

# Mutualisms: Assessing the Benefits to Hosts and Visitors

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*A great number and variety of interactions are widely assumed to be mutualistic because the species involved exchange goods or services from which they appear to derive benefit. A familiar example is pollination, in which animal vectors receive food in the form of nectar and/or pollen, while the ovules of plants are fertilized. Unfortunately, most studies fail to demonstrate that both participants benefit in any significant way and therefore lack the information necessary to determine whether a given interaction is mutualistic. While mutualism is thought to be a common type of species interaction, there is still little evidence for this belief.*

Mutualism involves a net increase in the fitness of participating individuals and populations, and is thought to be an abundant and taxonomically diverse form of species interaction<sup>1,2</sup>. Although the participants in such associations vary greatly in the services or resources they exchange, in their species specificity and in their degree of dependence on partners, most can be categorized as being either hosts or visitors (Table 1). Thompson<sup>3</sup> first proposed this idea, defining hosts as plants or animals that provide food and/or domicile to visitors, and visitors as animals that provide beneficial services – such as pollination, seed dispersal or protection from enemies – to hosts. This classification applies best to mutualisms that are direct and nonsymbiotic (see Box 1).

Even though the definition of mutualism states that both participants acquire benefits, most studies (including our own<sup>6,7</sup>) fail to verify this condition. Interactions are commonly regarded as mutualistic once hosts are shown to benefit from the services of visitors. In contrast, visitors are simply viewed as providers of services and generally assumed to receive unspecified benefits from the interaction. Even when hosts are studied, the existence and magnitude of benefits received by them are often found to be highly variable<sup>7-9</sup>. As a result, the assumption of mutualism is frequently premature, because current knowledge of interactions regarded as mutualistic is based on studies that ignore the perspective of one participant and

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often obtain equivocal results about the other (see Ref. 10 for discussion of related problems in endosymbiotic associations).

Visitors are less frequently overlooked in cases involving obligate interactions. Here, the life histories of visitors are constrained by the benefits that hosts provide (food and/or domicile), and the very existence of a visitor depends on the presence of its host. However, evidence to support the assertion that mutualisms are obligate is often weak or absent. In addition, most visitors participate in facultative associations where services provided by a single host are not necessarily essential to the visitor's

survival and reproduction<sup>1,2</sup>. In such cases, the precise benefits to visitors are much more difficult to assess, as their fitness is determined by the use of numerous resources in addition to those of a particular host.

We suspect that there will be skeptics who may argue that rigorous documentation of the obvious is unproductive. While many future studies will undoubtedly show that the fitness of visitors is significantly enhanced by certain hosts, other studies may provide counterintuitive findings which suggest that 'gut impressions' on the benefits to visitors are often simplistic or wrong. In either case,

**Table 1. Types of direct and nonsymbiotic mutualism, and the proposed benefits that each participant receives<sup>a</sup>**

Participants	Proposed benefits
Hosts: Plants with extrafloral nectaries <sup>b</sup> Visitors: Ants	Protection from herbivores Nectar with sugars and amino acids
Hosts: Plants with food bodies and/or domatia <sup>b</sup> Visitors: Ants	Protection from herbivores and encroaching vegetation Food (lipids, carbohydrates and proteins) and/or nest sites
Hosts: Epiphytic plants with domatia Visitors: Ants	Nutrients Nest sites
Hosts: Plants Visitors: Bats, birds and insects	Fertilization of ovules (pollination) Nectar and pollen
Hosts: Plants Visitors: Ants, bats and birds	Dispersal of seeds Fruits, arils, or elaiosomes with a wide range of nutrients
Hosts: Fungi <sup>c</sup> Visitors: Leaf-cutter ants <sup>c</sup>	Substrate on which to grow, a humid environment Larval food (specialized hyphae)
Hosts: Homoptera Visitors: Ants	Protection from predators and parasitoids Excretions with sugars and amino acids
Hosts: Lepidopteran larvae (lycaenids and riodinids) Visitors: Ants	Protection from predators and parasitoids Secretions with sugars and amino acids
Hosts: Anemones <sup>c</sup> Visitors: Clown fish <sup>c</sup>	Prey attraction, waste removal Protection from predators, food
Hosts: Fish Visitors: Cleaner fish	Removal of ectoparasites Food (ectoparasites)
Hosts: Corals Visitors: Shrimps and crabs	Protection from starfish Shelter, food

<sup>a</sup> Information compiled from Refs 3, 8 and 12.

<sup>b</sup> Plants may have a combination of extrafloral nectaries, food bodies and domatia.

<sup>c</sup> The distinction between host and visitor is less clear in these examples.

**Box 1. Direct and nonsymbiotic mutualisms**

In direct mutualisms, participants benefit each other through direct contact (e.g. many bird species benefit from collecting nectar of flowering plants as they pollinate them). In indirect mutualisms, participants benefit from each other's presence, but not through direct contact (e.g. intertidal starfish can benefit barnacles by preying on mussels that would otherwise competitively exclude barnacles from the shore<sup>4</sup>).

The distinction between symbiotic and nonsymbiotic mutualism is complicated by the immense confusion and disagreement over the meaning of symbiosis. There appear to be at least three definitions of symbiosis:

(1) Symbiosis is simply an interaction between species (i.e. symbiosis equals interaction). Sometimes this definition is amended to cover interactions in which the participants 'live together', but no attempt is made to elucidate what such qualification really means (e.g. how close together does a pair of species have to live before their association is classified as symbiotic?).

(2) Symbiosis is an interaction between species in which both participants benefit (i.e. symbiosis equals mutualism).

(3) Symbiosis is an interaction between species in which the participants are physiologically connected or integrated and may benefit, harm or have no effect on each other. Thus, symbioses can be parasitic, mutualistic or commensalistic. A well-known example is the association between mycorrhizal fungi and plants. While fungi are thought to benefit from the association under most conditions, the influence of fungi on host plants is often variable: it can be beneficial for plants when soil nutrients are low, whereas it can be harmful in nutrient-rich soils<sup>5</sup>.

Since the first and second definitions of symbiosis have less ambiguous and more appropriate alternatives (interaction and mutualism, respectively), it may be more useful to employ the third. Under this scheme, mutualisms can be classified as being symbiotic or nonsymbiotic.

examining the effects of hosts on visitors will shed light on the existence, strength and pattern of interdependences among species in nature.

**What are benefits?**

The meaning of 'benefit' is central to the study of mutualism and appears self evident: organisms benefit from a resource when use of it results in a greater number of viable offspring than would be produced without these resources. Unfortunately, 'benefit' is often used quite loosely, as studies rarely provide direct or indirect evidence of its existence, particularly for visitors. This practice is also evident in studies of optimal foraging, which commonly focus on indirect measures of fitness that are assumed to be correlated with reproductive success, such as the rates of energy acquisition, amounts of food consumed, digested, assimilated or converted into biomass, food preferences, nutritional quality of food and foraging economics<sup>11</sup>. While these measures may be useful approximations, the contribution of individual food items (and hosts) to forager fitness is usually unknown.

**Why are visitors overlooked?**

Measures of fitness (i.e. survivorship and fecundity) are comparatively simple to gather for hosts that are sedentary or have low mobility (such as plants, anemones, corals, homopterans and lepidopteran larvae)<sup>1,2,7,8,12</sup>. However, prac-

tical problems often abound with regard to visitors. For example, many pollinators and fruit dispersers are winged (insects, birds and bats), fast moving and elusive. This creates major difficulties in measuring the uptake of host resources and their influence on visitor fitness. The situation is further complicated by the varied and shifting use of hosts by visitors. Many hymenopteran visitors have complex trophic dynamics within their often subterranean colonies and these are difficult to monitor. Measuring the fitness of such colonies requires estimation of the production of reproductive castes, and opportunities for this can be infrequent and short lived<sup>13</sup>.

**Ants as visitors**

A large proportion of terrestrial visitors belong to the Hymenoptera, and the evolution of eusociality is widely believed to be a major factor responsible for their dominance in apparent mutualisms<sup>3,13</sup>. Ants are especially conspicuous in this regard: they are one of the most ubiquitous visitors found in nature, forming close associations with many plants, fungi and animals<sup>3,12</sup>. Here, we concentrate on ants and their interactions with plant and herbivore hosts. However, our comments apply to visitors as a whole, and we discuss ants only to provide examples.

Almost all studies of ants and their hosts invoke the term 'mutualism' without considering the effect of

interactions on any measure of ant colony fitness. For example, recent reviews of ant associations do not cite any studies that provide direct evidence that hosts benefit ants<sup>12-16</sup>. In associations with plants, ants provide services that vary according to the species involved, including provision of nutrients from colony wastes, protection from herbivores and dispersal of seeds. While many plant species develop specialized structures (inflated roots, hollow stems, leaf pouches) that serve as nest sites (domatia) for ants, very few studies demonstrate that ants nest exclusively in host domatia or compare the fitness of ant colonies that have access to domatia with those that do not. Similarly, while many studies have documented that plant food rewards (extrafloral nectars, elaiosomes and other food bodies) contain a wide range of nutrients<sup>12,13,16</sup>, none addresses the effect of these compounds on ant colonies, or whether they are available from alternative sources. However, a recent study by Fisher *et al.*<sup>17</sup> does provide indirect evidence for the importance of plant rewards, showing that the extrafloral nectar of an epiphytic orchid (*Caularthron bilamellatum*) comprises 11-48% of the diets of six ant species inhabiting its domatia.

Homopterans (such as aphids, coccids and membracids) and lepidopterans (lycaenids and riodinids) commonly benefit from ant tending, and their excretions or secretions are widely assumed to be important food resources for many ant species, as they contain a range of sugars and amino acids<sup>12,13,15,18,19</sup>. Three studies provide indirect evidence that ants benefit from their associations with tended herbivores. For *Polyrhachis simplex*, Degen *et al.*<sup>20</sup> estimated that daily energy gain from the honeydew of aphids (*Chaitophorus populialbae*) was from 4.4 to 9.4 times greater than energy expenditure. Pierce *et al.*<sup>21</sup> estimated that a single host plant (*Acacia* sp.) bearing 60 larvae of the lycaenid *Jalmenus evagoras* can result in the production of 100 new workers per day for the ant *Iridomyrmex anceps*. Fiedler and Maschwitz<sup>22</sup> also generated estimates suggesting that three ant species (*Tetramorium caespitum*, *Lasius alienus* and

*Plagiolepis pygmaea*) acquire a substantial proportion of their metabolic needs and produce a large number of workers when fed on secretions of the lycaenid *Polyommatus cordian*.

We know of only one study that provides direct evidence for the effect of tended herbivores on the fitness of ant colonies. D.R. Nash (PhD dissertation, Oxford University, 1989; see also Refs 19 and 23) showed that ant colonies (*Iridomyrmex vicinus*) given access to secretions of lycaenid larvae (*Jalmenus evagoras*) exhibited significantly higher growth rates than control colonies without larvae. However, the details were puzzling: colonies attained higher growth rates when consuming the secretions from one caterpillar than when they consumed the secretions from five caterpillars! Nash also showed that another ant (*I. anceps*) attained greater net energy from tending homopterans (psyllids) than from tending *J. evagoras*, even though more ants tended the lycaenids. These counterintuitive results suggest that this lycaenid host manipulates ant visitors into behaving in ways that reduce the latter's net benefits.

#### The importance of considering visitors

Future research on host-visitor interactions may reveal distinct kinds of hosts. First, 'key' hosts make large contributions to the fitness of specific visitors. Visitors may use other hosts, but only their key hosts provide them with major benefits. Second, 'cumulative' hosts make small contributions to the fitness of specific visitors. A visitor's key or cumulative host species may vary in space and time. Third, 'deceptive' hosts attract visitors but either (1) they make no detectable contribution to the fitness of visitors, even though they may provide apparent rewards that visitors attempt to harvest, or (2) they provide rewards to visitors but also parasitize them in some way, such that the net effect of the interaction on the visitor is negative.

Once we know the contribution of an array of hosts to visitor fitness, we may confirm that many mutualisms are genuinely diffuse, with cumulative contributions from many host species. Alternatively, we may find

that many visitors depend on the presence of key hosts, and that associations that appear to be diffuse are closer to pairwise and perhaps obligate associations.

A greater emphasis on visitors will establish which hosts and which visitors are involved in truly mutualistic interactions, and will shed light on the dynamics of interactions, their variation in time and space, and the degree and mode of dependence of participating species. It will also provide a better idea of the frequency of mutualisms in natural communities and their importance in community organization and assembly. There have been claims that mutualisms are as common as any other type of species interaction<sup>1,2</sup>, but until more is known about how visitors benefit, and from which hosts, these claims should remain speculative.

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#### References

- 1 Boucher, D.H., James, S. and Keeler, K.H. (1982) *Annu. Rev. Ecol. Syst.* 13, 315-347
- 2 Boucher, D.H., ed. (1985) *The Biology of Mutualism*, Oxford University Press
- 3 Thompson, J.N. (1982) *Interaction and Coevolution*, Wiley
- 4 Paine, R.T. (1966) *Am. Nat.* 100, 65-75
- 5 Bethlenfalvay, G.J., Bayne, H.G. and

- Pacovsky, R.S. (1983) *Physiol. Plant.* 57, 543-548
- 6 Culver, D.C. and Beattie, A.J. (1980) *Am. J. Bot.* 67, 710-714
- 7 Cushman, J.H. and Whitham, T.G. (1989) *Ecology* 70, 1040-1047
- 8 Addicott, J.F. (1984) in *A New Ecology: Novel Approaches to Interactive Systems* (Price, P.W., Slobodchikoff, C.N. and Gaud, W.S., eds), pp. 437-455, Wiley
- 9 Thompson, J.N. (1988) *Annu. Rev. Ecol. Syst.* 19, 65-87
- 10 Douglas, A.E. and Smith, D.C. (1989) *Trends Ecol. Evol.* 4, 350-352
- 11 Pyke, G.H. (1984) *Annu. Rev. Ecol. Syst.* 15, 523-575
- 12 Beattie, A.J. (1985) *Evolutionary Ecology of Ant-Plant Mutualisms*, Cambridge University Press
- 13 Hölldobler, B. and Wilson, E.O. (1990) *The Ants*, Harvard University Press
- 14 Buckley, R.C., ed. (1982) *Ant-Plant Interaction in Australia*, Dr W. Junk Publishers
- 15 Buckley, R. (1987) *Adv. Ecol. Res.* 16, 53-85
- 16 Keeler, K.H. (1989) in *Plant-Animal Interactions* (Abrahamson, W.G., ed.), pp. 207-242, McGraw-Hill
- 17 Fisher, B.L., Sternberg, L.S.L. and Price, D. (1990) *Oecologia* 83, 263-266
- 18 Pierce, N.E. (1987) in *Oxford Surveys in Evolutionary Biology* (Vol. 6) (Harvey, P.H. and Partridge L., eds), pp. 89-116, Oxford University Press
- 19 Pierce, N.E. (1989) in *Towards A More Exact Ecology* (Grubb, P.J. and Whittaker, J.B., eds), Blackwell Scientific Publications
- 20 Degen, A.A., Gersani, M., Avivi, Y. and Weisbrot, N. (1986) *Insectes Soc.* 33, 211-215
- 21 Pierce, N.E., Kitching, R.L., Buckley, R.C., Taylor, M.F.J. and Benbow, K.F. (1987) *Behav. Ecol. Sociobiol.* 21, 237-248
- 22 Fiedler, K. and Maschwitz, U. (1988) *Oecologia* 75, 204-206
- 23 Pierce, N.E., Nash, D.R., Baylis, M. and Carper, E.R. in *Ant-Plant Interactions* (Cutler, D.F. and Huxley, C.R., eds), Oxford University Press (in press)

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