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# VII.10

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## Cooperative Breeding

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### OUTLINE

1. Ecology and evolution of cooperative breeders
2. The evolution of helping
3. Individual differences in helping behavior
4. Reproductive conflict

Cooperative breeding is a relatively rare but taxonomically widespread social system in which adult helpers work to rear offspring that are not their own. Approximately 10 percent of birds and 2 percent of mammals are cooperative breeders; examples are also seen in insects, spiders, crustaceans, and some fish. These diverse systems present an opportunity to investigate how cooperation and helping can be favored in the face of natural selection, which is expected to work for self-interest. Cooperative breeding animals present concrete examples of altruism and helping, together with the possibility of measuring the lifetime fitness consequences of helping decisions. Research on cooperative breeding can also help elucidate the evolution of the unusual human life history, because humans evolved in cooperatively breeding groups in which grandparents, siblings, and other family members contributed to rearing offspring. Some of the main questions posed by cooperatively breeding animal societies are considered here: What ecological conditions favor cooperative breeding? Why do helpers help? Why do some individuals work much harder than others? How do competing individuals resolve conflicts of interest so that the cooperative team can function?

### GLOSSARY

- Altruism.** Acts or behaviors that result in a lifetime direct fitness increase for other individuals, at a lifetime direct fitness cost to the actor.
- Cooperation.** A social interaction in which individuals enhance each other's inclusive fitness.

**Direct Fitness.** The number of copies of alleles that an individual contributes to the next generation through offspring.

**Harming.** Acts or behaviors that reduce the number of offspring of other breeders that are raised to independence.

**Helping.** Acts or behaviors that increase the number of offspring of other breeders that are raised to independence.

**Inclusive Fitness.** Direct plus indirect fitness.

**Indirect Fitness.** The number of copies of alleles that an individual contributes to the next generation by helping nondescendant kin.

**Reproductive Division of Labor.** The partitioning of tasks involved in reproduction within animal societies among different individuals. Typically, socially dominant individuals produce offspring, while subordinate, nonbreeding individuals help provision or rear young.

**Reproductive Skew.** A measure of the evenness with which reproduction is distributed among the members of a cooperative group.

### 1. ECOLOGY AND EVOLUTION OF COOPERATIVE BREEDING

Cooperative breeding is a type of social system in which some adults (known as *helpers*) routinely assist in the raising of offspring that are not their own, even though they have the ability to produce offspring themselves currently or in the future. This broad definition includes a range of species, from social insects such as paper wasps, hover wasps, and halictid (sweat) bees to “helper-at-the-nest” bird systems (e.g., western bluebirds, white-fronted bee eaters), in which offspring delay dispersal and help their parents with the next clutch; and larger bird and mammal societies (e.g., acorn woodpeckers, banded mongooses) with multiple male and female breeders and

helpers per group. These systems have proven to be excellent models for studying the evolution of sociality and cooperation because they provide concrete examples of *altruism*, that is, behavior that boosts the lifetime fitness of others at a lifetime fitness cost to the actor (see also chapters VII.9 and VII.13). For example, in paper wasps, groups of overwintered females (called *foundresses*) emerge from hibernation in spring and form groups that cooperate to build a nest. In each group a single dominant female lays most of the eggs and remains safely on the nest while the other females forage for prey to feed the offspring and collect nest material to expand the nest. These helper foundresses are all mated and fully fertile, with the option of building their own nest or attempting to supplant the dominant, so why do they accept a non-breeding position and risk their lives to help the dominant instead? Studying cooperative breeders can help us understand how cooperation can be favored by natural selection and how cooperative groups remain stable despite conflict over reproduction and social rank. This is also a topic that is relevant to human evolution: many of the puzzling and unusual features of human life history (early reproductive cessation followed by menopause, a long period of offspring dependency, sequential production of multiple dependent young) appear to reflect an evolutionary history of cooperative breeding.

Cooperative societies, while very diverse in terms of social structure and basic biology, share some important features. Populations with cooperative breeders are usually made up of closely knit extended family groups, formed when offspring delay dispersal to remain in their natal groups. Within these groups there is usually (but not always) a reproductive division of labor in which older or socially dominant individuals breed, and lower-ranked or younger individuals provide most of the help. Because helpers retain the ability to reproduce, their behavior reflects a trade-off between their current and future fitness, and between direct and indirect components of inclusive fitness. In this way cooperative breeders differ from *eusocial* species (such as ants, honeybees, termites, some aphids, and naked mole rats) in which there are distinct reproductive and worker castes, and helpers remain functionally or morphologically sterile throughout their lives.

Ecological factors play a central role in both the evolution and maintenance of cooperative breeding. In birds, for example, comparative analyses show that the evolution of cooperative breeding is associated with high adult survival and intense competition among adults for breeding territories. Within species, offspring remain on their natal territory and serve as helpers if no suitable breeding habitat or territory is available but rapidly disperse to breed independently if ecological constraints are relaxed or vacant territories appear. In the Seychelles

warbler (*Acrocephalus sechellensis*), for example, adult males and females were transplanted from a saturated island in the Seychelles group (Cousin) to two adjacent uninhabited islands (Aride and Cousine), whereupon they formed breeding pairs and produced offspring who in turn went off to breed (Komdeur et al. 1995). As the vacant islands filled up and the best-quality territories were taken, offspring (particularly those born on high-quality territories) began to delay dispersal and to remain on their natal territory to help. This and other experimental studies of birds and fish (such as the cooperative cichlid *Neolamprologus pulcher*) suggest that ecological constraints on dispersal and high fitness benefits of remaining at home (known as the *benefits of philopatry*) together promote the formation of cooperative breeding groups. Similar constraints on dispersal promote delayed dispersal of helpers in cooperatively breeding mammals (such as lions, African wild dogs, meerkats, and banded mongooses), but here it is often aggressive territorial defense, rather than a lack of available habitat, that constrains immigration into existing groups (Clutton-Brock 2009).

In most cooperatively breeding insects, dispersal is not constrained by a lack of breeding habitat or territory, because nests can be constructed on a range of vegetation types or substrates. There are, however, often severe constraints on independent breeding because mothers have a high probability of dying in the extended period during which offspring are dependent on their care. Offspring that stay to help their mother or join the nests of same-generation females can provide insurance against the failure of the nest due to the death of the breeding female. Experiments have shown that these benefits are substantial and favor staying to help even when relatedness is low and breeding is monopolized by a single female (meaning that helpers stand to gain little indirect or direct fitness benefits from help). In cooperative insects such as paper wasps and tropical hoverflies, subordinates form a social queue and can inherit breeding status on the death of the dominant, which further increases the benefits of remaining in the natal group. Helping in these social queues ensures that nests quickly get through the vulnerable founding phase (i.e., the period before workers emerge), thus safeguarding the potential future fitness benefits that subordinates might gain through inheritance.

## 2. THE EVOLUTION OF HELPING

Ecological constraints on dispersal may set the stage for delayed dispersal and cooperative breeding, but on their own these constraints do not explain why helpers work to rear the young of breeders, rather than just waiting for

breeding vacancies to appear. A general theoretical framework for understanding the evolution of helping behavior (or indeed any trait that affects the fitness of social partners) was provided by William D. Hamilton's *inclusive fitness theory*, set out in a seminal 1964 paper. Hamilton showed that selection favors social traits that satisfy the following inequality (now known as *Hamilton's rule*):  $rB - C > 0$ , where  $B$  is the lifetime direct fitness benefit to the recipient of a social act (e.g., the recipient of help),  $C$  is the lifetime direct fitness cost to the actor or possessor of the social trait, and  $r$  is the coefficient of relatedness, a measure of genetic similarity between social partners relative to the average "background" genetic similarity in the wider population.

Ecological conditions can affect the magnitude of all three terms in Hamilton's rule: the fitness benefits ( $B$ ) to recipients of a given unit of help (for example, offspring may benefit more from help when food is scarce); the fitness cost ( $C$ ) of investing in help (for example, helping may be more costly when food is scarce); and even relatedness ( $r$ ), given that severe ecological constraints on dispersal mean that most interactions will occur between kin. Relatedness is also dependent on patterns of mating: other things being equal, monogamy is predicted to be more conducive to the evolution of altruism than is polygyny, since relatedness among family members is higher under the former than the latter. Recent phylogenetic analyses support this prediction and show that most cooperatively breeding insects, birds, and mammals arose from monogamous ancestors. It appears therefore that both ecology and family genetic structure exert important influences on the evolution of cooperative breeding.

Within the general framework of inclusive fitness theory, four main evolutionary mechanisms have been proposed to explain how helping behavior can evolve. The first two of these were proposed by Hamilton himself and are usually grouped under the term *kin selection*: (1) indiscriminate helping may be favored if dispersal is limited, so that the recipients of help are on average more closely related than the population at large; (2) individuals may recognize kin and preferentially direct care toward them; (3) there may be immediate or delayed direct fitness benefits that outweigh the immediate fitness costs; (4) helping may be enforced by social punishment, so that the alternative, not helping, results in even greater fitness costs. It is important to recognize that none of these explanations are mutually exclusive: for example, helping may involve both indirect fitness benefits (mechanisms 1 and 2) and direct fitness benefits (mechanisms 3 and 4).

### Indiscriminate Helping

The first mechanism based on dispersal constraints, or *population viscosity*, has been the subject of controversy,

because constraints on dispersal lead to both high relatedness and high local competition between relatives. There is little to be gained from raising extra offspring if these offspring compete with one another for the same limited number of breeding places. In fact, the first theoretical analysis of this problem by Peter J. Taylor in the early 1990s suggested that the costs of competition arising from dispersal constraints exactly cancel the benefits of increased relatedness for the evolution of altruism. According to this model, therefore, Hamilton's first mechanism for the evolution of altruism should not work. However, subsequent theory has shown that adding in biological features such as overlapping generations and sex differences in dispersal typically recovers Hamilton's prediction that increasing viscosity promotes the evolution of indiscriminate helping.

Extensions of Hamilton's theory can be used to predict harming as well as helping behavior, that is, acts or traits that *reduce* the fecundity of local group members, and can be applied to understand any social life history traits that have an impact on the direct fitness of fellow group members, such as reproduction and the rate at which individuals get old and die. For example, Rufus Johnstone and I have modeled how patterns of dispersal and mating may have predisposed humans and some cetaceans to the evolution of menopause and late life helping. Testing of these models is at an early stage, but proposals such as this with associated tests should lead to a better understanding of demographic influences on life history and helping behavior.

### Discriminate Helping

Hamilton's rule is easier to satisfy if helpers can direct care toward more closely related group members, since in this case relatedness is by definition higher than the average relatedness to all potential recipients. The ability to preferentially aid kin increases the inclusive fitness benefits of costly helping, so we might expect animals to evolve mechanisms to recognize close kin. In cooperatively breeding birds and mammals, kin recognition does occur and is typically based on cues that are learned during development, not on direct recognition of genetic similarity. In the long-tailed tit, for example, cross fostering experiments show that offspring preferentially help those individuals with which they were reared, rather than their genetic relatives. In fact, direct recognition of genetic similarity appears to be uncommon in social vertebrates, although there is evidence from laboratory mice and humans that individuals can detect similarity at some very variable genetic regions of the genome, such as the major histocompatibility complex (MHC) of genes that are involved in immune function.

In cooperatively breeding insects, helpers discriminate nest mates and non-nest mates but generally do not discriminate kin from nonkin within groups. In the paper wasp *Polistes dominulus*, for example, 20 to 30 percent of foundress helpers are nonrelatives, but there is no difference between related and unrelated helpers in foraging effort, nest defense, aggression, or inheritance rank. However, recent studies have also shown that these unrelated helpers have measurably different hydrocarbon profiles (volatile chemicals in the cuticle that in other insects are involved in signaling and kin recognition). Thus, although cues to discriminate kin exist, they are not used by wasps in helping decisions.

### Direct Fitness Benefits

Examples of hardworking, unrelated helpers (for example, in paper wasps and meerkats) suggest that helping may also yield direct fitness benefits, and that in some cases these direct benefits alone are sufficient to outweigh the costs of helping. Several direct fitness benefits of helping have been proposed. The *skills hypothesis* suggests that the experience of helping allows helpers to pick up parenting or foraging skills, which increases their reproductive success when they become breeders themselves. The *group augmentation hypothesis* suggests that helping can be favored if, as a consequence, helpers inherit a larger, more productive group within which to breed in the future. Finally, the *prestige hypothesis* suggests that helping results in elevated social status and an increased probability of inheriting breeding status in the future.

The skills hypothesis has been tested in several cooperatively breeding bird species by examining the correlation between helping effort and later reproductive success. These studies have found little evidence to support the hypothesis, and correlational tests of this kind are problematic, because any correlation may reflect differences in quality, state, or age of helpers, rather than a causal relationship between help and breeding success. Group augmentation seems a plausible idea, because larger groups are usually more productive in vertebrate cooperative breeders, but the key assumptions of the hypothesis have not been tested, namely, (1) that helping leads to increased recruitment and larger future group size, and (2) that larger group size is beneficial to the direct fitness of helpers. In paper wasps and hover wasps group augmentation benefits do not appear to be a major determinant of helper effort: helpers reduce their helping effort as they get closer to inheriting the breeding position, a pattern that is the opposite of that predicted by the group augmentation hypothesis. Finally, tests of the prestige hypothesis have also yielded little support, although there are intriguing observations of Arabian babblers competing with each other to help,

which are consistent with the hypothesis. Overall, evidence for direct fitness benefits of helping is thin on the ground, but more experiments are needed to manipulate helping effort and establish the causal consequences for later breeding success.

### Enforced Fitness Benefits

A great deal of theoretical interest in evolutionary biology has focused on the use of punishment and threats to induce cooperation and helping (Cant 2011, 3530) In the context of cooperative breeding, the *pay-to-stay hypothesis* suggests that dominants can use the threat of eviction from the group to induce subordinates to help or to pay “rent” to be allowed to stay. Alternatively, breeders could use acts of aggression to punish lazy helpers, rather than the threat of eviction. These two explanations are different because the pay-to-stay hypothesis is based on the use of a threat (namely, of eviction), whereas aggression represents a form of punishment. Threats differ from punishments because, if effective, a threat rarely needs to be exercised; punishments, however, require overt actions to be effective. There is evidence from cooperative insects and vertebrates that growth and behavior are influenced by “hidden” threats that are triggered only when the social rules they enforce are broken, but detecting these hidden threats requires experiments to break these rules, for example, by preventing helpers from helping or reducing their effort.

The key prediction of the pay-to-stay hypothesis is that experimental reduction of helper effort should lead to eviction from the group. In cooperative cichlid fish and splendid fairy wrens, helpers that were temporarily removed from the group or were prevented from helping were subjected to aggression from dominants, but were never evicted from the group. In naked mole rats dominant queens use aggressive “shoving” to activate lazy workers. Kern Reeve and his colleagues showed that in the paper wasp *Polistes fuscatus* the removal or inactivation of dominant foundresses (by cooling them) led to reduced helper effort, while wing clipping of subordinate helpers led to increased aggression from dominants, as expected if aggression is used to enforce help. There is no evidence from wasps or other cooperative insects that lazy helpers are evicted from the group. Thus, when enforcement does occur in cooperative societies, it appears to be achieved through the use of punishment, not the threat of eviction.

### 3. INDIVIDUAL DIFFERENCES IN HELPING BEHAVIOR

In most cooperatively breeding insects and vertebrates some helpers work hard to rear offspring, while other individuals in the same group do very little. Hamilton’s

rule suggests that these individual differences could be attributed to variation in relatedness between helpers and offspring, or to variation in the individual fitness costs of helping or of the benefits to recipients. The evidence for an effect of relatedness on helping effort is mixed. In birds and mammals, helping effort is positively associated with relatedness in some species but not others, while in social insects unrelated helpers typically work just as hard as more related nest mates. There is much stronger evidence that variation in the costs of helping underlies individual differences in helping effort. In meerkats and Arabian babblers, for example, experimental feeding of helpers results in increased helping effort. In paper wasps and banded mongooses, helpers with high expected future direct fitness (i.e., those that have most to lose) work less hard than those with little future direct fitness. Jeremy Field and colleagues tested the impact of future fitness experimentally on the Malaysian hover wasp, in which helpers form a strict age-based queue to inherit the position of breeder. In some groups they removed wasps from the bottom of the queue, which left the inheritance ranks of the remaining wasps unchanged. In other groups they removed wasps from the middle or upper part of the queue, which resulted in a promotion for all the wasps below the removed individual. As predicted, wasps that were promoted reduced their helping effort compared with wasps that did not ascend in rank. This experiment showed that in this social insect, helpers adjust their helping effort according to their expected future direct fitness.

There is also evidence of consistent individual differences or “personalities” within cooperatively breeding groups. In meerkats and banded mongooses for example, there are consistent differences among helpers in their contributions to pup feeding even when controlling for age, sex, and social status. Similar consistent differences in helping and other forms of social behavior have been found in cooperatively breeding cichlids. A plausible explanation for these differences comes from research on phenotypic plasticity that shows that early life conditions interact with genotype and exert a profound influence on an animal’s phenotype. In eusocial insects, variation in provisioning during the larval period triggers genetic switches that alter the developmental trajectory and result in distinct morphological and behavioral castes, even among individuals of the same genotype. Little is known about whether similar developmental effects underlie consistent individual differences in cooperative behavior in cooperatively breeding vertebrates and insects.

#### 4. REPRODUCTIVE CONFLICT

Cooperatively breeding groups can together raise many more young than can solitary breeders, but within groups

the role of breeder is much more profitable, in terms of inclusive fitness, than is the role of helper. This difference leads to intense competition over breeding status that can threaten the productivity and stability of cooperative groups. Much research over the last 20 years has focused on how this reproductive conflict is resolved and why there is so much variation among societies in the level of *reproductive skew*—a measure of the evenness with which reproduction is shared among group members. In high-skew societies reproduction is monopolized by one or a few dominant individuals; in low-skew societies all or most adults breed. Reproductive skew varies widely between species and between groups in the same species, and may be different for males and females in mixed-sex groups.

Two main types of model have been proposed to explain variation in skew within and between species. *Transactional* models assume that the stable distribution of reproduction is determined by threats to exercise *outside options*, such as leaving the group or evicting other group members. For example, if dominant individuals fully control reproduction, subordinates can use the threat of departure to extract a reproductive *concession* from dominants. If dominants have no control over subordinate reproduction, then the amount claimed by subordinates will be limited only by the threat of being evicted from the group. In both cases the stable level of reproductive skew is assumed to depend on the value of outside options, which are set by ecological constraint. In contrast with these models, *incomplete control* models assume that all group members can invest effort to exert partial, costly control over reproductive shares. In these models the stable outcome depends on the relative efficiency or strength of the players, and ecological constraints play no role. A key way to distinguish the models, therefore, is to test whether skew and group stability is sensitive to changes in ecological constraints.

Current data do not support the assumption of transactional models that skew is sensitive to outside options or ecological constraints on dispersal. Two studies (on cooperative cichlids, and a social bee) manipulated outside options experimentally and found no effect on reproductive skew. Observations of banded mongooses show that dominant females use eviction to limit reproductive competition, but subordinates do not forego breeding when the chance of being evicted is high, as would be expected if reproduction was limited by the threat of eviction. Finally, experiments to reduce the share of paternity of subordinate males in a cooperatively breeding group have never led to the breakup of the group, as one would expect if subordinates used the threat of departure to extract a share of reproduction from dominants. These lines of evidence suggest that

reproductive skew is not influenced by threats to leave or evict other group members, although more experiments are needed.

In light of these results, the focus of research has shifted to understanding the evolution of conflict strategies in cooperative groups: how animals suppress one another's breeding attempts, how conflicts are settled on a behavioral timescale, and why the outcome of reproductive conflict is so variable. Analogous questions can be asked about the resolution of conflict at other levels of biological organization, for example, between genes, cells, and groups. The evolution of biological complexity, from replicating molecules to animal and human societies, has occurred via repeated cooperative transitions whereby individual subunits have come together to form cooperative teams. These transitions require that individual subunits find ways to repress selfishness and resolve conflicts of interest over direct fitness, just as cooperative breeders must resolve conflicts if they are to reap the rewards of teamwork. Theory and experiments that help elucidate conflict resolution in cooperative breeders may therefore also shed light on the fundamental question of how biological complexity arose.

#### FURTHER READING

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