COMMUNITY CONTEXT OF AN OBLIGATE MUTUALISM: POLLINATOR AND FLORIVORE EFFECTS ON *YUCCA FILAMENTOSA*

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Abstract. Obligate pollination mutualisms have been central to our understanding of the ecology and evolution of mutualisms. Although usually viewed as pairwise interactions, obligate mutualists also interact with other community members that may impact the mutualism. In this study, we examined the community context of the obligate mutualism between the plant *Yucca filamentosa* and its yucca moth pollinator *Tegeticula cassandra* to determine the relationships among plant traits, the community assemblage, and fruit set. In addition to attracting its pollinator, *Y. filamentosa* in central Florida also attracts two insect florivores: the hemipteran *Leptoglossus phyllopus* and the beetle *Hymenorus densus*. We surveyed flowering *Y. filamentosa* in 2001 and 2002 to determine the abundance of the three insect species throughout the flowering period. We also measured fruit set and four plant traits thought to be important in attracting the moth pollinator. Path analysis revealed that *T. cassandra* was the most important determinant of relative fruit set for both years. Peak pollinator abundance was significantly earlier than peak flowering. Consequently, we found a negative relationship between plant flowering date and pollinator abundance. Furthermore, taller plants also attracted more pollinators. *Leptoglossus phyllopus* had a significantly negative impact on relative fruit set in 2001 but not in 2002, whereas *H. densus* had no effect in either year. Abundance of the two florivores was more closely tied to peak flowering of *Y. filamentosa* than was the peak abundance of the pollinator moths. Although both florivore species reached high densities on *Y. filamentosa*, their effect on relative fruit set through floral abscission may be partially masked by the characteristically high abscission rates found in yuccas. As a result, florivores may be feeding on flowers that are already destined to be abscised. Similarly, pollinator moths may be preadapted to handle the effects of florivores because females lay eggs across multiple plants and flowers. Hence, the obligate mutualism between yuccas and yucca moths may be somewhat buffered from the effects of local community members depending on whether florivores substantially increase floral abscission rates from year to year.

Key words: community context; florivory; mutualism; path analysis; Tegeticula cassandra; Yucca filamentosa; *yucca–yucca moth mutualism.*

INTRODUCTION

Much of the empirical and theoretical research on mutualism has treated the interaction as a pairwise relationship. In most mutualistic interactions, however, there are multiple mutualistic and nonmutualistic species that simultaneously interact with the focal participants (Stanton 2003). This complexity of interactions among mutualistic and nonmutualistic species coupled with changes in community composition over the geographic range of an interaction present a much more dynamic and realistic picture of mutualism. Relatively little research, however, has been directed at expanding the study of mutualism to understand the ecological and evolutionary roles of other species (Bronstein and Barbosa 2002).

Although comparatively rare in nature, obligate mutualisms between plants and their seed-eating pollinators have been a central focus for investigating the

evolution and maintenance of mutualisms and are a good starting point for incorporating the effects of other community members on mutualistic interactions. Each mutualistic partner has a direct and major effect on the other's fitness (Cook and Rasplus 2003, Kato et al. 2003, Pellmyr 2003), and identifying the cost–benefit ratio is much less complicated than in mutualisms in which plants and pollinators interact with a guild of mutualists. Species engaged in obligate pollination mutualisms are also part of a larger community, and they interact with many other species in addition to their mutualistic partners. These interactions may not necessarily influence the outcome of the mutualism, but they may shape the cost–benefit ratio, impact selection on traits important to the mutualism, and influence coevolutionary dynamics (Udovic 1981, Bronstein and Ziv 1997, Bronstein et al. 2003, Morris et al. 2003, Wilson et al. 2003). Understanding the evolution of traits important to obligate mutualisms, then, also requires examining the selection pressures exerted by other community members (West et al. 1996).

Research incorporating a community context into the study of obligate pollination mutualisms has focused mainly on the impact that seed-eating ''cheater'' or exploitative species have on the mutualism (West et al. 1996, Deprés and Jaeger 1998, Marr et al. 2001). In contrast, research on the community ecology of facultative pollination mutualisms has examined the direct and indirect effects of a wide range of community members. These studies have examined the influence of seed predators (Brody 1997, Cariveau et al. 2004) as well as florivores (e.g., Lohman et al. 1996, Krupnick and Weis 1999, Krupnick et al. 1999), herbivores (e.g., Strauss et al. 1999, Herrera 2000, Mothershead and Marquis 2000, Galen and Cuba 2001), nectar robbers (e.g., Irwin and Brody 1998, 1999, 2000), co-pollinators (e.g., Thompson and Pellmyr 1992, Holland and Fleming 2002), and host use by hemi-parasitic plants (Adler 2000, 2001). These results have demonstrated that plant interactions with other community members can have important consequences for pollinator attraction and both male and female components of plant reproductive success. In particular, florivores can have large effects by reducing nectar production within individual flowers and by reducing the overall size of floral displays. This can result in decreased pollinator visitation and a reduction in pollen receipt and transfer to other plants (Krupnick and Weis 1999). Incorporation of a broad spectrum of local community members provides an increased understanding of the multiple selection pressures placed on plant and pollinator mutualists (Schemske and Horvitz 1988, Strauss and Armbruster 1997, Herrera et al. 2002, Stanton 2003). This approach has rarely been taken for obligate pollination mutualisms, and whether the local community strongly impacts these types of mutualism remains unclear.

The pollination mutualism between yuccas and yucca moths is one of the classic examples of obligate mutualism. Yuccas are actively pollinated by yucca moth females, and the moth larvae complete their development by feeding on a subset of the developing yucca seeds. This interaction involves over 25 species of yuccas and 17 species of pollinator moths, 12 of which utilize only one yucca species (Pellmyr 2003). In addition to interacting with their mutualist pollinator moths, yuccas are also visited by a suite of other non-pollinating lepidopterans, xylophagous and florivorous beetles, and phloem-feeding hemipterans (Powell and Mackie 1966, Davis 1967, Powell 1984, Udovic 1986, Huth and Pellmyr 1997). Most of these species feed on or within the inflorescence scape, flowers, or fruits and have the potential to impact both yucca and pollinator fitness. For example, Bronstein and Ziv (1997) demonstrated that feeding by a bogus yucca moth species benefited the plant by reducing the number of yucca seeds eaten by pollinator larvae. In contrast, the beetle *Carpophilus longus* fed on seeds and added to the overall seed mortality in fruits.

In this study, we used the obligate pollination mutualism between *Yucca filamentosa* L. and its pollinator moth *Tegeticula cassandra* Pellmyr as the basis for examining how other insect species from the community can influence plant reproductive success and selection on floral traits. *Yucca filamentosa* is a particularly amenable focal species because there are already a number of studies that have examined patterns of flower and fruit production and characterized the fitness costs and benefits of the mutualism (Pellmyr and Huth 1994, Huth and Pellmyr 1997, 2000, Pellmyr 1997, Marr et al. 2000, Marr and Pellmyr 2003). Moreover, the effects of nonpollinating species have also been examined in some populations. For example, Huth and Pellmyr (1997) quantified the effect of the flower-infesting beetle *Carpophilus melanopterus* on floral abscission, and Marr et al. (2001) examined competition between larvae of seed-eating cheater moths and pollinator larvae. No studies, however, have addressed the collective impact of the assemblage of community members on plant reproductive success or examined selection on plant floral traits important to the mutualism.

Preliminary surveys of *Y. filamentosa* in central Florida indicated that this yucca is host to two insect florivores, *Leptoglossus phyllopus* (Hemiptera: Coreidae) and *Hymenorus densus* (Coleoptera: Tenebrionidae). Both species aggregate on the inflorescences, cause floral abscission through their feeding, and are likely to have a negative effect on fruit production. Thus, our goals were threefold. First, we determined how flowering characteristics influenced plant attractiveness to pollinators and florivores. Second, we quantified how pollinators and florivores influenced plant reproductive success. Third, we examined whether the impact of pollinators and florivores on reproductive success changed depending on differences in the local flowering conditions between years. Our main objective was to determine the effects exerted by these insect species in order to gain an understanding of the way in which the community assemblage may influence the pollination mutualism.

Methods

Study species

Yucca filamentosa (Agavaceae) is a native perennial that grows in disturbed areas in the southeastern United States. The study site was located in Placid Lakes, Florida (27°15′22″ N, 81°22′57″ W) near the Archbold Biological Station. Plants were located in a patchwork of undeveloped housing lots that were in various successional stages of Florida scrub. Individuals grow as a basal rosette of leaves for several years before flowering and typically flower once every 2–3 yr thereafter. Flowering at the study site began in April and continued into June. A *Y. filamentosa* inflorescence is a scape that can range between 0.5 and 4 m tall and has up to
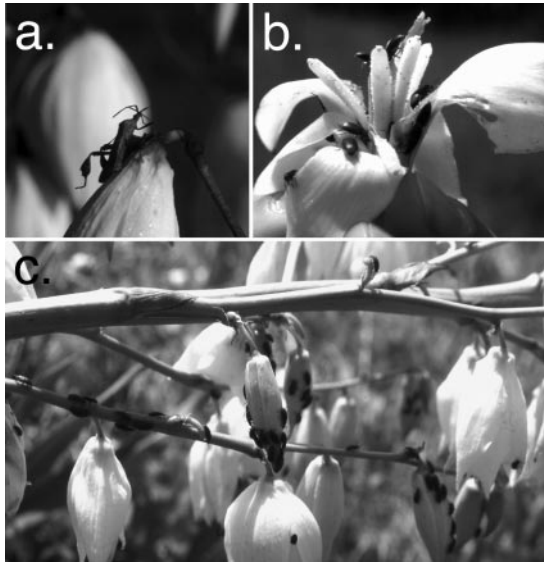
FIG. 1. The two florivores, (a) *Leptoglossus phyllopus* (Hemiptera: Coreidae) and (b) *Hymenorus densus* (Coleoptera: Tenebrionidae), on flowers of *Yucca filamentosa* (Agavaceae). (c) Example of moderate densities of *Hymenorus densus* individuals on an inflorescence.

300 or more flowers that open over the course of 6–15 d. Flowers open at dusk and close the following morning and those not pollinated the first night are abscised from the plant. Fruit mature in approximately 2 mo at which time the capsular fruit dehisces and the seeds are dispersed. Each fruit has the potential to produce more than 250 seeds. Plants may also reproduce vegetatively through the production of new rosettes from rhizomes.

At the study site, *Y. filamentosa* can be pollinated by two species of yucca moths, *T. cassandra* or *T. yuccasella*. Collections and observations over several years show that *T. cassandra* is the primary pollinator and accounts for more than 99% of pollination and fruit production of *Y. filamentosa* in the study area (K. A. Segraves, *unpublished data*). Female *T. cassandra* actively deposit pollen into the stigmatic cavity of *Y. filamentosa* flowers after ovipositing into the style. The moth larva chews into the locular cavity and feeds on the developing seeds for ~30 d. After completing feeding, the larva exits the fruit and burrows into the soil, where it undergoes diapause. Larvae may remain in diapause for 1 yr or longer. Adults eclose during a subsequent year's flowering event. The moths are active at night and rest within the flowers during the day.

Two insect species feed on the inflorescences of *Y. filamentosa* at the study site (Fig. 1). The generalist leaf-footed bug *Leptoglossus phyllopus* uses its stylets to pierce into the buds, flowers, or fruit to feed on plant fluids. Feeding usually results in abscission. At high density, this species can cause the complete loss of buds and flowers on an inflorescence (D. M. Althoff and K.

A. Segraves, *personal observation*). The host range of this species includes many plant families, and it has been recorded feeding on many agricultural species (Allen 1969). Adults appear to be attracted to the plants for both feeding and mating. The tall inflorescence may serve as convenient location for adults to congregate. Large aggregates of individuals can form on individual plants, and we have observed numerous matings on *Y. filamentosa*. In some cases, females lay eggs on the inflorescence and the developing nymphs can be found feeding on the plant.

The second inflorescence feeder is the beetle *Hymenorus densus* (Tenebrionidae: Alleculinae). Like the leaf-footed bug, adults feed and mate on the inflorescence. Adult beetles aggregate within individual flowers and feed on the anthers, style, and pistil tissue, sometimes completely consuming all. If damage to the ovary is severe, the flower is abscised. There may be thousands of beetles on a single inflorescence. In one of the first descriptions of the association between *H. densus* and yuccas, Brues (1926) estimated the number of adults collected from a single inflorescence to be well over 9800 individuals. There is little information on the natural history of *H. densus* and the feeding habits of the larvae are unknown.

Sampling methods

We surveyed flowering *Y. filamentosa* from April to July in 2001 and 2002. At the beginning of each flowering season we identified plants that were in bud. We surveyed nearly all of the flowering plants in a 533-ha area for the two years. Eighty plants were surveyed in 2001 and 224 plants in 2002. Some plants were excluded from the survey (<5%) because they were experimental plants used in another study, were covered with mesh cages, and thus were not available to visitors. Every third day, each plant was visited and the inflorescence was surveyed for the following: flowering stage (beginning, peak, or end), number of pollinator moths (both males and females separately), number of leaf-footed bugs, and degree of beetle infestation. Because beetle density can be extremely high (e.g., thousands of individuals on a single plant), we assessed the degree of infestation using a three-point subjective scale: 1, beetles in one or more flowers, little to no floral damage; 2, beetles in over half of the flowers, moderate floral damage; 3, beetles in most of the flowers, severe floral damage. Plants were surveyed twice after the completion of flowering. At this point, only leaf-footed bugs remained on the plants.

At the completion of fruit maturation, we measured the following plant characteristics: number of flowers (determined by pedicel count), number of fruits, rosette diameter, and inflorescence height. We chose these traits based on previous research that demonstrated their importance to reproduction and pollinator visitation in other species of yuccas (Udovic 1981, Aker 1982a, b, James et al. 1994, Addicott 1998).

We assessed differences in plant morphology and flowering duration between years with MANOVA. The data conformed to the assumptions of MANOVA. Percentage of fruit set was arcsine transformed, and ANOVA was used to test for differences between years. For each plant, we calculated the mean number of pollinators per day, leaf-footed bugs per day, and mean beetle score per day by summing values across days and dividing each summed variable by the total number of days the plant was surveyed. We used ANOVA to compare the mean number of pollinators, leaf-footed bugs, and mean beetle score per plant per day between the two years. We used Welch's ANOVA as the test statistic when variances were unequal. Statistics were performed using JMP version 3.2.1 (SAS 1998).

We used path analysis (Wright 1934, Mitchell 1992) to examine the influence of moth pollinators, leaf-footed bugs, and beetles on fruit production. The path diagram represents a conceptual model of the manner in which plant morphology and community assemblage could influence the relative fruit set of *Y. filamentosa*. We based the path diagram on the hypothesis that plant traits would influence the number of insects attracted to a plant and insect feeding and pollination behavior would in turn influence the number of fruit produced (Aker and Udovic 1981, Udovic 1981, Aker 1982*a, b*, James et al. 1993). Although seed set may have been a better measure of reproductive success, we used fruit set for three reasons. First, we surveyed nearly all of the flowering plants within the study area and were concerned about the potential effects on plant and moth recruitment by removing all of the fruit from the local population. Second, regression analysis on a subset of plants in the study population did not reveal a trade-off between the number of seeds per fruit and the number of fruits per plant ($N = 19$, $F_{1,18} = 1.16$, $P = 0.30$). Therefore plants with more fruit consistently matured more seeds. Third, many plants aborted 100% of their fruit, which meant their reproductive success was zero relative to plants that matured fruit.

We used the program Piste, version 3.1.2 (Vaudor 2000), to calculate and test the statistical significance of path coefficients for each year separately. Based on our path diagram, we tested whether each of the insects influenced relative fruit set. We also examined whether one or more of the plant traits were important in determining insect visitation and subsequent fruit set in *Y. filamentosa*.

RESULTS

There was a substantial difference in the number of plants flowering, plant morphology, and insect visitation between the two years (Fig. 2, Table 1). Nearly three times the number of plants flowered in 2002 as in 2001. Traits associated with plant morphology and flowering also differed between years (MANOVA, $F_{3,283} = 21.19$, $P < 0.0001$). Plants in 2001 had smaller rosettes (ANOVA, $F_{1,288} = 25.70$, $P < 0.0001$), but
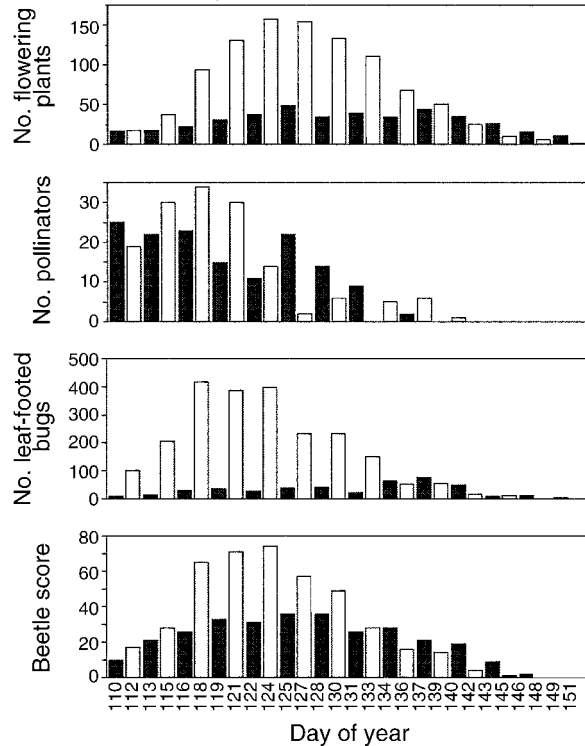

FIG. 2. Results of surveys for *Yucca filamentosa* flowering and abundances of the yucca moth pollinator *Tegeticula cassandra* and two florivores, the leaf-footed bug *Leptoglossus phyllopus* and the beetle *Hymenorus densus* for 2001 and 2002. Black bars show data for 2001 and open bars for 2002. Surveys were conducted every three days and started two days later in 2002 than in 2001. Beetle score was based on a subjective scale that assessed beetle numbers and damage to flowers (see *Methods* for further detail).

flowered longer than plants in 2002 (ANOVA, $F_{1,288} = 32.28$, $P < 0.0001$; Table 1). The mean flowering date was significantly earlier in 2002, and fruit set was significantly higher in 2001 (Table 1).

The total number of insects and the mean number of each insect per plant per day also differed between years (Fig. 2, Table 1). More pollinators were counted in 2001 and the mean number of pollinators per plant per day was over twice that of 2002. Similarly, the mean beetle score per plant per day was significantly lower in 2002. In contrast, leaf-footed bugs were more numerous in 2002, and this was reflected by a significantly higher mean number per plant per day. The mean day of year for insect presence on the surveyed plants also varied between years with the exception of the pollinators. Leaf-footed bugs and beetles were on the plants at early dates in 2002. In both years, peak pollinator abundance was significantly earlier than peak flowering of the *Y. filamentosa* population (2001, $F_{1,27} = 16.80$, $P = 0.0013$; 2002, $F_{1,27} = 232.28$, $P = 0.003$). For yucca moths in general, males emerge earlier than females. In 2002, we counted female and males moths separately to determine if the early bias

TABLE 1. Summary of flowering for *Yucca filamentosa* and visitation by pollinators and florivores (means ± 1 SE) for 2001 and 2002 at a study site in Placid Lakes, Florida, USA.

| | Year | | Comparisons between years | | |
Variable	2001	2002	F	df	P
Plant characteristics					
No. flowering plants surveyed	80	224			
Rosette diameter (cm)	76.12 ± 2.35	92.08 ± 1.69		(MANOVA)	
Inflorescence height (cm)	184.09 ± 4.08	182 ± 2.37	21.19	3, 283	<0.0001
No. flowers	88.31 ± 4.43	97.94 ± 3.47			
Flowering duration (d)	9.19 ± 0.26	7.46 ± 0.16			
Percentage of fruit set	9.49 ± 1.55	2.51 ± 0.32	23.26	1, 302	<0.001
Mean flowering date†	129.37 ± 0.40	127.17 ± 0.26	16.19	1, 1415	<0.0001
Insect characteristics					
No. pollinators counted	156	136			
No. leaf-footed bugs counted	441	2260			
No. pollinators·plant^{-1}·d^{-1}	0.21 ± 0.02	0.08 ± 0.01	12.60	1, 288	<0.0006
No. leaf-footed bugs·plant^{-1}·d^{-1}	0.68 ± 0.15	1.43 ± 0.09	24.65	1, 288	<0.0001
Beetle score·plant^{-1}·d^{-1}	0.42 ± 0.02	0.25 ± 0.01	48.47	1, 288	<0.0001

Notes: The pollinator yucca moth *Tegeticula cassandra* lays eggs into the pistils as well as pollinating the flowers. The two florivores, the leaf-footed bug, *Leptoglossus phyllopus*, and the beetle *Hymenorus densus*, cause abscission by feeding on buds, flowers, or fruit.

† Day 1 is 1 January.

in peak pollinator abundance was male-driven. Peak female moth abundance, however, was still significantly earlier than peak flowering of the *Y. filamentosa* population (date of female abundance = 119.48 ± 0.23 [mean ± 1 SE], $F_{1,27} = 63.12$, $P < 0.001$).

The path analyses were based on 74 plants in 2001 and 209 plants in 2002. In both years many plants lost all of their fruit (30 in 2001 and 127 in 2002). The number of fruit matured for plants retaining fruit ranged from 1 to 62 in 2001 and 1 to 66 in 2002. Path analysis relating plant characteristics to the insect community and the insect community to fruit set showed similar patterns between years (Fig. 3). The influence of plant characters on insect visitation varied among insect species and between years. For the pollinators, both peak flowering date and inflorescence height had significant and consistent effects across years. Peak flowering date had a negative influence on the number of pollinators per day, so that early flowering plants had more pollinator visits than plants that flowered later. In contrast, inflorescence height had a significantly positive effect. Plants with taller inflorescences attracted more pollinators per day relative to shorter inflorescences. Leaf-footed bugs were only weakly influenced by plant traits. In fact, the only plant trait that had a significant influence on visitation was peak flowering date, and this effect was only present in 2002. Whereas pollinator visitation positively increased with inflorescence height, leaf-footed bug visitation was unaffected. In 2001, all four of the plant traits significantly influenced beetle visitation. Rosette diameter and the number of flowers had significantly positive effects, whereas stalk height and peak flowering date had significantly negative effects. In 2002, only the number of flowers had a significant effect; plants with more flowers attracted more beetles. The path diagram

as a whole explained a significant amount of the total variation in both years, but explained more in 2001.

Pollinators had a significantly positive effect on fruit set in both years (Fig. 3). In 2001, leaf-footed bugs had a significantly negative effect on relative fruit set, whereas in 2002, the effect was negative but nonsignificant. Beetles had a nonsignificant effect on fruit set in both years. Pollinators were the most important determinant of relative fruit set among the three insect species. The path coefficient from pollinators to relative fruit set was at least three times larger than for path coefficients for leaf-footed bugs or beetles. In both years, peak flowering date and inflorescence height had the largest influence on pollinator visitation.

DISCUSSION

Our understanding of species interactions stems primarily from studies of pairwise interactions. These pairwise interactions, however, are nearly always embedded in a network of interactions that include other local community members. We know from studies of facultative pollination mutualisms that plant interactions with other community members can significantly influence plant fitness via reduced pollen transport, fruit set, and seed set (Juenger and Bergelson 1997, Strauss et al. 1999, Mothershead and Marquis 2000, Bronstein and Barbosa 2002, Stanton 2003, Cariveau et al. 2004).

In contrast, relatively little has been done to explore the impact of other community members on plant or pollinator fitness in obligate pollination mutualisms. In such interactions we might expect that other community members would have a large effect on both mutualist species. For the yucca–yucca moth association, community interactions that influence plant fitness also have fitness consequences for the moth. For example,
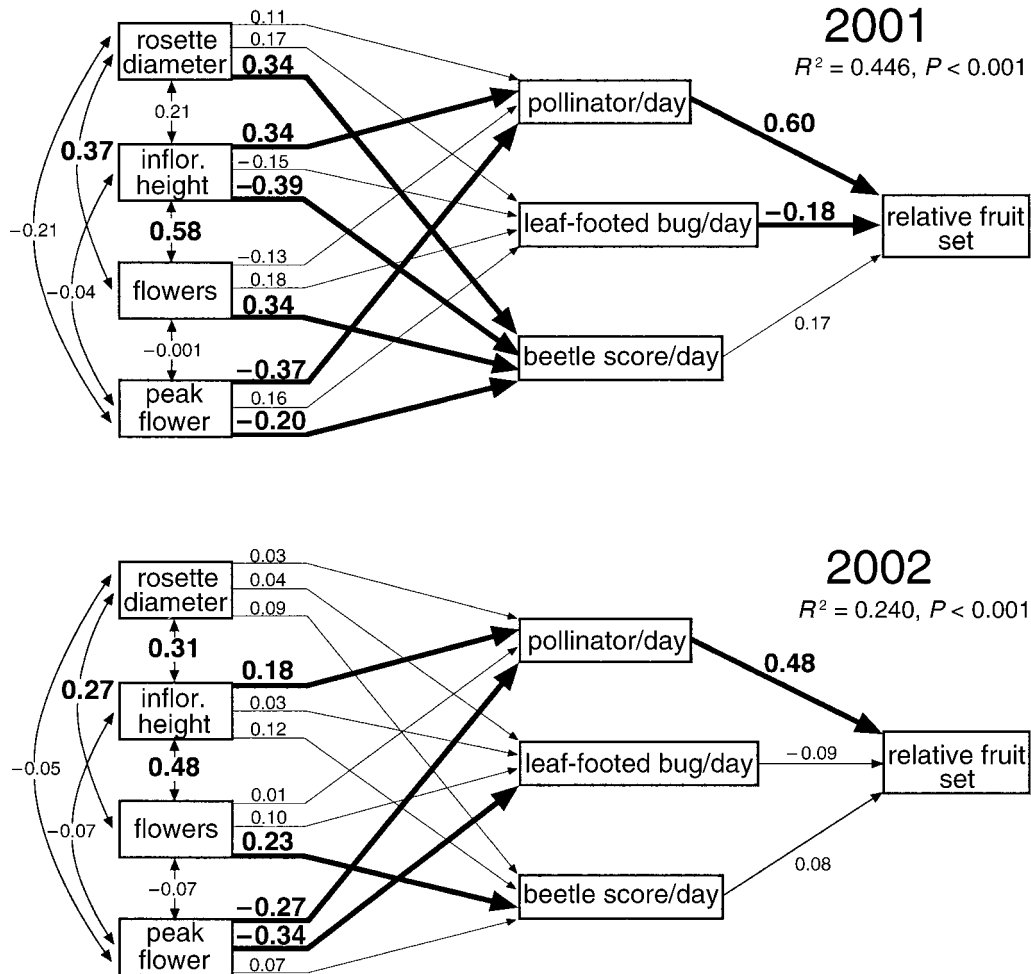
FIG. 3. Path diagrams representing the hypothesis of causal relationships between plant traits, insects, and relative fruit set for *Yucca filamentosa*. Pollinator/day is the presence of the yucca moth *Tegeticula cassandra*, leaf-footed bugs/day is the presence of *Leptoglossus phyllopus*, beetle score/day is the score for floral damage and presence of *Hymenorus densus*. The four plant traits measured were rosette diameter, inflorescence height, total number of flowers, and peak flowering date of each plant. Numbers above the arrows refer to the path coefficients, and those in boldface type were significant at the $P < 0.05$ level or better. A path with a double-headed arrow denotes a correlation between the two connected variables.

abscission of yucca flowers and fruit reduces resources needed by yucca moths and also kills moth eggs and larvae. The question remains, then, whether local community members can impact obligate mutualisms in the same way as has been demonstrated for facultative mutualisms.

For the mutualism between *Y. filamentosa* and *T. cassandra*, feeding by florivores influenced plant reproductive success as measured by fruit set. The leaf-footed bug *L. phyllopus* had a negative effect on fruit set in the first year of the study. Plants that attracted more *L. phyllopus* per day had reduced fruit set when compared to other individuals in the population. This effect, however, was not consistent across years. In the second year of the study, the path coefficient indicated a negative effect, but it was not statistically significant even though there were twice as many *L. phyllopus* per

day per plant than in 2001. This discrepancy between years suggests that the impact of community members on plant fitness can be temporally variable and dependent on local flowering conditions.

In contrast to *L. phyllopus*, the presence of the beetle florivore *H. densus* did not appear to have a significant negative effect on fruit set in either year. The path coefficients for both years were nonsignificant and were positive rather than negative. This result was somewhat surprising given that our measure of beetle presence took into account damage to the flowers as well as numbers of *H. densus* individuals. One possible explanation is that the subjective scale used to quantify beetle density may not have been detailed enough to accurately portray differences in beetle effects between plants. The contrasting effects between *H. densus* and *L. phyllopus* may also be a result of the difference in

how they feed on *Y. filamentosa*. *H. densus* uses its mandibles to feed exclusively on the style, anthers, and pistil tissue. Since yuccas abscise upwards of 80% of their flowers (Aker 1982*a, b,* Keeley et al. 1984, James et al. 1994, Pellmyr and Huth 1994, Richter and Weis 1995), many of the flowers fed upon by *H. densus* already have a high probability of being abscised. In contrast, *L. phyllopus* uses its stylets to pierce through buds, flowers, and fruit to feed on plant fluids. Feeding damage caused by both insect species can trigger floral abscission, but feeding by *L. phyllopus* may also result in bud and fruit abscission. Thus, this florivore has an opportunity to impact *Y. filamentosa* before, during, and after flowering. *L. phyllopus* additionally impacts the pollinator *T. cassandra* because all larvae in abscised fruit perish.

Irrespective of the effects of the two florivores, as expected, the presence of the pollinator *T. cassandra* had a significant and positive effect on relative fruit set. Although the effect was greater in 2001, it was also strong and positive in 2002. This may be explained by the twofold increase in the number of flowering plants in 2002 that may have reduced the magnitude of the effect of pollinators. The total number of moths surveyed was similar between the two years, but the number of pollinators per day was significantly lower in 2002. Correspondingly, fruit set for *Y. filamentosa* was also significantly lower in 2002. Previous studies on fruit set in *Y. filamentosa* (Huth and Pellmyr 1997) and *Y. elata* (James et al. 1994) suggest that fruit set in yuccas is primarily limited by resources rather than pollinator availability. For these two studies, hand pollinations of every flower on an inflorescence did not result in an increase in fruit set over plants pollinated naturally. For the present study, however, mean fruit set of 18 hand-pollinated *Y. filamentosa* was 15 ± 2% (2002, $N = 18$; D. M. Althoff and K. A. Seagraves, *unpublished data*) in contrast to the 2–9% for open-pollinated plants in the surveys. These results suggest that in addition to being resource limited, fruit set in *Y. filamentosa* may also be limited by pollinator availability.

Pollinator attraction in *Y. filamentosa* was driven primarily by the timing of flowering and inflorescence height. Plants that flowered earlier and had taller inflorescences had increased pollinator visitation. Both of these factors were important in determining moth visitation, and the path coefficients for these traits were the largest among the four plant traits for both years even though there was a large difference in the number of plants flowering. For 2001, leaf-footed bugs had a negative effect on fruit set, but none of the measured plant traits emerged as being particularly important for determining visitation. Thus, based on the current hypothesis about causal relationships, plants that flower earlier and are taller should have higher reproductive output. Moreover, early flowering was more beneficial

in terms of fruit production than having a taller inflorescence.

One striking pattern in the obligate pollination mutualism between *Y. filamentosa* and *T. cassandra* is that plant flowering and pollinator moth emergence are offset whereas plant flowering and florivore emergence were more synchronous. Pollinators emerged during the early stages of flowering of the plant population, and some plants flower when no moths are available. Law et al. (2001) demonstrated theoretically that in the absence of other antagonistic species, asynchrony in plant and pollinator phenologies can evolve in obligate associations such as the one between yuccas and yucca moths. Results from surveys of flowering phenology and pollinator visitation for two other yuccas and their pollinator moths, however, show that moth emergence is tightly coupled to flowering of the host plant. For *Hesperoyucca whipplei* (syn. *Y. whipplei*) peak flowering date and peak moth visitation were very similar at two sites (Aker 1982*b*). Addicott (1998) showed tight coupling of flowering and visitation between *Y. kanabensis* and its moth pollinator across three years of flowering, even when the peak flowering date changed significantly between years.

Although not experimentally tested in this study, the results suggest the possibility that the presence of florivores may, in the long term, shift the emergence phenology of the *T. cassandra* population. We hypothesize that the presence of florivores could influence yucca moth emergence in two ways. First, the presence of beetles within flowers may deter pollinators. *Hymenorus densus* aggregates within flowers during the day, and individual flowers can contain dozens of feeding and mating beetles. Because the flowers also serve as diurnal resting places for the pollinators, moths may avoid flowers containing beetles and spend extra time and energy searching for a suitable resting place in addition to experiencing increased exposure to predators. Second, both *H. densus* and *L. phyllopus* may increase moth mortality through their effects on floral abscission. *Tegeticula cassandra* experiences high egg and larval mortality independent of floral abscission (Segraves 2003); thus, additional pollinator mortality due to florivore-induced abscission may favor moths that emerge earlier and avoid mortality costs associated with florivores. Comparisons of the timing of moth emergence and flower phenology between this study population and populations in which the florivores are rare are needed.

The pairwise interactions of obligate pollination mutualisms has made them highly tractable for studies of the ecology and evolution of mutualism. The biological reality, however, is that these pairwise interactions can also be influenced by the surrounding community. We know that for two other similar obligate pollination mutualisms, figs and fig wasps and globeflowers and globeflower flies, additional species coexist or compete with mutualist species (West et al. 1996, Deprés and

Jaeger 1998), yet we know comparatively little about how these additional interactions affect the mutualism. The results of the present study suggest that community-level interactions may be variable in their impact on the yucca–yucca moth obligate mutualism. Florivores can reduce fruit set and consequently increase pollinator larvae mortality, but this effect may vary depending on local ecological conditions.

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