act is one that increases the welfare of another individual at an actual or potential **cost** of the individual who performs the act.

An example of altruism comes from ground squirrels, who may warn other members of their group about a predatory hawk overhead. This brings the hawk's attention to the individual giving the warning call. This risky behavior **benefits** other individuals in the squirrel's group. Other examples of altruistic behavior include sharing nesting space and helping to raise **offspring** of an unrelated individual.

The benefit of an altruistic behavior is ultimately measured in its effect on an animal's lifetime reproductive success. Evolutionary biologists and animal behaviorists have sought to identify the mechanisms that can explain what some have called the "problem of altruism." Natural **selection** operates against individuals who reduce their own fitness. Altruism by definition decreases the fitness of the individual, so how can this behavior persist? The solution to the "problem" of altruism comes from decades of research into genetics and animal behavior, which has taught us that altruism is a powerful demonstration of **natural selection** at work.

Reciprocity

Vampire bats (Figure 3) returning from an unsuccessful foraging bout will beg to share food from successful individuals. It is most directly in the interest of the solicited bat to keep its own food, as it requires the nutrients to survive and reproduce, and giving up part of its meal is in fact altruistic. Thus in both ecological and evolutionary terms, other members of this bat's own species are its greatest competitors.



Figure 3: A vampire bat, an excellent model system to test theories regarding the altruistic sharing of food

So why would a vampire bat share its meal of blood? The answer is **reciprocity**. In the early 1980s, graduate student and researcher Gerald Wilkinson conducted a series of experiments to demonstrate that vampire bats in Costa Rica often shared blood with other bats sharing their roosts. He found, however, that bats did not share their meals with all other bats equally.

Why would bats not share food equally? Based on long-term measurements of bat movements among roosts, Wilkinson found that some bats were more likely to interact with certain individuals more than others. Bats were far more likely to share blood with bats they were more likely to encounter in the future. In other words, when there was a greater opportunity for reciprocation, the bats were more likely to share their meals. Bats would not share blood meals with other bats if there was little chance that the other individual would be able to return the favor.

Reciprocity enables the existence of altruism because — in the long term — the benefits of altruism can outweigh the costs of altruism. In this particular example, the relative cost of sharing food, when available, is less than the potential future benefit of receiving food when hungry.

Kin Selection

Vampire bats share food not only because of the **anticipation** of reciprocation. They are far more likely to share blood meals with their relatives. After taking into account the potential for reciprocity, vampire bats are more inclined to share their blood meals with kin than with unrelated individuals. Using genetic analyses, researchers can calculate the **relatedness** among individuals. Bats that are more closely related are more likely to share resources.

Why are relatives more likely to be the recipients of altruistic acts than non-relatives? Individuals are far more likely perform altruistic acts for siblings than for nephews, and even less likely for third cousins. The mechanism behind the effect of relatedness on altruism is **kin selection**. Natural selection reflects how an individual passes on copies of their own **genes** through survival and **reproduction**, but kin selection reflects how copies of an individual's genes are passed down through the survival and reproduction of their relatives. Just

as the principle of natural selection predicts that an individual will act to maximize their own fitness, the principle of kin selection predicts that an individual will act altruistically to maximize the fitness of its relatives.

There are limits to altruism. An individual's **direct fitness** is measured by copies of her own genes passed on to children, grandchildren, and so on, whereas **indirect fitness** is the measure of copies of her genes passed on through her non-descendant relatives such as cousins, nieces, nephews, and siblings. Selection will favor an altruistic act if the benefit of the act (in terms of indirect fitness) exceeds the cost of the act (in terms of direct fitness). When individuals are more closely related, they have a greater relatedness (r) and altruism is more likely to occur. Relatedness is measured on a **scale** from 0–1 because it reflects the proportion of genes that are shared by two individuals. Zero indicates no relation among individuals. The coefficient r as measured in other pairs includes full siblings: 0.5; parent–offspring: 0.5; grandparent–grandchild: 0.25; cousins: 0.125.

In the 1960s, W. D. Hamilton formulated what is now commonly known as Hamilton's rule, in which relatedness is shown to moderate the **probability** that altruistic acts will occur. According to Hamilton's rule, altruism is favored when the benefits (B) of the altruistic act to the recipient, multiplied by the relatedness (r) to the actor, exceed the costs (C) to the actor; this is expressed mathematically as $rB > C$. In addition to vampire bats, other species such as ground squirrels, paper wasps, and wild turkeys follow Hamilton's rule.

Eusociality

The **evolution** of social behavior at its most intimate and complex degree is found in **eusocial** animals. Eusocial species live in colonies. Only a relatively small fraction of the animals in the colony reproduce; the non-reproductive colony members provide resources, defense, and collective care of the young. The list of known eusocial animals includes ants, termites, some wasps, some bees, a small number of aphid and thrip species, two species of mammal (the naked mole rat and the Damaraland mole rat), and multiple species of reef-dwelling shrimp.

How can selection produce an **organism** that has no chance of reproducing independently, whose fitness is entirely invested into colony mates? In other words, how can animals have no direct fitness and only indirect fitness? Individuals in colonies are usually related to one another, and relatedness can even be greater than 0.5 as a consequence of the unique genetics of some groups of insects or **inbreeding** (mating between close relatives). Hamilton's rule and kin selection provide at least a partial explanation for the evolution of eusociality.

An ecological explanation for the evolution of eusociality is that colonies often produce a very large number of offspring, such that even when relatedness is low the indirect fitness of the non-reproductive workers may be greater than if they had the capacity to reproduce independently. In eusocial animals, the high **productivity** resulting from communal life and the efficient division of labor among workers takes place in an **environment** which is usually well defended against natural enemies (Figure 4). In nearly all eusocial species, colonies are protected through structural means (such as termite nests in wood, or shrimp in marine sponges), with venom (of wasps, bees, and ants), or by both means.

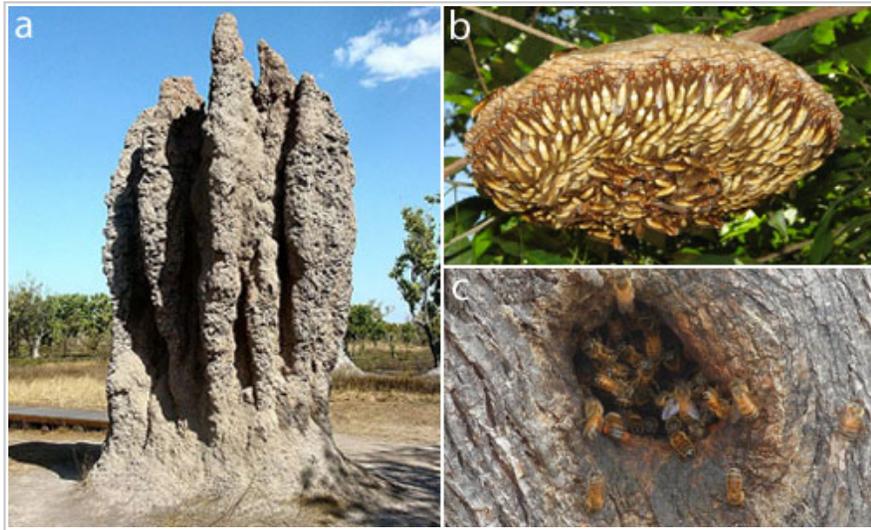


Figure 4: Social insects have well protected or defended nests, including termites (a), wasps (b), and bees (c).

Summary

Social and altruistic behaviors require a broad view of Darwinian fitness and an understanding that animals can perform behaviors that are responsive to short-term and long-term consequences for their fitness. By conducting research into how organisms interact with their environment and how the environment is predictive of their survival and reproductive success, researchers are able to explain how social behavior has evolved via the mechanism of natural selection.

References and Recommended Reading

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