



Cooperation in animals: An evolutionary overview¹

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Abstract. Evolutionary biologists have grappled with the question of the emergence and maintenance of cooperation since Darwin first listed animal cooperation as a potential problem for his theory of natural selection. Here I review four paths that have been delineated in the study of intra-specific cooperation among animals. These paths – kinship, reciprocity, byproduct mutualism and group selection – serve as a starting point for behavioral ecologists interested studying the initiation and maintenance of cooperation. After reviewing the empirical and theoretical underpinnings of these paths to cooperation, I touch upon some recent work that has attempted to examine (or reexamine) the role of phylogeny, punishment and morality in the light of cooperative behavior.

Introduction

Those on the forefront of evolutionary biology, from Charles Darwin through E.O. Wilson and W.D. Hamilton, have found the questions surrounding cooperation and altruism in animals to be both fascinating and frustrating. Darwin (1859) found the cooperative and altruistic behaviors that are typically displayed by sterile caste members in the social insects “one special difficulty, which at first appeared to me to be insuperable, and actually fatal to my whole theory,” while Wilson described such actions as “the central theoretical problem of sociobiology” in his classic *Sociobiology* (Wilson 1975). For Hamilton, cooperation and altruism were what drew him to tackle of kinship and social dynamics, ultimately leading to his inclusive fitness theory (Hamilton 1964).

The history of the study of cooperation and evolution is full of twists and turns, not only from a scientific perspective, but also from a political and social perspective. Take, for example, Thomas Henry Huxley and Peter Kropotkin’s 19th Century debate over cooperation. Huxley, one of the most well-respected scientists (as well as science writers) of the 19th Century was raised in the dog-eat-dog competitive world of Victorian Britain. Huxley didn’t mince words when it came to cooperation, or rather the lack of cooperation, in the natural world:

From the point of view of the moralist, the animal world is on about the same level as the gladiator’s show. The creatures are fairly well treated, and set to fight; whereby the strongest, the swiftest and the cunningest live to fight another day. The spectator has no need to turn his thumb down, as no quarter

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is given . . . the weakest and the stupidest went to the wall, while the toughest and the shrewdest, those who were best fitted to cope with their circumstances, but not the best in any other way, survived. Life was a continuous free fight, and . . . a war of each against all was the normal state of existence. (Huxley 1888)

Nor was Huxley shy about speculating about what such a view of the world meant for human behavior:

Let us understand, once and for all, that the ethical progress of society depends, not on imitating the cosmic process {evolution}, still less in running away from it, but in combating it. (Huxley 1888)

For Prince Petr Kropotkin, born and bred in Czarist Russia, intellectual and spiritual development went in hand-in-hand with the radical political movements of anarchism and socialism that were slowly, but surely, sweeping through Russia. Kropotkin despised Victorian capitalism and the way its long tentacles seemed to have seeped into English science (Woodcock and Avakumovic 1950). For Kropotkin, the natural world overflowed with “mutual aid.” Everywhere he looked in nature Kropotkin saw cooperation. This natural cooperation was a thing of beauty to Kropotkin:

The ants and the termites have renounced the “Hobbesian War” and they are the better for it. Their wonderful nests, their buildings superior in size relative to man; their paved roads and overground vaulted galleries; their spacious halls and granaries; their cornfields, harvesting and malting grain, their courage, pluck and superior intelligence – all of these are the normal outcome of the mutual aid which they practice at every stage of their busy and laborious lives. (Kropotkin 1902)

And as for what this tells us about ourselves, Kropotkin, too, was not afraid to express his opinions:

Don’t compete! . . . That is the watchword which comes to us from the bush, the forest, the river, the ocean. Therefore combine – practice mutual aid! That is what Nature teaches us; . . . this is what man – the most primitive man -has been doing; and that is why man has reached the position upon which we now stand. (Kropotkin 1902)

Daniel Todes has put forth a fascinating hypothesis regarding how Huxley and Kropotkin could have come to such markedly different views (Todes 1989). Todes argues that the scientists (and noblemen) that Huxley associated with spent their time studying life in the tropics. Huxley himself had a four-year stint (as a medical doctor and naturalist) on the HMS *Rattlesnake*, and his time in the tropics, as well as his stories, rivaled those of Darwin and his days on the *Beagle*. As opposed to the group living and group cohesion that was necessary for simple survival in the very harsh environment of Siberia, where Kropotkin did his observations, life in the

tropics may indeed have struck Huxley as more of a free fight. Huxley saw the nature of life through the prism of the tropics, while Kropotkin saw a very different world in his trek through Siberia.

There are still many debates over evolution and cooperation today, although they tend to be less dramatic than that of Huxley and Kropotkin. Here I will argue that there are four paths to cooperation – kin selection, reciprocity, byproduct mutualism and group selection. Subsequent to our discussion of these four paths, I shall examine the role of phylogeny in our understanding of cooperation, as well as the relationship between cooperation, punishment, play behavior and morality.

Four paths to cooperation

Kin selection

In the hope that it may provide a useful summary we therefore hazard the following generalized unrigorous statement of the main principle that has emerged from the model. The social behavior of a species evolves in such a way that in each distinct behavior-evoking situation the individual will seem to value his neighbors' fitness against his own according to the coefficients of relationship appropriate to that situation. {Hamilton's italics}. Hamilton (1964), (p. 19)

Hamilton (1964) tackled the question of kinship in his now famous pair of papers, "*The Genetical Theory of Social Behavior I and II*." The essence of Hamilton's "inclusive fitness" models is that they supplement "classical" models of natural selection by considering the effect of a gene not only on the individual that bears it, but on those sharing genes that are identical by descent (i.e., blood kin). The equations in Hamilton's original papers can be daunting, even to those with a mathematical background. Fortunately, these equations can be boiled down to what is now known as "Hamilton's Rule," which states that a gene increases in frequency whenever: $(\sum_A rb) - c > 0$ Where b = the benefit others receive from the trait the gene codes for, c = the cost accrued to the individual expressing the trait, r is a measure of relatedness (Grafen 1984), and A is a count of the individuals affected by the trait of interest. When individuals are highly related and a gene(s) codes for an action that provides a huge benefit at a small cost, selection strongly favors this trait. Conversely, the least likely trait to be selected is one in which those helped are not relatives, and where helping entails significant costs.

Hamilton's theory has had a large impact on the work of ethologists, behavioral ecologists and comparative psychologists. For example, although work had been going on in the field of cooperative breeding in birds for more than 30 years (Skutch 1935, 1987; Brown 1994), Hamilton's theory, in conjunction with Brown (1970) empirical work on Mexican Jays, caused a surge in studies in cooperative and communal breeding that is still in full force today (Brown 1987).

The impact of Hamilton's ideas were even greater than they may have been

otherwise as a result of Jerram Brown's reformulation of Hamilton's Rule. One restriction of Hamilton's approach is that inclusive fitness was cast *within* generations, but many studies of animal behavior examine interactions between individuals *across* generations. In addition, field workers found the *b* and *c* terms of Hamilton's model difficult to measure in nature. Brown (1975) "offspring rule" solved both these problems in that it examined kinship across generations and used offspring as the currency of measure (for more on how and how not to measure inclusive fitness, see Brown (1975, 1987), West-Eberhard (1975), Charnov (1977), Charlesworth (1980), Wade (1980), Michod and Hamilton (1980), Seger (1981), Michod (1982), Grafen (1984, 1985), Creel (1990), Queller (1992)).

Emlen's "evolutionary theory of family"

While Hamilton's Rule makes some very general predictions about animal social behavior, subsequent work by behavioral ecologists and evolutionary psychologists has generated a more specific list of predictions about cooperation and family dynamics (Emlen 1995). In particular, Emlen (1995) has been integral in the development of an "evolutionary theory of family." The building blocks for Emlen's predictions are: 1) kin selection theory, 2) ecological constraint theory – a set of models developed to examine dispersal options of mature offspring (Koenig and Pitelka 1981; Emlen 1982a, 1982b; Brown 1987; Koenig et al. 1992) and 3) reproductive skew theory, which seeks to understand how reproduction is divided among potential breeders by predicting conditions that should favor conflict or cooperation over breeding decisions.

Emlen (1995) puts forth fifteen specific predictions about animal family dynamics, and for each of these, he reviews the evidence from the animal literature, both for and against his predictions. Here, we shall take a look at one of Emlen's predictions that deals directly with kinship and cooperation. Namely, the prediction that, "Assistance in rearing offspring (cooperative breeding) will be expressed to the greatest extent between those family members that are the closest genetic relatives." Under Hamilton's Rule, increasing *r* has the effect of increasing prosocial interactions between individuals. As such, the higher the value of *r* between two individuals, the more likely they are to help one another. In addition, Hamilton's Rule suggests that, all else being equal, when given the choice between helping individuals who differ in *r*, aid should be differentially dispensed to individuals who are closest blood kin.

Emlen (1995) reports that in the nine studies published on cooperation in species of birds or mammals that live in extended families, eight uncovered individuals that preferentially extended aid as a function of blood relatedness. For example, in white-fronted bee-eaters (*Merops bullockiodes*; photo 4), helpers chose to aid the pair they themselves were most closely related to in 108 of 115 opportunities.

Policing the hive

In many ways, kinship and aiding relatives is best exemplified by social insects, who

show extreme levels of cooperation in conjunction with an odd genetic architecture that creates sisters that are “super relatives.” Social insects are haplodiploid, in that males have only a single copy of each (haploid), while females have two copies of each chromosome (diploid). As a result of the genetics underlying haplodiploidy, sisters are related to one another on average by a coefficient of relatedness of 0.75, which has the effect of making females more related to sisters than to their own offspring.

With an r of 0.75 between sisters, one would expect high levels of aid giving, and social insects are famous for such actions. However, if individuals are able to gauge their relatedness to others, then social insects may be influenced by kinship in more subtle ways. Consider the fascinating case of worker “policing” in honeybees (*Apis mellifera*).

Using the mathematics of inclusive fitness theory, Ratnieks and Visscher (1989) found that in honeybee colonies with a single queen who mates one time, female workers are more related to their nephews (their sister workers’ sons, $r = 0.375$) than to their brothers (offspring produced by their mother, the queen; $r = 0.25$). This inequality switches when the queen mates multiple times. In such a situation, workers may be more closely related to brothers than to nephews, with the exact values of relatedness depending on the number of different males with which a queen mates. Under such conditions, wherein female workers may now be more related to brothers than to nephews, Ratnieks and Visscher (1988, 1989) hypothesize that worker “policing” of honeybee reproduction may evolve. Such policing, for example, may take the form of workers favoring those eggs to which they are most highly related.

Ratnieks and Visscher (1989) examined the possibility that workers may favor brothers over nephews using the honeybee (*Apis mellifera*), where queens typically mate with 10–20 different males. They found that honeybee workers showed remarkable acumen in discriminating between worker-laid eggs which produce nephews and queen-laid eggs which produce brothers. After 24 h, only 2% of the worker-laid eggs remained alive, while 61% of the queen-laid eggs remained alive. Workers appear to use a specific egg-marking pheromone produced only by queens to distinguish which eggs to destroy and which eggs to leave unharmed (Ratnieks 1995), and in so doing, police the hive in a manner that increase their inclusive fitness.

Reciprocity

Outside of kinship, the path to cooperation that has received the most attention from behavioral ecologists, as well as social psychologists is reciprocal altruism. In his classic paper *The Evolution of Reciprocal Altruism*, Trivers (1971) notes that the Prisoner’s Dilemma Game may prove to be a useful mathematical tool for studying reciprocal altruism. The Prisoner’s Dilemma game, popularized by Von Neumann and Morgenstein (1953), takes its name from the following hypothetical scenario: Two individuals (prisoners) are interrogated by the police, while in separate rooms. Each player can choose to either cooperate or not cooperate (i.e. defect). In this

		Player 2	
		Cooperate	Defect
Player 1	Cooperate	R = 1 year	S = 5 years
	Defect	T = 0 years	P = 3 years

Figure 1.

situation, to defect means to tell the authorities that the other suspect is guilty and to cooperate is the converse.

The payoffs to the Prisoner's Dilemma game are set in advance. The authorities have enough circumstantial evidence to put away both suspects for 1 year, even without a confession from either. Should each suspect implicate the other, however, each prisoner is sent to jail for 3 years. If only one suspect cheats, such 'state's evidence' allows the cheater to walk away a free man, but causes his partner to go to jail for 5 years. On any single play of the game, a player receives a higher payoff for cheating, regardless of what player 2 does (Figure 1; $T > R$ and $P > S$). The dilemma in the Prisoner's Dilemma is that both prisoners would receive a higher payoff if they had both cooperated than had they both defected ($R > P$).

The Prisoner's Dilemma game came into the spotlight with Axelrod and Hamilton (1981) paper on the evolution of cooperation among unrelated individuals. Axelrod and Hamilton (1981) found that in the iterated version of the Prisoner's Dilemma game, if the probability of meeting a given partner in the future was above some critical threshold, then in addition to the success of a simple 'always defect' (ALLD) strategy, a conditionally cooperative strategy called TIT FOR TAT (TFT) was a robust solution to the iterated Prisoner's Dilemma.

TFT instructs a player to cooperate on the initial encounter with a partner and to subsequently copy its partner's last move. Axelrod (1984) hypothesized that TFT's success is attributable to its three defining characteristics: 1) 'Niceness' – TFT is never the first to defect, 2) Swift 'retaliation' – TFT immediately defects on a defecting partner, and 3) 'Forgiving' – TFT remembers only one move back in time. As such, TFT forgives prior defection, if a partner is currently cooperating (i.e., – it does not hold grudges). Brown et al. (1982) have argued that TFT succeeds because it segregates behavior at the phenotypic level – i.e., it matches moves of cooperation with cooperation, and defection with defection.

One difficulty in analyzing the iterated Prisoner's Dilemma centers on the question of which strategies to include in the game. On the one hand, the set of all possible strategies is infinitely large; on the other hand, a strategy can be an evolutionarily stable strategy with respect to the other strategies in the game, and not all strategies are guaranteed representation. As such, the practical implications of proofs that no strategy in the iterated Prisoner's Dilemma game can be an ESS (Boyd and Lorberbaum 1987; Farrell and Ware 1989; Lorberbaum 1994) is that theoretical work is limited to finding necessary conditions, because sufficient conditions can never be obtained – every strategy is invadable by some conceivable mix of mutant strategies. That being said, game theorists have found that TFT-like strategies (e.g., "contrite TFT", Tit for Two Tats, Pavlov) have proven to be quite robust with respect to numerous types of noncooperative strategies.

Coalitions and reciprocity in baboons

One of the best known examples of coalition formation centers on male reproductive coalitions in baboons, *Papio anubis*. *P. anubis* males solicit coalition partners by rapidly turning their heads between the solicited animal (i.e. the individual they are requesting aid from) and their opponent, while at the same time continuously threatening their opponent. Packer (1977) observed 97 solicitations that resulted in coalitions being formed. On 20 such occasions, the opponent was consorting with an estrous female, and this increased the probability of a coalition being formed between the other two individuals involved. On six of these 20 occasions, the estrous female deserted the opponent and went to the enlisting male, creating a clear benefit to coalition formation, at least for the enlisting individuals. Joining a coalition, on the other hand, may be fairly costly in that solicited individuals rarely obtained access to the estrous female, and risked attack from the opponent while the solicitor was with the female. Packer's study suggests that solicited individuals may overcome such costs by having the individual who enlisted them respond when they themselves need help (reciprocal coalitions). In fact, Packer discovered that baboons had "favorite partners," and that favorite partners solicited each other more often than they solicited other group members.

Other studies of coalition and alliance formation in baboons have generally supported Packer (1977) findings (Smuts 1985; Noe 1986). Bercovitch (1988), however, found that in olive baboons (*Papio cyanocephalus anubis*), males who solicited coalitions were no more likely to obtain the females than any other

coalition member, and that baboons who declined to join a coalition were again solicited in the future.

Reciprocity and food sharing in vampire bats

Females in a nest of vampire bats regurgitate blood meals to others that have failed to obtain food in the recent past (Wilkinson 1984, 1985). This form of food sharing can be a matter of life or death, as individual bats often starve if they don't receive a blood meal every 60 h. Wilkinson examined whether relatedness, reciprocity, or some combination of the two best explained the evolution and maintenance of blood sharing in this species. A typical group of vampire bats (*Desmodus rotundus*) is comprised largely of females, with an average coefficient of relatedness that ranges from 0.02 to 0.11 (Wilkinson 1984, 1990). While relatedness does play a role in regurgitating food, Wilkinson also created an "index of opportunity for reciprocity." When analyzing the vampire data with this sort of index, Wilkinson suggests three lines of evidence that reciprocity is important in this system: 1) the probability of future interaction is high as predicted by TFT models, 2) the blood meal obtained is critical, while the cost of giving up some blood may not be that great, thus satisfying one of the conditions stipulated by Triver's model of reciprocal altruism, and 3) vampires are able to recognize one another and are more likely to give blood to those that have donated in the past.

Byproduct mutualism

Brown (1983) introduced the concept of byproduct mutualism as follows:

In nature it is likely that many payoff matrices for potential cooperators depart from the requirement of the Prisoner's Dilemma. I predict that in many cases of mutualism, $CC > DC$ will be found to prevail rather than $DC > CC$ as required by the prisoner's dilemma . . . In by-product mutualism, each animal must perform a necessary minimum itself that may benefit another individual as a byproduct. These are typically behaviors that a solitary individual must do regardless of the presence of others, such as hunting for food. In many species these activities are more profitable in groups than alone, so that $CC > CD > DC = DD$. In other words, consistent defection (meaning depending completely on others) is impossible or foolhardy . . . (Brown (1983), p. 30)

A prerequisite for byproduct mutualism (Brown 1983; West-Eberhard 1975; Connor 1986; Rothstein and Pirotti 1987) is what Mesterton-Gibbons and Dugatkin (1992) call the boomerang factor. In essence, the boomerang effect is any uncertainty that increases the chances that a defector will be the victim of its actions. In byproduct mutualism models, the 'common enemy' of a sufficiently harsh environment can provide such a boomerang. For example, using the Mexican Jay (*Aphelocoma ultramarina*) as an example, Caraco and Brown (1986) model food-sharing behavior (versus $D =$ not sharing) when food is abundant. In their model, the

boomerang effect is the danger associated with a predator's attention being drawn to an individual's offspring, if the offspring of *others* are begging too loudly for food. Cheating, by not sharing food, can rebound against the cheater (via its offspring) in that the predator may be drawn toward the cheater's offspring by the general clatter of begging chicks.

Foraging bluejays and byproduct mutualism

One serious critique of much of the work on the evolution of cooperation is that it is very difficult to obtain the *precise* payoffs associated with acts of cooperation and defection (Clements and Stephens 1995). Without such knowledge, while it is possible to make qualitative predictions about cooperation, quantitative predictions are more difficult. A potential way around this problem is to use operant psychology-like Skinner boxes, that allow more exact control over the payoffs that animals encounter. Clements and Stephens (1995) did just this in their study of bluejay (*Cyanocitta cristata*) cooperation.

Clements and Stephens (1995) tested *pairs* of bluejays in what amounts to a Skinner-box of sorts. Each bird could peck one of two keys – the cooperate key or the defect key. Clements and Stephens (1995) presented birds with two different payoff matrices. The first matrix had payoffs that satisfy a Prisoner's Dilemma (P matrix), while the second matrix's payoffs matched those associated with byproduct mutualism in a harsh environment (M matrix; (Figure 2). Bluejay 1 would begin a trial by pecking one of the keys and bluejay 2 would end the trial, (again by pecking either the cooperation or defect key). Birds were given food according to the payoffs assigned to the game they were playing. For example, if a pair was in the P matrix part of the game and bluejay 1 cooperated, when bluejay 2 cheated, the latter obtained five food items, while the former would receive 1.

Birds were exposed to the P matrix, then to the M matrix, and finally to the P matrix once again. On any given day a pair of birds would play these games with each other more than 200 times. Clements and Stephens (1995) found that regardless of whether the jays could see each other, birds defected in the first P matrix, cooperated in the M matrix, and reverted to defection the second time they encountered the P matrix. As such, bluejays appeared to cooperate via byproduct mutualism and not reciprocity.

Byproduct mutualism and house sparrow food calls

When they come upon a newly-discovered food resource, house sparrows (*Passer domesticus*) produce a unique "chirrup" call (Summers-Smith 1963), and such calls often attract other birds to a newly-discovered bounty. To examine if cooperation was in play here, and if so, just what type, Elgar (1986) recorded chirrup calls at artificial feeders containing pieces of bread. The patches contained either bread that was divisible among sparrows, or bread that was just enough food for a single bird.

Elgar (1986) found some evidence that those sparrows arriving at a patch of food first were the most likely to produce chirrup calls, suggesting the possibility of

		Player 2			
		C		D	
Player 1	C	4		1	M matrix
	D	1		0	

		Player 2			
		C		D	
Player 1	C	3		0	P matrix
	D	5		1	

Figure 2.

cooperative recruitment. Importantly though, (Elgar 1986) found that chirrup call rates were higher when the food resource was large and divisible – often too large to remove from the foraging site. When food items were small enough such that sparrows could pick them up and fly away, that is what the sparrows did, and in so

doing, they didn't produce chirrup calls. It may be that given that sparrows needed to remain at a feeder with larger, divisible items, it was safer to do so in the company of other sparrows. That is, the benefits associated with predator detection may outweigh the costs of inviting other foragers to one's food at the site. If this proves to be the case, then chirrup calls are most easily understood in the context of byproduct mutualism. The calls are emitted when the immediate net benefit for calling is greater than for not calling (for large, divisible items), but not otherwise.

Group selection

For the most part, before the 1960s evolutionary biologists and ecologists did not argue all that much about the level at which natural selection acts. Group and individual selectionists lived side by side, most famously at The University of Chicago (Mitman 1988), in part because the levels-of-selection question was simply not recognized as an issue. This allowed the strong group selection of Kropotkin (1902), Allee (1943), Emerson (1960) to stand side by side with studies on selection at the level of the individual. This peaceful coexistence disappeared shortly after Wynne-Edwards (1962) presented his case for group selection as the major force controlling population size. Subsequent to this, Williams (1966) argued that virtually all cases of purported group selection could be understood within the framework of classical individual selection.

Citing Occam's razor, Williams proposed that we need not invoke group selection as an explanation in such cases. Williams presented a two-pronged case against group selection. First, selection at the group level, although possible, will be weak because of the relative speed of within vs. between-population selection. Second, Williams argued that almost no evidence existed that could not be understood using the logic of individual selection thinking. As Wilson (1983) noted, "For the next decade group selection rivaled Lamarckianism as the most thoroughly repudiated idea in evolutionary biology."

Group selection was reborn in the mid 1970s, primarily through the work of D.S. Wilson (Wilson 1975, 1977, 1980) and Michael Wade (Wade 1976, 1977, 1978). Three features distinguished Wilson and Wade's form of group selection from that of their predecessors. First, Wilson and Wade provided detailed genetic models, partitioning variance into within- and between-group components. Second, the definition of a group was no longer confined to a reproductively isolated deme. Wilson (1975) introduced the term 'trait group' and defined it as a population "within which every individual feels the effect of every other individual" (Wilson 1980), p. 22) and as such, trait groups exist within a larger inter-breeding population. Trait-group models rely on superior group-level production, whatever the mechanism, and are hence much more general than earlier models.

At their core, 'trait-group' models for the evolution of cooperation are quite straightforward. Cooperation can evolve even when it has a relative cost to the individual performing it, if such a *within-group cost* is countered by some *between group-benefit*, such that *cooperative groups are more productive than selfish groups*. For such group-level benefits to be manifest, groups must differ in the

frequency of cooperators within them, and groups must be able to ‘export’ the productivity associated with cooperation. Exporting productivity might take any number of forms and, for example, might include cooperative groups being able to outcompete less cooperative groups for access to some resource. If variation between groups exists, and cooperative groups can export their productivity, then within-group costs paid by cooperators, but not cheaters, can potentially be offset, allowing some degree of cooperation to evolve.

Group selection and colony foundation in ants

One putative case of trait-group selection in ants comes from Rissing et al. (1989) work on *Acromyrmex versicolor*. In *A. versicolor* many nests have multiple foundresses who are completely unrelated, no dominance hierarchy exists among queens, all queens produce workers. In addition, “brood raiding” among starting nests appears to be common. During brood raiding, brood are captured after some act of between-group aggression and are raised within the victorious nests, with “loser” colonies disappearing. In *A. versicolor* the probability of the nest surviving the brood-raiding period is again a function of the numbers of workers produced.

Foraging behavior in *A. versicolor* is a very dangerous activity, as a result of high predation pressure. Yet once a queen assumes the role of colony forager, she remains in that role and *shares* all the food brought into her nest with her co-founders. That is, foragers assume the risks of foraging and obtain the benefits, while other queens simply obtain the benefits, but pay no costs. Within-group selection favors cheating (not being the forager), while between-group selection favors cooperation, since cooperation on the part of a specialized forager appears to lead to increased productivity in the form of new workers. The number of new workers affects the probability that a given nest will be the one to survive the period of brood raiding, thus providing the between-group component necessary for cooperation to evolve (Seeger 1989; Rissing et al. 1989).

Phylogeny and cooperative breeding in birds

One of the most active areas of research on animal cooperation is cooperative breeding in birds and mammals (Skutch 1935, 1987; Brown 1987, 1994; Stacey and Koenig 1990; Emlen 1991; Jennions and Macdonald 1994; Solomon and French 1996). While we have been focusing primarily on the role of selection in shaping cooperative behavior, work on cooperative breeding allows us to consider the role that phylogeny plays in understanding cooperation, and how phylogenetic and adaptive analysis can work hand-in-hand.

Phylogenetic analysis allows behavioral ecologists to examine whether a trait may be common in a group of animal species as a result of common descent per se. Edwards and Naeem (1993) examined cooperative breeding from a phylogenetic perspective. Using 166 species of cooperatively-breeding passerine birds in 97 genera (Brown 1987), Edwards and Naeem (1993) began their work by testing

whether the distribution of cooperatively-breeding species was random. They found that the distribution of cooperative breeding in nature differed significantly from the random distribution generated by a computer simulation, with some genera having too many cooperatively-breeding species, and others too few.

Edwards and Naeem (1993) followed this analysis by using already published phylogenetic trees to examine the distribution of cooperative breeding. Their phylogenetic analysis of jays, Australian songbirds, Australian treecreepers and New World wrens, for example, suggests that cooperative breeding may have arisen a limited number of times in some common ancestor(s) to modern day species, and has simply been lost by those species that do not cooperate today.

The phylogenetic approach does not necessarily conflict with an adaptationist view of cooperative breeding. Arnold and Owens (1998, 1999) for example, addressed the question of whether ecological factors can help us explain why cooperative breeding is not randomly distributed across bird families. They found that increases in the level of cooperative breeding were correlated with decreases in annual adult mortality and clutch size. The low rate of mortality often seen in cooperatively-breeding birds is associated with increasing sedentariness, lower latitudes, and decreased environmental fluctuation. Arnold and Owens (1998, 1999) argued that “low annual mortality is the key factor that predisposes avian lineages to cooperative breeding; then ecological changes, such as becoming sedentary, further slow population turnover and reduce opportunities for independent breeding.”

Discussion

Ever since Darwin (1859) worried about the implications of cooperative and altruistic acts for his theory of natural selection, evolutionarily-oriented biologists have had something of a love/hate relationship with these subjects. On the one hand, these behaviors seem intrinsically important and something of a paradox to a gene's eye view of the world. On the other hand, studying cooperation and altruism, particularly in a controlled experimental manner, is very difficult. This is no less true today than 150 years ago, but we have made some progress in understanding the ultimate aspects of cooperation. In this review we have focused on intraspecific cooperation, but huge strides have been made in understanding interspecific cooperation as well (Boucher 1985; Kawanabe et al. 1993; Bronstein 1994; Frank 1994; Connor 1995; Nee 2000; Stachowicz 2001).

In addition to the work we have covered here, four recent developments also bode well for our understanding of the evolution of cooperation, and its implications. Reeve and his colleagues (Keller and Reeve 1994; Reeve and Keller 2001; Reeve et al. 1998, 2000), following early work by Emlen (1982a), Vehrencamp (1983), have built a number of “transactional models” of cooperation (also see; Johnstone and Cant (1999), Cant and Johnstone (2000), Johnstone (2000), Johnstone et al. (2000)). Transactional models unite genetics, ecology and behavioral dynamics under one theoretical umbrella, and have great potential to unravel some of the mysteries of cooperation.

Recent work has also focused on the role of punishment in the evolution and maintenance of cooperation (Axelrod 1986; Clutton-Brock and Parker 1995; Boyd and Richerson 1992; Sober and Wilson 1998; Heinrich and Boyd 2001; Nesse 2001; Sigmund et al. 2001). For example, in a tantalizingly titled article, "Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups", Boyd and Richerson argue that while many models fail to uncover cooperation when individuals live in large groups, this need not be the case. Rather than have cooperators simply withhold cooperation when they encounter noncooperators, Boyd and Richerson model "retribution," wherein cooperators punish specific noncooperators for their actions. Such retribution can take many forms including noncooperators being physically attacked, being made the victim of gossip (unlikely, but not impossible, in nonhumans) or being denied access to some important resource (Boyd and Richerson 1992). Once retribution is built into mathematical models, cooperation becomes a much more likely outcome.

Punishment may also be linked to cooperation via reputation. Pollock and Dugatkin (1992) first raised the possibility that reputation could facilitate cooperation in nonhumans and humans alike. Recently Sigmund et al. (2001) have shown that reputation is a much more powerful force when it is backed up by punishment vs. reward. More generally, it seems that the more sophisticated the underlying cognition that is assumed in a model, the greater the role punishment plays. For example, when Axelrod (1986) developed a game involving "metanorms" such as "punish those who fail to punish cooperators," cooperation again fared well. Similarly, when "commitments" are examined from an evolutionary perspective, punishment again facilitates cooperation. While metanorms are unlikely in many nonhuman animals, the possibility of commitments driving some social behavior in nonhumans is possible, at least in principle (Adams 2001; Dugatkin 2001; Nesse 2001; Silk 2001).

Animals are capable of punishing one another for violating established "rules" and such punishment is a powerful force. Rhesus macaques, for example, that fail to give food calls upon finding a new foraging patch are often punished by other group members (Hauser 1992; Hauser and Marler 1993), while adult female vervets that have been displaced from a food source often punish the displacer by attacking its relatives (Cheney and Seyfarth 1990). Punishment is usually dished out by dominants, but in some cases, such as egg production in the paper wasp, *Polistes fuscatus*, subordinates take on the role of punisher (Reeve and Nonacs 1992). Clutton-Brock and Parker (1995) list five contexts in which punishment plays a role in animal social life, and, not surprisingly, cooperative behavior is a prominent member of that list.

A number of sophisticated computer simulation models have tackled the complex question of what role population dynamics plays in the evolution of cooperation (Dugatkin 1997; Nowak and Sigmund 1998; Roberts and Sherratt 1998; Riolo et al. 2001). Such models often uncover new and fascinating heretofore unthought of twists and turns in our understanding of cooperative behavior. Finally, Bekoff (2000) has argued that social play in mammals is often how animals learn to cooperate and act fairly and that understanding the dynamics of such cooperation can help us better tackle the study of the evolution of morality.

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