

# 11

## By-product Benefits, Reciprocity, and Pseudoreciprocity in Mutualism

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### ABSTRACT

The concepts of by-product mutualism and reciprocal altruism have played important roles for theories of mutualistic interactions between unrelated organisms. By-product mutualism could explain the evolution of traits that primarily benefit their bearer and benefit other individuals as a side effect, whereas reciprocity could explain the evolution of traits that entail costly investments in other individuals. The concept of pseudoreciprocity — in which an individual invests in another to acquire or enhance by-product benefits obtained from that individual — is an alternative theory of the evolution of investment in unrelated individuals. Such pseudoreciprocity represents an important category of cooperation and may well be the main explanation for existing examples of investment in unrelated organisms. A reason for the prevalence of pseudoreciprocity, particularly in comparison with reciprocity, could be that there are many ways in which investments can yield by-product benefits, so that there will be many opportunities for the evolution of such investment from a noninvesting state.

### INTRODUCTION

For mutualistic interactions between unrelated organisms, including members of different species, a useful starting point for evolutionary analysis is that traits influencing the interaction can evolve only if they are advantageous for their bearers. There is a multitude of ways in which an advantage can be gained — some direct and others operating indirectly through an influence on other organisms — and there will be a corresponding richness in the types of interaction. An evolutionary theory of such interactions should focus on traits that play a role for the interaction; the net fitness effects, which form the basis for classification into

mutualism or parasitism, are less important for theoretical understanding. Nevertheless, there is scope for an evolutionary theory of traits that sometimes promote mutual benefit. A central issue for such a theory must be the evolution of traits that can benefit others.

There are several ways in which an individual could derive benefit from interacting with an unrelated organism (Table 11.1) (cf. Connor 1995). The transfer of benefit to the individual could primarily be the result of traits of the other organism. These characteristics of the other organism might be adaptations for generally benefiting the individual, provided that there is an element of common interest. For instance, if partners tend to succeed or fail together, there can be an incentive for investing in a partner's success, at least to some extent. In other cases it may be more appropriate to regard the transfer of benefit either as a means by the other organism to influence the behavior of the individual — perhaps attracting the individual with a food reward — or as a side effect of characteristics that are adaptive for the organism for other reasons. The transfer of benefit could also be a consequence of adaptations in the benefiting individual. In the latter case, the individual can be thought of as exploiting some characteristic of the other organism.

Our aim here is to examine and exemplify a number of concepts that are important for the evolutionary analysis of traits that play a role in providing benefit for others. In much previous work, two ideas stand out as having been particularly influential: that benefits to others may be by-products of traits or behaviors that directly benefit the individual itself (West-Eberhard 1975; Brown 1983) and that mechanisms of reciprocity could support the evolutionary stability of investing in a partner (Trivers 1971; Axelrod and Hamilton 1981). An important

**Table 11.1** Classification of benefits in mutualistic interactions.\*

Category	Description
invested benefits	An individual benefits as a consequence of traits in another, which traits have evolved for the purpose of influencing the individual in a way that has been advantageous for the other.
by-product benefits	An individual benefits as a consequence of traits in another, which traits have <i>not</i> evolved for the purpose of influencing the individual, but may instead have been advantageous for other reasons.
purloined benefits	An individual obtains a benefit from another as a consequence of its own traits, which traits have evolved for the purpose of obtaining this benefit from the other.

\*The classification emphasizes the selective background of traits and is highly idealized in ascribing simple functions to traits that may in reality have a more complex selective background, for instance because benefits appear as a consequence of the interaction of traits in different individuals.

distinction is that by-product mutualism appears not to explain traits that primarily benefit others, whereas such traits might be consistent with reciprocity. A tempting but incorrect conclusion is then that examples of investments in unrelated individuals ought to be examples of reciprocity. Instead, there is also the possibility that an individual invests in another because this would enhance the by-product benefits obtained from the other. This type of interaction has been called pseudoreciprocity (Connor 1986, 1995) and could be one of the main explanations for the occurrence of investments in unrelated individuals.

An entirely hypothetical illustration of pseudoreciprocity is as follows (Connor 1986): a bird whose nest is in a hot, sunlit area spends some time and effort “fertilizing” a nearby bush, causing the bush to grow taller and shade the bird’s nest. The bird has then performed a beneficent act for the bush, but the bush has not performed a beneficent act for the bird in return. Rather, the bird’s return benefit is an incidental effect or by-product of a self-promoting act (growth) on the part of the bush.

The suggestion that pseudoreciprocity is a major category of cooperation has been strongly criticized (Mesterton-Gibbons and Dugatkin 1992, 1997) on the grounds that it would be a redundant category and an unnecessary complication of the fundamental division into by-product mutualism and reciprocity. Here, we counter this criticism and argue that pseudoreciprocity and, more generally, the concept of investment in by-product benefits play natural and important roles when applying basic ideas of adaptation to the phenomenon of mutualism. In addition to providing an understanding of the evolution of investments in interspecific mutualisms, pseudoreciprocity may also be operating in intraspecific interactions, for instance in cooperatively breeding animals where helpers may gain by recruiting additional group members, and in some mating systems where sperm competition provides an incentive for males to transfer nuptial gifts to females at mating.

## **THE EVOLUTION OF INVESTMENT IN UNRELATED INDIVIDUALS**

The general procedure for determining whether some characteristic is an adaptation, and for what function it then has been adapted, is to identify the circumstances, either in the past or at the present time, that selected for the appearance or maintenance of the characteristic (Futuyma 1998). Let us apply this to traits entailing investment in unrelated individuals and entailing direct costs for the investing individual. If an individual would benefit in some way from the presence of another organism, it is clear that an investment in increasing the organism’s survival could be adaptive. Another general and important circumstance favoring investment would be the presence of behavioral mechanisms or plastic phenotypes in other organisms that make them respond to investment in a way that becomes favorable for the investing individual. The hypothetical example

of the fertilization–growth response in the bush is one such mechanism. There are many others, for example, the propensity of potentially beneficial visitors, like pollinators, to be attracted by rewards.

### **Reciprocity as an Adaptation**

Although there is no universally agreed upon definition of reciprocity, an unambiguous case would be unilateral investment by one individual in another on one occasion, followed by a reverse investment on a clearly separate occasion, and so on in an alternating fashion (Trivers 1971). Usually, one would also include situations showing similarity to the play of Tit-for-Tat in a two-person repeated Prisoner's Dilemma game (PD) (Axelrod and Hamilton 1981). If the investments are concurrent, ongoing activities that are regulated by some sort of bookkeeping mechanism, i.e., a mechanism serving to regulate current investment based on benefits received and previous investments, it may be preferable to speak of trading rather than reciprocity, since it may not be possible to identify any discrete "chunks" of investment that are reciprocated. In either case, whether there is ideal reciprocity or just some form of trading, investing in the partner could be viewed as an adaptation to a behavioral mechanism in the partner, namely the partner's tendency to deliver returns in proportion to the investment. Note that there may also be other situations where two organisms invest in each other, and these investments are adaptations to behavioral mechanisms in the partner, but where the mechanisms are different from bookkeeping. For instance, each organism could invest in by-product benefits from the other (Connor 1995). For mobile organisms, behaviors such as abandoning an unproductive partner but staying with a sufficiently productive one, which is not really bookkeeping, can also promote investment, provided there is some cost of partner switching (e.g., Friedman and Hammerstein 1991; Connor 1992; Enquist and Leimar 1993).

Strictly from the point of view of evolutionary game theory, the perspective above would seem incomplete, because the requirement that investment is an adaptation to a mechanism in the partner is only part of a demonstration of evolutionary stability. Thus, one might also require that each individual's behavioral mechanism is an adaptation to the circumstances of the interaction and, even further, that it is an optimal adaptation, in order to say, for instance, that there is adaptive reciprocity. The Tit-for-Tat strategy for the repeated PD game cannot be regarded as an adaptation in this sense (Selten and Hammerstein 1984). However, with random errors in the execution of investments, strategies based on "good standing" can be optimal adaptations (Boyd 1989); similar kinds of strategies can be optimal adaptations when there is random variation in the ability to perform investment or in the partner's need for the investment (Leimar 1997). Nevertheless, when thinking about the characteristics of real

organisms, it seems wise to be somewhat more lenient in one's requirements to avoid falling into the trap of extreme adaptationism.

### **A General Definition of Pseudoreciprocity**

The term pseudoreciprocity was originally applied to situations where one individual invests to acquire or enhance by-product benefits from the other, but where there is no similar investment in the other direction (Connor 1986, 1995). It seems rather natural to broaden the definition of the term to also include cases where each party invests in by-product benefits from the other (such relationships were classified as by-product investment – by-product investment in Connor 1995). Thus, the term pseudoreciprocity could cover any mutualistic interaction where there are investments in by-product benefits. This usage has the advantage of making pseudoreciprocity a main competing alternative to reciprocity and trading as an explanation for mutualistic relationships with costly investments in unrelated individuals.

### **Pseudoreciprocity and Evolutionary Stability**

When an individual invests in by-product benefits from another organism, the traits of the other organism that produce the by-product benefits need not be adaptations for the particular circumstances of the interaction. Thus, in the bird-bush example, the growth response of the bush need not be an adaptation for interacting with fertilizing birds but might just be a plastic response to variation in the availability of nutrients that has evolved independently of any interactions with birds. The example illustrates that pseudoreciprocity could evolve through adaptation of only one of the parties of the interaction. In such a case, one would not expect complete evolutionary stability. Although the organism producing the by-product effect would tend to benefit from its own response, the response would not be adaptively fine-tuned to the particular situation. The fact that pseudoreciprocity identifies only the minimal circumstances for investment in others to evolve should be seen as an advantage of the concept because this gives it a potentially broad range of application.

Pseudoreciprocity can, of course, also be an evolutionarily stable strategy (ESS). The analysis is particularly simple if an interaction can be modeled as a sequence of two unambiguous steps: an initial investment by one individual, followed by the response of the other. In such a case, backward induction can be used to determine evolutionary stability. For an ongoing or repeated interaction, the issue of evolutionary stability becomes more delicate if one allows for the possibility that the organism receiving investment might adjust its response in a way that leads to increased investment. Thus, the bush in our example might do better by growing more laterally before increasing its height, in this way forcing the bird to perform greater fertilization to achieve the desired shade. Just as in

any other interaction between unrelated individuals with little common interest, there is always the possibility that various means of exploitation evolve.

### **Is Pseudoreciprocity a Case of By-product Mutualism?**

According to Mesterton-Gibbons and Dugatkin (1992, p. 278; 1997, p. 556), “pseudoreciprocity, in which one individual manipulates another for the benefit of both, ... is simply asymmetric by-product mutualism (with asymmetry caused by sequential action).” It is, of course, true that the individual’s investment in another is ultimately self-serving, so that the fitness effect on the other individual can in this sense be regarded as a by-product. Similar things can be said about any adaptation with fitness effects on others, including reciprocity, which thus has no particular status in this regard. However, when discussing the transfer of benefits between unrelated individuals, it is of basic interest to identify the circumstances under which investing in another organism can be an adaptation. Investments in by-product benefits, which pseudoreciprocity entails, correspond to a broad set of such circumstances and may apply to many existing mutualistic interactions, making it an important concept.

## **EXAMPLES OF INVESTMENT IN BY-PRODUCT BENEFITS**

Activities such as seeking nourishment and shelter are ubiquitous among animals. This may be a reason why cases of investment in by-product benefits often follow the pattern of “hosts” offering food or shelter to “visitors,” in this way gaining by-product benefits from the visits (Cushman and Beattie 1991). The benefits can, for instance, be that visitors act to defend their food source or shelter against enemies of the host. In the following, we use the mutualism between lycaenid larvae and ants to illustrate this kind of interaction. For interactions within species, the host–visitor situation is less common; however, there are other possibilities for investment in by-product benefits. We discuss helping at the nest and nuptial gift giving as examples that may be interpreted in this way.

### **Interactions between Lycaenid Larvae and Ants**

The Lycaenidae is a large family of butterflies that contains the blues, coppers, and hairstreaks. A considerable proportion of the over six thousand lycaenid species associate with ants during parts of the life cycle, most commonly during the larval stage (reviewed in Pierce 1987; Fiedler 1991; Pierce et al. 2002). A small minority of the associations are clearly parasitic, with lycaenid larvae either being predators on ant brood or acting as cuckoos inside ant nests. The majority of the associations are usually considered mutualistic and are based on nutritional rewards delivered by lycaenid larvae in exchange for protective benefits of ant attendance. The interactions typically take place on the larval host

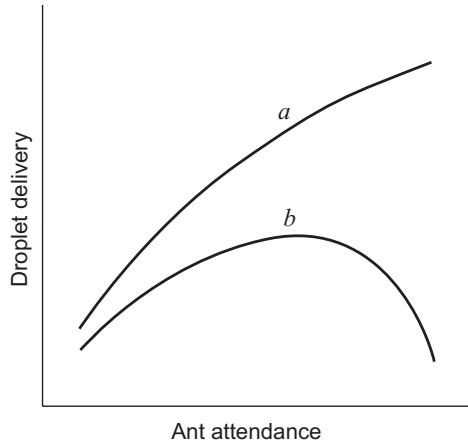
plant. Lycaenid larvae possess—in varying degrees—a suite of adaptations for influencing ant behavior. The most important of these adaptations may be the so-called dorsal nectar organ, which is a gland situated dorsally on the seventh abdominal segment of a larva and which is capable of secreting a nutritious liquid, packaged into discrete droplets. The delivery of droplets is stimulated by ant attendance and causes the ants to treat a larva as a food source to be defended against possibly competing intruders. As a result, a larva's mortality rate from attacks by invertebrate predators and parasitoids is reduced. For some lycaenid species, larvae in the field have only a small or no chance of surviving into adulthood without ant protection, making ant association an obligate relationship, whereas other species have a looser, facultative association with ants.

The lycaenid–ant relationship seems to be a case of pseudoreciprocity, in which lycaenid larvae invest in food rewards and receive the by-product benefits of ant defence. The ant defence should be regarded as a by-product because it is typical of ant behavior vis-à-vis any food source. Some enemies of a larva, such as predatory insects, would also be enemies of the ants, since these predators will remove the food source. The most important enemies of lycaenid larvae are likely to be parasitoids, which lay eggs that hatch into parasitic larvae that grow inside and eventually kill the butterfly larva, often around the time it pupates. The parasitoids are not really enemies of the ants, since they seem not to interfere with a lycaenid larva's ability to deliver food rewards. The reason the ants still protect lycaenid larvae from parasitoids is probably that ants attack more or less any type of seeming intruder.

### **Behavioral Mechanisms of Lycaenid Larvae and Attending Ants**

Looking more closely at the behavioral mechanisms regulating lycaenid–ant interactions, the overall impression is that lycaenid adaptations serve to control the number of attending ants to a level that corresponds to a larva's need for protection. For instance, lycaenid larvae tend to deliver more droplets as a response to higher ant attendance; however, for species that are not completely dependent on ants for survival, this relationship holds only up to a moderate degree of attendance, after which the delivery rate of rewards either levels off or decreases with increasing attendance (Figure 11.1) (Leimar and Axén 1993; Fiedler and Hageman 1995; Fiedler and Hummel 1995; Axén et al. 1996; Axén and Pierce 1998). As a result, more ants will attend larvae with greater need for ant protection. For ant allocation of workers to a food source, the general principle is that more workers will be allocated to a richer source (Figure 11.2) (Crawford and Rissing 1983). Joint operation of the lycaenid and ant behavioral mechanisms (Figures 11.1, 11.2) will then determine the delivery of reward and level of ant attendance in a given situation. This outcome should be regarded as a dynamic balance that adjusts itself over a period of a few minutes (Axén et al. 1996).

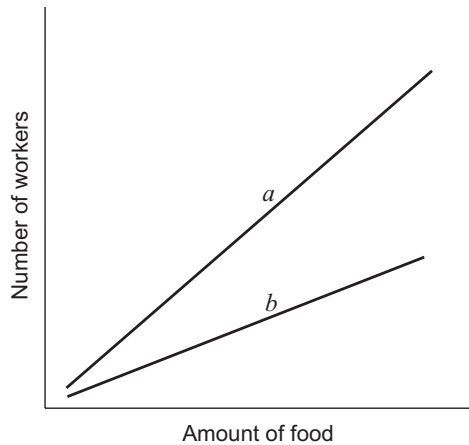
This picture is complicated by a situation that leads us to believe that ants often allocate more workers to lycaenid larvae than would in principle be needed



**Figure 11.1** Schema of a lycaenid larva's rate of reward delivery as a function of ant attendance. Curve (a) encourages a high level of attendance and could be a lycaenid species with strong dependence on ant protection. For curve (b), which could correspond to a species less dependent on ants, the ants ought not to allocate very many workers to the larva, since this decreases the rewards. Note that the curves depict a hypothetical steady state situation under some given circumstances. Other factors influence droplet delivery in addition to the average level of ant attendance, e.g., a larva's age and the quality of its diet.

to collect the nutritious reward. When several ants tend a larva, most of them are not retrieving droplets but are standing or walking either on the larva or next to it, while sometimes palpating it with their antennae. Assuming—for the sake of the argument—that ant behavior has been adapted for efficient handling of lycaenid larvae, these “extra” workers could play the role of an investment by the ant colony, serving to stimulate a larva to increase its rate of reward delivery. At least for certain ranges of investment, the combination of ant and larval behavioral mechanisms would then show some similarity to bookkeeping (see Figures 11.1 and 11.2; cf. Leimar 1997). Another explanation for the “extra” workers is that they are there to defend the colony's food source. Since tending ant species are not known to allocate such extra workers to other types of food sources, this latter explanation is perhaps unlikely. In either case, the benefit to lycaenid larvae of ant defence would be a by-product of normal ant behavior.

The assumption that ant behavior is well adapted to the handling of lycaenid larvae is, however, rather doubtful. It may well be that lycaenid larvae—through skillful interference with the chemical communication system of the ants—manage to manipulate the ants into overestimating their value as food sources. There are also several ways in which ants could increase the average rate of reward delivery of a larva, but which they seldom use. It has been found that a larva will sharply increase its delivery of droplets when it perceives itself to be under attack from enemies or when ants return to it after an interruption in attendance (Leimar and Axén 1993; Axén et al. 1996; Agrawal and Fordyce



**Figure 11.2** An ant colony's allocation of workers as a function of the rate of delivery of a food source. For efficient (ideal free) foraging, one would expect the allocation of workers to be directly proportional to the rate of delivery. This will hold over small additional food sources that are simultaneously available at equivalent positions near the colony. The allocation of workers per amount of resource will also depend on factors like the colony state (e.g., the level of "hunger"), the overall availability of food sources, the distance from the food source to the colony, and the time of day. For instance, line (a) could correspond to a situation where the colony has a strong need for the particular resource (e.g., carbohydrates vs. protein) and line (b) to a situation with less intense need. A number of aspects of ant behavior will jointly determine the allocation of workers illustrated in the figure, for instance the individual worker's tendency to deposit trail pheromones when returning from the food source — which is influenced by how readily she was able to obtain her load — and the degree of "enthusiasm" with which she is met when she hands over her load to nest mates inside the colony.

2000). Thus, if ants "attack" a larva occasionally or leave it unattended for a few minutes and then return, they would substantially increase their benefits.

If allocating too many workers to lycaenid larvae in fact hurts a colony, the interaction would be a case of parasitism. However, if the ants still benefit from the interaction and the larvae actually need the protection, the larval investment and ant protection would be pseudoreciprocity. Since ecological conditions like the food abundance for ants and the population densities of enemies of lycaenid larvae may fluctuate in time and space, the nature of the lycaenid–ant interaction may also vary from mutualism to parasitism (cf. Bronstein 1994).

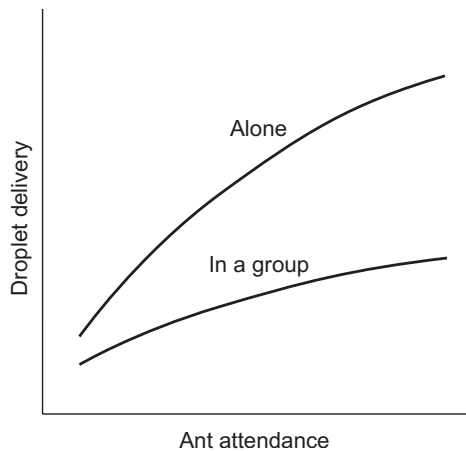
### Markets and Investment

A situation where hosts invest to attract visitors can be likened to a market where hosts supply a commodity for which there is demand among the visitors. One might then expect the evolutionarily stable level of host investment to be influenced by "market forces" (Noë and Hammerstein 1994, 1995). Examples of

such market forces are the relative population sizes of hosts and visitors as well as the availability of alternative commodities for the visitors. The host–visitor association could still be described as pseudoreciprocity, but the relationship between supply and demand would influence the evolution of investment. One might even argue that the market situation provides a very basic explanation for the presence and the magnitude of investment.

Several issues make the matter more complex. Visitors could be attracted by traits that do not directly benefit them but only signal the presence of reward. Competition for visitors might then just increase investment in advertisement, perhaps even at the expense of investment in reward, as might be the case in flowers lacking nectar. The by-product benefits of the visits could also be shared among a group of hosts, for instance among neighbors, resulting in decreased investment by the hosts (“tragedy of the commons”).

Lycaenid–ant interactions provide an example. The larvae of some lycaenid species occur in aggregations, and these species invariably associate with ants. Pierce et al. (1987) have suggested that group living could be a way for the larvae to increase the protection from ant attendance and/or to decrease the cost of the association. In a series of experiments, Axén and Pierce (1998) demonstrated that larvae of the group-living lycaenid *Jalmenus evagoras* modify the rate of reward delivery as a function of group size. A solitary larva secretes considerably more droplets than a group member (when controlling for the number of ants directly attending the larva; see Figure 11.3). A likely explanation is that a larva will, to some extent, be protected by the presence of ants on other group members. The reason why the rate of secretion does not drop to zero may be that a larva needs some directly attending ants, which can alert other nearby ants in



**Figure 11.3** Illustration of a normally group-living lycaenid larva’s rate of reward delivery as a function of per capita ant attendance, in two different situations. The rate of delivery is considerably higher when the larva happens to be alone compared to when it is in a larval group.

case of danger. Another reason could be that the larvae in a group are related; however, since several females oviposit on the same host plant and the larvae move about on the plant, the within-group relatedness is probably not so high (Pierce et al. 1987). From the point of view of the ants, the larval aggregations seem disadvantageous. Axén and Pierce (1998) estimated that ants would nearly triple their rewards if they were to break up naturally occurring aggregations into singletons (but the ants do not attempt this). The study indicates that larvae do not compete for ant attendance within a group. Nevertheless, larvae have to compete with other food sources of the ants, which could be other larval groups. For instance, the reason a singleton larva delivers more droplets should be to attract enough ants away from foraging elsewhere. The idea of a market (Noë and Hammerstein 1994, 1995), at least within the home range of a single ant colony, thus seems valid.

### **Intraspecific Helping at the Nest**

Several authors have suggested that subordinates in communally breeding birds and mammals might “help at the nest” because of benefits received later when the subordinate becomes a breeder and the young it helped have survived to engage in anti-predator behavior, territorial defence, or feeding the former helper’s offspring (Woolfenden 1975; Brown 1978, 1983; Rood 1978; Clutton-Brock 2002). As noted by Connor (1986), this would make helping at the nest a candidate for intraspecific pseudoreciprocity. Connor (1986) also pointed out that selection would not favor helping to promote the survival of young that help in return unless helping is already favored by kin selection, or there are return benefits that derive from nonhelping behaviors (e.g., territorial defence). In either case, there would be by-product benefits from the presence of additional group members acting in their own interest. A recent formal model of cooperative breeding and group augmentation by Kokko et al. (2001) substantiates this. They found that helping was readily favored with “passive group augmentation,” i.e., return benefits from territorial defence, etc. When there was only “active group augmentation,” i.e., return benefits only from active helping, Kokko et al. (2001) concluded that helping must occur initially for other reasons (e.g., helping kin) before selection would favor helping to augment group size.

### **Pseudoreciprocity in Insect Mating Systems**

Mating effort can sometimes represent an investment in by-product benefits (Connor 1986). An example could be the nutritious “nuptial gifts” that are part of male mating effort in certain insects (Boggs 1990). The gift is transferred to the female at mating and may increase her reproductive output. Nuptial gifts could function to increase a male’s chances of acquiring matings, but they could also function as investments in a male’s own offspring or devices to increase a male’s success in sperm competition. In insect groups where nuptial gifts are

part of the male ejaculate, there is no effect on the probability of mating; however, the relative importance of investment in the male's own offspring versus sperm competition has been debated. For butterflies, where the issue has been studied experimentally (Wiklund et al. 1993), it appears that nuptial gifts partly represent an investment in eggs that the male will fertilize and partly serve to increase the male's sperm competition success. Butterfly sperm competition is characterized by last male advantage, meaning that the male that most recently copulated with a female will fertilize most eggs laid by her, up to the time she mates again. The importance of nutritious ejaculates for sperm competition is that a female will wait longer until remating if she receives a larger gift (Kaitala and Wiklund 1995), and thus will lay more eggs fathered by the male. In this way, a larger investment serves to increase the male's success in sperm competition. For a female, the delay in remating after receiving a larger nuptial gift is directly in her own interest. Females in species with nuptial gifts can be said to forage for matings (Kaitala and Wiklund 1994) to increase their own reproductive output. Since there will be a limit on the rate at which a female processes the resources in gifts, it will be in the female's interest to vary the intervals between matings in proportion to the resources received. Only part of the resources in a male's ejaculate will find their way into eggs fertilized by the male; the remainder will provision eggs that are fertilized by other males (Wiklund et al. 1993). The overall conclusion is then that males invest partly in their own offspring and partly in by-product benefits from female reproductive behavior. The relative importance of these two factors for the evolution of male investment is, however, not known. Nevertheless, it seems likely that pseudoreciprocity plays an important role in certain insect mating systems.

## MUTUAL INVESTMENTS

For cases where there are clear investments from both sides of a relationship, and only a limited degree of common interest, it is of interest to determine for what function the investments are adaptations. Some form of bookkeeping is, of course, a possibility but may be unusual. The return benefits of an investment could come about in many other ways, more resembling by-product benefits than bookkeeping.

### **Mycorrhizal Symbiosis and Investment in By-product Benefits**

The majority of the species of vascular plants form mycorrhiza with fungal mycelium in the soil (Smith and Read 1997). It is thought that this association was instrumental for the original colonization of land by plants more than 400 million years ago (Simon et al. 1993). The association is based on transport of organic carbon from plant photosynthesis to the fungal partner as well as a transport of soil mineral nutrients, such as like phosphorus, from fungus to plant.

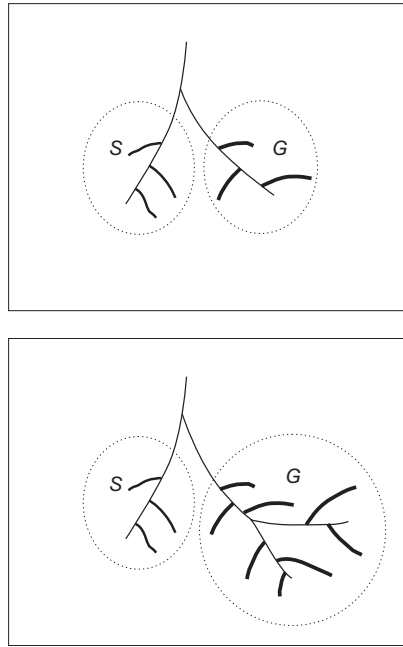
The physiology and molecular biology of the interaction are quite complex and not yet completely understood for any of the various types of mycorrhiza (Smith and Read 1997). However, barring some examples of parasitism, it seems likely that mycorrhizal symbiosis is a case of mutual investment of plant and fungus in each other. The transport of molecules — of organic carbon by the plant and of mineral nutrients by the fungus — to the site of contact between the organisms, across a plasma membrane to a so-called interfacial apoplast, where the partner can extract the molecules, is a process that involves the expression of several genes of both plant and fungus (Harrison 1999).

Many mycorrhizal fungi depend obligately on plants, and most plants benefit from mycorrhizal interactions, although they can grow without them. If a single plant interacted with a single fungus, their mutual investments could be explained by common interest in a “team project” of joint growth. In reality, plants often interact with several mycelial networks, corresponding to different fungi, and each of these networks may be connected to several plants. Thus, a plant can perhaps avoid investing in a fungus and still draw benefit from it if the fungus is maintained by other plants, and vice versa for the fungus. This might severely limit the evolution of investment on both sides, in a way analogous to the “tragedy of the commons.”

One could speculate that some kind of bookkeeping, localized to a single mycorrhizal site of interaction, would maintain the investments. There is, however, no evidence for any such trading mechanism. On the contrary, there are reasons to doubt that the interaction works in this way. A common observation is that a young seedling plant can benefit from being surrounded by mature plants, because the seedling can draw nutrients from a hyphal network that is being maintained by the mature plants (Smith and Read 1997). Thus, it seems that it is quite possible for a plant to receive nutrients without “paying for them.”

It is perhaps more likely that by-product benefits play a role in maintaining the investments. One potentially important factor is that the plant–fungus interaction takes place in a dynamical and spatial setting, where roots grow and senesce and where different fungal mycelia compete with each other for access to plants. For instance, a fungus could invest in a plant to stimulate additional root growth, which the fungus will be in a good position to colonize (Figure 11.4). It is known that root growth can be plastic, resembling foraging for elevated nutrient concentrations in the soil (Robinson 1994). This kind of response is particularly strong for non-mycorrhizal plants, where roots absorb the nutrients directly, and it is less pronounced when fungal hyphae of mycorrhizal symbionts instead explore the soil. Nevertheless, the roots of mycorrhizal plants also respond to nutrients (e.g., Jackson et al. 1990), so that local root growth as a by-product benefit of fungal investment is a reasonable hypothesis.

Competition between mycorrhizal fungi could also be responsible for by-product effects of plant investment. In an experiment with the Scots pine, Saikkonen et al. (1999) found that defoliation of a tree led to a changed composition of mycorrhizal associates. Since defoliation reduces a plant’s ability to



**Figure 11.4** Local root growth is a possible by-product benefit of fungal investment in a plant. The top panel shows a hypothetical situation where two fungi have colonized different parts of a growing root. One fungus (S) is “stingy” and contributes few nutrients to the plant, whereas the other fungus (G) is more “generous.” Assuming that the plant will allocate root growth primarily to those parts of the root that are successful in collecting nutrients, the investing fungus may have a competitive advantage (because of spatial proximity) in attempting to colonize new parts of the root. As shown in the bottom panel, the investing fungus might then form mycorrhiza with a greater proportion of the root, and thus enjoy the benefit of a greater proportion of the flow of carbon from the plant.

photosynthesize, the response was interpreted as an outcome of competition between fungal types with different carbon demands. This interpretation by Saikkonen et al. (1999) implies that a plant’s level of photosynthate investment in associated fungi has the effect of a choice of fungal partner. Provided that a more “expensive” partner gives better returns to a plant that can “afford” this partner, there may thus be an incentive for the plant to invest in giving such a partner a competitive advantage.

### **BY-PRODUCT MUTUALISM AND COORDINATION**

In by-product mutualism, there is little or no investment in other organisms, and the transfer of benefit is a side effect of traits that are present for other reasons, for instance, for providing direct benefit to their bearer. This concept of by-product mutualism can be elaborated by noting that there may be traits that benefit

their bearer directly, but which have been selectively modified because of feedback of fitness effects from an influence on the behavioral mechanisms of other organisms. One example could be aphid secretion of “honeydew,” which may be collected by attending ants (Way 1963). Since the aphid honeydew is a waste product that needs to be excreted regardless of the presence of ants, it cannot be regarded as an investment in the ants. However, aphids seem to benefit from the presence of ants, protecting them from enemies and keeping their local environment clean. Consequently, aphids time their secretions to the presence of ants and use special body postures to display and deliver droplets. The ants also communicate with the aphids, stroking them with the antennae to encourage the release of honeydew. Both ants and aphids act essentially in their own immediate interest and cannot be said to invest in each other; however, they show a considerable degree of coordination of their actions (Douglas and Sudd 1980). Such coordinated by-product mutualism, where the partners are adapted both to pursue their own immediate interests and to deal with each other’s behavioral mechanisms, represents an important category of cooperation.

A common form of coordinated by-product mutualism is when individuals join together for the purpose of some project, such as cooperative hunting (e.g., Dugatkin 1997). In addition to coordinating their activities, individuals may also modify the degree to which they invest in the activities of the project (Leimar and Tuomi 1998). If benefits of the project are shared among group members, there may typically be a decrease in each individual’s investment in the activity with increasing group size, following the logic of the “tragedy of the commons.” In bird parental care, a single female shows a higher rate of brood provisioning than one working with a mate (Houston and Davies 1985).

### **Joint Tasks and Division of Labor**

Recently, Anderson and Franks (2001) defined teams as exhibiting a division of labor and team tasks as comprised of different subtasks that must be performed concurrently. They defined group tasks as requiring concurrent action by multiple individuals, but where everybody performs the same task, without any division of labor. A group task might well be regarded as a special case of a team task. An example of a group task is coordinated fishing by cormorants (Bartholomew 1942). Stander (1992) described a team task performed by lions in which individuals take different strategic positions, “wing” or “center,” in a group hunt. In these examples, both group and team tasks represent coordinated by-product mutualism.

Anderson and Franks (2001) extended the team concept to putative cases of reciprocal altruism. For example, they recognized three subtasks performed by supposedly reciprocating vampire bats (Wilkinson 1984): foraging, regurgitation (which is reciprocated), and receiving blood. However, it seems unhelpful to consider the acts of giving and receiving altruism to be subtasks in a team task,

because the receiving individual does not invest in the execution of any project but rather just receives a benefit.

Team tasks can include reciprocity if it is demonstrated that two individuals perform subtasks concurrently to acquire a benefit that only one of them enjoys, and that individuals take turns receiving the benefit in a series of tasks. In the same sense, reciprocity can be a part of group behavior with no division of labor, provided there is concurrent action and turn taking in receiving benefits. A hypothetical example would be a pair of individuals jointly hunting a single prey that only one of them will eat, and where this role of beneficiary alternates. A second example discussed by Anderson and Franks (2001) — coalition formation in male olive baboons (Packer 1977) — could in principle correspond to a team task with reciprocity. The suggestion has been that a male solicits the assistance of his coalition partner to engage a high-ranking male, giving the soliciting male an opportunity to mate with a female that is guarded by the high ranking male (Packer 1977). However, further studies have shown that male baboons do not exhibit a division of labor, nor do they take turns consorting females taken from high-ranking males (Bercovitch 1988; Noë 1992). Rather, their coalitions are by-product mutualisms in which, by coordinating their actions, each male enjoys a better chance of obtaining a female than he would have by acting alone.

A striking example of teams in interspecific mutualism is the cooperative feeding association between humans and dolphins, of which the most detailed accounts come from Mauritania and Brazil (Busnel 1973; Pryor et al. 1990). In the team task, humans and dolphins perform concurrent subtasks to reach the common goal of capturing fish. The humans place or throw nets into the water, which serve as a barrier against which the dolphins can catch fish. Since the dolphins drive fish into the nets, they also produce benefit for their human partners. This is a by-product mutualism with a division of labor, but with some investment by humans in the Mauritania case as they signal to the dolphins upon sighting a school of fish. Presumably, the association is a result of cultural evolution on both the human and the dolphin side. The signals produced by humans to initiate cooperative foraging with dolphins can be seen as (rather small) investments needed to initiate the execution of coordinated by-product mutualism, so that these interactions contain elements of pseudoreciprocity.

## DISCUSSION

Distinguishing in which way benefits acquired in interactions are consequences of adaptations of either of the interacting parties is a useful method of analysis of mutualism. This may seem like stating the obvious, but in our opinion the study of mutualism is in need of a more thorough analysis, both of the selective background of traits playing a role in interactions and of the side effects of these traits. Important traits may also have evolved in other contexts than the mutualistic interaction, or otherwise not be perfectly fine-tuned to the circumstances of the interaction.

Our presentation has primarily dealt with benefits deriving from traits of other organisms, either invested benefits or by-product benefits. Benefits can also be adaptive consequences of an individual's own traits, and these benefits have been referred to as purloined by Connor (1995; see Table 11.1). In principle, there could be interspecific mutualisms with purloined benefits on both sides, resulting in net benefits for the parties involved, although interactions where one organism gains by-product benefits from the exploitative behavior of another seem more likely. An example would be a seed predator that benefits a plant through the dispersal of some of its seeds.

By exploitation, one often means the presence of traits for which the advantage is directly linked to a disadvantage for another organism, although one might also regard other traits, including investments, as ultimately a form of exploitation (Bronstein 2001 and this volume). Adaptations for exploitation may lead from mutualism to parasitism, either through reduced investments by one party or through increased benefits purloined by one party, as well as the appearance of novel ways to purloin benefits. Concerning by-product benefits, they could be lost or reduced if there is a change in the original adaptation that produced the by-product benefits. Such a change may well shift the interaction from mutualistic to parasitic, but saying that there is increased exploitation seems inappropriate as an explanation of the change. Although the interaction may have shifted from mutualistic to parasitic, there has not been selection on the former mutualist to reduce benefits; the reduction simply occurs as a side effect. An example might be a pollinator becoming more efficient at extracting nectar rewards and, at the same time, becoming less efficient in transporting pollen (cf. Bronstein 2001).

The perspective we have used that benefits to an individual are either primarily due to its own traits or to the traits of another (Table 11.1) is clearly an idealization. For certain cases of mutualism, the basic principle is that benefits are obtained only through the interaction of traits of different individuals: warning coloration and Müllerian mimicry would be examples. These can be regarded as special forms of by-product mutualism, where coordination — in behavior or in other traits — is crucial for any benefit to be obtained. The concept of synergistic selection (Maynard Smith 1982) can be applied to such phenomena. More generally, coordination of directly beneficial behaviors or traits to acquire or enhance by-product benefits, which we have referred to as coordinated by-product mutualism, is a very widespread type of mutualistic adaptation.

Nevertheless, the evolution of investment in unrelated organisms is conceptually perhaps the most basic mutualistic adaptation, and reciprocity and pseudoreciprocity are the main competing explanations for such investments. Our arguments in favor of pseudoreciprocity have been that reciprocity is a quite special adaptation, whereas pseudoreciprocity could come about in many ways. Game theory analyses show that reciprocity in principle may evolve; however, these arguments say rather little about the likelihood of this happening for real organisms, in comparison with the likelihood of the evolution of investment in

by-product benefits. There are several ways in which investment can yield by-product benefits, and some of these are associated with ubiquitous activities, such as foraging and growth. This could be the reason for the scarcity of reciprocity and the much wider distribution of pseudoreciprocity.

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### REFERENCES

- Agrawal, A.A., and J.A. Fordyce. 2000. Induced indirect defence in a lycaenid-ant association: The regulation of a resource in a mutualism. *Proc. Roy. Soc. Lond. B* **267**: 1857–1861.
- Anderson, C., and N.R. Franks. 2001. Teams in animal societies. *Behav. Ecol.* **12**:534–540.
- Axelrod, R., and W.D. Hamilton. 1981. The evolution of cooperation. *Science* **211**: 1390–1396.
- Axén, A.H., O. Leimar, and V. Hoffman. 1996. Signalling in a mutualistic interaction. *Anim. Behav.* **52**:321–333.
- Axén, A. H., and N. Pierce. 1998. Aggregation as a cost-reducing strategy for lycaenid larvae. *Behav. Ecol.* **9**:109–115.
- Bartholomew, G.A. 1942. The fishing activities of double-crested cormorants on San Francisco Bay. *Condor* **44**:13–21.
- Bercovitch, F.B. 1988. Coalitions, cooperation, and reproductive tactics among adult male baboons. *Anim Behav.* **36**:1198–1209.
- Boggs, C.L. 1990. A general model of the role of male-donated nutrients in female insects' reproduction. *Am. Nat.* **136**:598–617.
- Boyd, R. 1989. Mistakes allow evolutionary stability in the repeated Prisoner's Dilemma game. *J. Theor. Biol.* **136**:47–56.
- Bronstein, J.L. 1994. Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* **9**:214–217.
- Bronstein, J.L. 2001. The exploitation of mutualisms. *Ecol. Lett.* **4**:277–287.
- Brown, J.L. 1978. Avian communal breeding systems. *Ann. Rev. Ecol. Syst.* **9**:123–156.
- Brown, J.L. 1983. Cooperation: A biologist's dilemma. *Adv. Study Behav.* **13**:1–37.
- Busnel, R.G. 1973. Symbiotic relationship between man and dolphins. *NY Acad. Sci. Trans.* **35**:112–131.
- Clutton-Brock, T. 2002. Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* **296**:69–72.
- Connor, R.C. 1986. Pseudo-reciprocity: Investing in mutualism. *Anim. Behav.* **34**: 1562–1584.
- Connor, R.C. 1992. Egg-trading in simultaneous hermaphrodites: An alternative to Tit-for-Tat. *J. Evol. Biol.* **5**:523–528.
- Connor, R.C. 1995. The benefits of mutualism: A conceptual framework. *Biol. Rev.* **70**: 427–457.

- Crawford, D.L., and S.W. Rissing. 1983. Regulation of recruitment by individual scouts in *Formica oreas* Wheeler (Hymenoptera, Formicidae). *Insectes Soc.* **30**: 177–183.
- Cushman, J.H., and A.J. Beattie. 1991. Mutualism: Assessing the benefits to hosts and visitors. *Trends Ecol. Evol.* **6**:193–195.
- Douglas, J.M., and J.H. Sudd. 1980. Behavioural coordination between an aphid (*Symydobius oblongus* von Heyden; Hemiptera, Callaphidae) and the ant that attends it (*Formica lugubris* Zetterstedt; Hymenoptera, Formicidae): An ethological analysis. *Anim. Behav.* **28**:1127–1139.
- Dugatkin, L.A. 1997. Cooperation among Animals. Oxford: Oxford Univ. Press.
- Enquist, M., and O. Leimar. 1993. The evolution of cooperation in mobile organisms. *Anim. Behav.* **45**:747–757.
- Fiedler, K. 1991. Systematic, Evolutionary, and Ecological Implications of Myrmecophily within the Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zool. Monog.* **31**. Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig.
- Fiedler, K., and D. Hageman. 1995. The influence of larval age and ant number on myrmecophilous interactions of the African grass blue butterfly, *Zizeeria knysna* (Lepidoptera: Lycaenidae). *J. Res. Lepid.* **31**:213–232.
- Fiedler, K., and V. Hummel. 1995. Myrmecophily in the brown argus butterfly, *Aricia agestis* (Lepidoptera: Lycaenidae): Effects of larval age, ant number, and persistence of contact with ants. *Zoology* **99**:128–137.
- Friedman, J.W., and P. Hammerstein. 1991. To trade or not to trade: That is the question. In: *Game Equilibrium Models. I. Evolutionary and Game Dynamics*, ed. R. Selten, pp. 257–275. Berlin: Springer.
- Futuyma, D.J. 1998. *Evolutionary Biology*. 3d ed. Sunderland, MA: Sinauer.
- Harrison, M.J. 1999. Molecular and cellular aspects of the arbuscular mycorrhizal symbiosis. *Ann. Rev. Plant Physiol.* **50**:361–389.
- Houston, A.I., and N.B. Davies. 1985. The evolution of cooperation and life history of the dunnock, *Prunella modularis*. In: *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*, ed. R.M. Sibly and R.H. Smith, pp. 471–487. Oxford: Blackwell.
- Jackson, R.B., J.H. Manwaring, and M.M. Caldwell. 1990. Rapid physiological adjustment of roots to localized soil enrichment. *Nature* **344**:58–60.
- Kaitala, A., and C. Wiklund. 1994. Polyandrous female butterflies forage for matings. *Behav. Ecol. Sociobiol.* **35**:385–388.
- Kaitala, A., and C. Wiklund. 1995. Female mate choice and mating costs in the polyandrous butterfly *Pieris napi* (Lepidoptera: Pieridae). *J. Insect Behav.* **8**:355–363.
- Kokko, H., R.A. Johnstone, and T.H. Clutton-Brock. 2001. The evolution of cooperative breeding through group augmentation. *Proc. Roy. Soc. Lond. B* **268**:187–196.
- Leimar, O. 1997. Reciprocity and communication of partner quality. *Proc. Roy. Soc. Lond. B* **264**:1209–1215.
- Leimar, O., and A.H. Axén. 1993. Strategic behaviour in an interspecific mutualism: Interactions between lycaenid larvae and ants. *Anim. Behav.* **46**:1177–1182.
- Leimar, O., and J. Tuomi. 1998. Synergistic selection and graded traits. *Evol. Ecol.* **12**: 59–71.
- Maynard Smith, J. 1982. The evolution of social behaviour: A classification of models. In: *Current Problems in Sociobiology*, ed. Kings College Sociobiology Group, pp. 22–44. Cambridge: Cambridge Univ. Press.
- Mesterton-Gibbons, M., and L.A. Dugatkin. 1992. Cooperation among unrelated individuals: Evolutionary factors. *Q. Rev. Biol.* **67**:267–281.

- Mesterton-Gibbons, M., and L.A. Dugatkin. 1997. Cooperation and the Prisoner's Dilemma: Towards testable models of mutualism versus reciprocity. *Anim. Behav.* **54**:551–557.
- Noë, R. 1992. Alliance formation among male baboons: Shopping for profitable partners. In: *Coalitions and Alliances in Humans and Other Animals*, ed. A.H. Harcourt and F.B.M. de Waal, pp. 285–321. Oxford: Oxford Univ. Press.
- 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.
- Packer, C. 1977. Reciprocal altruism in *Papio anubis*. *Nature* **265**:441–443.
- 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., 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.
- Pierce, N.E., R.L. Kitching, R.C. Buckley et al. 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly, *Jalmenus evagoras*, and its attendant ants. *Behav. Ecol. Sociobiol.* **21**:237–248.
- Pryor, K., J. Lindbergh, S. Lindbergh, and R. Milano. 1990. A human-dolphin fishing cooperative in Brazil. *Mar. Mamm. Sci.* **6**:77–82.
- Robinson, D. 1994. The response of plants and their roots to non-uniform supplies of nutrients. *New Phytol.* **127**:635–674.
- Rood, J.P. 1978. Dwarf mongoose helpers at the den. *Zeitschrift Tierpsychol.* **48**:277–278.
- Saikkonen, K., U. Ahonen-Jonnarth, A.M. Markkola et al. 1999. Defoliation and mycorrhizal symbiosis: A functional balance between carbon sources and below-ground sinks. *Ecol. Lett.* **2**:19–26.
- Selten, R., and P. Hammerstein. 1984. Gaps in Harley's argument on the evolutionary stability of learning rules and in the logic of "tit for tat." *Behav. Brain Sci.* **7**:115–116.
- Simon, L., J. Bousquet, R.C. Levesque, and M. Lalonde. 1993. Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* **363**:67–69.
- Smith, S.E., and D.J. Read. 1997. *Mycorrhizal Symbiosis*. San Diego: Academic Press.
- Stander, P.E. 1992. Cooperative hunting in lions: The role of the individual. *Behav. Ecol. Sociobiol.* **29**:445–454.
- Trivers, R.L. 1971. The evolution of reciprocal altruism. *Qtlly. Rev. Biol.* **46**:33–57.
- Way, M.J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Ann. Rev. Entomol.* **8**:307–341.
- West-Eberhard, M.J. 1975. The evolution of social behavior by kin selection. *Qtlly. Rev. Biol.* **50**:1–33.
- Wiklund, C., A. Kaitala, V. Lindfors, and J. Abenius. 1993. Polyandry and its effect on female reproduction in the green-veined white butterfly (*Pieris napi* L.). *Behav. Ecol. Sociobiol.* **33**:25–33.
- Wilkinson, G.S. 1984. Reciprocal food sharing in the vampire bat. *Nature* **308**:181–184.
- Woolfenden, G.E. 1975. Florida scrub jay helpers at the nest. *Auk* **92**:1–15.