ANNUAL REVIEWS

Annual Review of Entomology

150 Years of Coevolution Research: Evolution and Ecology of Yucca Moths (Prodoxidae) and Their Hosts

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Annu. Rev. Entomol. 2024. 69:375–91

First published as a Review in Advance on
September 27, 2023

The *Annual Review of Entomology* is online at
ento.annualreviews.org

https://doi.org/10.1146/annurev-ento-022723-104346

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Keywords

pollination, mutualism, coevolution, Agavoideae, *Tegeticula*, antagonism

Abstract

Yucca moths (*Tegeticula* and *Parategeticula*) are specialized pollinators of yucca plants, possessing unique, tentacle-like mouthparts used to actively collect pollen and deposit it onto the flowers of their hosts. The moths' larvae feed on the developing seeds and fruit tissue. First described in 1873, the yucca–yucca moth pollination system is now considered the archetypical example of a coevolved intimate mutualism. Research conducted over the past three decades has transformed our understanding of yucca moth diversity and host plant interactions. We summarize the current understanding of the diversity, ecology, and evolution of this group, review evidence for coevolution of the insects and their hosts, and describe how the nature of the interaction varies across evolutionary time and ecological contexts. Finally, we identify unresolved questions and areas for future research.

INTRODUCTION

Yucca moths (*Tegeticula* and *Parategeticula*) and yuccas (*Yucca* and *Hesperoyucca*) constitute perhaps the best known of the obligate pollination mutualisms (also called brood pollination systems) (44), where plant reproduction is dependent on the service of one or a few closely related pollinators, and the pollinators feed on developing seeds. The uncommon pollination interaction between yucca and yucca moths involves active pollen collection and deposition employing behaviors that serve the exclusive function of transferring pollen between flowers. Female yucca moths possess tentacle-like mouthparts—uniquely derived outgrowths of the maxillary palps—that they use to collect pollen and deliver it to another flower, ensuring the production of seeds to provision their offspring. In a letter to J.D. Hooker (29), Darwin described yucca's pollination by yucca moths as "the most wonderful case of fertilisation ever published" (p. 361).

The yucca–yucca moth interaction is now considered an archetypical example of coevolution and a model for understanding the ecology of mutualisms. The past 30 years brought an explosion of research on all aspects of yucca and yucca moth biology, including taxonomic revisions and new species circumscriptions, as well as ecological, phylogenetic, and phylogenomic studies. In this article, we review the current state of knowledge and identify outstanding problems in need of further research.

NATURAL HISTORY OF OBLIGATE POLLINATION MUTUALISMS

At the time of Darwin's letter to Hooker, active pollination was virtually unknown. A handful of other active pollination systems have since been identified, including fig wasps (117), leaf-flower moths (53), and *Upigia* moths pollinating *Lophocereus* cacti (47). In each case, the plants and insects show morphological and physiological adaptations to the interaction. For example, female yucca moths exhibit differences in ovipositor morphology associated with the host plant and the mode of oviposition. In yuccas, nectar production is scant (see, e.g., 32, 86), and the plants produce less pollen per ovule than their closest relatives (79). Brood pollination mutualisms frequently show high levels of host–pollinator specificity; roughly two-thirds of *Tegeticula* and *Parategeticula* species are specialized on a single host (72, 75). This specificity may be mediated by floral scent; *Yucca* flowers produce unique volatiles that appear to attract moths (107, 108, 115), and in some cases, yuccas pollinated by different moths produce distinct scents (109).

Seed-feeding pollinators also show behavioral adaptations to the mutualism (4). This is particularly true for yucca moths (30, 73). Males and females aggregate on the yucca flowers, mating within the inflorescence. Females collect pollen by dragging their tentacles across the floral anthers. Prior to pollination, *Tegeticula* females use their piercing ovipositors to place eggs in yucca floral ovaries or styles. In contrast, *Parategeticula* females use rake-like ovipositors to cut grooves in yucca pedicels, petals, or other flower parts and then deposit their eggs into them (75, 77, 88). Females of both genera deposit pollen on stigmas and into styles using their tentacles. The moths' eggs typically hatch within 7 days. In *Tegeticula*, the larvae then feed on the developing ovules. In *Parategeticula*, larvae hatch and make their way to yucca carpels, where they induce cyst formation and feed on cyst and carpel tissues (88). After feeding, the larvae burrow out of the fruits and descend to the ground, where they dig into the soil, spin a cocoon, and diapause for one or more years (30). They pupate shortly before emerging as adults, but the signals that prompt pupation and emergence are unknown.

DIVERSITY AND TAXONOMY

A total of 54 species of yucca moths are distributed across three genera in the Prodoxidae (Adeloidea, Lepidoptera): *Tegeticula*, *Parategeticula*, and the bogus yucca moths *Prodoxus*. Most members of *Tegeticula* and all known species of *Parategeticula* are pollinators, with females possessing the characteristic pollination tentacles. No species within *Prodoxus* pollinate their hosts, and they do not feed on seeds. Instead, they oviposit into fruits, stems, and leaves, sometimes forming gall-like structures (76). Davis (30) reported that some *Prodoxus* possess rudimentary tentacles, though none were identified in scanning electron micrographs (SEMs) of *Prodoxus decipiens* (80).

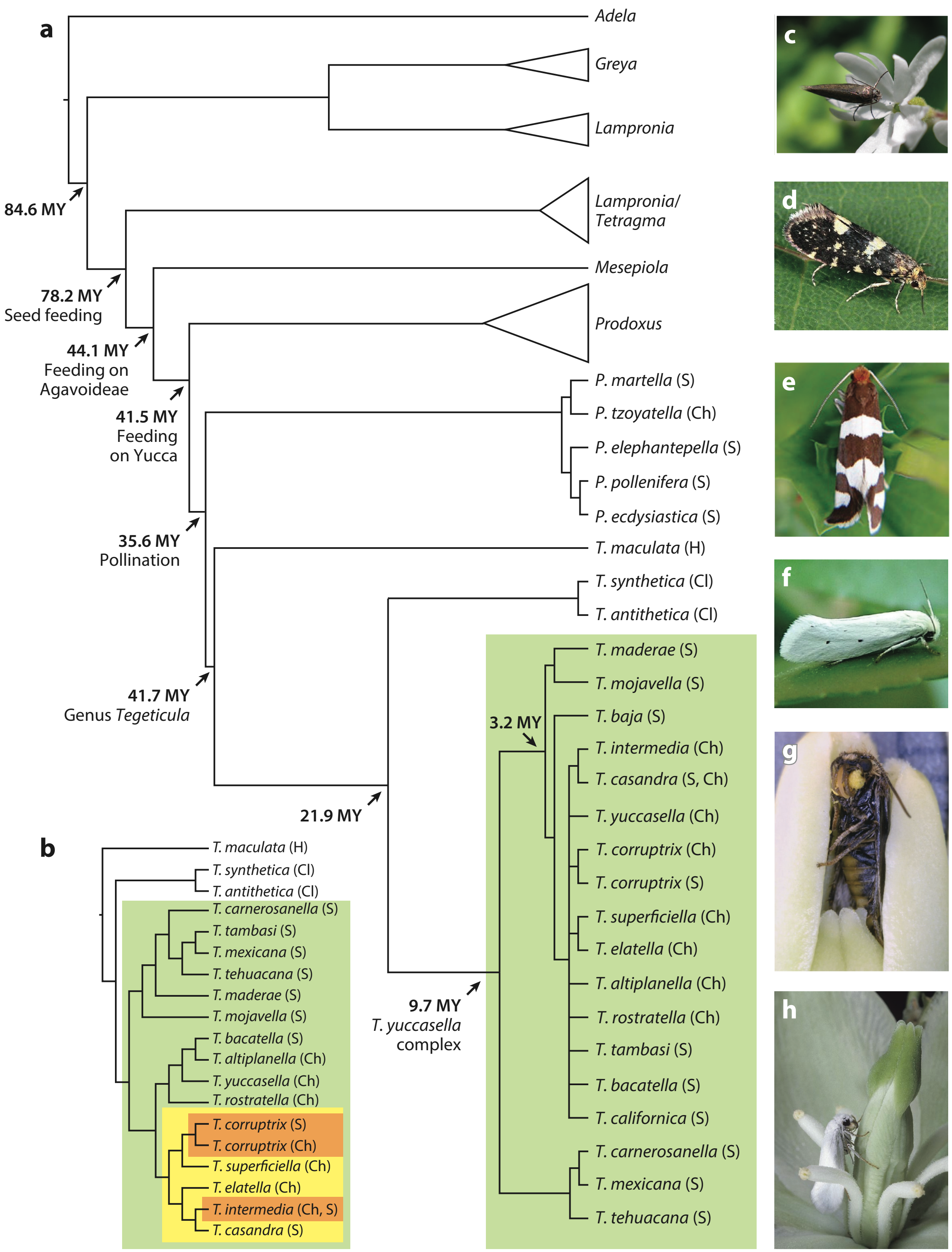
Although yucca moths were discovered in 1872 (36), and the first formal taxonomic descriptions were completed in 1873 (92), most of the diversity in the three genera was not uncovered until recently. Much of the twentieth century saw little taxonomic work on the group, and until recently, only three species of *Tegeticula* were recognized (30): *Tegeticula synthetica* pollinating Joshua tree (*Yucca brevifolia sensu lato*); *Tegeticula maculata* associated with Whipple's yucca (*Hesperoyucca whipplei*); and *Tegeticula yuccasella*, thought to be the pollinator of all other yuccas (30). In the 1960s, Davis (30) described *Parategeticula*, as well as two species of *Prodoxus*. Davis also suggested that there might be cryptic species within *T. yuccasella*, documenting morphological differences in the genitalia of male moths associated with different host plants. In the 1980s and 1990s, extensive morphological and genetic studies revealed multiple species within *T. yuccasella*. Addicott (1) identified nonpollinating cheater moths that are morphologically and ecologically different from pollinating moths (5). Subsequently, Pellmyr and collaborators (72, 81–83) circumscribed 10 genetically distinct lineages within *T. yuccasella*, as well as five other species of *Tegeticula* (77, 84), four species of *Parategeticula* (75, 77), and nine species of *Prodoxus* (76, 87).

There are likely still undescribed species in all three genera. Pollinators of nine *Yucca* species are unknown, and two other yuccas pollinated by *Parategeticula* have no known *Tegeticula* associates. Furthermore, *Prodoxus* moths have yet to be documented on several understudied yuccas. There are also likely to be additional distinct taxa within the currently described species. Segraves & Pellmyr (100) identified three deeply divergent lineages within *T. maculata*, and populations of the cheater moth *Tegeticula corruptrix* associated with either fleshy or capsular fruited yuccas appear to be genetically distinct (10). Pellmyr (72) suggested that there might be additional cryptic species or host races within his more narrowly circumscribed *T. yuccasella*, though a population survey of mitochondrial sequence variation did not detect host-specific population structure beyond genetic structure due to geographic isolation (57).

PHYLOGENY AND EVOLUTION

The evolutionary origins of such tightly interdependent mutualists may seem difficult to imagine, but macroevolutionary analyses suggest a stepwise evolution of the interaction, involving small, gradual changes over approximately 40 million years (MY) (81) (**Figure 1**). Feeding within the floral ovary was probably the ancestral condition within the Prodoxidae (119), and approximately 50% of species feed on woody monocots. Local host specificity also appears to be common. Active pollination and maxillary tentacles are the only features not already established in the prodoxid ancestors of *Tegeticula* and *Parategeticula*. In fact, passive pollination and probing of flowers appear to have evolved repeatedly within Prodoxidae (86). Furthermore, the origin of novel pollination tentacles may be driven by minor changes in gene regulation and development (80).

Surprisingly, age estimates for yuccas and pollinating yucca moths have consistently differed. The only fossil for either lineage—*Protoyucca shadishii*—provides an upper bound on the origin of *Yucca* at approximately 14.5 million years ago (MYA) (113), but a molecular clock analysis of moth mitochondrial DNA (81) suggests that active pollination originated approximately 35.6 MYA. That analysis used the break-up of Gondwana 95 MYA as a calibration point for the last common ancestor of Incurvariidae and Prodoxidae. Subsequent phylogenetic studies using different calibrations have produced similar or even older ages. Gaunt & Miles (39) estimated the age of the



(*Caption appears on following page*)

Figure 1 (*Figure appears on preceding page*)

Phylogeny of the Prodoxidae and species of pollinating yucca moths (*Tegeticula* and *Parategeticula*). (*a*) Phylogeny of the Prodoxidae based on Yoder et al. (119) and Pellmyr et al. (77). Branch lengths are not to scale; node heights are arbitrary except where indicated. Age estimates are based on Pellmyr & Leebens-Mack (81); ancestral states are based on Yoder et al. (119). The green highlight shows the *Tegeticula yuccasella* species complex. (*b*) Alternative resolution of relationships with the *T. yuccasella* complex based on Darwell et al. (28). The yellow highlight indicates superficial ovipositors; orange highlights indicate nonpollinating moths arising from superficial ovipositors. Branch lengths are arbitrary. (*c–h*) Images of key genera and species within the Prodoxidae. (*c*) *Greya politella*. Photo courtesy of Jeremy B. Yoder. (*d*) *Lampronia corticella*. Photo courtesy of Tom Murray. (*e*) *Lampronia oregonella*. Photo courtesy of Rick Avis. (*f*) *Prodoxus quinquepunctellus*. Photo courtesy of Cynthia Van Den Broeke. (*g*) *Tegeticula antithetica*. Photo courtesy of William Cole. (*h*) *Tegeticula altiplanella*. Photo courtesy of United States National Parks Service. All photos are used with permission.

prodoxids and the incurvariids to be 121 MY and that of the common ancestor of *Yucca* moths to be 66.7 MY. Kawahara et al. (54) estimated the age of the Adelodiea (the common ancestor of *Tegeticula* and *Nemophora*) to be 113–144 MY. Meanwhile, four studies have produced much younger age estimates for the origin of *Yucca*. Good-Avila et al. (42) estimated the age of the common ancestor of *Yucca* to be between 13.4 and 18.1 MY, whereas Smith et al. (104), using multiple fossil calibrations, estimated the age of *Yucca* to be between 6.4 and 15.8 MY. Two more recent studies using the complete set of chloroplast genes estimated the age of *Yucca* as either 4.1 MY (103) or 12.4 MY (66), which reflects differences in which nodes were constrained and what fossils were included in the analyses. Questionable placement of a rogue taxon, *Yucca queretaroensis*, adds uncertainty to some of these age estimates; different studies have placed it either within *Yucca* (46, 66, 103) or as sister to the rest of the genus (37, 85, 104).

Nevertheless, all of the results point to an origin of *Yucca* that is more recent than that of their pollinators and the origins of active pollination. There are several potential biological explanations for the discrepancy. One possibility is that the moths initially diversified on a different group of plants—perhaps an extinct stem group that diverged prior to the common ancestor of *Yucca* and *Agave*. This would require independent shifts of pollinating moths from an extinct host onto *Yucca* and *Hesperoyucca*. Although such extensive convergence seems implausible, it is clear that there have been multiple shifts between extant host lineages, including colonization of *Agave* and *Hesperoyucca* within *Prodoxus* (76) and an independent origin of yucca moth pollination in *Hesperoyucca* (16, 66). Furthermore, whereas *Yucca* subgenera diversified early in the history of the genus (66, 104), phylogenetic analysis of the moths suggests that both *Tegeticula* and *Parategeticula* initially diversified on fleshy fruited species (*Yucca* section Sarcocarpa), with pollinators of capsular-fruited species (Chaenocarpa) evolving secondarily within these groups (**Figure 1**). This implies additional host shifts and replacements of now extinct moth lineages on Chaenocarpa yuccas and *Yucca baccata* (Sarcocarpa) (10, 73).

MUTUALISM, CHEATING, AND PARASITISM

The yucca–yucca moth system is frequently described as a prime example of a mutualism, but various authors have suggested that the interaction may be more antagonistic than mutualistic (32, 43). Mutualisms, by definition, are interactions in which the benefits outweigh the costs for both players (18) but are typically conceptualized as reduced antagonisms in which mechanisms have evolved to limit the costs of the interaction for each species (51). However, mutualists commonly exploit their partners by failing to provide a benefit or by imposing an especially high cost (20, 52). Likewise, in certain ecological contexts, the value of the benefit provided may be lower, or the cost of cooperating may be higher, such that interaction becomes antagonistic (22). Evolutionary theory of cooperation predicts that mechanisms for retaliation against overexploitation should prevent the proliferation of defectors (14). All of these phenomena occur within the yucca–yucca moth interaction.

It can be difficult to evaluate the extent to which the yucca–yucca moth interaction is mutualistic because measuring the costs to each player is not necessarily straightforward (19). For the plants, potential costs include seeds lost to feeding by moth larvae and vegetative reproduction foregone to produce flowers, fruit, and seeds (43). Seed consumption by moths varies within and between species of yuccas. Typically, 5–30% of the seed crop is consumed (17, 31, 32), but mature fruits sometimes contain no larvae, and thus no seeds are consumed (17, 21, 31, 32, 97). At the same time, consumption can sometimes be as high as 90%. Some reports of high seed mortality might include seeds lost to cheater moths that exploit the system (e.g., 32), but some studies have found high seed mortality in yucca species where cheaters are not known to occur (e.g., 17). Thus, there may be instances in which high seed consumption outweighs the value of pollination.

One mechanism by which the plants may limit these costs is through selective abscission or abortion of fruits (78, 118). Up to 90% of yucca flowers abscise before reaching maturity (2). In both *Yucca filamentosa* and *Yucca kanabensis*, increasing numbers of moth eggs deposited in the locules has been shown to be associated with higher rates of abscission (3, 78), prompted by wounding of the ovules during oviposition (65). Interestingly, abscission seems to be correlated with the number of eggs laid, not with oviposition attempts. As oviposition attempts are correlated with bouts of pollination, flowers receiving more oviposition attempts may have better-quality pollination (48)—perhaps including more pollen grains and greater genetic diversity among pollen donors. The mechanism underlying differential fruit retention remains unknown, but resource limitation may explain the effects of both ovule wounding and pollination quality (78). If water, sugars, and other nutrients are insufficient to mature all flowers, then fruits with more developing ovules may draw more resources from the plant, reducing resources available to other flowers. Flowers have higher abscission rates on inflorescences with fruits that have already begun to develop (thus reducing the available resources for additional fruit), supporting the resource limitation hypothesis (49). Resource limitation on fruit production may have been the ancestral condition in the Agavoideae, and thus, differential abortion may have been an exaptation facilitating the origin of the pollination mutualism.

There may also be cases in which the plants are able to cheat their pollinators, enjoying the benefits of pollination without providing the reward of seeds (15). *Yucca baccatta* has an exceptionally long pistil, sometimes >60 mm. In some plants, the pistil contains very few viable ovules, clustered near the base of the pistil, whereas yucca moth oviposition typically takes place near the middle of the pistil. These cheater morphs make fewer flowers but produce more fruit per inflorescence, with fewer larvae and greater seed mass per fruit. It is unclear, however, whether the fitness of cheater plants is higher than the fitness of cooperators; the cheaters produce nearly 50% fewer ovules overall, so the plants would need to produce nearly twice as many fruits over the course of a lifetime to offset this cost. Bao & Addicott (15) suggest that cheating may occur in several other yuccas, but Crabb & Pellmyr (25) found very limited evidence of cheating in *Yucca treculeana*.

For the moths, costs of cooperation include time and energy expended in collecting, carrying, and depositing pollen. Dispersal between hosts, necessary for outcrossing between individual plants, may induce additional costs through increased predation (5, 64). Individual females can carry up to 10,000 pollen grains (74), which comprise a small (<10%) but significant portion of the moth's body weight. Pellmyr (71) argues that the costs of cooperation are small, noting that female moths allocate only approximately 4% of their time toward pollen collection and deposition. However, Aker & Udovic (6) report that some females may spend several hours searching for pollen and found that, on average, females spend approximately 25% of their time engaged in search behavior (71). It is unclear how much of this is time spent searching for pollen versus time spent searching for flowers for pollination and oviposition. It is possible that time spent searching for pollen varies depending on seasonal changes in the availability of pollen.

Nevertheless, there are multiple behavioral mechanisms by which moths may facultatively reduce the costs of mutualism, and there appear to have been at least two evolutionary transitions within *Tegeticula* that minimize or eliminate these costs. *Tegeticula yuccasella* females frequently pollinate *Y. filamentosa* flowers with pollen from the same plant (selfing), despite low retention rates of flowers that have been selfed and high mortality of any moth eggs laid in them (64). Selfing may be a bet-hedging response if there are high costs of dispersal between plants, for example, when flowering plant density is low or predation risk is high for moths flying between flowering plants (5). To our knowledge, the predation rates for moths dispersing between plants have never been measured, but studies of *T. maculata* suggest that movement between plants is common. Aker & Udovic (6) found that females almost always disperse immediately after pollen collection and never appear to self the plants. In a mark-recapture study, Powell (89) found that, whereas *T. maculata* male moths rarely dispersed between plants, only 17% of females were recaptured on the same plant.

Several studies have reported that individual moths may facultatively oviposit without pollinating, thus cheating the plants (5, 6, 116). In addition, two species, *T. corruptrix* and *Tegeticula intermedia*, have lost both pollination behavior and tentacles entirely, ovipositing onto fruit that has already begun to mature following pollination by other yucca moths (1, 81, 83). Reports of facultative cheating could represent misidentification of obligate cheaters. However, *T. maculata* has also been observed to attempt oviposition without pollinating (6), and obligate cheaters have never been reported on its host, *H. whipplei*, so misidentification seems unlikely in this case. Aker & Udovic (6) report observing oviposition into developing fruit by *T. maculata* females that were carrying pollen but could not or did not deposit pollen on the floral stigma, which would no longer be receptive to pollination. This observation is remarkable in that it unambiguously implicates pollinating *T. maculata* females as facultative cheaters.

Another way in which pollinating moths may increase their net benefit from the interaction is by changing oviposition depth or location in a way that does not induce the plants' abscission response. *Tegeticula cassandra*, *Tegeticula elatella*, and *Tegeticula superficiella* oviposit superficially on the surface of the flower, and the larvae burrow into the ovary afterward, thus avoiding damaging the ovules and circumventing the plants' defense against overexploitation (3, 72). Unlike moths that oviposit in the locules, among superficial ovipositors, increasing egg load does not increase rates of abscission. In fact, a greater number of ovipositions seems to actually increase the probability of fruit retention (3). Pellmyr & Leebens-Mack (82) speculated that transitions to superficial oviposition may be a precursor to the loss of pollination: Superficially ovipositing moths sometimes co-occur on the same host with locule ovipositors, so the loss of pollination behavior might not be disfavored if another moth is available to ensure fruit set. Phylogenetic analysis reveals that both species of cheaters are derived from superficial ovipositing ancestors (28, 82). In addition, differences in ovipositor morphology might allow superficial ovipositors to lay eggs in fruit, like the obligate cheaters (82). However, behavioral studies of the superficially ovipositing species *T. cassandra* found weak support for this hypothesis (99).

The behavior and morphology of moths and plants that fail to provide benefits notwithstanding, there remains an outstanding question of whether this failure qualifies as cheating, strictly speaking. Jones and colleagues (52) define cheaters as individuals derived from mutualists who engage in behaviors that reduce the fitness of the other player and have higher fitness than cooperators. Although cheater moths increase the net costs for the yucca, it is not necessarily clear that they have higher fitness than pollinators. No study has empirically measured the costs and benefits of cheating, but Pellmyr (71) argues that the overall cost of pollination is low (see above).

With this in mind, Jones and colleagues argue that nonpollinating moths are not a threat to the mutualism and may not be cheaters strictly speaking.

A final question is how the costs and benefits of the interaction vary across environments. Where the costs of yucca moth pollination for plants have been measured, a recurring finding is that seed consumption varies strongly between years and between populations within species (17, 31). High-elevation sites, where colder temperatures may inhibit moth development, are frequently reported to have lower rates of fruit production and higher rates of vegetative reproduction (32, 43). There have also been sporadic reports of pollination by other species of insects, including bees (91) and lauxuniid flies (32). The presence of copollinators is known to have the potential to change the costs and benefits of pollination mutualisms (112). The most persuasive case for copollinators in yuccas (91) examined pollination in *Yucca aloifolia* using a combination of pollinator observations, daytime and nighttime pollinator exclusion experiments, and quantification of seed consumption in developed fruits. *Yucca aloifolia* fruiting has long been documented in the absence of yucca moths (114), and observations of fruiting plants in Israel led Galil (38) to hypothesize pollination by European honeybees (*Apis mellifera*). Experimental exclusion data collected by Rentsch & Leebens-Mack (91) support this hypothesis, suggesting that even highly specialized mutualisms such as the yucca–yucca moth pollination system are not evolutionary dead ends. To date, all evidence of pollination by other insects has been in settings where the native moth pollinator is absent, and fruit set is typically sporadic, so it is unclear whether non-yucca-moth pollination occurs often enough to make the interaction with yucca moths more parasitic than mutualistic.

Nonpollinating herbivorous insects, predators, and extrinsic environmental factors may also shape the nature of the interaction. Bronstein & Ziv (21) found that the presence of galls made by the nonpollinating *Prodoxus y-inversus* in *Yucca schottii* fruits reduced the number of seeds lost to feeding by *Tegeticula* larvae. Because *Prodoxus* does not destroy seeds, their presence might limit the cost of yucca moth pollination. Similarly, Segraves (97) found that *Carpophilus* beetles will consume yucca moth eggs laid superficially on *Y. filamentosa*, which may translate to a significant increase in seed survival. Parasitoid wasps that prey on yucca moth larvae may also reduce the costs that yuccas pay for pollination (26) if parasitoid attack rates are density dependent. Lastly, Segraves (96) found that superficially ovipositing moths suffer higher rates of egg mortality due to desiccation, which may also limit seed predation.

COEVOLUTION

The relationship between yucca moths and yuccas is referenced as an example of coevolution in nearly every paper or textbook chapter on the topic. Although the term coevolution was not coined until the 1960s (35), the suggestion that moths evolved in concert with *Yucca* date to Riley's (92) original description. The strikingly low pollen production per ovule (79), the scant nectar production, and the abortion of fruits that have been overexploited (78) all suggest adaptation by the plants to yucca moth pollination. Likewise, the moths' active pollination behavior and the presence of tentacles on the maxillary palps—a feature that is unique within the Insecta—seem self-evidently to be adaptations to pollination. Further supporting adaptation, SEM studies identified hook-tipped sensilla on the ventral surface of the tentacles that are similar to structures found in multiple groups of pollen-collecting bees (80). Finally, variation in the ovipositor morphology associated with different hosts and oviposition strategies suggests adaptation by the moths (72).

Even so, several authors have expressed skepticism about the case for coevolution (11, 40, 104). The lack of consensus is in some measure a problem of definitions. Multiple authors have employed different conceptions of coevolution and suggested different tests and standards of evidence (23). Ehrlich & Raven (35) proposed a model of coevolution now termed the escape and radiate model, in which each of two interacting lineages undergoes successive adaptive radiations following the evolution of defenses and counter-defenses. A key innovation releases one group of organisms from constraints of competition or natural enemies, prompting an adaptive radiation as these organisms enter a novel adaptive zone. This innovation is eventually matched by a counter-defense in the second group, causing it to diversify in turn. Several studies have proposed that such a mechanism may be at work within yuccas and yucca moths (80, 82). Whereas selective abortion of flowers containing many moth eggs may be a mechanism to limit overexploitation of seeds, both the superficial ovipositors and cheater moths (discussed above) appear to have evolved counter-defenses to avoid the abscission response. These counter-defenses may have prompted rapid adaptive radiation as these moths colonized different hosts. *Tegeticula corruptrix* is known to utilize six species of *Yucca* (72) and likely feeds on many others. These different populations may be in the process of host race and ultimately species formation (10).

Several studies have attempted to reconstruct phylogenetic relationships among cryptic species previously lumped into *T. yuccasella* (10, 81, 82). They all found support for the monophyly of most species but with poor resolution of relationships between species, conflict between nuclear and mitochondrial data sets, and retention of ancestral polymorphisms, all of which may be consistent with rapid diversification. Recent work using restriction site–associated DNA sequencing seems to have resolved relationships within the *T. yuccasella* complex and shows a single transition to superficial oviposition with two independent transitions to cheating from superficial ovipositors (28) (**Figure 1**). However, no research to date has directly tested for escape and radiate coevolution in the yucca–yucca moth system. Addressing the question of whether yuccas and yucca moths conform to Ehrlich & Raven's (35) model would require an evaluation of whether changes in oviposition habit or loss of pollination resulted in changes in diversification rates, using a method that jointly estimates character evolution and diversification rates. However, a single origin of superficial oviposition makes it difficult to test the hypothesis that changes in oviposition strategy promote adaptive radiation. It may be possible to evaluate the simpler question of whether rates of diversification are higher among superficial ovipositing species and cheaters, but low overall diversity will still limit statistical power.

In contrast to Ehrlich & Raven (35), Janzen (50) suggests a quite strict definition of coevolution focused on microevolutionary processes: "Evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first" (p. 611). Thus, simple filtering of species into ecological roles to which they are preadapted cannot be considered coevolution. Because of the specific emphasis on population-level processes, under this definition, evolutionary changes that occur in a stepwise manner in each of two interacting lineages over long periods of time—as suggested by Ehrlich & Raven—might arguably not qualify as coevolution. Likewise, adaptations in one species that benefit the mutualism (e.g., active pollination by moths) might not be seen as coevolutionary if they are not associated with a resulting coadaptation in the other. Even ongoing evolutionary responses by a pollinator to evolution of the plant that it pollinates—known as host tracking—do not constitute coevolution under Janzen's definition.

Several studies have applied Janzen's (50) definition to studies of yuccas and yucca moths (24, 41, 102). Joshua trees (*Y. brevifolia* and *Yucca jaegeriana*) and their pollinators (*Tegeticula antithetica* and *T. synthetica*) have been a particular focus for testing coevolution as described by Janzen. The two moth pollinators are each other's sister species and differ markedly in body size and in the length of the ovipositor (84). They pollinate each of two sister species of *Yucca* that show strongly divergent floral morphology (41, 59, 103, 120), particularly in the length of the style, where the moths oviposit. This system may be an example of selection for phenotype matching: Increasing body size and ovipositor length in the moths may increase larval survival by allowing the eggs to be deposited closer to the ovules. However, overly long ovipositors may wound the ovules, prompting abscission. Increasing style length in the trees may provide a counter-defense that reduces larval survival, thus diminishing the cost paid by the trees for pollination. Several studies suggest that reciprocal selection may have produced differences in morphology in both the plants and their pollinators. Single nucleotide polymorphisms associated with style length seem to be under divergent selection between species and disruptive selection within a hybrid population (93). Within the moths, *T. antithetica* place their eggs further from the ovules when ovipositing onto plants with longer styles (24) and produce fewer larvae per clutch when ovipositing onto the longer-styled *Y. brevifolia* (101). These studies stop short, however, of demonstrating reciprocal selection as Janzen proposes, as the costs and benefits of phenotype matching have yet to be measured in an experimental framework. To date, no published study of yucca moths and their hosts has examined whether reciprocal selection at a population scale translates to correlated changes over macroevolutionary time. Althoff (8) found that shifts in egg-laying strategy are associated with higher rates of evolution in ovipositor morphology, suggesting adaptation on the part of the moths, but it is unclear whether changes in ovipositors are correlated with changes in floral morphology across *Yucca*.

A final question is whether diversifying coevolution may have promoted speciation in yuccas and yucca moths. Althoff and colleagues (9) define diversifying coevolution as "the process by which coevolution between two or more taxa increases net diversification" (pp. 82–83) and suggest several direct mechanisms by which coevolution could promote speciation: generating assortative mating, reducing gene flow between populations, or causing correlated changes in reproductive traits. Systems in which one player controls the movement of gametes in the other are thought to be particularly likely to undergo diversifying coevolution (111), and many authors have therefore suggested that coevolution between plants and their pollinators promotes diversification of both taxa (55, 56, 95). As the yucca–yucca moth mutualism involves all of these mechanisms, it is a case where diversifying coevolution is likely to occur.

A common test for diversifying coevolution is to assess phylogenetic congruence, which could indicate a long history of cospeciation. Althoff et al. (11) found significant phylogenetic congruence between *Yucca* and both *Tegeticula* and *Prodoxus* but observed that patterns of phylogenetic congruence can be generated by processes other than coevolution, including a shared biogeographic history. They argued that the diversification of both *Yucca* and associated insects may have been driven primarily by allopatric speciation and geographic isolation. They point out that there is no significant association between genetic divergence between species and the degree of range overlap—as might be expected if speciation occurs primarily through diversifying selection in sympatry—and that the extent of phylogenetic congruence between yuccas and *Tegeticula* is not greater than that between yuccas and *Prodoxus*, which is less likely to exert selection on the plants.

Althoff and colleagues' (11) results illustrate that evolutionary patterns provide only circumstantial evidence of coevolution (see also 69). Althoff et al. (9) highlighted four lines of evidence that strongly implicate diversifying coevolution: (*a*) Divergent selection acts on coevolving traits, (*b*) there is limited gene flow between populations with different phenotypes, (*c*) coevolution of traits influences mating success, and (*d*) the species interaction is associated with increases in net diversification rates for one or both taxa. Each of these have been explored in the yucca–yucca moth system and yielded varying conclusions.

There is circumstantial evidence of divergent selection in Joshua trees and their pollinators (discussed above), and there is also some evidence that coevolved traits may be involved in reproductive isolation. Hybridization is thought to be widespread in *Yucca* (12, 45, 90, 106, 110), including between species from different sections within the genus (45, 61, 90). Within Joshua trees, there is compelling evidence of hybridization (93, 94, 103, 106), but hybrids are rarer than would be expected (94), and asymmetric gene flow between the two species seems to reflect differences in pollinator behavior (106). A handful of studies have used genetic approaches to test for hybridization in *Tegeticula* (33, 58, 101). Although some cases have been identified (98), it is rare overall. Host specificity (58, 101) likely generates strong assortative mating, and changes in ovipositor length associated with adaptation to different hosts could cause correlated changes in male morphology, reducing heterospecific mating success (8).

Three studies have examined diversification rates in *Yucca* and relatives. Good-Avila et al. (42) estimated diversification in *Agave* and in *Yucca* and found that overall diversification rates in *Agave* were higher than in *Yucca*. In a similar analysis, Smith et al. (104) found slightly higher rates of diversification in *Yucca* than in its sister clade (including *Agave*, *Beschorneria*, *Furcraea*, *Manfreda*, *Polianthes*, and *Prochnyanthes*), but the estimated diversification rate (0.33 ± 0.06 species/MY) was modest and differed depending on the placement of *Y. queretaroensis* (see above). Lastly, Flores-Abreu and colleagues (37), using maximum likelihood model-fitting, inferred increasing rates of diversification through time in *Agave* (but not in *Yucca*), with contemporary rates of diversification (1.47 species/MY) three times higher than those in *Yucca* (0.473 species/MY). Together, these studies provide little evidence for increased diversification associated with yucca moth pollination. To date, no researchers have estimated diversification rates in yucca moths. A single origin of pollination in the common ancestor of *Tegeticula* and *Parategeticula* makes it impossible to address the question of whether active pollination promotes diversification generally, but it would be straightforward to evaluate whether there was an increase in diversification rates following the single origin of active pollination. Another approach would be to compare the absolute diversification rates in Prodoxidae with other groups in the Lepidoptera.

FUTURE DIRECTIONS

The revolution in molecular phylogenetics enabled enormous advances in our understanding of the diversity, ecology, and evolution of yucca moths and their hosts. In a similar fashion, third-generation, long-read DNA sequencing and advances in genome assembly are making it possible to address previously intractable questions. These technologies are proving particularly useful in understanding the diversity and evolution of the host plants. *Yucca* has historically been considered "one of the most difficult genera" in the flora of North America (110, p. 364). Frequent hybridization (12, 45, 61, 90, 106); intraspecific variation (13, 40, 68); and large, complex genomes (67) make both taxonomy and phylogenetics difficult (60, 104, 110). However, transcriptome assemblies are now available for multiple species of *Yucca* (70), and phylogenetic studies using both plastid genomes (66, 103) and sequence-capture technologies (46) have improved our understanding of evolutionary relationships. In addition, complete genome sequences will soon be available for some species (105), which could elucidate the molecular basis of adaptations to yucca moth pollination, including reduced nectar production and changes in floral form and volatile profiles.

Although we still lack a complete genome for any member of the Prodoxidae, assembled transcriptome sequences are available (27), and genome-scale data have already improved our understanding of phylogenetic relationships within *Tegeticula* (28). Future genomic investigations could reveal the genetic basis of adaptive innovations in *Tegeticula*, including the formation of the tentacles—an exceptionally rare instance of the evolution of a novel limb. Pellmyr & Krenn (80) speculated that the *distal-less* (*Dll*) and *bric-a-brac* (*bab*) genes may be involved, but these ideas have not been explored further. Variable tentacle development in *T. intermedia* (72) and reported hybridization between *T. intermedia* and *T. cassandra* (98) might provide an opportunity to study this question.

There are also unresolved questions about how the interaction generates and maintains differences between species in the moths and their hosts. While natural selection associated with different oviposition strategies may contribute to reproductive isolation (8), it does not explain divergence between moth species with the same mode of oviposition on different hosts. Allopatry likely plays an important role in the initial divergence between species (11), but the processes maintaining isolation on secondary contact are not clear. These might include responses to host-specific volatiles (109) or divergent selection due to differences in floral morphology (101). For *Yucca*, pollinator-mediated reproductive isolation seems at first glance to be a principal factor in maintaining species boundaries (106), but divergent selection (93) and genetic incompatibilities (94) may prove to be more important. The many areas of sympatry and frequent hybridization between *Yucca* species offer significant opportunities to explore these ideas.

The greatest advances, however, may be achieved through continued exploration of the diversity of these insects. Historically, the researchers investigating yucca moths have been based in the United States, and nearly all of the research on the group has focused on species and populations in the United States (but see 75, 77). However, the majority of described species of *Yucca* occur in Mexico, as do most *Yucca* species from which moths have never been identified. A growing community of scientists in Mexico exploring the ecology, evolution, and genetics of *Yucca* and its pollinators (7, 12, 13, 31, 34, 62, 63) promises to uncover hidden diversity in both groups. Improving our knowledge of this diversity will deepen our understanding of the yucca–yucca moth interactions and identify new opportunities to test the hypotheses developed over the past 150 years of research into this most remarkable case of fertilization.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

While preparing this manuscript, C.I.S. was supported by funding from the National Science Foundation (award ID 2001190) and the Fulbright–Garcia Robles US Scholars Program. David Althoff and Jeremy Yoder provided useful discussion and commentary on drafts of this manuscript. We are grateful for this assistance and support. Olle Pellmyr provided mentorship, guidance, and inspiration to us both. We are proud to dedicate this article to his memory.

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