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THE EVOLUTION OF COOPERATION

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ABSTRACT

Darwin recognized that natural selection could not favor a trait in one species solely for the benefit of another species. The modern, selfish-gene view of the world suggests that cooperation between individuals, whether of the same species or different species, should be especially vulnerable to the evolution of noncooperators. Yet, cooperation is prevalent in nature both within and between species. What special circumstances or mechanisms thus favor cooperation? Currently, evolutionary biology offers a set of disparate explanations, and a general framework for this breadth of models has not emerged. Here, we offer a tripartite structure that links previously disconnected views of cooperation. We distinguish three general models by which cooperation can evolve and be maintained: (i) directed reciprocity—cooperation with individuals who give in return; (ii) shared genes—cooperation with relatives (e.g., kin selection); and (iii) byproduct benefits—cooperation as an incidental consequence of selfish action. Each general model is further subdivided. Several renowned examples of cooperation that have lacked explanation until recently—plant-rhizobium symbioses and bacteria-squid light organs—fit squarely within this framework. Natural systems of cooperation often involve more than one model, and a fruitful direction for future research is to understand how these models interact to maintain cooperation in the long term.

A FEW KEY STUDIES in the 1960s led to a radical change in the way biologists viewed the evolution of cooperative interactions. Challenging the nearly pervasive and casual attitude of most biologists that held that interactions evolve for the good of the species, Hamilton (1964a,b) and Williams (1966) explained how natural selection was intrinsically selfish, and that cooperative acts were likely to evolve only under restrictive conditions. This shift in paradigm then set the stage for a major focus on the evolution of cooperation in the last two decades.

The evolution of cooperation contrasts with the evolution of traits that directly and solely benefit the individual possessing them, such as sharp teeth, visual acuity, or crypsis. Cooperation by definition involves an interaction between individuals that benefits the recipient but not necessarily the donor. At face value, therefore, cooperation presents an evolutionary dilemma, one that underlies a famous quote of Darwin (1859): “Natural selection cannot possibly produce any modification in any one species exclusively for the good of another species” (p 228). Darwin realized that the bearers of a trait must themselves benefit if the trait is to be favored under natural selection. The modern version of Darwin’s criterion is that the genes underlying a cooperative trait must themselves benefit disproportionately if they are to increase in frequency. How then do cooperative traits overcome this evolutionary hurdle?

Hamilton (1964a, 1964b) proposed one

solution that can operate within species: the genes for cooperation tend to benefit copies of themselves in others, and thus are favored by a process of “kin selection” (Maynard Smith 1964). While kin selection has provided the conceptual framework for understanding cooperation between relatives, a vast number of cooperative traits are not explained by Hamilton’s solution (cooperation between species, for example). Today, a pluralistic approach has emerged, in which multiple models attempt to explain various idiosyncratic examples of selfless behavior. The full account of models for cooperation includes not only kin selection, but the iterated prisoner’s dilemma of reciprocal altruism (Trivers 1971; Axelrod and Hamilton 1981), synergism (Queller 1985), indirect reciprocity (Alexander 1987; Nowak and Sigmund 1998), partner choice (Eshel and Cavalli-Sforza 1982; Noë 1990; Bull and Rice 1991), policing (Frank 1995, 2003), pseudo-reciprocity and parceling (Connor 1995b), to name a few. However, this panoply of models does not offer obvious themes that underlie our modern understanding of the evolution of cooperation.

This paper offers a hierarchical framework in which the principal models of cooperative evolution are readily compared, and in which known examples can be accommodated. Alternative frameworks have been proposed: inclusive fitness theory (Queller 1985), trait-group selection (Wilson 1975; Wilson and Dugatkin 1997), and repression of competi-

tion/policing (Frank 1995, 2003). We think that the framework offered here is the most comprehensive and provides a more natural accommodation of the diverse biological examples of cooperation. We suggest that multiple frameworks are desirable, however, and are motivated by the belief that enlightenment emerges out of the contrast between different conceptual frameworks.

The structure for this paper is as follows. We define cooperation and then proceed to explain our framework using traditional examples and models. Since none of the models presented are original to us, it is the organization of models that distinguishes this paper from others. Next, we apply this framework to diverse biological systems, ranging from well-studied and well-understood examples to cases that are complex and enigmatic. Finally, we suggest avenues of further study.

WHAT IS COOPERATION

All cooperation involves acts by one individual (X) that benefit one or more other individuals (Y). Beyond this deceptively simple core, there is an intricacy that complicates attempts to unite different models under a single approach. The greatest focus in the field has been on “costly” acts by individual X that benefit Y, because the challenge in such cases is to understand how natural selection can tolerate the maintenance of acts by X that potentially lower X’s fitness. More recently, however, the field has included cases in which acts by individual X benefit both X and Y. These cases, known as byproducts, can be understood by relatively straightforward selective mechanisms.

Cooperation is usually considered a two-way interaction, such as a mutualism or symbiosis. For the sake of deconstructing the evolution of cooperation, we adopt a one-sided perspective that considers the costs and benefits accruing to one partner at a time. This one-sided perspective is essential for addressing the evolution of cooperation between species, because the evolutionary process leading to and maintaining cooperation is operating separately in each species. The critical mechanisms stabilizing cooperation can be different in two interacting species.

This one-sided perspective also expands the realm of examples that are relevant to the evolution of cooperation to include exploitation and parasitism. This generalization can be realized by considering a one-dimensional continuum of possible actions of individual X on individual Y, with cooperation at the left end and antagonistic/exploitative interactions at the right. Evolution in X that shifts its location on the continuum toward the left has, by definition, evolved to be more cooperative, regardless of where it sits on that continuum. Thus, the framework applies beyond interactions that are strictly cooperative.

THE FRAMEWORK

Our classification divides types of cooperation into three general models: i) *directed reciprocity*—cooperation with individuals that return benefits; ii) *shared genes*—cooperation with relatives (e.g., kin selection); and iii) *byproduct benefits*—cooperation with others as a coincident of selfish actions (Table 1). Each general model can be further subdivided. Directed reciprocity is divided into *partner choice* (benefits are returned by specifically chosen partners) and *partner fidelity feedback* (benefits are returned by partners that are coupled in fitness). Shared genes is divided into *kin choice* (cooperation with relatives based on phenotypic recognition of those relatives) and *kin fidelity* (cooperation with relatives based on a social context of spatial association). Finally, byproducts is divided into: *one-way byproducts*—one individual receives incidental benefits from another individual; *two-way byproducts*—two or more individuals receive incidental benefits from each other; and *byproduct reciprocity*—where an individual maximizes incidental benefits it receives from another by actively helping that individual.

Each of these models have been proposed before (Hamilton 1964a, 1964b; Eshel and Cavalli-Sforza 1982; Queller 1985; Bull and Rice 1991; Noë and Hammerstein 1994, 1995; Connor 1995a, 1995b; Frank 1995, 2003; Noë 2001; Wilkinson and Sherratt 2001; Simms and Taylor 2002), but without the overall structure presented here. We attempt to provide a comprehensive hierarchy of models in

TABLE 1

General Models	Specific Models	Examples in Text
Directed Reciprocation		
X undertakes a significant cost to benefit Y, and Y in turn reciprocates that benefit back to X. Operates within or between species. (Trivers 1971)	<i>Partner Fidelity Feedback</i> X and Y are associated for an extended series of exchanges that last long enough that a feedback operates: the effect of benefits transferred from X to Y returns and enhances the fitness of X. Thus, by failing to cooperate, individual X ultimately curtails its own fitness (Bull and Rice 1991; Nowak and May 1992; Frank 1994; Doebeli and Knowlton 1998; Simms and Taylor 2002).	—Vertically transmitted symbionts, optimal virulence evolution, ant-acacia mutualism.
	<i>Partner Choice</i> Either individual X ₁ or X ₂ receives a benefit from Y, depending on Y's choice. Y chooses to interact with the X individual that offers greater fitness returns (Darwin 1859; Eshel and Cavalli-Sforza 1982; Noë 1990; Bull and Rice 1991; Peck 1993; Noë and Hammerstein 1994; Batali and Kitcher 1995; Frank 1995; Wilson and Dugatkin 1997; West et al 2002b).	—Squid-light organ symbiosis, legume-rhizobium symbiosis, yucca-yucca moth symbiosis, image-scoring in reef fish, allogrooming in impala.
Shared Genes		
X benefits Y ₁ with which X shares alleles through descent from a common ancestor. Operates within species only. (Hamilton 1964a,b)	<i>Kin Choice</i> X recognizes and directs benefits to more closely related Y ₁ as opposed to more distantly related Y ₂ based on phenotype(s) of Y ₁ , Y ₂ (Hamilton 1964a; Eshel and Cavalli-Sforza 1982; Reeve 1989; Queller 2000).	—Exclusion of non-relatives in tunicates, GP9 locus in fire-ants, M-factors in beetles, cell adhesion genes in social amoebae.
	<i>Kin Fidelity</i> X directs benefits to Y ₁ based upon Y ₁ 's context-dependent spatial association with X. This proximity denotes shared genes with X (Hamilton 1964a; Eshel and Cavalli-Sforza 1982; Reeve 1989; West et al. 2002a).	—Parental care in birds, coinfection in clonal microbes, aposematism in family groups of aphids.
Byproducts		
X benefits Y as a byproduct of an otherwise selfish act of X. Operates within or between species. (West-Eberhard 1975; Brown 1983)	<i>One Way</i> An act of X benefits Y as an automatic consequence (byproduct) of X's self interested action (West-Eberhard 1975; Brown 1983; Connor 1995a).	—Vultures and lions, carrion feeders.
	<i>Two Way</i> Both X and Y each benefit the other as automatic consequences (byproducts) of their own selfish actions. Includes synergism: actions or coordinated behavior that are automatically more fitness-enhancing when performed in groups (Hamilton 1971; Queller 1985; Connor 1995a).	—Predator dilution in bugs, selfish herds, Mullerian mimicry, unrelated helpers at the nest, ant colonies founded by multiple queens.
	<i>Byproducts Reciprocity</i> Y evolves to enhance its benefit to X, which in turn increases the byproducts it receives from X. The byproduct from X does not evolve, but the effect of Y on X does (Connor 1986).	—Honeyguide-man mutualism, food sharing in cliff swallows.

which each model invokes the fewest assumptions required to evolve (or maintain) cooperation and does not invoke any of the other models. This emphasis on “minimal” models stands in contrast to some other approaches. In particular, Noë (whose approach shares similarities with ours) has developed a framework around “biological markets” (Noë and Hammerstein 1994, 1995; Noë 2001). Markets combine several models present in our framework and thus can be dissected with our approach. Frank (1995, 2003) has developed a framework around policing (repression of competition), which we dissect and reclassify under several models below. Likewise, as we will explain below, the collection of examples that have been lumped under the well-known “iterated prisoner’s dilemma” model are subdivided here into partner choice and partner fidelity feedback. We first introduce the models for the evolution of cooperation, then apply that framework to specific examples of cooperation to identify the mechanisms driving cooperation in each case.

DIRECTED RECIPROCATION

In directed reciprocity, an individual accepts a cost to benefit a specific partner, and the partner in turn compensates or reciprocates that benefit back to the donating individual (hence the reciprocity is “directed” to the partner). To anticipate the other models in our framework, directed reciprocity is distinguished from shared genes because it can operate between nonrelatives and between species, and it is distinguished from byproduct benefits because the cooperative traits are potentially costly, not directly benefiting the individual expressing them.

Of these three classes of models, directed reciprocity best epitomizes the Darwinian dilemma, because most examples involve adaptations in one species that benefit another species. Furthermore, the mere fact that directed reciprocity has been established does not ensure its persistence—these systems are potentially vulnerable to exploitation, in which an individual receives the benefit from its partner and then enjoys a further benefit by not reciprocating (also known as “cheating”). Models that account for the

evolution of directed reciprocity must thus account for the stability of cooperation against cheating.

The iterated prisoner’s dilemma (IPD) game is the most celebrated model of directed reciprocity. The mechanism driving the evolution of cooperation under this model was first explained by Trivers (1971) but was later developed by Axelrod and Hamilton (1981). This model has two main requirements: (i) an extended series of interactions within a pair of individuals, and (ii) the ability of each individual to vary its behavior in each interaction according to a partner’s previous action. The conclusion from the Axelrod-Hamilton paper was that the simple strategy of “tit-for-tat” evolved under a wide range of conditions if the likelihood of future interactions between the same partners was high. (The tit-for-tat strategy is the rule of “cooperate when your partner has cooperated in the previous iteration but refuse to cooperate if your partner did not cooperate in the previous iteration.”) The Axelrod-Hamilton paper inspired a surge of theoretical and empirical studies on cooperation, mostly supporting the generality of the original conclusions.

Many empirical examples of cooperation were initially interpreted as fitting this model, including intracellular symbionts, parasite virulence (Axelrod and Hamilton 1981), the cooperative behavior of fish (Dugatkin 1997), and even dynamics of WWI trench warfare (Trivers 1985). While there is no question that the IPD model describes conditions that can favor cooperation, there are few examples that are now thought to adequately satisfy its assumptions. Many between-species examples clearly do not fit, such as two-species cooperative systems that lack long-term interactions between the same partners.

The IPD has two main components: repeated interactions of partners and the ability of interactants to alter their behavior in response to the other’s action. As has been realized previously, either component alone can drive the evolution of cooperation. Our framework for directed reciprocity thus separates these two components of the IPD into *partner fidelity feedback* (involving repeated interactions between partners) and

partner choice (differential response to partners). Connor (1995b) has also partitioned and reclassified examples formerly interpreted as IPD, but along different lines than ours.

Partner Fidelity Feedback

Two partners (X, Y) are associated for an extended series of either discrete or continuous exchanges (Figure 1). The association lasts long enough that a feedback operates: changes to the fitness of individual Y affect the fitness of its partner X. Thus, by failing to cooperate, individual X ultimately curtails its own fitness because its partner's fitness loss feeds back as a fitness loss to X (merely because its partner cannot provide as much benefit). This feedback is automatic and, unlike tit-for-tat, does not require recognition or conditional response. Biological examples to be described below include vertically transmitted symbionts, commensals and parasites (e.g., mitochondria), and ant-acacia symbioses.

It has also been suggested on theoretical grounds that partner fidelity feedback operates in viscous populations, where spatial structure enforces the long-term association of different lineages living in proximity to each other (Nowak and May 1992; Frank 1994; Doebeli and Knowlton 1998). However, theoretical work in the field of kin-selected cooperation has noted that competition between neighbors may override selection for cooperation (Taylor and Wilson 1988; West et al. 2001, 2002a). This latter work, however, studies competition between neighbors of the same species, and competition may be weaker when cooperative partners are of different species.

Partner fidelity feedback is not merely an extended series of contests. Rather it is a *coupling of fitness* between two individuals through repeated interactions (Bull and Rice 1991); the fitness effects may extend across generations, as in vertically transmitted symbionts, or not, as is described below for ant-acacia symbioses. The stability of partner fidelity feedback is strongly dependent upon the strength of fitness feedback between partners. In theory, fitness feedback is strongest

under uniparental vertical transmission of symbionts, and this is the application of the model for which there is the greatest empirical support (Axelrod and Hamilton 1981). However, a number of other factors can facilitate strong fitness feedback (fitness coupling) between partners. Factors that limit the dispersal abilities of partners, including high population viscosity, are frequently discussed mechanisms to facilitate cooperation under partner fidelity feedback (Nowak and May 1992; Doebeli and Knowlton 1998; but see Taylor and Wilson 1988; West et al. 2001, 2002a). Partner fidelity feedback is also facilitated if small short-term fitness gains by cheating result in a large fitness loss to the partner. Thus, the negative effect of cheating on partner fitness increases disproportionately with the degree of exploitation. This is a common assumption in models of virulence evolution (discussed below).

Partner fidelity feedback differs from the explicit IPD in two basic ways. First, under partner fidelity feedback, interaction between partners involves automatic fitness feedback. Under the rules of the IPD, a cheater paired with a cooperator achieves the highest fitness attainable. In partner fidelity feedback a cheater's fitness declines by failing to maintain its cooperative partner's fitness. Second, in partner fidelity feedback no choice of partners is required to stabilize cooperation, and cheaters fail to receive benefits solely because of the automatic fitness feedback. The IPD, however, leads to maintenance of cooperation only with a conditional strategy for reciprocation (e.g., tit-for-tat), which involves an element of partner choice manifested as termination of the cooperation.

Partner Choice

An individual X interacts with and rewards a specific cooperative partner Y and avoids rewarding less cooperative partners (Figure 2). By choosing a cooperative partner Y, individual X not only enhances its own fitness but it promotes the evolution of cooperation in species Y. This latter effect occurs because X selectively benefits cooperative individuals of Y through its cooperation. (However, it

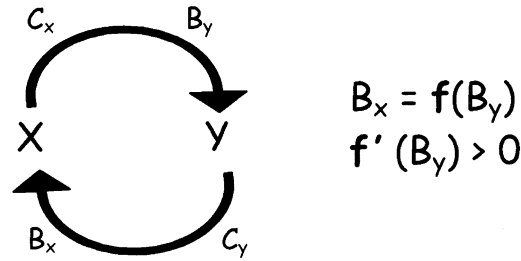


FIGURE 1. PARTNER FIDELITY FEEDBACK

Benefits transferred from X to Y feed back through an extended series of exchanges. (B_x, B_y = Benefits to X, Y respectively; C_x, C_y = Costs to X, Y, respectively. $B_x = f(B_y)$ means that benefits to X are a function of the benefits to Y. $f'(B_y) > 0$ indicates that B_x increases as B_y increase. B, C are always positive.)

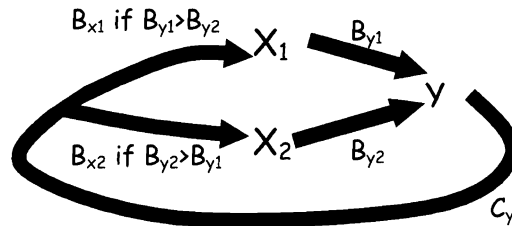


FIGURE 2. PARTNER CHOICE

Either individual X_1 or X_2 receives a benefit from Y, depending on Y's choice. Y chooses to interact with the more cooperative X individual. (B_{x1}, B_{x2} = Benefits to X_1, X_2 , respectively, B_{y1}, B_{y2} = Benefits to Y from X_1, X_2 , respectively; C_y , is the cost to Y.)

should be emphasized that X is selected to choose a cooperative partner only because of the immediate benefit to itself and not through the effect it has on Y's fitness.) Choice may take several forms, ranging from establishing cooperation with only one of several potential partners, to altering the duration of cooperation with a partner according to its actions, to actually reducing the fitness of selfish partners. Thus, partner choice differs from the IPD in one critical respect: partners need not interact repeatedly for cooperation to be maintained by partner choice. Cooperation can evolve by partner choice even if individuals interact only once.

Partner choice is easy to contemplate as a mechanism for the evolution of cooperation, but several quantitative factors determine whether it is sufficient to maintain cooperation (Bull and Rice 1991; Noë and Hammerstein 1994; Batali and Kitcher 1995; Noë 2001). For example, there is an inherent density dependence in which choices become

more limited when few partners are available than when many are available (Noë and Hammerstein 1994; Noë 2001). That is, the costs of rejecting a potential partner are lower if many alternative partners are available.

Partner choice involves both an *assessment* of how cooperative a partner is and a *decision rule* about whether to accept exchange with that partner (and how much to exchange). Decision rules may be relative, "accept the most cooperative individuals," or absolute "accept any partner above some value" (West et al. 2002b). Decision rules may be behavioral, as with partner choice in baboons (Noë 1990), or chemical, as is in the yucca-yucca moth symbiosis discussed below. "Tit-for-tat," for example, is a type of decision rule commonly modeled in the IPD.

Decision rules are often coupled with an assessment system. The assessment system is the biological arena in which one or more potential partners are observed for their cooperative tendencies, such that their level

of cooperation in further interactions can be predicted. While a decision rule is the basis by which an individual chooses a partner, the assessment system allows an individual to gain information about which partners are cooperative and how cooperative they are. Three different assessment systems have been described in the empirical literature: parceling, distributing, and image scoring. In *parceling*, a single resource is presented to a partner incrementally, over time (Connor 1995b). A simple example of parceling involves grooming in impalas (Connor 1995b) in which individuals exchange short bouts of grooming in pairs. A cheating individual, in this case a nongrooming impala, can at best exploit a single grooming bout before its selfish tendencies are revealed. The choosing partner then avoids spending time grooming the selfish partner. Parceling is an integral part of the classic IPD model—it represents the iterations.

Yucca plants use a *distributing* assessment system to evaluate the cooperative tendencies of their obligate pollinating moths. Distributing is a spatial portioning of the resource. Moths oviposit into the ovary before pollinating the flower, and the developing seeds are used as food by the larvae. Uncooperative moths lay more than the average number of eggs per flower, thus lowering plant fitness. *Yucca* assessment is thought to depend on the number of larvae within each ovary. In contrast to parceling, there is no sequential exchange of benefits over time: if the plant aborts the flower, then both the plant and the moth lose all offspring from that flower (Pellmyr and Huth 1994; Huth and Pellmyr 2000). In contrast to parceling, therefore, distributing divides a resource into spatial allotments rather than temporal allotments. Distributing further differs from parceling in that the decision rule may act separately in each allotment (e.g., ovary). While a decision in parceling is made one partner at a time, decisions in distributing can be made simultaneously upon many partners.

A third type of assessment system, *image scoring* (Nowak and Sigmund 1998), exists in reef fish that choose among “cleaner fish” (Bshary 2002). Some species of reef fish, termed clients, benefit from cleaner fish that

remove and eat their mouth parasites or dead infected tissue (Grutter 1999). However, the cleaner may cheat the client by biting healthy tissue off the client instead of, or in addition to, the removal of parasites (Bshary and Grutter 2002). Some species of client fish choose cleaners after observing the cleaner’s behavior with a previous client; clients choose cleaners that they observe to be cooperative (Bshary 2002). This form of cooperation has been termed image scoring (Nowak and Sigmund 1998; Riolo et al. 2001) or more generally “indirect reciprocity” (Alexander 1987); a benevolent act by X to Y increases the chance that X receives benefit from others.

A History of Partner Choice

Partner choice is clearly a widespread evolutionary mechanism for cooperation, yet it is neglected in many reviews. This omission seems to stem from a widespread emphasis on the IPD as the model for the evolution of cooperation between unrelated individuals. Historically, however, partner choice underlies Darwin’s contemplation on the evolution of nectaries in flowers (1859:139, see below), Dawkins’s model of female choice of males differing in levels of paternal care of the brood (1976), the fig-wasp model described by Axelrod and Hamilton (1981), Eshel and Cavalli-Sforza’s (1982) model of assortment of encounters, and Bell’s model for the evolution of empty flowers (1986). Nonetheless, both Dawkins (1989) and Axelrod and Hamilton attempted to use the IPD to explain the evolution of cooperation where repeated interactions were absent, and Bull and Rice (1991) included one model involving partner choice under partner fidelity (feedback), illustrating the common difficulty and confusion over these mechanisms.

Noë (1990) proposed that certain types of choice-based games in baboons constituted an alternative to the IPD model as a way to maintain cooperation. Bull and Rice (1991) proposed the two basic models we recognize here, partner choice and partner fidelity (feedback). Noë and Hammerstein and their collaborators have since elaborated variations of partner choice and illustrated that the efficacy of choice increases with the number of

partners in a density dependent manner (Noë and Hammerstein 1994, 1995; Noë 2001).

We view some group-level selection models of *active* assortative interactions as partner choice models (Eshel and Cavalli-Sforza 1982; Peck 1993; Wilson and Dugatkin 1997). Choice of partners by individuals can drive the assortative interactions of cooperators. Assorted interaction then leads to between-group variance, and thus could allow selection to favor some groups over others. These models may be particularly predictive for within-species cooperation, though more empirical work is needed to test the importance of partner choice within species.

SHARED GENES

Cooperation by shared genes occurs when one individual benefits another individual with which it shares alleles through descent from a common ancestor. By definition, this mechanism operates only when the partners are members of the same species. A shared genes model for the evolution of cooperation (altruism) was first proposed and developed quantitatively in the classic papers of Hamilton (1964a, 1964b). In Hamilton's model, interactions occur among relatives, and evolved cooperative acts are directed toward other individuals, depending on the average degrees of relatedness of those individuals (Figure 3). Thus, genes that encode for (shared genes) cooperation tend to benefit copies of themselves in others (Dawkins 1976). Shared genes cooperation differs from all other models considered here in that the cooperative individual need not benefit from its act. This section is included in our review for completeness but is otherwise brief, since this subject already has several excellent reviews (Queller 2000; Alonso and Schuck-Paim 2002; West et al. 2002a).

We recognize two classes of mechanisms by which an individual preferentially gives benefits to others with shared genes: *kin fidelity* and *kin choice*. This distinction highlights the different mechanisms by which cooperative acts are directed to kin and the divergent ways that shared genes cooperation may be vulnerable to cheating. Kin fidelity versus kin

choice have been variously described as passive versus active assortment (Eshel and Cavalli-Sforza 1982), spatial association versus kin recognition (Grosberg and Quinn 1986), spatial location mechanism versus phenotype matching (Reeve 1989), and phenotypic versus nonphenotypic kin recognition (Pfennig 1997), though the context of these various terms are not always completely overlapping. This structure is obviously parallel to that of directed reciprocation.

Kin Fidelity

With kin fidelity, benefits are given to relatives based on context-dependent spatial association, as in offspring sharing a nest (Hamilton 1964a). By definition, no recognition of individuals per se is involved, because the act is performed to benefit individuals nearby. Although kin fidelity originally seemed to be an obvious mechanism for kin selection, it has recently been challenged as a sufficient mechanism to promote cooperation. The main problem is that relatives living in close proximity may also compete for common resources, and competition between close relatives can overwhelm selection for cooperation (Taylor and Wilson 1988; West et al. 2001, 2002a). Despite this problem, kin fidelity may be important in the evolution of cooperation, especially where kin recognition systems are unable to evolve (Crespi 2001).

Perhaps the first kin fidelity hypothesis was Fisher's model (1930) for the evolution of aposematism through the clustering of brightly colored sibling larvae. A predator tasting the first larva would learn to avoid the siblings because of their spatial proximity and similar appearance. This model has since received empirical support: in experiments, two predator species learned to avoid a conspicuous-distasteful species of aphid while continuing to eat a cryptic-tasteful species after limited experience with both (Malcolm 1986). The aposematic aphids live in large familial congregations, so the kin-selected benefits of aposematism are only received by nearby relatives, as in Fisher's model.

Another unambiguous example of kin fidelity is revealed in the experiment of Turner and Chao (1999), in which a bacteriophage evolved lower levels of selfishness when

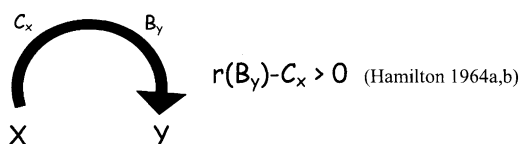


FIGURE 3. KIN SELECTION

X evolves to benefit Y if $rb_y - c_x > 0$. (r = coefficient of relatedness between X and Y; c_x = the cost of the act to X; b_y = the benefit of the act to Y.)

bacteria were infected with phage clone mates than when infected with nonclone mates. The level of kin fidelity is merely the extent that bacteria were coinfecting by related phage genotypes versus unrelated genotypes, and the results showed that higher levels of kin fidelity selected higher levels of cooperation.

For many birds that invest significantly in their brood, parents often feed or incubate whichever young are in that parent's nest, even when those young are not their offspring (as in cuckoldry or experimental crossfostering). This fundamentally involves kin fidelity rather than kin choice. In contrast to the two preceding examples, however, there is a certain level of recognition required: parents recognize their nest even if not their offspring in that nest. Hence this example has also been classified as nonphenotypic recognition (Pfennig 1997).

Kin fidelity is vulnerable to a specific kind of cheating because a nonkin individual can receive kin fidelity benefits simply by being present in the correct context or location, as in the brood parasitic birds just described. Kin fidelity is no doubt important in many contexts: even when proximity leads to competition, kin fidelity may moderate the competitive interactions of relatives.

Kin Choice

Individuals benefit others whose phenotypes indicate shared genes. Kin choice implies (kin) recognition, and the mechanisms of recognition are diverse. There are two dimensions to kin recognition: which phenotypes are used in recognition, and how the discrimination is acquired. The phenotypes include visual or auditory cues as well as odors, pheromones, and other diffusible chemicals (Greenberg 1979; Gamboa et al.

1986, 1996). Most commonly, the recognition is acquired by learning some type of environmental cue (Gamboa et al. 1986; Neff and Sherman 2002), and this learning often has elements of kin fidelity (because the individuals who are learned as kin are neighbors). One example of kin choice that does not involve kin fidelity comes from colonial tunicates that fuse to form colonies. The fusion systems typically exclude nonrelatives from colonies, and this "choice" appears to be based solely on heritable cues (Grosberg and Quinn 1986; Rinkevich and Weissman 1992; Bishop and Sommerfeldt 1999).

Although learned recognition may blur our distinction between kin choice and kin fidelity, it operates in most animals with kin recognition (Pfennig 2002). Learned discrimination often has elements of kin fidelity, because the individuals learned as kin are those of the same nest or other immediate environment. Kin recognition is often learned simply by exposure, so that an individual's specific phenotype becomes familiar. Experiments involving exposure of naïve social wasps to nonkin nests have shown that nonkin can become accepted and that quarantined kin can be forgotten and excluded (Pfennig et al. 1983). In wood frogs, naïve individuals kept free of variable environmental cues prefer kin to nonkin, suggesting an intrinsic ability to discriminate. However, this effect is overcome by exposing nonkin groups to similar environmental cues, whence they now recognize each other as kin (Gamboa et al. 1991).

Although recognition can be based on a phenotype that reflects kinship per se (whole-genome relatedness), it can also be based on specific genes that are the true targets of selection. A case in point is what has been described as "green beard" selection (Ham-

ilton 1964a). Three properties are required for green-beard selection: (i) a gene which causes a phenotypic effect; (ii) recognition of the phenotype; and (iii) differential behavior by bearers of the gene to those with the phenotype (Hamilton 1964a). In this model, first proposed merely as a hypothetical principle, benefits are directed to individuals who are phenotypically recognized as carrying the cooperative gene(s). The interacting individuals need not be kin per se (may not share whole-genome relatedness), but the recognized phenotype enables the benefits to be bestowed directly on the genes affecting the cooperation. (We include the green-beard model in this section on kin choice for convenience, even though it does not require choice of *kin* per se.) Green-beard mechanisms may operate to specifically reward individuals carrying the proper genes, or to harm individuals that lack those genes, regardless of how many alleles individuals share throughout the rest of the genome. Empirical work matches the predictions of green-beard selection for the fire ant Gp-9 locus (Keller and Ross 1998), M-factors in flour beetles (Beeman et al. 1992), and cell adhesion genes in social amoebae (Queller et al. 2003). As far as we know, all the above examples of green beard are pure examples of kin choice; they work irrespective of environmental or context dependent cues.

In contrast to kin fidelity, kin choice can be exploited by nonkin that imposter as of mimic relatives (Alexander and Borgia 1978). We are unaware of exploitation of this specific type, but it may well exist. One interesting line of research will be to study specifically how cooperation is stabilized against cheaters in each case, and whether recognition or proximity maintains cooperation between relatives.

BYPRODUCT BENEFITS

Byproduct models have only recently been emphasized in the cooperation literature. They are potentially confusing because they do not obviously qualify as cooperation in the classic sense, but they overlap with cases that clearly do qualify. Byproduct benefits are integral parts of some cooperation systems, and they likely formed the origins of many systems

that evolved into more elaborate cooperative interactions. We distinguish three categories.

One-Way Byproduct Benefit: No Evolution of Cooperation

The benefit that Y receives is an automatic consequence of the otherwise selfish act in which individual X does something to benefit itself (West-Eberhard 1975; Brown 1983; Figure 4). For example, the feces from large ungulates are food for dung beetles; vultures and carrion-feeding insects benefit from abandoned lion kills. Following Connor (1995b), there has been no evolution of cooperation per se in these cases. That is, lion behavior has not been evolutionarily modified to benefit vultures or other carrion feeders, and vulture behavior has not evolved to increase the chance of a kill. Whatever evolves in the case of this byproducts model, it is not selected to offer a cooperative act. In byproduct models, there is no potential Darwinian dilemma, because the basic cooperative trait directly benefits its bearer and only incidentally benefits others.

Two-Way Byproduct Benefits: Byproduct Mutualism

Byproduct benefits can be one sided, in which X performs an act that benefits itself and coincidentally benefits another, Y, but benefits may also go in both directions to give byproduct "mutualisms" (West-Eberhard 1975; Brown 1983; Figure 4). Two-way byproducts can be simple extensions of one-way examples, or can promote group behavior. One general class of byproduct mutualism is *synergism*: actions or coordinated behaviors that are automatically more profitable when performed in groups (Queller 1985), such as flocking, selfish herds (Hamilton 1971), and Müllerian mimicry (Connor 1995a). Synergism has the appealing and simple formulation that group behavior evolves via individual selection whenever benefits increase disproportionately with group size. As a specific example, empirical work on aquatic hemipterans, which congregate in large groups, suggests that per capita predation risk decreases with group size (Foster and Treherne 1981). Thus, an individual join-

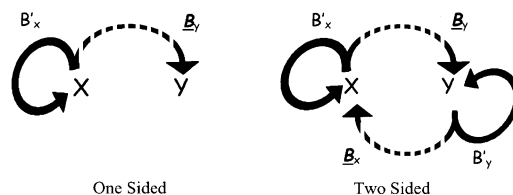


FIGURE 4. BASIC BYPRODUCT BENEFITS

Left: An act of X benefits Y as an automatic consequence (byproduct) X's self interested action (one sided). *Right:* Likewise, individual Y may, when performing an act that benefits itself, also benefit X (two sided). (B'_x , B'_y are benefits of self interest to X, Y respectively. B_x , B_y are byproduct benefits to X, Y, respectively. Dashed lines refer to byproduct benefits.)

ing a group reduces its own per capita predation rate as well as reducing the per capita predation rate of the other group members through simple predator dilution (Foster and Treherne 1981). Everyone benefits, and no special mechanism for "cooperation" need be invoked.

Although controversial in the details, cooperative founding of colonies between unrelated ant queens also fits the requirements of byproduct mutualisms, because grouped queens automatically achieve higher mean (expected) fitness than solitary females (reviewed in Bernasconi and Strassmann 1999). Two-way byproduct cooperation also extends to examples of "helping at the nest" by unrelated individuals. At least 300 species of birds exhibit cooperative breeding, in which some individuals forgo independent nesting to act instead as helpers at a conspecific's nest (Arnold and Owens 1998). In some cooperatively breeding birds, the helpers are unrelated to the individuals they assist in raising young (Cockburn 1998). Recent work on cooperatively breeding warblers showed that unrelated helpers gained significantly more direct fitness benefits via breeding opportunities than through indirect fitness benefits (Richardson et al. 2002). Thus, the benefits that other birds receive from the unrelated helpers is a byproduct of the helpers' pursuit of direct fitness benefits.

Maximizing Byproduct Benefits Without Evolving Cooperation

When byproduct benefits exist, individuals may be selected to increase the benefit they can obtain. Evolution of byproducts may take the form of "harvesting" the byproduct bene-

fits *without* benefiting the partner that produces the benefit. As an imaginative example, dung beetles might evolve to search for large mammals that provide dung, limiting their foraging to the vicinity of these animals. There would be no specific evolution of cooperation—promoting a benefit to another individual—but this evolution may increase the appearance of the cooperation because the "harvesting" individual has undergone evolutionary modification to increase its dependence on the byproduct.

Byproduct Reciprocity: Evolution of Cooperation from Byproducts

When one individual (X) receives automatic byproduct benefits from another individual (Y), natural selection can shape X to maximize these benefits by being cooperative toward Y. The greater cooperation *toward* Y yields greater byproduct benefits *from* Y (pseudoreciprocity: Connor 1986; Figure 5). For example, consider the remarkable case of the greater honeyguide, an African bird that guides humans to beehives for collection of honey (Hoesch 1937; Isack and Reyer 1989). In Africa, humans have foraged for beehives for many thousands of years. As a consequence of diminishing returns during hive destruction, there is generally honey left behind after human foraging (Dean et al. 1990). Upon destruction of the hive by the human, the bird forages on the discarded hive remnants, and thus receives automatic benefits as a byproduct of the human foragers' selfish act. Presumably to maximize this benefit, the bird has evolved to call the humans and lead them to beehive locations. Although the coevolutionary history of this

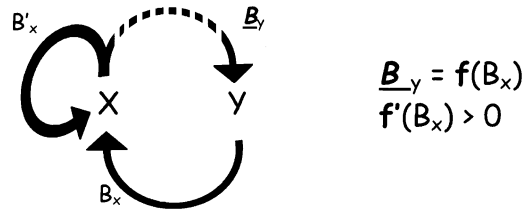


FIGURE 5. BYPRODUCT RECIPROCITY

Y evolves to enhance its benefit to X, which in turn increases the byproducts it receives from X. (B'_x is a benefit of self-interest to X, B_y is a byproduct benefit to Y. B_x is a benefit to X. Dashed lines refer to byproduct benefits.)

apparent human-bird mutualism is speculative (Dean et al. 1990), the inescapable conclusion is that this bird behavior evolved to benefit another species because the bird is incapable of attacking an intact hive by itself. The behavior of the other species in turn benefits the bird. No special mechanisms are needed to prevent exploitation of bird behavior, because the cooperator (human) automatically returns the benefit by unavoidably leaving scraps of the hive behind.

Why is byproduct reciprocity not prone to exploitation? For all examples of byproduct reciprocity known to us, the underlying feature is a common resource not totally monopolizable by either party: each interactant is assured adequate benefits. For example, the honeyguide requires only a small fraction of the hive, which is unavoidably left over during dismemberment of the hive by humans; honeyguiding behavior would presumably not have evolved if humans harvested entire hives without leaving scraps. A parallel case is food sharing in social cliff swallows, which alert conspecifics when insect swarms are found. Efficient group tracking of swarms can benefit the caller through increased foraging (Brown et al. 1991).

EMPIRICAL EXAMPLES OF COOPERATION

We now review examples of cooperation in nature, illustrating the application of this framework. Our examples focus heavily on partner fidelity feedback and partner choice because the other examples, listed in the tables above, do not present the difficulties in interpretation that directed reciprocation does. Some systems of interspecific cooperation involve multiple mechanisms. Further-

more, for a given cooperative interaction between species, the mechanism maintaining cooperation in one species may differ from the mechanism maintaining cooperation in the other species.

PARTNER FIDELITY FEEDBACK:
A DIVERSITY OF CONTEXTS

Organelles and Maternally Inherited
Microorganisms

Strong partner fidelity feedback (PFF) exists between eukaryotes and their vertically transmitted bacteria-derived symbionts, such as mitochondria and chloroplasts. The evolution of these symbionts has been sometimes accompanied by extreme reduction in gene content and genome size of the bacterial symbionts, and by tight interdependence of physiologies between the symbiont and host cell (Palmer 1997; Moran and Wernegreen 2000). Axelrod and Hamilton considered this case under the IPD game (1981), but in most cases there is no element of choice (e.g., mitochondria cannot be rejected) and cooperation is maintained entirely by PFF.

Parasite Virulence Evolution

One of the most prominent applications of the PFF principle has been to understand the evolution of virulence in infectious diseases. Beginning with Fine (1975), Axelrod and Hamilton (1981), Anderson and May (1982), and Ewald (1983), the standard model for the evolution of virulence invokes a strict negative correlation between the parasite's propensity to be transmitted and the harm it causes its host (the virulence). Thus, an increased ability to infect new hosts comes at the expense of a shorter life span and/or

fecundity of the current host (higher virulence). The optimal virulence along this tradeoff depends on how long the parasite occupies its current host before it is transmitted to other hosts, the duration of the infection (limited by the longevity of the infected host and the speed of immune clearance), whether the populations of infected hosts are expanding or at a dynamic equilibrium (Lenzki and May 1994), and whether the infection is transmitted vertically or horizontally (Fine 1975; Axelrod and Hamilton 1981). All of these factors affect the PFF between the parasite and host, and in general, *the greater the PFF, the lower the optimal virulence*. For example, a strictly vertically transmitted parasite can afford but limited virulence (Ewald 1983). PFF is thus a central part of the framework for understanding the evolution of virulence, although the extent to which optimal virulence models are supported empirically is not clear (Ebert and Bull 2003). Note also that these examples focus on PFF from the perspective of the parasite, not the host, since the host does not benefit from the infection.

Fungal Endophytes

Various groups of fungi are specialized to invade plant tissues and exist inside living plants, for example, in the interstitium between leaf cells, or even inside of cells. Many of these endophytic fungi are parasitic and cause disease symptoms in the plant host, but others form mutualistic relationships with plants (Clay 1988; Saikkonen et al. 1998). The best-studied mutualist endophytes are in grasses, within which the fungi are vertically transmitted via the seeds (Schardl and Clay 1997). The fungus grows into the seed tissue during seed formation, subsequently infecting any developing seedling and ultimately the seeds of the next generation, thus spanning the fungus-host life cycle. The tight vertical transmission sets up conditions of PFF, and both partners are therefore expected to enhance each other's fitness. Indeed, grass endophytes produce secondary compounds (e.g., ergot alkaloids) that protect the grass host against herbivores; the grass host in turn provides the fungus with nutrients and facilitates fungal persistence. Investment by the

fungus into secondary compounds thus feeds back via protection of the nourishing plant host (feedback returning to fungus). Likewise, nutritional provisioning of the fungus by the host feeds back via increased delivery of secondary compounds (feedback returning to grass host). Interestingly, horizontally transmitted endophytes of plants generally have deleterious effects on their hosts, consistent with reduced or absent PFF between horizontally transmitted endophytes and their hosts.

Ants and Acacias

PFF exists in a short-term setting in the mutualism between bullhorn acacia plants (Mimosoideae) and ants in the genus *Pseudomyrmex*. The acacia plant grows chambers to house ants and provides protein and lipid rich "Beltian" bodies that nourish the ants (Belt 1874). In turn, the ants attack animals that contact the plant, preventing loss from herbivory. The ants also remove local vegetation in the immediate vicinity of the plant to reduce competition (Belt 1874; Janzen 1966). From the perspective of PFF, plant protection by the ants ensures the ants a future home and food supply that would not exist (or not be as extensive) if herbivores were allowed to reign freely on the plant. Likewise, the plant promotes positive feedback to its fitness by providing a home and food for the ants living on it. This PFF can only operate when plants are a limiting resource for the ants, so that ants cannot completely exhaust resources of the current plant and then move on to a new plant.

Although fitnesses in PFF are often coupled between partners across generations (as in the case of the endophytes), PFF does not operate across generations in the ant-acacia case. Each new plant starts from seed and must be colonized by ants, and those ants do not necessarily come from the parent plant producing the seeds. These short-term PFFs are less intrinsically stable than across-generation cases. For example, the ant-acacia system is ultimately maintained because plants attended by ants enjoy enhanced reproductive success. If ants evolved to consume flowers and all seeds of the plants they attended, the short-

term PFF would continue to operate and benefit the growth of existing adult plants as well as the ants, but recruitment of new plants would decline until the system collapsed when the acacia goes extinct. Plant castration occasionally occurs in a related ant-plant symbiosis, and the plant minimizes this cheating by restricting ant domatias (hollow structures that house ants) to certain parts of the plants (Izzo and Vasconcelos 2002). Finally, some plant-ants are effectively parasites on their plants (Janzen 1975) and recent work by Stanton et al. (1999) proposes that this parasitism is favored by a high density of ant trees. This supports the prediction that PFF can only occur in this system when plants are a limiting resource for ants. Thus, the success of PFF in maintaining cooperation must ultimately be assessed for its consequences across generations, even if the feedback operates on a shorter time scale.

Partner choice could also operate in this system, depending on the availability of empty plants. Ants whose plant "cheated" them and did not provide a home or food for them could potentially move out in search of a new home, rather than die with the current plant. Also, PFF would fail to operate if ant turnover was high, because ants that did not remain in their home for long would be unlikely to reap the return benefits of maintaining it (akin to arguments about the evolution of parasite virulence under high levels of horizontal transmission). Thus, depending on environment and relative abundances of the two partner species, the ant-acacia system could potentially exhibit a turnover of mechanisms from pure PFF, to a mix of PFF and partner choice, to a destabilization of cooperation.

Breakdown of Partner Fidelity Feedback

The automatic feedback of PFF can operate at different levels of organization and different time scales, and is correspondingly vulnerable to exploitation. Specifically, PFF may sporadically break down when one of the partners has a different generation time than the other. For example, and perhaps surprisingly, mitochondria are the cause of some profoundly deleterious phenotypes, such as

male sterility in plants (Schnable and Wise 1998) and some degenerative diseases of aging (Wallace 1999). The evolution of mitochondrial male sterility derives from the fact that the PFF between mitochondria and host is matrilineal, so sons do not contribute positively to the feedback loop of mitochondrial fitness. Moreover, mitochondrial diseases of aging may be due to within-cell evolution of the mitochondrial population. This is a consequence of the within-cell evolution of mitochondria operating faster than the between-host evolution of cooperation (akin to cancer in this respect). PFF still operates and stabilizes host mitochondrion cooperation over the long run, but some invasion of cheater mitochondria can be expected, given their faster evolutionary rate and their resulting temporary liberation from PFF.

PARTNER CHOICE:

MANY ENIGMAS RESOLVED

In partner choice, individuals engage in one or more exchanges in which one partner can vary its response to accept or exclude the other partner. The strongest data for partner choice in a cooperative interaction is a variable and effective response to alternative partners. These data are not trivial to generate, but such responses are being worked out in elegant detail in two eukaryote-bacterial symbioses described below: the legume-rhizobium symbiosis and the bobtail squid-*Vibrio fischeri* symbiosis.

One of the biggest difficulties in exploring and understanding natural systems of cooperation is that partner choice, which is evidently rampant, is inherently density dependent and cannot operate effectively unless the preferred chosen partners are common (Noë and Hammerstein 1994; Noë 2001). Thus for systems in which the chosen partner is at least sporadically uncommon (Nuismer et al. 2000), cooperation may need to be supplemented by another mechanism, or otherwise the choosing partner may be exploited (see Bshary 2001 for this effect in cleaner fish). However, partner choice has the advantage over partner fidelity feedback in that, once established, it can work to the individual's benefit over short time-scales (e.g., within

generations). In contrast, many cases of partner fidelity feedback operate through differential reproductive success of the interacting lineages, hence across generations.

Yuccas and Yucca Moths

Yucca plants (Agavaceae), the plant family that includes Spanish daggers, have a highly specialized and largely obligate mutualism (Pellmyr and Thompson 1992). Yucca flowers require pollination by a yucca moth, and in return the developing yucca fruit provides an essential resource for the moth larvae. The larvae consume developing seeds and so reduce plant seed set directly. Thus, there is a potential evolutionary conflict in which moths try to maximize egg loads while the plant tries to maximize the number of developed seeds (Pellmyr and Huth 1994). Since the yucca system was first described, various intricacies have been discovered that paint a complicated picture for the maintenance of these systems (Pellmyr and Huth 1994; West and Herre 1994; Herre and West 1997; Huth and Pellmyr 1999, 2000; Marr et al. 2001).

In the “basic” mutualism, the moth gathers pollen from one or more flowers, typically flies to a new plant, oviposits into a flower, and then (often) pollinates that flower before moving to other flowers on the same plant (Huth and Pellmyr 1999). Moth species that exhibit this type of behavior could potentially violate the mutualism in two ways. First, they could oviposit but fail to pollinate. This is in fact a common but puzzling behavior, because unpollinated flowers do not develop and thus are dead ends for the offspring of the nonpollinating moths. However, at high moth density, an oviposited flower will sometimes be pollinated by another moth, which could save the eggs of a moth that did not pollinate. A second type of violation is to lay excessive numbers of eggs per flower, such that the plant produces few or no seeds (the same effect would be achieved by ovipositing in flowers with eggs deposited by another moth). Through selective maturation of fruit with low moth egg loads and high pollen loads the plant has a partner choice mechanism to reward moths that do not overload plant ovaries with larvae (Pellmyr and Huth

1994; Huth and Pellmyr 2000). A high percentage of flowers are normally abscised early; floral abortion not only prevents seed development, it also kills all moth larvae in that flower (Marr et al. 2001). The “choice” is discriminatory in that pollinated flowers with many oviposition scars are more likely to be abscised than those with few scars (Pellmyr and Huth 1994; Huth and Pellmyr 2000). The plant is thus able to ensure that seeds are produced, although the final distribution of egg loads per ovary may vary with the density of moths. In order for the plant to exercise choice, one would expect that the plants have evolved to produce initially more ovaries than they can actually support, allowing the plant to eliminate the least desirable flowers and thus select against the most undesirable moths.

Virtually nothing is known about how the plant is prevented from cheating the moth, which could be any form of killing the larvae while retaining pollinated ovaries. An additional complication is that there are moths that do not exhibit the above form of mutualism. Nonpollinating “parasitic” moth species are known that lay eggs in developing ovaries, after the plant has made its choice of which ovaries to abort (West and Herre 1994; Pellmyr et al. 1996). These parasites can only be maintained in the presence of the mutualists. Yet other species pollinate flowers but lay eggs near the surface of the ovary (Pellmyr and Leebens-Mack 2000). These scars do not affect the plant’s abscission decision, so it is not known how the fecundity of these (apparently mutualistic) moths is maintained at an acceptable level.

Squid Light Organs

The symbiosis between the bobtail squid, *Euprymna scolopes*, and the luminescent bacterium, *Vibrio fischeri*, is an elegantly studied example of partner choice. The squid houses luminescent *V. fischeri* cells in a specialized light organ on its mantle. The bacteria benefit from maximal growth conditions in the light organ, conditions that can barely be improved upon in lab cultures (Boettcher and Ruby 1990). The nocturnal foraging squid (Berry 1912) probably uses the bacteria

in a camouflaging behavior called counterillumination (McFall-Ngai 1990). Partner fidelity feedback via vertical transmission across generations is unlikely to occur because squids are born symbiont free and acquire their bacteria from the environment (Wei and Young 1989). There is no evidence that adults remain near their eggs (Singley 1983), nor that there are sufficient bacteria on the coating of the eggs to inoculate them (see Ruby and Lee 1998), thus there is no evidence for PFF. However, partner choice appears to occur at two steps in the interaction: initiation and maintenance of the symbiosis.

Initiation—For the squid, initiation of the interaction is specific to the bacterial species level, and even between strains (McFall-Ngai and Ruby 1991). While the light organ tissues remain open to new strains after initial infection (Lee and Ruby 1994a), they are resistant to all other marine bacteria but *V. fischeri* (McFall-Ngai and Ruby 1991) and its congener *V. logei* (Ruby 1996). A surface peptide on the bacterium plays a critical role in its recognition by a squid host and the specificity of the interaction (Hensey and McFall-Ngai 1992).

Maintenance—Once *V. fischeri* infects the squids, the mechanisms of partner choice are both elegant and specific. Even if hosts are infected with a single strain, new strains could arise through mutation or superinfection, so partner choice must also occur after initial infection, particularly since the bacteria are evolving faster than the host. Each morning, squids expel 90% to 95% of their symbiont population into the environment (Lee and Ruby 1994b), the remaining symbionts being tightly bound to microvillus structures lining the light organ (Montgomery and McFall-Ngai 1994). Although differential retention may be a mechanism for partner choice, no work has specifically addressed this aspect. However, there is intriguing evidence that the squid can select directly on luminescence as a bacterial trait. Visick et al. (2000) developed several mutant *V. fischeri* strains, defective for either the luciferase enzyme or a step in its regulation. These mutants were unable to completely colonize the light organs of the squids unless luciferase activity was replaced

experimentally. An elegant mechanism has been hypothesized for how the host can choose specific partners based on their luciferase activity. The crypts of the squid light organs produce poisonous concentrations of peroxidase (McFall-Ngai and Hensey 1992), which may function to act specifically against nonluminescent strains. Because the functioning bacterial luciferase has a higher binding affinity for oxygen than for the peroxidases, luminous strains may escape the effects of the deadly poison (Visick et al. 2000). Ruby (1996) pointed out that, of the thousands of *V. fischeri* strains isolated from bobtail squids, no nonluminescent strain has been found. Thus, partner choice seems to be an effective mechanism selecting against light cheaters in the *V. fischeri* / *E. scolopes* symbiosis.

The Legume-Rhizobium Symbiosis

The legume-rhizobium symbiosis offers a near parallel to the squid-*Vibrio* system described above, with partner choice occurring at both initiation and maintenance of the symbiosis. Legumes form symbioses with rhizobial bacteria that fix atmospheric nitrogen into organic form. The rhizobia reside as differentiated bacteroids harbored within root swellings called nodules. Plants usually benefit from this interaction, as nitrogen is often a factor limiting their growth (Tamm 1991), but it is difficult to measure the benefits to rhizobia. Studies show that there are higher concentrations of rhizobia surrounding symbiotic legumes (Reyes and Schmidt 1979; Kuykendall 1989), but evidence is scant beyond this (reviewed in Denison 2000; Simms and Taylor 2002). Partner fidelity feedback is unlikely to be a force in this system: rhizobia are not transmitted directly from parent to offspring but are spread between plants in the soil, and most plants are infected with several strains (Dowling and Broughton 1986). Experiments show much more bacterial genetic diversity within plants than between them (Hagen and Hamrick 1996).

Initiation—Two factors contribute to legume choice of rhizobia at the initiation of the interaction (Simms and Taylor 2002). Host plants produce flavonoids that are spe-

cifically recognized and matched by some rhizobial strains, and transcriptional regulators (NodD factors) on rhizobia induce critical stages of infection (Perret et al. 2000). Though strain specificity at initiation is important, it is unlikely to be immune to cheating (Denison 2000; Simms and Taylor 2002; West et al. 2002b).

Maintenance—Recent work has suggested that cooperation is maintained via postinfection legume sanctions of nonsymbiotic rhizobial strains (Denison 2000; Simms and Taylor 2002; West et al. 2002b; Kiers et al. 2003). Experimental evidence suggests that legumes punish nonfixing strains through limiting oxygen supply (Uvardi and Kahn 1993; Kiers et al. 2003). It seems likely that the elegant research on this system will soon unravel the mechanistic basis underlying rhizobial cooperation.

A Rule About Partner Choice?

Partner choice between species often operates on just one side of a mutualism. In particular, if there is an asymmetry in population size and/or generation time, the chosen partner is typically the one with the more rapid generation time and larger population size. There may be a meaningful generality in this pattern: that choice is a mechanism that the more slowly evolving species can use against the more rapid evolutionary changes of the partner. At present, we can offer no more than speculation of the possible existence or significance of such a pattern.

MULTIPLE MECHANISMS AND POTENTIAL PUZZLES

The application of our framework to even a modest number of examples from nature leads quickly to the realization that multiple mechanisms operate in many systems. In many cases, for example, one species uses partner choice to prevent exploitation, but the other partner species relies on a different mechanism. A system may also involve multiple mechanisms within one of the partner species. For some of the systems we analyze below, the evolution of cooperation is not well understood. We apply our framework to illustrate what kind of data need to be gath-

ered to identify the mechanisms maintaining cooperation in each system.

Generalized Animal Pollinators of Nectar-Producing Flowers

An example of cooperation that is familiar to everyone is the use of insects or vertebrates as pollen vectors for flowering plants. The flower offers the pollinator nectar or other reward, and the pollinator deposits pollen to fertilize the flower and/or carries pollen off from that flower in search of other flower rewards. The degrees of sophistication and specialization in this relationship vary widely across plant species, from largely nonspecific pollinators of sunflowers to the highly coevolved systems of euglossine bees and orchids. In most cases, the delivery and dispensing of pollen by the animal is inadvertent, a byproduct of the fact that pollen sticks to the pollinator and that the animal cannot easily remove it. To attract the pollinator, the plant offers a reward in the form of nectar. However, the pollinator is vulnerable to being cheated (Bell 1986; Gilbert et al. 1991), because some pollen will already have been deposited before the insect can determine whether there is a reward present in that flower. Partner choice is at work in at least some cases: insects (Chittka et al. 1999) and hummingbirds (Waser and Price 1981; Meléndez-Ackerman et al. 1997; Schemske and Bradshaw 1999) remember plant characteristics that do and do not offer rewards, such that the selfish plant receives fewer visits (see Noë 2001 for a model of this effect). As far as we know, no work has specifically tested partner choice mechanisms in pollinators, as work has focused on choice by pollinators between plant *species* and according to flower characteristics (Meléndez-Ackerman et al. 1997). It is therefore unclear how partner choice is operating on individual flowers. Perhaps insects visit few flowers on a plant if that plant has little nectar, thus potentially reducing plant fitness through its choice to leave quickly. Interestingly, Darwin (1859) recognized that partner choice acts in nectar-producing flowers (though not identified as such):

Those individual flowers which had the largest glands or nectaries, and which

excreted most nectar, would be oftenest visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. Those flowers, also, which had their stamens and pistils placed, in relation to the size and habits of the particular insects which visited them, so as to favour in any degree the transportal of their pollen from flower to flower, would likewise be favoured . . . ” (p 139).

In the first sentence Darwin describes partner choice by pollinators; the second sentence, however, he describes maximization of the byproduct benefits received by the plants. This latter effect should not be confused with byproduct reciprocity, since the insect does not necessarily reap benefits from the plant's specialization.

Leaf-Cutter Ants that Cultivate Gardens

Fungus-growing ants require the cultivation of fungus for food. When associated with ants, the fungal cultivars are clonally propagated within ant nests, and also between ant generations through the transfer by foundress queens of clonal inocula from maternal to offspring nest. Cultivar clones are occasionally exchanged laterally between different ant nests (Mueller et al. 1998; Adams et al. 2000; Green et al. 2002). Associations of ant and fungal lineages thus persist for prolonged evolutionary times through partner fidelity feedback, but are occasionally punctuated by novel fungal imports or lateral cultivar transfer.

Partner fidelity feedback is certainly one mechanism that will curb the spread of unproductive or exploitative “cheater” cultivars, but partner choice is a second *reinforcing mechanism* (Mueller 2002). For example, ants may be able to pick between productive and unproductive cultivars that coexist in a given nest, using indicators of cultivar productivity (e.g., nutrient level, growth rate). Behavioral assays in which ants were presented with genetically differentiated cultivars indicates that attine ants are indeed capable of exerting “symbiont choice” necessary for the operation of partner choice (Mueller et al.

2004). Moreover, cultivar substitution involving lateral transfer from other nests is inherently based on partner choice of cultivars selecting for cultivar productivity because: i) the substituting ants may screen against cultivars that appear suboptimal; and ii) cultivars are most likely to be picked up from ant lineages with large productive nests (nests that have nonexploitative cultivars, which are mutualisms that persist because of partner fidelity feedback). Both partner fidelity feedback and partner choice thus interact, but both can also operate independently and modulate the evolution of cooperation between ants and their fungi.

Algal-Invertebrate Symbioses

A wide variety of symbioses are known among tropical marine invertebrates in which large populations of photosynthetic unicellular algae live within the tissues of the host (Trench 1993). The majority of the algal symbionts are dinoflagellates; the hosts include sponges, cnidarians, mollusks, flatworms, and foraminiferans (Trench 1993). In some species there is evidence that the algae provide the host with carbohydrates derived from photosynthesis (Balderston and Claus 1969). The algae, in turn, presumably have access to the rich store of nitrogen present in the host tissue, which enables them to reproduce in a protected environment (Muscatine 1990).

Approximately 85% of corals and other invertebrate host species acquire their complement of symbionts horizontally, from the external environment rather than from their parents (Fadlallah 1983; Babcock and Heyward 1986; Harrison and Wallace 1990). Symbionts available to colonize new hosts likely arise from neighboring conspecific hosts. Within-host symbiont growth rates are generally in excess of host growth rates, and some fraction of the excess symbiont population is expelled into the environment. Expelled symbionts are viable, and are presumably available to infect additional hosts. Thus, in systems with horizontal transmission, symbiont within-host fitness can translate into among-host fitness. Invertebrate hosts can harbor one or more species of algal symbiont, with the number of algal partners varying among

host species (Rowan and Knowlton 1995; Baker and Rowan 1997; Belda-Baille et al. 2001). Changes in the relative abundances of different symbiont species have been noted for hosts that can simultaneously harbor multiple symbiont types, particularly when the host is stressed (Rowan and Knowlton 1995; Baker 2001). However, dynamic symbiont populations are not found in all hosts (Goulet 1999, Goulet in prep), and generally little is known about how much turnover occurs within that intracellular population, either via further colonization or via competition within the host.

The horizontal transmission and large algal populations within the host suggests that partner choice may be the mechanism required to maintain cooperative algae. Variants of algae are known that infect and kill the host or otherwise retard host growth (Sachs, personal communication), so a byproduct benefit seems unlikely as a universal mechanism. The turnover that can occur within hosts questions whether partner fidelity feedback operates across host lifetimes, although it may operate early in the critical stages of the host life history (Wilcox, personal communication). By analogy with the squid-*Vibrio* and plant-rhizobium systems, we should expect that partner choice plays an essential role in maintaining these dinoflagellate symbioses, but there has been scant investigation of this possibility. Several experiments have shown that hosts infected with multiple strains of dinoflagellates ultimately resolve to a single strain, but whether this resolution is due to the host (choice) or simply competition among dinoflagellates is not clear (Belda-Baille et al. 2001; Coffroth et al. 2001). Thus, the forces maintaining symbiont cooperation remain unresolved in these systems.

Policing

As a final example of multiple mechanisms, we consider how our framework relates to a concept (policing) that has been presented in a different framework. Frank (1995, 2003) considered policing to be one of the two major classes of models for the evolution of cooperation. By analogy to human societies, policing is the imposition of costs by one indi-

vidual on another in response to their uncooperative behavior (Frank 1995). Models of policing overlap with several parts of our framework. We neither defend nor challenge the biological evidence that policing evolves in ways consistent with Frank's models, rather we merely illustrate how the two frameworks overlap.

(i) Partner choice. Virtually all policing models involve some form of partner choice within species, because one individual imposes a cost/punishment on specific individuals who are behaving noncooperatively. Models of policing thus differ in the nature of partner choice and in how the benefits from partner choice are distributed to others, as described next.

(ii) Shared genes combined with byproduct benefits. In one model that applies to social Hymenoptera, policing is the consumption of worker-derived eggs by other workers. It is favored as a worker behavior because it results in queen-laid eggs automatically replacing worker-laid eggs—the policing individual shares more genes with queen-laid eggs than with worker-laid eggs (Ratnieks and Visscher 1989). The policer thus benefits via shared genes. The main difference between this policing model and our kin-choice model is that the policing act is not cooperative between the two interactants. Instead, policing is cooperative to other workers in the colony (because they too share more genes with queen-laid eggs than with eggs laid by other workers).

(iii) Byproduct benefits only. In yet another model, group benefit occurs when the policing action reduces selfish interactions, enhancing group productivity. Although this mechanism is typically thought to apply in groups with related members, in principle it can operate when group members are unrelated: by policing others, an individual directly improves its own fitness through its fair share of the improved group productivity (Frank, 2003). Noncheating group members benefit as a byproduct of the selfish action of the policer, and their byproduct benefit helps maintain the policing.

CONCLUSIONS AND FUTURE DIRECTIONS

The study of cooperation has progressed greatly in the past thirty years, and there are now many evolutionary models to explain a wide array of empirical systems. Our goal has been to consolidate the models and examples into a framework of relatively few evolutionary mechanisms. This framework allows the recognition of parallels between seemingly disparate systems (e.g., rhizobium-legume mutualisms and squid-bacterial mutualisms), and also suggests studies of empirical mechanisms to identify the detailed ways that mutualisms are maintained against exploitation (cheating). Discoveries of new systems are also easily classified in this system, and those additions may lead to the recognition of new mechanisms.

Our framework recognizes: (i) directed reciprocity; (ii) shared genes; and (iii) by-product benefits as three classes of models for the evolutionary maintenance of cooperation. The perspective of this framework is individual selection (why cooperating individuals are favored over noncooperators), but most or all of the underlying mechanisms can be modeled with no loss of generality in various frameworks (e.g., trait-group selection or policing, as detailed above). Thus, we suggest that the mechanisms at work here transcend the specific formulation of the model.

The framework is also a starting point that opens many avenues for further study, some of which could lead to discoveries that expand the framework or even change its perceived relevance. We discuss a few unexplored problems that seem worthy of further attention.

(1) Incorporating other models. The framework here attempts to organize the known empirical examples. Several models have been proposed in which cooperation can evolve, but for which there is scant empirical evidence, and those models have not necessarily been accommodated here. It would be useful to know whether new models can be incorporated into this framework; if not, then the search for examples that satisfy those models could be intensified, and a new framework proposed if examples are found.

(2) Embedding ecological factors. The framework attempts to isolate the minimal elements that allow the maintenance of cooperation within a species or between two species. Yet nearly all natural examples are embedded in complex ecologies involving multispecies interactions. How do these ecological dynamics impinge on the evolution of cooperation? A mild parasite may become a mutualist in the presence of a more severe parasite, if the mild parasite can prevent infection by the severe one or reduce its harmful effect. How do the dynamics of the two parasites affect the evolution of cooperation? Alternatively, can a third species interact with a mutualist to prevent the evolution of cheating via some mechanism that we have not identified? Investigators who conduct field studies of mutualisms certainly convey a suspicion that ecological dynamics may provide key insights into the maintenance of cooperation in ways that have not been anticipated (A Herre and O Pellmyr, personal communication).

(3) Origins of cooperation and the evolution of parameters. The maintenance of cooperation in our framework requires many conditions that are treated as invariant in our mechanisms. For example, partner fidelity feedback requires that partners are associated for an appropriate duration, possibly across generations. Partner choice typically assumes an asymmetry in which the chosen individual is forced to accept the consequences of being chosen or rejected; there is an appropriate level of "control" for the persistence of cooperation, whereby choice operates effectively but cannot enslave an individual. A broader perspective for the evolution of cooperation would consider the evolution of these parameters, ultimately addressing the origins of cooperation.

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