

The Costs of Mutualism¹

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SYNOPSIS. Mutualisms are of central importance in biological systems. Despite growing attention in recent years, however, few conceptual themes have yet to be identified that span mutualisms differing in natural history. Here I examine the idea that the ecology and evolution of mutualisms are shaped by diverse costs, not only by the benefits they confer. This concept helps link mutualism to antagonisms such as herbivory, predation, and parasitism, interactions defined largely by the existence of costs. I first briefly review the range of costs associated with mutualisms, then describe how one cost, the consumption of seeds by pollinator offspring, was quantified for one fig/pollinator mutualism. I compare this cost to published values for other fig/pollinator mutualisms and for other kinds of pollinating seed parasite mutualisms, notably the yucca/yucca moth interaction. I then discuss four issues that fundamentally complicate comparative studies of the cost of mutualism: problems of knowing how to measure the magnitude of any one cost accurately; problems associated with using average estimates in the absence of data on sources of variation; complications arising from the complex correlates of costs, such as functional linkages between costs and benefits; and problems that arise from considering the cost of mutualism as a unilateral issue in what is fundamentally a reciprocal interaction. The rich diversity of as-yet unaddressed questions surrounding the costs of mutualism may best be investigated via detailed studies of individual interactions.

INTRODUCTION

Mutualisms (reciprocally beneficial interactions between species) have finally come to be recognized as critical components of ecological and evolutionary processes occurring at scales ranging from the individual to the ecosystem. Every organism on earth is probably involved in at least one and usually several mutualisms during its lifetime (Janzen, 1985). In tropical rainforests, the large majority of flowering plants depend on mutualistic pollinators and seed dispersers. Deserts are dominated by nitrogen-fixing legumes, lichens dominate tundra habitats, and most northern hardwood forest and grassland plant species depend on mycorrhizal fungi to survive and persist. In the ocean, both coral and deep-sea vent communities are rich with mutualisms; coral itself is the product of a mutualistic sym-

biosis. Organisms from every kingdom are involved in mutualisms, and certain kingdoms may in fact have originated as a consequence of symbiotic innovations. Other key events in the history of life on earth have been linked to mutualism as well, including the origin of the eukaryotic cell, invasion of the land by plants, and the radiation of the angiosperms (Boucher *et al.*, 1982; Janzen, 1985; Herre *et al.*, 1999; Bronstein, 2001a).

There are more researchers studying mutualisms now than ever before, and the level of mechanistic detail now available about many of these interactions is impressive. However, the study of these interactions has not yet progressed very far beyond the descriptive phase (Bronstein, 1994a). Few general concepts have yet emerged. Furthermore, the few that do exist have rarely been used as tools to detect parallels and differences between mutualisms with highly contrasting natural histories. In this paper I examine one such conceptual theme, the idea that mutualisms are shaped not only by their benefits but by their costs as well.

¹ From the Symposium *An Integrative Approach to the Study of Terrestrial Plant-Animal Interactions* presented at the Annual Meeting of the Society for Comparative and Integrative Biology, 5–8 January 2000, at Atlanta, Georgia.

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The idea that mutualisms involve costs is not new. Cost/benefit analysis has long been a standard approach in studying the ecological dynamics of these interactions (Roughgarden, 1975; Keeler, 1985). There are by now hundreds of articles that describe one or another cost incurred in one or another sort of mutualism. Furthermore, a growing number of studies have rigorously measured a subset of those costs. It has been estimated, for instance, for different plant species, that up to 20% of the total carbon budget can be allocated to support mycorrhizae (Johnson *et al.*, 1997), 3% of total energy investment is devoted to floral nectar for pollinators (Harder and Barrett, 1992), and 0.2–1% of the energy costs of leaf production may be invested in production of extrafloral nectar and other food rewards for ant guards (O'Dowd, 1979, 1980). No comparisons of these kinds of figures have yet been attempted, however. Are the costs of rewarding mutualists that provide different kinds of services really as divergent as these figures seem to indicate? If so, how might this influence when and where different mutualisms are likely to arise and persist? Or are these differences illusory, a simple outcome of comparing not only across plant species but across sites and times, using different techniques to measure different physiological currencies? My aim here is to encourage a rigorous comparative approach to studying the costs of mutualism that eventually will allow us to answer these questions. Equally importantly, however, I argue for the value of conducting considerably more detailed studies of the phenomena generating costs within individual pairwise interactions.

MOST MUTUALISMS INVOLVE COSTS AS WELL AS BENEFITS

Organisms use mutualists to obtain goods and services that they cannot, or cannot affordably, produce or acquire otherwise. Thus, mutualists transport organisms or their gametes to places they could not otherwise reach (in pollination, seed dispersal, and phoretic mutualisms); they protect organisms from their natural enemies (*e.g.*, in cleaning symbioses and ant defensive mutualisms); and they provide organisms with

essential nutrients (in most mutualistic symbioses). Most of these goods and services are costly for organisms to provide to their partners. They certainly do not provide them out of some altruistic impulse, as was once believed. Rather, it is because organisms must give in order to get. It is useful to think of mutualisms as “biological markets,” in which organisms trade commodities that are relatively inexpensive for them to produce for those that they require but that are expensive or impossible for them to produce (Noë and Hammerstein, 1994; Schwartz and Hoeksema, 1998). Thus, for instance, in most pollination mutualisms, plants trade nectar to obtain pollen transport, while in mycorrhizal symbioses, plants trade carbon for access to phosphorus.

Investment in reward production is only one of many costs of mutualism, however. Mutualists themselves can inflict costly damage. For instance, ant defenders sometimes consume aphids rather than protecting them from natural enemies (Offenberg, 2001), while some coevolved seed dispersers consistently destroy a significant proportion of seeds (Vander Wall, 1994). “Exploiters,” opportunists that benefit from the commodities traded within mutualisms but do not reciprocate, can likewise inflict costs (Bronstein, 2001*b*). One well-known example involves animals that feed on floral nectar but do not transfer pollen between flowers. Irwin and Brody (1998), for example, document that hummingbird pollinators avoid bumblebee-robbed *Ipomopsis aggregata* flowers, at a significant cost to potential fruit set. Somewhat more abstract costs are associated with an organism's inability to succeed in the absence of mutualists. For instance, biotically pollinated plants may perform poorly in parts of their range where their best pollinators are unable to persist (Aizen and Feinsinger, 1994). Finally, there are costs associated with the loss of evolutionary flexibility, particularly in organisms or lineages obligately dependent upon mutualists (but see, for instance, Armbruster and Baldwin, 1998). A full accounting of the total cost of any given mutualism would need to take into account all of these highly diverse phenomena. Clearly,

however, some of these costs are difficult or impossible to quantify, let alone to compare across different interactions. To begin building a rigorous comparative approach to studying the costs of mutualism, it is easiest to focus first on the most easily measured cost, investment into rewards.

COSTS OF SEED LOSS IN POLLINATING SEED PARASITE MUTUALISMS

One of the best-known forms of mutualism involves insects that pollinate a host plant, then deposit offspring that will ultimately consume many of the seeds. Most of these “pollinating seed parasite” mutualisms are both obligate (*i.e.*, neither partner can persist without the other) and species-specific (there is a one-to-one correspondence between partner species). The two most thoroughly studied cases involve figs (*Ficus*, Moraceae) and fig wasps (Agaonidae, Hymenoptera) (Anstett *et al.*, 1997), and yuccas (*Yucca*, Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula*, Incurvariidae) (Pellmyr and Leebens-Mack, 2000). Less well-known interactions of the same type take place between some species of globeflower (*Trollius*, Ranunculaceae) and *Chiastocheta* flies (Anthomyiidae) (Jaeger *et al.*, 2000) and between senita cactus (*Lophocereus schottii*, Cactaceae) and the senita moth (*Upiga virescens*, Pyralidae) (Fleming and Holland, 1998). Pollinating seed parasites are also associated with *Lithophragma parviflorum* (Saxifragaceae) (Thompson and Pellmyr, 1992) and *Silene vulgaris* (Caryophyllaceae) (Pettersson, 1991), although in these cases they occur alongside generalist pollinator species.

As in other mutualisms, participants in these interactions are afflicted with diverse costs. However, one cost incurred by the plants is of particular interest: the destruction of seeds by the pollinators' offspring. In Janzen's (1979) words, how many babies must be sacrificed to make babies? It is relatively straightforward to take a comparative approach to seed loss to pollinator offspring, because it can be measured the same way (via fruit dissections) in any pollinating seed parasite mutualism. Furthermore, the costs and benefits of these mutualisms to the plants can be measured in the same

currency: numbers of seeds. This allows unusual resolution of their net benefits, that is, the gross benefits (numbers of seeds initiated) minus costs (numbers of seeds consumed). Because of these advantages, the costs these mutualisms have been investigated in exceptional detail. In fact, it would be fair to say that these interactions form the centerpiece of our understanding of the costs of mutualism.

How much, then, has been learned about the costs of pollinating seed parasite mutualisms, and how reliable is that information? Below, I first describe how I measured the average cost of seed destruction in one fig/fig wasp interaction. I then compare this cost with published data from other fig pollination mutualisms and from other pollinating seed parasite relationships. Finally, I present a critique of how the costs of mutualism can be measured. This analysis casts a highly critical eye on our ability to take a quantitatively rigorous comparative approach to the costs of mutualism. However, it also suggests a number of other issues surrounding costs that should prove enlightening and quite amenable to further investigation.

Costs in the Florida Strangling Fig

Ficus aurea Nuttall, the Florida Strangling Fig, is a Caribbean species that reaches its northern limit in south central Florida; it is one of only two figs native to the United States. In Florida, these large trees grow abundantly in patches of woodland, as well as along canals and other watercourses. Like the large majority of other fig species, *F. aurea* is associated with a single pollinator species throughout its range, in this case *Pegoscapus mexicanus* (Grandi) Wiebes. The biology of this wasp and its interactions with *F. aurea* are unusually well known (*e.g.*, Bronstein and Hossaert-McKey, 1995, 1996; Anstett *et al.*, 1996; Bronstein *et al.*, 1998), especially for the sites in Coral Gables, Florida where the data presented here were collected (see Bronstein and Hossaert-McKey, 1996 for site and species descriptions).

The natural history of this interaction is typical of mutualisms between monoecious figs (about half the genus *Ficus*) and fig

wasps. The millimeter-long, pollen-carrying female wasps arrive at fig trees when they are in flower. Figs (or, more properly, syconia) are hollow multiple receptacles lined with numerous male and female florets. At the time the wasps arrive, only the female florets are receptive. The wasps enter the fig via a bract-covered pore, often becoming trapped in the process. Once inside, they deposit pollen on the stigmas, then oviposit via the styles into some of the ovaries; each wasp offspring ends up occupying space that would otherwise have been taken up with one developing seed. Wasps and some intact seeds mature over the next several weeks. Also occupying florets and developing within the fig are members of a large, poorly known community of non-pollinating wasps nearly as specialized to the fig as are the pollinators themselves. When the pollinator offspring reach adulthood, they mate within the fig. Females then actively collect pollen from the newly mature anthers and pack it into special structures ("pollen pockets") on their mesothoracic sternites, while the wingless males tunnel back through the fig wall. The inseminated female wasps then depart with pollen in search of a receptive fig. They can survive a few days at most as free-living adults; they do not feed, and mortality in flight is extremely high (Bronstein, 1992). Considerable flowering asynchrony among fig trees in any population increases the likelihood that a fig wasp emerging at any time of year will be able to locate a receptive fig.

I quantified the extent to which seed production in *F. aurea* was reduced due to the actions of its pollinator's offspring. I collected figs just prior to the time wasps were expected to depart from them; the sample analyzed here included over 400 figs from 23 trees sampled every few days from February through December 1991. In most cases, four to ten figs were collected from a given tree during a single sampling period. Figs were placed into individual mesh-covered vials and placed in the dark until wasps exited naturally, usually within 24 hr of removal from the tree. Wasps were later counted under the dissecting microscope and identified to species and sex. The re-

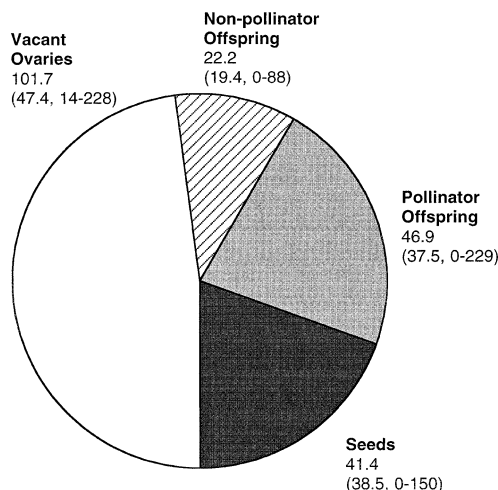


FIG. 1. Contents of 195 *Ficus aurea* figs. Average numbers of female ovaries that were vacant and that matured a seed, pollinator offspring, or non-pollinator offspring are listed; standard deviations and ranges are given in parentheses.

mains of each fig were later dissected. The number of seeds, the number of florets that had been exited by wasps, the number that contained mature but unemerged wasps of each species and sex, and the number of florets that appeared to be vacant were recorded. In the analysis presented here, I included figs only if the number of wasps counted fell within 15% of the number of exited florets counted. Although these numbers should be equal, in practice some figs were collected after some or all of the wasps had departed.

Figure 1 summarizes data on the average contents of a mature *F. aurea* fig. Note first that the contents of matured figs were exceedingly variable, as shown by the great ranges and standard deviations listed in the figure. Second, note that well over half the female flowers contributed neither to fig nor pollinator reproduction, because they either matured a non-pollinating wasp or were entirely vacant at maturity. Finally, 53% of the ovaries that presumably could have matured seeds contained the offspring of the pollinators instead. That is, reproduction by the obligate mutualist costs *F. aurea* about half its potential seed production.

The comparative costs of seed loss

The cost of seed loss to pollinator offspring in *F. aurea* seems *a priori* to be extremely high. However, this figure is impossible to interpret in the absence of something to compare it to. Two kinds of comparisons can be envisioned. In one approach, seed loss to pollinator offspring would be compared quantitatively to seed loss inflicted by other mortality factors, such as post-dispersal seed predation and dispersal to unsuitable microsites. The data simply do not exist yet to attempt such a demographic analysis for figs (but see Holland [2001] for a pioneering effort to analyze another pollinating seed parasite mutualism with this approach). A different kind of comparison would involve examining how seed loss to pollinators compares between *F. aurea* and other plants associated with pollinating seed parasites. The data are currently available to do this; therefore, it is this approach that I take here to explore the comparative costs of seed loss.

Table 1 summarizes published values for the average cost of seed destruction across the four best-known obligate pollinating seed parasite systems. Although there are some important differences in the way that the authors obtained and reported their data, for the purposes of this paper I have chosen to express all of them in the same way: as the proportion of all initiated seeds consumed by pollinator larvae, averaged across all fruits sampled within a population.

Consider first the data on fig pollination mutualisms. (I have tabulated data on monoecious figs only; in the gynodioecious [commonly called dioecious] fig species, seeds and pollinator offspring mature on different trees, complicating the comparisons of interest.) These data indicate that across species, figs typically lose 30–55% of their seeds to their pollinators' offspring, with *Ficus aurea* coming in on the high side of that range. These values are markedly lower than the heavily-cited data of Janzen (1979) on five monoecious fig species; he reported values ranging from 41% to 77%. However, Janzen did not count pol-

linator offspring directly, but rather the number of fig ovaries from which wasps of any sort had exited. This method fails to separate out non-pollinator wasps, most of which do not directly destroy seeds (Compton *et al.*, 1994; West *et al.*, 1996; Kerdellu   and Rasplus, 1996; Herre, 1999); hence, I chose not to include Janzen's data in the table.

Table 1 also shows data for a large number of yucca pollination mutualisms. Seed loss to yucca moth larvae lies in the range of 5–20%, although outliers are common; striking variation is evident across different yucca species. Several of these mutualisms have been studied at multiple sites, permitting comparisons across populations as well as across species. In some cases, differences among population averages are as large as some of the species differences in the table. For instance, there is a threefold difference in average cost of mutualism across populations of *Yucca angustissima* and *Yucca elata* (Keeley *et al.*, 1984). Even in light of these population differences, however, it is clear that yuccas lose proportionately fewer seeds to pollinator offspring than do monoecious figs. This observation is not new (*e.g.*, see Addicott, 1986), but it is worth reiterating since earlier comparisons had used Janzen's (1979) inflated values for figs. Pellmyr and Leebens-Mack (2000) believe that the published values for yuccas are themselves inflated, and for largely the same reason: seed loss to non-pollinator species has generally not been separated out, because pollinator and non-pollinator larvae and the damage they cause are essentially indistinguishable. Note, however, that even if the tabulated yucca values could somehow be properly deflated, it would only strengthen the general conclusion: monoecious figs lose more seeds to their pollinating seed parasites than do yuccas. Although other systems have been much less studied, *Trollius* seems similar to yuccas and senita mid-way between yuccas and figs in terms of this cost of mutualism.

There has been some discussion in the literature about certain patterns shown in Table 1. For instance, Herre (1989) points out that in the Panamanian community he has studied, fig species with smaller inflo-

TABLE 1. Estimates of the "cost of mutualism" (the average percentage of initiated seeds lost to offspring of the obligate pollinators) for four pollinating seed parasite mutualisms. Ranges of average seed loss are listed in cases where data on more than one plant population were reported.

Plant	Average % seeds lost to pollinator offspring	Citation
Monoecious fig/fig wasp mutualisms		
<i>Ficus sur</i> ^a	18%, 29%	Kerdelhué <i>et al.</i> , 1997
<i>Ficus pertusa</i>	31%	Bronstein, 1988
<i>Ficus pertusa</i>	37%	Herre and West, 1997
<i>Ficus rubiginosa</i>	38%	Cook and Power, 1996
<i>Ficus nr. trigonata</i>	42%	Herre and West, 1997
<i>Ficus burtt-davyi</i>	43%	Compton and Nefdt, 1990
<i>Ficus nymphaefolia</i>	43%	Herre and West, 1997
<i>Ficus benjamina</i>	45%	Corlett <i>et al.</i> , 1990
<i>Ficus turbinata</i>	47%	Herre and West, 1997
<i>Ficus obtusifolia</i>	48%	Herre and West, 1997
<i>Ficus bullenei</i>	49%	Herre and West, 1997
<i>Ficus columbrinae</i>	50%	Herre and West, 1997
<i>Ficus aurea</i>	53%	this paper
<i>Ficus citrifolia</i>	55%	Herre and West, 1997
<i>Ficus yoponensis</i>	55%	Herre and West, 1997
<i>Ficus microcarpa</i>	60%	Corlett <i>et al.</i> , 1990
Trollius/Chiastocheta mutualism		
<i>Trollius europaeus</i> ^b	8.7–19.5%	Pellmyr, 1989
	10–35%	Hemborg and Deprés, 1999
Senita/senita moth mutualism		
<i>Lophocereus schottii</i>	19–29%	Holland and Fleming, 1999
Yucca/yucca moth mutualisms		
<i>Yucca arizonica</i>	1%	Addicott, 1986
<i>Yucca whipplei parishii</i>	2.4–7.1%	Keeley <i>et al.</i> , 1986
<i>Yucca whipplei whipplei</i>	2.5–8.7%	Keeley <i>et al.</i> , 1986
<i>Yucca schidigera</i>	3%	Keeley <i>et al.</i> , 1984
<i>Yucca torreyi</i>	4–11%	Keeley <i>et al.</i> , 1984
<i>Yucca whipplei caespitosa</i>	4.2–11.6%	Keeley <i>et al.</i> , 1986
<i>Yucca schottii</i>	5–10%	Keeley <i>et al.</i> , 1984
<i>Yucca whippei percursa</i>	5.6–24.5%	Keeley <i>et al.</i> , 1986
<i>Yucca baccata</i>	6%	Addicott, 1986
<i>Yucca whipplei intermedia</i>	6.8–11.9%	Keeley <i>et al.</i> , 1986
<i>Yucca brevifolia</i>	7%	Keeley <i>et al.</i> , 1984
<i>Yucca glauca</i>	7%	Keeley <i>et al.</i> , 1984
<i>Yucca elata</i>	7–22%	Keeley <i>et al.</i> , 1984
<i>Yucca baccata</i>	10–12%	Keeley <i>et al.</i> , 1984
<i>Yucca baileyi</i>	11%	Addicott, 1986
<i>Yucca reverchoni</i>	12–18%	Keeley <i>et al.</i> , 1984
<i>Yucca schottii</i>	14%	Addicott, 1986
<i>Yucca angustissima</i>	15–45%	Keeley <i>et al.</i> , 1984
<i>Yucca elata</i>	16%	Addicott, 1986
<i>Yucca glauca</i>	19%	Addicott, 1986
<i>Yucca angustissima</i>	19%	Addicott, 1986
<i>Yucca kanabensis</i>	19%	Addicott, 1986

^a The two values tabulated are for *Ceratosolen silvestrianus* and *Ceratosolen flabellatus* respectively, both effective pollinators of *Ficus sur*.

^b Total seed destruction by a group of four obligate pollinator flies in the genus *Chiastocheta* is tabulated.

rescences tend to experience disproportionately high seed loss to fig wasp offspring. For yuccas, Addicott (1986) notes that the baccate (fleshy-fruited) species typically lose more seeds to yucca moth larvae than do the dry-fruited capsular yuccas. The

comparatively high seed loss to fig wasps has been linked to the fact that, in contrast to all other pollinating seed parasites, fig wasps also transfer pollen between inflorescences. I discuss this idea in greater depth in a later section of this paper.

MEASURING THE COST OF MUTUALISM: A CRITIQUE

Taking a comparative approach to the costs of mutualism thus can reveal striking patterns that may prove very informative about the ecology and evolution of these interactions. However, rather than attempting to explain patterns in Table 1 any further, I wish to step back and take a very skeptical look at the kinds of comparisons we might be tempted to draw. There are at least two weaknesses inherent to searching for patterns from data like these. The first is a problem common to many comparative studies, and relates to whether the taxa we would be comparing are truly independent data points. In this brief look at the comparative costs of mutualism, I have made no effort to factor out phylogenetic relationships. A more detailed comparison should take this approach to examine whether (for instance) the costs of fig seed consumption are more similar among more closely related figs, due to shared ancestry rather than shared ecological pressures.

The second problem relates to how one interprets any single measure of a cost (or, for that matter, a benefit) of mutualism. Thus, it is a problem of how one rigorously studies mutualism, rather than of how one conducts comparative studies. The pitfalls of the comparative approach have been addressed extensively in recent years (*e.g.*, Felsenstein, 1985; Harvey and Pagel, 1991), but the difficulty of quantifying mutualistic effects has not. For this reason, it is this latter problem that I examine in the remainder of this paper. To do this, I use the illustration of the cost of mutualism calculated from my own data on the Florida Strangling Fig.

The problem of an accurate measure

If a given cost of mutualism has not been calculated fairly accurately, its value is clearly limited. This becomes particularly important if the intention is to compare mutualisms whose costs are unlikely to be affected by the same sources of error.

How accurate, then, is the conclusion that the offspring of *F. aurea*'s obligate pollinators destroy an average of 53% of its

potential seeds (Fig. 1)? Two important caveats need to be stated. The first relates to whether these insects actually *destroy* seeds, a point on which I have been intentionally vague up to this point. It has almost universally been assumed that fig wasp larvae consume seeds that are initiated as a consequence of their mothers' pollination behaviors. Surprisingly, this may not be true. It has recently been shown that the larvae can alternatively feed on sterile tissue that females induce when they oviposit within unfertilized florets, although they develop less successfully there than when they feed on endosperm in fertilized florets (Jousselin and Kjellberg, 2001; F. Kjellberg, personal communication). However, this does not significantly alter the analysis I present here, because experimental evidence has confirmed that seed production is proportionately reduced by pollinator oviposition just as if seeds were actually consumed. Anstett *et al.* (1996) injected excess pollen into *F. aurea* figs, then introduced a single pollinator into half of them. Figs receiving only pollen produced 175 seeds on average, whereas those receiving both pollen and a pollinator matured an average of 100 seeds and 75 pollinator offspring.

The second caveat relates to whether the figure of 53% seed loss may be an underestimate. It is not clear whether some or all of the numerous vacant ovaries and non-pollinator wasps (Fig. 1) should be added into this cost of mutualism. Vacant ovaries include those that were never occupied, but also those whose contents failed to develop successfully; these categories cannot be distinguished in *F. aurea* (Bronstein and Hossaert-McKey, 1996). While none of the non-pollinator wasp species associated with this fig directly feeds on seeds or wasps, some may well outcompete the pollinators for oviposition space and/or food; one particularly large non-pollinator crushes some larval pollinators as it develops within the fig (Bronstein, 1999). Thus, some vacancies and non-pollinators might represent seeds destroyed by pollinator larvae, which themselves then died before maturation. My earlier observation that Janzen (1979) erred in counting non-pollinators as part of the cost of mutualism may therefore have been too

dismissive (see also Herre, 1999). Note, however, that if I had in fact added some or all of the non-pollinator wasps and vacant ovaries into the cost of this mutualism, that cost would have been substantially larger than 53%. This actually strengthens the conclusion that monoecious figs sacrifice more than yuccas do to their pollinating seed parasites.

These two complications with obtaining an accurate account of seed loss are likely to afflict studies of all fig pollination mutualisms, although not necessarily to the identical degree. (New World figs, for instance, carry much higher non-pollinator wasp loads than do Old World figs [Bronstein, 1992].) The general point, then, is that the accuracy problem will be most vexing when comparing a group of mutualisms subject to one particular kind of error with mutualisms not subject to that error.

The problem of an average measure

Most of the few published measures of the costs of mutualism have been expressed as averages such as those shown in Table 1 and Figure 1. Average costs are certainly handy for drawing comparisons across different mutualisms, but their weaknesses are legion (as most of the researchers whose data are tabulated here have themselves discussed at length). For example, how many pairs of interacting individuals should be studied before one has some assurance that a useful estimate has been obtained of the cost of a given mutualism? The data in Table 1 were drawn from studies using as many as 600 and as few as 10 fruit per species; several authors did not report sample sizes. Furthermore, how many populations should go into calculating this average? Studies of yuccas by Keeley *et al.* (1984, 1986) and Addicott (1986), of globeflowers by Pellmyr (1989), and senita by Holland and Fleming (1999) clearly demonstrate that great population-level variation can exist in the costs of mutualism.

To address these sampling issues, it is essential to have some idea of the variables that generate variation in costs. In fact, a number of arguments can be made for the value of identifying factors that lead costs to vary within a single mutualism. For ex-

ample, this information is necessary for predicting the range of conditions under which costs will exceed benefits, and hence when an interaction will function antagonistically rather than mutualistically (Thompson, 1988; Bronstein, 1994b). This information is also valuable for generating predictions about when selection can act to lower the costs of mutualism.

With regard to *F. aurea*, the extreme variability of the cost of seed loss is as least as striking as the high average (Fig. 1). On average, 47 seeds are replaced by pollinator offspring, but the range is from zero to 229. How much of this variation can we explain, and what do the sources of that variation tell us about this mutualism that an average measure cannot reveal?

As a first approach to this problem, we examined whether differences in costs could be explained in part by differences in the figs themselves. Single pollinators (foundresses) were introduced into 60 receptive *F. aurea* figs on six trees during May–July 1991–1993. (Methods are described in Bronstein *et al.*, 1998.) All foundresses introduced to figs on a single tree came from a single pollen source, a randomly chosen tree from the same population. Figs on each marked branch had been mapped and labeled prior to the introductions. Hence, we knew the location of each fig relative to the nearest leaf (from which it might obtain its resources for seed and wasp maturation) and the nearest neighboring fig (with which it might compete for those resources). Figs were covered to exclude oviposition by non-pollinator species, then collected several weeks later when the seeds and pollinator offspring were mature. We then counted seeds, wasps (by sex), and vacant ovaries in each fig. To look at the factors accounting for wasp numbers, we designed an ANCOVA analysis in GLIM; female flower number was used as a covariate since it was found to be highly correlated with fig contents. To look at what might account for the variation in flower numbers itself, we used a fixed-effects ANOVA. In each case, the best model was determined by using a step-forward selection of variables. At the end of the analysis, we

TABLE 2. Wasp production per fruit: GLIM variance-covariance analysis of the numbers of wasp offspring maturing in 60 single-foundress *Ficus aurea* figs, as a function of four independent factors. See text for definition of the factors.

Factor	<i>r</i> (estimated)	df	F	<i>P</i>
Female flowers	+0.405 ± 0.108	1, 60	55.9	≤0.0001
Crop		5, 55	4.32	<0.002
Leaf/no leaf		1, 54	1.39	0.24
Single/paired		1, 54	1.29	0.26
Crop × female flowers		5, 50	2.21	0.07

verified that all variables were still significant in the final model.

In these single-foundress figs, by far the greatest variation in wasp numbers—that is, in the cost of the mutualism—was accounted for by the number of flowers per fig (Table 2): figs that contained more flowers lost more seeds to the pollinators' offspring. Once this variable was removed statistically, there was an important residual effect of crop (a composite variable incorporating time of year, maternal tree, and paternal tree, *i.e.*, the natal tree of the pollinators we introduced). Flower numbers themselves varied significantly with crop and with the position of the nearest leaf: figs located adjacent to leaves contained significantly more flowers (Table 3). In single-foundress figs, then, the absolute magnitude of seed loss reflected traits of the maternal trees themselves. This was not an inevitable result: seed loss might, for instance, have been a function only of the foundresses' own fecundities.

In our study population, the modal fig is entered by a single foundress. However, more than half are entered by more than one and up to at least 24 foundresses per fig (Bronstein and Hossaert-McKey, 1996). For this reason, we conducted a number of experiments similar to those described

above, but in which seed and wasp production were compared between figs entered by single and multiple foundresses (Anstett *et al.*, 1996; Bronstein *et al.*, 1998). The cost of this mutualism was always found to vary with the number of foundresses entering the fig. For example, foundress number accounted for most of the variation in wasp offspring production when single-foundress and five-foundress figs were compared: five-foundress figs produced about twice as many wasps and half as many seeds (Anstett *et al.*, 1996).

A discussion of the ecological and evolutionary implications of these results lies beyond the scope of this paper (but see Anstett *et al.*, 1996; Bronstein and Hossaert-McKey, 1996; and Bronstein *et al.*, 1998). Here, I will simply highlight two observations about the costs of mutualism that the averages shown in Figure 1 could not reveal. First, the exact magnitude of seed loss within a fig is related to that fig's own morphological traits. Second, this cost also varies with the number of mutualists attracted. Seed loss rises and then probably levels off as more and more pollinators enter a given fig. Generally similar patterns have been documented now for several other fig species (Cook and Power, 1996; Nefdt and Compton, 1996; Herre and West, 1997; Herre, 1999).

The problem of interpreting the significance of a cost

The use of the term "cost" implies something that is to be avoided if at all possible. In theory, lowering the costs should increase the net beneficial effect of a mutualism, since net benefit equals the gross benefits of the interaction minus its costs. Consequently, the recent literature on mu-

TABLE 3. Female flower numbers: GLIM variance-covariance analysis of the number of female flowers per fig in 60 single-foundress *Ficus aurea* figs, as a function of three independent factors. See text for definition of the factors.

Factor	df	F	<i>P</i>
Crop	5, 56	10.3	≤0.0001
Leaf/no leaf	1, 55	18.2	≤0.0001
Single/paired	1, 54	3.36	0.07

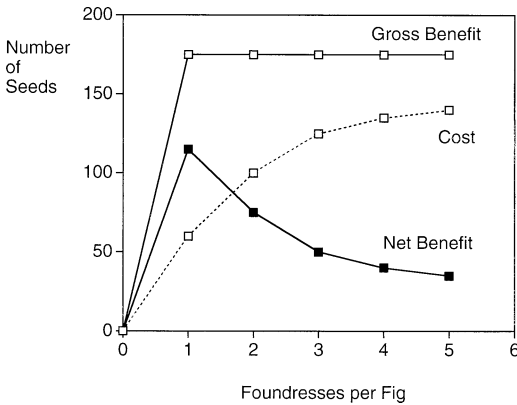


FIG. 2. A graphical model of costs and benefits of mutualism to *Ficus aurea* female function (seed production). Gross benefits quickly saturate since a single foundress imports sufficient pollen into a fig to initiate a full complement of seeds; costs (seed loss to foundress offspring) rise and then saturate as available oviposition space fills up. The net benefit (*i.e.*, gross benefits minus costs) is therefore maximal when a single foundress enters each fig.

tualism has dealt extensively with how organisms might be able to reduce the costs of the mutualisms in which they are involved (*e.g.*, Johnson *et al.*, 1997; Axén and Pierce, 1998; Addicott and Bao, 1999; Bultman *et al.*, 2000).

If this view of mutualism were accurate for monoecious fig/pollinator interactions, then we might conclude from the previous section that (from the perspective of the plant) the ideal number of foundresses that should enter a *F. aurea* fig would equal one. The graphical model shown in Figure 2 illustrates the logic underlying this conclusion. A single pollinator imports sufficient pollen into an individual fig to initiate a full complement of seeds (Anstett *et al.*, 1996). That is, seed set is not pollen-limited within a fig, as long as at least one pollinator enters. Hence, gross benefits rise sharply and then plateau even though more foundresses import more pollen into the fig. Costs also rise with foundress number, although more slowly, and then level off. Subtracting costs from gross benefits, we would conclude that seed production per fig is highest when a single foundress is allowed access. That is, the net benefits curve is unimodal.

This analysis makes two assumptions.

First, it assumes that, like seed quantity, seed *quality* does not rise with an increased diversity of pollen imported into the fig. This assumption seems reasonable. *F. aurea* seed set and germination rate are indistinguishable between experimentally outcrossed and self-fertilized figs (Hossaert-McKey and Bronstein, 2001). If seed quality doesn't vary between those treatments, it seems unlikely that it would vary perceptibly according to which outcrossed individual contributed pollen.

The second assumption underlying the interpretation of the graphical model is that the evolutionary interests of the fig are directed towards maximizing seed production. This assumption is deeply flawed. *Ficus aurea* is monoecious: it reproduces both as a female (via seed production) and as a male (via pollen donation). But in monoecious figs, the only possible pollen vectors are the seed-consuming female offspring of the pollinators! Hence, the *benefit* of success via the male reproductive function is directly achieved via a *cost* to the female reproductive function.

As it happens, *F. aurea*'s pollen donation success is unlikely to be maximal at the same number of foundresses per fig that maximizes seed production. A graphical model illustrating this point is shown in Figure 3. Once again, it is possible to sketch curves of gross benefits, costs, and net benefits as functions of foundress number per fig. Gross benefits to male function are equal to the number of offspring that pollinators deposit in a fig; note that this male-function gross-benefits curve is identical to the female-function costs curve shown in Figure 2. Costs to male function are the number of those pollinator offspring that are male, since these individuals do not act as pollen vectors. (Fig wasp sex ratios are highly female-biased, but this bias becomes progressively less prominent as the number of foundresses per fig increases, in general accord with predictions from local mate competition theory [Herre, 1985]. This explains why the male-function cost curve is generally very low, but rises with foundress numbers.) Subtracting costs from gross benefits, we see that net benefits in terms of pollen donation for an *F. aurea*-

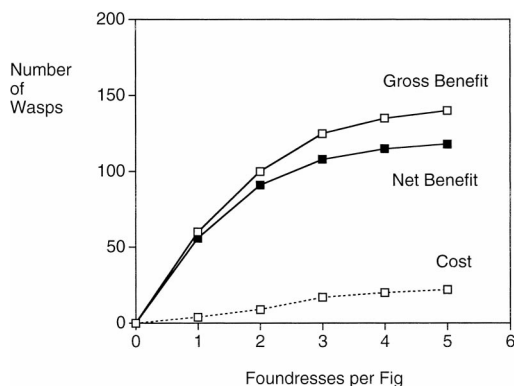


FIG. 3. A graphical model of costs and benefits of mutualism to *Ficus aurea* male function (pollen donation). Gross benefits equal all foundress offspring, while costs equal the subset that are male (and hence are not pollen vectors). The net benefit (*i.e.*, gross benefits minus costs, or the foundress' female offspring) approaches an asymptote when about 4–6 foundresses enter each fig. This net benefit curve is the same as the cost curve in Figure 2.

like fig only begins to level off at around four foundresses, much higher than the number that maximized female success (Fig. 2).

This analysis highlights a fundamental complication of comparing the cost of pollination between monoecious figs and other plants. In no other plant species—not even those pollinated by other seed parasites—are the cost of seed consumption and the benefit of pollen donation functionally coupled. Recognizing this unique feature of figs sheds light on certain striking differences among pollinating seed parasite systems. For example, it is well-known that certain yuccas selectively abort developing fruits in which pollinator offspring have inflicted particularly high costs (Pellmyr and Huth, 1994; Addicott and Bao, 1999). Despite some claims in the theoretical literature, figs appear never to do this (Bronstein, 1992). The fact that fruit abortion would cause figs but not yuccas to sacrifice part of their pollen-donation success is certainly part of the explanation for this difference. The implication is that seed loss is so high in monoecious figs (Table 1) because it is an inescapable byproduct of adaptations allowing these plants to achieve high success as pollen donors.

To summarize, exploration of the complex correlates of one particularly easily measured cost raises more doubts about how to treat the costs of mutualism in a comparative context. At the same time, however, it opens up diverse new questions about the evolution of mutualism, and may help explain differences among mutualisms that superficially appear quite similar.

The problem of a unilateral measure

Tabulating and comparing costs of mutualism can reveal some interesting patterns, but it is a decidedly one-sided enterprise. For example, in Table 1, costs of pollinating seed parasite mutualisms are compared strictly from the plant perspective. We might come up with a very different assessment of costs of these mutualisms were we to compare them from the perspective of the insect partners. Those costs are largely unknown, although Pellmyr (1997) has argued that they are probably quite low.

At least from the perspective of the evolutionary dynamics of mutualism, however, it is most interesting to compare costs between the two partners in a single mutualism, rather than across single partners from many mutualisms. In this paper I have frequently referred to “the cost of mutualism,” but this is actually a very misleading phrase: costs will almost inevitably differ both in nature and in magnitude for the two partners. In fact, the cost of mutualism to one species often translates directly into the *benefit* of mutualism for its partner, not unlike the coupling we have just seen to exist between the cost of mutualism to figs' female function and its benefit to figs' male function. For example, energetic investment into nectar production is an important cost of biotic pollination to many plants; in contrast, energy gained from consuming that nectar is a benefit of that association from the perspective of their pollinators. In theory, a plant that produced more and more nectar would experience a greater and greater cost, while the animal that collected that nectar would enjoy a greater and greater benefit. Consequently, optimal nectar production rate will likely differ from the perspective of the plant and of its pollinator

(Rathcke, 1992). Logic like this has given rise to the general idea that conflicts of interest underlie most mutualisms, and are a primary evolutionary force that generates their dynamics (Thompson, 1982; Janzen, 1985; Bronstein, 1994a; Frank, 1996; Herre *et al.*, 1999).

Figures 2 and 3 hint at the rich complexity of conflicts between monoecious figs and their obligate pollinators. As we have seen, these figs benefit from the mutualism by producing some balance of seeds and female pollinator offspring, which cause seed loss but which also transfer pollen. The wasps benefit by producing female offspring (which are part of both the benefit and the cost of the mutualism to the plant), but male offspring as well (which are only part of the plant's cost of mutualism). At first glance, the only thing that seems clear is that a fig does not benefit when its pollinator produces sons. Yet it is not that simple, because in most species, the pollen-carrying female offspring cannot escape the fig by themselves: their brothers must chew an exit passage for them. It is little wonder that consideration of how the diverse conflicts and concordances of interest in this mutualism play out evolutionarily is generating a vigorous literature (Herre, 1989, 1999; Ganeshaiah *et al.*, 1995; Anstett *et al.*, 1996, 1997; Herre and West, 1997). Similar conflicts of interest and the costs that generate them are now being described for a growing number of mutualisms (*e.g.*, Patel *et al.*, 1995; Frank, 1996; Smith and Smith, 1996; Willmer and Stone, 1997; Yu and Pierce, 1998; Wagner, 2000; Jaeger *et al.*, 2000; Denison, 2000; Weiblen *et al.*, 2001).

Costs, then, lie at the heart of the conflicts of interest that underlie mutualism, and hence contribute critically to the evolutionary dynamics of these interactions. Studying this aspect of the cost of mutualism, however, demands comparisons not across individual partners in different pairwise interactions, but rather between members of a single interacting pair.

CONCLUSIONS

Mutualisms have long been perceived as poorly studied relative to their true biological significance. This attitude is not well-

justified based on the amount of attention paid to these interactions in recent years: almost a quarter of all published studies on interspecific interactions now investigate a mutualism (Bronstein, 1994a, 2001a). The large majority of these studies, however, describe mechanistic details of individual mutualisms, rather than testing hypotheses or searching out broad patterns. In fact, there have been very few agreed-upon general themes than inform our understanding of mutualisms that contrast greatly in natural history.

I have argued here that the idea that mutualisms involve costs as well as benefits is one such theme. Costs set limits on when mutualisms are likely to evolve, and where they will be able to stably persist. Costs lie at the root of the conflicts of interest between mutualists that may be a major driving force in the evolution of their interactions. The existence of costs also helps us understand where and when organisms that "cheat" by avoiding investment into mutualism will enjoy an advantage. Finally, this concept serves as a major link between mutualisms and far better-studied antagonistic (plus/minus) interactions such as herbivory, predation, and parasitism. Recognizing that mutualisms have costs immediately raises the question of when, why, and how these costs will exceed the better-known benefits, in other words, when they will function as antagonisms. From there, it is only a small step to the view that forms of interaction traditionally regarded as quite separate may in fact grade smoothly into one other, a perspective that itself raises diverse new ecological and evolutionary questions. Hence, the cost of mutualism is a central issue for the study of species interactions as a whole.

In light of the centrality of this issue, it is surprising that only a handful of hypotheses have ever been offered to explain which kinds of mutualisms will have greater and lesser costs, and which kinds of costs will themselves be greater and lesser. The sobering lesson from this paper is, I believe, that such hypotheses, once they have been formulated, are likely to be very difficult to test rigorously via comparative studies. Using the example of one form of mutualism

with a particularly easily recognized cost, I have discussed four difficulties with interpreting costs: problems of knowing how to measure their magnitude accurately; problems associated with using average estimates in the absence of data on sources of variation in costs; complications arising from the complex correlates of costs, such as functional linkages between costs and certain benefits; and problems arising from considering the cost of mutualism as a unilateral issue in what is fundamentally a reciprocal interaction. I would note that each of these same difficulties is equally likely to pertain to comparative studies of the much better-known *benefits* of mutualism.

On the other hand, examining these concerns has pointed to a number of fascinating and important phenomena that will bear a closer look in the coming years. First, the magnitude of costs that an individual mutualist experiences is likely to be a function of its own traits, its partner's traits, and the abundance of its partner. There is likely to be an optimal number of partners that maximize the net benefit of mutualism, although whether mechanisms have evolved that increase the likelihood of associating with that number of partners is an open question. Second, natural selection may be expected to reduce the costs of mutualism, but whether or not this is likely depends on, among other things, whether those costs are functionally linked to the benefits of mutualism experienced both by that organism and by its partner. Finally, links between the costs experienced by one organism and the benefits enjoyed by its partner generate conflicts of interest that seem likely to drive the evolutionary dynamics of these interactions. Each of these phenomena need to be explored via studies within individual pairwise interactions. I began this paper by arguing the need for studies of general themes that cut across single mutualisms. The somewhat paradoxical conclusion is that those themes may in fact best be addressed by further investigation of single mutualisms.

ACKNOWLEDGMENTS

The data on *Ficus pertusa* presented here were collected and analyzed in collabora-

tion with Drs. Martine Hossaert-McKey and Marie-Charlotte Anstett; they also played a major role in interpreting their evolutionary significance. I thank Allen Herre, Finn Kjellberg, and Olle Pellmyr for access to unpublished information, and Bill Morris, Nat Holland, Ted Fleming, Greg Dimijian, and Goggy Davidowitz for comments on the manuscript. My studies of fig/pollinator interactions have been supported by grants from NSF (BSR 9007492, BSR 9407615, and INT 9218330) and NATO (CRG 921294). Preparation of the manuscript was supported by a grant from NSF (POWRE 9973521) and the hospitality of the Duke University Department of Zoology.

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