

## Defection by plants in the yucca–yucca moth association: a test of the cheater plant hypothesis for *Yucca treculeana*

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In mutualisms, an underlying conflict of interests may select for defection from providing benefits. In the obligate mutualism between yuccas and yucca moths, where pollination service and seeds for pollinator larvae are traded, it has been suggested that some individuals in a population of *Y. baccata* may defect by preventing pollinator egg or larvae from development. We tested this hypothesis in *Y. treculeana*, another species suggested to contain cheater plants. Five specific predictions were tested during two years of study. A prediction that a surplus of plants without pollinator larvae should be present was met. Predicted existence of two distinct fruit morphs was rejected, and none of several highly variable morphological traits were linked to presence/absence of larvae. Predicted excess of intact seeds in the fruits of plants without larvae was not found; in fact, such plants produced fewer seeds, contrary to the hypothesis. A suggestion that inverse frequency-dependent fitness could explain the pattern was rejected. Contrary to prediction, distribution of larvae of a closely related cheater yucca moth was positively associated with pollinator larvae, even though it would not be affected by the proposed killing mechanism. The results together provide strong support against the existence of cheater plants in *Y. treculeana*.

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In mutualistic interactions, species benefit from interacting with one another. While each species benefits, it also must reciprocate, which incurs a cost. In the case of the obligate mutualism between yuccas and yucca moths, the plant benefits from pollination by the adult moth, but sustains the cost of seed consumption by the moth larva. The moth in turn gains the benefit of food for her larvae, but pays potential costs of being a pollinator (Riley 1892, Pellmyr 1997, 2003).

Underlying this reciprocation is a conflict of interests, in that individuals that can improve the benefit:cost ratio at the expense of their mutualism partner are expected to have higher fitness (Bull and Rice 1991, Pellmyr and Huth 1994, Yu 2001). Long-term stability can be maintained despite this conflict of interest if there are

mechanisms that prevent over-exploitation by either partner. One example of such a mechanism is selective floral abscission of heavily moth-infested flowers in the yucca–yucca moth association (Pellmyr and Huth 1994, Richter and Weis 1995, Wilson and Addicott 1998, Addicott and Bao 1999). Some models suggest that this conflict can result in intraspecific polymorphism for cheating, with a subset of all individuals cheating the partner by not reciprocating (Soberon Mainero and Martinez del Rio 1985, Addicott and Bao 1998); frequency-dependent selection can provide a mechanism in such models to allow for long-term persistence of both mutualists and cheaters.

Bao and Addicott (1998) suggested that many individuals in one population of *Yucca baccata* might cheat

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their pollinator. They characterized individual plants in a population as falling into either of two categories based on fruit shape: one category had fruit that were short, bulbous, and sharply constricted at the tip ("narrowed"), whereas the other category had long and uniformly tapered fruit ("tapered"). Narrowed fruit had few or no larvae present in their fruit, whereas larvae were present in large numbers in tapered fruit. The authors suggested that this was due to a large number of inviable ovules present at the top of narrowed fruit, which they speculated could cause the death of emerging larvae. They hypothesized that larvae moving through the fruit fail to encounter developing seeds quickly enough and therefore perish. In this manner, individual plants would benefit from yucca moth pollination, but avoid seed predation. They further suggested that other fleshy-fruited *Yucca* species have similar variation in fruit shape and that they may also have evolved this mechanism of cheating. We tested this hypothesis and related questions using one of the proposed species, *Y. treculeana*, its pollinating mutualist *Tegeticula treculeanella*, and a coexisting cheating yucca moth, *T. corruptrix*.

We asked five questions to specifically test predictions that derive from the cheater plant hypothesis: 1) how were *T. treculeanella* larvae distributed within and among plants in the population? The hypothesis predicts that larvae should not be distributed evenly among plants, in that there should be an excess of plants in which all fruits lack larvae relative to a Poisson distribution of larvae among the plants. 2) Were there morphological differences between fruits on plants with and without *T. treculeanella* larvae? The hypothesis predicts that there should be shape differences of fruits on plants with and without *T. treculeanella* larvae. 3) Were plants with a large larval load a result of more oviposition attempts or more eggs laid in their flowers? Variation in larval density could result from plant factors, but also from differences in moth behavior. Moths may attempt fewer ovipositions, or be less successful in laying eggs. We asked whether there were fewer ovipositions into flowers on plants without larvae and if there were fewer eggs in flowers on plants without larvae. The cheater hypothesis predicts that there should be successful ovipositions into fruits without larvae. 4) Did fruits on plants that lack *T. treculeanella* larvae have more intact viable seeds than plants that contain larvae? The hypothesis predicts that the plant would benefit by eliminating seed predation by the pollinator, which would result in an increase in the number of intact viable seeds produced. 5) Did larvae of the cheater yucca moth *T. corruptrix* that coexist with pollinators show random distribution across fruits? The cheater moth oviposits directly into full-size fruits, so larval distribution should not be affected by the proposed killing mechanism. Thus the hypothesis pre-

dicts that cheater larval distribution should be independent of pollinator larval distribution.

## Material and methods

### Study species

*Yucca treculeana* Carrière (= *Y. torreyi* Shafer; Robbins 1983) is widely distributed throughout the northern Chihuahuan desert and adjacent grasslands in southwestern Texas, southeastern New Mexico, and northern Mexico (Correll and Johnston 1979, Robbins 1983). An individual plant produces one or a few inflorescences, each consisting of several hundred flowers. The white, sometimes purple-tinged flowers are open for 1–2 days each, and flowering within an inflorescence is progressive over the course of 1–2 weeks. Flowering extends from late February and to mid April in the study area. The green, fleshy fruits of *Y. treculeana* ranged in size in the study area between 4–12 cm in length.

*Tegeticula treculeanella* Pellmyr (Prodoxidae) is the only documented pollinator of *Y. treculeana* (Pellmyr 1999). The female lays her eggs inside the ovaries of yucca flowers, in a cavity above the topmost ovule in a locule. After oviposition, she uses specialized mouthparts to deliberately pollinate the flower with pollen gathered from flowers. The larva feeds on a portion of the developing seeds inside the fruit, generally starting at the top of locules and feeding downward. Upon completion of development, the larva chews its way out of the fruit, and descends to the ground where it burrows down to diapause in a dense cocoon. The adult emerges during a subsequent flowering period one or a few years later (Riley 1892).

The larva of a comparatively uncommon cheater yucca moth, *T. corruptrix*, also was found inside some fruits. Whereas *T. treculeanella* larvae generally start feeding at the top of the seed stacks, *T. corruptrix* typically feed in the lower two thirds, and we used this criterion to remove the cheater larvae from the analyses. DNA-sequence based identification of a separate set of 82 larvae indicated that this criterion is 87–89% accurate (Crabb and Pellmyr, unpubl.). Removal of cheater larvae in calculations had a weak conservative effect on rejection of the hypothesis as pollinator and cheater larvae were positively associated, and cheater moth damage thus increased probability that the cheater plant hypothesis would be accepted.

### Fruit collection

Sample collection was performed in Big Bend National Park, Texas, USA (N29°15' W103°15') in May 2000 and March–May of 2001. Some observations were made in the adjacent Black Gap Wildlife Management Area. In

each year, 100 flowering plants were located during the flowering season and then used for fruit collection. To assure that seed consumption had ceased, we monitored the study plants daily for larval exit holes. When most fruits on a given plant had exit holes, we haphazardly harvested five fruits distributed within the infructescence from each plant. Fruits from study plants that did not show exit holes early on were harvested when adjacent plants with holes were ready. Pilot dissections of longer series of fruits within plants showed that five fruits would suffice to document most of the intraplant variation. In 2000, eighteen of the 100 selected plants failed to set any fruit, thus only 82 plants were used in pertinent analyses.

Before dissecting the fruit to assess larval damage, we measured mass to the nearest 0.01 g using a Mettler Toledo PB1502 balance, and length and diameter of each fruit to the nearest 0.01 mm using calipers. We also made a photocopy of each fruit before dissection. Fruits were then dissected and we counted the total number of larvae present in each fruit and the total number of intact viable seeds produced.

To calculate the degree of tapering, we used the photocopies of fruits (Fig. 1). The picture of each fruit was cut out, using the bottom half of the fruit (which in general is rounded and non-tapered) as a template for the upper part of the fruit (where the tapering occurs) to give the relative weight of a non-tapered fruit. This piece

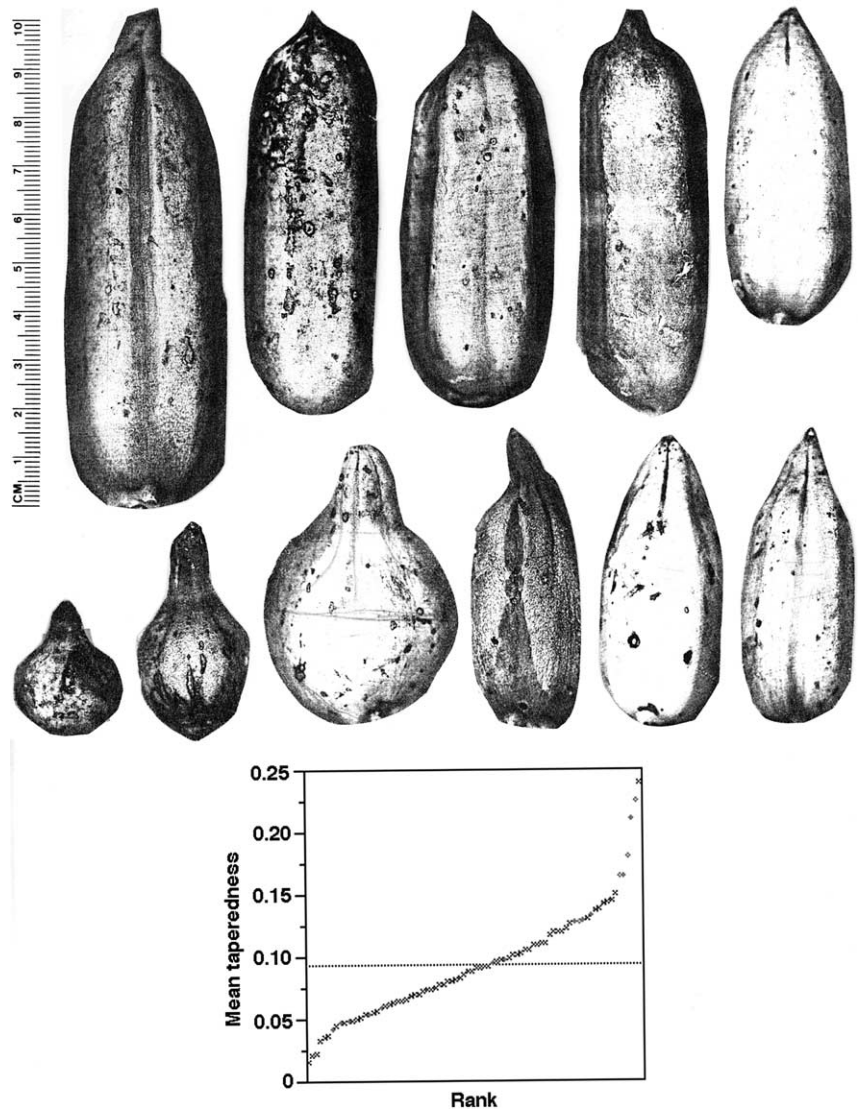


Fig. 1. Variation in fruit shape in *Y. treculeana*. Top, fruits from 11 study plants; ruler = 10 cm. Below, rank plot of mean taperedness among all plants in 2000, computed as described in text.

of paper was weighed to the nearest 0.0001 g using a Mettler Toledo AB104 balance. Next the actual shape of the upper portion of the fruit (with tapering) was cut out and the paper was weighed again. To estimate a tapering index, we then calculated the difference between the two and divided by the non-tapered number to get a percent tapering value.

### Distribution of oviposition scars and moth eggs

Samples were collected from a sub-set of the 100 plants used for the 2001 flower and fruit collection. We selected five flowers per plant that had been open for a night and had been pollinated by at least one moth. Pollinated flowers were easily distinguished from unpollinated flowers by the presence of pollen on the stigmatic tissue. Flowers were removed from the plant, immediately preserved in 70% ethanol, and transported back to Vanderbilt University to be analyzed.

Oviposition scars were counted using an Olympus SZ40 dissecting microscope (magnification  $10 \times -30 \times$ ). Scars appeared as minute holes on the exterior of the ovary surface approximately 1 cm below the top of the style. Each flower was then divided into thirds by cutting along the wall of each carpel, and the number of eggs deposited inside the flower was counted under the microscope. The eggs of *T. treculeanella* appeared as white, semi-translucent elongate structures 1–2 mm in length found in the cavity above the topmost ovule.

### Statistical and morphological analyses

If *T. treculeanella* females lay their eggs randomly among plants and those eggs translated into larvae, the number of larvae within and among plants should fit a Poisson distribution. Using this assumption, we calculated expected frequencies of larvae both within and among plants in the population. We compared observed and expected frequencies using a G-test. Since the results did not conform to a Poisson distribution, we used the coefficient of dispersion (CD; Sokal and Rohlf 1981) to determine whether or not the distribution was a case of clumping ( $CD > 1$ ) or repulsion ( $CD < 1$ ).

To determine whether plants with and without larvae differed in fruit traits, we performed a MANOVA of the fruit character plant means using the presence/absence of *T. treculeanella* larvae as the effect. Only the results of the 2000 fruit data-set MANOVA were significant. For this significant MANOVA result, we ran independent tests on each morphological trait for all fruits to determine which individual traits differed. No transformations produced normal distributions, so we used the nonparametric Wilcoxon signed-ranks test.

To test if there was a difference in the number of oviposition scars or eggs laid on plants with and without

larvae, we used the Wilcoxon signed-ranks test as neither of the distributions could be normalized.

We tested whether plants that lacked larvae produced more intact viable seeds in their fruit using an Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf 1995) since the viable-seed data did not conform to the assumptions of normality of a two-way ANOVA. Year was the block in the design and presence/absence of *T. treculeanella* larvae was the treatment.

## Results

### *Tegeticula treculeanella* larvae distribution within and among plants

In both 2000 and 2001, the distributions of the number of fruits per plant that contained *T. treculeanella* larvae did not conform to a Poisson distribution (Fig. 2A). In both instances there was an excess of plants that had either no fruits containing larvae or all five fruits containing larvae. In both years, the distribution of *T. treculeanella* larvae per fruit also did not conform to a Poisson distribution (Fig. 2B). The two distributions were clumped with an excess of fruits that contained no larvae and fruits that contained many larvae.

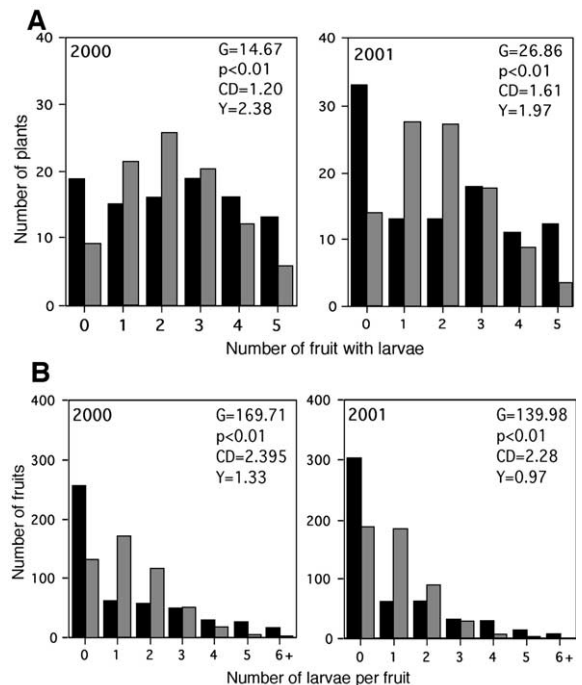


Fig. 2. Observed (black bars) and expected distribution (gray bars) based on a Poisson distribution of (A) the number of fruits per plant containing moth larvae, and (B) the number of moth larvae in fruits.

### Morphological differences between fruits that did and did not have *T. treculeanella* larvae?

The cheater plant hypothesis states that there are two fruit types: narrowed fruit (which are short, bulbous, sharply constricted at the tip, and do not contain larvae) and tapered fruit (which are long, uniformly tapered, and contain larvae). *Yucca treculeana* did not have two discrete fruit types but rather showed a continuous distribution (Fig. 1).

MANOVAs using the plant means of each fruit trait as the variable and presence/absence of *T. treculeanella* larvae as the effect yielded very different results between years. There were significant differences in fruit trait means on plants with and without larvae in 2000 ( $F = 4.8810$ ,  $p = 0.030$ ,  $N = 82$ ,  $df = 1, 80$ ), but no differences in 2001 ( $F = 0.4058$ ,  $p = 0.526$ ,  $N = 100$ ,  $df = 1, 98$ ).

Since there was no overall difference in fruit characteristics in 2001, we only performed independent tests on the data from 2000. Fruits on plants that contained larvae had significantly higher mass, were longer, had a larger length:diameter ratio, and were less constricted at the tip than plants with fruit that did not contain larvae (Table 1). Plants with fruits with or without larvae, respectively, did not have significantly different fruit diameter (Table 1).

### Reasons for a large larval load

Oviposition scar counts indicated that there was no difference in the number of oviposition attempts in flowers on plants that ended up having larvae than plants that did not end up having larvae (Table 2). Similarly, there was no difference in the number of eggs successfully laid into flowers on plants that ended up having larvae than plants that did not end up having larvae (Table 2).

### *T. treculeanella* larvae and intact viable seeds

Contrary to the predictions of the cheater plant hypothesis, fruits on plants with larvae produced significantly

more intact, viable seeds than fruits on plants without larvae (Table 3). There was also a year effect in that plants in 2001 produced more intact viable seeds than plants in 2000. There was also an interaction effect in that the difference in intact viable seeds produced between plants with and without larvae was greater in 2001 than in 2000 (Table 4).

### Distribution of the cheater yucca moth *T. corruptrix* across fruits?

Since *T. corruptrix* oviposits straight into fruits with developed seeds, primarily in the lower two thirds, they should now show any association in distribution among fruits with *T. treculeanella*. Contrary to this prediction we found a highly significant positive association between larvae of the two species (2000:  $\chi^2 = 6.5$ ,  $p = 0.0108$ ; 2001:  $\chi^2 = 14.1$ ,  $p = 0.0002$ ).

### Discussion

There are relatively few reported cases in the literature of individual plants that defect in pollination mutualisms by not providing a reward (Bell 1986, Gilbert et al. 1991, López-Portillo et al. 1993, Golubov et al. 1999). The suggestion that yucca plants may defect by killing pollinator moth eggs or larvae (Bao and Addicott 1998) is unusual in this context, as it is an obligate mutualism, where defection under many circumstances may be evolutionarily unstable (Bull and Rice 1991; but note defection by all females in dioecious figs, Patel et al. 1995). Based on observational data, Bao and Addicott laid out a verbal model involving frequency- and density-dependent selection on plant morphs, and suggested that the phenomenon may be applicable to several other yucca species. The present analysis of *Y. treculeana* is the first test of this cheater plant hypothesis.

Data to test the first prediction provided support for the cheater plant hypothesis. We found that the distribution of larvae within and among plants conformed to the predictions of the cheater plant hypothesis, in that there

Table 1. Summary of non-parametric independent tests of the fruit traits in 2000 for plants with larvae and plants without larvae.

Fruit trait	N	Mean ( $\pm$ SE)	Z	p
Mass (g) with larvae	325	37.8 $\pm$ 1.14		
Mass (g) without larvae	80	27.9 $\pm$ 1.33	-3.46837	0.0005
Length (cm) with larvae	325	7.76 $\pm$ 0.10		
Length (cm) without larvae	80	6.36 $\pm$ 0.17	-5.90682	<0.0001
Diameter (cm) with larvae	325	3.28 $\pm$ 0.03		
Diameter (cm) without larvae	80	3.15 $\pm$ 0.05	-1.20273	0.2291
Length:diameter ratio with larvae	325	2.38 $\pm$ 0.02		
Length:diameter ratio without larvae	80	2.02 $\pm$ 0.05	-6.11416	<0.0001
Tapering with larvae	325	0.09 $\pm$ 0.002		
Tapering without larvae	80	0.12 $\pm$ 0.008	3.56646	0.0004

Table 2. Comparison of the number of oviposition scars and eggs laid in flowers on plants eventually with or without larvae, N = number of flowers.

Trait	N	Mean $\pm$ SE	Z	p
Oviposition scars, plants with larvae	129	4.53 $\pm$ 0.20		
Oviposition scars, plants without larvae	63	4.75 $\pm$ 0.45	-0.89983	0.3682
Eggs laid, plants with larvae	129	1.66 $\pm$ 0.14		
Eggs laid, plants without larvae	63	1.63 $\pm$ 0.20	-0.10646	0.9152

were many more plants and fruits without larvae than expected based on a Poisson distribution (Fig. 2). This difference could be a result of plants actually preventing seed consumption, but could alternatively be a result of differential oviposition attempts or eggs laid by the adult moths. The results showed no significant difference in oviposition attempts or eggs laid between plants with and without larvae (Table 2), so we can exclude that possibility.

Most of our data do not support the cheater plant hypothesis. *Yucca treculeana* individuals do not have two discrete fruit morphs ("narrowed" and "tapered") as defined a priori for *Y. baccata* (Bao and Addicott 1998). The distribution of fruit shape was effectively continuous in *Y. treculeana* (Fig. 1). This result alone does not prevent the possibility of there being fruits of a certain shape that contain larvae, as there could be a continuous distribution of fruit forms, with fruits on cheater plants having a different morphology than fruits on non-cheater plants. This was not the case. The multivariate analysis of variance of fruit characteristics on plants with and without larvae did not produce consistent results between years. In 2000, but not in 2001, there was a significant difference in the fruit traits between plants with and without larvae. The independent tests for the 2000 data showed that fruits on plants with larvae were heavier and longer, had larger length:diameter ratios, and were less constricted at the tip. Since fruit diameter did not differ between categories, the difference found in the length:diameter ratio is attributable to difference in fruit length. Despite these differences in 2000, the fact that the overall MANOVA results were not consistent between years conflicts with the cheater plant hypothesis. In order for the hypothesis of fruit shape to be accepted, shape differences should be a reliable predictor of the distribution of *T. treculeanella* larvae across years.

The strongest evidence against the cheater plant hypothesis comes from the patterns of intact seeds among plants, and from the distribution of *T. corruptrix*. The implicit assumption of the cheater plant hypothesis

is that cheater plants may benefit because they avoid seed predation by the pollinator and thus would have more intact seeds. The results did not show this predicted net benefit for plants without larvae. In fact, the plants without larvae actually produce significantly fewer intact viable seeds than plants that contained larvae. No comparison can be made to the *Y. baccata* study, as intact seed counts were not provided for the two fruit categories.

This result is not likely due to inverse frequency dependence, as hypothesized by Bao and Addicott (1998). They speculated that cheater plants could be maintained in the population by inverse frequency-dependent fitness of fruit forms. When cheater plants are common in the population, the numbers of yucca moth larvae in the fruit of non-cheater plants would be low and thus those plants would produce more seeds per fruit. As the frequency of non-cheaters increases, moth densities would increase, which would increase the number of seeds consumed in fruits of non-cheaters, giving a fitness advantage to cheater plants. Number of intact viable seeds produced in each fruit was not reported in *Y. baccata*, but instead the number of inviable ovules per locule was used to define cheater and non-cheater plants. Over 70% of the individuals in the population were characterized as cheaters by this definition. In the present study of *Y. treculeana*, plants lacking larvae were infrequent in the population. In 2000, 19 of 100 study plants lacked larvae, and 33 of 100 plants in 2001 lacked larvae. Given this low frequency, population densities of moths and resulting seed consumption should be high, thus giving a fitness advantage to cheater plants. This was not the case, as our data show that plants without larvae were at a fitness disadvantage when estimated by intact seed production.

Why would fruits on plants with larvae contain significantly more intact viable seeds than fruits on plants without larvae? One possibility is that seed consumption by larvae of the cheater moth *T. corruptrix*

Table 3. Number of intact viable seeds produced in fruits on plants with and without larvae in 2000 and 2001.

Year	Presence/absence	Number of fruits	Mean $\pm$ 1 SE
2000	No larvae	94	65.14 $\pm$ 2.99
2000	Larvae	397	69.82 $\pm$ 1.46
2001	No larvae	164	65.90 $\pm$ 2.17
2001	Larvae	333	81.99 $\pm$ 1.57

Table 4. Results of rank test comparing total number of intact viable seeds produced in fruit with and without *T. treculeanella* larvae, between years, and their interaction.

Source	df	H	p
Presence/absence	1	21.4178	<0.001
Year	1	8.5373	<0.01
Year $\times$ presence/absence	1	7.6849	<0.025

may eliminate the benefit for cheater plants. In 2000, they constituted 5.3% of all larvae ( $n=681$ ) and, in 2001, 18.7% of all larvae ( $n=572$ ). *Tegeticula corruptrix* could preferentially oviposit into fruits on plants without *T. treculeanella* larvae to avoid possible competition for seeds. If correct, such a distribution of *T. corruptrix* larvae could result in seed predation in fruits without pollinator larvae that would eliminate the advantage given to cheaters. This would result in a negative association between pollinator and cheater larvae. In the two years of the study, however, we found only one fruit in which there was a *T. corruptrix* larva present on a plant that lacked *T. treculeanella* larvae. There was in fact a significant positive association of pollinator larvae and cheater larvae in both years, refuting this explanation for the low intact seed count in fruits without pollinator larvae. Either *T. corruptrix* selectively oviposits in the same plants as *T. treculeanella* or the same mechanism that is causing the death of *T. treculeanella* is causing the death of *T. corruptrix*. Inviability of topmost ovules would be ineffective as *T. corruptrix* oviposits anywhere on the fruit, and at a time when seeds are well developed (Pellmyr 1999). By inference, shared oviposition preference or a shared mortality factor other than that proposed by the cheater plant hypothesis is needed to explain these patterns.

Another possibility is that plants without larvae are a result of poor quality pollination. This could result for example through small amounts of pollen or autogamous pollination (Pellmyr et al. 1997, Huth and Pellmyr 2000, Marr et al. 2000). The lack of quality pollination might cause the fruit to develop abnormally, which results in oddly shaped fruit, more non-developing ovules in the fruit, and the death of larvae. This hypothesis assumes that there can be differential pollination of flowers in the absence of differential oviposition into flowers, since we found no significant differences in the number of oviposition attempts or eggs laid in flowers that did and did not contain larvae. Available data do not allow us to assess pollination quality, but it could be determined by observing moth behavior and quantifying the amount and genotype of pollen deposited by a moth.

The evolution of non-pollinating cheater moth species in the yucca–yucca moth obligate mutualism has been well documented (Addicott 1996, Pellmyr et al. 1996), but it appears to have been a non-adaptive change secondary to a niche shift to access an unexploited seed resource (Pellmyr and Leebens-Mack 2000) rather than direct selection for defection. The proposed presence of a trait for defection in yuccas (Bao and Addicott 1998) yielded several testable hypotheses. Our test using *Y. treculeana* provided limited support for one prediction, but all other predictions were quite strongly rejected for this species. Whereas the verbal, rather complex model for balanced dimorphism in *Y. baccata*

may be theoretically possible, data are needed to test it. The data from *Y. treculeana* do not support the hypothesis that defecting plants exist in this species.

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