Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates

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In cooperatively breeding vertebrates, nonbreeding helpers raise young produced by dominant breeders. Although the evolution of cooperative breeding has often been attributed primarily to kin selection (whereby individuals gain "indirect" benefits to their fitness by assisting collateral relatives), there is increasing evidence that helpers can be unrelated to the young they are raising. Recent studies also suggest that the indirect benefits of cooperative behavior may often have been overestimated while the direct benefits of helping to the helper's own fitness have probably been underestimated. It now seems likely that the evolutionary mechanisms maintaining cooperative breeding are diverse and that, in some species, the direct benefits of helping may be sufficient to maintain cooperative societies. The benefits of cooperation in vertebrate societies may consequently show parallels with those in human societies, where cooperation between unrelated individuals is frequent and social institutions are often maintained by generalized reciprocity.

Kin selection (*1*) is widely thought to play a dominant role in the evolution of specialized cooperative societies, where breeding individuals rely on the assistance of nonbreeding helpers to raise their young (*2–5*). In eusocial insects, kin selection provides the only viable explanation for the evolution and maintenance of worker sterility (*6–8*), while in many obligately cooperative birds and mammals, helpers are usually relatives of dominant breeders that have not yet left the group, or individuals whose own breeding attempts have failed and who have returned to assist kin in their original group (*3–5*). In several facultatively cooperative birds, individuals are more likely to return and help in groups that contain close relatives (*9, 10*) and, in a few cooperative societies, close relatives contribute more to cooperative activities than do distant relatives or unrelated individuals (*11*).

Although relatedness between group members will usually facilitate the evolution of cooperation (*7*), the view that kin selection provides a satisfactory general explanation of specialized cooperative societies now appears less compelling than it did 20 years ago (*5*), for several reasons. First, most permanent groups of social animals consist of relatives and, if haplodiploid species are excluded, it is not clear that the degree of relatedness is consistently higher in cooperative breeders than in other species that live in stable groups but do not breed cooperatively. In many societies of vertebrates as well as invertebrates, differences in contributions to rearing young do not appear to vary with the relatedness of helpers (*5, 12–14*), and several studies of cooperative birds and mammals have shown that helpers can be unrelated to the young they are raising and that unrelated helpers invest as heavily as close relatives (*14–16*). Second, the relative importance of "indirect" fitness benefits acquired by helping collateral kin has probably been overestimated. Estimates of indirect benefits have sometimes incorporated the effects of helping on direct descendants (offspring and grand-offspring) as well as on collateral kin. Benefits received by helpers from their kin and those they confer on kin have often both been included, leading to double accounting of kin-selected benefits (*17*). Also, costs arising from competition between relatives for resources or mates have seldom been set against the indirect benefits of cooperation (*18*). Third, the costs of helping may often have been overestimated. Estimates of the costs of helping based on comparisons of the fitness of helpers versus established breeders can be misleading. This is because younger animals may increase their survival by waiting in their natal group so that the actual costs of helping may be limited to the costs of cooperative behavior per se. Moreover, individual contributions to helping behavior are commonly adjusted to variation in nutrition (*14*) so that even where cooperation has substantial energetic costs, effects on the survival or breeding success of helpers may be small. While the indirect benefits of cooperative behavior may have been overestimated, direct benefits to the helpers' own fitness have probably been underestimated. Recent studies of vertebrates show that contributing to cooperative activities can increase the direct fitness of helpers by raising their survival, mating success (*5, 19, 20*), ability to rear offspring (*21*), or chances of successful dispersal. In some cases, this is because fitness increases with group size and helpers gain substantial deferred benefits by contributing to rearing young in their own group (*22, 23*). In addition, helping may sometimes reduce the chance that helpers will be ejected from their original group by dominants (*24*), although there is little empirical evidence that this is the case.

Fig. 1. In lions (*Panthera leo*), larger groups of males are more likely to acquire and maintain access to breeding females, while larger female groups are better able to defend their young and their territories against immigrant males as well as against neighboring prides (*25*).

Parasitism, By-Product Mutualism, and Coercion

In some societies, it may be to the advantage of individuals to coordinate their activities with those of other group members, but the consequences of an individual's behavior for the fitness of the animals it interacts with may be neutral or even negative. For example, it may often be to the advantage of solitary lions to join groups even if this reduces the feeding success or fitness of the individuals they join, because group membership increases their capacity to defend their territory

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or their young against rival groups (*25, 26*) (Fig. 1). Interactions of this kind may best be regarded as parasitic rather than cooperative, because one individual exploits another. Another possibility is that some (perhaps many) forms of apparently cooperative behavior are "by-product mutualisms," in which an individual's behavior maximizes its own immediate fitness and any positive effects on the fitness of other individuals are coincidental and do not contribute to the selection pressures maintaining the behavior (*4, 27*). For example, Arabian babblers (Fig. 2) may go on sentinel duty once they have collected sufficient food because this maximizes their own survival in a predator-rich environment if no other individual is on guard (*28*). The fact that other individuals can detect the approach of predators by watching them may not contribute to the maintenance of "sentinel" behavior.

Although parasitism and by-product mutualism may be common and may often lead to the formation of groups, neither provides a satisfactory explanation of cases where helpers contribute to risky or costly activities (such as feeding and guarding young) and where their contributions are adjusted to the age and needs of the individuals they are assisting (*29, 30*). One possibility is that group members are coerced into contributing to these activities through harassment or the threat of punishment or eviction by dominant breeders (*31*). However, theoretical models suggest that coercion is only capable of maintaining specialized cooperative behavior under rather restrictive conditions (*32*). Occasional coercion probably occurs in many cooperative societies (*31, 33, 34*), but, in specialized cooperative breeders, there is little evidence that individuals who contribute little to cooperative activities are ejected from groups. Helpers commonly continue to care for young when dominant breeders are removed, although their work levels may fall (*35*).

Mutualism and Reciprocity

For more specialized cooperative societies, the likely alternative explanation to kin selection is probably some form of mutualism or reciprocity. Like interspecific mutualism (*36*), intraspecific mutualism can take a wide variety of forms. Benefits may be immediate (as in cases where individuals groom each other simultaneously) or may be deferred (for example, where social birds contribute as juveniles to building a communal nest that they may use in adulthood). Two or more participating individuals may exchange beneficial acts in turn ("reciprocal altruism" or "cost-counting" reciprocity). Alternatively, all individuals may contribute to some common good, such as a communal nest, from which all group members subsequently draw automatic benefits ("generalized" reciprocity). Where large groups can displace smaller ones, it may even be to the advantage of all group members to contribute to rearing young because this maintains or increases the size of their group ("group augmentation").

The nature of the direct benefits that different participants gain from cooperative interactions may also vary. In some cases, benefits may be in the same currency; in others, they may contribute to different components of fitness. In some avian societies, for example, the breeding female is a potential mate for male helpers in the future, and individuals may benefit from feeding her or her young because this increases their subsequent chances of mating with her (*5, 11*). The benefits of cooperative behavior may be shared equally or unequally between participants, eventually grading into parasitism (see above). Similarly, the behavior of both (or all) participants may be adapted to increasing each other's fitness (to their own eventual benefit), or the behavior of some parties may be adapted to increasing the fitness of others while any beneficial consequences of the behavior of others may be an unselected by-product ("pseudo-reciprocity") (*37*). Few of these different kinds of mutualistic interactions have been clearly defined, and in practice they may often be combined with each other as well as with components of kin selection.

By far the largest body of theoretical research devoted to direct benefits of this kind has focused on reciprocal exchanges of beneficial behavior between individuals. Many studies have explored the evolution of cooperative strategies in models of the Iterated Prisoner's Dilemma (IPD) (*38, 39*), which envisage a situation where two partners can either exchange mutually beneficial acts ("cooperate") or refuse to do so ("defect"). In these models, payoffs are normally set so that pairs of individuals that cooperate achieve higher fitness than pairs that defect, whereas individuals that defect while their partners cooperate gain the highest payoffs of all (*4*). Because of this distribution of payoffs and the consequent benefits of cheating, it is difficult for pure cooperation to spread, and retaliatory strategies that involve copying the partner's previous actions (such as "tit for tat") or strategies based on the success of previous outcomes (such as "win-stay, lose-shift") are usually most successful (*4*).

Although reciprocal altruism is evidently involved in the evolution of some forms of cooperation (*4*), the relevance of IPD models to the evolution of specialized cooperative breeding is debatable. Breeders and helpers rarely exchange roles in cooperative societies, and the most convincing examples of reciprocal altruism involve less valuable commodities, such as food or grooming (*4*). Moreover, there is little evidence that helpers retaliate to reductions in the level of other group members' contributions by reducing their own input, as IPD models predict; instead, they commonly appear to "cover" for each other by increasing their level of contributions when others are indisposed (*40*). Finally, IPD models seldom consider a range of processes that are likely to strengthen the benefits of cooperation. These include asymmetries in the costs and benefits of cooperating, competition for cooperative partners (*41*), the possibility that defectors will be punished by partners or by other group members (*31*), and competition with other groups (*22*). Where these mechanisms increase the payoffs of cooperation above those of defection, the Prisoner's Dilemma can evaporate and simple cooperative strategies may be favored.

Fig. 2. In Arabian babblers (*Turdoides squamiceps*), sentinels may maximize their own individual fitness by guarding (*28*).

Group Augmentation

Although group augmentation has been suggested many times (*42*), it has received less attention from theoreticians than reciprocal altruism, partly because it has been supposed that cooperative strategies maintained by group augmentation would be susceptible to erosion by cheats (*4*). However, recent models show that if group members automatically share benefits derived from increased group size, cooperative behavior can be maintained in small groups by group augmentation alone, and that (in combination with kin selection) group augmentation can produce elevated levels of cooperative behavior and cheating may not be favored unless the costs of helping are high (*43, 44*). Where the benefits of increasing group size are not automatic and depend on the contributions of group members to cooperative activities, coopera-

Fig. 3. In meerkats (*Suricata suricatta*), the foraging success, growth, breeding success, and survival of all group members increase with group size (*50*).

tion can still be maintained by group augmentation, but its initial evolution requires some previous tendency to help. As long as the costs of low levels of cooperation are small, this can be very low and could be provided by by-product mutualism (*27, 45*) or by weak kin selection.

In specialized cooperative societies of vertebrates as well as in some invertebrates, there is increasing empirical evidence that the fitness of all group members commonly increases with the size of their group, because group size increases the capacity of group members to catch, produce, or defend food (*46, 47*), to detect or repel predators (*13, 40*), to disperse in large subgroups (*48, 49*), or to raise young successfully (*2, 50*) (Fig. 3). In addition, both among vertebrates and among invertebrates, larger groups usually compete successfully against smaller ones, sometimes killing their members or driving them out of their territories (*51, 52*) (Fig. 4). Consequently, individuals living in small groups often have slow growth rates (*50*), low survival, and low breeding success (*47*), and hence small groups may frequently become extinct (*53*). Group augmentation appears to offer an alternative explanation for many forms of cooperative behavior that are often attributed to kin selection and also provides a possible explanation for a number of phenomena that kin selection cannot easily account for. These include the involvement of unrelated animals in cooperative activities (*5, 14*), the acceptance or kidnapping of unrelated juveniles from neighboring groups (*54, 55*), and the tendency for groups to kill litters born to their neighbors (*56*).

Like kin selection and by-product mutualism, group augmentation cannot account for all forms of cooperative breeding. Breeding alliances between unrelated males are unlikely to affect group size and may often be maintained by reciprocal altruism or by-product mutualism (*19, 26*); in some facultatively cooperative breeders, helpers do not appear to increase the growth or survival of the young they are rearing (*57, 58*); and, unless group selection is invoked, group augmentation cannot account for the evolution of sterile worker castes in social insects. In practice, the effects of group augmentation and kin selection may often be difficult to separate. For example, cooperative behavior that increases a helper's direct fitness by increasing group size may also increase the fitness of its relatives in the same group, while nepotistic acts that increase the survival of relatives will also increase a helper's direct fitness if survival increases with group size.

Synthesis

Recent research into the evolution of specialized cooperative societies has at least four important implications. First, many apparently cooperative actions may generate immediate direct benefits to individuals and any effects on "recipients" may be negative, neutral, or coincidental. In the future, it may be useful to tighten the definition of cooperative behavior by distinguishing between socially coordinated behavior (where individuals adjust their actions to the presence or activities of others so as to maximize their own immediate direct fitness) and cooperative behavior (where individuals perform activities that are adapted to increasing the fitness of others because this ultimately contributes to their own direct or indirect fitness). Socially coordinated behavior is widespread in animal societies and may be maintained by parasitism or by-product mutualism, but these mechanisms are less likely to account for cooperative behavior defined in this way.

Second, mutualism may play a more important role in the evolution of specialized cooperative societies than has previously been supposed. Where the fitness of group members increases with group size, strong selection pressures may favor simple cooperative strategies, and there is no reason to suppose that these will necessarily be eroded by cheating (*23, 43*). There is now a need to estimate the relative magnitude of direct and indirect benefits of cooperative behavior, to investigate whether mutualistic benefits are large enough to maintain cooperative behavior on their own, and to identify and test predictions about the distribution of cooperative behavior that discriminate between hypotheses based on kin selection and those based on mutualism. We also need to investigate the ways in which different selection pressures interact, because the relative importance of particular mechanisms may change during the evolution of cooperative societies. For example, an initial tendency for kin selection to favor cooperation could encourage the development of cooperative breeding, leading to the co-adaptation of life-history variables and the eventual evolution of an obligately cooperative society where all group members benefit from assisting breeders.

Third, despite superficial similarities between cooperative societies, it seems likely that there are qualitative as well as quantitative differences in the evolutionary mechanisms maintaining cooperation in different species. For example, in some avian societies, helpers may increase their chances of breeding with the dominant female by feed-

Fig. 4. In fire ants (*Solenopsis wagneri*), new breeding groups consisting of several unrelated queens and their progeny compete intensely with their neighbors, and the success of groups increases with their size (*51*).

ing her young, whereas in others, helpers are unlikely to breed with the dominant female, and either kin selection or mutualism probably maintains cooperation (*5*). Similarly, the available evidence suggests that the relative importance of mutualism and kin selection may vary between societies.

Finally, if mutualism proves to be important in maintaining cooperative animal societies, the benefits of cooperation in animals may be more similar to those of cooperation in humans than has been previously supposed. In humans, unrelated individuals commonly assist each other (*59*), generalized reciprocity appears to be important in maintaining many social institutions (*60*), and, where human groups compete, their size often has an important effect on the outcome (*61*). "God," as Shaw's cynical Bastard of Orléans remarks to an optimistic Joan of Arc, "is on the side of the big battalions." All three trends appear to have close parallels in other cooperative animals.

References and Notes

→ W. D. Hamilton, *J. Theor. Biol.* **7**, 1 (1964).
2. J. L. Brown, *Helping and Communal Breeding in Birds* (Princeton Univ. Press, Princeton, NJ, 1987).
3. S. T. Emlen, in *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs, N. B. Davies, Eds. (Blackwell Scientific, Oxford, 1991), pp. 301–337.
4. L. A. Dugatkin, *Cooperation Among Animals* (Oxford Univ. Press, Oxford, 1997).
5. A. Cockburn, *Annu. Rev. Ecol. Syst.* **29**, 141 (1998).
6. R. H. Crozier, P. Pamilo, *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection* (Oxford Univ. Press, Oxford, 1996).
7. A. F. G. Bourke, in *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs, N. B. Davies, Eds. (Blackwell Scientific, Oxford, 1997), pp. 203–227.
8. ———, N. R. Franks, *Social Evolution in Ants* (Princeton Univ. Press, Princeton, NJ, 1995).
9. S. T. Emlen, P. H. Wrege, *Behav. Ecol. Sociobiol.* **23**, 305 (1988).
→ A. F. Russell, B. J. Hatchwell, *Proc. R. Soc. London Ser. B* **268**, 2169 (2001).
11. H. U. Reyer, *Anim. Behav.* **32**, 1163 (1984).
12. J. E. Strassmann, C. R. Solis, C. R. Hughes, K. F. Goodnight, D. C. Queller, *Behav. Ecol. Sociobiol.* **40**, 71 (1997).
13. D. C. Queller, J. E. Strassmann, *Bioscience* **48**, 165 (1998).
→ T. H. Clutton-Brock *et al.*, *Proc. R. Soc. London Ser. B* **267**, 301 (2000).
→ P. O. Dunn, A. Cockburn, R. A. Mulder, *Proc. R. Soc. London Ser. B* **259**, 339 (1995).
16. R. D. Magrath, L. A. Whittingham, *Behav. Ecol. Sociobiol.* **41**, 185 (1997).
→ S. Creel, *Proc. R. Soc. London Ser. B* **241**, 229 (1990).
18. S. A. West, M. G. Murray, C. A. Machado, A. S. Griffin, E. Herre, *Nature* **409**, 510 (2001).
19. J. Grinnell, C. Packer, A. E. Pusey, *Anim. Behav.* **49**, 95 (1995).
20. A. Zahavi, A. Zahavi, *The Handicap Principle: A Missing Piece of Darwin's Puzzle* (Oxford Univ. Press, Oxford, 1997).
21. J. Komdeur, *Behav. Ecol.* **7**, 326 (1996).
22. A. E. Pusey, C. R. Packer, in *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs, N. B. Davies, Eds. (Blackwell Scientific, Oxford, 1997), pp. 254–283.
23. T. H. Clutton-Brock *et al.*, *J. Anim. Ecol.* **68**, 672 (1999).
24. A. J. Gaston, *Am. Nat.* **112**, 1091 (1978).
25. C. R. Packer *et al.*, *Am. Nat.* **136**, 1 (1990).
26. R. G. Heinsohn, C. R. Packer, *Science* **269**, 1260 (1995).
27. P. A. Bednekoff, *Am. Nat.* **150**, 373 (1997).
→ J. Wright, E. Berg, S. R. de Kort, V. Khazin, A. A. Maklakov, *Proc. R. Soc. London Ser. B* **268**, 821 (2001).
29. R. G. Heinsohn, S. Legge, *Trends Ecol. Evol.* **14**, 53 (1999).
→ M. B. Manser, *Proc. R. Soc. London Ser. B* **266**, 1013 (1999).
31. T. H. Clutton-Brock, G. A. Parker, *Nature* **373**, 209 (1995).
32. H. Kokko, R. A. Johnstone, J. Wright, *Behav. Ecol.*, in press.
33. R. A. Mulder, N. E. Langmore, *Anim. Behav.* **45**, 830 (1993).
34. S. Balshine Earn, C. Neal, H. Reid, M. Taborsky, *Behav. Ecol.* **9**, 432 (1998).
35. H. K. Reeve, *Nature* **358**, 147 (1991).
36. J. D. Hoeksema, E. M. Bruna, *Oecologia* **125**, 321 (2000).
37. R. C. Connor, *Biol. Rev.* **34**, 1652 (1995).
38. R. Axelrod, W. D. Hamilton, *Science* **211**, 1390 (1981).
39. R. Axelrod, L. D'Ambrosio, *Annotated Bibliography on the Evolution of Cooperation* (1994), http://pscs.physics.lsa.umich.edu/RESEARCH/Evol_of_Coop_Bibliography.html.
40. T. H. Clutton-Brock *et al.*, *Science* **284**, 1640 (1999).
41. R. Noë, *Anim. Behav.* **39**, 78 (1990).
42. P. Kropotkin, *Mutual Aid* (Heinemann, London, ed. 3, 1908).
→ H. Kokko, R. A. Johnstone, T. H. Clutton-Brock, *Proc. R. Soc. London Ser. B* **268**, 187 (2001).
→ G. Roberts, *Proc. R. Soc. London Ser. B* **265**, 427 (1998).
45. I. G. Jamieson, *Am. Nat.* **133**, 394 (1989).
46. E. O. Wilson, *The Insect Societies* (Belknap, Cambridge, MA, 1971).
47. S. Creel, N. M. Creel, *The African Wild Dog* (Princeton Univ. Press, Princeton, NJ, in press).
48. J. D. Ligon, S. A. Ligon, *Nature* **280**, 174 (1978).
→ F. Courchamp, B. T. Grenfell, T. H. Clutton-Brock, *Oikos* **91**, 311 (2000).
50. T. H. Clutton-Brock *et al.*, *Science* **293**, 2446 (2001).
51. G. Bernasconi, J. E. Strassmann, *Trends Ecol. Evol.* **14**, 477 (1999).
52. J. D. Bygott, in *The Great Apes*, D. A. Hamburg, R. McCown, Eds. (Cummings, Menlo Park, CA, 1979), pp. 405–427.
53. F. Courchamp, T. H. Clutton-Brock, B. Grenfell, *Trends Ecol. Evol.* **14**, 405 (1999).
→ G. Bernasconi, L. Keller, *Proc. R. Soc. London Ser. B* **263**, 509 (1996).
55. R. G. Heinsohn, *Anim. Behav.* **41**, 1097 (1991).
→ T. H. Clutton-Brock *et al.*, *Proc. R. Soc. London Ser. B* **265**, 2291 (1998).
57. M. L. Leonard, A. G. Horn, S. F. Eden, *Behav. Ecol. Sociobiol.* **25**, 357 (1989).
58. R. D. Magrath, I. S. M. Yezerinac, *J. Anim. Ecol.* **66**, 658 (1997).
59. M. Ridley, *The Origins of Virtue* (Viking, London, 1996).
60. R. D. Putnam, *Bowling Alone* (Simon & Schuster, New York, 2000).
61. N. A. Chagnon, in *Evolutionary Biology and Human Social Behaviour*, N. A. Chagnon, W. Irons, Eds. (Duxbury, Belmont, CA, 1979), pp. 86–131.

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REVIEW: CONFLICT AND COOPERATION

Cooperation and Competition Between Relatives

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Individuals are predicted to behave more altruistically and less competitively toward their relatives, because they share a relatively high proportion of their genes (e.g., one-half for siblings and one-eighth for cousins). Consequently, by helping a relative reproduce, an individual passes its genes to the next generation, increasing their Darwinian fitness. This idea, termed kin selection, has been applied to a wide range of phenomena in systems ranging from replicating molecules to humans. Nevertheless, competition between relatives can reduce, and even totally negate, the kin-selected benefits of altruism toward relatives. Recent theoretical work has clarified the processes and selective forces underlying this effect and has demonstrated the generality of the effect of competition between relatives.

Kin selection theory provides a solution to the problem of altruism (*1*, *2*). The problem is, why should an individual forego reproduction, and instead help another to breed (e.g., in cooperatively breeding birds, in mammals such as meerkats, or in social insects such as ants, bees, wasps, and termites)? This can be explained relatively easily if they are helping their close relatives reproduce and hence are still passing on their genes to the next generation, albeit indirectly. A pleasingly simple and elegant way of quantifying this idea of kin selection is Hamilton's rule (*1*, *2*). This states that individuals will be selected to perform altruistic behaviors for the benefit of relatives when $rb - c > 0$, where c is the fitness cost to the altruist, b is the fitness benefit to the beneficiary, and r is their genetic relatedness.

More generally, kin selection theory and Hamilton's rule can be applied to any situation involving conflict or cooperation. For example, it has been suggested that in birds and mammals, individuals are more likely to warn close relatives about the approach of predators; or that higher relatedness between parasites within a host will lead to less intense competition for the host