

Altruistic Behavior, Vertebrates

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GLOSSARY

cooperative breeding Collaboration by the members of a stable social group in rearing the offspring produced by only some of the group's members.

Hamilton's rule A sufficient condition for the evolution of altruistic behavior toward genealogical relatives.

iterated Prisoner's Dilemma A model in game theory for repeated social interactions in which individuals can play either of two strategies: "cooperate" (accept benefits and return them) or "defect" (accept but not return benefits).

kin selection Changes in the spread of alleles in a population as a result of their influence on the survival or reproduction of genealogical relatives.

reciprocal altruism The return of benefits to the original actor by the beneficiary of an altruistic act.

tit for tat A conditional strategy which can eventually win (or spread during evolution) when played against defect in a game of iterated Prisoner's Dilemma.

Altruism occurs when an individual's actions benefit another at some cost to itself. Until the 1960s the occurrence of such behavior in animals was explained as a consequence of evolution for the overall good of the species. If an individual's actions resulted in a net benefit for its species, population, or social group, then its evolution seemed adequately explained. The appearance of W. D. Hamilton's paper, "The Genetical Evolution of Social Behavior" and G. C. Williams' book, *Adaptation and Natural Selection* abruptly reoriented thinking about the evolution of

altruistic behavior. Although an allele associated with altruistic behavior might make the persistence of a species or a population more likely in the long term, it is not obvious how it could spread within a population in the short term. Because altruistic individuals incur costs in order to provide benefits for others, alleles associated with altruism do not spread within a population as rapidly as others. Because of this apparent paradox, altruistic behavior quickly became one of the central issues in the study of the evolution of behavior. In the ensuing three decades much mathematical theory and intensive fieldwork has clarified these issues and raised some new ones.

I. INTRODUCTION

To appreciate these advances in understanding the evolution of altruism, it is necessary to be clear about some basic issues. Altruism is defined in terms of benefits and costs to individuals. In evolutionary biology, these benefits and costs are increases and decreases in "fitness." This term is used in modern population genetics for the rate of spread of alleles in populations. To apply it to individuals requires some care: A change in an individual's fitness means a change in its prospects for reproduction or survival that in turn affects the spread of its alleles. Altruistic behavior is thus action that tends to increase the spread of another individual's alleles and to decrease the spread of the actor's alleles. Like many words adopted by science, fitness has acquired a more restricted meaning than in ordinary usage.

Another issue that needs attention is the association between alleles and altruistic behavior. Most comparative studies of altruistic behavior have not identified the genes involved nor attempted standard genetic analyses. Most information about the genetics

of behavior comes from a relatively small number of organisms, mostly those permitting large-scale breeding. Nevertheless, diverse kinds of behavior have received attention from behavioral geneticists: aggression, mating behavior, learning, responses to stimulation, and others. The variety of behavior investigated suggests that virtually any aspect of behavior, like any other feature of organisms, has some—however small—association with particular alleles.

To reach this conclusion, we do not need to assume that any one or a few alleles “determine” a particular behavior, like a switch, nor do we need to suppose that much of the behavioral variation among individuals is associated with genetic variation. We do not need to assume that learning or culture has no influence on individuals’ behavior. Indeed, alleles might be associated with a propensity to learn a particular form of behavior. Often, the development of behavior depends as much on environmental as on genetic variation. Evolutionary biologists studying altruism, however, do assume that behavioral differences in natural environments are associated, to some degree, with genetic differences. In technical terms, this position is equivalent to assuming that altruistic behavior, like other forms of behavior, often is heritable in natural environments.

To keep the evolutionary arguments clear, altruism must refer to the immediate consequences of an action, not to the eventual possibilities. The new developments in evolutionary theory have sought conditions under which the long-term advantages of alleles associated with altruism can overcome the short-term disadvantages. The fundamental problem is to explain how alleles associated with disadvantages in the short term can persist or increase in a population in the long term.

Two prominent possibilities for the evolution of altruism in the long run are kin selection and reciprocal altruism. Kin selection occurs when the behavior of individuals affects the survival or reproduction of their genealogical relatives. Reciprocal altruism occurs when an individual receiving altruism is likely to return the favor in the future. Both possibilities were first proposed in detail in the 1960s—kin selection by W. D. Hamilton and reciprocal altruism by R. Trivers. Both have subsequently received much empirical and theoretical investigation.

II. KIN SELECTION

Kin selection occurs whenever individuals affect the reproduction and survival of their genealogical relatives. Because relatives have a greater chance of sharing identical alleles than do randomly chosen individuals, an allele can spread in a population if an individual carrying it has a sufficiently large influence on the survival or reproduction of a relative, even at some cost to its own survival or reproduction. This cost (c) to the actor must be less than the benefit (b) to the relative weighted by the coefficient of genealogical relatedness (r , the probability that the relative has a copy of the actor’s allele as a result of descent from a common ancestor): $c < br$. This expression is a sufficient condition for the evolution of altruism among genealogical relatives and is known as Hamilton’s rule.

This rule applies strictly only to large randomly mating populations and to alleles not subject to strong selection. If there is significant inbreeding in the population, then the coefficient of relatedness needs adjustment for the background sharing of alleles identical by descent. Alternatively, the rule can be rephrased to include any background relatedness. Consider the decision an individual faces when it can promote the spread of its alleles either by direct or by collateral descent. An allele associated with altruism will spread provided that the number of additional progeny produced by a relative as a result of an altruist’s actions (g_a) \times the probability that those progeny will have the altruist’s allele (r_a) exceeds the number of progeny a nonaltruist (egotist) individual could instead produce (g_e) \times the probability that these progeny will have the egotist’s allele (r_e): $g_e r_e < g_a r_a$. This corollary of Hamilton’s rule incorporates any background sharing of alleles identical by descent as a result of inbreeding in the population because inbreeding increases the probability that an individual will share alleles with its own progeny.

This rephrased rule also resolves the problem of whether or not to consider parental behavior as altruism. Clearly, parental behavior often involves costs for the parents and benefits for the offspring, but in this case the recipients of benefits are also the direct bearers of the actors’ genes. Application of Hamilton’s

original rule to this sort of cross-generational helping is problematic. The situation is clearer when we focus on alternatives for producing new copies of alleles at any one time: copies of alleles in an individual's own offspring versus copies of alleles identical by descent in the contemporaneous offspring of relatives. The rephrased rule, which applies explicitly to this case, makes the condition for the evolution of altruism by kin selection clear: Altruism evolves when alleles associated with it are more likely to be passed to new individuals in the population than are alleles associated with egotism.

In many cases of helping, several individuals assist a recipient. For instance, the cooperatively breeding species discussed later often have several helpers associated with each breeding pair. Note that Hamilton's rule (in the original or rephrased form) requires careful accounting for each individual's contribution to the breeders' reproduction. Each individual's assistance is that portion of the breeders' reproduction that would not occur if the helping individual were not present. Studies of kin selection in vertebrates have focused on measuring the effects of helpers on survival and reproduction of relatives, on establishing genealogical relationships within groups, and on determining which members of groups in fact reproduce (see Section IV).

III. RECIPROCAL ALTRUISM

If an altruist incurs an immediate cost that is more than recuperated in the future, then alleles associated with altruism will have a long-term advantage in a population. Thus, reciprocal altruism addresses the long-term advantages of altruism by considering the probability that an altruist and its beneficiary will exchange roles at some time in the future. A simple model from game theory, the iterated prisoner's dilemma, clarifies a fundamental issue for reciprocal altruism. This two-person game supposes that individuals can follow either of two strategies, "cooperate" or "defect," in repeated encounters. Because there is usually no necessary connection between the providing of assistance and its subsequent return, there is always the possibility that some individuals

might defect by accepting but not returning favors. The question thus becomes, under what conditions can alleles associated with altruism spread in a population that also includes alleles associated with defection?

In their seminal analysis of the iterated prisoner's dilemma from an evolutionary point of view, Axelrod and Hamilton proposed that a combination of conditional behavior (cooperate only when your partner has cooperated in the preceding encounter) and memory (recognition) of individual partners can prevail against defection. To ensure cooperation when possible, individuals must also either try cooperation at the outset or randomly at low frequencies. This conditional behavior, called tit for tat, requires substantial cognitive abilities. Few studies have managed to demonstrate all the assumptions: conditional behavior, memory of interactors, and costs for the actors and benefits for the recipients.

Both field and laboratory studies have sought to confirm that animals are capable of the kinds of contingent behavior required by these theoretical analyses. For instance, both baboons and antelopes are more likely to groom individuals that have groomed them previously than other individuals of equal kinship. Rhesus monkeys are more likely to behave aggressively toward an individual that finds food but does not announce it with a characteristic call than toward those that do announce food. Vampire bats in Central America share their meals of blood only with others that have shared their meals in the past. A territorial male hooded warbler mostly ignores an established neighbor singing near its territorial boundary, but only when the neighbor has not recently intruded into its territory. Small fish provide a laboratory model of reciprocal altruism. Guppies and three-spined sticklebacks will approach a predatory fish visible in an adjacent aquarium, apparently for inspection. An inspecting fish will come closer to the predator when a parallel mirror makes it appear that another fish accompanies it than when a diagonal mirror makes the accompanying fish appear to lag behind. These studies of a variety of vertebrates suggest that individuals are often capable of behaving contingently toward social partners in the way required for the evolution of reciprocal altruism.

IV. COOPERATIVE BREEDING

The most prominent example of altruistic behavior in vertebrates is cooperative breeding, as practiced by many birds and mammals. In these species, individuals live in stable social groups that include more than two individuals old enough to breed when an opportunity arises. In many cases, only a subset of these individuals actually breed, yet all individuals participate in activities that promote the breeders' reproduction. These activities can include building or maintaining nests or dens, defending territories, guarding against predators, feeding the young, and feeding the parents while they in turn care for the young. Because these groups often consist of genealogical relatives, some of which breed and others help, they provide possibilities for the evolution of altruism by kin selection. In addition, the stability of membership in these groups provides opportunities for reciprocity. Several examples can illustrate both these common themes and also the diversity among them.

White-fronted bee-eaters in east Africa nest in colonies in earth banks, where each pair digs a long burrow for its nest. Offspring from previous years often assist in feeding the young. The number of progeny produced in a nest increases linearly with the number of adults feeding the young, with each additional helper adding about 0.3 additional fledged young. Complexities arise as helpers eventually acquire mates of their own. They then often concentrate on their own nests. If, however, a nest fails, the birds often return to their parents' nests to help there; mates usually separate temporarily in this case. On occasion, a parent interferes with the nesting attempts of its previous offspring so that they abandon their own nests and return to help the parents.

Florida scrub jays nest in large territories in which the birds find all of their food. Young often remain in their parents' territories for 1 or more years and help to defend the territory against other jays, to feed the parents' young (usually their siblings), and to defend the parents' nests against predators. The help from a previous years' offspring increases a pair's annual reproductive success by almost one additional offspring, but there is no additional increase as the number of helpers increases above one. Males stay

longer on average than females, in some cases long enough to inherit the territory if their father dies. Females eventually leave to find a mate on another territory. Male helpers provide significantly more assistance in raising the young than do females. By helping, males thus adopt a long-term strategy for enhancing their chances for reproduction.

Stripe-backed wrens illustrate this pattern even more clearly. They live in groups averaging five or six adults, although some pairs and single birds also defend territories. Young almost always remain in their natal territories until opportunities arise to breed. A male usually stays in his natal territory for life; if he survives long enough, he succeeds to the breeding position after the deaths of his father and older brothers. A female remains until she finds a vacancy in a nearby group. DNA fingerprinting has established that only one pair breeds in most groups. Exceptions occur in 10% of groups, always those in which the female breeder has recently been replaced. In these groups, the oldest male helper sires on average 15% of offspring. Males never breed with their mothers because the oldest helping male in a group never mates with the breeding female unless she has immigrated since he was born. On average, all ages and both sexes of helpers provide equal contributions to raising the young, although individuals vary considerably in the amount of help they provide. Pairs without helpers, or with only one, produce very few young on average, and consequently few individuals attempt to breed as unassisted pairs. The assistance of two helpers, in contrast, results in a significant increase in nesting success, apparently mostly as a result of better protection of the nest from predators. Because there is such a premium on breeding in a large group, competition among young females to fill vacancies in large groups is intense. Probably for this reason, young females suffer higher mortality than any other segment of the adult population.

Acorn woodpeckers also live in groups on large territories in which the entire group works to store acorns during autumn and winter. Each territory includes several trees in which innumerable small holes are prepared in the bark or dead wood, each to receive one acorn. A group cannot breed successfully without this stored food to provide nutrients in late winter and early spring. Parentage is much more

complex in this species. Often a group of males defends a territory, and these males, as revealed by DNA fingerprinting, mate jointly with the females present. Females compete to have their eggs retained in the nest by removing each other's eggs. Eventually one or more females produce the eggs raised by the entire group. Young remain in their natal territory for a year or more and during this time do not mate with their parents nor interfere with their reproduction, so some groups can eventually resemble the extended families seen in stripe-backed wrens or Florida scrub jays. Most groups, however, consist of several males, all of which mate with several females, which in turn compete with each other to have their eggs incubated.

Fairy wrens of several species represent a few of the dozens of species of Australian birds that breed cooperatively. In this case young remain in their natal territory but, unlike the species already considered, the males do not usually breed there. Instead, DNA fingerprinting shows that they routinely court and mate with females in neighboring territories. In these species, the adult sex ratio is skewed strongly toward males, apparently because of high mortality of females during nesting. Because there are so many vacancies for females, young females usually emigrate at an early age, whereas males remain in their natal territories and attempt to mate with neighboring females. The presence of these extra males does not have a significant influence on nesting success.

Pied kingfishers in African woodlands often remain with their parents after independence and help to raise subsequent broods, particularly when conditions are harsh. Sometimes individuals abandon their parents and take subordinate positions helping other adults. In this case, the advantage of taking a subordinate position in a good territory can pay off if the breeder of the same sex dies. The subordinate is then in line to succeed to the breeding position.

Gray wolves and African hunting dogs provide cases of mammals that breed cooperatively. In both species, normally one pair in a pack reproduces, although exceptions apparently occur when food is abundant. Nevertheless, all members of the pack share food with the lactating mother and later with the growing puppies. Pack members are often previ-

ous years' offspring, but at least in African hunting dogs a cohort of the same sex sometimes leaves its natal pack to evict like-sex individuals from another pack. Reports of multiple paternity in packs might apply to such cases, much as in acorn woodpeckers.

Dwarf mongooses provide a more thoroughly documented case of cooperative breeding in mammals. Social groups average about nine individuals at least 1 year old, of which two normally breed, although the extent of multiple paternity has not yet been thoroughly investigated. In this species, as in many cooperatively breeding birds, helpers have only modest effects on reproductive success in the group. As a consequence, helping to produce collateral relatives makes a relatively minor contribution to the transmission of an individual's genes.

Naked mole rats' bizarre social behavior has evoked much interest. These obligately subterranean rodents live in large social groups, each of which includes a single exceptionally large reproductive female. The analogy with social insects is inviting, except that the reproductive female mates with several males in her own colony. Almost nothing is known about acquisition of breeding status or dispersal among colonies in natural circumstances.

African lions, like wolves and hunting dogs, hunt together and rear their young communally. One female in a pride usually remains with young cubs of several pride members while the others are hunting, and the attendant female then nurses all cubs indiscriminately. Females usually remain in their natal pride, so the females in a pride are usually close relatives. Nevertheless, pride members do not all contribute equally to the group's welfare; for instance, individual females differ consistently in their roles in approaching simulated intruders in the pride's territory.

Another example of communal breeding is the groove-billed ani, one of several species of black tropical American cuckoos. Breeding often involves two or three pairs using the same nest. Most young disperse from their natal territory in their first year, with the exception of a minority of males, so that pairs sharing a nest are usually not closely related genealogically. Females compete to have their own eggs retained in the communal nest. Each female ejects others' eggs from the nest until she herself

begins to lay, so one female in each group, the last to begin laying, usually produces most of the eggs incubated. The size of a group has modest effects on the survival of adults in the group and on young reared to independence.

These examples of cooperative breeding vary in important ways. In particular, there is much variation in the influence of potential helpers on reproductive success by breeders, in the relatedness of helpers to breeders, and in the distribution of reproduction among group members. Nevertheless, four important generalities emerge.

First, nonbreeding individuals usually remain with their close relatives. Although the contributions of helpers to the success of breeders are too low, in most cases, for kin selection to provide a sufficient explanation for helping, kin selection does successfully predict whom an individual helps. If nonbreeders help at all, they overwhelmingly help relatives.

Second, most long-term studies of cooperative breeders have revealed that individuals stand to gain by joining groups as nonbreeders and queuing for subsequent opportunities to breed. In this way, cooperative breeding is often a long-term strategy for maximizing reproductive success combined with some short-term advantages from kin selection. For the breeders, retention of offspring in their territory is a long-term form of parental care.

Third, the association of relatives in cooperative breeders does not preclude competition among them. Although it is often clear that individuals help relatives rather than unrelated individuals, they do not necessarily help relatives rather than promote their own interests; for example, competition for breeding opportunities within groups of bee-eaters or acorn woodpeckers.

Finally, individuals do not necessarily have to discriminate degrees of relatedness in order to associate with relatives. In many cooperatively breeding species, individuals associate with relatives simply as a consequence of remaining in their natal groups or with individuals that raised them.

Much about cooperative breeding remains to be clarified. In only a few cases has DNA fingerprinting actually established the patterns of paternity. Even so, only long-term studies of large marked populations can establish the genealogical structure of

populations with such complex social structure. In addition, little is known about the behavioral mechanisms that produce the complex social interactions in cooperatively breeding species, especially individuals' capabilities for discriminating degrees of relatedness or recognizing other group members.

See Also the Following Articles

AGGRESSIVE BEHAVIOR; ALTRUISM IN INSECT REPRODUCTION

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