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# Costs of two non-mutualistic species in a yucca/yucca moth mutualism

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**Abstract** Mutualisms often involve significant costs for participants. Costs are inflicted by mutualists themselves, as well as by associated, non-mutualistic species. These costs are rarely quantified, however, particularly the ones extrinsic to the pairwise interaction. We compare costs inflicted by an obligate mutualist pollinator and two common exploiters of an Arizona yucca over a 2-year period. The magnitude of seed damage from seed and fruit-feeding beetle larvae (*Carpophilus longus*, Nitidulidae) was similar to damage from the seed-eating larvae of *Yucca schottii*'s pollinator moth *Tegeticula yuccasella* (Prodoxidae), averaging about 15 seeds destroyed per fruit in each case. The two seed predators usually fed within the same fruits, although rarely side by side. In contrast, the presence of fruit-galling moth larvae (*Prodoxus y-inversus*, Prodoxidae) appeared to benefit the yucca: individual *Tegeticula* destroyed only half as many seeds in galled fruits as they did in ungalled fruits. We discuss three general implications of these results. Firstly, the costs of non-mutualists to the two mutualistic partners are not necessarily parallel. Secondly, measurable costs of non-mutualists do not necessarily translate into an impact on the success of the mutualism itself, because they may be incurred after mutualistic activities take place. Finally, the costs of mutualists to each other can differ substantially depending on the presence or absence of non-mutualistic species.

**Key words** *Yucca* · *Tegeticula* · Yucca moth · Mutualism · Seed predation

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## Introduction

Mutualisms are interactions that confer net benefits on two species. While the nature of these benefits (e.g., pollination, seed dispersal) has long received substantial attention, it has been less widely recognized that mutualism can also impose substantial costs on the partners. These include costs of locating, attracting, and/or rewarding the partners that confer benefits. Costs like these arise from forces intrinsic to the mutualistic interaction. Many costs of mutualism originate from extrinsic phenomena, however. For example, foraging by other species (e.g., nectar robbers and fruit predators) can reduce the rewards available to mutualistic partners, causing mutualists to abandon the reward producer. Certain partnerships persist only under the restricted set of extrinsic conditions in which benefits of the interaction exceed its costs (Thompson 1988; Cushman and Addicott 1991; Bronstein 1994). These observations suggest that an understanding of mutualism critically depends on knowledge of important extrinsic factors, including the presence of other species. Nonetheless, the community context in which mutualisms take place remains very poorly known, with the focus almost exclusively on the pair of mutualistic species themselves.

Costs of mutualism have been unusually well-studied in the interaction between yuccas (*Yucca* spp., Agavaceae) and their obligate yucca moth pollinators (*Tegeticula* and *Parategeticula*, Prodoxidae, Lepidoptera) (Keeley et al. 1984; Addicott 1986; James et al. 1994; Pellmyr and Huth 1994; Ziv and Bronstein 1996). Female moths both pollinate and oviposit within the flower; their offspring feed on a large fraction of the developing seeds. Many of the costs and benefits of this interaction can therefore be expressed in a single currency, numbers of seeds: yuccas benefit by maturing seeds and are harmed by having seeds eaten, while yucca moths benefit by consuming those seeds. Yuccas show several traits that act to reduce costs inflicted by their pollinators without discouraging attention from them.

Fruits containing particularly large numbers of moth eggs may be aborted (Pellmyr and Huth 1994; Richter and Weis 1995), infertile seeds may be present within the fruit in an arrangement that protects some fertile seeds from being consumed (Ziv and Bronstein 1996), and thick membranes restrict moths to feeding in only one of the six locules (Ziv and Bronstein 1996).

The ecology and evolution of this mutualism can only be understood in light of the substantial costs of seed consumption. However, not all yucca seed consumers are mutualists. Yucca seeds are also fed upon by an array of non-mutualistic insect species (Addicott et al. 1990; Pellmyr et al. 1996), as well as by individuals of the mutualist species that fail to pollinate under certain circumstances (Riley 1892; Tyre and Addicott 1993; Addicott and Tyre 1995). Other insects, many of them specialists, are known to consume or gall the yucca fruit (Powell 1984, 1989), feed on yucca flowers (Udovic 1986; Pellmyr and Huth 1994), and parasitize yucca moth larvae (Powell 1984; Force and Thompson 1984). The costs of these organisms to yuccas have only been measured in one instance: Pellmyr et al. (1996) showed that on a per-individual basis, certain non-mutualistic moths inflict far greater costs on one yucca than do the mutualists themselves. If these results are typical, then the cost of this mutualism, as well as putative adaptations to reduce it, may be interpretable only in the context of the broader community of exploiters.

The purpose of this study was to compare costs inflicted by two abundant exploiters and by the pollinator moth (*Tegeticula yuccasella*) of one yucca species, *Yucca schottii*. One non-mutualistic species is a beetle (*Carpophilus longus*, Nitidulidae) that consumes seeds and fruit. The other (*Prodoxus y-inversus*, Incurvariidae), a moth closely related to the pollinator, initiates and feeds within woody galls in the fruit tissue. We report on the relative abundance of the three insects over two seasons, and the relative numbers of seeds that *Y. schottii* loses to each of them. We also examine evidence for interactions among these insects, and explore how these interactions may affect the success of the yucca/yucca moth mutualism.

## Methods

### Study system

*Yucca schottii* (Engelmann) is a forest species that occurs in the mountains of Arizona at 1200–2400 m elevation, from the lower limits of oak woodland to the pine forests. It ranges from the Santa Catalina Mountains north of Tucson, Arizona, to southwestern New Mexico and northern Sonora and Chihuahua, Mexico (Powell 1984).

This study was conducted at Madera Canyon, located in the Santa Rita Mountains 55 km southeast of Tucson.

Like most yuccas, *Y. schottii* is perennial and polycarpic. The inflorescence bud appears about mid-June and the scape rapidly elongates, reaching the point at which flower buds are ready to begin opening after 12–14 days. In the study population, the mean flowering period for each plant is approximately 13.4 days, with a total of 26 days for the entire population (Z. Forsman and J. Bronstein, unpublished data). Following pollination, fruits reach full size in 25–30 days and seed maturation requires an additional month (Powell 1984).

*Y. schottii* is unusual among yuccas in being pollinated by two different yucca moths, *Tegeticula yuccasella* (Riley) and *Parategeticula pollenifera* (Davis). Nearly all yucca species are associated with *Tegeticula* moths; *P. pollenifera* is found only on *Y. schottii* and *Y. elephantipes* (Davis 1967). Here we focus on the mutualism between *Y. schottii* and *T. yuccasella*, since *P. pollenifera* was largely absent from our site during the two years of this study (Z. Forsman, Y. Ziv, and J. Bronstein, personal observations).

The pollination behavior of *Tegeticula yuccasella* on *Y. schottii* has been described by Powell (1984). Briefly, adults emerge from pupation in the ground near a yucca plant around the time when the plants come into bloom. They mate within the yucca flowers. The female then locates a freshly opened yucca flower and actively collects pollen. She then flies to another receptive flower, enters it, and, aligning herself appropriately, deposits an egg in one or more of the six locules. Subsequently, she deposits some or all of her pollen load in the stigmatic groove. Each larva develops within a single locule, consuming seeds in its immediate vicinity; it feeds preferentially on fertile seeds, avoiding the 15–40% of seeds within the locule that are infertile (Ziv and Bronstein 1996). After approximately 4 weeks, the larva chews a hole through the fruit wall, emerges, and drops to the ground. It forms a cocoon in the soil and remains there at least until the following summer.

The genus *Prodoxus* is one of the closest relatives of the two yucca moth genera (Brown et al. 1994). *Prodoxus* species feed within leaves or in the sterile tissue of the yucca inflorescence (either within the main scape or more rarely the fruit), rather than on yucca seeds, and do not pollinate their host plant (Powell 1984, 1989; Wagner and Powell 1988). *P. y-inversus* Riley, a fruit-feeding species, is restricted to *Y. schottii* and *Y. baccata*; Powell (1984, 1989) has described its natural history. Adults oviposit into recently initiated fruits several days after *Tegeticula* and *Parategeticula* activity. Larvae develop in the fleshy tissue immediately outside the seed-containing locules. Feeding occurs in the direct vicinity of their oviposition site, within spherical woody galls apparently initiated by larval secretions. Galls reach 8–10 mm in diameter, growing tightly apressed to the outside of the locule but not interfering with seed development in any obvious way (Y. Ziv, personal observation). In October, larvae enter pupation within the galls. Soon afterwards, the fruits drop from the plant. As the fruits decay or are fed upon by animals, the woody galls remain intact, scattered in the forest litter. The moths spend winter in diapause, normally completing development the following season. However, diapause can be extremely prolonged, lasting as long as 17 years (Powell 1989).

*Carpophilus* beetle larvae have frequently been noted in mature fruits of *Y. schottii* and other yucca species, sometimes in very high numbers (Connell 1956; Davis 1967; Powell 1984). However, their natural history is essentially unknown. Davis (1967) believed that larvae first mine in *Y. schottii's* petals, then, when the petals have decayed, commence burrowing in young fruit. Powell (1984) never found beetles in immature *Y. schottii* fruits, and suggested instead that they invade mature fruits via the pollinator larvae's emergence holes. However, as we document below, *Carpophilus longus* also occurred in fruits never occupied by moth larvae. Damage caused by these beetles has not to our knowledge been previously described or quantified.

In September 1992 and August 1993, we collected *Y. schottii* fruits from around the Bog Springs Campground in Madera Canyon. We collected 4–8 fruits from each of four plants in 1992 (for a total of 20 fruits) and 5–24 fruits from each of eight plants in 1993 (for a total of 116 fruits). Fruits were generally collected after exit holes of moth larvae were found, but before fruits fell or were removed from the plant by frugivores.

In the laboratory, we dissected each fruit and mapped the sequence of different seed types within each of the six locules (see Ziv and Bronstein 1996 for further details). Seeds were first designated as fertile or infertile: fertile yucca seeds are thick and black, whereas infertile ones are thinner and white. Each seed was then classified as uneaten or eaten, and, if eaten, whether the damage was inflicted by a yucca moth or beetle. A seed fed upon by a yucca moth had a large hole bored through it; the series of adjacent seeds bored through by yucca moths will be referred to hereafter as an eaten-seed sequence. Each eaten-seed sequence was usually associated with a feeding moth larva, a dead larva, or a larval exit hole. In contrast, beetle-fed seeds had small punctures, and they and the surrounding fruit tissue were often partially or entirely rotten; many of these damaged areas had beetle larvae present within them. If both beetle and moth larvae were present either within or close to a given eaten seed, this was recorded. The organism responsible for seed damage was recorded as unknown when there was any ambiguity. Fruits whose sources of damage were unknown were excluded from analyses where appropriate. An index of damage was recorded for each eaten seed (1, 1–25% eaten; 2, 26–50% eaten; 3, 51–75% eaten; 4, 76–99% eaten); it should be noted that regardless of the amount of perisperm removed, the embryo was destroyed in all cases (authors, personal observations).

In addition, we noted the presence of any other insects and (in 1993 only) the presence of woody galls formed by *Prodoxus y-inversus*. We did not attempt to count the number of beetles per fruit; *Carpophilus* larvae are very small, may enter and leave the fruit frequently while feeding, and can occur in numbers as high as 300 per fruit at this site (H. Harvey and J. Freeh, unpublished work). Nor did we count the number of *Prodoxus* galls per fruit. We therefore use presence/absence data to quantify attack by these insects.

In our analyses, we first compared proportions of fruits containing *Tegeticula* (mutualist) moths, *Prodoxus* (galler) moths, and *Carpophilus* beetles, and examined whether there were any significant associations among them. We then contrasted patterns and levels of seed damage between *Tegeticula* and *Carpophilus*, and examined how the presence of *Prodoxus* (which does not eat seeds) might affect costs of these insects to the plant. We pooled data across plants and, in some analyses, across years. However, it should be noted that levels of attack by each insect can differ substantially both in space and in time (Ziv and Bronstein 1996; J. Freeh, H. Harvey and J. Bronstein, unpublished work; this paper).

## Results

### Levels of attack by mutualists and non-mutualists

Percentages of sampled fruits exploited by *Tegeticula, Prodoxus,* and/or *Carpophilus* are shown in Table 1. In both 1992 and 1993, fruits were most commonly inhabited by larval yucca moths (*Tegeticula*). However, they were not ubiquitous: 28% (in 1992) and 56% (in 1993) of fruits contained no evidence that yucca moths had matured within them, an observation not uncommon in studies of this and other yuccas (Addicott 1986). Furthermore, rates of fruit occupancy by the non-mutualistic beetles and (in 1993) gall-forming moths were nearly as high as occupancy by the mutualist yucca moths. Attack by both *Tegeticula* and *Carpophilus* was more common in 1992 than in 1993, considering the proportions of fruit containing each insect (Table 1). We do not have data on relative beetle numbers, but the number of *Tegeticula* larvae per infested fruit was also higher in 1992 than in 1993 (3.7 vs. 1.9 larvae per fruit; *t*-test, $t = 3.305, P = 0.0016, df = 60$).

**Table 1** Sample sizes and levels of *Yucca schottii* fruit attack by three insects. Percentages are calculated from fruits that had unambiguous patterns of damage. *Prodoxus y-inversus* damage was recorded only in 1993

| | 1992 | 1993 |
|---|---|---|
| Number of plants sampled | 4 | 20 |
| Number of fruits sampled | 20 | 116 |
| Number of fruits with unambiguous damage pattern | 18 | 100 |
| *Fruits damaged by:* | | |
| *Tegeticula* (mutualist) | 72.2% | 44.0% |
| *Carpophilus* (beetle) | 50.0% | 36.0% |
| *Prodoxus* (galler) | | 42.0% |
| No damage | | 25.0% |
| *Damaged fruits containing:* | | |
| *Teg.* only | | 11.0% |
| *Carp.* only | | 9.0% |
| *Prod.* only | | 17.0% |
| *Teg.* + *Carp.* | | 13.0% |
| *Teg.* + *Prod.* | | 11.0% |
| *Carp.* + *Prod.* | | 5.0% |
| *Teg.* + *Carp.* + *Prod.* | | 9.0% |

Each of the three insects sometimes occurred alone within fruits, as well as in every possible combination (Table 1). *Carpophilus* beetles and *Tegeticula* moths occurred together much more often than expected by chance (1992 and 1993: chi-square test, $\chi = 40.77$, $P < 0.0001, n = 136$). In contrast, *Prodoxus* was not significantly associated with either *Tegeticula* (1993: $\chi^2 = 0.626, P = 0.73, n = 116$) or with *Carpophilus* (1993: $\chi^2 = 0.325, P = 0.85, n = 116$). In 1993, when all three insects were sampled, 25% of fruits contained no evidence that either *Tegeticula*, *Prodoxus*, or *Carpophilus* had fed within them.

### Seed damage in fruits attacked by mutualists and non-mutualists

Pooling across fruits, 12.4% of all *Y. schottii* seeds produced in 1992 and 7.3% produced in 1993 were destroyed by either a yucca moth or a beetle. Seed loss differed significantly between years. There was more damage to all seeds (*t*-test, $t = 2.67, P = 0.008, df = 134$) and to fertile seeds ($t = 2.71, P = 0.007$, $df = 134$) in 1992, the year with higher rates of infestation by both *Tegeticula* moths and *Carpophilus* beetles, than in 1993.

Total levels of seed damage were quite similar between the two insects. Of all destroyed seeds, 46.0% could be attributed to feeding by yucca moths and 42.5% to feeding by beetles; another 11.5% showed some evidence of damage by both insects. Of all seeds eaten by these insects, 83% were fertile. Patterns of damage to fertile seeds reflected those to all seeds: of the fertile seeds that were destroyed, 44.5% were eaten by yucca moths, 43.2% by beetles, and 12.1% by both insects. These data slightly underestimate the level of damage caused by each insect, since fruits were dissected while 22% of yucca moths, as well as many beetles, were still feeding. Furthermore, fruits with beetle damage often had large rotten spots (Y. Ziv and Z. Forsman, personal observations), suggesting an additional cost to beetle feeding not measured in our analyses.

The similarity in magnitudes of damage between mutualist moths and non-mutualist beetles is also seen when considered on a per-fruit basis (Figure 1). (We excluded fruits that contained feeding yucca moths from this analysis, using only those fruits from which moths had exited or died while feeding; we used data from 1993 only, due to small sample sizes in 1992.). The total number of seeds consumed in fruits occupied by *Tegeticula* moths only, beetles only, or both *Tegeticula* and beetles did not differ significantly from one another, averaging 15.4 seeds/fruit across all categories. Nor did the number of fertile seeds eaten (averaging 12.4/fruit) differ across these three categories. The trend in both cases was for fruits with *Tegeticula* only to have the fewest damaged seeds, those with beetles only to have intermediate numbers, and those with both insects to have the most damaged seeds (Fig. 1).

## Spatial arrangement of seed damage from mutualists and non-mutualists

Yucca moth (*Tegeticula*) larvae fed on a series of adjacent seeds within a locule, only rarely moving successfully between locules; there was usually a single yucca moth larva per locule (Ziv and Bronstein 1996). In the absence of *Carpophilus* beetles, individual yucca moths tunneled through 1–13 seeds ($5.2 \pm 2.4$, $n = 72$), of which 0–10 were fertile ($4.2 \pm 2.2$, $n = 72$), before they exited the fruit.

In contrast to yucca moths, *Carpophilus* beetle larvae moved freely between locules of the fruit, and possibly between fruits as well. Membranes separating the locules, as well as the fruit wall itself, were found perforated with many tiny holes when beetles were present. Up to five beetle-fed sequences could be found within a single locule. Because of their evidently great mobility and occasionally very high numbers within a fruit, we were not able to examine damage on a per-beetle basis. However, comparisons between eaten-seed sequences were possible. Sequences eaten by beetles were significantly shorter than those eaten by moths that had survived to exit the fruit (an average of 5.2 vesus 3.5 seeds eaten; *t*-test, $t = 4.13, df = 203, P < 0.0001$). Although the range of lengths of eaten-seed sequences was nearly identical for the two insects, most beetle-fed sequences were only a single seed in length, whereas lengths of moth-fed sequences were roughly normally distributed.

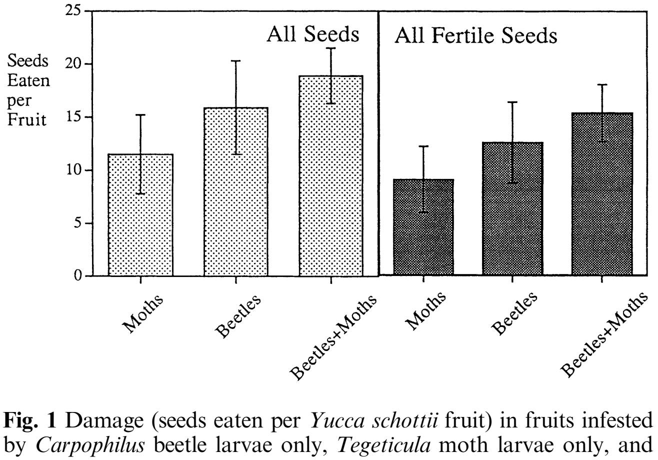

**Fig. 1** Damage (seeds eaten per *Yucca schottii* fruit) in fruits infested by *Carpophilus* beetle larvae only, *Tegeticula* moth larvae only, and the two insects in combination. Damage to all seeds (fertile + infertile) is shown on the *left* and damage to fertile seeds is shown on the *right*. Damage was similar across the three classes of fruit (all seeds: ANOVA, $F_{2,44} = 1.10$, $P = 0.341$; fertile seeds: $F_{2,44} = 1.02$, $P = 0.370$)

Although *Tegeticula* moths and *Carpophilus* beetles usually occurred together in fruits (see above), they were only rarely found in the same eaten-seed sequence. *Tegeticula* accounted for 33.0% and beetles for 61.4% of all eaten-seed sequences in fruits they shared ($n = 218$ sequences); the insects were found together in the remaining 5.5% of eaten sequences. Eaten-seed sequences in which both species were present averaged 7.2 seeds in length, significantly longer than those in which either species occurred alone (*t*-tests, $P \leq 0.001$). Although seeds damaged by both moths and beetles had been noted during the dissections (see above), the amount eaten per fertile seed was found to be statistically similar in rows attacked both by moths and beetles and in rows attacked by beetles only (Mann-Whitney test, $U_{21,14} = 127, P = 0.50$). It is possible that beetles consume so little of each seed that our index of seed damage was unable to detect doubly damaged seeds; alternatively, such seed-sharing may be rare in nature.

## Seed Damage in the Presence of a Fruit Galler

*Prodoxus y-inversus* is a fruit galler that does not consume or otherwise damage yucca seeds. We examined whether the presence of this moth or its galls might influence the number of seeds fed upon by *Carpophilus* beetles and/or *Tegeticula* moths, which do consume seeds.

Fruits containing at least one *Prodoxus* gall in fact had significantly fewer total seeds destroyed (*t*-test, $t = 1.97, P = 0.050, df = 114$), as well as fewer fertile seeds destroyed ($t = 2.08, P = 0.039, df = 114$), than fruits lacking galls. This unexpected reduction in seed damage associated with *Prodoxus* was significant only in fruits in which *Tegeticula* had fed: in fruits infested by beetles but not *Tegeticula*, there was no difference in damage to all seeds ($P > 0.50$) or to fertile seeds ($P > 0.50$) depending on the presence or absence of galls, although the trend was again towards lower damage in the presence of galls. In contrast, in fruits containing *Tegeticula*, there was significantly reduced destruction of all seeds ($t = 2.568, P = 0.013, df = 47$) and of fertile seeds ($t = 2.445, P = 0.018, df = 47$) when galls were present. More than twice as many seeds were destroyed by *Tegeticula* when galls were absent as when they were present (15.6 versus 6.7 seeds eaten).

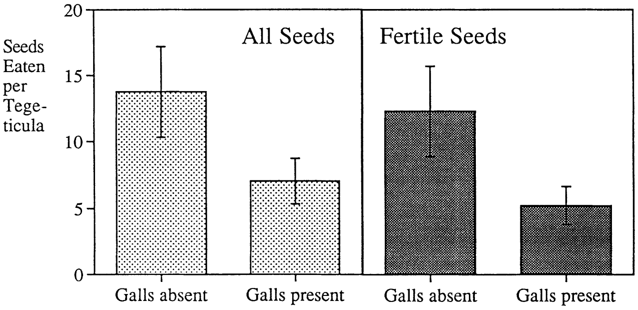

**Fig. 2** Seed damage per *Tegeticula* moth larva in relation to the presence of a fruit galler, *Prodoxus y-inversus*. *Tegeticula* surviving to exit the fruit ate fewer fertile seeds (*right*: *t*-test, $t = 2.20$, $P = 0.0431$, $df = 16$) and tended to eat fewer total (fertile + infertile) seeds (*left*: $t = 1.96$, $P = 0.0681$, $df = 16$) when feeding in fruits with galls

We further investigated possible causes of this reduced seed damage in galled fruits. *Tegeticula* larvae were no rarer in galled fruits than in ungalled ones, although there was a trend in this direction ($t = 1.724$, $P = 0.091, df = 47$). Nor was *Tegeticula* mortality associated with the presence of galls (chi-square test, $\chi^2 = 0.029, P = 0.865, n = 56$). Rather, each *Tegeticula* larva surviving to exit the fruit ate significantly fewer seeds when galls were present in the same fruit (Fig. 2). Larvae eating fewer seeds did not consume more of each seed. There was no significant difference in the average index of yucca moth seed damage between seeds in galled versus ungalled fruits (Mann-Whitney test, $U_{11,11} = 49, P = 0.45$); consistently, about 75% of an attacked fertile seed was consumed.

## Discussion

Pairwise interactions do not take place in isolation from their community context. The outcome of competitive interactions can be altered by the presence of a predator (Paine 1966), parasite (Price et al. 1986), or mutualist (Clay et al. 1993). Predator-prey interactions are often influenced by organisms at a third trophic level (Price et al. 1986). Mutualisms, in turn, attract species that can exploit the rewards offered to mutualists, without providing any service in return. Examples include certain hummingbirds and bees that obtain nectar without pollinating flowers (Inouye 1983), unaggressive ant species that exploit food rewards that swollen-thorn acacias offer their ant guards (Janzen 1975), and frugivorous birds that digest seeds rather than disperse them (Janzen 1981). The cost of such exploitation to the mutualists is potentially great. The reward-providing species loses its investment in the reward, which may not be renewable, and often the attention of its mutualist as well. The partner loses a necessary resource that may not be obtainable elsewhere.

Despite the potential significance of such exploitation of mutualism, its magnitude and importance in nature have as yet received scant attention (but see, e.g., Soberon and Martinez del Rio 1985; Bronstein 1991; West and Herre 1994; Addicott and Tyre 1995; Pellmyr et al. 1996). In part, this is related to difficulties of measuring the cost of exploiters, particularly relative to costs inflicted by the mutualists themselves. In many cases, the costs of exploitation (e.g., loss of a small amount of nectar to nectar-robbers) may be so slight as to have no measurable impact on the success of the mutualism. In other situations, however, the costs may be so great that it is impossible to understand the evolution and current function of certain traits except in light of this exploitation. For example, a variety of floral traits (Inouye 1983; Prys-Jones and Willmer 1992) and fruit traits (Cipollini and Stiles 1992; Sallabanks and Courtney 1992) have been interpreted as adaptations to exclude costly nonmutualistic species such as nectar-robbers and fruit predators. Furthermore, attempts to interpret mutualisms in terms of the costs mutualists are apparently willing to pay to receive service (e.g., Janzen 1979; Addicott 1986; Noë and Hammerstein 1994) may have to be significantly altered if much of the observed costs are actually attributable to non-mutualistic organisms.

One advantage that yuccas offer for quantifying the importance of such exploitation in nature is that the benefits of their mutualists, the costs of their mutualists, and the costs of some of their non-mutualistic exploiters can all be expressed in the same currency: numbers of intact, fertile seeds matured. This study was explicitly designed to compare the costs of mutualists versus nonmutualists. We found that ubiquitous seed-predator beetles inflicted damage on *Y. schottii* roughly equivalent in magnitude to the damage inflicted by the offspring of the mutualist pollinators. We have presented data here from two years, 1992 and 1993; similar results were obtained in smaller studies in 1994 and 1995 (B. McCormack and H. Harvey, unpublished data). These data probably underestimate beetle damage to the yucca, since (1) beetles continue to feed within fruits after moths depart and until fruits are removed or fall to the ground; and (2) beetle damage is associated with extensive fruit rot, which we did not attempt to quantify.

It is less clear whether the beetles also have negative effects on the yucca moths. Moths and beetles were positively associated within fruit, but tended to feed in different locations within those fruits. When they occurred together in the same eaten-seed sequence, that sequence was about 16% shorter than would be expected if damage from the two insects were simply additive (7.2 seeds vs. an expectation of 8.4 seeds; Fig. 2). This could indicate that beetles interfere with moth feeding, an effect that would be incidentally beneficial for the plant. However, there are at least two other explanations for this pattern: moths might interfere with beetle feeding, rather than vice versa, or fewer beetles might choose to feed alongside moths than away from moths. Further observations are required to separate these possibilities.

The impact of the fruit-galling moth *P. y-inversus* was quite different. Its presence within a fruit may, surprisingly, be beneficial to *Y. schottii*. This benefit arises because galling apparently reduces the cost of mutualism: when galls are present, individual yucca moth larvae destroy fewer seeds before leaving the fruit to pupate. Many questions remain about this unexpected positive effect of galling. First, its proximate mechanism is still unknown. There is no physical contact between the gall or galler and the feeding yucca moths. It is possible that galls interfere so much with moth exit from the fruit that moths avoid feeding in galled areas, departing the fruit early if necessary (much as they do when they encounter infertile seeds; Ziv and Bronstein 1996). Alternatively, galling may change the chemical content of the seeds. It remains to be investigated whether galling imposes any costs on the yucca, e.g., by causing fruits to be rejected by seed dispersers. Finally, the fitness costs to yucca moths of departing a galled fruit early, having consumed less than half the number of seeds they would in an ungalled fruit, have not yet been measured.

It is clear from this study that exploiters can have quite different impacts on each mutualistic partner. *Carpophilus* beetles have a negative effect on yuccas, but may actually be attracted to the fruit by the yucca's mutualistic moths; their presence has possibly no impact on the moths themselves. *Prodoxus* moths change yucca moth feeding behavior in a way that appears to be costly to yucca moths and hence beneficial to yuccas. These results are one more indication that the interests of mutualists are not parallel, and in fact often come directly into conflict (Axelrod and Hamilton 1981, Bull and Rice 1991; Thompson 1994). They also suggest that the magnitude of that conflict (in this case, the costliness of yucca moths to yuccas) can be a function of the presence of other species in the community.

Effects of exploiters on mutualist species do not necessarily translate simply into effects on the success of the mutualistic interaction *per se*. In the case described here, beetles and galling moths attack yuccas well after yucca moths have pollinated and oviposited within them. Therefore, neither of them directly interferes with the mutualistic stage of the yucca/yucca moth interaction; rather, their effects take place during its subsequent antagonistic component (seed predation). Less obvious effects of these exploiters on the success of the mutualism can certainly be envisioned. For example, if beetles and gallers are significant sources of mortality for yuccas and/or yucca moths, their presence could affect the population dynamics of the mutualism. That impact is not necessarily disruptive, however: some models show that the presence of predators can stabilize mutualist population dynamics (Heithaus et al. 1980; Tonkyn 1986).

Recent theories argue that costs of exploiters on beneficial interactions can be so large that selection to exclude them can be a major force driving the evolution of mutualism (e.g., Axelrod and Hamilton 1981; Bull and Rice 1991; Weisbuch and Duchateau 1993). In fact, our knowledge about the natural magnitude of these costs is still negligible. In this study we have documented three perhaps unexpected complexities regarding costs of such exploitation: exploiters can affect mutualists asymmetrically, can alter both the costs and benefits of mutualism, and can reduce the success of mutualists even if they do not affect the success of the mutualism *per se*. However, it should be pointed out that our results pertain primarily to the costs, not to the net effects (i.e., benefits minus costs), of exploiters. It is possible, for instance, that the net effect of galling on yuccas will turn out to be small, because its documented benefit of reducing seed predation is counterbalanced by an as yet uninvestigated cost of reduced seed dispersal. Moreover, factors such as variable ovule numbers per fruit or variable resources available for seed maturation may swamp out the impact of beetle (or moth) predation on seed set (cf. Anstett et al. 1996). Such data are methodologically challenging to obtain, but ultimately will be essential for evaluating the evolutionary impact of exploiters in mutualistic interactions.

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