Specialization in the yucca–yucca moth obligate pollination mutualism: A role for antagonism? 1

David M. Althoff 2

PREMISE OF THE STUDY: Specialized brood pollination systems involve both mutualism and antagonism in the overall interaction and have led to diversification in both plants and insects. Although largely known for mutualism, the role of the antagonistic side of the interaction in these systems has been overlooked. Specialization may be driven by plant defenses to feeding by the insect larvae that consume and kill developing plant ovules. The interaction among yuccas and yucca moths is cited as a classic example of the importance of mutualism in specialization and diversification. Pollinators moths are very host specific, but whether this specificity is due to adult pollination ability or larval feeding ability is unclear. Here, I test the potential role of antagonism in driving specialization among yuccas and yucca moths.

METHODS: I examined the ability of the most-polyphagous yucca moth pollinator, Tegeticula yuccasella, to pollinate and develop on five Yucca species used across its range. Yucca species endemic to the Great Plains and Texas were transplanted to a common garden in Syracuse, New York and exposed to the local pollinator moth population over 3 years.

KEY RESULTS: Local moths visited all but one of the Yucca species, but had drastically lower rates of successful larval development on non-natal Yucca species in comparison to the local host species.

CONCLUSION: Specialization in many brood pollination systems may be strongly influenced by the antagonistic rather than the mutualistic side of the overall interaction, suggesting that antagonistic coevolution is a possible source of diversification.

KEY WORDS: Asparagaceae; Agavoideae; coevolution; diversification; Lepidoptera; mutualism; plant defense; Prodoxidae; specialization; yucca moths

Species interactions are integral to the origin of biodiversity, particularly for insects and plants. Indeed, the overwhelming assortment of flowering plants and the associated insects that pollinate and feed upon them comprise a dominant component of Earth’s known biodiversity (Gaston, 1991; Mora et al., 2011). As such, much of the theoretical and empirical studies on species interactions have focused on the myriad interactions of plants and insects. From these studies, concepts such as diversifying coevolution, escape and radiate coevolution, and chemical arms races have been proposed as major mechanisms by which plants and insects diversify either in tandem or sequentially (Ehrlich and Raven, 1964; Berenbaum, 1983; Farrell et al., 1991; Thompson, 1994; Zangerl and Berenbaum, 2003; Janz et al., 2006; Agrawal et al., 2009; Janz, 2011). The underlying premise of these concepts is that coevolution between interacting lineages is responsible for or promotes speciation in both groups (Vermelj, 1994).

Thompson (1994) suggested that the key to whether coevolution will lead to adaptive divergence in traits and potentially speciation is the degree to which different types of interactions will generate specialization and local adaptation. He further suggested that interactions in which one species controls the mating patterns of another, such as between plants and pollinators or between hosts and inherited symbionts, could directly lead to reproductive isolation. Theoretical studies have modeled the conditions under which coevolution and different types of interactions such as mutualism, parasitism, predation, and competition will potentially lead to diversification (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000; Bolnick, 2006; Kopp and Gavrilets, 2006; Yoder and Nuismer, 2010). Results suggest that the conditions under which mutualism will facilitate diversification may be limited, and it is victim–exploiter relationships such as predation and parasitism that appear to be more likely to cause specialization and phenotypic divergence among interacting groups (Kopp and Gavrilets, 2006; Yoder and Nuismer, 2010). Part of the reason for this finding is that the phenotype

---

1 Manuscript received 5 February 2016; revision accepted 19 May 2016.
Department of Biology, 107 College Place, Syracuse University, Syracuse, New York 13244 USA

2 E-mail for correspondence: dmalthof@syr.edu
doi:10.3732/ajb.1600053
matching commonly observed among mutualist species may decrease the propensity for adaptive divergence among populations that could lead to speciation (Yoder and Nuisser, 2010). These theoretical results provide the impetus for re-evaluating model systems in which specialized, mutualistic interactions have been implicated as the driver of diversification. An ideal system would allow the simultaneous assessment of whether mutualism or antagonism is more likely to contribute to specialization that could lead to coevolutionary diversification.

One such system is the obligate pollination seed-feeding mutualism between yucca plants (Asparagaceae: Agavoideae) and yucca moths (Lepidoptera: Prodoxidae) (Powell, 1992; Pellmyr, 2003) that has both mutualistic and antagonistic components. Yuccas are only pollinated by yucca moths, and yucca moth larvae only feed on yucca seeds. A female oviposits eggs into the flowers and then actively pollinates using specialized mouthparts called tentacles, ensuring food for her developing offspring. The overall interaction is mutualistic because moth larvae only eat a small proportion of the developing seeds (Powell, 1992; Pellmyr, 2003). Thus, this interaction involves a suite of mutualistic (pollination) and antagonistic (oviposition) traits. The yucca–yucca moth interaction includes over 22 species of pollinating moths in two genera, Parategeticula and Tegeticula, 2–3 species of cheater moths that have lost the tentacles and pollination behavior, and over 35 species of yuccas (Pellmyr et al., 1996, 2007; Pellmyr, 1999, 2003; Pellmyr and Leebens-Mack, 1999; Smith et al., 2008). Taken as a whole, this interaction has been used as the basis for many theoretical models of mutualism, coevolution, and the evolution of cheating (Holland et al., 2002; Bronstein et al., 2003; Morris et al., 2003; Wilson et al., 2003; Jones et al., 2009).

Although the yucca–yucca moth interaction is best known as a mutualism, it is unclear whether the mutualistic or the antagonistic aspects of the overall interaction best explain levels of specialization and the evolution of moth and plant diversification. For example, moth larvae feed solely on seeds and complete their entire development on one plant. Thus, there is strong selection for moths to be effective seed feeders, and the evolution of pollination ability is likely the result of selection to increase moth offspring survival. Viewed in this light, changes in plant traits such as floral morphology or defensive chemistry that limit moth damage may be important in generating specialization. For yuccas, death of plant ovules as a result of mechanical damage from a moth’s ovipositor is used by plants as a proxy for gauging the potential number of moth eggs within flowers (Pellmyr and Huth, 1994, 1995; Huth and Pellmyr, 2000; Marr and Pellmyr, 2003). Flowers with high levels of ovule death are preferentially absconded from the plant, resulting in moth egg/larval death (Marr and Pellmyr, 2003). This selective abscission mechanism provided the selective environment for the changes in moth oviposition behavior and morphology among species (Pellmyr and Leebens-Mack, 2000). Yuccas are also heavily defended by a suite of saponins and concentrations within the seeds of some species can be quite high (Wall and Fenske, 1961; Stohs and Obrist, 1975; Hostettmann and Marston, 1995). Recent work on figs and fig wasps, another obligate brood pollination mutualism, provides support for the idea that selection for being an effective plant feeder is important for host specificity. Use of different fig species can be determined by the ability of wasps to gall figs, rather than the ability to pollinate (Ghana et al., 2015a, b).

Within Tegeticula, in which most pollinator diversity resides (17 species), moth species differ significantly in ovipositor morphology as a consequence of whether females lay eggs deep within the pistil (locular oviposition) or on the pistil surface (superficial oviposition) (Pellmyr, 1999, 2012; Pellmyr and Leebens-Mack, 2000; Pellmyr et al., 2008). Superficial oviposition does not trigger selective abscission. Moth species also differ significantly in body size, the number of eggs they lay in flowers, and larvae differ in the number of seeds they consume (Addicott, 1998; Pellmyr, 1999). Differences among moth species in how they deposit eggs and use seed resources suggest the possibility that selection to be a seed feeder may influence specialization in host use. In contrast to changes in ovipositor morphology, there are no data on variation in tentacle morphology, a key mutualistic trait, or how this variation might relate to changes in flower morphology across Yucca species (Pellmyr and Krenn, 2002). Comparisons of changes in mutualistic traits and antagonistic traits in the context of determining specialization in host use are needed to understanding the underlying dynamics of coevolution and diversification in yuccas and yucca moths and other brood polination mutualisms.

To begin to explore the relative role of the mutualistic and antagonistic sides of the overall interaction in determining specialization in host use, I tested whether pollinator species are able to pollinate and develop on non-natal Yucca species. Specifically, I allowed a local population of the geographically widespread and most polyphagous pollinator moth, T. yuccasella, to visit flowering individuals of five non-natal Yucca species that are used in different parts of the moth’s range (Fig. 1). This test is very conservative in that there is little host-associated genetic structure across the entire range of T. yuccasella, suggesting that moths would likely be able to pollinate and develop at least to some degree on host plant species used by different populations across its range (Leebens-Mack and Pellmyr, 2004). Thus, any differences in the ability of moths to be pollinators and seed feeders are likely much less pronounced than would be expected among comparisons from moth species that are extreme specialists. I examined the following questions: (1) Will moths visit non-natal Yucca species? (2) Will moths pollinate flowers on non-natal Yucca species with resulting fruit production? (3) Will moth attempts to oviposit into flowers and be successful in depositing eggs? (4) Can moth larvae successful feed and complete development on non-natal Yucca species? Behavioral observations coupled with flower and fruit dissections demonstrate that moths visit and are able to successfully pollinate non-natal Yucca species and deposit eggs, but larvae are only able to successfully develop within the local host plant species.

**MATERIALS AND METHODS**

**Study system**—Tegeticula yuccasella is the most geographic widespread and polyphagous yucca moth pollinator. This moth species uses seven Yucca species that are distributed mostly allopatrically across eastern North America (Pellmyr, 1999) (Fig. 1). Females of this species deposit eggs next to developing plant ovules (locule oviposition), which leaves a characteristic kink in the yucca fruit as a result of ovule death during oviposition. The Yucca species used by T. yuccasella are from the Chamaecarpa section of Yucca with the exception of Y. aloifolia, that is from section Sarcocarp (Pellmyr, 1999). All of these plants have a basal rosette that produces a 1–3 m tall inflorescence that contains greater than 300 flowers. Within the Chamaecarpa, Y. rupicola, Y. reverchonii, and Y. pallida are from the Rupicoleae series that is endemic to Texas and northwestern Mexico (Clary and Simpson, 1995; Hochstätter, 2000). Yucca glauca occurs
across the Great Plains and Y. constricta in northern Texas, while Y. filamentosa occurs along the Gulf of Mexico east of Louisiana and into the interior of eastern North America (Pellmyr et al., 2007).

In 2006 and 2007, approximately 25 individual plants each of Y. constricta, Y. glauca, Y. pallida, Y. reverchoni, and Y. ripicola, and Y. filamentosa from Florida were collected from natural populations and planted in a common garden on the Syracuse University campus (Appendix S1; see Supplemental Data with online version of this article). The local host plant of T. yuccasella in Syracuse, New York is Y. filamentosa that occurs throughout the surrounding area as ornamentals in landscaping. We used Y. filamentosa from Florida as a control to assess whether any differences in moth use of host plants were due to the host plant species and not just to plants being from a different geographic locality. For each plant, a rosette and approximately 30 cm of the underlying rhizome were harvested and planted in 20-L plastic nursery pots containing a mix of equal parts Metro-Mix 360 (Sun Gro Horticulture, Vancouver, British Columbia, Canada) and sand. The pots were placed in the ground so that the top of each pot was flush with the ground surface. Plants began to consistently flower starting in 2013, and flowering phenology and insect visitation were recorded for all individuals at the common garden.

In 2013 and 2014, I recorded the number of flowers per day as well as the number of T. yuccasella present within flowers of each plant. I also surveyed fruit for the presence of exit holes that indicate the successful development of fifth instar larvae that leave the fruit to diapause in the soil. In 2015, I recorded flowering phenology but did not record insect visitation because the previous years data demonstrated that T. yuccasella consistently visited plants at the common garden. Instead, I observed pollination and oviposition behavior of moths to visually confirm that pollination and oviposition were occurring. I also dissected haphazardly selected flowers after observing moth oviposition to check for the presence of eggs. All fruit that were produced were collected after moth larvae had exited the fruit to diapause in the soil below the plants. I dissected each fruit to determine the number of exit holes, the number of feeding rows produced by larvae, and the number of viable (black) and nonviable (yellow) seeds that were eaten by larvae. I used an ANOVA to test for differences in flower phenology and a Kruskal–Wallis test to determine any differences in the number of T. yuccasella adults visiting each Yucca species per day. For 2015, I used a Mann–Whitney test to examine differences in the median number of constrictions per fruit and the number of exit holes per fruit among Yucca species. All statistical analyses were performed in JMP 9.0.2 (SAS Institute, Cary, North Carolina, USA).

RESULTS

The transplanted Yucca species differed in flowering phenology for 2013 ($F_{4, 450} = 830, P < 0.001$) and 2014 ($F_{4, 224} = 189, P < 0.001$) (Table 1). Yucca glauca flowered the earliest, followed by Y. pallida, and then Y. constricta, Y. reverchoni, and Y. filamentosa from Florida (Appendix S1, see Supplemental Data with online version of this article). The local population of Y. filamentosa flowered from late June to mid or late July each year. As a consequence, some individuals of Y. glauca completed flowering before any local pollinator moths were available. Moths were found in the flowers of all species with the exception of Y. ripicola in both years and Y. reverchoni in 2013 (Table 1). In 2013 and 2014, Y. pallida attracted the most moths, while Y. reverchoni and Y. constricta attracted only a few individuals (Appendix S2, see online Supplemental Data). Yucca glauca also consistently attracted moths. In 2014, Y. filamentosa from Florida attracted similar numbers of moths as Y. pallida. Given the low numbers of moths, I only observed pollination behavior of T. yuccasella on Y. pallida and Y. filamentosa from Florida. In terms of oviposition behavior, I was able to dissect flowers of Y. pallida after observing moth oviposition to confirm that T. yuccasella can deposit eggs into the flower locule (Fig. 2). Examination of fully developed fruit also confirmed that female moths were able to reach the locule during oviposition (Fig. 2). Many, but not all, fruit had the characteristic constriction as a result of ovule damage during moth oviposition.

The only two Yucca species that consistently produced mature fruit at the common garden were Y. pallida and Y. filamentosa from Florida. This result was somewhat surprising, especially for Y. glauca, which had similar numbers of T. yuccasella observed in the flowers as Y. pallida and Y. filamentosa. For Y. ripicola, Y. reverchoni, and Y. constricta, moth visitation was very low based on the number of moths recorded within the flowers, and there was no fruit set. Additional, focused observations of moths on Y. glauca, Y. ripicola, Y. reverchoni, and Y. constricta are needed to positively identify that moths are pollinating the plants.

In terms of successful larval development in yucca fruit, the normal host of T. yuccasella in Syracuse, Y. filamentosa, consistently produced a much greater number of fifth instar larvae that exited the fruit to diapause in the soil ($\chi^2 = 61.46, df = 1, P < 0.0001$). On average, there were $1.12 \pm 0.34$ exit holes per fruit across the 3 years.
of this study (2013–2015). In contrast, there was a grand total of two exit holes from 397 fruit of *Y. pallida*. The lack of exit holes could be the result of two factors. First, female moths may pollinate yucca flowers but not successfully oviposit, or female moths may oviposit eggs but the eggs or larvae perish during development. Of the 125 fruits dissected in 2015, 30 did not show any evidence of constrictions that are typical of successful oviposition. The remaining 94 fruit, however, had an average of 3.41 ± 0.16 constrictions that was similar to the number for *Y. filamentosa* ($\chi^2 = 2.06, df = 1, P = 0.36$), demonstrating that *T. yuccasella* females had reached the locule with their ovipositors. Strikingly, only two of these fruit had exit holes and evidence of eaten seeds.

**DISCUSSION**

Understanding the processes that have led to the diversification of plants and insects, two of the most species-rich groups on Earth, has been a long-standing goal in evolutionary biology. In particular, a number of hypotheses such as diversifying coevolution, arms races, and escape and radiate coevolution have been proposed as mechanisms to explain the incredible diversity of both groups. Central to these speciation mechanisms is the idea that insect and plant lineages specialize to one another and coevolve, which in turn leads to diversification in both lineages (Ehrlich and Raven, 1964; Thompson, 1994). Although there is little doubt that insects and plants have specialized to one another, the link between coevolution and speciation remains elusive (Althoff et al., 2014b; Hembry et al., 2014). Moreover, the relative roles of mutualism vs. antagonism in generating specialization, coevolution, and speciation are also unclear. Here, I examined an obligate brood pollination interaction to begin to unravel the relative contributions of mutualism vs. antagonism in the specialization process that ultimately influences coevolution and speciation.

As is typical for these types of systems, many of the species of pollinating yucca moths are extremely host specific, pollinating just one or two species of *Yucca* (Pellmyr, 1999). A recent test of cospeciation between the pollinator moth genus *Tegeticula* and *Yucca* detected significant levels of cospeciation between the lineages (Althoff et al., 2012), yet disentangling the mechanisms that might be responsible for these linked speciation events is more challenging. For example, geography, selection for the pollination mutualism, and selection for feeding on seeds could all be contributing to speciation in both lineages. Plants will be under selection to limit the behavior of pollinator moths to visit only conspecific individuals, moths will be under selection to increase larval survivorship, and selection for these two aspects will be variable given the overlapping and non-overlapping geographic distributions of *Yucca* species (Pellmyr et al., 2007; Althoff et al., 2012). Determining the contributions of each of these factors is important for understanding their roles in specialization that will influence coevolution and diversification.

The results from *T. yuccasella* demonstrate that although moths will visit, pollinate, and oviposit into non-natal *Yucca* species they appear to be less successful as antagonists than mutualists. For

---

**TABLE 1.** Flowering phenology of five *Yucca* species and visitation by the pollinator moth *Tegeticula yuccasella* at a common garden in Syracuse, New York. Letters denote statistically significant differences among species.

<table>
<thead>
<tr>
<th>Year</th>
<th>Observation</th>
<th><em>Y. constricta</em></th>
<th><em>Y. filamentosa</em></th>
<th><em>Y. glauca</em></th>
<th><em>Y. pallida</em></th>
<th><em>Y. reverchoni</em></th>
<th><em>Y. rupicola</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td>Peak flowering date</td>
<td>14 July c</td>
<td>–</td>
<td>21 June a</td>
<td>1 July b</td>
<td>19 July c</td>
<td>26 June c</td>
</tr>
<tr>
<td></td>
<td>Median moths per day</td>
<td>0.5</td>
<td>–</td>
<td>0</td>
<td>2.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Range of moths per day</td>
<td>0–2</td>
<td>–</td>
<td>0–10</td>
<td>0–10</td>
<td>0–1</td>
<td>0</td>
</tr>
<tr>
<td>2014</td>
<td>Peak flowering date</td>
<td>–</td>
<td>13 July c</td>
<td>24 June a</td>
<td>3 July b</td>
<td>11 July c</td>
<td>11 July c</td>
</tr>
<tr>
<td></td>
<td>Median moths per day</td>
<td>–</td>
<td>0.5</td>
<td>0.2</td>
<td>0.5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Range of moths per day</td>
<td>–</td>
<td>0–5</td>
<td>0–2</td>
<td>0–5</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

---

**FIGURE 2** Left: Interior of a dissected pistil with ovules (large, white round structures) moved to reveal eggs to show evidence of egg deposition by *Tegeticula yuccasella* into the locular cavity of *Yucca pallida* flowers. The arrow points to two elongate eggs of *T. yuccasella*. Magnification is 10×. Right: Example of constricted (top) and unconstricted (bottom) fruit of *Y. pallida*.
example, while many fruit were produced on the non-natal *Y. pallida*, only two larvae survived to the fifth instar. The performance of *T. yuccasella* on *Y. pallida* suggests that the ability of larvae to feed on the seeds of different *Yucca* species is a critical aspect of specialization to host use by the moths. Female moths will pollinate and lay eggs into *Y. pallida* flowers; however, less than 2% of fruit had exit holes that demonstrated successful development of larvae. This result was somewhat surprising given that *T. yuccasella* uses *Y. pallida* in Texas, suggesting that this moth may be undergoing divergent selection across its range. One possibility is that *T. yuccasella* is locally adapting to individual plant populations; however, the results from the garden suggest instead that this moth is undergoing host-associated specialization. For example, in the common garden, greater than 90% of fruit from *Y. filamentosa* transplanted from Florida had exit holes. This success rate is similar to that on local *Y. filamentosa* (D. M. Althoff, personal observations), suggesting that the parasitic side of the interaction may limit moth host range.

This striking difference in larval development could be due to unsuccessful oviposition or mortality of eggs and/or early instar larvae developing within non-natal host species. On the basis of dissections of *Y. pallida* fruit, female moths attempt oviposition, as there were many constrictions on the fruit (Table 2). Fruit dissections, however, also demonstrated that there was no damage to seeds from larval feeding, except in the rare instances in which there was an exit hole in the fruit. Although I did confirm that female moths are able to lay eggs into *Y. pallida* flowers (Fig. 2), I did not estimate the success rate of egg deposition. In *Y. filamentosa* from Florida, Segraves (2003) reported an oviposition success rate of approximately 45% for *T. yuccasella*. If I assume a similar oviposition rate for *Y. pallida*, I would have expected about 42 of the 94 *Y. pallida* fruit with constrictions to have larvae. Furthermore, larval loads in fruits of *Y. pallida* at the site from Texas were 1.35 ± 0.12 larvae per fruit (D. M. Althoff, unpublished data), indicating that *T. yuccasella* from Texas are able to effectively use *Y. pallida* as hosts. The fact that two larvae from the local *T. yuccasella* in Syracuse were able to develop, suggests that there is the potential for moth populations to adapt to new *Yucca* species they encounter, but that selection will be intense.

Although much of the emphasis on the yucca–yucca moth interaction has been on the mutualism, the ability of moth larvae to feed on yucca seeds is a critical component to the overall interaction. Plants will be selected to limit feeding damage, and moths will be under selection to maximize the number of larvae that can develop within a fruit and to do so at a rate that makes them competitive with other moth individuals. The importance of selective abscission in regulating moth larval loads within flowers is a testament to this dynamic (Pellmyr et al., 1996; Pellmyr and Leebens-Mack, 1999; Marr and Pellmyr, 2003). One of the major overlooked aspects of this interaction, however, is the fact that yucca leaves, inflorescences, and seeds are chemically defended primarily by saponins, a class of amphiphilic glycosides that are bitter, soapy feeding deterrents (Bahuguna et al., 1991; Hostettmann and Marston, 1995; Zhang et al., 2008). The dry mass of seeds of some *Yucca* species can be up to 18% saponins (Wall and Fenske, 1961; Stohs and Obrist, 1975; Hostettmann and Marston, 1995) and at least two species, *Y. schidigera* and *Y. gloriosa* are grown commercially for this resource (Piacente et al., 2005; Skhirtladze et al., 2011). Thus, moth larvae potentially have to contend with high levels of saponins in their diet in addition to other secondary plant chemicals. These high levels lead to the intriguing possibility that adaptation to plant defensive chemistry might be a major factor determining specialization in the yucca–yucca moth interaction.

The idea that plant chemistry may be important in host use by pollinators is further supported by recent work on a species of bogus yucca moth, *Prodoxus decipiens*. This moth species feeds within the flowering stalk of yuccas, but not on seeds. Across much of its range, *P. decipiens* uses *Y. filamentosa* (Groman and Pellmyr, 2000; Althoff et al., 2001; Althoff and Pellmyr, 2002). Althoff et al. (2014a) demonstrated that females of *P. decipiens* recognize *Y. pallida* and successfully deposit eggs into the inflorescence stalks, but no fully developed larvae were produced because of early larval mortality. In addition, *P. decipiens* was also unable to complete development on two other species within the Rupicolae, *Y. rupicola*, the sister to *Y. pallida*, and *Y. reverchoni*. Once again, feeding by the moth larvae was detected, but larvae perished in the early instar stages (Althoff et al., 2014a). The sister species to *P. decipiens*, *P. quinquepunctellus*, however, uses the Rupicolae as hosts (Althoff et al., 2001).

For many brood pollination mutualisms, perhaps it is not surprising that host specificity will likely be strongly influenced by the ability of insects to act as seed feeders. During the evolutionary history of many of these pollinating-seed feeders, ancestors of the pollinating species were herbivores that evolved pollination and seed feeding. For the prodoxid moths in general, there have been multiple shifts from pure antagonism to a pollinating-seed eating mutualism as pollination became important as a means to ensure a food source for developing offspring (Pellmyr and Thompson, 1992). Whether the evolution of pollination led to an increase in specialization and diversification is untested. If I compare just the number of bosgus yucca moth species to the number of pollinator species, however, there is roughly equal species diversity, suggesting that perhaps it is not the evolution of active pollination per se that has been important for determining host use and patterns of diversification (Althoff et al., 2001; Pellmyr et al., 2006). Additional evidence that host specificity can be driven by the antagonistic side of the overall interaction in brood pollination mutualisms comes from recent work in figs. Ghana et al. (2015a, b) demonstrated that fig wasps are attracted to their normal host, *Ficus montana*, the closely related fig, *F. asperifolia* that is normally pollinated by a different fig wasp species, and hybrids and backcrosses of these two fig species. Fig wasp females were able to enter figs and lay eggs in all plant crosses, but the galls necessary for wasp larval development failed to form in hybrids, backcrosses, and pure *F. asperifolia* individuals. Ghana et al. (2015a, b) suggest that the ability to form galls may be a major determinant of host specificity in fig wasps.

**Table 2.** Results of fruit dissections to determine whether *Tegeticula yuccasella* larvae are able to successfully complete development on different *Yucca* species. “Constrictions” refers to the characteristic morphology of fruit caused by ovule death from moth oviposition (see Fig. 2). “Exit holes” refers to the feeding pathway that larvae chew as they leave the fruit to diapause in the soil. *Filamentosa-FL* refers to *Y. filamentosa* from the Florida population.

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>Plants</th>
<th>Fruit</th>
<th>Constrictions</th>
<th>Exit holes</th>
</tr>
</thead>
<tbody>
<tr>
<td>2013</td>
<td><em>Filamentosa-FL</em></td>
<td>2</td>
<td>15</td>
<td>59</td>
<td>25</td>
</tr>
<tr>
<td>2014</td>
<td><em>Filamentosa-FL</em></td>
<td>17</td>
<td>125</td>
<td>321</td>
<td>2</td>
</tr>
<tr>
<td>2015</td>
<td><em>Filamentosa-FL</em></td>
<td>5</td>
<td>6</td>
<td>–</td>
<td>3</td>
</tr>
<tr>
<td>2016</td>
<td><em>Filamentosa-FL</em></td>
<td>10</td>
<td>11</td>
<td>–</td>
<td>0</td>
</tr>
<tr>
<td>2017</td>
<td><em>Filamentosa-FL</em></td>
<td>2</td>
<td>12</td>
<td>–</td>
<td>12</td>
</tr>
<tr>
<td>2018</td>
<td><em>Filamentosa-FL</em></td>
<td>9</td>
<td>261</td>
<td>–</td>
<td>0</td>
</tr>
</tbody>
</table>
In contrast to the results for yucca moths and fig wasps, Kawakita et al. (2010) suggested that it is the mutualism that drives specialization in the brood pollination interaction between leafflowers and leafflower moths. Comparisons of host use between mutualistic lineages of *Epicephala* moths and a sister group of leaf miners, demonstrate that the mutualists are more specialized, and this pattern also holds true when comparing *Epicephala* to other more distantly related seed-feeding moths that use the same host plants. Visitation and fruit set data for *T. yuccasella* suggest that mutualistic side of the interaction may also influence specialization to some degree. Moths visited all species except *Y. rupicola*, but fruit were consistently produced only in one of the non-natal species, *Y. pallida*. With the current experiment, it was not possible to determine why, but the results leave open the possible role of mutualistic traits. Particularly intriguing is the fact that although many individuals of *Y. glauca* flowered and were visited by moths, no fruit was set. Additional tests in the yucca–yucca moth system as well as other brood pollination systems are clearly needed to examine the relative roles of mutualistic vs. antagonistic traits in promoting specialization. Once these tests are in place, we will have a more accurate and robust view of the ecological and evolutionary forces that have promoted specialization, coevolution, and diversification of plants and their associated insects.

**ACKNOWLEDGEMENTS**

I thank A. Fox for assisting with phenology surveys and Georgia Chaniotaki and Pristine Mei with fruit dissections. Kari Segraves provided valuable comments to previous versions of the manuscript. I especially thank Jim Leebens-Mack and Jeremy Yoder for organizing the colloquium, the chance to participate and overseeing the editing of the special feature. The manuscript was also improved greatly from comments by Jeremy Yoder and two anonymous reviewers.

**LITERATURE CITED**