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Cooperative Breeding

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Synonyms

Primitively Eusocial; Quasisocial

Definition

Group living with alloparental care

Introduction

Cooperative breeding is characterized by a combination of group living and alloparental care, i.e., the care of others' offspring. Typically, young of previous broods remain in their natal territory and help raising subsequent offspring of dominant breeders. Hence, the characteristic of cooperative breeding is the joint occurrence of delayed dispersal of young with a propensity to help caring for offspring they have not produced. Such "helpers" may or may not participate in reproduction, but if they do, the majority of young is still produced by more dominant group members. In other words, the "reproductive skew" within groups is usually high.

There are numerous variations of this general pattern, which differs also systematically between taxonomic groups. In birds and mammals, for example, there are two prevailing patterns: either young that delay dispersal from their natal territory help raising their later born siblings, or several females produce offspring jointly and raise them cooperatively, which is usually referred to as "communal breeding"(Koenig and Dickinson 2016). In fishes, insects, and spiders, there are sometimes different variations of these patterns. For instance, in fishes young delaying dispersal may help raising offspring of unrelated breeders that have replaced their own parents, or they may join forces to raise a brood that has been sired by several different males (Taborsky 1994). In some insects, several females jointly found a nest, in which only the dominant takes over the reproductive role, while subordinates help raising the latter's offspring irrespective of their degree of relatedness to them (Field and Leadbeater 2016). In social spiders, allofeeding of offspring that were not produced by the helpers may reach extreme levels, where helpers are consumed by these young even if they are unrelated to them (Lubin and Bilde 2007).

From an evolutionary perspective, cooperative breeding is of fundamental interest because it involves alloparental care, i.e., apparently altruistic behavior. This provides exceptional opportunities to ask under which circumstances selection

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will favor individuals accepting an apparent fitness cost at a benefit to the recipients of their helpful behavior.

Evolution of Cooperation

There are two principle ways how such behavior can evolve (Taborsky et al. 2016). Firstly, cooperative behavior may be mutualistic, i.e., the act itself has immediate fitness benefits to the actor; in this case, the behavior will be selected regardless of its beneficial effects on potential receivers. Secondly, cooperative behavior may be altruistic, which means that one individual helps another at immediate fitness costs exceeding the immediate fitness benefits of the act, i.e., the act bears immediate net costs. There are four possibilities how altruism, that is, cooperative behavior bearing immediate fitness costs, can be selected for.

(1) Kin selection. If the donor and the beneficiaries of the helpful act share a common genealogy, i.e., if they are related by common descent, genetic predispositions for helpful behavior may be favored if the fitness benefits to the receiver times the degree of relatedness between donor and receiver surpass the fitness costs to the donor. This algorithm has been termed "Hamilton's rule" after its originator William Hamilton (1964).
(2) Green beard effects. If there is a genetic correlation between cooperative behavior and traits allowing individuals to identify carriers of such genetic cooperation predisposition, co-operators can exercise selective altruism towards other co-operators. Identifier traits can be arbitrary like a green beard, which is the reason why this potential mechanism has been coined "green-beard effect" by its originator (Richard Dawkins 1976).
(3) Reciprocity. Altruistic behavior may be positively selected if it increases the chance of the actor to get something back in the future that overcompensates the immediate net costs of the act (Trivers 1971).
(4) Coercion. Prospective receivers may enforce cooperative behavior on potential donors against the latter's fitness interests. As in this case the cooperative behavior reduces the lifetime fitness of donors, countermeasures against such exploitation will be selected. This can lead to an evolutionary arms race just like in brood parasite – host interactions.

Regarding the evolution of cooperative breeding, there is evidence for a role of both mutualism and altruism, and regarding the latter possibility, kin selection and reciprocity seem to be the most important underlying mechanisms (Taborsky et al. 2016).

Why Delay Dispersal?

There are two major ecological constraints that may select for delayed dispersal of offspring, i.e., for a prolonged stay in the natal territory. (1) Habitat saturation, which occurs when all areas suitable for breeding are already occupied by superior competitors. This constraint has been implied to explain cooperative breeding in many bird species (Koenig and Dickinson 2016). (2) High risk, which may prevent dispersal if either the dispersal itself or the subsequent settlement entail exceptionally high risk. This ecological constraint has been identified in cooperatively breeding fishes (Heg et al. 2004).

Why Help?

Staying in the natal territory will usually lead to some form of family formation, but this does not compel individuals to help raising the dominants' offspring. As alloparental care usually entails fitness costs, there must be some benefits compensating for such seemingly altruistic behavior. As has been outlined above, there are in principle two evolutionary mechanisms responsible for costly helpful behavior shown by subordinate group members. (1) They may be related to the beneficiaries, i.e., to the dominant breeders and their offspring. (2) Alternatively, there may be reciprocal benefits to dominants and subordinates, i.e., some sort of trading of commodities between the different types of group members. In Lake Tanganyika cichlids, for instance, it has been shown that the brood care helpers benefit from being protected in the territory of dominants, and in turn they help caring for the latter's brood; in other words, they "pay-to-stay" in a safe territory. The amount of "rent" to be paid by subordinates depends on the need for help and on the demands of dominants, which are communicated to their helpers by restrained aggressive behaviors (Taborsky 2016).

Proximate Mechanisms

Important prerequisites for a proper operation of group living and cooperation in highly social species is the ability of individuals to recognize conspecifics by their group affiliation, rank, role, and/or relatedness. In some cooperative breeders, individuals specialize in different duties. This is most prominent in animals continuing to grow after maturation such as fish, because this results in body size variation between group members; small and large individuals can perform diverse duties with different efficiencies, for instance direct brood care, digging out burrows, or territory defense. Such behavioral specialization of group members is most highly developed in eusocial insects, but it sometimes occurs also in cooperatively breeding vertebrates where individuals maintain their reproductive potential such as mole rats and cichlids (Taborsky 2016).

Most importantly, relatives should be distinguished from nonrelatives, because this allows differential allocation of altruistic help towards related beneficiaries. Such distinction has been shown to exist in several species of mammals, birds, and fish. While the cooperation propensity rises with increasing relatedness in many mammals and birds, there are cases where this does not hold. In vampire bats, for example, a blood meal is often donated to related young, but most blood donations depend on reciprocal exchanges and not on relatedness. In cooperatively breeding cichlids, relatedness even reduces the helpers' propensity to care for the eggs of dominants, as the latter demand more help from unrelated subordinates. If the alternative "outside options" of subordinates are bad, for instance, because of a high mortality risk outside of a territory, the helpers are prepared to pay a high price for protection and resource use in the dominants' safe territory (Taborsky 2016).

Some studies have shown that individuals may differ consistently in their propensity to cooperate, i.e., they show "helping personalities" which are heritable and hence subject to natural selection. Dominants may respond to such personality differences of subordinate group members.

The hormonal, genetic, and epigenetic mechanisms underlying behavioral decisions of dominant and subordinate group members are hitherto little understood. As many behavioral and physiological traits of several different individuals are involved, this topic features considerable complexity, which makes it both challenging and rewarding to unravel these mechanisms. As the underlying neurophysiological and endocrine mechanisms seem to be deeply conserved among vertebrates, this allows to study general regulatory mechanisms in cooperative breeders that can be investigated under standardized experimental conditions, like cooperatively breeding cichlids (Taborsky and Taborsky 2015).

Conclusion

Cooperative breeding reflects the most complex form of social organization known among animals, featuring the highest degrees of cooperation and altruism. This applies particularly to its most extreme manifestation, eusocial organization, where individuals forego own reproduction for their entire lives to raise offspring of close relatives. The evolution of such altruism is explained through the action of kin selection or green-beard effects, as the genetic causes for lifelong reproductive abstinence can only be transmitted between generations by the offspring of individuals sharing the same genetic makeup with above average probability. In cooperative breeders that do not cross the line to complete celibacy, which is a social organization occurring in many different taxa, some form of reciprocity may also be responsible for cooperation and sharing of tasks among group members. This makes cooperative breeders a particularly useful target for studies of ultimate and proximate mechanisms of cooperation and social evolution.

Cross-References

- ▶ Adaptation
- ▶ Altruism
- ▶ Brood Care
- ▶ Cooperation
- ▶ Cooperative Foraging
- ▶ Division of Labor and Eusociality
- ▶ Evolution of Cooperation
- ▶ Food Sharing
- ▶ Helpers at the Nest
- ▶ Skin Selection
- ▶ Non-human Reciprocal Altruism
- ▶ Proximate Mechanisms
- ▶ Reciprocal Altruism and Cooperation for Mutual Benefit
- ▶ Social

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