Infertile seeds of *Yucca schottii*: a beneficial role for the plant in the yucca-yucca moth mutualism?

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Summary

The yucca-yucca moth interaction is a classic case of obligate mutualism. Female moths pollinate and oviposit in the gynoecium of the flower; however, maturing larvae eat a fraction of the developing seeds. We studied within-fruit distributions of four seed types (fertile, infertile, eaten and uneaten seeds) in order to evaluate costs and benefits in a *Yucca schottii* population in southeastern Arizona. We focused on how the spatial arrangement of seeds affected larval behaviour and, hence, the costs of the mutualism to the yucca. Infertile seeds were distributed throughout both infested and uninfested locules. Additionally, moth larvae feeding in a single locule preferred fertile seeds and even avoided infertile seeds and left the fruit significantly more often when they encountered infertile seeds. We suggest that, regardless of the cause of infertile seeds, they function as blocking units within seed locules and therefore reduce seed predation by moth larvae. We also suggest that, together with certain other fruit traits, the presence of infertile seeds promotes the evolutionary stability of this pollination mutualism.

Keywords: obligate mutualism; yucca-yucca moth interaction; seed predation; resource limitation; pollination

Introduction

Mutualism is an important interaction for many taxa and communities and is widely found in many environments (Boucher *et al.*, 1982; Addicott, 1984; Bronstein, 1994). A species interaction is considered to be mutualistic whenever each species experiences a higher net benefit when associated with the other species than when it is alone (Boucher *et al.*, 1982; Addicott, 1984, 1986a). A classic example of an obligate mutualism, in which a pair of species are completely dependent on each other, is the yucca-yucca moth interaction (*Yucca* spp., Agavaceae-*Tegeticula* spp. and *Parategeticula pollenifera*, Prodoxinae, Incurvariidae, Lepidoptera). The study of this interaction has a long history in the ecological literature, tracing back to Engelmann (1872) and Riley (1872, 1892) and it continues to make major contributions to our understanding of mutualism (e.g. Aker and Udovic, 1981; Keeley *et al.*, 1984; Addicott, 1986b; Johnson, 1988; Tyre and Addicott, 1993; Dodd and Linhart, 1994; James *et al.*, 1994; Pellmyr and Huth, 1994). Although a few studies have suggested that processes other than obligate pollination by yucca moths may be responsible for fruit initiation – other effective pollinators and self-fertilization (see Baker, 1986; Dodd and Linhart, 1994, for reviews) – it is well accepted that yucca moths are the major agent of pollination (Addicott, 1986b; Powell, 1992).

To maintain a mutualistic relationship, each partner species must reward its mutualist. Because this usually demands the allocation of energy and nutrients, benefits almost always come at some cost. The balance between net costs and benefits determines the net gain by each species (Boucher *et al.*, 1982; Addicott, 1984). Therefore, to evaluate any mutualism, it is necessary to

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measure the costs and benefits to each species (e.g. Keeley *et al.*, 1984; Addicott, 1986b). In contrast to many other mutualistic systems, in which costs and benefits are relatively unrelated (e.g. nectar production as a cost and pollen dispersal and delivery as a benefit), in the yucca-yucca moth pollination mutualism the costs and benefits for the plant are tightly related – seeds produced by the plant serve as food resources for the developing moth larvae. The more viable seeds produced by an individual plant, the higher fitness it might be expected to have, whereas one might expect that the more seeds that are eaten by the larva, the higher its probability of survival and hence fitness. The latter statement can be extended to the adult moth: the more of its offspring that mature successfully, the higher its fitness. This relationship between yucca seeds and the fitness of both partners demonstrates the fundamental, short-term conflict between these mutualists (Janzen, 1985; Addicott, 1986a).

The existence of this conflict suggests that to better understand the yucca-yucca moth mutualism, we must focus on ways in which each partner increases its short-term fitness or, equivalently, in this case, decrease its partner's benefits. From the point of view of the plant, it needs to reduce seed predation by moth larvae. Hence, studies of the yucca-yucca moth mutualism that focus on costs and benefits to the plant have measured relative numbers of eaten and uneaten seeds and fertile and infertile seeds (Keeley *et al.*, 1984; Keeley and Ikeda, 1986; Addicott, 1986b; Johnson, 1988). Fertile and infertile seeds are important in this context because it is only the fertile seeds that are of benefit to the plant within this mutualism. In contrast, studies suggest that infertile seeds are either neutral with respect to the mutualism (e.g. the result of a lack of resources, independent of moth behaviour; Addicott, 1986b) or a cost intrinsic to the mutualism (e.g. the result of damage by the yucca moth's ovipositor; Riley, 1892; Powell, 1984).

We initially studied relative numbers of fertile, infertile, eaten and uneaten seeds produced by an Arizona yucca species, *Yucca schottii*, in order to compare costs and benefits of this mutualism to patterns documented in other yuccas. However, preliminary data suggested a spatial arrangement of infertile seeds relative to fertile seeds within fruits that might influence the behaviour of the feeding yucca moth larvae. Therefore, the goal of this paper is to describe within-locule distributions of different seed types in *Y. schottii* and to suggest a potential beneficial function of infertile seeds to the plant.

We show that infertile seeds are distributed throughout fruit locules and that infertile seeds are found in both infested and uninfested locules. We then show that a moth larva feeding in a single locule prefers fertile seeds and even avoids infertile seeds and that moth larvae leave the fruit significantly more often when they encounter infertile seeds. Finally, we suggest that regardless of the cause of infertile seeds, they function as blocking units within seed locules and therefore reduce seed predation by moth larvae.

Methods

Study species

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). 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).

Two mutualist moth species are associated with *Y. schottii*: *Tegeticula yuccasella* (Riley) and *Parategeticula pollenifera* (Davis). While *T. yuccasella* (as currently defined taxonomically) is associated with almost all yucca species, *P. pollenifera* is associated only with *Y. schottii* and *Yucca elephantipes*. In general, both moth species perform similar pollination behaviours (Powell, 1984). Here, we describe the behaviour of *T. yuccasella*, by far the most common pollinator present at our site during this study. Moths emerge from pupae in the ground near a yucca plant around the time when the plants come into bloom. They mate in the yucca flowers. The female then flies to a freshy 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 of the six locules. She then actively deposits some or all of her pollen load in the stigmatic groove. Constrictions are usually formed in areas where the female's ovipositor penetrates the ovary walls, causing ovules to fail to develop in areas close to both sides of the constriction (Baker, 1986).

Each larva develops in one of the six locules and consumes seeds in its immediate vicinity. 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 next summer.

Data collection

In September 1992 and August 1993, we collected fruits of *Y. schottii* from around the Bog Springs Campground in Madera Canyon, located in the Santa Rita Mountains, 55 km southeast of Tucson, Arizona. We sampled four plants in 1992 and eight plants in 1993, with fruit numbers per plant ranging from four to eight in 1992 and from five to 24 in 1993. Fruits were collected after exit holes of moth larvae were found but before fruits were damaged or harvested by other animals. We dissected each fruit and mapped the sequence of different types of seeds (fertile, infertile, uneaten and eaten seeds by moth larva) within each of the six locules. Fertile yucca seeds are thick and black, whereas infertile ones are thinner and white, allowing them to be distinguished easily; eaten seeds have an obvious hole bored through them. In addition, we recorded the following information: fruit length, presence and location of any constrictions, areas where ovules failed to develop within locules, external and internal holes, the presence of other insects and damage to individual seeds. Damage was recorded on a scale from 1 to 4, representing 0–25, 25–50, 50–75 and 75–100% damage per seed, respectively. Damage from moth larvae is easily distinguished from other forms of damage and we specifically noted it. Figure 1 shows typical examples of fruit locules as recorded by our mapping method. The mapping method allowed us to record the exact location of each seed, as well as the sequence of eaten seeds that a larva consumed (hereafter, 'eaten-seed sequence').

Certain locules were excluded from the analyses due to damage by other insects (e.g. pyralid moths) and the presence of dead areas and hard galls found in fruits, which prevented us from determining the seed arrangement unambiguously. In particular, intensive seed predation by beetles (*Carpophilus* sp., Nitidulidae (Coleoptera)), especially in 1993, forced us to exclude most of the locule data when we analysed locule infestation and seed predation by moth larvae. Beetles left no characteristic pattern of damage to seeds or fruit material, occasionally producing rotten areas within a locule or several locules. This, in turn, promoted further seed and fruit damage, probably by bacteria. Therefore, despite the large number of locules examined, some of the statistical analyses, especially on seed predation by moth larvae in 1993, had small sample sizes (see Results for specific comments).
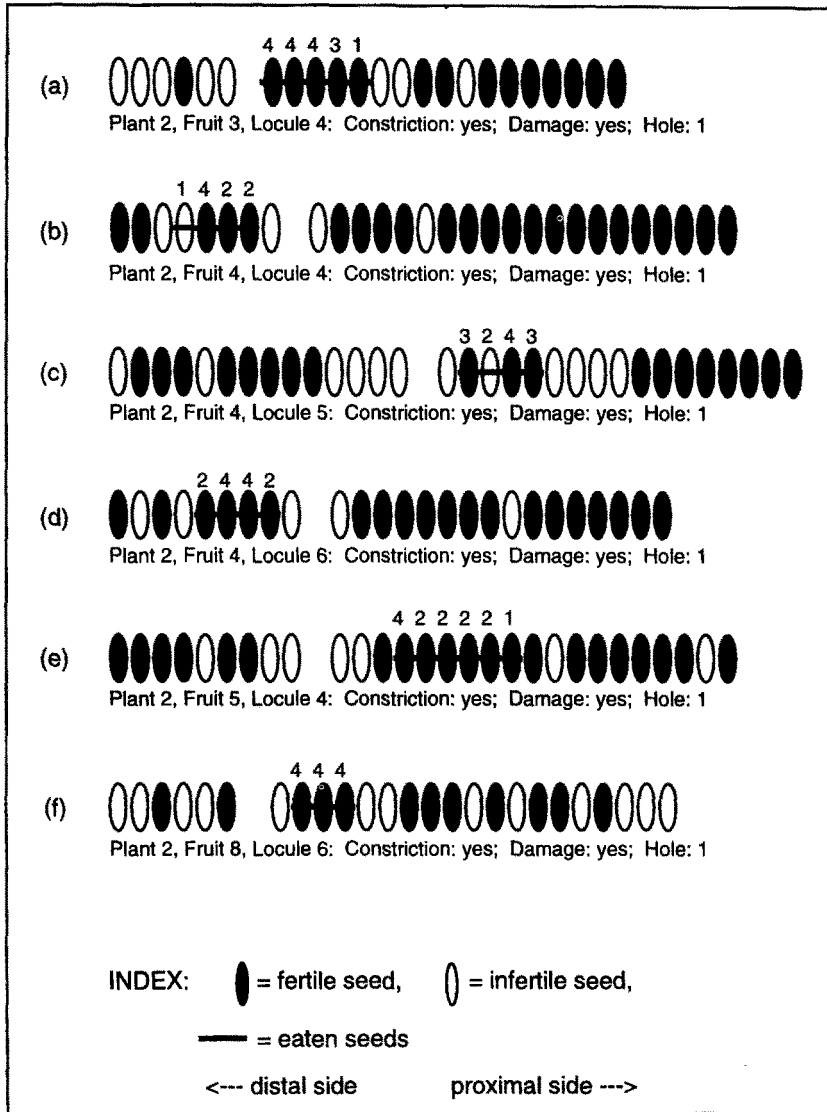
Figure 1. Maps of *Y. schottii* locules with actual examples from different plants and fruits. A line indicates an eaten-seed sequence, while a number above each seed of the sequence indicates the damage class, ranging from 1 to 4 (see text). A gap in a locule map indicates a constriction. Note that infertile seeds are distributed throughout a locule with no obvious pattern.

In addition, because of a potential effect of intraspecific competition between moth larvae (Powell, 1984), we usually analysed the infestation data only in those locules that had only one larva. This decision did not bias our analyses because the large majority of infested locules in both years contained only one larva (93.9 and 72% for 1992 and 1993, respectively).

Most of the infestations we found were by *T. yuccasella*, while only the minority were by *P. pollenifera*. *Parategeticula pollenifera*'s infestations were sometimes indistinguishable from beetle

damage and therefore did not allow for an accurate assessment of the behaviour of the larva of this species. Hence, our data on eaten and uneaten seeds are restricted to infestations by *T. yuccasella* only.

Because we were interested in larval behaviour with regard to seed distributions that it encountered and because larvae only rarely moved from one locule to another ($\approx$ 2%; see Discussion), we collected and analysed our data on a per locule basis.

Statistical tests that deal with proportions use arcsine-square root transformation of the original data for the analyses.

Results

Between- and within-year variability of seed numbers

Seed numbers per locule varied greatly both between and within years. The most striking difference between the two years was due to the heavy damage by seed-eating *Carpophilus* beetles (see Methods) in 1993. Seventy-five percent of seed locules were infested by beetles in 1993, compared to 25% in 1992 (Z. Forsman, Y. Ziv and J. Bronstein, *unpublished data*).

We compared seed numbers per locule between the two years using one-way ANOVA (Table 1). The total number of seeds, number of fertile seed and proportion of seeds per locule that were infertile were significantly different between years (p $<$ 0.05). Additionally, years differed in the proportion of seeds that were eaten ((fertile eaten + infertile eaten)/total seeds) ($N = 698, F = 11.51, P = 0.001$). Hence, we analysed data from the two years separately to avoid between-year bias on the tested variance.

Seed numbers per locule also varied among plants within each year (Table 2). However, the proportion of seeds that were infertile varied within a limited range in both 1992 and 1993 (0.15–0.33 and 0.2–0.41 for 1992 and 1993, respectively). Because we were interested in studying the effect of infertile seeds on larval behaviour, we included all locules of a given year in further analyses.

Number, proportion and arrangement of infertile seeds

In both years, infertile seeds were distributed throughout a locule with no obvious pattern. Typical examples of infertile seed distribution are shown in Fig. 1 a–f. Often, we observed a few infertile seeds in areas of constriction, which caused an apparent clumped distribution of infertile seeds in some locules. However, these infertile seeds were distinctly different from the other infertile seeds both in location and shape.

Table 1. Number of seeds and proportion of seeds that were infertile per locule in different years (mean $\pm$ SE)

	1992	1993	*F* value	*P*
Total seeds	26.24	19.55	40.92	$<$0.001
	(0.85)	(0.45)		
Fertile seeds	19.83	13.67	60.40	$<$0.001
	(0.71)	(0.33)		
Infertile seeds	6.41	5.88	1.06	0.305
	(0.46)	(0.22)		
Proportion of seeds infertile	0.24	0.29	4.605	0.032
	(0.01)	(0.01)		

Date include 124 and 578 points for 1992 and 1993, respectively.

Table 2. Number of seeds and proportion of seeds that were infertile per locule in different plants (mean ± 1 se)

Plant	Total seeds	Fertile	Infertile	Proportion infertile
1992				
1	15.1[b]	12.86[b]	2.23[b]	(0.15[c]
	(1.04)	(1.09)	(0.50)	(0.015)
2	28[a]	21.08[a]	7.51[a]	(0.265[ab]
	(2.32)	(1.89)	(1.27)	(0.016)
3	31.16[a]	24.79[a]	6.37[a]	(0.2[bc]
	(5.1)	(4.06)	(2.24)	(0.019)
4	29.54[a]	21.17[a]	9.65[a]	(0.33[a]
	(5.74)	(5.33)	(3.88)	(0.047)
1993				
1	29.51[a]	18.43[a]	11.01[a]	(0.4[a]
	(1.29)	(1.32)	(0.81)	(0.03)
2	14.43[c]	10.27[bc]	4.17[cd]	(0.3[ab]
	(0.64)	(0.65)	(0.33)	(0.03)
3	28.16[a]	19.04[a]	9.01[ab]	(0.32[a]
	(0.72)	(0.59)	(0.38)	(0.01)
4	22.55[b]	15.3[ab]	7.13[bc]	(0.29[ab]
	(1.46)	(1.08)	(1.06)	(0.03)
5	12.16[c]	9.56[c]	2.84[d]	(0.24[b]
	(0.55)	(0.43)	(0.2)	(0.01)
6	22.52[b]	18.26[a]	4.26[cd]	(0.21[b]
	(0.85)	(0.98)	(0.49)	(0.03)
7	8.62[d]	6.58[c]	2.02[d]	(0.26[b]
	(0.46)	(0.41)	(0.15)	(0.02)
8	27.97[ab]	16.5[a]	11.5[a]	(0.41[a]
	(1.22)	(1.22)	(1.07)	(0.03)

Numbers within a category (e.g. total seeds) that share the same letter are not significantly different ($p < 0.05$, Scheffé multiple range test).
Data include 124 and 578 points for 1992 and 1993, respectively.
For 1992: total seeds, $F = 34.13$, $p < 0.001$; Fertile, $F = 15.65$, $p < 0.001$; Infertile $F = 13.577$, $p < 0.001$; Proportion infertile $F = 9.253$, $p < 0.001$.
For 1993: total seeds, $F = 115.434$, $p < 0.001$; Fertile, $F = 55.679$, $p < 0.001$; Infertile $F = 63.277$, $p < 0.001$; Proportion infertile $F = 9.672$, $p < 0.001$.

In order to see whether the occurrence of infertile seeds was independent of moth infestation, we compared the proportion of infertile seeds between locules uninfested and infested with larvae. We found no significant difference in 1992 ($n = 86$, $F = 1.625$, $P = 0.206$). In contrast, uninfested and infested locules differed significantly in 1993 ($n = 408$, $F = 4.767$, $P = 0.03$): infested locules contained a higher proportion of seeds that were infertile. Hence, infertile seeds are as common or even more common in infested locules compared to uninfested ones.

Damage to infertile and fertile seeds by larvae

We examined the preference of moth larvae for infertile and fertile seeds by asking questions regarding the proportions of all seeds versus eaten-seeds infertile and the average damage to infertile versus fertile seeds.
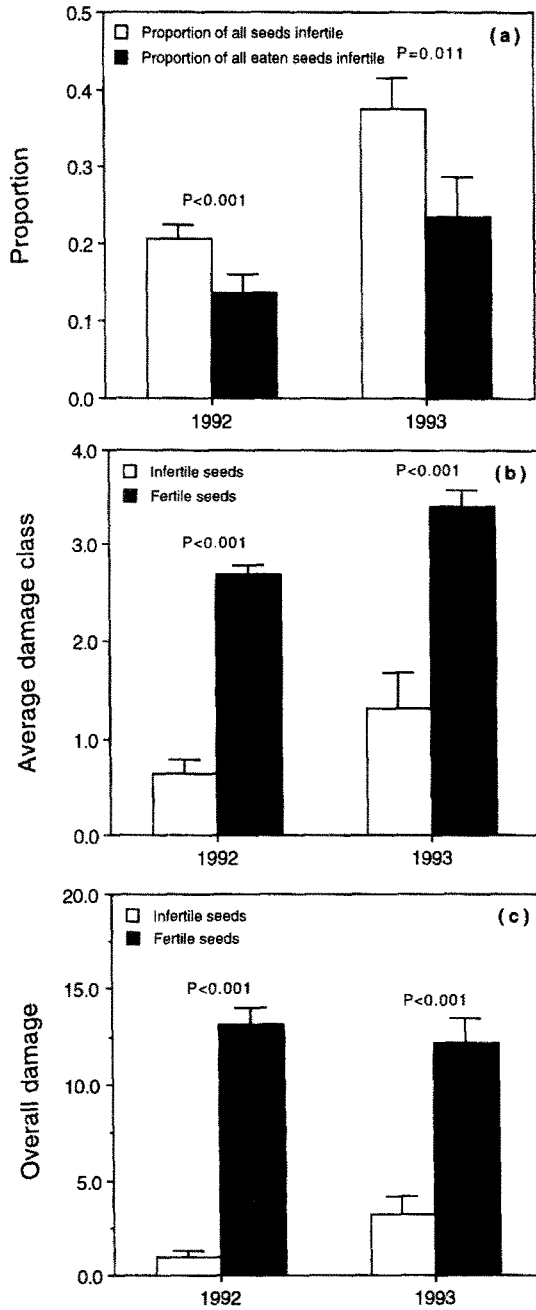
Figure 2. (a) Proportions of all seeds infertile (infertile seeds/(fertile seeds + infertile seeds)) and all eaten-seeds infertile (eaten-seeds infertile/(eaten seeds fertile + eaten-seeds infertile)). (b) Mean damage class of fertile and infertile seeds in each year (damage classes range from 1 to 4, where 1 = 0–25%, 2 = 25–50%, 3 = 50–75% and 4 = 75–100% damage; see text). (c) Overall damage to fertile and infertile seeds in each year. Overall damage is calculated by summing the damage class of each seed of a particular type (fertile or infertile) in each eaten-seed sequence in a locule; see text.

First, we asked whether moth larvae preferred to consume infertile or fertile seeds. If larvae were indifferent, we would expect no significant difference between the mean proportions of all seeds that were infertile and all eaten seeds that were infertile per locule. In fact, the proportion of all seeds infertile was significantly higher than the proportion of all eaten seeds infertile in both years (Fig. 2a; paired t-tests, $n = 66$, $t = 4.513$, $P < 0.001$ for 1992 and $n = 18$, $t = 2.835$, $p = 0.011$ for 1993). (For this analysis, for both 1992 and 1993, we included locules that were infested both by one and by two larvae in our analysis. We assumed that competition between larvae, although it might affect the number of seeds eaten per larva, would not change the way in which each larva treated the different type of seeds.) Moth larvae consumed approximately 36% fewer infertile seeds (34.5 and 37.8% for 1992 and 1993, respectively) than the proportion of these seeds in locules.

Second, we asked whether larvae damaged an infertile seed more or less than a fertile seed when one was encountered. If larvae fed on infertile and fertile seeds to the same degree, we would expect no difference between the mean amount of damage done to each of them. However, in both years an infertile seed was damaged significantly less, on average, than a fertile one (Fig. 2b; paired t-tests, $n = 30$, $t = 11.209$, p < 0.001 for 1992, and $n = 11$, $t = 5.396$, $p < 0.001$ for 1993). Moth larvae consumed four and 2.5 times more from a fertile seed than from an infertile seed in 1992 and 1993, respectively.

The proportion of eaten seeds that were infertile and the amount of damage done to an infertile seed are not independent. When exploiting a locule in a yucca fruit, a larva needs to decide how many seeds, as well as how much of each seed, to consume. In order to evaluate the joint effect of these phenomena, we calculated the overall damage (OD) to fertile and infertile seeds in a locule using the following equation:

$$OD = \sum_{i=1}^{NE} d_i \quad \text{or } OD = NE * d_i \tag{1}$$

where d_i is the amount of damage to seed i and NE is the number of damaged seeds of each type (fertile or infertile). The OD for each type of seed represents the overall amount of material of each type of seeds eaten by moth larvae in a locule. As expected, in both years overall damage by larvae was significantly higher on fertile seeds (Fig. 2c; $n = 30$, $t = 13.352$, $p < 0.001$ for 1992 and $n = 12$, $t = 7.582$, $p < 0.001$ for 1993). In 1992, fertile seeds in a locule were damaged approximately 13 times more than infertile seeds, while in 1993 the damage was approximately four times higher.

Location of infertile seeds and the number of eaten seeds

Evidence that the presence of infertile seeds might reduce the number of seeds eaten by moth larvae led us to examine whether the presence of infertile seeds affected a larva's decision as to when to depart the fruit. That is, did the presence of infertile seeds within a locule change the total number of seeds eaten by a larva in its lifetime? If larvae preferred fertile seeds (or avoided infertile seeds), then the total number of eaten seeds could be strongly affected by the presence of infertile seeds in a locule. We would expect in this case to see fewer seeds eaten when an infertile seed was immediately adjacent to an eaten-seed sequence (hereafter, 'blocking effect') than when a fertile seed was the next seed available. Practically speaking, we could not determine which side of the eaten-seed sequence was encountered last by a larva before it left the fruit. We therefore distinguished among three categories: (1) both sides of an eaten-seed sequence next to fertile seeds; (2) one side of an eaten-seed sequence next to a fertile and the other next to an infertile seed; and (3) both sides of an eaten-seed sequence next to infertile seeds. We assumed
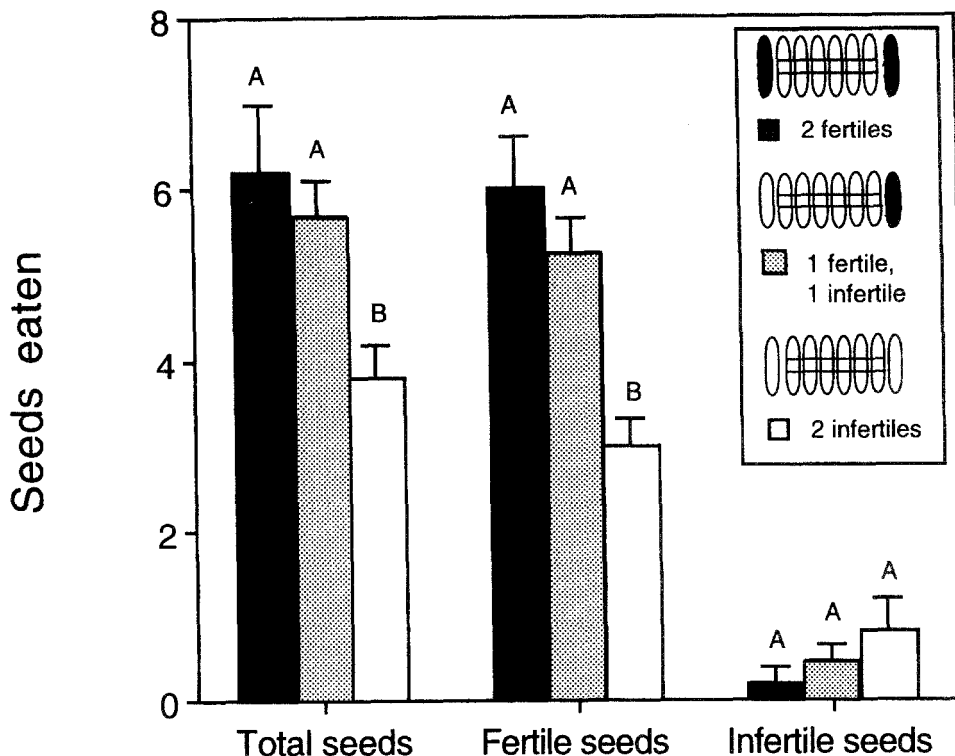
Figure 3. Total number of eaten seeds, number of eaten fertile seeds and number of eaten infertile seeds in three categories defined according to the location of an infertile or fertile seed on the side next to an eaten-seed sequence (both sides next to fertile seeds, one side next to a fertile seed and the other next to an infertile seed and both sides next to infertile seeds). Box in the upper right corner of the graph shows the three categories in the order in which their columns are shown for each type of seeds.

that in category 2, some of the cases resulted from an infertile seed being the last seed that the larva encountered before its departure from the fruit; therefore, if there were any negative effect of infertile seeds on larva behaviour, the number of seeds eaten would have an intermediate value between the numbers of seeds eaten in the two other categories. We purposely ignored those eaten-seed sequences that ended at a constriction or the end of the locule, focusing only on those eaten-seed sequences that were surrounded by seeds on both sides.

Figure 3 shows the number of eaten seeds (total, fertile and infertile) in each of the three categories of eaten-seed sequences in 1992. Sample sizes were too low to conduct similar analyses in 1993. We used a one-sided Mann-Whitney test (Daniel, 1983) to test the hypothesis of a blocking effect by infertile seeds. Significantly more total seeds were eaten ($T_{5,5}$ = 2.5, p < 0.025) in category 1 sequences (both sides next to fertile seeds) than in category 3 sequences (both sides next to infertile seeds) and significantly more seeds were eaten ($T_{14,5}$ = 10.5, p < 0.01) in category 2 sequences (one side next to a fertile and the other next to an infertile seed) than in category 3 sequences. No significant difference was found between category 1 and 2 sequences ($T_{5,14}$ = 120, p ≫ 0.1). Additionally, as predicted, the number of eaten seeds in category 2 had a value between those of the two other categories (Fig. 3).

Similarly, significantly more fertile seeds were eaten ($T_{5,5}$ = 0.5, p < 0.005) in category 1 sequences than in category 3 sequences and significantly more seeds were eaten ($T_{14,5}$ = 5.5, p

< 0.005) in category 2 sequences than in category 3 sequences. No significant difference was found between categories 1 and 2 ($T_{5,14} = 112, p \gg 0.1$).

The above analyses take as a null hypothesis (i.e. the absence of a blocking effect) that the three categories of eaten-seed sequences will be equally common. However, considering that infertile seeds are less common than fertile seeds, one might expect that, simply by chance, short eaten-seed sequences will more frequently end at a fertile seed. Therefore, statistically speaking, we would expect to have, on average, shorter eaten-seed sequences in category 1 (both sides of eaten-seed sequences next to fertile seeds). Our analyses revealed significantly reverse results. This may indicate that in this regard, our analyses are conservative and the above results may, if anything, underestimate the real effect of infertile seeds.

In addition, a chi-square test for goodness of fit showed that category 3 (infertile seeds on both sides of an eaten-seed sequence) compared with category 1 (fertile seeds on both sides of an eaten-seed sequence) was significantly more common than expected, given the low proportion of infertile seeds ($X^2_{(1)} = 5.76, p < 0.025$). In other words, moth larvae emerged significantly more often when an infertile seed would have been the next one encountered, than when a fertile seed would have been the next one encountered.

Correlations between different seed types

If infertile seeds affect the total number of seeds eaten and the number of fertile seeds eaten, then it is reasonable to predict that the more infertile seeds produced within a locule, the fewer fertile seeds will be eaten. This correlation is based on the simple assumption that, although a larva does not necessarily encounter all infertile seeds, it has a higher probability of encountering one when more infertile seeds exist. To test this prediction, we conducted correlation analyses between the different seed types (i.e. total seeds, total fertile seeds, total infertile seeds, fertile seeds eaten and infertile seeds eaten). We found significant positive correlations between the number of fertile or infertile seeds and the total number of seeds in a locule in 1992 ($n = 43, r^2 = 0.773, p < 0.001$ and $n = 43, r^2 = 0.607, p < 0.001$ for fertile and infertile seeds, respectively), indicating that locules with more seeds have both more infertile and more fertile seeds. The total number of seeds eaten decreased significantly as the number of infertile seeds increased (partial correlation $= -0.408, p = 0.007, n = 43$), but not as the number of fertile seeds increased (partial correlation $= -0.163, p = 0.303, n = 43$). Supporting our prediction, the number of fertile seeds eaten decreased significantly as the number of infertile seeds increased (partial correlation $= -0.441, p = 0.003, n = 43$; Fig. 4). Although the number of fertile seeds eaten also decreased significantly as the total number of seeds increased (partial correlation $= -0.428, p = 0.004, n = 43$), they were not significantly correlated with the number of fertile seeds (partial correlation $= -0.295, p > 0.05, n = 43$).

As in 1992, we found significant positive correlations between fertile or infertile seeds and the total number of seeds in a locule in 1993 ($n = 13, r^2 = 0.767, p < 0.001$ and $n = 13, r^2 = 0.637, p = 0.001$ for fertile and infertile seeds, respectively). However, no correlation was found between fertile seeds eaten and total seeds or infertile seeds.

Discussion

Our results can be summarized briefly as follows.

(1) *Yucca schottii* shows a high variability in the numbers of infertile and fertile seeds in locules between plants, both between years and within years (our results are similar to those given for *Y. schottii* by Keeley *et al.* (1984) and Addicott (1986b)). However, the proportion of infertile seeds stays within a relatively limited range, a result similar to that of Addicott (1986b).
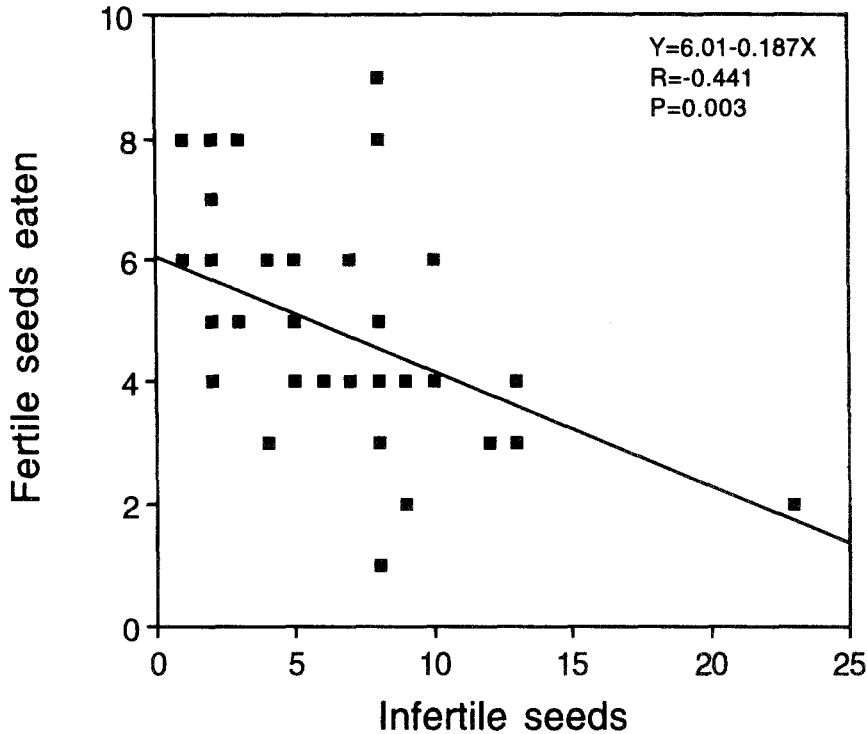
Figure 4. Relationship between fertile seeds eaten and the number of infertile seeds in the same locule.

(2) Infertile seeds are distributed throughout a seed locule, both in uninfested and infested locules.

(3) Fewer infertile seeds are eaten than would be expected at random and less of an infertile seed than a fertile seed is eaten, on average. Overall damage to infertile seeds (a combined measure of number of seeds eaten and the damage each seed suffers in a locule) is much lower than to fertile seeds.

(4) Moth larvae leave the fruit more frequently when they encounter infertile seeds than when they encounter fertile seeds. (The phenomenon of infertile seeds present next to an eaten-seed sequence can be seen also in Powell's (1984) monograph (his Figs 24 and 25).)

(5) Correlation analysis suggests that the more infertile seeds are present, the fewer fertile seeds are eaten.

These results suggest that the presence of infertile seeds reduces the number of fertile seeds eaten in *Y. schottii*. Furthermore, the fact that yucca moth larvae depart the fruit more frequently when they encounter infertile seeds and as a result consume fewer seeds, as well as the fact that infertile seeds and fertile seeds eaten are negatively correlated, may suggest that infertile seeds function to block larvae from feeding on additional seeds in a way that limits the number of seeds eaten. It is important to note here that we suggest that infertile seeds help reduce seed predation but do not prevent it. Furthermore, this is not an absolute effect. For instance, Fig. 1e shows that the moth larva in this case was not affected by an infertile seed before emerging from the yucca fruit. In addition, Fig. 1c shows that the moth larva penetrated an infertile seed and continued

consuming fertile seeds thereafter (but note that the infertile seed itself was consumed less than the fertile seeds around it).

Given the 'partnership conflict' underlying this mutualism, in which each mutualist may experience higher benefits when reducing costs imposed by its partner, plant traits that reduce consumption by the mutualist species may help to stabilize this interaction. Such traits should be essential especially when resources are limited and consumption can potentially cause an absolute reduction of the benefits for the mutualist. In the case where costs and benefits are tightly interwined (Addicott, 1986a), reducing the benefits to the partner will often mean increasing the mutualist's own benefits. With regard to our study species, having infertile seeds distributed throughout a seed locule might prove advantageous to a *Y. schottii* individual, by reducing the number of fertile seeds destroyed by its pollinator's offspring. Addicott (1986b) found yucca fruits in which all fertile seeds were lost to yucca moth larvae, while Powell (1984) provides a few indications that seeds are occasionally limited for the moths and that competition between and within yucca moth species occurs. Therefore, in *Y. schottii*, using infertile seeds as blocking units may help a plant to ensure that at least some fertile seeds matured successfully.

We do not yet know the cause of infertile seeds. Three explanations have been suggested by other researchers. First, Riley (1892) suggested that the yucca moth's ovipositor may damage ovules or interfere with seed development, leading to constriction of the mature fruit at the site where oviposition occurred. In our study, we frequently observed areas of infertile seeds at either side of a constriction. Often these seeds produced a clumped distribution of infertile seeds. However, these seeds are distinctly different from the infertile seeds distributed throughout a seed locule and so cannot account for the results we present here. Second, Powell (1984) and Addicott (1986b) mention that insufficient pollen transfer may cause ovules to fail to develop. Powell's (1984) study on *Y. schottii* at our study site suggested that moth density is very high and pollen might not be an important limiting factor in this case; however, we have no information about pollen limitation during the period of our study. Third and most likely, fertilized seeds may abort because of insufficient resources for seed development (Addicott, 1986b). Infertile seeds distributed between fertile seeds reached the size of fertile seeds, although they were thinner. In addition, numerous studies on yuccas have suggested that resource limitation is common and leads to abortion at all levels – flowers (Riley, 1892; Aker and Udovic, 1981; Udovic, 1981; Udovic and Aker, 1981; Aker, 1982; James *et al.*, 1994), fruits (Riley, 1892; Udovic and Aker, 1981; Aker, 1982; Powell, 1992; James *et al.*, 1994) and seeds within locules (Addicott, 1986b).

More generally, theoretical studies conflict regarding whether mutualism is structurally stable over evolutionary time, whether it tends to evolve towards parasitism or whether it is likely to lead to global extinction (e.g. Addicott, 1981; May, 1981; Wright, 1989). We suggest that internal effects, such as fruit constrictions (see below) and infertile seeds serving as blocking units, can provide mechanisms favouring stability of this mutualistic interaction, by reducing the degree to which the moths exploit yucca seeds.

It is important to emphasize that we do not argue that infertile seeds have primarily evolved to allow the plant to avoid intensive seed predation. Rather, we suggest that whatever the origin of infertile seeds (e.g. seed abortion due to insufficient resources), having those infertile seeds distributed throughout the seed locules may prove advantageous to the plant. However, we might speculate on some evolutionary scenarios regarding the secondary use of infertile seeds as reducing the predation cost imposed by moth larvae. Given the presence of infertile seeds due to either pollen limitation or seed abortion, infertile seeds might have evolved towards a haphazard distribution throughout the locule, because of its beneficial effects in the context of the mutualism with yucca moths. If pollen is usually limited, directed growth of pollen tubes towards certain

ovules might have evolved to generate this seed distribution, whereas if seed abortion is the cause of infertile seeds, spatially haphazard abortion might have evolved to produce the observed pattern. In any case, such evolution could promote the stability of this mutualism without the necessity of evolving the cause of the effect itself (i.e. seed infertility).

We also do not yet know why moth larvae prefer fertile over infertile seeds or, in other words, what infertile seeds have that larvae try to avoid. Tentatively, we suggest three possibilities: infertile seeds may contain less energy and cause larvae to experience a lower energy gain, infertile seeds are tougher and more difficult for the larvae to pentrate and infertile seeds may contain chemical feeding deterrents. This final possibility is particularly intriguing, since it would normally be expected that fertile seeds would be the best defended.

The blocking effect of infertile seeds might not be the only mechanism that reduces seed predation by moth larvae (and maybe other yucca seed predators). Two fruit structures may have the same effect: the wall that occurs between locules and the constriction of the fruit created after an oviposition by the female moth. Regarding the fruit walls, in our study, of all moth infestations, only in one case ($\approx$ 2%) did a larva move from one locule to another. (This is why we chose to analyse our data by locule rather than by fruit; see Methods.) Furthermore, we occasionally observed a dead larva between areas having only infertile seeds in them, while in an adjacent locule, fertile seeds were available. Regarding the constriction effect, Fig. 1a shows a situation in which an eaten-seed sequence is blocked by a constriction. In our study, there was not a single case in which larvae consumed seeds on both sides of the constriction. This, of course, means that the fertile seeds on one side of the constriction remained untouched.

In the present work we have focused on the short-term conflict between mutualists in a case in which each may benefit from over-exploitation of its partner and processes that may reduce this over-exploitation. Future studies on such processes might help us to better understand mutualism and the ways in which it can be stabilized.

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References

Addicott, J.F. (1981) Stability properties of 2–species models of mutualism: simulation studies. *Oecologia* **49**, 42–9.

Addicott, J.F. (1984) Mutualistic interactions in population and community ecology. In *A new ecology: novel approaches to interactive systems* (P.W. Price, C.N. Slobodchikoff and B.S. Gaud, eds) pp. 437–55. John Wiley & Sons, New York.

Addicott, J.F. (1986a) On the population consequences of mutualism. In *Community ecology* (J.M. Diamond and T.J. Case, eds) pp. 425–36. Harper and Row, New York.

Addicott, J.F. (1986b) Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. *Oecologia* **70**, 486–94.

Aker, C.L. (1982) Regulation of flower, fruit and seed production by monocarpic perennial, *Yucca whipplei*. *J. Ecol.* **70**, 357–72.

Aker, C. and Udovic, D. (1981) Oviposition and pollination behavior of the yucca moth *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). *Oecologia* **49**, 96–101.

Baker, H.G. (1986) Yuccas and yucca moths – a historical commentary. *Ann. Missouri Bot. Gard.* **73**, 556–64.

Boucher, D.H., James, S. and Keeler, K.H. (1982) The ecology of mutualism. *Annu. Rev. of Ecol. and System.* **13**, 315–47.

Bronstein, J.L. (1994) Our current understanding of mutualism. *Q. Rev. Biol.* **69**, 31–51.

Daniel, W.W. (1983) *Biostatistics: A Foundation for Analysis in the Health Sciences.* John Wiley & Sons, New York.

Dodd, R.J. and Linhart, Y.B. (1994) Reproductive consequences of interactions between *Yucca glauca* (Agavaceae) and *Tegeticula yuccasella* (Lepidoptera) in Colorado. *Am. J. Bot.* **81**, 815–25.

Engelmann, G. (1872) The flower of yucca and its fertilization. *Bull. Torrey Bot. Club* **3**, 33.

James, C.D., Hoffman, M.T., Lightfoot, D.C., Forbes, G.S. and Whitford, W.G. (1994) Fruit abortion in *Yucca elata* and its implications for the mutualistic association with yucca moths. *Oikos* **69**, 207–16.

Janzen, D.H. (1985) The natural history of mutualism. In *The biology of mutualism* (D.H. Boucher, ed.) pp. 40–99. Croom Helm, London.

Johnson, R. (1988) The reproductive cost to the yucca plant (*Yucca filamentosa* L.) in its mutualistic relationship with the yucca moth (*Tegeticula yuccasella* Riley). *J. Tennessee Acad. Sci.* **63**, 77–8.

Keeley, J.E. and Ikeda, D.A. (1986) Seed predation by yucca moths on semelparous, iteroparous and vegetatively reproducing subspecies of *Yucca whipplei* (Agavaceae). *Am. Midl. Nat.* **115**, 1–9.

Keeley, J.E., Keeley, S.C., Swift, C.C. and Lee, J. (1984) Seed predation due to the yucca-moth symbiosis. *Ame. Midl. Nat.* **112**, 187–91.

May, R.M. (1981) *Theoretical Ecology: Principles and Applications.* Blackwell Scientific Publications, Oxford.

Pellmyr, O. and Huth, C.H. (1994) Evolutionary stability of mutualism between yuccas and yucca moths. *Nature* **372**, 257–60.

Powell, J.A. (1984) Biological interrelationships of moths and *Yucca schottii.* *Univ. Calif. Publ. Entomol.* **100**, 1–99.

Powell, J.A. (1992) Interrelationships of yuccas and yucca moths. *Trends Ecol. Evol.* **7**, 10–15.

Riley, C.V. (1872) The fertilization of the yucca plant by *Pronuba yuccasella. Can. Entomol.* **4**, 182.

Riley, C.V. (1892) The yucca moth and the yucca pollination. *Missouri Bot. Gard. Rep.* **3**, 99–159.

Tyre, A.J. and Addicott, J.F. (1993) Facultative non-mutualistic behavior by an 'obligate' mutualist: 'cheating' by yucca moths. *Oecologia* **94**, 173–5.

Udovic, D. (1981) Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availabilty. *Oecologia* **48**, 389–99.

Udovic, D. and Aker, C. (1981) Fruit abortion and the regulation of fruit number in *Yucca whipplei. Oecologia* **49**, 245–8.

Wohlin, C.L. and Lawlor, L.R. (1984) Models of facultative mutualism: density effects. *Am. Natu.* **124**, 843–2.

Wright, D.H. (1989) A simple, stable model of mutualism incorporating handling time. *Am. Nat.* **134**, 664–7.