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Game Structures in Mutualistic Interactions: What Can the Evidence Tell Us About the Kind of Models We Need?

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I. THE PUZZLE OF COOPERATIVE BEHAVIOR

Nature is full of examples in which individuals of different species cooperate with each other. Some of these interactions (mutualisms) are crucial to the persistence of the world that we know: most plants need mycorrhizal fungi and/or rhizobial bacteria for successful growth, as well as pollinators for reproduction; coral reefs are the result of a mutualistic symbiosis between polyps and algae; and virtually all animals appear to have endosymbionts that help with digestion of food. Other mutualisms attract human attention because of their oddity: birds and fish that enter the mouths of predators in search of food, birds that lead other animals to a mutually appreciated food source, and anemones that defend the crabs on whose backs they ride.

Darwin (1859) was well aware that interspecific mutualism, like intraspecific cooperation, provided a challenge to his theory of evolution. Selection favors individuals that behave selfishly and maximize their own benefit. Cooperative behavior, however, often involves costly investment by one individual for the benefit of its partner. This puzzle of cooperative behavior is best illustrated with the so-called prisoner's dilemma game. In this game, each of two genetically unrelated players can either cooperate or defect. Both players receive a payoff from the interaction (assumed to be of some relevance to the players' fitness) that depends on the combination of

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behaviors the two players have performed. The payoff matrix is constructed such that (1) both players receive a higher payoff from mutual cooperation than from mutual defection, (2) each player receives a higher payoff from defecting than from cooperating, irrespective of the partner's action, and (3) the player invariably receives a higher payoff if the partner cooperates than when the partner defects. Thus, cooperative behavior is an altruistic act in this game, an investment in the partner's fitness. Not surprisingly, mutual defection is the only evolutionarily stable outcome under these conditions. Thus, even if the partner cooperates and invests, selection should favor individuals that do not invest in return (both reduced investment and active exploitation are what we refer to as cheating). Why, then, does cooperative behavior seem to be ubiquitous in nature? Furthermore, why do individuals of one species invest in individuals of another species?

II. Game Theoretical Approaches to Mutualism

Initially, most theoretical work on the evolutionary stability of cooperative behavior/altruism focused on cooperation *within* species. Here, the explanation for many cases seems to be linked to the existence of kin selection (Hamilton, 1964). However, examples of within-species cooperation exist in which the partners are unrelated. Furthermore, kin selection cannot explain any example of interspecific mutualism.

Trivers (1971) proposed that both intraspecific cooperation and interspecific mutualism can evolve and be maintained when the same individuals interact repeatedly with each other. His idea of reciprocal altruism was formalized by Axelrod and Hamilton (1981) via an iterated version of the prisoner's dilemma game. In brief, Axelrod and Hamilton found, in a computer simulation tournament with a variety of strategies, that a simple strategy called ''Tit-for-Tat'' could emerge as a cooperative solution to the game. Tit-for-Tat players begin the game by cooperating and then, in subsequent rounds, do what their partners did in the previous round. For some time, the iterated prisoner's dilemma was the paradigm for theoretical studies on the evolution of cooperation (reviewed by Dugatkin, 1997). However, empiricists seem to have found it difficult to relate the cooperative strategies proposed by theoreticians, including Tit-for-Tat and its successors (Dugatkin, 1997), to real-world cooperative interactions. There are a few examples in which an observed case of intraspecific cooperation seems consistent with game theory models (Dugatkin, 1997). The situation is different with regard to interspecific mutualism, however. Researchers at the 90th Dahlem workshop, on the evolution of cooperation, argued that there is not a single suspected example of mutualism for which (1) the payoff matrix can be described adequately by the prisoner's dilemma game, and (2) the partners behave as predicted from cooperative solutions to the iterated prisoner's dilemma game (Bergstrom *et al.*, 2003).

Three other game theoretic concepts that until now have attracted less attention have been seen to be more promising frameworks to explain the evolutionary stability of cooperation and mutualism: by-product mutualism, pseudoreciprocity, and biological market theory. By-product mutualism (Brown, 1983) is a confusing term, because it was developed to explain intraspecific cooperation rather than interspecific mutualism. However, the concept applies to both sets of interactions, and yields a simple, straightforward explanation for the occurrence of cooperative behavior: each individual acts selfishly, and the benefits to other individuals accrue as a simple by-product of their behavior. As there is no costly investment on the part of the partners, no altruistic behavior must be explained. This may be the reason why many researchers, in particular theoreticians, tend to ignore this explanation (Dugatkin, 1997): it takes away the most interesting aspect of cooperation. But at the same time, that is the very argument for why this form of cooperation should be found frequently in nature: because it does not pose any problems to either player.

Pseudoreciprocity (Connor, 1986) differs from by-product mutualism in two ways: (1) one or both partners invest in each other, and (2) investment makes cooperative behavior the best option for the investing partner. The second point is also the crucial difference between pseudoreciprocity and the prisoner's dilemma game, in which cheating invariably yields a higher payoff in each round. In pseudoreciprocity, cooperative behavior yields the highest possible payoff in each single round as long as the partner cooperates. The selfishness of cooperative behavior can be understood best with optimality theory. If and only if investment by the partner is above a critical threshold, it pays to perform an act that returns the investment. Thus, there is still no risk that the altruist will be exploited.

Biological market theory proposes that cooperative or mutualistic interactions can be viewed as an exchange of goods or commodities between individuals that differ in the degree of control over these goods/commodities (Noë, 2001). Control is used in a loose sense here; it may simply imply that a commodity/good is easier to produce for one partner than for the other. Trading partners can be chosen from a number of potential partners. The focus of biological market theory has been to understand how supply and demand ratios of the goods/commodities traded in combination with partner choice opportunities determine the exchange rate (Hoeksema and Schwartz, 2001, 2003; Noë, 2001; Noë and Hammerstein, 1994; Noë *et al.*, 1991; Schwartz and Hoeksema, 1998). For example, market theory predicts that the nectar-provisioning rate by lycaenid butterfly larvae to tending ants (that would defend the larvae against predators) depends on variables like predation risk, and the number of ants or other larvae present: decreasing predation risk and increasing number of ants reduces the larvae's demand for tending, hence larvae should reduce nectar production. The ability to choose between partners may also be a mechanism that promotes costly cooperative behavior in the form of investment (Bshary and Noë, 2003; Bshary and Schäffer, 2002; Bull and Rice, 1991; Ferrière *et al*., 2002). In particular, if a cheater that refrains from investing belongs to the abundant trading class, it risks being abandoned by the choosing partner and remaining partnerless for a long time, while the choosing partner will easily find a new and hopefully more cooperative partner.

The concepts of by-product mutualism, pseudoreciprocity, and partner choice may explain why cooperative behavior persists in mutualistic interactions: either cooperative behavior may not be costly, or investment may yield predictable benefits, or investment may secure repeated interactions. However, these game theoretic concepts are not the focus of most scientists working on mutualism; most work on these interactions is ecological in nature (Bronstein, 1994). One reason might be that game theoretical analyses of mutualism have tended to treat the core interaction quite abstractly, focusing on few aspects rather than explicitly considering a broad range of its ecological or behavioral features. Admittedly, these features vary enormously across particular forms of mutualism (pollination, dispersal, etc.), often obscuring fundamental similarities across interactions differing greatly in natural history (Bronstein, 1994, 2001a). On the other hand, since mutualisms are real interactions that function in real ecological settings, excessive abstraction risks meaningless results. Here, we evaluate the game theoretic approach, with its focus on behavioral strategies of individuals, to identify its potential strength but also its shortcomings in light of empirical knowledge about mutualistic systems. We identify 12 parameters that, in combination, describe features of a mutualism that are relevant for generating a meaningful so-called game structure (Table I). By meaningful, we mean that the game structure allows an exploration of the fitness consequences of individual behavioral strategies that may resemble those that partners actually use in the real world. The parameters can be seen as important modules for the construction of a game, for which evolutionarily stable behavioral strategies can be explored. For example, individuals may interact once or repeatedly, both partners (or one partner, or neither) may be mobile, and so on. We have chosen to examine eight relatively well-understood kinds of mutualism. We have selected these mutualisms on the basis of the following criteria: (1) the reciprocal benefits of the mutualism

TABLE I
Parameters Evaluated in Mutualistic Systems[a]

Parameter	Possible combinations (species 1/species 2)
Dependency	high/high, high/low, low/high, low/low
Specificity	high/high, high/low, low/high, low/low
N interactions	repeated, one-off
Offer produced	prior/during, during/during, during/prior, during/after
Moves	simultaneous, alternating, sequential
Mobility	mobile/mobile, mobile/sessile, sessile/mobile, sessile/sessile
Active choice	yes/yes, yes/no, no/yes, no/no
Partner recognition	yes/yes, yes/no, no/yes, no/no
Behavioral options	allC/allC, C or D/allC, allC/C or D, C or D/C or D
Investment	yes-no/yes-no, variable/yes-no, yes-no/variable, variable/variable
Payoff symmetry	symmetrical, asymmetrical
Control over interaction	full/full, full/limited, limited/full, limited/limited

[a] Behavioral options: individuals can either only cooperate (''allC'') or they can cooperate or defect (''C or D'').

appear clear, and (2) enough is known about the natural history of both species and their interactions to allow us to assess the various parameter states. We recognize, however, that as more is learned about these interactions, we are likely to find that we have misidentified one or more of these parameter states. Indeed, one of our aims is to point to problematic gaps in our empirical knowledge of these mutualisms.

III. Goals of This Article

1. We aim to evaluate the extent to which there are general features that underlie many different mutualisms with respect to game structure. The evolutionary and ecological backgrounds of different mutualisms are highly diverse, prompting the question of whether it is appropriate to categorize them at all. With respect to game theory and questions about the evolutionary stability of mutualisms, one must ask how many different game structures will be found. Does every mutualistic interaction exhibit a unique game structure, or are there important common features? How uniform are game structures within broad classes of mutualism, such as ''cleaning mutualisms'' or ''pollination mutualisms,'' which are defined by the actions of partners but may include a wide range of taxa? How uniform are game structures within taxon-specific mutualisms, such as ant–lycaenid interactions, which appear to be relatively uniform with respect to what is traded between partners

and with respect to phylogeny, but which involve several thousand different species with potentially very different ecological demands?

2. We aim to identify gaps in our empirical knowledge that limit our ability to assess the game structure for certain mutualistic systems.
3. We aim to identify important ecological parameters. Ecological parameters are usually not captured by game theoretic approaches, but still may be of fundamental importance for explaining individual behavior.

More generally, we hope to describe natural systems in a way that will facilitate the development of theoretical concepts for mutualism. This in turn will allow us to understand the basic rules for how cooperative behavior between unrelated individuals may persist in nature. At this stage, a descriptive, rather than abstract, theory-driven approach seems necessary to facilitate communication between empiricists and theoreticians. More specifically, we hope to provide empiricists with a framework for the kinds of data theoreticians may find useful, and we hope to provide theoreticians with a wealth of empirical information as a basis for future models. This task is big enough to force us to refrain from using the data to develop theoretical predictions ourselves, or to evaluate the various existing concepts of partner control. We also restrict ourselves to interspecific mutualism and do not further discuss intraspecific cooperation. Intraspecific cooperation often involves cases in which some partners are related to varying degrees, while other partners are unrelated. In practice, it may therefore often be difficult to distinguish between reciprocity arguments and kin selection arguments for the evolution of cooperation in intraspecific interactions. Nevertheless, we would predict that the principles that lead to stable mutualism may also be relevant for intraspecific cooperation between unrelated individuals.

IV. Terminology

There has been considerable confusion about the use of terms like cooperation, mutualism, and symbiosis. In brief, the verb ‘‘to cooperate’’ refers to a positive consequence (increased fitness) of the behavior of individuals on the partners with which they interact (which can either be conspecifics or allospecifics), without implying any cognitive abilities such as intentionality. Cooperative behavior may be selfish (it directly increases the fitness of the actor, irrespective of the partner’s action), cost-free, or a costly investment. In the latter case, we refer to cooperative behavior as being altruistic. We use this term with the knowledge that ultimately, we will try to give a functional explanation for such altruistic behavior by explaining how the investment behavior promotes benefits that outweigh the costs. Note that kin selection theory too starts with the observation of one animal investing into another, and then explains this oddity away with the concept of relatedness. The same is true for reciprocity based on the iterated prisoner's dilemma. ''Cooperation'' and ''mutualism'' refer to the outcome of interactions: the terms are used if both partners receive a net benefit from the interaction. We use the term ''cooperation'' as the outcome of intraspecific cooperative behavior, and ''mutualism'' as the outcome of interspecific cooperative behavior. ''Symbiosis'' is an intimate spatial relationship between individuals of different species; the outcome can be mutualistic, commensal, or parasitic.

Another important terminological issue is what we mean by ''cheating.'' There has been reasonable confusion in the literature about what cheating refers to and who cheaters are. For a definition of the behavior, we refer to Bull and Rice (1991): an individual cheats if it provides less to its partner than the average individual of its species would provide. This definition acknowledges that cheating may be both a discrete behavior (e.g., an ant eating an aphid) but more often a continuous one (a lycaenid butterfly larva providing less nectar to tending ants than other larvae do). It also acknowledges the existence of what Sherratt and Roberts (2001) called phenotypic defectors. These are individuals who cannot invest (as much as others) because they are in poor condition. From the partner's point of view, it should always respond to low payoffs, no matter whether its own investment is not reciprocated because the other individual defects or because it cannot reciprocate. We use the term ''cheater'' only for individuals that belong to the mutualist species under investigation. They may either be individuals who always cheat (designated by Bronstein, 2001b, as ''pure exploiters''), or individuals that cooperate under some defined range of conditions (''conditional exploiters''). Bronstein (2001b) also identified ''exploiter species,'' allospecific exploiters of mutualisms that cannot provide benefits but that take advantage of rewards and services designated for the mutualistic partner. While they are an important ecological and evolutionary problem for mutualisms (Bronstein, 2001b), we set exploiter species aside for the purposes of this article.

V. Parameters Considered for the Assessment of Game Structures

The prisoner's dilemma game is a good starting point to illustrate the kinds of parameters that might be important in defining the game structure of mutualisms, and hence in exploring how evolutionary stability of cooperative behavior might be achieved. The version of the iterated prisoner's dilemma used by Axelrod and Hamilton (1981) for exploring mutualism made the following assumptions: (1) players interact repeatedly; (2) players are assigned randomly to each other as partners; (3) players do not know *a priori* how many rounds they will play; (4) both players have the same behavioral options (i.e., to cooperate or to cheat); (5) investment in the partner is an all-or-nothing behavior; (6) the payoffs are symmetrical for both players; (7) the payoffs are constructed in such a way that cheating invariably yields a higher payoff than cooperating; (8) the players' moves are simultaneous; and (9) the offers are produced during the interaction. No assumptions are made regarding mobility of partners, nor whether partners recognize each other on an individual basis (although it may be implied by the repeated game structure). Nor are there any assumptions regarding whether individuals are limited in any way in their choice of partner species, or whether they are strongly or weakly dependent on each other.

This particular combination of assumptions allows cooperative solutions for mutualism, including Tit-for-Tat and its successors (Dugatkin, 1997). Theorists have more recently recognized the artificiality of some of these assumptions, however, and have altered them to generate alternative conditions for the evolutionary stability of mutualism. Our goal here is not to evaluate the newer modeling approaches (e.g., Doebeli and Knowlton, 1998; Ferrière *et al*., 2002; Roberts and Sherratt, 1998), but to describe empirical examples of mutualism according to the list of parameters identified below. Note that each of the following 12 parameters may have several potential states. We list possible states for all parameters based on the empirical examples that we discuss in this article in Table I, and briefly describe them below. We recognize that this list may be incomplete, since in many cases other parameter states seem possible, at least in principle.

Dependency: Mutualisms vary greatly in how crucial they are to survival and reproduction of each partner. We distinguish between ''high'' dependency for obligate mutualisms and ''low'' dependency for facultative mutualisms (those in which individuals can survive and reproduce at some level without mutualist partners). Dependency can be mutually high, mutually low, or asymmetric.

Specificity: In some mutualisms, single partner species are matched (''high specificity''), while in other systems, several partner species can function as mutualists (''low specificity''). Again, specificity can be mutually high, mutually low, or asymmetric. Note that specificity may be low even if one partner is very dependent on mutualistic interactions (i.e., in cleaning mutualisms).

N interactions: The number of interactions between two individual partners in their lifetimes can be mutually repeated, mutually single, or asymmetric.

Offer produced: Mutualisms are based on the provision of goods and/or services to partners; we refer to these as ''offers.'' Note that offers are not necessarily investments, as some offers in mutualisms are cost-free. Of major interest to us is that offers can be produced before the interaction, during the interaction, or even after the interaction. In addition, individuals may produce an initial offer prior to the interaction, but produce more during the interaction. Consequently, there are many parameter state combinations possible for the two partners (before–during, during–during, etc.).

Moves: The two players can make decisions about their behavior simultaneously or not. We refer to these decisions as ''moves.'' When moves are not simultaneous, we use the term ''alternating moves'' if there are several rounds of interactions between two individuals, and the term ''sequential moves'' if there is only one round of interactions with a fixed sequence of decisions.

Mobility: Individuals may be capable of moving around freely (although they may be constrained considerably through ecological limitations), or may be sessile. Mobility can be mutual, one-sided, or nonexistent.

Active choice: This refers to the ability of individuals to seek out mutualists by choosing to visit a subset of all possible partners. It is usually but not always closely linked to mobility. Active choice can be mutual, one-sided, or nonexistent.

Partner recognition: Recognition may be possible either because partners have cognitive abilities that allow them to recognize partners individually, or because one or both partners show site fidelity. In the absence of empirical evidence for the presence or absence of partner recognition (as is the case for most systems), it may be more appropriate to ask, when it seems feasible, whether or not partner recognition would yield advantages. Advantages of partner recognition may be mutual, one-sided, or nonexistent.

Behavioral options: Whenever individuals invest in their partner, they are able to cooperate or to cheat and hence have the option to choose between these two behaviors. If a player lacks the option to cheat in a sense that would be meaningful (receiving benefits out of cheating the partner), it is unconditionally cooperative. Options may be symmetrical in that both partners can either cooperate or cheat [i.e., both are ''conditional exploiters'' in Bronstein's (2001b) terminology], or asymmetrical in that only one partner has this strategic option. Finally, both players may lack the option to cheat.

Investment: Players may or may not invest in their partner. As any investment is by definition costly, we call the act of investing altruistic. If a player invests, this investment can be all or nothing (a player either cooperates or cheats) or variable, in that individuals must decide precisely how much they give to their partner.

Payoff symmetry: This parameter is quite specific in that it needs evaluation only when both partners can cheat. In the absence of any quantitative knowledge on exact payoff values for any mutualism, we distinguish between ''asymmetric payoff values'' (e.g., costs of being cheated are small for one partner, but fatal for the other) and ''symmetric payoff values,'' in which both partners appear to experience more or less similar costs of being cheated. When only one partner can cheat, there is an obvious asymmetry. In cases where neither partner can cheat, this parameter is not relevant.

Control over interaction: Partners may have ''full control'' over the interaction, in that they can withhold the reward/service that they are offering without any costs, can steal the reward/service, or can force it to be handed over. Both, one, or neither partner may have control over the interaction.

In the following section, we review the mutualism literature and report on states of these 12 parameters for each of 8 well-studied forms of mutualism. However, one must keep in mind that these 12 parameters still do not represent the full complexity of mutualistic interactions. Each mutualistic system may have its specific additional features that are important for a thorough understanding of individual behavior (and hence the outcome of the interaction). We list such additional features for each system as well.

VI. Evaluation of the Literature

We have organized our presentation of individual mutualisms according to the three widely recognized classes of benefits mutualists receive: transportation, protection, and nutrition (Boucher *et al.*, 1982; Bronstein, 2001a). We briefly describe the important features of each system. To facilitate comparison of the sections, we present the parameters in the order in which they are listed in Table I.

A. Transportation Mutualisms

In transportation mutualisms, one partner offers the other a commodity, usually food, in exchange for transport of itself or its gametes.

1. Pollination

In pollination mutualisms, plants offer a resource (usually nectar or pollen as food) in exchange for transport of pollen and hence pollination of the flowers. Most pollinator species are insects, but birds and mammals, especially bats and primates, may also function as pollinators. The crucial issues about pollination mutualisms that game theory may be able to address are why plant investment in nectar apparently does not usually drop toward zero (it is well known that it has in some systems), and under what conditions individuals of some species shift between pollination and cheating (nectar-robbing) behaviors.

1. Dependency: Dependency can be mutually high, mutually low, or asymmetric. Certain plants (not all: some are wind-pollinated) absolutely require pollinators if they are to outbreed (although self-fertilization may often be possible). Conversely, pollinators often rely heavily or exclusively on floral resources as food. When specificity is low, however, there may be very little dependency on a particular partner species.
2. Specificity: Like dependency, specificity varies from mutually low to mutually high to asymmetric. Certain plants can be pollinated only by a single pollinator species that can obtain resources only from that plant; some of these are discussed in the following section. Most plant–pollinator interactions are considerably less specific than this, however. An increasing number of pollination mutualisms are being found to be distincly asymmetric in specificity (Vázquez and Simberloff, 2002).
3. *N* interactions: Interactions may be repeated or one-off. The situation is sometimes more complex than this, however, as an individual pollinator may interact only once with a particular flower but several times with the same plant. Conversely, a plant may interact only once with an individual pollinator, but with many individuals from a single colony of Hymenoptera. Hence, the question arises whether one should look at individual flowers or plants and at individual insects or colonies.
4. Offer produced: Plants produce their offer prior to the interaction. In contrast, pollinators make their offer during the interaction (they deposit pollen, and/or collect pollen, in varying amounts) and after the interaction (they may deposit the pollen they have collected on conspecific flowers or heterospecific ones; in the latter case, the pollen is wasted).
5. Moves: In principle, moves are sequential in that the plant puts out an offer and then the pollinator decides whether or not to visit. This simple view becomes complicated through the possibility that several pollinators may visit the same flower, in which case the amount of

nectar in a flower may partially reflect how much prior visitors left behind rather than exactly what the plant offered.

6. Mobility: The pollinators are mobile, whereas plants are not.
7. Active choice: The pollinators can actively choose which plant/flower to visit, whereas the plant has no control (in a behavioral sense) over who visits. Flowers may have features that exclude certain pollinator species or individuals of a certain size, shape, or behavior, but this does not translate into active choice on the part of plants during the course of an individual flower visit.
8. Partner recognition: If interactions are repeated, it may pay the pollinator to recognize partners (''site recognition''). Indeed, certain bees pheromone-mark flowers they have visited, and avoid revisiting those flowers (e.g., Giurfa and Nunez, 1992).
9. Behavioral options: Pollinator species usually cooperate by default, as they bring in pollen from plants visited previously for food, and pollen is usually collected passively. However, there are certain pollinator species in which individuals can choose to cheat by robbing nectar without collecting or depositing pollen (Irwin *et al.*, 2001), a strategy that may save time. Conversely, plants may invest more or less energy into the production of food for their pollinators, and low (or zero) investment can be called cheating.
10. Investment: Whenever pollinators passively transfer and collect pollen, questions about investment into the partner usually do not apply. In species in which individuals can alternatively pollinate or rob, investment in the mutualism is an all (visiting the regular way and collecting/depositing pollen) or nothing (bypassing the floral sexual organs to get directly to the nectar) phenomenon. As mentioned above, investment of plants into their partners is variable.
11. Payoff symmetry: In pollination interactions with passive pollen transfer, cheating opportunities are asymmetric (only the plant can reduce investment). When nectar robbing is possible, both partners may cooperate or cheat. For a pollinator, being cheated by a single flower probably inflicts little cost, although marking of empty flowers and the ability to learn to avoid entirely nectarless plants suggests that significant costs of fruitless visits must exist. Nectar robbing can inflict costs to plants that range from high to low to nonexistent (Maloof and Inouye, 2000).

12. Control over interaction: Individual plants may control their investment into nectar at ecological time scales (Castellanos *et al*., 2002). More generally, however, nectar production most likely reflects evolutionary history and is thus quite inflexible. Some pollinators may access the food source without pollinating. Some pollinators may be able to preassess the food content of flowers and avoid empty flowers. Except for the very few active pollination systems (see the next section), they do not withhold pollen or avoid collecting pollen if the flower is empty, although less pollen may be transferred if the visit is shorter.

Important features of pollinator–plant mutualisms not covered by our game structure assessment: (1) When pollinators have access to alternative food sources, whether interacting with the flowering plants is beneficial depends on the quality of these alternatives; (2) a pollinator may encounter empty flowers not only because some plants invest little into nectar production, but also because the flower may have been visited recently. The effect on the pollinator is the same, however; and (3) whether interactions are repeated or not may depend on how an interaction is defined. The two crucial problems are whether an insect visiting multiple flowers of a single plant during one inspection interacts repeatedly with the plant, and whether plants pollinated by social insects interact with individual insects or with the colony, in which more foragers may be recruited through communication.

2. *Pollinating Seed Parasite Mutualisms*

In this small subset of pollination mutualisms (reviewed by Dufaÿ and Anstett, 2003), insects pollinate plants and simultaneously lay their eggs in or near the flowers; the larvae eat some of the developing seeds. The fig–fig wasp and yucca–yucca moth interactions are the best-known pollinating seed parasite mutualisms, although several similar but independently evolved interactions have been discovered. These include the senita cactus–senita moth and globeflower–*Chiastocheta* fly interactions. The key questions for these mutualisms include what limits the number of eggs laid per female pollinator, how variation in population density of the pollinators affects the mutualistic outcome, how plants can cope with destructively high pollinator densities, and why a few of these plant species have evolved mechanisms to (completely) prevent oviposition by the insects, while most have not.

1. Dependency: These mutualisms are obligate for both partners. The plants can be pollinated only by these insects, and the insects can lay their eggs nowhere else.

2. Specificity: The yucca, senita, and fig systems show very high specificity, in that plant species and insect species are almost matched one to one (but see Molbo *et al.*, 2003). For *Trollius*, *Chiastocheta* flies appear specific to a particular plant species, while the plant may be pollinated by several species of *Chiastocheta*.
3. *N* interactions: Interactions are usually one-off between fig wasps and figs, since an inflorescence is usually visited only once by an individual insect. However, in other pollinating seed parasite mutualisms, individual insects will visit more than one inflorescence on the same or on different plants.
4. Offer produced: As in other pollination mutualisms, plants produce their offer (an oviposition site, in this case) prior to the interaction, while the insects provide their offer during the interaction. The insects' offer has a benefit component and a cost component: (a) how many flowers they pollinate, and (b) how many eggs they lay.
5. Moves: Moves are sequential: first the flower makes an offer, then the insect makes hers. Plants may make a further move later, through random (senita) or selective (yucca) fruit abortion (Holland *et al.*, 2004).
6. Mobility: Plants are immobile, and the insects visit them.
7. Active choice: This varies across different pollinating seed parasite mutualisms. Fig wasps apparently do not compare among inflorescences; they may enter the first one that they encounter. In the process, they lose their wings and rarely leave. Thus, the wasps are unlikely to exert active choice at the level of the inflorescence (it is possible that they do make choices among flowers within it, however). In contrast, yucca moths, senita moths, and *Chiastocheta* flies visit several flowers, and at least have the potential to make choices among them.
8. Partner recognition: Partner recognition is unlikely to play a role in these mutualisms, although in some cases (e.g., Huth and Pellmyr, 1999), the insect has mechanisms to avoid visiting the same flower twice.
9. Behavioral options: The plants have limited options to cheat their pollinators, although some yuccas may kill the offspring of pollinators before they begin to feed (Bao and Addicott, 1998) and female fig trees (in the dioecious fig species) prevent fig wasp oviposition and thus obtain the benefits of pollination without paying a cost for it. The

insects can cheat in two possible ways: (a) they may not pollinate, and (b) they may lay more eggs than average.

10. Investment: In the dioecious fig species, cheating is all or nothing: female trees prevent fig wasp oviposition while males allow it (Kjellberg *et al*., 1987). Insects show variable investment, which could be expressed as the ratio of pollinating acts to eggs laid.
11. Payoff symmetry: In systems in which the plant cannot cheat, the strategy set is asymmetric in that only the insect can cheat (hence the payoff matrix is asymmetric). In the dioecious fig species, where both individual plants and insects may cheat, the payoffs are asymmetric, in that the trees (which reproduce many times in their lives) would lose little from a wasp that cheated, while the wasp dies without reproducing if it enters an inflorescence on a female fig tree.
12. Control over interaction: The pollinators have full control over the interaction, in that they come to the plant and set the conditions of the game by deciding how many flowers to pollinate and how many eggs to lay. Plants may have morphological adaptations that make ovipositing in some flowers more difficult.

Important features of pollinating seed parasite mutualisms not covered by our game structure assessment: (1) Fig trees and yuccas make many flowers in each reproductive episode, whereas *Trollius* usually bears only a single flower at a time; (2) all plants have multiple reproductive episodes, whereas the insects have only one; (3) *Trollius* also offers nectar, not only oviposition space, for its mutualists. Hence, male as well as female flies visit the flowers, and may in fact be responsible for most of the pollination (Després, 2003); (4) fig wasps collect and move the pollen in the inflorescence in which they develop. Any emerging female wasp thus contributes to the fitness of the very same tree whose female function was reduced by the larval seed predators. In contrast, other pollinating seed parasites do not collect pollen from the flower in which they matured (Addicott *et al*., 1990); (5) there is a temporal component to how cooperative the pollinators are that has nothing to do with the pollinators' behavioral strategies (Law *et al*., 2001). The first individual to arrive at a flower must cooperate by pollinating, or else her offspring will starve (unless a second female visits and pollinates). Later female visitors may not contribute much more to plant fitness, as pollination has already occurred and may be sufficient to permit initiation of every seed (Bronstein, 2001c); however, they may lay some additional eggs, which decreases plant fitness; and (6) plants may abort fruits, either selectively (ones with many eggs; yucca) or unselectively (senita). This means that although plants cannot control directly what insects are doing (see point 12; control over interaction), they may respond to insect behavior at later stages.

3. Seed Dispersal

In these mutualisms, plants provide food in exchange for transport of seeds (reviewed by Herrera, 2002). Typical seed dispersers are birds, mammals, and ants. The plant benefits from the great mobility of the fruit/seed consumer that results in seeds being removed from the maternal plant. Seeds are sometimes moved long distances and/or to superior germination spots. The animal gets a meal in return. With respect to this article, the major goal is to understand what factors determine plant investment in fruit flesh.

1. Dependency: Partners are moderately dependent on each other. Plants may require seed dispersal for their seeds to have any chance to germinate, although undispersed seeds may have a low likelihood of success. Most disperser species have a wide range of food sources, although at certain times of year they may be heavily dependent on fruit.
2. Specificity: Specificity is generally low. Certain plants may rely on a given class of animals as seed dispersers (e.g., small birds, or seed-harvesting ants), but in only very rare cases is specificity higher than this. Similarly, almost no animals rely on fruits of a single species for food.
3. *N* interactions: Interactions may often be repeated but could also be one-off: an individual fruit usually has only a single interaction—the interaction in which it gets eaten. But almost all plants bear multiple ripe fruits at once, and most animals visit the same plant repeatedly for food.
4. Offer produced: The plants produce their offer prior to the interaction, whereas the seed dispersers produce theirs during the interaction (when they select a fruit) and afterward (when they drop or defecate the seeds).
5. Moves: Moves may be termed sequential (first the plant, then the seed disperser makes a move).
6. Mobility: The plants are sessile, whereas the dispersers are mobile.
7. Active choice: The plant cannot choose (in a behavioral sense) who eats the fruits, although, as in plant–pollinator interactions, selection may have shaped the subset of animals that are attracted to and rewarded by the fruit. Seed dispersers have the potential to compare

and actively choose among several plants, although the extent to which they actually do so is little known.

8. Partner recognition: Plants lack this ability, whereas the seed dispersers have the potential to remember plants with large fruit crops and with fruits in the correct stage of ripeness.
9. Behavioral options: Plants could potentially cheat by reducing their effort in the production of fruit flesh. Seed dispersers would appear to lack the option to cheat.
10. Investment: Investment of the plants is variable; among other things, it depends on the ratio of fruit flesh to seeds. Seed disperser species do not invest in the interaction; presumably, they defecate whenever they must.
11. Payoff symmetry: As only the plant invests, the question of how mutual cheating affects each partner's fitness does not apply. For the dispersers, picking fruits with little flesh probably bears little cost.
12. Control over interaction: The seed dispersers have full control, in that they choose the fruits they prefer. Plants would appear to have little control over where the seed disperser will defecate, although the recent discovery of laxatives in certain fruits (Murray *et al.*, 1994) suggests some control over *when* they will do so (and, hence, where they may be when they defecate).

B. Protection Mutualisms

In this category of mutualisms, one species offers its partner some form of protection from the abiotic environment or natural enemies. In return, the other partner receives either a food reward (e.g., in cleaning and ant protection mutualisms) or reciprocal protection (in group foraging and Müllerian mimicry associations).

1. Cleaning Mutualism

In cleaning mutualisms, a ''cleaner'' species benefits by obtaining access to a food source, while a ''client'' species has its ectoparasites and possibly dead or infected tissue removed (see reviews by Côté, 2000; Losey *et al.*, 1999). Cleaning mutualisms involve a very diverse group of animals. On the cleaner side, there are shrimps, fish, and birds. Clients can be fish, turtles, crocodiles, and various mammals. The key questions in understanding cleaning mutualisms are how the conflict between cleaner and client over what the cleaner should eat is resolved, and how cleaners avoid being eaten by predatory clients.

With respect to our parameters, cleaning mutualisms have the following features.

1. Dependency: Clients generally show low dependency, in that they survive long periods without being cleaned. Most cleaner species described so far are also relatively independent of their clients in that they eat plenty of alternative food items under natural conditions. However, a few cleaner fish of the genus *Labroides* and *Elacatinus*, and possibly some shrimp species, accrue 80% or more of their diet from cleaning interaction (Côté, 2000).
2. Specificity: Partner species usually show very low specificity: each cleaner species interacts with several client species and vice versa (although clients are less specific to cleaners than cleaners are to clients).
3. *N* interactions: Depending on the home range sizes of the pair of species involved, interactions between individuals can be repeated or one-off.
4. Offer produced: Offers are produced during the interaction. Neither cleaner nor client can preassess how its partner will behave. The cleaner ''produces'' a certain level of service (i.e., parasite removal) during the interaction; similarly, during the interaction, the client makes a decision on how long to interact with the cleaner, and in the case of predatory clients whether it will try to eat it.
5. Moves: Moves are made simultaneously.
6. Mobility: Cleaner shrimps and some cleaner fish show very limited mobility, while other cleaner fish and birds are quite mobile. Similarly, there is great variation among client species in their mobility.
7. Active choice: The relatively immobile cleaner shrimps and fish mentioned above lack the option to actively visit clients and start interactions. Nevertheless, they are sometimes able to choose, when two or more clients seek their service simultaneously. Similarly, client species with small home ranges or territories usually have at best access to one cleaning station and hence cannot choose between cleaners unless they have cleaner fish and cleaner shrimp present, which happens occasionally (R. Bshary, unpublished observation). Cleaner species and client species with large home ranges, however, are in a position to actively seek the partners they prefer.

8. Partner recognition: Individual recognition of clients has been shown experimentally for the cleaner wrasse *Labroides dimidiatus* (Tebbich *et al*., 2002). In this system and in some other cases, individual cleaners show strong site fidelity and hence may be recognized through location. Generally, individual recognition would be advantageous if the partners have the option to cheat and if interactions are repeated.
9. Behavioral options: It is known for some cleaner fish and bird species that they can cheat the clients by feeding on healthy client tissue (Randall, 1958; Weeks, 2000). Cleaner shrimps may lack this option, but this remains to be confirmed. Two categories of clients need to be distinguished (Bshary, 2001). Clients that are potential predators of their cleaners could cheat by eating their cleaner, whereas nonpredatory clients have no means to exploit a cleaner.
10. Investment: The investment of cleaners with cheating abilities into their clients is variable (in the sense that the rate of cheating bites to cooperative bites is variable). The investment of predators is all or nothing: they either cooperate or try to eat the cleaner.
11. Payoff symmetry: In most cases, only the cleaner is able to cheat, hence the payoff matrix is asymmetric. An exception are interactions between cleaners with cheating abilities and predatory clients. Here, the payoffs are asymmetric, as a cheated predator would lose a bit of healthy tissue while the cleaner would lose its life.
12. Control over interaction: Cleaners have full control over the service quality they provide. Clients can only respond to cleaner fish behavior. Nevertheless, most client species have high control, in that they can terminate interactions immediately whenever they decide to. However, some species may move slowly relative to cleaners and therefore have difficulties avoiding a cleaner that wants to interact with them.

Important features of cleaning mutualisms not covered by our game structure assessment: (1) The benefits that cleaners can offer to the clients depend critically on the population dynamics of other species, namely the parasites. If parasite abundance is low, cleaners cannot provide great benefits to their clients (Grutter, 1997); and (2) cleaner-to-client ratios may determine whether or not cleaners get sufficient food from their interactions with clients. If cleaners are very abundant, facultative cleaners might switch to other food sources, while full-time cleaners may cheat more frequently by feeding on healthy client tissue. Finally, territorial clients might face significant costs when visiting cleaning stations means leaving their territory, due to risk of territory loss and aggression by conspecifics (Cheney and Côté, 2001).

2. *Ant Protection Mutualisms*

In these mutualisms, ants provide protection against natural enemies, while the partners provide a food source, and in certain cases, shelter. Well-studied examples include mutualisms between ants and lycaenid caterpillars (Pierce *et al.*, 2002), ants and a variety of Homoptera, including aphids and treehoppers (Buckley, 1987), and ants and plants (Heil and McKey, 2003). Protection results either when ants chase away predators/herbivores, or when they actively consume them. Food sources include excretions (in the case of aphids), glandular secretions (lycaenids), and extrafloral nectar and lipid-rich food bodies (plants). The key questions for understanding ant protection mutualisms are why ants protect their partners at all, why insect mutualists are not eaten by the ants, and what keeps the production of food and shelter by the tended partners as high as it is.

1. Dependency: There is a continuum of dependence, from species that cannot survive unless ant tended, to species whose success is only marginally increased by tending. Ants usually have food sources in addition to what they receive from their partners. Only in certain highly specialized ant–‘‘myrmecophytic’’ plant mutualisms (e.g., the association between neotropical *Acacia* species and *Pseudomyrmex* ants) are the ants highly dependent on their partners.
2. Specificity: Ants and myrmecophytic plants, as well as ants and some lycaenid species, form relatively species-specific relationships; specificity in most other ant protection systems is low.
3. *N* interactions: Individuals interact repeatedly with each other.
4. Offer produced: Offers are generally produced continuously during the interaction, although partners in need of protection may produce an initial offer before ants are present, in order to attract them.
5. Moves: It is difficult to apply the terms ‘‘simultaneous’’ or ‘‘sequential’’ to ant protection mutualisms. The partner species continually invest in the ants by providing food, although they may modulate the amount and quality in relation to their need for protection. Ants, on the other hand, do not do anything beneficial for their partners most of the time. Benefits accrue only when the partner is at risk of attack.
6. Mobility: Partner species move little or not at all, while the ants are generally highly mobile. Exceptions are ant species associated with myrmecophytic plants that occupy nest space on or in the plant.

Hence, they have strongly reduced mobility compared with most ant protectors.

7. Active choice: The tended species appear to have no ability for active choice, while ants usually have access to several partners. Again, the exceptions are ant species associated with myrmecophytic plants. Here, the ant queen could initially choose a plant on which to settle, but once the colony grows, movement to other plants and hence the ability to actively choose among partners may be constrained.
8. Partner recognition: Ants may be able to recognize individual partners through site recognition (mediated via trail-marking pheromones), since most ant-protected species are immobile or nearly so. Partners seem highly unlikely to be able to recognize individual ants.
9. Behavioral options: Ants could in principle cooperate or cheat, in one of two ways: they could avoid risks associated with defending their partners, or they could actively consume them (relevant for Homoptera and some lycaenid species). Tended partners may cheat by reducing the amount or quality of food or shelter that they provide to ants. This option is limited in aphids, as aphids honeydew is mainly an excretion that cannot be stopped completely.
10. Investment: Investment is usually variable on both sides of the interaction: both protection effort and food production can be adjusted (with the possible exception of Homoptera). In the case of possible ant predation of partners, investment is all or nothing.
11. Payoff symmetry: The effects of reduced investment in the partner are asymmetrical in ant–insect protection. If ants do not defend, predators/parasites can kill the insect, whereas ants just lose a bit of food if cheated. The payoffs are more symmetrical in ant–plant mutualisms, since the cost of lack of defense by a single ant individual is a marginally higher rate of herbivory for the plant rather than a matter of life and death.
12. Control over interaction: Ants usually have full control over their own behavior: they can presumably choose how much protection they give, and they can quickly adjust to environmental conditions. Tended partners could in principle control to some extent how much food they offer; Homoptera may have limited control over what they offer, although there is some evidence that they control its chemistry (Fischer and Shingleton, 2001). A major problem might be that tended partners cannot respond instantaneously to changes in their most important variable in the environment, namely predator attack.

However, the ability of lycaenids to alter secretion rates according to their perceived need for protection, and of some lycaenids and plants to increase secretion on attack, may reduce subsequent attack rates (Axén *et al*., 1996; Leimar and Axén, 1993; Ness, 2003).

Important features of ant protection mutualisms not covered by our game structure assessment: (1) Most importantly, the magnitude of the benefits ants can offer to their partners depends crucially on the identity and density of the partners' natural enemies. If there are no enemies, ant tending may confer no benefit (but see Morales, 2000); and (2) the benefits that the partner species provide depend on the identity and quality of alternative food sources available to the ants. Under some circumstances, partner species may not be able to provide food of high enough quality to make tending a profitable option for ants.

3. *Mixed Species Aggregations*

Individuals or groups of different species of vertebrates aggregate for some or all of their lives. Detailed studies have investigated mixed species associations in forest primates (Höner *et al*., 1997), ungulates (FitzGibbon, 1990), a large variety of bird species (Moynihan, 1962), and fish (Ehrlich and Ehrlich, 1973). For most of these interspecific associations, it is assumed that a reduction in predation risk is the primary advantage. There is good evidence for this claim in birds and mammals (Bshary and Noë, 1997; Fitzgibbon, 1990; Greig-Smith, 1981; Noë and Bshary, 1997). Potential mechanisms facilitating increased protection include dilution effects, confusion effects, increased early warning, and improved defense. Increasing group size with allospecifics rather than conspecifics may reduce competition over food or mating partners. It may also lead to the joining of complementary skills in predator avoidance, or may reduce predation risk if the partner species is ''preferred'' by predators (references in Noë and Bshary, 1997). Increased foraging efficiency for individuals of one or both partner species is an alternative hypothesis to explain mixed species associations (references in Cords, 1987).

1. Dependency: Dependency in these associations is probably low, and each species could survive without its partner. Nevertheless, there will often be an asymmetry, in that one partner species benefits more from the association than the other partner species.
2. Specificity: Associations can be quite partner specific (e.g., olive colobus seek Diana monkeys at Tiwai Island; Whitesides, 1989). Often, however, several partner species are involved in the association. Still, some species may be better partner species than others because of their vigilance abilities, active predator defense, or passive food provisioning.

3. *N* interactions: Interactions are usually repeated between the same individuals or groups. In some bird flocks or fish schools, individuals may only meet once, although this has rarely been documented.
4. Offer produced: Offers here mean that (a) the presence of each individual adds to the safety for all other individuals through early warning, dilution, or confusion effects, and (b) one partner species facilitates access to a food source for the other one in association when foraging benefits exist. Offers are produced during the interaction.
5. Moves: This term is difficult to apply to interspecific associations. Moves may be termed simultaneous in that everybody responds to the presence of a predator. If access to food is traded for increased protection (as possibly in some marine associations), food may be accessed continuously while predatory attacks are unpredictable.
6. Mobility: Partners are generally mobile.
7. Active choice: Because of their mobility, individuals may often be able to actively choose with whom to associate. Territoriality and living in stable groups may constrain active choice options in some species, however.
8. Partner recognition: Partner recognition below the species or sometimes group level appears not to be necessary unless it can be shown that cheating the partner species is a problem in interspecific interactions (see below).
9. Behavioral options: Cheating appears not to be an option within these interactions. The benefits of mixed species associations are usually an emergent property of the increase in group size: improved early detection of predators due to ''many eyes and ears,'' dilution effects, and confusion effects. Note, however, that there may be individual differences with respect to the likelihood of giving alarm calls, although these differences are seen as intraspecific strategies (Sherman, 1977).
10. Investment: There is no investment that benefits the partner directly, although there are costs of staying together and synchronizing activity patterns.
11. Payoff symmetry: As there is no cheating, the payoff symmetry is of no concern.
12. Control over interaction: As mentioned above, the benefits are a result of simply associating together. No active exchange between partners

occurs. Hence, every participating partner gets the increased protection by default.

Important feature of mixed species associations not covered by our assessment of game structures: The costs and benefits of mixed species associations depend on group size. Costs of being in a group larger than some optimal level cannot be attributed to the behavior of individuals. Individuals do not cheat, but competition for food increases with the number of individuals present. Population densities may hence become a crucial parameter.

4. Müllerian Mimicry

In Müllerian mimicry, two or more partner species (1) strongly resemble each other in colors and morphology, and (2) are to some degree unpalatable or poisonous (Ruxton *et al*., 2004; Speed, 1999). Individuals of partner species do not interact directly with each other. On exposure to the same potential predator species, look-alikes benefit from the dilution effects associated with individual predators learning to avoid prey with certain characteristics (color, smell). The best-studied Müllerian mimicry complexes involve Lepidoptera. The crucial question is what prevents individuals of partner species from reducing the unpalatable or poisonous products in their body and becoming Batesian mimics that resemble unpalatable species but are harmless.

1. Dependency: Dependency is probably mutually low: each species can survive without the partner species, although fitness may be higher in its presence.
2. Specificity: All species that resemble each other, are unpalatable, and occur in the same place should be good partners. The number of partner species may therefore range from one to many.
3. *N* interactions: Individuals do not interact directly with each other. Potential predators, however, may repeatedly interact with (i.e., encounter) individuals of all species involved.
4. Offer produced: Nothing is exchanged between mimicry species. Hence, the ''offer,'' if it can be said to exist at all, is the degree of unpalatability, which is produced continuously.
5. Moves: This parameter is difficult to apply to Müllerian mimicry. Moves can be termed simultaneous in that all individuals involved may be encountered by a predator at any time.
6. Mobility: Partner species are mobile.

7. Active choice: There is usually no potential for active choice in Müllerian mimicry, since mimics do not appear to intentionally flock together.
8. Partner recognition: Partners do not need to recognize each other in order to share benefits, and it is unlikely that they do.
9. Behavioral options: The crucial questions are whether (a) the unpalatable substances are costly to produce, and (b) if they are costly, whether the exact investment of individuals depends critically on what individuals of partner species do rather than on what conspecifics do. For example, kin selection and low dispersal rates may stabilize unpalatability independently of the existence of a Müllerian look-alike. If the answer to both questions is ''yes,'' then cheating is possible. With respect to production, there is evidence in some systems that sequestering secondary compounds from food is costly (Ruxton *et al*., 2004).
10. Investment: If unpalatability is costly, investment is variable in that the production or incorporation of compounds is variable. But as mentioned above, it is critical to know whether investment is a game between conspecifics or between all look-alikes.
11. Payoff symmetry: The payoffs should be symmetrical, as costs and benefits to each partner are similar.
12. Control over interaction: Individuals do not directly interact with each other. Each individual may control to some extent its production or sequestration of toxic compounds; however, it has no control over what other individuals are doing.

Important features of Mullerian mimicry not covered by our assessment of game structures: (1) Population densities of partners may be crucial to understand how a reduction in unpalatability in one species would affect predator behavior and hence the fitness of all Müllerian mimic species; and (2) as mentioned above, dispersal patterns might be another important variable. If dispersal rates are low, then kin selection advantages associated with predator defense may override any advantages of reduced investment. In contrast, if dispersal rates are high, a reduction in investment may be advantageous.

C. Nutrition Mutualisms

Until this point, we have focused on nonsymbiotic mutualisms, simply because more relevant ecological data are available to infer their game structures. In this section, we deal relatively briefly with a suite of mutualistic symbioses based on the benefit of nutrition (reviewed by Douglas, 1994): nitrogen-fixing symbioses, plant–mycorrhizal mutualisms, coral–zooxanthellae associations, and lichens (mutualistic symbioses between fungus and algae). In these interactions, one partner acts as host to a microbial associate that lives in or on it. The two partners trade substances that are either of nutritional value or essential for physiological activities. Shelter offered by the host may be an additional offer. The crucial question in symbioses is how the nutrient transfer between partners is regulated. We stress that our parameter descriptions below are somewhat conjectural, in light of limited study of some of the critical features of these interactions.

1. Dependency: In most cases, hosts are highly dependent for survival and/or growth on their symbionts. Certain symbiont species are known to occur only in association with hosts, but in general, information is lacking on this point.

2. Specificity: While it was once assumed that nutritional symbioses exhibit low partner specificity, more recent molecular evidence suggests higher or even complete specificity, at least in vertically transmitted symbioses (Herre *et al*., 1999).

3. *N* interactions: There is usually one prolonged interaction between individual partners during which partners may alter their behavior repeatedly. From a theoretical point of view, the interaction can therefore be seen as repeated. On the brief end, some corals readjust the number of algae on a daily basis; on the long end, the interactions last a lifetime in lichens. Things become even more complex as there can be long-term associations between cell lineages, not just individuals.

4. Offer produced: Offers are produced continuously by both partners. Hosts sometimes must invest first, however, by producing a structure in which the symbiont can live.

5. Moves: Moves are simultaneous, and both partners may continuously provide nutrients to each other.

6. Mobility: In many symbioses, both partners are sessile and cannot move freely. Zooxanthellae, however, move in the water column.

7. Active choice: There is no choice possible in vertically transmitted symbioses (i.e., those passed internally between host generations). With regard to horizontally transmitted symbioses, at least some marine symbionts actively locate hosts, usually via chemical detection (Douglas, 1994).

8. Partner recognition: In this context, partner recognition refers to being able to assess the amount of nutrient received from different partners. Partner recognition of some form would be advantageous in all cases in which one individual interacts with several partner individuals, especially hosts associated with several symbiont lineages that may confer greater or lesser benefits. In mycorrhizae, an individual fungal genotype may be in contact simultaneously with several plants; in this case, both partners could benefit from partner recognition.
9. Behavioral options: Both sides invest in their partner, so both sides can in principle cooperate or cheat. A variety of forms of cheating have in fact been detected in both hosts and symbionts (e.g., Kiers *et al*., 2003; Smith and Smith, 1996).
10. Investment: The investment into the partner is variable rather than all or nothing.
11. Payoff symmetry: The payoffs may be relatively symmetrical in most systems, as being cheated usually means not receiving nutrients from the partner. However, being cheated may have greater consequences for a unicellular symbiont compared with its multicellular host. The payoffs in corals can also be asymmetric, as some polyps can eat their zooxanthellae.
12. Control over interaction: This point is of crucial importance for the outcome of the game, but is still unresolved. In corals, it is hypothesized that polyps have some control over nutrient flow, as the algae are placed into a host vacuole. Polyps may also expel the algae (Titlyanov *et al*., 1996). In nitrogen-fixing symbioses, plants must offer an initial investment that may or may not be reciprocated later on. During later stages of the interactions, evidence suggests that there is a complex amino acid transfer between plant and rhizobia that prevents either partner from dominating the interaction (Kiers *et al*., 2003; Lodwig *et al*., 2003). Such information is essential for all symbioses. We need to know how well each partner can control how much it gives and how much its partner has to give in return.

Important features of nutritional symbioses not covered by our game structure assessment: (1) There is one important variable that exists only in symbioses: do partners associate horizontally or vertically? Vertical transmission of symbionts has been shown empirically and theoretically to reduce the potential for conflict among partners; and (2) Hosts and symbionts usually have radically different generation times. How generation times affect the outcome of interactions at evolutionary time scales has barely been addressed (Bergstrom and Lachmann, 2003).

VII. How Similar/Different Are Mutualisms?

In the previous section, we reviewed the best-studied mutualistic systems in order to extract their game structures. A summary of our results is presented in Table II. We now attempt to assess the similarities between these interactions in the context of game structure. The importance of ecology for our understanding of behavioral strategies and their consequences on the fitness of each partner are evaluated later.

One might expect that the huge diversity mutualisms exhibit with respect to evolutionary origin, species identity, and ecology would also be reflected in game structures. If so, it is likely that general principles cannot be found. We promote a more optimistic view, based on the game theoretic concepts that we presented in Section I. These concepts focus on the question of how mutualistic systems may be stable against erosion through the evolution of cheating strategies. Below, we review the main features of game structure that mutualisms share, even when differing greatly in natural history.

A. Investment

In the majority of mutualistic systems investigated in this article, one or both partners invest in each other. In most cases, investment is variable; for example, plants may produce greater or lesser amounts of nectar per flower, and pollinators may deposit and carry a variable number of pollen grains between plants. Exceptions are protectors and clients that can act as predators of their partners. In these cases, individual investment may be all or nothing (i.e., the partner is either allowed to live or is eaten), as the original prisoner's dilemma game assumed (Axelrod and Hamilton, 1981). However, cheating by predators terminates the game and hence violates the iterated prisoner's dilemma game in another important way (Hammerstein and Hoekstra, 1995). For all mutualisms in which investment occurs, one can ask what factors may stabilize cooperative behavior by disfavoring individuals that play a strategy of reduced investment in the partner.

In other mutualisms, however, there appears to be no investment whatsoever. In particular, in mixed-species foraging associations, mutual benefits appear to be a simple by-product of group enlargement. Many other, less well-studied mutualisms similarly involve no investment. Examples include gabar goshawks placing webs with social spiders into their nest

TABLE II

Summary of Evaluated Parameters That May Have Important Implications for the Outcome of Interspecific Interactions[a]

Parameter	Plant–pollinator	Plant–seed parasites	Plant–seed dispersers	Cleaner–client	Ants–partner	Mixed species	Mimicry	Host–symbiont
Dependency	High/div	High/high	Low/low	Div/low	Div/div	Low/low	Low/low	High/high
Specificity	Low/low	High/high	Low/low	Low/low	Div/div	Variable	Variable	Often high
N interactions	Variable	One-off	Variable	Variable	Repeated	Repeated	d n a	Lasting
Offer produced	Before/during	Before/during	Before/after	During/during	During/during	During/during	Constant/constant	During/during
Moves	Seq	Seq	Seq	Simult	Simult	Simult	Simult	Simult
Mobility	No/yes	No/yes	No/yes	Var/var	Var/no	Yes/yes	Yes/yes	No/var
Active choice	No/yes	No/var	No/yes	Var/var	Var/no	Both	d n a	No/no
Partner recognition	No/var	No-pos/no	No/pos	Var/var	Pos/no	Pos or no	No/no	Pos/no
Behavioral options	cd/cd or c	cd/cd	cd/c	cd or c/cd or c	cd/cd	c/c	cd or c/cd or c	cd/cd
Investment	Cont/a–n	Cont, a–n/cont	Cont/no	Cont/a–n	Cont, a–n/cont	No/no	Cont/cont	Cont/cont
Payoff symmetry	Sym	Life-din	d n a	Life–din	Sym or life–din	d n a	Sym	Sym or life–din
Control	Var/full	No/var	No/full	Full/var	Full/var	Full/full	Full/full	?/?

[a] If two parameter states are given, separated by “/,” the first information applies to the mutualist named first in row 1, and the second information applies to the mutualist named second in row 1. For example, in plant–pollinator mutualisms, dependency is high for the plants and diverse for the pollinators (some species are highly dependent whereas others are not). *Abbreviations*: div, diverse parameter states occur in the system; d n a, does not apply; simult, simultaneous; seq, sequential; pos, possible (the ability would yield fitness advantages); c, to cooperate is the only behavioral option; cd, individuals could cooperate or cheat, at least in theory; cont, continuous; a–n, all or nothing; life–din: one partner would lose little if cheated whereas the other partner would lose its life; sym, symmetrical; var, variable.

to reduce parasite densities on young (Henschel *et al*., 1992) and cooperative hunting between groupers and moray eels (Bshary *et al*., 2001). Since there is no (or minimal) investment, there is presumably nothing for these species to gain by cheating in the interaction; in fact, it is difficult even to define what cheating would consist of. There can be opportunity costs in these systems, that is groupers may spend a considerable amount of time (up to 60 min; R. Bshary, unpublished observation) signalling to the moray eel, trying to elicit joint hunting. But these costs do not translate into benefits for the moray eel. We do not deal with these mutualisms further in this article, as game theory does not appear to have much to offer as a tool to study their stability. Furthermore, we cannot discuss Müllerian mimicry examples properly without knowing whether or not there is selection on partner species to become palatable Batesian mimics. In any case, individuals of partner species do not invest in each other in interactions and hence our game structures do not yield important insights.

B. Investment at the Outset of the Interaction

In a diverse range of mutualisms, one partner may have to produce an initial investment for the interaction to begin. Some species must produce a reward in order to attract a partner, including plants (floral nectar, extrafloral nectar, and fruits) and lycaenid caterpillars (secretions). Other mutualisms are only initiated once one partner has produced a shelter for the other to inhabit (e.g., myrmecophytic plants and reef-building corals). Finally, the cleaner wrasse *L. dimidiatus* must invest initially in its resident clients by providing tactile stimulation before it is allowed to search each client's surface for parasites (Bshary, 2002). In all these cases, any potential benefit for the investing partner is delayed until after substantial investment has been made. Hence, the question of when the other partners will cheat by taking the offer without returning any benefits becomes particularly interesting. Such behaviors are well documented in most of these mutualisms. For example, nectar robbers take floral nectar while bypassing the pollen and stigmas; it is difficult to see how plants could sanction these behaviors in a behavioral sense.

C. Partner Choice

A common feature of mutualisms (with the exception of mutualistic symbioses involving vertical transmission) is that individuals of one species may have, at least theoretically, the option to choose among several individuals of their partner species. Pollinators and seed dispersers are usually mobile and visit several plants, many clients are mobile and visit different cleaner individuals, and ants tend a variety of individual partners, often belonging to several partner species. In all these systems, the predictions of biological market theory (Hoeksema and Schwartz, 2001, 2003; Noë, 2001; Noë and Hammerstein, 1994; Noë *et al.*, 1991) could be tested. Biological market theory treats mutualistic interactions as an exchange of goods between partners that differ in the degree of control they have over the goods they trade. Predictions based on market theory would be as follows. (1) The chosen partner species adjust their offers according to supply and demand ratios. If they have few competitors for access to partners, they should offer less than if there are many competitors, because in the latter situation, individuals of the partner species can be choosy; and (2) individuals of the choosy partner species should stop interacting with cheating individuals and search for more cooperative partners. Such active choice would stabilize the occurrence of cooperative behavior in the partner species (Ferrière *et al.*, 2002). In one marine cleaning mutualism, Bshary and Schäffer (2002) found that client species with large home ranges do choose between cleaners on the basis of the quality of the service that cleaners provide. More specifically, clients switch to a new cleaner if they are bitten by their current one, and return with high probability if the cleaner behaves cooperatively (Bshary and Schäffer, 2002). In addition, partner choice options may affect an array of other parameters, at least in the *L. dimidiatus* cleaning mutualism (Bshary and Noë, 2003). However, evidence that choosiness of clients stabilizes cooperative behavior of cleaners is still lacking.

While individuals need to move freely in order to be able to actively choose between potential partners, there is also a way of choosing that may be called ''passive.'' For example, in most mutualistic symbioses, each host interacts simultaneously with several genetically distinct symbiont lineages. If these symbionts vary in quality, any ability of the host to sanction unproductive symbionts would be favored by natural selection. Evidence in nitrogen-fixing symbioses between plants and *Rhizobium* bacteria shows that plants do in fact discriminate between nodules with different N_2 production (Kiers *et al.*, 2003; Lodwig *et al.*, 2003). Similarly, some yucca plants selectively abort fruits that contain high numbers of pollinator eggs (Pellmyr and Huth, 1994). Like active choice, this passive choice arguably stabilizes cooperative behavior of the symbionts. Similar ''sanctions'' have been argued to exist in some other mutualisms as well (e.g., West *et al.*, 2002).

D. Dependency and Specificity

Dependency on the partner is typically high in nutritional symbioses, pollinating seed parasite mutualisms, and interactions between ants and myrmecophytic plants. In addition, a few cleaner species and many plants can survive or reproduce only when clients/pollinators visit them. Interestingly, high dependency does not necessarily translate into high partner specificity. In particular, cleaner fish and shrimps access many client species, and many self-incompatible plants can be pollinated by a wide range of small insects. On the other hand, partner specificity may be high in some mixed species and mimicry associations, although dependency is probably relatively low in these cases.

Dependency appears to be a parameter that may affect mutualistic interactions in ways that go beyond the game structures we presented. With respect to game structures, dependency may simply affect payoff values: if one partner is very dependent on the other, the payoff values for receiving a cooperative act from the partner are higher if an individual is critically dependent on the partner's cooperation than if the individual can survive well without the partner. But the degree of dependency may also affect interactions more deeply, through increased selection pressure favoring mutants with greater access to resources provided by the partner. The result can be seen as increased sophistication of behavioral strategies, but also as potential threats to the evolutionary persistence of cooperative behavior, as the following examples indicate: (1) only obligate cleaners of the genus *Labroides* are known to manipulate client decisions through tactile stimulation of the client with the pelvic and pectoral fins (Bshary and Würth, 2001); and (2) flower mimicry of female pollinators instead of nectar provisioning is found in systems with high pollinator specificity (Dafni, 1984).

E. Similarities within Different Mutualistic Classes

It is important to note that the similarities in game structures across mutualisms mentioned above are not necessarily linked to the particular commodities that are exchanged by partners, but are more general. As a consequence, for example, some ant-tending mutualisms may share more features with pollination mutualisms than with mixed species associations or Müllerian mimicry, although the latter two are protection mutualisms as well. As an example, interactions between plants with extrafloral nectar and ants have a game structure similar to interactions between plants and pollinators that can rob nectar (Table III). On the other hand, there can be remarkable similarities between specific systems in which similar commodities are exchanged. A striking case is the comparison between cleaner wrasse *L. dimidiatus*–predatory client interactions and aphid–ant interactions (Table III). These specific examples emphasize that insights gained from one mutualistic system may shed light on other mutualisms that at first sight appear to be very different.

Generally, transportation mutualisms appear to be more coherent in game structure than protection mutualisms. The transportation mutualisms discussed here generally share the following features (Table II): they involve one sessile and one highly mobile partner, the sessile partner invests prior to the interaction and moves are therefore sequential, the mobile partner may be able to actively choose while the sessile partner cannot, and the sessile partner has little immediate control over the course of interaction, which is determined mainly by the behavior of the mobile partner. Among protection mutualisms, mimicry and mixed-species associations are very peculiar. Mimicry differs from all other examples because partners do not interact directly with each other. This generates a suite of consequences for the game structure; even the game's terminology is difficult to apply (Table II). Mixed-species associations differ from all other examples in that partners do not invest in each other, with another suite of consequences for the game structure (Table II).

TABLE III
Specific Examples of Strong Similarity in Game Structures Between Mutualisms That May Initially Appear Different

Parameter	*L. dimidiatus*–predator	Aphid–ant	Plant–ant	Plant–bumblebee
Dependency	High/low	High/low	High/low	High/high
Specificity	Low/low	Low/low	Low/low	Low/low
N interactions	Repeated	Repeated	Repeated	Variable
Offer produced	During/during	During/during	Before/during	Before/during
Moves	Simult	Simult	Seq	Seq
Mobility	No/yes	No/yes	No/yes	No/yes
Active choice	No/yes	No/yes	No/yes	No/yes
Partner recognition	Pos/pos	No/pos	No/pos	No/pos
Behavioral options	cd/cd	cd/cd	cd/cd	cd/cd
Investment	Cont/a–n	Cont/a–n	Cont/cont	Cont/a–n
Payoff symmetry	Life–din	Life–din	Sym	Sym
Control	Full/high	Low/full	No/full	No/full

[a] The first comparison is between the mutualism of the cleaner wrasse *L. dimidiatus* and a predatory client with access to several cleaning stations (e.g., a giant moray eel, *Gymnothorax javanicus*), and an aphid–ant mutualism (both examples are of protection mutualisms). The second comparison is between the mutualism of a plant with extrafloral nectar and ants (protection mutualism), and the mutualism between a plant and bumble bees as pollinator (transport mutualism). Bumble bees have been chosen as a representative of a pollinator that can rob nectar. For abbreviations, see Table II.

The different types of mutualism that we have reviewed are quite diverse with respect to the degree of variation they exhibit in the states of individual parameters (Table II). Plant–seed disperser mutualisms appear to be very uniform, as are mixed-species associations. In Müllerian mimicry cases, crucial information is lacking for a proper assessment. Other types of mutualisms show considerably more variation. For example, pollination mutualisms range from species-specific and obligate to highly generalized and facultative. Nevertheless, the number of game structures is not overwhelming. Cleaning mutualisms appear to be the most diverse system with respect to the number of game structures possible. But even here, the number of different game structures is limited to about 15 different combinations of parameter states. In each of the other systems, free combinations of observed parameter states yield less than 10 potential game structures. Hence, the diversity in game structures is not so large that it could not be tackled by theoreticians.

VIII. The Importance of Ecology

The approach to mutualisms that we have taken here focuses on the question of what factors may promote the persistence of cooperative behavior and keep cheating at levels that do not threaten the overall mutualistic outcome. Ideally, to address this question theoretically, the behavioral options of individuals are identified, the payoffs for each behavioral option are determined, and the interaction is formalized as a game. If the game yields a solution in which both partners show cooperative behavior, the mutualism is assumed to be evolutionarily stable against cheating. However, both short-term and evolutionary stability may depend on additional, ecological variables that are not easily covered by game theoretic assessments. Some of these are as follows.

A. The Influence of Population Densities

We identified several mutualistic systems in which population dynamics of partner species are almost certainly of major importance in determining payoff values. For example, in pollinating seed parasite mutualisms, high pollinator densities mean that flowers/inflorescences will become heavily laden with eggs, raising the possibility that the larvae will eat most of the developing seeds. Pollinator females arriving after all flowers have been pollinated also lay eggs, contributing to the cost of the mutualism but adding no extra benefits. The investment of a pollinator in its partner, as measured by the ratio of pollination acts to eggs laid, is therefore determined strongly by sequence effects (being the first or second or third visitor), not only by female strategies. The problem for the plants is that they appear to have little control over the course of the interaction; various mechanisms have been invoked that would give them control (e.g., Bao and Addicott, 1998; Ganeshaiah *et al*., 1995), although most of these have been challenged on empirical or theoretical grounds. Theoreticians are beginning to explore how pollinator densities may be kept low enough to yield a net benefit to the plants, focusing on fruit abortion mechanisms that have been reported in some systems (e.g., Holland and DeAngelis, 2002; Holland *et al*., 2001).

In cleaning mutualisms, a high cleaner-to-client ratio means that cleaners will not find enough parasites on clients to meet their daily food intake. Some cleaner species, in particular facultative cleaner species, may switch to other food sources under such circumstances. Full-time cleaners, however, may behave more parasitically under these conditions and increase feeding on healthy client tissue, resulting in conflicts between client and cleaner.

Finally, in Müllerian mimicry systems, relative population sizes of species within the complex may determine whether individuals of a rarer species can benefit from a reduction in the production of toxic material (assuming that it is costly to produce). That is, the balance between cooperation and conflict in these interactions may be frequency dependent (Ruxton *et al*., 2004). A common view, however, is that systems do not shift back and forth between Müllerian and Batesian mimicry (Mallet, 1999).

B. Population Densities of Third Species

In protection mutualisms, the benefits for the protected partner generally depend critically on the population dynamics of third species, specifically, the natural enemies that the protector consumes or deters (Bronstein and Barbosa, 2002). Cleaners and ants generally do not improve the fitness of their partners if the partners' enemies are rare or absent. In cleaning mutualisms, low parasite densities mean that clients simply seek cleaning less frequently. Hence, as long as clients can control number and duration of interactions with cleaners, no negative payoffs are to be expected, although the benefits would shift toward zero under circumstances of extreme parasite shortage (Johnstone and Bshary, 2002). The concept of ''power'' in the economic literature is very similar to what we have called ''control over interaction'' (Bowles and Hammerstein, 2003). Ant mutualisms differ from cleaning mutualisms in that partners are usually producing at least some reward for ants even when they do not require attendance. Therefore, partner species can incur net fitness costs from their interactions with ants during periods in which attack risk is low. These costs depend in part on the costliness of the reward. For example, lycaenids involved in relatively obligate and species-specific ant-tending mutualisms produce particularly high-nutrient secretions, and experience reduced success when tended in the absence of a predation risk (Pierce *et al.*, 1987). Untended, secreting lycaenids engaged in more facultative ant-tending mutualisms have not been found to experience these costs (e.g., Wagner, 1993).

C. The Environment as ''Competitor''

Any partner in mutualisms involving food offers must outcompete alternative food sources that are available and acceptable to individuals of the partner species. These alternative food sources could be other potential mutualist species. For example, plants and Homoptera may compete for access to ant defenders (Sakata and Hashimoto, 2000), and several client species may compete among each other over access to cleaners (Bshary, 2001). In most cases, however, alternative foods are not associated with potential mutualists. Cleaners may feed from free-swimming invertebrates, ants must feed on protein as well as sugar-rich secretions and excretions, and vertebrate pollinators feed on insects as well as nectar. In addition, in some nutritional symbioses, critical nutrients may at some times be obtained directly from the environment (e.g., Johnson *et al.*, 1997). Interacting with the partner is therefore at the expense of looking for alternative options in the environment, thus there are opportunity costs. If these costs are higher than the benefits of the mutualistic interactions, because of high abundances of alternative commodities in the environment, a (temporary) breakdown of mutualistic relationships may be observed, not because one partner starts cheating, but because it terminates the interaction.

D. Mode of Transmission

In symbioses, a critical question appears to be whether symbionts are transmitted vertically or horizontally. Any vertical transmission of symbionts into the next host generation may greatly reduce potential for conflicts, as it is then in the interest of both sides that the partner fares well (but see Frank, 1996). In contrast, if both sides reproduce independently and partners must locate each other at later stages of their life cycle, it is theoretically possible that exploitation of the partner to such a point that the partner is no longer able to reproduce (but is still able to offer the commodity in demand) may be favored in the short term (in the long term, of course, this may lead the mutualism to break down). A variation of this question exists in seed parasite pollination mutualisms. Fig wasp females collect the pollen within the inflorescence from which they emerge and use it to pollinate the inflorescence that they enter. Hence, the male reproductive success of the tree is positively coupled with the reproductive success of the wasp. In contrast, female yucca and senita moths collect pollen elsewhere and the male reproductive success of their host plant is therefore not coupled to the reproductive success of the moths.

IX. Future Avenues with Respect to Evaluation of Game Structures

There are three major gaps in our knowledge that must be filled if we are to reach a deeper understanding of how mutualistic behaviors persist. These points are crucial issues for future empirical studies to address.

1. We need to know more about the exact payoffs associated with different individual behaviors. There are two main problems to solve: (a) we need to know whether a reduction in investment into the partner yields a higher or lower (short-term) benefit to the actor. This distinction is crucial because it influences the game in the most fundamental way. If a reduction in investment yields a higher payoff, then cheating is a profitable option, and partner control mechanisms must reinforce cooperative behavior if the mutualism is not to be driven to extinction. If reduced investment in fact carries no net benefit because it predictably lowers the partner's investment in return, then investment into the partner would be a form of pseudoreciprocity (Connor, 1986), and cheating is highly unlikely to be an issue; and (b) we must put all potential costs into the equation. Costs arise if an individual invests in the partner, if the partner performs a discrete cheating act (nectar robbing, eating a cleaner, etc.) or if it reduces the benefits through decreased investment, and if there are opportunity costs. These latter costs may not influence the course of interactions, but interactions may simply not take place if opportunity costs are too high.
2. We need to learn more about how well each player can control how much it offers to its partner, and the extent to which it can force its partner to provide commodities in return. Such information is particularly crucial to assess in mutualistic symbioses. Research on mechanisms of nutrient transfer in nitrogen-fixing associations by Lodwig *et al.* (2003) sets a prime example of what should be investigated in other symbioses as well. As long as each player has control over what it gives but not over what it receives, cooperative behavior may be more stable against cheating strategies than in situations in which one player has some power to rob/steal/purloin commodities from its partner.

3. We need to understand generalized mutualisms, that is, mutualisms that involve several potential partner species, in more detail. For example, it needs to be established whether or not a suboptimal partner species (e.g., an ant species that does not protect its partner species as efficiently as does another ant species) has a higher gain from the interaction than the partner species that provides the optimal service. Alternatively, suboptimal partners also do not gain high benefits from the interaction. In other words, suboptimal partners may be better exploiters, or they may be adapted to other partners themselves, and perform suboptimally in the association as well.

X. Conclusions

We still have a long way to go to understand how cooperative behavior persists in mutualisms. To achieve this goal, we need more empirical information that is structured in a way that it is of direct value for theoreticians. An interactive approach, which involves developing theoretical concepts based on empirical information that are then amenable to further empirical tests, seems to be most promising at this stage. We hope that our review provides a step in this direction. While it seems impossible at this point to develop a single unifying concept for behavioral strategies that may explain the persistence of cooperative behavior in mutualisms, the diversity of game structures is not so large that it could not be tackled by theoreticians. Detailed theoretical and empirical studies of single parameters may yield building blocks for more sophisticated integrative models (Bshary and Noë, 2003). Such building blocks must not be confined to behavior and game theory, but we must incorporate ecological information and population dynamics as well.

XI. Summary

Currently, there is little information transfer between empiricists working on cooperative interactions between species (mutualism) and theoreticians who model possible scenarios for the evolution and maintenance of cooperation between unrelated individuals. Furthermore, both theoretical and behavioral approaches often fail to consider ecological parameters that influence behavior. Our goal is to present the wealth of empirical knowledge (both behavioral and ecological) on mutualistic systems in a structure that may facilitate communication between empiricists and theoreticians.

We have chosen eight broad categories of mutualisms that have been intensely studied and that are relatively well understood. For each system, we assess possible states of 12 parameters that can help theoreticians to construct game structures of mutualisms that are built on current empirical knowledge. We point out how ecological variables may influence behavioral decisions in ways not identified by our parameters. Finally, we elucidate similarities between mutualistic systems with respect to game structures that may not be expected given the diversity of mutualisms with respect to ecological and evolutionary background. On the basis of these results, we promote an interactive approach with models based on empirical knowledge, amenable to further testing.

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