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FLORIVORES LIMIT COST OF MUTUALISM IN THE YUCCA–YUCCA MOTH ASSOCIATION

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Abstract. Multispecies interactions may have important consequences for the ecology and evolution of mutualism by changing the cost-to-benefit ratio. Here I determine whether florivorous beetles can limit moth populations and influence the costs of the mutualism between yuccas and their pollinating moths. Yucca moths actively pollinate yucca flowers, and their larvae feed on a portion of the seeds. I used a manipulative field experiment to examine the hypothesis that the characteristic feeding behavior of the florivorous beetle *Hymenorus densus* may increase mortality of pollinator moth eggs and reduce the costs incurred by the plant. The results indicated that *H. densus* consumes moth eggs and that the consumption rate matches levels of moth mortality typically observed in these populations. On average, beetles consumed 1–2 eggs per flower, which translates into an increase in seed production of ~16–32% per fruit. Counterintuitively, these results suggest that florivores can limit moth populations and reduce the costs incurred by the plant.

Key words: beetle; community context; florivory; Hymenorus; *multi-species interaction; obligate pollination mutualism;* Tegeticula cassandra; *yucca;* Yucca filamentosa; *yucca moth.*

Introduction

Recent syntheses on the evolutionary ecology of species interactions and mutualism in particular have highlighted that integrating a community context is vitally important to our understanding of population dynamics and the evolution of species interactions (Herre 1996, Stanton 2003, Strauss and Irwin 2004). Studies on the evolutionary ecology of mutualism have increasingly incorporated the biological reality that mutualisms are embedded within a community of interacting species (Bronstein and Barbosa 2002, Stanton 2003, Hay et al. 2004, Strauss and Irwin 2004). For several decades, researchers have recognized the importance of additional partners in influencing the outcome of species interactions (e.g., Fritz 1983, Cushman and Whitham 1989, Bronstein 1994, Thompson and Fernandez 2006) and in the evolution of traits important to the interaction (e.g., Brody 1992, Armbruster 1997, Galen 1999, Mothershead and Marquis 2000, Herrera et al. 2002, Cariveau et al. 2004, Rudgers 2004, Gómez 2005). These studies demonstrate that a more complete view of mutualism may only be gained by the additional insight provided when we examine the collective group of organisms interacting with the focal mutualistic species.

This complexity of interactions between mutualists and non-mutualists in combination with spatiotemporal variation in species composition will ultimately determine the ecological and evolutionary trajectories of a mutualism. For example, the presence of particular community members may alter the cost/benefit ratio of a mutualistic interaction (e.g., Morales 2000) or may serve to regulate the mutualism by controlling population dynamics of mutualists (Bacher and Friedli 2002, Hofstetter et al. 2006). Such extrinsic mechanisms are infrequently examined in mutualisms, but yet they may play an important role in the maintenance and persistence of these interactions. One of the drawbacks to this community-wide approach is that assessing the relative contribution of each mutualistic partner may be daunting in diffuse mutualisms, as there can be a complex array of interacting mutualists. As a result, incorporating a community context may become even more difficult when interactions with non-mutualists are also considered. For this reason, obligate mutualisms offer an excellent starting point, as they are often pairwise between mutualists, yet the mutualists interact within a community of other species.

Studies of the influence of other partners on obligate mutualisms demonstrate that the presence of additional

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species may generate complex interactions and have important consequences for the mutualism. In the interaction between figs and fig wasps, ants may serve as indirect mutualists of both pollinator wasps and figs (Schatz et al. 2006), or in other instances, ants may destroy figs and consume pollinator wasps (Dejean et al. 1997). Temporal and spatial variation in the presence and abundance of pollinator wasps, non-pollinator wasps, nematode parasites, and seed-dispersing birds and bats demonstrates that there are many levels of interaction that can influence the pairwise mutualism (Herre 1996).

Until recently, the obligate pollination mutualism between yuccas and yucca moths has been examined nearly exclusively with regard to the pairwise mutualism between the plants and pollinators. Some notable exceptions include experiments that show that the presence of ants on yucca infructescences decreases seed predation by parasitic yucca moths, but does not deter pollinator moths (Perry et al. 2004) and that parasitoids that attack yucca moth larvae can reduce the number of seeds consumed in a fruit (Crabb and Pellmyr 2006). Furthermore, considerable attention has been devoted to understanding the intrinsic mechanisms that plants use to reduce costs in this mutualism (e.g., Pellmyr and Huth 1994, Addicott 1998, Addicott and Bao 1999, Shapiro and Addicott 2003, Humphries and Addicott 2004), but these studies have primarily focused on mechanisms pertaining to the pairwise interaction. For example, yuccas can selectively abscise yucca fruit with many moth eggs within them and limit the number of eggs within retained fruits (Pellmyr and Huth 1994, Marr and Pellmyr 2003; but see Shapiro and Addicott 2004, Holland and DeAngelis 2006). This mechanism, however, only works for the yucca moths that damage ovules as they deposit their eggs into the floral tissue (e.g., Addicott and Bao 1999, Marr and Pellmyr 2003). For species that oviposit superficially in flowers, we lack an explanation for how plants limit moth overexploitation (Wilson and Addicott 1998, Addicott and Bao 1999). Although many eggs are often laid within single flowers by superficially ovipositing species, only a few of these will survive to mature larvae (Addicott 1986, Segraves 2003). Segraves (2003) proposed that exposure to desiccation reduced survivorship of superficially deposited moth eggs and, thus, may potentially limit the number of moths feeding within single yucca fruit. This study, however, could not exclude the possibility that flying predators were responsible for reducing the number of moths developing within fruit. Here I examine this hypothesis by conducting a manipulative experiment on a potential flying predator of yucca moth eggs.

Hymenorus densus, a florivorous tenebrionid beetle, is a common visitor of *Yucca filamentosa* flowers in Florida (Brues 1926). The beetles mate and feed within the flowers and have been observed consuming floral tissue: in particular, the style. The common pollinator of *Y. filamentosa* in Florida is *Tegeticula cassandra*, a superficially ovipositing yucca moth. This pollinator has a characteristic oviposition habit that involves depositing eggs in the basal portion of the style tissue. Given that the beetles feed on tissue in the same location as the oviposition site of *T. cassandra*, beetles may consume moth eggs while feeding (Fig. 1). This study addresses whether florivorous beetles consume moth eggs and, as a result, reduce the costs of mutualism for the plant.

MATERIALS AND METHODS

All studies were conducted near or on the property of the Archbold Biological Station in Lake Placid, Florida, USA (27°11′18″ N, 81°20′16″ W) in the spring of 2006. In this population, *Yucca filamentosa* is pollinated by the yucca moth *Tegeticula cassandra*. Female moths lay their eggs superficially within the style tissue of flowers and then actively pollinate using specialized mouthparts. The larvae feed within the style tissue for a brief period as they burrow into the locule where they complete development feeding on seeds. The tenebrionid beetle *Hymenorus densus* is a frequent visitor of *Y. filamentosa* flowers. Adults feed and mate within the flowers and can occur in very high densities. Brues (1926) discovered their peculiar aggregation behavior, and rather than individually counting beetles, he determined the number of beetles in a gram and weighed a collection from one inflorescence. This extrapolation led to an estimate of 15 000 beetles on a single plant. The life history of this beetle is unknown, and I have never observed them feeding or resting on plants aside from *Yucca*.

Beetle experiment

To determine whether *H. densus* consumes moth eggs while feeding in the flowers, I conducted a manipulative experiment. On 10 plants, I counted the number of moth oviposition scars on 250 flowers and randomly assigned one of three treatments to each flower. The treatments were either control flowers with zero beetles, flowers with four beetles, or flowers with 16 beetles. These beetle densities were based on the results obtained in the beetle survey described here. Beetles were collected from a nearby population ~16 km from the study site. Beetles were trapped onto flowers by placing them in small mesh bags (11 × 13 cm) and then securing the bags around the flowers by wrapping a plastic coated twist tie at the base of the pedicel. Mesh bags were extremely effective in preventing escape by beetles, and beetles appeared to behave normally. After two days, the flowers were harvested, beetles removed, and the flowers were immediately dissected under a dissecting scope (Leica S8 Apo; Leica, Bannockburn, Illinois, USA) to determine the number of eggs remaining. Because *T. cassandra* eggs do not hatch before day 4 (K. A.

FIG. 1. *Hymenorus densus* damage and feeding on *Yucca filamentosa*. (a) Minor beetle damage in pollinator moth oviposition zone. (b) Moderate beetle damage resulting in complete loss of style, but no damage to ovary or ovules. (c) Acute infestation resulting in severe damage to pistil and petals.

Segraves, *unpublished data*), the number of eggs missing from the style tissue should reflect differences caused by beetle feeding and not by hatching of larvae. The length of time that treatments were left on the flowers was determined from the results obtained in the beetle survey described here and by limitations caused by natural floral abscission. Because the data did not conform to the assumptions of parametric statistics even when transformed, I used two different approaches for the analysis. In the first approach, I used the R statistical package (R Development Core Team 2006) to implement a generalized linear mixed model with a quasipoisson error distribution to correct for overdisperson (Crawley 2005). This model tested the effect of beetle density on the number of missing eggs and included the random factor plant as a block effect. In the second approach, I used the same generalized linear mixed model; however, I implemented the model in SAS using PROC MIXED (Littell et al. 2006), and assessed the *P* value by using a randomization test (Cassell 2002). The randomization test compared the *P* value of the model to the distribution of *P* values generated under the assumption that there were no differences among beetle treatments. The distribution of *P* values was generated from 10 000 replicate data sets where the dependent variables were randomized, while the independent variables remained fixed. Significance of treatment means were examined with Tukey's hsd tests to control for multiple comparisons, and the resulting *P* values were assessed with the randomization procedure just described. Because both approaches yielded similar results, I only report the findings from the latter analysis.

Surveys of H. densus

A population of *Y. filamentosa* was surveyed to provide an estimate of the number of *H. densus* typically found within yucca flowers. This range of beetle density was then used in the above manipulative experiment. I determined the number of beetles per flower for 1120 flowers on 36 plants. For flowers with <20 beetles, the number of beetles was determined by counting them on the plant. For flowers with >20 beetles, all beetles from a single flower were collected in a small mesh bag and counted. Beetles were released back onto the plant from which they were collected. From this survey, I determined the mean, variance, and range of beetles residing within flowers. For each flower, I also determined whether there was obvious damage caused by *H. densus* feeding. I examined whether there was a difference in the number of beetles on damaged and undamaged flowers using a Wilcoxon signed rank test.

A separate set of 106 flowers distributed over 10 plants was surveyed for four days to determine the number of consecutive days that *H. densus* are typically found in flowers. This survey was used to determine the length of time to allow beetles to remain on flowers in the above manipulative experiment. These plants were located in the same population as the survey previously described, but utilized different individual plants and were conducted in consecutive weeks. On the first day of the survey, newly opened flowers that contained beetles were individually labeled with a small hanging tag tied around the pedicel. The number of beetles per flower was recorded. On the next three days, I determined the number of beetles per flower and whether the flower had abscised or been damaged by *H. densus*. Beetle damage is distinct and typically involves consumption of the style tissue and inner tepal margins (Fig. 1). At very high densities, *H. densus* can completely consume the pistil. From these data, I determined the attrition rate of beetles. For example, if beetles were present in a flower on day one, how likely was it that beetles would also be present on day two? I used a Fisher sign test to determine whether the relative change in beetle density per flower increased, decreased, or remained the same between consecutive days.

Survey of moth survival and cost to plants

Because survival of moth eggs will ultimately determine the fraction of seeds consumed per fruit and, thus, the cost to the plant, I conducted a survey to determine the number of seeds consumed by moth larvae, the number of larvae per fruit, and the number of eggs deposited per flower. I determined the total number of fertilized and unfertilized seeds per fruit. Fertilized and unfertilized seeds are readily distinguished via color. Fertilized seeds are black and tend to be larger, while unfertilized seeds range in color from white to yellow and are small. Seed consumption was determined by fruit dissection of 79 fruit collected from 10 plants. I determined the number of fertilized and unfertilized seeds consumed per larva. Distinguishing feeding paths by yucca moths is straightforward because larvae feed within a row of seeds, eating only the central core from each seed. Once they are done feeding, they spin cocoons within the feeding path, causing the seeds to cling together. This characteristic feeding makes sorting the intact and damaged seeds simple. In addition, species identification of larvae at this site is nearly always possible because *T. cassandra* damage the interior of the apical tip of the fruit wall at the point of entry into the locule from the style.

The distribution of mature larvae within fruit was examined by dissection of 750 fruit ~30 days after flowering. The number of larval exit holes was added to the number of larvae remaining within the fruit to obtain the total larval count per fruit. Exit holes were always associated with an empty feeding path characteristic of a yucca moth larva.

The distribution of eggs per flower was determined by directly counting the number of oviposition scars on flowers that had opened the previous night. I used a 20× hand lens to count the characteristic oviposition punctures of *T. cassandra* in the style tissue on 433 pollinated flowers. Pollinated flowers are readily distinguished by checking for the presence of pollen in the stigmatic cup. All flowers were left on the plants. Because there is a tight 1:1 relationship between the number of eggs laid and the number of oviposition scars (Segraves 2003), by determining the number of scars we effectively know how many moth eggs were originally placed within flowers and how many potential larvae reside within fruit. I examined whether there was a difference in the distributions of the number of eggs per flower and the number of larvae in mature fruit using a Wilcoxon signed rank test.

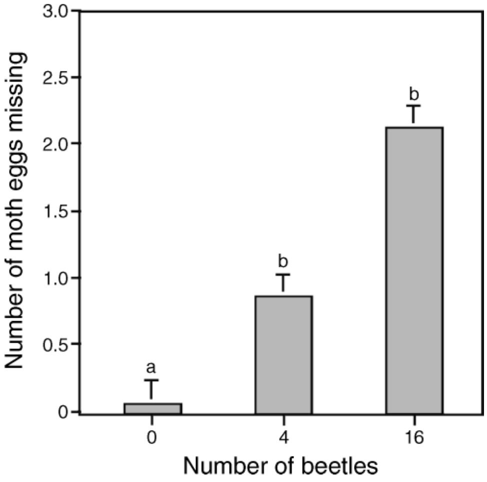

FIG. 2. Yucca moth egg consumption by the florivorous beetle *Hymenorus densus*. The number of moth eggs missing from flowers with beetles was significantly greater than from control flowers lacking beetles ($F = 11.72$, df = 2, 100, $P < 0.0001$). The error bars represent standard errors, and the letters over the bars show statistical significance with differing letters representing statistically significant results ($P < 0.001$). The comparison of 4 and 16 beetles was not significant ($P = 0.083$).

RESULTS

The manipulative experiment showed that the number of moth eggs missing increased with the addition of beetles to flower cages (Fig. 2). The number of eggs missing from the control treatment lacking beetles did not differ statistically from 0 (Wilcoxon $P > 0.13$). Posteriori pairwise comparisons indicated that the number of eggs missing was significant between the control and both treatments (Fig. 2).

The survey of the natural population of beetles residing on *Yucca filamentosa* indicated that 4.53 ± 11.59 beetles/flower (mean ± SD; range = 0–148) are typically found within yucca flowers. There was a significant difference in the number of beetles feeding within damaged and undamaged flowers (Wilcoxon, $Z = 14.15$, $P < 0.0001$). Damaged flowers had 15.92 ± 0.91 beetles/flower (mean ± SE) whereas undamaged flowers had ~2.51 ± 0.45 beetles/flower (mean ± SE). These values were used to determine beetle density in the manipulative experiment.

The survey of the number of consecutive days that beetles remain in flowers indicated that if *H. densus* is found on the first day a flower is open, ~96% of these flowers will retain beetles on the second day. Following day two, there is a gradual attrition of beetles, declining to 41% on day 4. At the same time, the abscission rate of flowers increases sharply between days 2 and 4 (2.8% on day 2 to 72% on day 4) and drops after day 5. The number of beetles within flowers increased between days 1 and 2 (Fisher sign test $P < 0.0001$), whereas the number of beetles decreased between days 2 and 3 and between 3 and 4 (Fisher sign test: for days 2–3, $P = 0.0003$; for days 3–4, $P = 0.0009$). For these reasons, the manipulative beetle experiment was conducted on the first and second days after flowers opened.

Tegeticula cassandra consumed 41.1 ± 0.82 seeds/larva (mean ± SE). This number corresponds to ~16% of the total number of seeds per fruit (total seeds per fruit, mean = 246.92 ± 3.82 [mean ± SE], range 129–298). The number of fertilized and unfertilized seeds consumed was similar (fertilized, 22.0 ± 0.80; unfertilized, 19.1 ± 0.88 [mean ± SE]).

There were 1.35 mature *T. cassandra* larvae (SE = 0.07) per fruit with a range of 0–11 larvae, and 391 fruit lacked larvae altogether. The distribution of the number of eggs (scars) per pollinated flower differed significantly from the distribution of the number of larvae per mature fruit (Wilcoxon $Z = 22.92$, $P < 0.0001$). On average, there were 4.99 eggs per flower (SE = 0.12) with a range of 1–18 eggs per flower.

Discussion

The web of interactions between mutualists, non-mutualists, and variation in species composition can impact the ecology and evolution of mutualism. For many diffuse mutualisms, assessing the relative contribution of each mutualistic partner may be difficult, especially when interactions with non-mutualists are also included. Because of this, obligate mutualisms offer a unique circumstance as they are often pairwise but are also embedded within a community of other interacting species. Here I show that the presence of a non-mutualistic species may limit a mutualistic partner and decrease the costs for the plants in the obligate pollination mutualism between yuccas and their pollinating moths.

The present study finds that florivorous beetles can act as predators of pollinator moths by simultaneously consuming moth eggs with floral tissue. A significant number of moth eggs were missing from flowers containing *Hymenorus densus* as compared to control flowers and the number of eggs consumed increased with increasing beetle density. In addition, >66% of flowers in the beetle treatments had obvious beetle feeding damage, and 85% of flowers with high beetle density had severe damage. Severe damage often resulted in the complete loss of the style, including the region where moth eggs are deposited (Fig. 1). In the field, beetles have been observed entirely consuming the pistil, but this tends to occur only at very high beetle densities (K. A. Segraves, *personal observation*). This characteristic feeding behavior of *H. densus* increases mortality of moth eggs. Although beetles may be actively searching for eggs, egg consumption is most likely an inadvertent result of flower feeding, and I have observed damage on flower styles in the region of moth oviposition in flowers lacking eggs. As a result, the beetles are unlikely to regulate the mutualism between yuccas and yucca moths. For this to be regulatory, the mortality rate of eggs would need to increase nonlinearly with increasing moth egg density and damage to the plant would need to be less costly than the gain in reproductive success due to egg mortality.

A reduction in the number of moth eggs may, however, reduce the cost of mutualism for the plant. For example, a *Tegeticula cassandra* larva typically consumes 16% of *Yucca filamentosa* seeds per fruit. In the high density treatment, *H. densus* consumed approximately two eggs per flower, thus potentially reducing the cost by 32% per fruit. This reduction in egg survival could be particularly important since the population surveys demonstrated that there were approximately five eggs per flower, which translates into a substantial loss to the plant (80% of the seeds per fruit). Observations of egg survival in the natural population showed that only ~1.35 larvae matured per fruit, or ~73% moth mortality. The results suggest that this egg mortality could largely be attributed to consumption by *H. densus*. Florivory resulted in up to a 70% reduction in the number of eggs present on a flower, very similar to the egg mortality typically observed in this population. Other factors such as egg viability and abiotic conditions are involved in determining egg survival, but florivores may have a significant impact on pollinator survivorship. As a result, feeding by beetles may reduce the cost of the mutualism; however, these benefits could be masked by the negative effects associated with florivory. At very high beetle densities, the entire pistil can be consumed and these flowers abscise (K. A. Segraves, *personal observation*). Because yuccas typically abscise 80–90% of their flowers, beetles would only negatively impact plant reproductive success if they increase this rate of abscission or if they damaged ovules of retained flowers. Otherwise, counterintuitively, florivory by beetles may be beneficial to the plant.

Although the experimental design did not allow me to directly measure seed set, there are several lines of evidence that indicate that florivory by *H. densus* can benefit the plant. First, in a previous study, I determined that flowers protected from beetles had significantly more moth larvae feeding within fruit than flowers unprotected from beetles (Segraves 2003). The proportion of larvae surviving from the egg to mature larval stage tripled in flowers protected from beetles, and the mean number of larvae doubled in protected flowers. Any increase in larval loads will increase the costs of seed damage. Second, previous work indicated that the presence of *H. densus* had no impact on fruit set in *Y. filamentosa*. Althoff et al. (2005) used a path-analysis approach to determine whether qualitative differences in the density of beetles influenced fruit production. Fruit production was unaffected by *H. densus*; however, the presence of beetles on plants should reduce the number of larvae per fruit, and as a consequence, increase seed production per fruit. Because seed production was not directly measured, the potential benefits of beetle presence may have gone undetected. Finally, preliminary data corroborate the findings of Althoff et al. (2005) by indicating that, at low to average density, the presence of beetles does not increase the rate of floral abscission (K. A. Segraves and D. M. Althoff, *unpublished data*). Therefore, at low to moderate density, beetles decrease moth larval loads in flowers without causing enhanced floral abscission or a reduction in fruit set. Additional studies are required to assess the magnitude of the benefits of beetles on seed production. Although *H. densus* may benefit the plants by enhancing female plant fitness, the potential for negative consequences on male plant fitness also needs to be considered.

The present results, then, suggest that at low to average densities, feeding by *H. densus* may decrease moth survival and increase the number of seeds produced per fruit. Other studies have demonstrated an increase in yucca seed production due to the presence of non-mutualists. Perry et al. (2004) show that the presence of ants may deter oviposition by non-pollinator yucca moths, but because ants have no effect on pollinator moths, they do not reduce the cost of the mutualism for the plant. In contrast, Crabb and Pellmyr (2006) show that parasitoid wasps can serve as indirect mutualists of yuccas by attacking pollinator larvae. Parasitoids can reduce the costs of the mutualism because parasitized larvae eat fewer seeds than unparasitized larvae. Of these community members, *H. densus* provides the greatest potential benefit to the plant because the beetles consume pollinator moths prior to any seed damage.

Understanding species interactions requires focus at multiple scales, from characterizing the pairwise interactions between species to the web of interactions at the community level. Here I show that community-level interactions may have important consequences for a pairwise mutualism between a plant and pollinating seed predator. Superficially, the presence of a florivore would seem to have a negative effect on seed production, but in this case, florivores may actually benefit the plant by reducing seed predation by pollinator moth larvae. The outcome of this interaction will depend on the community context in terms of yucca moth density, beetle density, and other factors that influence survivorship of moth eggs and larvae. Clearly, factors extrinsic to a given interaction, even a tightly coevolved and specialized mutualism, may have important consequences for its outcome.

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