

13

Group Report: Interspecific Mutualism

Puzzles and Predictions

Carl T. Bergstrom, Rapporteur

Judith L. Bronstein, Redouan Bshary, Richard C. Connor,
Martin Daly, Steven A. Frank, Herbert Gintis, Laurent Keller,
Olof Leimar, Ronald Noë, and David C. Queller

INTRODUCTION

In 1859, Charles Darwin wrote:

If it could be proved that any part of the structure of any one species had been formed for the exclusive good of another species, it would annihilate my theory, for such could not have been produced through natural selection.

—*The Origin of Species*, Chapter 6

This was a bold prediction indeed! Many species were known to provide one another with benefits, and a good fraction of these appeared to have evolved elaborate mechanisms by which to do so. The evolutionary study of *interspecific mutualism*—defined as mutually positive interactions between species—aims to explain such observations by identifying the direct or indirect benefits that accrue to an actor from the actions that benefit its partner.

A hundred and forty years after Darwin stepped out onto this proverbial limb, where do we stand? Has the branch given way under the weight of his bold prediction, or has the branch held firm as theory and observation remain in close accord? Have we addressed Darwin's challenge to our full satisfaction, or do we need to seek new principles by which to explain the full range of observed interactions? More specifically, what observations do we need to explain, and what explanations do we have to offer? In this report, we describe the major conceptual foundations that are applied to the study of mutualism, and we ask what questions remain unanswered.

MAJOR QUESTIONS

To provide a thorough and satisfying evolutionary explanation of a given phenomenon, we typically need to identify mechanisms responsible for two separate processes: First, how did the phenomenon of interest initially arise? Second, what prevents its dissolution once established? These two questions stand at the center of the study of mutualism and comprise our first two major questions in the field of mutualism:

- By what processes do mutualisms form?
- How do mutualisms persist over time, despite the ever-present threat of exploitation from within or by third parties?

Beyond obtaining a basic answer to each of these problems, we would like to be able to say at least something about how the ecological and evolutionary context affects the biological outcomes observed. In essence, we seek to understand how the properties of mutualisms change in response to changes in underlying parameters. In general, we would like to know:

- What factors promote or inhibit the formation and persistence of mutualisms?
- What factors influence the partitioning of benefits between the mutualist partners?

All of these questions can be addressed on both ecological and evolutionary timescales. For example, if we ask how mutualisms are formed, we can explore how partners find one another in real time and how the ecological dynamics of growth and dispersal act to structure the patterns of mutualistic association in time and space. Alternatively, we could explore the processes by which novel mutualisms arise over evolutionary time among previously unassociated species pairs or out of other forms of interspecies interaction (e.g., parasitism; see Table 13.4). In this report we focus primarily on what happens over evolutionary time; however, we recognize the crucial importance (and ultimate interdependence) of both scales.

THE RANGE OF MUTUALISMS

Biological mutualisms span such a broad range of natural histories and evolutionary origins that mutualism as a concept cannot easily be shoehorned into any simple, single situational template. For this reason, it would be a tremendous stretch to argue that any particular system is itself the “archetypal” mutualism. That said, would it even be useful to consider mutualisms as a class of interactions delimited by a set of common features and subject to some single conceptual framework? A pessimist might answer “no” and argue that mutualism is a catch-all category, an unrelated grab bag of interactions with no hope for conceptual unification.

We, the authors (or at least some subset thereof), prefer a more optimistic view: Mutualism represents an ecologically, evolutionarily, and taxonomically rich spectrum of biological phenomena that remain in large part unexplored or even undescribed. By identifying the salient structural features of mutualistic interactions — both those features relevant to the nature of the interaction in real time and those relevant to the ontogeny of the mutualism on an evolutionary scale — we should ultimately be able to highlight relevant connections among these diverse systems. Moreover, we expect the diversity of mutualistic systems to manifest these various structural features in a multiplicity of combinations, creating a network of relationships whereby any pair of different mutualisms share some characters in common and differ in others. In Table 13.1, we list some of the key features that we consider to be important in determining the nature, outcome, and evolutionary history of mutualistic systems. Any one mutualism is characterized by a number of features from this list, and different pairs have different features in common (an ideal situation in which to take a comparative approach to understanding the consequences of game structure!)

In Table 13.2, we briefly summarize a few of the better-studied examples of mutualism and describe them in terms of combinations of the properties listed in Table 13.1. Among the various types of mutualism listed in Table 13.2, only in the shared-benefit mutualisms do all individuals, regardless of species, contribute the same good. In these mutualisms, there is not really a trading market (Bowles and Hammerstein, this volume; Bshary and Noë, this volume) at all, nor can a “price” or “exchange rate” be computed. Instead, these shared benefit mutualisms typically involve exchange (or production) of *information*. The laws governing information-sharing work differently from those governing the exchange of ordinary physical commodities, for information can be transferred to another without reducing that enjoyed by the donor (Lachmann et al. 2001).

CONCEPTUAL TOOLS AND FOUNDATIONS

In the field of intraspecific cooperation, theoretical foundations (e.g., Hamilton 1964; Trivers 1971; Axelrod and Hamilton 1981) developed alongside empirical observation and experimentation. The study of mutualism biology has had quite a different history; this history may in part explain the relation (or lack thereof!) between theory and empirical work in this area. The study of mutualism largely arose out of efforts to understand the elaborate natural histories of species pairs interacting to their mutual benefit (e.g., Buchner 1965; Janzen 1966). When theorists first began to take note of the “mutualism problem,” they brought with them a body of conceptual and mathematical models largely developed within other disciplines. The theory of reciprocal altruism, based largely on models of the iterated Prisoner’s Dilemma (PD) game, was an early colonist, having been imported from the study of intraspecific cooperation. More recently, a second wave of theoretical concepts — market theory and

Table 13.1 Key variables that differ across mutualisms.*Properties of the Game Payoffs*

1. Magnitude of benefits: The benefit that members of a given species reap from their participation in a mutualism can range from marginally greater than zero to an opposite extreme in which all fitness comes through the mutualism, as is the case for obligate mutualists.
2. Magnitude of investment: For each partner, investment can range from nothing to enormous; investments can be fixed at the onset of the interaction or variable across its course; investments can be symmetric or asymmetric between partners; investments can be concealed, revealed, or even extravagantly signaled.
3. Cost of being cheated: The consequences of a partner's defection range from negligible to fatal.
4. Potential for sanction: Some species may be able to impose substantial costs on their mutualist partners; others will have little opportunity to negatively influence their associates.

Availability of "Outside Options"

5. Obligacy: Mutualistic association can increase an individual's fitness from a baseline of zero (in obligate mutualisms) or from something greater than zero (in facultative mutualisms).
6. Specificity: Some mutualisms feature only one partner species for each species (species-specific mutualism); in others, partner species are substitutable such that any of a number of species may be able to step into a partner role (nonspecific mutualism).
7. Opportunity for choice: Partner choice can range from highly important to nonexistent.

Ecological Structure and Evolutionary Dynamics

8. Population structure: Partners may be clumped or spread evenly across the habitat; there may or may not be significant genetic structure across space.
9. Symmetry: Both obligacy and specialization can be symmetrical between partners or asymmetrical (e.g., obligate on one side, facultative on the other).
10. Duration of association: The durations of mutualistic associations can range from single-shot and fleeting encounters to life-long partnerships with highly iterated interactions.
11. Influence of third parties: Though typically modeled as dyadic interactions, mutualisms commonly involve third species that influence the outcome or magnitude of the mutualism. The third species may be responsible for raising (or even creating) the benefits of the mutualism. Alternatively, it may lower the benefits and/or stability of the mutualism by exploitation.
12. Evolutionary rate: Mutualist partners may have similar or widely divergent generation times and evolutionary rates.

a suite of related ideas — has been imported from the field of economics. In this section, we consider these and other conceptual foundations for understanding mutualistic interactions.

To understand the relations among these core concepts, we find it helpful to distinguish clearly between the structure of the pair formation, on one hand, and

Table 13.2 Well-studied empirical systems and some phenomena they exemplify.**Protection Mutualisms**

General features: Mutualistic only in the presence of third species (antagonists of one partner); protection traded for food

Examples:

- Cleaning: (Bshary and Noë, this volume): Generalized; facultative; extensive and reciprocal partner choice and partner-recognition mechanisms; high cognitive abilities; minimal investment
- Ant-tending of lycaenids (Bronstein, this volume; Leimar and Connor, this volume): Range from generalized to specialized, from obligate to facultative, from mutualistic to parasitic; partner recognition at least by ants; adaptively plastic reward production ranging from cheap to expensive

Similar mutualisms: Ant-tending of aphids, ant-tending of plants

Transportation Mutualisms

General features: Food traded for transport of self or gametes

Examples:

- Obligate pollination of yuccas (Bronstein, this volume): Symmetrically obligate and species-specific; high reward investment, fixed before onset of interaction; costly exploitation by mutualists and other species
- Generalized pollination: Varying symmetry of obligacy and specificity; reward investment fixed before outset of interaction; exploitation by mutualists and other species that varies widely in costs.

Similar mutualisms: Obligate pollination of figs; generalized seed dispersal

Nutrition Mutualisms

General features: Food traded for food/protection; often but not always symbiotic

Examples:

- Plant–mycorrhizal symbiosis: Varying symmetry of obligacy and specificity; can range from mutualistic to parasitic across species and across gradients of resource availability for individual species pairs; at least one-sided partner choice

Similar mutualisms: Plant–rhizobium symbiosis; light organ symbioses; gut symbioses

Shared-benefit Mutualisms

General features: Multispecies aggregations that benefit participants via shared vigilance or defense

Examples:

- Mixed-species foraging: Highly facultative and generalized; negligible investment; may involve more than two species simultaneously

Similar mutualisms: Müllerian mimicry complexes

the population-genetic structure in which mutualistic phenotypes and behaviors evolve, on the other. The former essentially concerns the number of separate classes or categories from which partnerships are assembled. Are mutualist

Table 13.3 Types of cooperative interaction.

<i>Partner Classes</i>	<i>Gene Pools</i>	<i>Example</i>
1	1	Coalition formation among baboons (Noë 1994)
2	1	Lazuli bunting “tenant” system (Bowles and Hammerstein, this volume) Biparental care (Clutton-Brock 1991)
1	2	Mixed flock aggregations (Lima 1995)
2	2	Cleaning mutualisms (Bshary and Noë, this volume) Protection mutualisms (Bronstein, this volume) Pollination mutualisms (Bronstein, this volume)

pairs composed of individuals paired from each of two mutually exclusive groups (e.g., mating pairs of one male and one female; cleaning mutualistic pairs composed of one cleaner species and one client species), or are they drawn from one homogeneous class (e.g., coalition partners taken from the set of all individuals in a population)? The structure of pair formation can play a significant role in determining the nature of the interaction as well as the structure and stability of the pairing (see e.g., the two-sided matching literature: Roth and Sotomayer 1990; Bergstrom and Real 2000).

We contrast this to the structure of the *gene pool* in which the cooperative strategies evolve. Do both partners belong to a common gene pool (as is the case in examples of intraspecific cooperation), or is each pair composed of one member from each of two separate populations (as is the case in interspecific mutualism)? This distinction can be crucial in determining the evolutionary dynamics by which strategies are ultimately selected. In Table 13.3, we summarize the possible combinations of pairing structure and gene pool structure, and provide biological examples of each combination. Four basic theoretical frameworks used to understand mutualism evolution are described below.

Reciprocity

As mentioned above, reciprocal altruism was an early — and largely unsuccessful — invader from intraspecific cooperation theory. In his treatment of reciprocity, Trivers (1971) gave a detailed account of cleaning symbiosis and argued that the phenomenon is likely to be an example of interspecific reciprocal altruism. Axelrod and Hamilton (1981) extended this theoretical stance, by applying the repeated PD game to interspecific interactions. In addition to cleaning symbiosis, Axelrod and Hamilton suggested a range of applications covering most of the general categories of mutualism listed in Table 13.2. Both Trivers (1971) and Axelrod and Hamilton (1981) stressed the importance of detecting and punishing cheaters: an individual must not be able to get away with defection without others being able to retaliate effectively.

The papers by Trivers (1971) and by Axelrod and Hamilton (1981) came to be regarded as providing a general conceptual foundation for the evolution of cooperation between unrelated individuals, between as well as within species. However, this position has in turn resulted in a growing discontent among biologists interested in the evolution of mutualism. The perceived weakness of the theory of reciprocal altruism is not that the logic of the arguments supporting it appear faulty, but rather that there appear to be few examples of reciprocal altruism that have held up to closer scrutiny (e.g., Bronstein, this volume; Bshary and Noë, this volume; Hammerstein, Chapter 5, this volume; Leimar and Connor, this volume). Thus, it would seem that Tit-for-Tat reciprocity is a logically feasible, but in practice marginal, form of interspecific cooperation.

By-product Effects and Pseudoreciprocity

Certain traits or behaviors that have evolved to benefit an individual directly might also benefit others, as a side effect of their primary function. For example, Müllerian mimics receive by-product benefits from one another, as members of one species “train” predators to avoid other similarly colored and similarly dangerous species as well. Such by-product benefits may have been instrumental for the evolutionary origin of many existing mutualisms (Connor 1995).

Nevertheless, all benefits of mutualism cannot be regarded as by-products of other activities. Many costly traits, such as nectar production, must be interpreted as investments that primarily benefit other organisms and, as suggested in the introduction, these are the traits that most desperately need to be explained by any successful evolutionary theory of mutualism.

Reciprocal altruism provides a candidate explanatory framework, but as we have noted it appears to have limited applicability. *Pseudoreciprocity*—that idea that investments in unrelated individuals have evolved to enhance by-product benefits obtained from these individuals—may be a more common explanation for both the origin and the maintenance of mutualistic associations. Investment in by-product benefits could have played a role for the origin of certain mutualisms. For example, Tilman (1978) discovered that ants that are attracted to extrafloral nectaries on black cherry trees reduced herbivore damage from caterpillars. Apparently, this reduction in herbivory was the by-product benefit that favored investment in the ants by the trees, in the form of nectar production. Such investment is likely to be of even greater importance for the further adaptive modification of mutualistic interactions, whether derived from by-product benefits or from initially parasitic interactions (Table 13.4). Leimar and Connor (this volume) argue that pseudoreciprocity should replace reciprocity as the dominant explanatory framework for the evolution of investments in unrelated individuals.

Markets and Partner Choice

The term “biological market” was introduced to highlight the commonalities among human economic markets, mating markets, and cooperation markets

Table 13.4 Mutualism may arise in different ways depending upon the nature of the benefits exchanged. Traits that have evolved to benefit an individual directly may produce incidental or *by-product* benefits for others; individuals may extract benefits at a cost to others (*purloined*), or individuals may *invest* in others at a cost to themselves. All mutualisms may originate with one or both parties receiving by-product benefits, yielding three different routes to mutualism (see text for discussion of the examples). If it were discovered that the origin of any mutualism fell into one of the three categories that does not include by-product benefits, including reciprocal altruism, **Prediction 3** (see text) would be falsified. Adapted from Connor (1995).

		Mutualist 2		
		<i>By-product</i>	<i>Purloined</i>	<i>Invested</i>
Mutualist 1	<i>By-product</i>	Müllerian mimicry	Origin of insect pollination mutualisms	Ant–black cherry tree
	<i>Purloined</i>		?	?
	<i>Invested</i>			? (Reciprocal altruism)

(Noë and Hammerstein 1994, 1995). In human markets, buyers are “choosy”: they seek out sellers who offer the best prices. This choosiness pressures sellers to compete with one another to offer lower prices, thus forming a crucial link between supply, demand, and the exchange ratio of commodities. As Bshary and Noë (this volume) illustrate for cleaner fish – client interactions, the same process and basic principles apply to nonhuman systems as well; market theory can be used to understand the flow of resources among any organisms that exchange commodities that they cannot take from one another by force.

The biological market approach has two major goals:

1. To explain adaptations in organisms involved in cooperation or mutualism that are due to “market selection,” i.e., that have evolved under the pressure of partner choice. The obvious parallel is the evolution of secondary sexual characters driven by mate choice.
2. To predict changes in exchange rates of commodities due to shifts in the supply and demand curves. Again, these dynamics have been well studied in the context of economics and sexual selection, but have received far less attention in the context of cooperation and mutualism.

Sanctions, Power, and Partner Control

Although the biological market analogy can be extremely useful, biological markets and their economic counterparts — at least as typically abstracted — differ from one another in important ways. In standard neoclassical economic theory, agents (e.g., buyers and sellers, employers and employees) are assumed

to be able to establish complete contracts. That is, individuals are able to make fully binding commitments regarding the terms of any exchange, and these commitments are enforceable at zero cost. By contrast, biological markets typically offer no analogous way of establishing binding and freely enforceable contracts.

In the absence of complete contracts, the participants in market exchanges have to bring about their desired outcomes by alternative means, for example, by the strategic use of rewards for fulfilling an agreement or punishment for failing to do so. The ability to make effective use of such strategic incentives is termed *power* in recent economic models designed to address situations such as labor agreements, in which contracts are not in practice complete (see Bowles and Hammerstein, this volume). In short, we can describe power as follows:

We say that agent A has *power* over agent B if A can gain advantage over B by threatening B with punishment, and B has no analogous counter-response.

With an example drawn from lazuli bunting mating systems, Bowles and Hammerstein (this volume) illustrate the way in which power can be exerted in biological systems. They find that in this system, models accounting for power relations better explain the division of benefits among participants than do models based upon biological markets with complete contracts (see also Bergstrom and Lachmann, this volume).

Models based on power can also account for observed inefficiencies in social equilibria among animals that cannot be explained in a simple biological markets framework. Bowles and Hammerstein (unpublished manuscript) stress that in biological markets *or* economic markets, when power is employed in lieu of complete contracts and neither party has absolute power, equilibrium outcomes will often be Pareto inefficient, because Pareto efficiency can often be obtained only through trade with enforceable contracts. Although, in principle, these ideas will apply to interspecific mutualisms, we stress that many current examples are drawn from intraspecific interactions: Bowles and Hammerstein examine the landlord-tenant system among lazuli bunting, Reuter and Keller (2001) predict this sort of inefficiency arising from the exercise of power in hymenopteran sex-ratio conflict, and of course the original economic theories were derived to explain human intraspecific behavior.

PREDICTIONS

In the previous section, we briefly surveyed the current suite of conceptual tools available to address the issues surrounding the evolution of mutualism. Each is appealing in its own way, but how do we know which of these tools are right for the job? How do we avoid driving nails with a screwdriver and turning bolts with a hammer? Conceptual constructs can prove their utility by helping us organize the facts that we already have collected, but often a stronger challenge can be brought to bear upon our conceptual foundations through direct contact between theory and empirical data (Hilborn and Mangel 1997).

To bring about such an encounter, one requires that the theory generate testable predictions. In this spirit, we offer (and briefly motivate) a set of such predictions here. Rather than hedging our bets in mortal terror of possibly being proven wrong at some future date, we have deliberately stated these predictions in strong forms that are more likely than their timorous counterparts both to generate debate and to collapse ultimately under the weight of an accumulated body of empirical evidence.

Prediction 1: Reciprocal altruism will never be observed in interspecific mutualism. Reciprocal altruism requires both the presence of adequate cognitive complexity to handle accounting and individual recognition as well as the absence of alternative mechanisms sufficient to enforce mutualistic behavior. We conjecture that this combination of circumstances will rarely, if ever, be present in the interspecies associations that spawn interspecies mutualisms.

Prediction 2: Among organisms with relatively well-developed cognitive systems, many by-product mutualisms are the results of learning rather than the results of adaptation for that particular interaction. Therefore, if one partner is replaced with some phylogenetically related and/or physiologically similar but typically nonsympatric species, the individuals involved will be able to establish mutually beneficial interactions despite the novelty of the partnership, and they will be able to do so on the timescale of individual lifetimes.

Prediction 3: All interspecific mutualisms began, evolutionarily, from an association with by-product benefits to at least one party. Some by-product benefits are necessary on at least one side in order to select for further development of the interspecific association.

Prediction 4: Most mutualisms neither require nor exhibit sanctioning behavior on the part of either partner. Partner choice and individually beneficial response to undercontributing partners will be sufficient to motivate and enforce cooperative behavior. Where mechanisms for imposing sanctions do exist, they will be co-opted rather than evolved directly as sanctions.

PUZZLES

Thus far in our understanding of mutualism, a number of observations remain baffling. Although, at this point, we cannot lay out a set of Hilbertian problems for the study of mutualism, we would like to suggest the following puzzles as possible areas of focus for future empirical and theoretical development.

Puzzle 1: Many mutualist partners appear to be quite poorly coadapted and poorly fine-tuned to profit maximally from the mutualistic interaction. This is surprising, given that opportunities for exploitation of mutualist partners appear to be plentiful (Leimar and Connor, this volume; Bronstein, this volume). How can we explain the limited success of mutualist partners in finding adaptive

solutions to the problem of extracting maximal resources from the interspecific interaction?

Puzzle 2: Why do adaptations for imposing sanctions on an interspecific mutualist partner appear to be so rare? Individuals commonly engage in self-interested behavior (e.g., switching partners when paired with a noncooperator), which has the side effect of imposing costs on an uncooperative partner. (Could we call this by-product punishment, in analogy to by-product mutualism?) However, we rarely find examples in which an individual regulates or manipulates the behavior of an interspecific partner behavior by actively imposing costs on the partner at a direct cost to itself. Are there basic theoretical reasons why such behaviors are unlikely to evolve, much as the evolution of intraspecific punishment presents a free-rider problem (Frank 1995)? Is partner choice and/or “by-product punishment” sufficiently effective such that selection is simply too weak to generate active sanctioning? Are we failing to observe active sanctioning behavior even though it *is* present in a considerable number of systems? Is sanctioning simply unnecessary, because the evolutionary process rarely generates the mutational combinations to produce variants capable of taking advantage of their partners?

Puzzle 3: Why are mutualisms so commonly exploited by third parties, and why do they so seldom have built-in mechanisms for the prevention of such exploitation? Is the answer to this question more or less the same as the answer to Puzzle 2, or is dealing with “exploitation from outside” a fundamentally different sort of evolutionary problem?

Puzzle 4: Mutualist partners often use signals to coordinate their actions and contributions. What mechanisms (if any) prevent the evolution or persistence of deceptive signaling strategies and the ultimate dissolution of the communication system? Should we expect these mechanisms to be similar to those involved in the maintenance of intraspecific honest signaling?

By way of closing this section, we should note that each of these puzzles challenges the reader to explain a claim or pattern derived from our current assessment of the body of empirical evidence. In any or all of these cases, the resolution may lie in further theoretical or conceptual development; alternatively, it is possible that our current assessment of the data is incorrect and that the patterns around which the puzzles are founded could prove to be unsupported. In either case, explicit theoretical models can serve to create the logical framework in which to organize these data and address these puzzles. We hope that these puzzles will serve to stimulate development of such models.

Model Systems and Experimental Tests

The field of mutualism biology has been blessed with a spectacular diversity of field systems. However, the flip side of this lucky coin is that the particular

systems that have received thorough attention thus far may be neither the most representative of mutualistic interactions in general (see Bronstein, this volume), nor the most tractable for observational and experimental study. Although no single system can capture the range of processes and phenomena observed across all mutualisms, the development of a small number of model systems could conceivably serve to accelerate progress in the field.

What makes a good model system? Clearly, this will depend on which questions one wishes to ask. In the study of nonobligate interspecific mutualism, we are often particularly interested in the consequences of the parameters listed in Table 13.1. Unfortunately, for most systems, many of these parameters either cannot be, or have not been, quantified. As a result, quantitative prediction will at best be difficult and at worst be a futile exercise in curve-fitting. We propose an alternative approach: Within a particular model system, one can manipulate these basic parameters and then observe the qualitative consequences. If one were interested in the role of partner choice on the frequency of punishment behavior, one could manipulate partner availability on each side of a facultative mutualism and measure the resulting changes in punishment frequency.

Another important consideration is the ability to perform experimental manipulations; potential model systems differ substantially in this respect. Some are more easily brought into the laboratory than others. Obligate mutualisms may be more difficult to manipulate broadly than facultative ones. Generation times, and thus the potential for experimental evolution, vary by orders of magnitude. So which systems would make good models? We propose two sets, corresponding to two timescales. Although this list is unavoidably biased toward the inclusion of the research systems that we know the best, we hope that it can nonetheless serve as a useful starting point.

Single-generation Experimental Manipulation

By observing short-term responses of species to changes in the behavior, condition, availability, and other characteristics of their mutualist partners, one can explore possible answers to some of the major questions with which this report began: How are mutualisms stabilized, and to what degree do species exhibit adaptive plasticity in their responses to the specific circumstances of the mutualism? However, a caveat is in order for studies of this kind. It will be crucial to work with a system that exhibits natural variation in the parameters that will be manipulated. Otherwise, one would not expect an evolved plasticity of response to be manifested by members of the population.

Possible model systems:

1. *Cleaner fish – client mutualism.* In this volume, Bshary and Noë describe the cleaner fish – client mutualism, a strong candidate for study on this timescale. The system has the notable advantage of being amenable to both field and laboratory study. Moreover, the relatively advanced

cognitive capabilities of the partners and evidence of extensive learning suggests that this system may be a particularly good place to study the role of cognitive function and learning mechanisms in the establishment and maintenance of mutualism.

2. *Ant–lycaenid systems.* Evolutionary associations between ants and lycaenid butterflies are some of the most extensive in terms of the number of species involved, with an estimated 4500 related species on the lepidopteran side spanning the range of symbiotic associations from parasitism through mutualism (Pierce 1987, 2001; Pierce et al. 2002; Bronstein, this volume) As such, this ensemble appears to be a particularly promising system for comparative research. Because of the huge number of species involved, this system also offers extraordinary potential for investigation of the underexplored relationships between phylogeny and mutualistic association; ongoing phylogenetic work by Pierce and colleagues will provide the necessary background for such investigations.

Experimental Evolution

Over the past decade, evolutionary biology has been deeply enriched by the development of procedures and model systems allowing the experimental study of evolution in real time in the laboratory. This approach would also seem to be highly promising for the study of mutualism. Mutualistic interactions, including biofilm formation, syntrophy, and various forms of environmental conditioning, appear to be common in bacterial communities. Moreover, recent evidence of interspecific bacterial signaling (Bassler 2002) strongly suggests coordinated mutualistic activity.

Possible model systems:

1. *Bacterial systems:* Several investigators have developed laboratory models of multispecies bacterial biofilms (see, e.g., Tolker-Nielsen and Molin 2000); these could serve as useful evolutionary models. Bacterial mutualisms — obligate or facultative — could also be constructed de novo. An artificial obligate mutualism could be created by knocking out complementary functions from two bacterial species so as to induce mutual dependence in certain selective environments. Such a protocol would allow the investigator to observe actually the initial steps in the ontology of mutualism and to explore the role of the gene transfer in the mutualism evolution. Moreover, biofilm systems are likely to provide useful insight into the population dynamics and regulation of mutualist partners.
2. *Bacterium–plasmid associations:* The interaction between bacteria and their semi-autonomous, horizontally transferred plasmid molecules may also merit consideration as a model system for the study of mutualism.

Unlike bacteriophages and other parasitic replicons, plasmids most likely enjoy a mutually beneficial relationship with their hosts. Current theory and empirical work suggests that plasmids persist in bacterial populations only when they actively benefit their hosts under at least some environmental conditions (Bergstrom et al. 2000). Bacteria and novel plasmids are known to exhibit rapid coevolution in response to one another's genetic makeup (Levin and Lenski 1983) and may also provide interesting models of fitness compensation or even "addiction" in the absence of beneficial effects (Levin et al. 2000).

Other promising potential systems include plant–rhizobium interactions (Denison 2000), cnidarian–algae symbioses (Baghdasarian and Muscatine 2000), and bacterial–insect (Moran 2001) or bacterial–nematode associations (Burnell and Stock 2000).

CONCLUSION: WHY STUDY MUTUALISM?

To date, the study of mutualism has proceeded largely out of a desire to explore the extraordinary natural histories of mutualist species and mutualistic associations. This remains a fascinating area, a rich and still proportionally uncharted territory. In addition, there are further reasons why the study of mutualism will serve to address important, basic issues in ecology and evolutionary biology.

First, the study of interspecific mutualistic associations offers the opportunity to explore the mechanisms — from sanctioning to partner choice to pseudoreciprocity — that maintain cooperative behavior even in the absence of kin selection. These mechanisms are likely to be of fundamental importance as guarantors of prosocial behavior not only in interspecific interactions throughout the tree of life, but also in the human (intraspecific) interactions among nonkin that are ubiquitous in large modern societies (McElreath et al., this volume; Henrich et al., this volume).

Second, many of the major transitions in evolution (Maynard Smith and Szathmáry 1995) have involved the formation of mutually beneficial associations that ultimately became new levels of organization. A more detailed understanding of the origin and ontogeny of interspecific mutualisms can further help our efforts to understand the most important occurrences in the history of life.

Third, the study of mutualism to date has focused on the dyadic relationship between partner–species pairs. Of course, each of these pairwise species interactions is in fact embedded in a larger community-level context. To understand the function of mutualistic systems *fully*, we will have to understand the community-level context as well. As such, the study of mutualism dynamics should stimulate the development of additional connections between ecological and evolutionary processes and timescales. Ultimately, studies of multispecies phenomena that build upon mutualism should have significance for conserving and restoring species in a rapidly changing world.

REFERENCES

- Axelrod, R., and W.D. Hamilton. 1981. The evolution of cooperation. *Science* **211**:1390–1396.
- Baghdasarian, G., and L. Muscatine. 2000. Preferential expulsion of dividing algal cells as a mechanism for regulating algal-cnidarian symbiosis. *Biol. Bull.* **199**:278–286.
- Bassler, B.L. 2002. Small talk: Cell-to-cell communication in bacteria. *Cell* **109**:421–424.
- Bergstrom, C.T., M. Lipsitch, and B.R. Levin. 2000. Natural selection, infectious transfer, and the existence conditions for bacterial plasmids. *Genetics* **155**: 1505–1519.
- Bergstrom, C.T., and L.A. Real. 2000. Toward a theory of mutual mate choice: Lessons from two-sided matching. *Evol. Ecol. Res.* **2**:493–508.
- Buchner, P. 1965. Endosymbiosis of Animals with Plant Microorganisms. rev. Engl. ed. New York: Interscience Publ.
- Burnell, A.M., and S.P. Stock. 2000. Heterorhabditis, Steinernema and their bacterial symbionts: Lethal pathogens of insects. *Nematology* **2**:31–41.
- Clutton-Brock, T.H. 1991. The Evolution of Parental Care. Monographs in Behavior and Ecology. Princeton, NJ: Princeton Univ. Press.
- Connor, R.C. 1995. The benefits of mutualism: A conceptual framework. *Biol. Rev.* **70**:427–457.
- Denison, R.F. 2000. Legume sanctions and the evolution of symbiotic cooperation by rhizobia. *Am. Nat.* **156**:567–576.
- Frank, S.A. 1995. Mutual policing and repression of competition in the evolution of cooperative groups. *Nature* **377**:520–522.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**:1–52.
- Hilborn, R., and M. Mangel. 1997. The Ecological Detective: Confronting Models with Data. Princeton, NJ: Princeton Univ. Press.
- Janzen, D.H. 1966. Coevolution of mutualism between ants and acacias in Central America. *Evolution* **20**:249–275.
- Lachmann, M., S. Szamado, and C.T. Bergstrom. 2001. Cost and conflict in animal signals and human language. *Proc. Natl. Acad. Sci. USA* **98**:13,189–13,194.
- Levin, B.R., and R.E. Lenski. 1983. Coevolution in bacteria and their viruses and plasmids. In: Coevolution, ed. J. Futuyama and M. Slatkin, chap. 5, pp. 99–127. Sunderland, MA: Sinauer Associates.
- Levin, B.R., V. Perrot, and N.W. Walker. 2000. Compensatory mutations and the population genetics of adaptive evolution in asexual populations. *Genetics* **154**: 985–997.
- Lima, S.L. 1995. Collective detection of predatory attack by social foragers: Fraught with ambiguity? *Anim. Behav.* **50**:1097–1108.
- Maynard Smith, J., and E. Szathmáry. 1995. The Major Transitions in Evolution. Oxford: Oxford Univ. Press.
- Moran, N.A. 2001. The coevolution of bacterial endosymbionts and phloem-feeding insects. *Ann. Missouri Bot. Gard.* **88**:35–44.
- Noë, R. 1994. A model of coalition formation among male baboons with fighting ability as the crucial parameter. *Anim. Behav.* **47**:211–213.
- Noë, R., and P. Hammerstein. 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav. Ecol. Sociobiol.* **35**:1–11.

- Noë, R., and P. Hammerstein. 1995. Biological markets. *Trends Ecol. Evol.* **10**:336–339.
- Pierce, N.E. 1987. The evolution and biogeography of associations between lycaenid butterflies and ants. In: *Oxford Surveys in Evolutionary Biology*, ed. P.H. Harvey and L. Partridge, vol. 4, pp. 89–116. Oxford: Oxford Univ. Press.
- Pierce, N.E. 2001. Peeling the onion: Symbioses between ants and blue butterflies. In: *Model Systems in Behavioral Ecology*, ed. L.A. Dugatkin, pp. 41–56. Princeton, NJ: Princeton Univ. Press.
- Pierce, N.E., M.F. Braby, A. Heath et al. 2002. The ecology and evolution of ant association in the lycaenidae Lepidoptera. *Ann. Rev. Entomol.* **47**:733–771.
- Reuter, M., and L. Keller. 2001. Sex ratio conflict and worker production in eusocial hymenoptera. *Am. Nat.* **158**:166–177.
- Roth, A.E., and M.A.O. Sotomayer. 1990. *Two-sided Matching*. Cambridge: Cambridge Univ. Press.
- Tilman, D. 1978. Cherries, ants and tent caterpillars: Timing of nectar production in relation to susceptibility of caterpillars to ant predation. *Ecology* **59**:686–692.
- Tolker-Nielsen, T., and S. Molin. 2000. Spatial organization of microbial biofilm communities. *Microb. Ecol.* **40**:75–84.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *Qtlly. Rev. Biol.* **46**:35–57.