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## Characterizing the interaction between the bogus yucca moth and yuccas: do bogus yucca moths impact yucca reproductive success?

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**Abstract** Yucca moths are most well known for their obligate pollination mutualism with yuccas, where pollinator moths provide yuccas with pollen and, in exchange, the moth larvae feed on a subset of the developing yucca seeds. The pollinators, however, comprise only two of the three genera of yucca moths. Members of the third genus, *Prodoxus*, are the “bogus yucca moths” and are sister to the pollinator moths. Adult *Prodoxus* lack the specialized mouthparts used for pollination and the larvae feed on plant tissues other than seeds. *Prodoxus* larvae feed within the same plants as pollinator larvae and have the potential to influence yucca reproductive success directly by drawing resources away from flowers and fruit, or indirectly by modifying the costs of the mutualism with pollinators. We examined the interaction between the scape-feeding bogus yucca moth, *Prodoxus decipiens*, and one of its yucca hosts, *Yucca filamentosa*, by comparing female reproductive success of plants with and without moth larvae. We determined reproductive success by measuring a set of common reproductive traits such as flowering characteristics, seed set, and seed germination. In addition, we also quantified the percent total nitrogen in the seeds to determine whether the presence of larvae could potentially reduce seed quality. Flowering characteristics, seed set, and seed germination were not significantly different between plants with and without bogus yucca moth larvae. In contrast, the percent total nitrogen content of seeds was significantly lower in plants with *P. decipiens* larvae, and nitrogen content was negatively correlated with the number of larvae feeding

within the inflorescence scape. Surveys of percent total nitrogen at three time periods during the flowering and fruiting of *Y. filamentosa* also showed that larval feeding decreased the amount of nitrogen in fruit tissue. Taken together, the results suggest that although *P. decipiens* influences nitrogen distribution in *Y. filamentosa*, this physiological effect does not appear to impact the female components of reproductive success.

**Keywords** Mutualism · Community context · Herbivory · Plant physiology · Species interactions

### Introduction

Our understanding of mutualism has been based largely on studies of pairwise interactions between mutualists (Bacher and Friedli 2002; Bronstein and Barbosa 2002; Stanton 2003). From these studies, we have learned that the evolution and maintenance of mutualisms are dependent on the fitness benefits and costs of engaging in the interaction. Mutualisms are viewed as balanced antagonistic interactions in which the net outcome is beneficial to both participants (Thompson 1982; Herre et al. 1999; Bronstein 1994, 2001). This view has spurred research on identifying the benefits and costs across a wide range of mutualisms and has also focused attention on model systems such as the pairwise interactions in obligate pollination mutualisms. For these interactions in particular, progress has been made in identifying, not only the benefits and costs, but also the mechanisms that balance these factors to prevent overexploitation by the mutualists themselves (Pellmyr and Huth 1994; West and Herre 1994; Nefdt and Compton 1996; Addicott 1998; Wilson and Addicott 1998; Herre 1999; Weiblen et al. 2001; Segraves 2003). Although studies of these pairwise interactions have been essential to our understanding of mutualism, we know, however, that mutualists are part of a greater community and must simultaneously interact with other species.

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Such interactions with other community members may directly or indirectly influence mutualisms by modifying their cost-benefit ratios (e.g., Gaume et al. 1998). To fully understand the evolution and maintenance of mutualisms, we need to place them in the community context in which they occur (Cushman and Whitham 1989; Cushman 1991; Thompson and Pellmyr 1992; Thompson 1994; Bacher and Friedli 2002; Bronstein and Barbosa 2002; Stanton 2003). Examining how mutualists interact with other community members is the first step in identifying the direct and indirect effects third parties may have on mutualisms.

The specialized interactions between plants and their obligate pollinators represent good starting points for incorporating a community context into studies of mutualism. The interaction between yuccas (Agavaceae) and yucca moths in the genus *Tegeticula* (Prodoxidae) is a well-studied, classic example of an obligate pollination mutualism (Riley 1892; Powell 1992; Pellmyr 2003). This interaction is one of several that have formed the basis of our knowledge about mutualisms in general, and many models of mutualism have been formulated with this interaction in mind (e.g., Bull and Rice 1991; Law et al. 2001; Holland and DeAngelis 2001, 2002; Bronstein et al. 2003; Morris et al. 2003; Wilson et al. 2003). Pollinator yucca moth larvae feed exclusively on yuccas, and the female moths actively pollinate the flowers into which they lay eggs (Powell 1992; Pellmyr 2003). Because the developing moth larvae only consume a portion of the seeds within a fruit, the overall interaction is beneficial to both partners. This mutualism is balanced by both intrinsic plant factors and extrinsic mortality factors that reduce seed damage caused by moth larvae (Pellmyr and Huth 1994; Addicott 1998; Wilson and Addicott 1998; Segraves 2003). The obligate nature of the interaction has made it tractable for studying the evolution of mutualism because there is usually only one or two pollinator species utilizing a yucca species at a given locality (Pellmyr 2003).

In addition to interacting with the pollinator moths, yuccas are also utilized by other prodoxid moths that are not mutualists. Within the *Tegeticula* pollinator lineage, two cheater species have evolved that do not pollinate, yet feed on the developing seeds (Pellmyr and Leebens-Mack 1999, 2000; Pellmyr 1999; Marr et al. 2001). Another genus of yucca specialists, *Prodoxus*, also does not pollinate, but feeds on plant parts other than seeds (Davis 1967). This genus is widespread and species co-occur with the pollinator moths on almost every species of yucca with the possible exception of *Yucca reverchoni* (O. Pellmyr, personal communication). Adults rest in the flowers during the day and mate within yucca flowers at night, but they lack the specialized mouthparts used for pollination. Riley (1880) labeled *Prodoxus decipiens* as the “bogus yucca moth” because it was repeatedly misidentified as a pollinator. Since then, the name bogus yucca moth has been applied to the genus as a whole. There are currently 11 described bogus yucca moth species that differ in the yucca species utilized and the location of larval feeding (Davis 1967; Powell 1984; Wagner and

Powell 1988; Powell 1992). Seven of the species feed within the inflorescence scape, three in the fruit wall, and one as a leafminer. Unlike the wealth of information about the interactions between the true pollinator yucca moths and yuccas, there are no studies that specifically examine the interactions between bogus yucca moths and yuccas. Characterizing these interactions is important for incorporating a community context into the pollination mutualism between *Tegeticula* and yuccas, and for addressing hypotheses about the diversification of yucca moths in general (Althoff et al. 2001). Moreover, recent theoretical models have shown that community members can influence the temporal and spatial dynamics of mutualisms such as the one between yuccas and yucca moths (Bronstein et al. 2003; Morris et al. 2003; Wilson et al. 2003).

In this study, we examined the interaction between a scape-feeding *Prodoxus* species, *P. decipiens*, and one of its hosts, *Y. filamentosa*. We chose this system because there are already a number of studies on flowering and fruit production in *Y. filamentosa* (Huth and Pellmyr 1997; Marr et al. 2000), on the costs and benefits of the mutualism between *Y. filamentosa* and its pollinators (Pellmyr and Huth 1994; Huth and Pellmyr 2000; Marr and Pellmyr 2003), and on the impact of the cheater yucca moths on the mutualism (Marr et al. 2001). Specifically, we asked whether *P. decipiens* feeding reduces the reproductive success of *Y. filamentosa*. We addressed this question in two ways. First, we compared commonly measured components of female reproductive success such as flowering phenology, fruit set, and seed production between plants in which *P. decipiens* was excluded and those with naturally occurring densities of moth larvae. For these plants, we also measured seed nitrogen content. Second, we quantified whether *P. decipiens* larvae represent a drain on plant nutrients allocated to the entire inflorescence, and the temporal component of this effect. We harvested another subset of plants with naturally occurring densities of moth larvae and measured the percent nitrogen content of the scape, flower, and fruit tissues. These plants were harvested at three time points during the flowering and seed-provisioning periods for *Y. filamentosa*. We chose to examine nitrogen content, because nitrogen is a key component in both seed provisioning (e.g., Parrish and Bazzaz 1985) and insect larval development (Bernays and Chapman 1994; Schoonhoven et al. 1998).

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## Methods

### Study system

We studied the interaction between *P. decipiens* and *Y. filamentosa* at two sites located on the Lake Wales Ridge in central Florida. One site was west of Sebring, Fla. (27° 32' 06"N, 81°32' 5"W) and the other was located in Placid Lakes, Fla. (27°15' 22"N, 81°22'57"W). These sites are approximately 45 km apart. *Y. filamentosa* (Agavaceae) is a perennial that grows in recently disturbed areas and can reproduce sexually or clonally through the production of

new rosettes from rhizomes. Individuals typically flower once every 2–3 years and produce a 1- to 2-m panicle inflorescence. Flowering at the study sites begins in April and continues into June. An inflorescence may contain up to 300 or more flowers that open over the course of 6–15 days. Flowers open at dusk and close the following morning. Flowers not pollinated the first night are abscised from the plant. Each capsular fruit has the potential to produce over 250 seeds.

*P. decipiens* Riley (Lepidoptera: Prodoxidae) occurs from the east coast of the United States west to the Edwards Plateau in central Texas and feeds on four *Yucca* species across its range (Davis 1967; Althoff et al. 2001). At the study sites, it only feeds on *Y. filamentosa*. Adults are active at night, and mate within yucca flowers. Female moths oviposit into the scape, and larvae feed within the scape tissue throughout their development (Fig. 1). Fifth instar larvae feed to within a few millimeters of the scape exterior and then diapause within a silken cocoon. Larvae can remain in diapause for several years, and adults emerge from the previous years' scapes throughout the flowering period of *Y. filamentosa* (D. M. Althoff, unpublished data).

#### Moth exclusion and reproductive success of *Yucca filamentosa*

To assess the effect of *P. decipiens* on female reproductive success, we compared commonly measured traits of reproductive success between ten plants exposed to larval feeding and ten plants from which *P. decipiens* was excluded. This experimental manipulation was conducted at the Placid Lakes site. Moths were excluded from the whole inflorescence of ten plants by enclosing each inflorescence within a cage prior to *P. decipiens* emergence for the flowering season. The cages were made from 1×1 mm fiberglass screening and were held approximately 15 mm from the scape exterior with foam pipe insulation cut into 2-cm strips and wrapped around the scape at 30- to 40-cm intervals. This was done to ensure that female moths could not reach the scape surface with their ovipositors. The tube of screening extended from the base of the scape to the first side branch of the inflorescence. The remaining part of the inflorescence was enclosed in a mesh bag made of veil material (0.5×0.5 mm mesh) to exclude florivores and the pollinator moths. For the ten plants to which *P. decipiens* were allowed access, the inflorescences were enclosed in the same way except that the fiberglass screening around the scapes was only partly sealed. Each day we used an excess of outcross pollen to hand pollinate all the newly open flowers on all 20 plants to ensure that differences in fruit set or seed set were not due to differences in pollen quantity or quality.

For each plant, we measured a suite of variables associated with plant size and reproductive success. Rosette diameter and inflorescence height were measured to estimate plant size. The following traits were measured to assess female reproductive success: flowering duration, number of flowers, number of fruits, total number of unfertilized ovules, and total number of seeds. We also dissected all scapes to count the number of larvae present and to check the effectiveness of the cages. We used MANCOVA to test for differences in the number of flowers, flowering duration, proportion

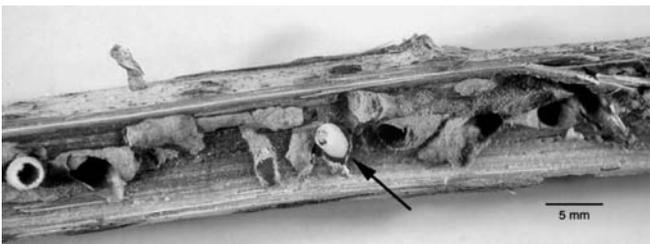
fruit set, number of ovules per fruit, and proportion of seeds matured. Proportion fruit set and seeds matured were arcsine-transformed before performing statistical analyses. Rosette diameter and inflorescence height were used as the covariates to account for effects due to differences in plant size. Each variable was checked for normality and equality of variances before performing the MANCOVA.

We also tested for differences in seed quality by quantifying germination ability and the percent nitrogen content of seeds. The seeds from all fruits produced by an individual plant were mixed, and 50 seeds were haphazardly chosen to assess germination ability. The germination procedure followed Marr et al. (2000) and was carried out at the Archbold Biological Station in Lake Placid, Florida. Seeds were soaked in water for 48 h in complete darkness and then placed in 150×15 mm polyethylene petri plates with a piece of 120-mm filter paper in the bottom. The plates were placed in complete darkness inside an ice cooler at room temperature and seeds were kept moist by spraying them with deionized water. We recorded the number of seeds germinated per plant per day, and germinated seeds were removed from the plates daily. For some plates, the seeds were rinsed in water and the filter paper replaced when fungal infections appeared. Germination was monitored for 37 days. The experiment was terminated on day 37 because it was the fifth consecutive day without any seed germination. We used ANCOVA to test for differences in the total number of seeds germinated and the number of seeds germinating per day between the two groups. Rosette diameter and inflorescence height were used as the covariates.

#### Moth effects on tissue nitrogen content in *Yucca filamentosa*

We examined the temporal component to effects of *P. decipiens* larvae on plant nitrogen content by harvesting inflorescences/infructescences from plants at the Sebring site. Twenty inflorescences/infructescences were harvested at three time points: during flowering, 14 days after plants had completed flowering and were provisioning seeds, and 30 days after flowering when seed provisioning was nearly complete. For each scape, the number of larvae present was determined through dissections. Each scape was then divided into tissue below larval feeding, tissue above larval feeding, and floral/fruit tissue. We removed the ovules and seeds from the pistils and fruits. For this experiment, our goal was to quantify changes in nitrogen content in the structures that support seed development. All tissue types were dried for 3–4 days at 54°C in a drying oven, frozen in liquid nitrogen, and ground to a fine powder in a mortar and pestle. Fibrous scape material was also ground with a Wiley Mill before freezing. Sub-samples of 3–6 mg were weighed on a microbalance (Model 4504 MP8, Sartorius, Edgewood, N.Y.) and analyzed for total nitrogen content using a carbon/nitrogen analyzer (Model EA 1112, CE Elantech, Lakewood, N.J.). All values were referenced to an aspartic acid standard (CE Elantech, Lakewood, N.J.). We examined the effects of *P. decipiens* larvae on percent total nitrogen by using linear regression. Percent total nitrogen was regressed against the number of larvae present in the scape. Separate regressions were conducted for the pistil/fruit tissue for each of the three time periods. Because there was a gradient in nitrogen content along the length of the scape (percent total nitrogen increased from bottom to top), we examined the difference in percent total nitrogen between the scape below and above larval feeding for each of the time periods. If *P. decipiens* was consuming a significant amount of plant resources, we expected that the difference in percent nitrogen content would be less in plants that contained many larvae. Larvae would be reducing the amount of nitrogen reaching the top portion of the scape.

To assess the effect of larval feeding on seed provisioning, we also analyzed the nitrogen content of seeds from plants in the exclusion experiment. We used ANOVA to test for differences in percent nitrogen content of seeds between the two groups. The percent nitrogen content values were arcsine-transformed and tested for normality and equality of variances before performing ANOVA.



**Fig. 1** Close-up of *Prodoxus decipiens* larval feeding galleries and cocoons used for diapause. Larva is present in middle of photograph. Note how galleries completely fill center of *Yucca filamentosa* scape

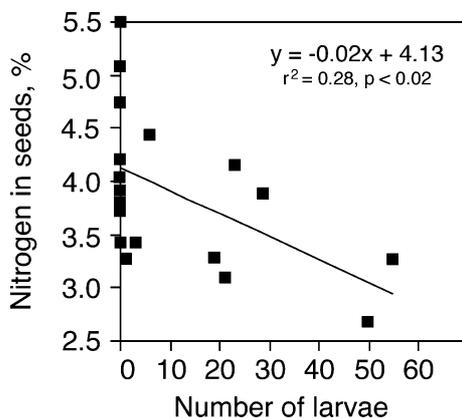
All statistical tests were performed using JMP 3.2.1 (SAS Institute 1997).

## Results

The exclusion cages were 100% effective at preventing *P. decipiens* from ovipositing into the scapes. No larvae were found in the scapes of the ten plants in the exclusion treatment. The mean number of larvae in the scapes of plants exposed to moths was  $23.00 \pm 6.44$  and ranged from 1 to 55 larvae. One of the plants in this group was vandalized and was removed from the experiment.

The exclusion of feeding by *P. decipiens* larvae appeared to have no significant effect on the measured traits of female reproductive success (MANCOVA,  $F=2.55$ ,  $P=0.14$ ). There was no difference in the number of flowers produced, flowering duration, or fruit set between plants with and without larvae feeding in the scape. Seed production was also unaffected. The number of ovules produced and the proportion of seeds matured were not statistically different. There was also no difference in the total number of seeds germinated or in germination rate ( $F_{1,16}=0.519$ ,  $P=0.49$  for both). Plant size as estimated by rosette diameter did not have a significant effect on any of the variables ( $F=1.62$ ,  $P=0.29$ ), whereas inflorescence height significantly influenced seed germination ( $F=8.90$ ,  $P=0.01$ ). Plants with taller inflorescences had more seeds germinate and had a faster germination rate than plants with shorter inflorescences.

Feeding by *P. decipiens* larvae, however, did influence the distribution and quantity of nitrogen within the reproductive structures of *Y. filamentosa*. For the exclusion experiment, seeds from plants containing moth larvae had significantly reduced nitrogen levels ( $F_{1,16}=7.459$ ,  $P=0.02$ ), and the magnitude of this reduction was dependent upon the number of larvae present in the scape (Fig. 2). There was a significant negative association between the number of larvae feeding in a scape and the percent total nitrogen content of fully mature seeds.

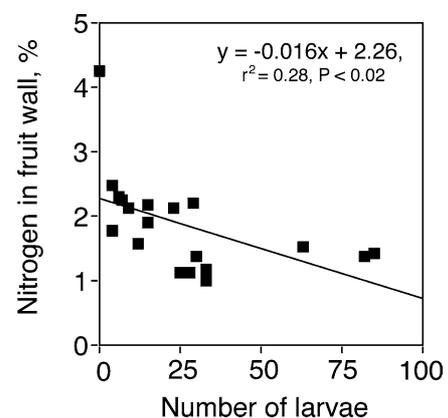


**Fig. 2** Relationship between the number of *Prodoxus decipiens* larvae present in a *Yucca filamentosa* scape and percent total nitrogen of mature seeds

Surveys of percent total nitrogen content for *Y. filamentosa* at the Sebring site also demonstrated that feeding by *P. decipiens* larvae decreased nitrogen levels (Fig. 3). This effect was only apparent in fruit tissue at the end of seed provisioning. As with the effect on seeds, larger numbers of larvae in a scape were negatively correlated with percent total nitrogen. Larval feeding did not affect nitrogen levels in either pistil tissue or in fruit tissue sampled approximately mid-way through the seed-provisioning period. Interestingly, larval feeding only appeared to influence nitrogen levels in mature fruit tissue. For the three time periods sampled, there was no statistically significant relationship between the relative change in percent total nitrogen along the scape and the number of larvae present.

## Discussion

Although yuccas are well known for their obligate pollination mutualism with prodoxid moths, they also have important interactions with several non-pollinating prodoxids. These moths include cheaters that exploit the mutualism and feed on developing seeds, and the bogus yucca moths that feed on plant tissue other than seeds. The interactions between the pollinators and yuccas and between cheaters and yuccas are easily quantified because the costs and benefits of the interaction are measured with the common currency of seeds produced or consumed. For the bogus yucca moths, however, the interaction is more difficult to quantify. There are two potential avenues by which *Prodoxus* species may influence yucca reproductive success—directly, by consuming plant resources that could be used for reproduction, and indirectly, by modifying the mutualism between yuccas and the pollinators. Studies from other plant-pollinator systems have shown that herbivores may negatively impact pollination mutualisms by reducing pollinator attractiveness through decreases in flower number, flower size, or nectar rewards presented to pollinators (Strauss et al. 1999; Mothershead and Marquis 2000; Adler 2001).



**Fig. 3** Regression of percent total nitrogen of fruit tissue excluding seeds in *Yucca filamentosa* as a function of the number of *Prodoxus decipiens* larvae in the scape

In the present study, we examined the direct effects that the scape-feeder *P. decipiens* can have on *Y. filamentosa*. Assays of percent nitrogen content demonstrated that *P. decipiens* consumed plant resources that were directed towards reproduction. Feeding by *P. decipiens* larvae significantly reduced levels of nitrogen in the seeds and surrounding fruit tissue, and the magnitude of the reduction was associated with the number of larvae present within a scape. This decrease in percent total nitrogen was only evident in seeds and fruit tissue that had fully developed, which suggests that the effect of *P. decipiens* feeding may be relatively small but cumulative, or alternatively, may not be present until larvae reach later instars in development. For many insect larvae, both feeding and growth rate are higher in the later instars (Chapman 1998), and for *P. decipiens*, this may correspond with a diversion of nitrogen away from seeds. In either case, plants with *P. decipiens* larvae produced seeds that had lower percent total nitrogen content.

Research on stem-boring insects in agricultural systems has demonstrated that larval feeding can have significant effects on plant reproductive output. Many of the insect pests of corn and cereal grains are stem-borers and cause significant losses to crop yields through the disruption of nutrient flow and the destruction of plant tissue (e.g., Kfir et al. 2003). To the best of our knowledge, however, only a single study has documented the physiological effects of stem-borers in a natural system, and this study focused on plant growth traits rather than reproduction. Moon and Stiling (2000) demonstrated that a lepidopteran stem-borer did not impact growth of the shrub *Borrchia frutescens* as measured by stem height and leaf area. Furthermore, the stem-borer also had no effect on the nitrogen content of leaves. Although the physiological impacts of other types of herbivores such as leaf feeders and gallers has been well documented, the paucity of studies on stem-borers makes it difficult to categorize their general effects on plant reproductive success.

For *P. decipiens*, larval feeding did affect plant physiology by influencing the allocation of nitrogen to seeds, but feeding did not influence other components of *Y. filamentosa* reproductive success. The number of flowers produced and the duration of flowering were not different between plants with and without larvae. Similarly, the number of ovules produced per fruit, the number of seeds matured per fruit, and the overall percent fruit set were unaffected. Interestingly, seed germination was also unaffected even though percent nitrogen content was lower for seeds from plants that contained larvae. This decrease in percent nitrogen content may be more important later in the ontogeny of the seedling rather than in the germination process. For example, less available nitrogen can decrease the window of time available for seedling establishment (Milberg and Lamont 1997; Vaughton and Ramsey 2001; Kitajima 2002). Taken together, these measures of reproductive success suggest that *P. decipiens* feeding may not be an important determinant of *Y. filamentosa* fitness.

How, then, do we characterize the interaction between *P. decipiens* and *Y. filamentosa*? The lack of an effect on plant traits associated with reproductive success suggests that the interaction is largely commensalistic. There was a decrease in seed nitrogen content, but this decrease did not appear to influence seed set or seed germination. The magnitude of the direct effects on plant reproductive success, however, may be partly dependent on local ecological conditions. For example, the reduction of percent nitrogen was significantly correlated with the number of larvae within a scape. In years of limited flowering by *Y. filamentosa*, the effect of *P. decipiens* larvae may be more pronounced because of increased density of larvae within scapes. Flowering in yucca populations can be variable (Rau 1945), and surveys of flowering plants at the Lake Placid site from 1999 to 2003 indicated that the year of this study (2002) was the year with the highest number of flowering *Y. filamentosa* (K. Segraves and D. Althoff, unpublished data). Thus, depending on the availability of flowering plants, the number of larvae in scapes could become quite high and reduce nitrogen levels even further than documented here.

Although not tested in the present study, feeding by *P. decipiens* could also influence plant fitness indirectly by modifying the cost of the mutualism between *Y. filamentosa* and its *Tegeticula* pollinators. For another *Prodoxus* species, *P. y-inversus*, Bronstein and Ziv (1997) demonstrated that the presence of larvae in the fruit wall had a positive effect on *Y. schottii*. Although the mechanism is unknown, fruit with larvae of *P. y-inversus* had significantly reduced seed destruction by pollinator larvae. In the case of *P. decipiens*, we might expect the opposite trend where the presence of larvae results in an increase in the cost of the mutualism for *Y. filamentosa*. The decrease in percent nitrogen content of seeds caused by *P. decipiens* may increase the number of seeds eaten by pollinator larvae during their development. One of the major limitations for the development of phytophagous insect larvae is the acquisition of nitrogen (Bernays and Chapman 1994; Schoonhoven et al. 1998). Even a modest increase in seed consumption per pollinator larva could scale up to a large impact for an individual *Y. filamentosa* because there are multiple larvae per fruit and multiple fruit per plant.

In conclusion, the present study documents that feeding by bogus yucca moth larvae reduces the availability of plant nitrogen for reproduction. This reduction, however, does not appear to influence seed output or seed quality as measured by germination ability. Although we did not detect a direct effect on plant reproductive success, an interesting possibility raised by the study is that the reduction in seed nitrogen content caused by bogus yucca moths may indirectly influence the cost to benefit ratio for the pollination mutualism. Based on the current study, we conclude that the interaction between the bogus yucca moth and yuccas is largely commensalistic, and any direct effects on plant fitness are likely to be sporadic and dependent on yearly variation in flowering conditions.

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