

- FREAN, M. R. (1994). *Proc. R. Soc. London B* **257**, 75–79.
- HAMILTON, W. D. (1964). *J. Theor. Biol.* **7**, 1–51.
- HEINSOHN, R., and PACKER, C. (1995). *Science* **269**, 1260–1262.
- MANNING, C. J., WAKELAND, E. K., and POTTS, W. K. (1992). *Nature* **360**, 581–583.
- MAYNARD-SMITH, J., and SZATHMARY, E. (1995). *The Major Transitions in Evolution*. Freeman, San Francisco.
- NOË, R., and HAMMERSTEIN, P. (1994). *Behav. Ecol. Sociobiol.* **35**, 1–11.
- NOWAK, M., and SIGMUND, K. (1993). *Nature* **364**, 56–58.
- PUSEY, A. E., and PACKER, C. (1994). *Behav. Ecol.* **5**, 362–374.
- RATNIEKS, F. L. W., and VISSCHER, P. K. (1989). *Nature* **342**, 796–797.
- TRIVERS, R. L. (1971). *Q. Rev. Biol.* **46**, 35–57.
- VEHRENCAMP, S. L. (1983). *Anim. Behav.* **31**, 667–682.
- VRIES, P. J. (1992). *Scienze*, 76–82.
- WADE, M. J. (1977). *Evolution* **33**, 749–764.
- WEST EBERHARD, M. J. (1975). *Q. Rev. Biol.* **50**, 1–33.
- WILKINSON, G. S. (1984). *Nature* **309**, 181–184.
- WILLIAMS, G. C. (1966). *Adaptation and Natural Selection*. Princeton Univ. Press, Princeton, NJ.
- WILSON, D. S., and SOBER, E. (1994). *Behav. Brain Sci.* **17**, 585–654.

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transmission, thereby limiting the opportunity for genetic conflict. For example, considerable evidence supports the view that mitochondria and chloroplasts developed from bacteria that formed symbiotic associations with primitive eukaryotic cells. These organelles are now passed from mother to offspring. Such uniparental inheritance ensures that a zygote only contains organelles from a single genetic lineage. Biparental inheritance of organelles, in contrast, would lower relatedness among organelles within and between cells. Genetic variation among mitochondria could influence metabolic performance and lead to competition among cell lineages for transmission into the next generation. As any cancer victim will attest, intercellular competition is harmful to the parent organism. Uniparental inheritance therefore acts to maintain high levels of relatedness.

The most compelling evidence in support of uniparental vertical transmission-enforcing cooperation derives from examining variation in the degree to which parasitic organisms harm their hosts as a function of their mode of transmission. Virulence of both prokaryote and eukaryote parasites is associated with forms of transmission that permit infection by multiple genetic lineages (Maynard-Smith and Szathmary, 1995). Multiple infections are more prevalent with horizontal transmission than vertical transmission, especially when vertical transmission is uniparental. Experimental evidence in support of an association between virulence and horizontal transmission has been obtained for the bacterium *Escherichia coli* infected by a filamentous DNA phage (Bull *et al.*, 1991). When growth conditions permitted only vertical transmission, phage evolved to have minimal deleterious effects on bacterial growth rates. However, when the bacteria were grown to induce conjugation, thereby allowing horizontal transmission, phages with more harmful effects appeared. Comparative data on the effects of phage on bacteria also support an association between horizontal transmission and virulence (Maynard-Smith and Szathmary, 1995).

Several events in the history of life may also be interpreted as ways to ensure high levels of relatedness among potentially variable genetic entities that must cooperate to function properly (Maynard-Smith and Szathmary, 1995). For example, the ubiquity of reproduction from a single cell in multicellular organisms results in all the cells in a developing embryo being genetically identical. The early separation of germline cells from cells which give rise to the rest of the body may further control any possible cell lineage competition within the body. Early separation of germline cells also reduces the number of divisions that those cells must undergo and decreases the chance that somatic mutations will decrease genetic relatedness among the gamete-producing cells. A parallel case of separating potentially competitive cell lineages has been noted for many symbiotic organisms which are often housed in special organs within the body of the host (Frank, 1996).

Human Cooperation

Which, if any, of these mechanisms have been important for promoting cooperation among our ancestors? The answer is almost certainly all of them. Cooperative interactions in nonhuman vertebrate and human families are often consistent with expectations derived from kin selection and kin manipulation theories (Emlen, 1995). For example, assistance in rearing children is expressed to the greatest extent among the closest relatives. Kin selection, however, is less likely to explain interactions among families. To the extent that families banded together to form larger social units, repeated interactions must have created opportunities for temporary as well as more stable alliances based on partner choice and reciprocity. Ecological circumstances favoring long-term durable relationships between individuals in small groups would have laid the foundation for cooperation. Longevity coupled with an ability to remember individuals and their interactions provide all the necessary ingredients for stable reciprocity. As long as groups of individuals can anticipate many future opportunities for profitable exchange, cooperation in small groups seems inevitable.

Neither reciprocity nor kin selection adequately explain examples of ethnic cooperation in which very large groups of individuals develop common goals and will often go so far as to defend those goals by warfare. Examples of such large-scale cooperation do not exist among unrelated non-human animals. This suggests that ethnic cooperation may be the result of some cultural inheritance system in which the group, rather than the individual, is under selection. Cultural group selection has been proposed as an explanation for why humans differ from all other animals in cooperating, often against their own interests, with other unrelated individuals (Boyd and Richerson, 1991).

References Cited

- AXELROD, R. (1984). *The Evolution of Cooperation*. Basic Books, New York.
- BOYD, R., and RICHESON, P. J. (1991). In *Cooperation and Prosocial Behaviour* (R. A. Hinde and J. Groebel, Eds.), pp. 27–48. Cambridge Univ. Press, New York.
- BULL, J., and RICE, W. R. (1991). *J. Theor. Biol.* **149**, 63–74.
- BULL, J. J., MOLINEAUX, I. L., and RICE, W. R. (1991). *Evolution* **45**, 875–882.
- CONNOR, R. C., SMOLKER, R. A., and RICHARDS, A. F. (1992). *Proc. Natl. Acad. Sci. USA* **89**, 987–990.
- CREEL, S., and CREEL, N. M. (1995). *Anim. Behav.* **50**, 1325–1339.
- DE VRIES, P. (1992). *Sci. Am.* **267**, 76–82.
- DUGATKIN, L. A. (1997). *Cooperation among Animals: A Modern Perspective*. Oxford Univ. Press, New York.
- EMLEN, S. T. (1995). *Proc. Natl. Acad. Sci. USA* **92**, 8092–8099.
- FRANK, S. A. (1995). *Nature* **377**, 520–522.
- FRANK, S. A. (1996). *Am. Nat.* **148**, 1113–1124.



FIGURE 15 Two bottlenosed dolphin (*Tursiops truncatus*) males, on opposite sides of a female, engaged in a simultaneous courtship display consisting of belly slapping with their fins. Males will form long-term alliances to gain access to receptive females. All the males in alliances appear to mate equally often with the escorted receptive females (photo courtesy of R. Connor).

lation. For example, a male baboon, *Papio anubis*, only enlists the support of another male in his troop when attempting to mate with a female currently in consort with a higher ranking male. If the alliance is successful, the dominant individual in the alliance has priority in mating. In contrast, some bottlenose dolphin, *Tursiops truncatus*, alliances persist for long periods with two or even three males working together on multiple occasions to display to and herd females. No evidence for asymmetrical mating success has been observed (Fig. 15). All males in an alliance often mate with the female being herded (Connor *et al.*, 1992). Greater cooperation among male dolphins than male baboons is therefore consistent with randomized reproduction, probably acting in addition to partner choice, as a mechanism to prevent cheating and foster cooperation.

Mutual Policing

An alternative to partner choice for enforcing cooperation is to repress competition among individuals in a potentially cooperating group. The best way to repress competition is to maintain a sufficiently high level of relatedness among all individuals in the group such that their reproductive interests coincide. For example, mutual policing in honeybees, *Apis mellifera*, depends on the level of relatedness. Female worker bees reproduce by laying unfertilized eggs which develop into haploid males. If, as usually happens, the queen has mated many times, then workers are less closely related to the haploid male offspring of their

sisters than they are to their mother's offspring (Maynard-Smith and Szathmary, 1995). As expected, worker bees continuously inspect comb cells for the presence of eggs laid by other workers. If a worker-laid egg is discovered, it is promptly destroyed. Worker policing behavior (Fig. 16) breaks down if the queen dies (Ratnieks and Visscher, 1989).

An analogous situation occurs during the transmission of cytoplasmic genetic elements, including symbiotic organelles. In eukaryotes, genetic lineages of symbiotic cytoplasmic elements are prevented from mixing during

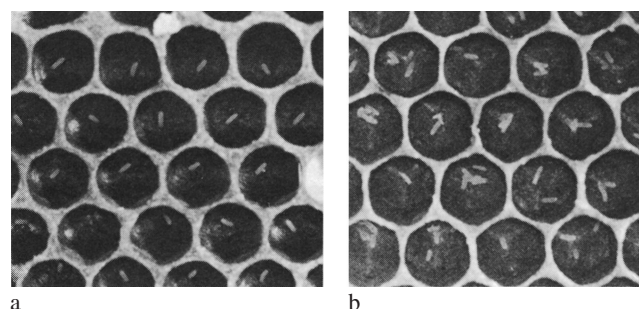


FIGURE 16 Egg-laying patterns in honeybee (*Apis mellifera*) colonies in which a queen is present (a) or in queenless colonies (b). In the presence of a queen, the workers actively police the cells, destroying the eggs laid by other workers, whereas in the absence of a queen they actively compete among themselves for reproductive success (photo courtesy of B. Thorne).

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FIGURE 13 Ants tending a membracid leaf hopper. These ants will feed on the exudate provided by the leaf hoppers and in return will attack and repel its potential predators (photo courtesy of R. Cocroft).

Partner Choice

Mutualistic interactions between a variety of species provide good examples for how an alternative mechanism, partner choice (Bull and Rice, 1991), controls cheaters and maintains cooperation. Many species of homopterans, such as aphids and membracids, the larvae of many lycaenid and riodinid butterflies, and some plants such as ant acacias, provide sugar-rich solutions to ants in exchange for protection from predators or competitors (Fig. 13). Individual plants or insects could cheat by not producing rewards for the ants. Cooperation should persist as long as the ants are

able to choose alternate plant or insect partners that provide higher rewards. At the same time, the insects or plants may withhold rewards if the attending ants do not provide adequate protection. Thus, cooperation may be regulated by partner choice as in any market economy (Noë and Hammerstein, 1994).

Evidence for partner choice derives from studies of mutualistic associations between some butterfly caterpillars and attending ants. Lycaenid and riodinid caterpillars produce sugar-rich solutions from a dorsal nectary organ, which functions only to produce rewards for ants (Fig. 14). Some caterpillars even attract ants by emitting vibratory acoustic calls and may emit chemical signals that cause the ants to attack approaching predators (De Vries, 1992). Isolated caterpillars produced more nectar when the number of attending ants was increased from one to two. Similarly, in those species of lycaenids which form large clusters, individual caterpillars failing to produce nectar are often killed by attending ants. Although the pupae remain attractive to ants by continuing to produce nectar, once eclosed, the emergent butterflies are vulnerable to ant predation, further demonstrating that cooperation in this system depends on the market value of nectar (Noë and Hammerstein, 1994).

Partner choice may also enforce mutualistic behavior within species. For example, in some primates and dolphins, males work together in alliances to gain access to sexually receptive females. Primate alliances appear to differ from dolphin alliances, however, in at least two ways. Primate alliances tend to be temporary and result in asymmetrical benefits to participants, much like in cases of kin manipu-

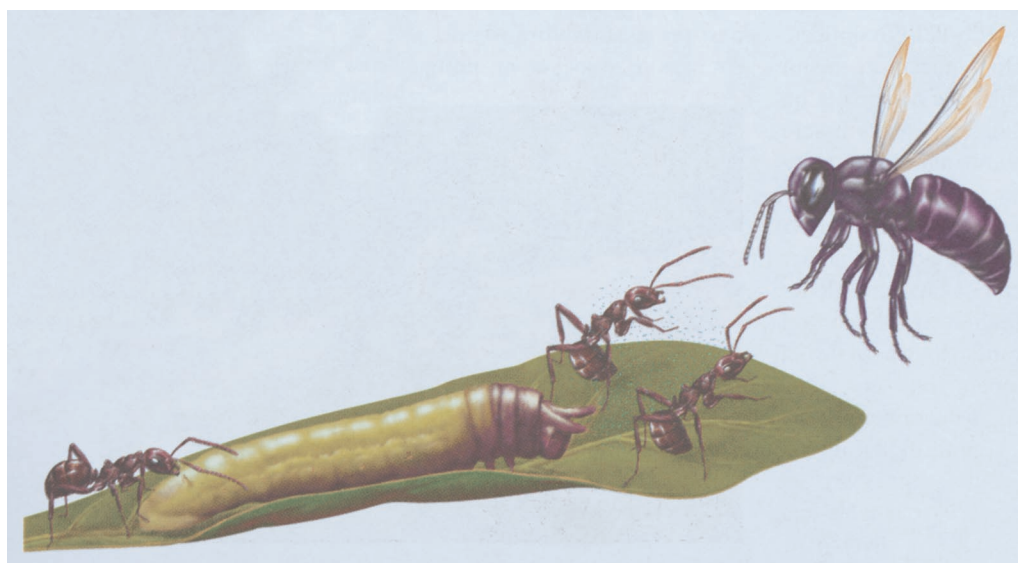


FIGURE 14 Riodinid caterpillars feed attending ants from their nectary organs (left). The caterpillars can elicit an attack response to predators from the ants by releasing chemicals that mimic the ants' alarm pheromone (right) (adapted from Vries, 1992).



FIGURE 11 Thirty-three primary queens (with extended abdomens) and 17 primary kings (2 of which are visible at top right) of *Nasutitermes corniger* termites collected from a single colony in Panama (photo courtesy of B. Thorne).

much longer periods. Nevertheless, cooperative reproduction by multiple foundresses appears to represent a transient period typical only of the early phase of any social insect colony. In most cases, conflict eventually erupts and only a single queen survives. A plausible explanation for such temporary cooperation depends on foundresses being unable to determine who will eventually gain reproductive control. If every foundress has an equal chance of becoming the dominant reproductive in a colony, then sustained cooperation is expected.

Another intriguing potential example of equal reproductive opportunity acting to ensure cooperation involves the slime mold, *Dictyostelium discoideum*. The life cycle of this organism passes from a dispersed single-celled feeding stage to a multicellular aggregate or slug capable of coordinated movement (Fig. 12). When the slug reaches an ecologically appropriate location, a fruiting body containing spore cells is erected on a long stalk. Although kin selection may be part of the explanation for why stalk cells should sacrifice

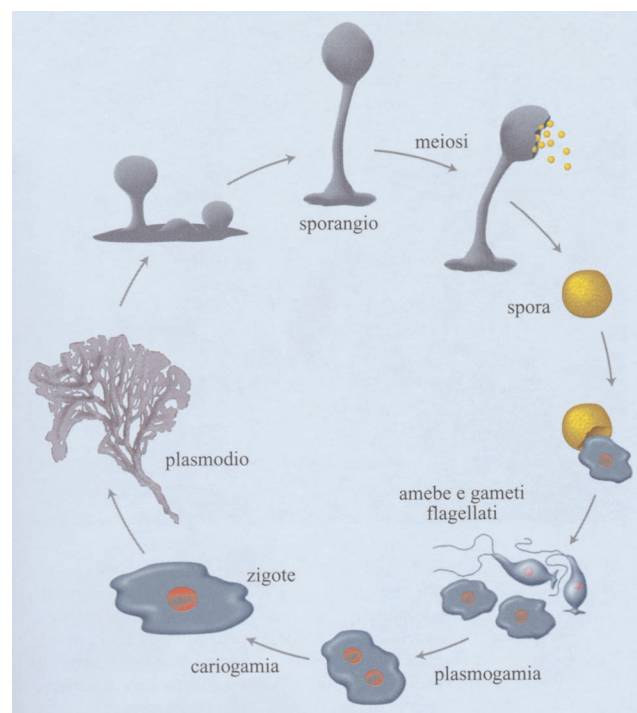


FIGURE 12 Life cycle of the slime mold *Dictyostelium discoideum*. The mature fruiting body (sporangium), held on a long stalk, produces the haploid spores. These hatch into amoebae, which multiply asexually. Amoebae aggregate, first by plasmogamy and then karyogamy, to form a migrating diploid slug (plasmodium), which eventually develops into a fruiting body.

themselves for their spore brethren, some slugs develop from up to 100,000 aggregated cells. Cooperation without kin selection may be favored if cell fate is determined at random in the developing slug. This proposition is supported by a random spatial distribution of cell types when fate is determined (Frank, 1995).

Equal reproductive opportunity also typifies biological cooperation of a very different kind — the passage of chromosomes from a diploid cell into haploid gametes. Through the process of meiosis, each chromosome has a 50% chance of ending up in a gamete. Evidence that meiosis represents a bona fide example of cooperation derives from observations of cheaters. In a variety of organisms, meiotic drive occurs, i.e., one chromosome ends up in a disproportionate fraction of gametes. When a sex chromosome disobeys the laws of Mendelian segregation, distortion of the primary sex ratio results. Although such selfish behavior may be advantageous for genes on the cheating chromosome, the outcome of meiotic drive for a sex chromosome is eventual extinction when the limiting sex disappears unless some force intervenes to restore transmission frequencies. Thus, meiosis may be viewed as an elaborate mechanism for ensuring cooperation among the chromosomes (Maynard-Smith and Szathmary, 1995).

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FIGURE 10 A pregnant female naked mole rat (*Heterocephala glaber*) in the midst of a communal nesting area. This female gave birth to 27 pups the next day. The reproductive female in a colony is much larger than either males or females and is provisioned by scouts which collect tubers (photo courtesy of P. Sherman).

Workers advertise their find by vocalizations which recruit colony members to the food source. Even though workers may never reproduce, they indirectly benefit by helping the reproductive female because relatedness within a colony may be extremely high due to inbreeding, almost certainly from past incestuous mating. In contrast to most animals, naked mole rats rarely disperse.

Kin manipulation has also been reported in *Polistes* wasps (West Eberhard, 1975). In many species of paper wasps, sisters disperse together and found a new nest. Due to an unusual sex determination system known as *haplodiploidy* in which males carry one copy of chromosomes and females carry two copies, sisters from a singly inseminated mother have a 75% chance of sharing a gene which is identical by descent. Although sisters may initially cooperate to construct a nest, only one or perhaps two dominant individuals eventually develop ovaries and lay eggs. The remaining sisters often become workers which continue to build the nest and care for the brood. Once again, a subordinate wasp should, in an evolutionary sense, be willing to help as long as more copies of her genes will be carried by her sister's offspring than by her own offspring if she departed and attempted to nest on her own.

The Problem with Group Selection

Until the mid-1960s, cooperative behavior was commonly invoked as a mechanism for population regulation. This point of view is best captured by the phrase, "Cooperation occurs because it is good for the species." A detailed critique by Williams (1966) illustrated the flaw in this perspective. Unless there is little or no migration between groups

of interbreeding organisms and frequent extinction of such populations, those individuals which selfishly reproduce as much as possible will outcompete those which limit reproduction to reduce competition. The primary exception to this conclusion occurs when animals are related to each other. The discovery that reproductive sacrifice is typically found in animals which form groups composed of close kin is therefore consistent with kin selection, rather than group selection, favoring cooperation.

During the past 15 years, however, an alternative form of selection at the group level has been advocated by some evolutionary biologists. Rather than depend on differential extinction of populations, this new type of group selection, *trait group selection*, depends on differential productivity of groups. Theoretical studies have shown that trait group selection may favor cooperative behavior among organisms if they mate at random prior to dispersal into groups on the basis of their predisposition to act cooperatively. In theory, such trait groups could be composed of unrelated animals, but the simplest mechanism producing such nonrandom assortment into groups is kinship association. When trait groups are composed of close relatives, kin selection, as outlined previously, is sufficient to explain the occurrence of cooperation. Although group selection has been demonstrated in the laboratory (Wade, 1977), few if any unequivocal examples have been identified in nature. Currently, perhaps the most plausible case of trait group selection involves cooperation among unrelated human groups (Wilson and Sober, 1994).

Enforcing Cooperation

Equal Reproductive Opportunity

The behavior of groove-billed anis, naked mole rats, and paper wasps might lead one to predict that all cases of cooperative breeding must involve closely related animals. However, in several species of ants and termites, nests may be founded by multiple reproductive females which may be distantly related if at all (Fig. 11). Where data are available, colonies founded by multiple queens tend to grow faster and are more likely to survive and produce reproductive individuals than colonies founded by single females. As a consequence, per capita reproduction is often higher in these multiple queen or polygynous colonies. Termites and ants differ from wasps, birds, and mole rats in that the decision to become reproductive is not reversible. Whereas workers in these other taxa are able to develop reproductive organs, most ants and termites do not have such physiological flexibility. Queens of the latter species typically must develop ovaries and extended abdomens before they can lay eggs. Also, although supernumerary wasp queens are invariably eliminated or end up helping but not reproducing within a few months after colony formation, some termite and ant queens may live together and continue to reproduce for



FIGURE 7 A female lion snarls at a large cub while nursing her two small offspring and a third cub belonging to another female. Females give an average of 30% of their nursing to cubs other than their own (photo courtesy of C. Packer).

with unequal benefits among participants may occur. Communal breeding in groove-billed anis, *Crotophaga sulcirostris*, provides an example. These glossy black cuckoos live in social groups containing one to four pairs of birds and share a single nest. Each female lays all of her eggs in succession, with the most subordinate female laying first and the most dominant laying last. Before each bird begins laying, it removes several eggs already in the nest. As a consequence of this egg-tossing behavior, the dominant female contributes more eggs to the final clutch than any of the other females (Fig. 9). Once the eggs hatch, all members of the group participate in feeding and protecting the chicks. Why don't subordinate females leave and nest on their own? The reason appears to be that quality breeding habitat



FIGURE 9 Two pairs of groove-billed anis (*Crotophaga sulcirostris*) at a communal nest. The dominant female lays in the nest only after removing several of the subordinate's eggs.

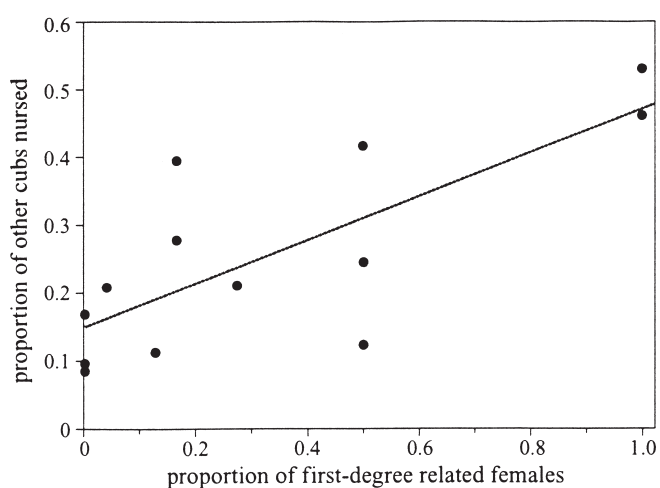


FIGURE 8 The proportion of cubs of other mothers nursed by female lions in a crèche as a function of the proportion of all females which are first-degree relatives. The interpolation line implies a direct relationship between the two variables.

is typically unavailable in those parts of Central America where this bird is found. Consequently, a subordinate may produce more young in a cooperative group than she could on her own. If she is also related to the dominant, then she may gain further benefits by increasing the survival of related offspring (Vehrencamp, 1983).

Kin manipulation also occurs in mammals, including dwarf mongoose (*Helogale parvula*), African hunting dogs, cotton-top marmosets (*Saguinus oedipus*), and naked mole rats (*Heterocephalus glaber*). In each of these species, only a single female usually succeeds in rearing young (Fig. 10). Reproduction by other females in the social group is suppressed by yet to be determined pheromones or their young are killed at birth. Despite such treatment, these nonreproductive, but typically related, animals remain in the group, collect food, and help care for the young of the dominant pair. Naked mole rats represent an extreme example because they occur in large colonies in desert areas of eastern and southern Africa where they feed on large tubers of a few species of plants. Successful exploitation of this widely dispersed food source requires that a colony develop an extensive and ever-expanding network of tunnels. Once a tuber is found, workers carry pieces back to the communal nest and share them with other members of the colony.

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Kinship is important because cheating on a potentially cooperative interaction may not pay if a potential partner is related. Recall that natural selection favors traits that increase an individual's lifetime production of offspring and their survival. The reason for this is that parents are related to and share genes with their offspring. From the perspective of a gene, any behavior that increases its frequency in the next generation will be favored. Consequently, natural selection should also favor traits that increase the production and survival of other relatives, such as siblings or cousins. However, because siblings have a higher degree of relatedness than cousins, we expect animals to discriminate among and preferentially interact with their closest relatives.

If two animals are sufficiently related, even altruistic behavior may be favored. A gene influencing altruistic behavior will spread when the benefit to the recipient (B) times the degree of relatedness (r) minus the cost to the individual initiating the act (C) exceeds zero; in other words, when $rB - C > 0$ (Hamilton, 1964). This simple inequality, known as Hamilton's rule, forms the basis for a powerful theory called kin selection (Maynard-Smith and Szathmari, 1995). Kin selection influences the evolution of aid-giving and cooperative behavior, as well as many other forms of social behavior, in a variety of animals.

To illustrate how kin selection influences cooperative behavior, consider nesting and nursing behavior among house mice, *Mus domesticus*. House mice often give birth and nest with one or two other females and then indiscriminately nurse all the young in a communal nest (Fig. 6). An important advantage to forming a communal nest appears to be that two or more females are better at protecting their vulnerable pups from potentially infanticidal males. However, since lactation is usually the most energetically expensive period of any female mammal's life, why doesn't a fe-

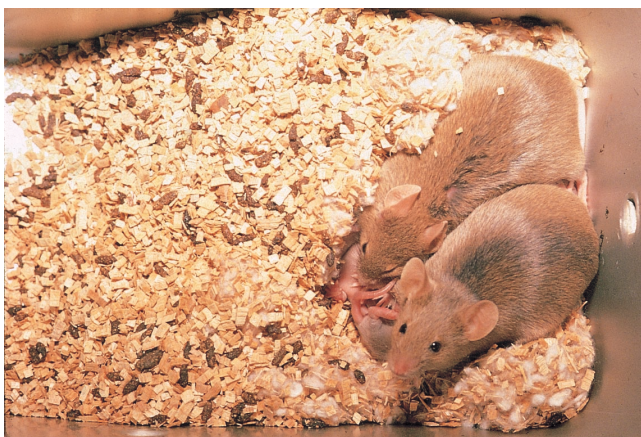


FIGURE 6 A communal nest occupied by two female house mice (*Mus domesticus*). Females will nurse all the pups without discrimination. Experiments with congenic mice indicate that communal nesting females use the major histocompatibility complex (MHC) system to identify their relatives.

male mouse try to avoid nursing pups in the communal nest? The answer appears to be that she is usually related to all the pups. House mice preferentially form communal nests with close relatives, such as sisters or daughters (Manning *et al.*, 1992). Consequently, females that provide milk to their own pups as well as their relative's pups leave more copies of their genes in future generations than females who are less cooperative.

Kin Recognition

For kin selection to operate, female mice must be able to recognize and preferentially nest with close relatives. In other words, they need to be able to discriminate kin from nonkin. In some animals, kin recognition is based on past association. For example, a common smell acquired by two individuals that grew up together and fed on similar foods may impart a recognizable scent. Although a nest-specific odor might allow an animal to make simple categorizations, such as distinguishing siblings from unrelated individuals, it will not predict very well genetic relatedness in those animals that exhibit variation in relatedness within a brood, as will happen if two or more males share paternity. In these cases, animals would do better if they could somehow directly compare genes to assess relatedness.

Genetic kin recognition requires the presence of variable regions in the genome and the sensory ability to detect and discriminate individuals on the basis of these differences. Otherwise, genetic similarity caused by past ancestry may be confused with similarity due to chance. Studies using congenic house mice bred to be genetically identical except for alleles at the multiple histocompatibility loci (MHC) demonstrated that female mice form nests together depending on whether they have the same MHC haplotype (Manning *et al.*, 1992). Tremendous genetic variation at the MHC is maintained in all vertebrates to facilitate cell-cell recognition in the face of parasitic cell invasions from disease-producing organisms. Consequently, MHC loci are ideally suited to function as genetic indicators of relatedness and may do so in many vertebrates from tunicates to humans.

African lions resemble house mice in that females living together routinely nurse each other's pups (Fig. 7). A major cause of cub mortality is male infanticide following replacement of a coalition of males. Just as in house mice, the number of females living together determines how well cubs are protected from infanticidal males. However, lions go further than mice. Lactating females selectively permit more suckling by closely related cubs than by distantly related cubs (Pusey and Packer, 1994) (Fig. 8). How female lions recognize cub kinship levels is not known, but age, past association, and MHC similarity are all likely possibilities.

Kin Manipulation

When relatives differ in dominance and have restricted opportunities to live away from a social group, cooperation

sumed to benefit approaching pairs of fish because each learns what kind of predator is nearby and how likely it is to attack. Paired individuals interact repeatedly over time and take turns moving toward the predator, as predicted if each pair of moves represents one round in a prisoner's dilemma game.

The importance of the iterated prisoner's dilemma in explaining cooperation in animals remains controversial, however, because even though each of these examples is generally consistent with TFT, most have alternate explanations and some fail to mimic the payoff situation envisioned by the prisoner's dilemma. In particular, the iterated prisoner's dilemma assumes that both players make simultaneous decisions about their next move. If, instead, animals alternate moves, as is the case for food sharing, predator inspection, and territorial defense, then computer simulations show that yet another strategy, firm but fair (FBF), eventually outcompetes generous TFT and the Pavlovian win-stay, lose-shift (Frean, 1994). This new strategy is "firm" because it retaliates by defecting if it was a sucker. FBF is "fair" because it does not retaliate against a defector if it defected itself, and it cooperates with suckers rather than continue to exploit them. Thus, even though the order of play does not influence the outcome of a single round of the game, it will influence how to behave in situations in which partners exchange interactions over time.

Territorial defense in African lions, *Panthera leo*, provides an instructive exception to much of this theory because some individuals appear to exhibit unconditional cooperation, even when defection occurs. Male lions band together to form coalitions that compete for control of a pride of females. Small male coalitions are usually composed of unrelated individuals, whereas large coalitions invariably contain brothers. Although takeovers of prides by male coalitions occur infrequently—only every 2 or 3 years—territorial defense has been studied extensively by broadcasting roars through speakers to simulate intrusions by a competing coalition. All males in a coalition currently in possession of a pride approach playbacks independently of the behavior or relatedness of their companions (Fig. 5). The lack of any apparent cheating among males in a coalition makes sense because the reproductive success of each male hinges on retaining possession of the pride. Since all members of a coalition mate and share paternity, every male benefits by helping to drive away a competing coalition.

In contrast to the unfettered defense displayed by males, most female lions facing the same situation are less likely to rush out and defend the pride (Heinsohn and Packer, 1995). Females only approach speakers when the number of lions emitting roars is less than the size of the pride—in other words, when the odds are in their favor. Furthermore, individual females consistently differ in their willingness to lead the charge. Some females always act boldly and move to-



FIGURE 5 Male lions in a coalition always exhibit a form of cooperative in defense. When a playback speaker broadcasts the roar of a simulated intruder, the male lion approaches the source of the noise (photo courtesy of C. Packer).

ward playbacks, whereas others act fearful and lag behind. Although lead females often look back at their tentative pride mates, they continue to approach playbacks without exhibiting any form of retaliatory behavior. Female lions, therefore, appear to tolerate cheaters, at least in the context of territorial defense. Although such repeated cooperation in the face of apparent defection is inconsistent with even the most forgiving successful strategies for the iterated prisoner's dilemma, other examples of asymmetrical benefits to cooperation have been observed, but always among relatives. As discussed next, kinship provides an important reason for cooperation in these situations.

Kinship Promotes Cooperation

Kin Selection

Kinship refers to genetic relatedness. Reproduction in all animals involves duplicating and transmitting genes to offspring. The probability that an exact copy of a gene is located in another individual is called the degree of relatedness, symbolized by r . In humans and other diploid organisms (i.e., those that possess copies of genes on paired chromosomes), the degree of relatedness between a mother and her son is one-half because the son gets half of his genes from his mother and half from his father. Similarly, the degree of relatedness between a son and his mother is one-half for the same reason. Any pair of individuals with a common ancestor has some degree of relatedness, although r may be very small if the ancestor occurred many generations in the past. In all cases, r is measured by the probability that a typical gene in one individual has an exact copy in another due to direct descent from a common ancestor.

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as expected if grooming is involved in monitoring past feeding history. Since both mutual grooming and blood sharing in the wild only occur between individuals that have reliably roosted together in the same hollow trees for many months or years, partner fidelity appears essential for maintaining this cooperative system.

The Iterated Prisoner's Dilemma

The effect of partner fidelity on the evolution of cooperation has received considerable theoretical attention. Much of this theory involves analysis of a repeated two-person game known as the *iterated prisoner's dilemma*. Rather than barter money, biological players of this game win or lose points that reflect differences in their lifetime reproductive success or fitness — the currency of evolution. In one play of the game, when both players cooperate each receives a reward R compared with a punishment P if each fails to cooperate. The temptation T for a player to defect when it encounters a cooperative opponent provides the highest payoff, whereas a cooperating sucker receives the lowest score, S . In algebraic terms, a prisoner's dilemma is defined to exist when $T > R > P > S$ and $R > (T + S)/2$ (Fig. 4). In a single round of this game, the best strategy is to defect even though both players would receive higher payoffs if they both cooperated. This is because a player who defects either avoids receiving the sucker's payoff or obtains the temptation. Thus, defection by player A yields the best re-

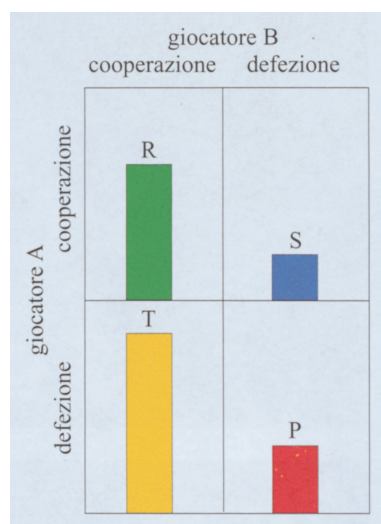


FIGURE 4 Matrix of the relative payoffs for player A in a prisoner's dilemma game. Players A and B gain points which reflect the difference in their success. In a round of the game, each player obtains a reward (R) if both cooperate and a punishment (P) if both fail to cooperate (defect). The temptation to defect if the other cooperates depends on the highest payoff (T), whereas cooperation with a defecting opponent gives the lowest score (S). To qualify as a prisoner's dilemma, the conditions must be respected that $T > R > P > S$ and $R > (T + S)/2$.

sponse to either possible action by player B for a single play of the prisoner's dilemma.

When this game is repeated over and over again, however, and the players base their decisions on previous interactions, then cooperation can emerge. In a series of computer tournaments, Axelrod (1984) discovered that the simple strategy tit-for-tat (TFT) outperformed all other competing strategies. TFT embodies the golden rule: It always begins by cooperating and on subsequent interactions simply copies whatever its partner did. Consequently, TFT is nice because it is never the first to defect and forgiving because it only defects once as long as its partner resumes cooperating. The success of TFT depends on there being a sufficiently large probability that two individuals will encounter each other again. In this way, TFT uses partner fidelity to exclude cheaters.

Recent theory indicates that TFT may represent only the first stage in the evolution of cooperation. Although TFT does as well or better than any alternative strategy in a constant environment, TFT is vulnerable to inadvertent errors. One accidental defection between two individuals playing TFT will lead to cycles of mutual defections until another mistake corrects the misunderstanding. Generous tit-for-tat (GTFT), a strategy which retaliates only two-thirds of the time in response to a defection, is more forgiving than TFT and therefore is immune to such occasional mistakes. Computer simulations by Nowak and Sigmund (1993) show that GTFT often gives rise to a strategy called PAVLOV. The terminology PAVLOV derives from the conditioned reflex response of this strategy to the payoff: It repeats its previous move when rewarded with either of the two more profitable payoffs, R or T , but changes behavior when punished with the least profitable payoffs, S or P . In other words, PAVLOV obeys the rule win-stay, lose-shift. PAVLOV outperforms TFT in an environment in which errors occur because it corrects mistakes and exploits an unconditional cooperator.

Several animal examples of cooperation appear to involve reciprocation and are consistent with strategies involving retaliation, such as TFT and PAVLOV (Dugatkin, 1997). For example, hooded warblers, *Wilsonia citrina*, exhibit increased aggressiveness in response to playbacks that simulate territorial incursions by neighbors rather than by strangers, as expected if there is retaliation against neighbors for not observing a territorial boundary. In some hermaphroditic serranid fish and polychaete worms, eggs and sperm are sequentially traded in small aliquots presumably to minimize the potential gain obtained from cheating by only transferring small, energetically inexpensive sperm rather than the larger, and therefore more energetically costly, eggs. Also, a series of experiments on sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*) have shown that these fish often leave a school and approach a much larger predator in pairs. Predator inspection is as-

Nevertheless, much of the theory has direct relevance to interactions between cells within organisms, interactions between different genetic elements within a cell, and even interactions between molecules in a primordial soup. Thus, the evolution of cooperation has implications for understanding parasite virulence, diseases such as cancer in which cell lineages compete instead of cooperate, and key transitions in the evolution of life from the origins of replicating molecules to multicelled organisms (Maynard-Smith and Szathmary, 1995).

Partner Fidelity Permits Cooperation

Reciprocity

Partner fidelity forms the basis for reciprocity. Trivers (1971) first pointed out that as long as two individuals help each other repeatedly, then over time cooperative pairs will survive and reproduce better than uncooperative pairs. Trivers termed this form of cooperation reciprocal altruism because he wished to explain cases in which aid is exchanged despite an immediate cost to reproduction or survival. If the benefit exceeds the cost, over time each participant profits from the interaction. However, individuals that fail to return the benefit do even better. Thus, for reciprocity to remain advantageous, prior association and memory are necessary for cooperative individuals to identify or retaliate against uncooperative individuals.

Food sharing in vampire bats, *Desmodus rotundus*, illustrates the potential advantage of reciprocity (Fig. 3). Female vampire bats regurgitate blood to their offspring and to each other when one has failed to obtain a blood meal on its own (Wilkinson, 1984). Each night, 7% of adults and 33% of juveniles fail to feed. Feeding failure occurs because the prey, which in most parts of Latin America is either cattle or horses, often detect and dislodge the bats. Young bats apparently do not avoid detection as readily as more experienced animals. Experiments with captive animals indicate that the bats not only identify and preferentially feed individuals from the same roosting group but also are more likely to give blood to a bat that has previously fed them. Such aid may be tremendously beneficial since a bat that fails to feed on three consecutive nights will die. In the absence of reciprocal blood sharing, annual mortality should exceed 80%, but female vampire bats are known to survive more than 20 years in the wild.

The mechanism by which vampire bats detect and exclude cheaters, those individuals which take blood without ever reciprocating, remains to be demonstrated. However, successful bats can ingest their body weight (more than 30 g) in blood. The stomach distention caused by such gorging sessions is likely to be noticed by another bat during episodes of mutual grooming. Mutual grooming frequently occurs between individuals just prior to blood regurgitation,



a



b



c

FIGURE 3 Vampire bats, of which the most common species is *Desmodus rotundus* (a), show various cooperative behaviors, such as blood sharing with other members of the colony and reciprocal grooming (b). During feeding, the bat, distending its stomach like a balloon, can consume its own body weight in blood (c).

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nation example, this could occur if the pollinator discriminated among plants and failed to carry pollen from those flowers that did not produce adequate nectar. Finally, some level of cheating may actually be tolerated. This is expected only when the cooperating individuals are genetically related and partner choice is not possible. Relatedness enables the recipient to benefit by genetic proxy from the more selfish action of its partner.

The degree to which cheating occurs in any cooperative system depends on when partners benefit and whether mutual benefits require collective action. Mutualisms involving two individuals of either the same or different species are characterized by situations in which benefits are received immediately by all individuals as a direct consequence of their joint behavior. For example, African hunting dogs, *Lycaon pictus*, pursue and kill prey much larger than themselves by hunting in packs (Fig. 1). Foraging success, as measured by the amount of food killed per dog for each kilometer traveled, is highest for dogs living in large packs (Creel and Creel, 1995). As long as participation in cooperative hunts is required to capture and kill prey, cheating will not pay. Simultaneously received benefits almost certainly characterize other examples of cooperative hunting, including some tropical group-hunting ants that capture and consume prey much larger than themselves (Fig. 2).

If cooperation is defined solely as mutual benefit from any action, then a wide variety of selfish behaviors may also be considered cooperative when they inadvertently benefit other individuals. Any selfish acts by an individual that improve its ability to feed, warn, or defend itself or its young may simultaneously benefit other individuals by showing them where to feed, warning them of danger, or chasing off predators (West Eberhard, 1975). These types of situations



FIGURE 1 A pack of African hunting dogs (*Lycaon pictus*) dismembering an antelope during a cooperative hunt. Each dog, by hunting in a pack, improves its success as measured in terms of the amount of meat obtained per kilometer traveled during hunting (photo courtesy of S. Creel).



FIGURE 2 An army of ponerine ants attacks and dismembers an earthworm.

have been termed *by-product mutualisms* and cannot be exploited by cheaters as long as there is no alternative behavior that provides greater reproductive success or survival to the selfish individual.

Opportunities for cheating arise whenever beneficial acts require collective action or are separated in time. Exchanges involving some kind of donation, such as food, are referred to as *return benefit mutualism* when there is little or no cost to providing the donation and *reciprocal altruism* when the donation is costly (Trivers, 1971). Although reciprocal exchanges involving long time delays characterize a variety of human cultural practices, many evolutionary biologists believe reciprocity should be uncommon among animals because keeping cheaters out of such a system is likely to be difficult. For all individuals to profit from reciprocity, the value of past exchanges and identity of trading partners must be remembered. Cheaters which only infrequently repay their debts would be difficult to detect without considerable bookkeeping by the participants.

Although controversy remains over the extent and evolution of cooperation in nature, substantial theory and evidence indicate that faithful, repeated interactions as well as kinship among partners provide two important mechanisms for the evolution of cooperation. In the absence of partner fidelity or kinship, other social mechanisms are required to control the presence and behavior of individuals which attempt to garner more than their fair share of the benefits of cooperation. Several interesting possibilities for enforcing cooperation, including equal reproductive opportunity, partner choice, and mutual policing, have received attention recently. Although some evidence is consistent with each of these ideas, future empirical and theoretical studies will undoubtedly improve our understanding of how cooperation is maintained in different systems.

Many of the examples used in this article illustrate forms and mechanisms of cooperation among interacting animals.

GERALD S. WILKINSON

Department of Zoology
University of Maryland
College Park, Maryland 20742, USA

Cooperation occurs when two organisms benefit as a consequence of their joint action. Cooperation poses an evolutionary dilemma when it is possible for individuals to cheat by receiving the benefits of cooperation without participation. Theoretical investigations and detailed study of many biological systems suggest that kinship and partner fidelity provide the most important mechanisms for explaining the evolution of cooperation in animals. Cooperation may also be enforced by equalizing reproductive opportunities, allowing choice among partners, and mutual policing. Understanding cooperation may shed light on parasite virulence, key transitions in the evolution of life from the origins of replicating molecules to meiosis, and human behavior.

Cooperation

Cooperation Poses an Evolutionary Dilemma

Some organisms often behave in such a way as to help each other reproduce or survive. For example, many flowering plants provide nectar as a source of food to animals that, in turn, carry pollen between flowers resulting in fertilization. Although this behavior might appear practical for efficient survival of these species, a simple thought experiment illustrates the evolutionary problem posed by such cooperation. Given a population of nectar-producing plants, why doesn't a rogue plant attempt to produce less nectar and more pollen? As long as such a mutant continues to be visited by pollinators, it should increase in frequency in the

next generation because it will be able to produce more pollen and thereby fertilize more seeds. Clearly, cooperation between plant and pollinator should only persist if individuals that cheat — in this case, fail to produce appropriate levels of nectar — are excluded or eliminated.

Several mechanisms may regulate cheaters in cooperative systems. One widely acknowledged mechanism is *partner fidelity*, i.e., cooperation is restricted only to those individuals which interact repeatedly. Such interactions may occur because the animals live in closed societies or because they can recognize each other and remember past interactions. An alternative possibility when interactions are not repeated is that in some situations an animal may be able to restrict aid to the most cooperative partner. In the polli-