

Reversal of Mutualism as a Mechanism for Adaptive Radiation in Yucca Moths

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ABSTRACT: Species interactions are a major source of adaptive radiation. In mutualisms, such diversification can take the form of evolution of parasites that exploit the resources needed for maintenance of the mutualism. Mutualistic associations often have associated parasitic species, and in some cases, parasitic species have indeed evolved from the mutualists. For example, obligate mutualisms, such as those involving seed-eating pollinators, have on a few occasions given rise to nonmutualist species. These systems are relatively simple and provide models for identifying factors that facilitate the stable reversal of a mutualistic interaction. We used ecological data in a phylogenetic framework to analyze the origins of two nonmutualist cheater yucca moths. Phylogenetic analysis suggests that the evolution of cheating may be preceded by a change in oviposition behavior. Two different modes of oviposition among moth species cause density-dependent moth egg mortality through flower abscission in one case (locule-ovipositing species) but density-independent mortality in the other (superficially ovipositing species). A mtDNA-based phylogeny indicated that cheating and superficial oviposition have evolved twice each and that the cheater clades are sisters to the superficially ovipositing species clades. Consideration of the fitness consequences of two trait changes—loss of pollination and phenological delay in oviposition—in which cheaters have diverged from ancestral pollinators suggest that the shift to oviposition into fruit may have occurred first and that loss of pollination behavior was a secondary event. We suggest that secondary coexistence of two pollinator species of opposite oviposition modes may facilitate the shift to fruit oviposition and cheating and that this is applicable in the best documented of the cheater yucca moths. Superficially ovipositing species suffer dual sources of egg mortality when in coexistence with locule-ovipositing species. Shift to fruit oviposition under this circumstance can be facilitated by access to a seed resource not available to the copollinator, preadaptations in ovipositor morphology, and pollinator phenology late relative to the copollinator. Thus the adaptive radiation of nonmutualists from mutualists may have taken place in specific ecological contexts through few trait

changes, and the reversal of mutualism would be a by-product of a shift to reliance on a previously inaccessible seed resource.

Keywords: obligate mutualism, Prodoxidae, life-history evolution, macroevolution, indirect effects.

Interaction between species is one of the major ecological causes of adaptive radiation (Darwin 1859; Mayr 1942; Thompson 1994; Howard and Berlocher 1998; Schluter 2000). Mutualistic interactions in particular provide opportunities for the evolution of parasites that exploit the resources that maintain the mutualism. For example, a large proportion, if not a majority, of all pollination mutualisms involve several animal species for a given plant species, and some of those associates are likely facultative or obligate parasites on floral rewards (Lindsey 1982; Herrera 1987; Wilson and Thomson 1991; Morris 1996; Pellmyr and Thompson 1996; Irwin and Brody 1998). In such complex webs, spatiotemporal variation in associates and outcomes of interaction present a challenge in understanding the factors that cause adaptive radiation in general and of life-habit shifts from mutualism to antagonism in particular.

Obligate mutualisms, such as those between seed-eating pollinators and their host plants, represent relatively simple systems in this regard. Reciprocal exploitation must be constrained for the mutualism to persist, and the evolution of nonmutualist genotypes is expected on theoretical grounds to be evolutionarily unstable except in specific circumstances (Bull and Rice 1991; Nowak et al. 1994; Herre and West 1997; Herre et al. 1999). There are a few identified cases of mutualism reversal in the two most species-rich models of seed-eating pollinators: a single instance among the many fig wasp species that pollinate 750–800 species of figs (Compton et al. 1991; Machado 1998) and one or more reversals among more than 15 species of yucca moths that pollinate yuccas (Pellmyr et al. 1996). The potential development of a general theory of evolution of parasites amid mutualists will require identification of the specific attributes and mechanisms that have led to reversal of mutualism in these cases as well as

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in other examples of reversed mutualisms. What facets of the biology of these organisms permitted the seemingly uncommon adaptive radiation of cheaters? Whether general principles can be found or whether the originating circumstances are too case specific and diverse will only be understood once the history and ecology of numerous models have been analyzed.

Here we present results from empirical studies of specific interactions in the obligate mutualism between yuccas and yucca moths, with emphasis on how this particular mutualism has set the stage for the origin of nonmutualistic moth species. We will use phylogenetic and ecological data to suggest that the coexistence of mutualists may not only allow for the evolution and persistence of non-pollinating cheaters but moreover that coexistence actually may change the adaptive landscape for one species such that cheating may evolve as a secondary result of a niche change.

This article has several different parts. First, we review recent advances in our understanding of the natural history of various yucca-yucca moth interactions. We then present a phylogeny for the pollinating yucca moths and derived cheater yucca moths and outline species differences in a specific life-history trait, namely mode of oviposition. We emphasize how change in oviposition behavior causes different moth-plant dynamics and may be critical to understanding the origin of cheater yucca moths. In the final section, we focus on one cheater and its sister species to erect hypotheses for mechanisms that may have facilitated its origins. We surmise that the coexistence of pollinating moth species on a single host would favor delayed phenology in one of the two pollinator species. The loss of pollination behavior, hence reversal of mutualism, may have followed that shift toward oviposition in developing yucca fruits.

Natural History of the Interacting Organisms

The obligate mutualism between yucca moths (Lepidoptera, Prodoxidae) and yuccas (Agavaceae) has been known for over a century (Engelmann 1872; Riley 1892), but the known diversity of interactions has increased dramatically in recent years. For this reason, a brief review of the moths and their interactions with yuccas is provided to set the stage.

All of the 35–50 recognized species of yuccas, which occur in North and Central America (fig. 1), rely on yucca moths for their pollination. There are currently 17 recognized pollinator species, 13 of which have been described since 1999. This increase in moth species has come from the realization that one traditionally recognized species (*Tegeticula yuccasella*) actually is a large complex as well as from the discovery of new species in the field

(Powell 1992; Pellmyr 1999; Pellmyr and Balcázar-Lara 2000). In all instances, the female moth uses unique tentacles on the maxillary palps to gather and to manipulate host yucca pollen. Females of the genus *Tegeticula* use a cutting ovipositor to lay eggs one at a time into the floral ovary, whereas those of *Parategeticula* lay eggs on plant tissue near the ovary. The larvae of all species require developing yucca seeds to complete development. The mature larva exits the fruit shortly before the fruit is ripe and diapauses and pupates underground in a dense cocoon. The adult emerges during a subsequent flowering episode. The majority of all pollinator species are monophagous, but some use at least seven yucca species (Pellmyr 1999).

There are two described nonpollinating yucca moth species that are referred to as “cheaters” because they have lost the habit of pollinating while maintaining the habit of seed consumption (Addicott 1996; Pellmyr et al. 1996; Pellmyr 1999). Cheaters thus rely on pollinator species for the availability of yucca seeds. Not only have these species lost the behavioral traits associated with active pollination, but both cheater species lack functional maxillary tentacles for pollen manipulation. They oviposit into yucca fruits, either early during development or once full fruit size has been reached. The phenologically early species, *Tegeticula intermedia*, oviposits very superficially into the fruit wall, and the larva chews its way into the locule to reach the seeds. In contrast, the later *Tegeticula corruptrix* oviposits through the fruit wall straight into the seeds of full-size fruits. The larvae of both species feed on seeds together with coexisting pollinator larvae but are two or more instars behind in development (D. Marr, M. Brock, and O. Pellmyr, unpublished data). *Tegeticula intermedia* is primarily eastern in distribution, ranging from the eastern seaboard of the United States to central New Mexico, while *T. corruptrix* is found in western North America, ranging from the Pacific coast eastward to southern Texas (fig. 1; Pellmyr 1999). The host plant range of these two cheaters is mostly separate. At least eight of the 11 described pollinator species within the *T. yuccasella* complex coexist with one or both cheater species. For the remaining three pollinators, the existence of cheaters has not yet been investigated. Cheaters have not been found on two highly distinctive yuccas (*Yucca brevifolia* and *Hesperoyucca whipplei*) that have highly distinctive pollinators (*Tegeticula synthetica* and *Tegeticula maculata*, respectively) basal to the *T. yuccasella* complex.

Phylogenetic Analysis of Life-History Diversification

Phylogeny of the Yucca Moths

We developed a phylogeny for all described species of *Tegeticula* and *Parategeticula* using a 2,103-bp stretch of

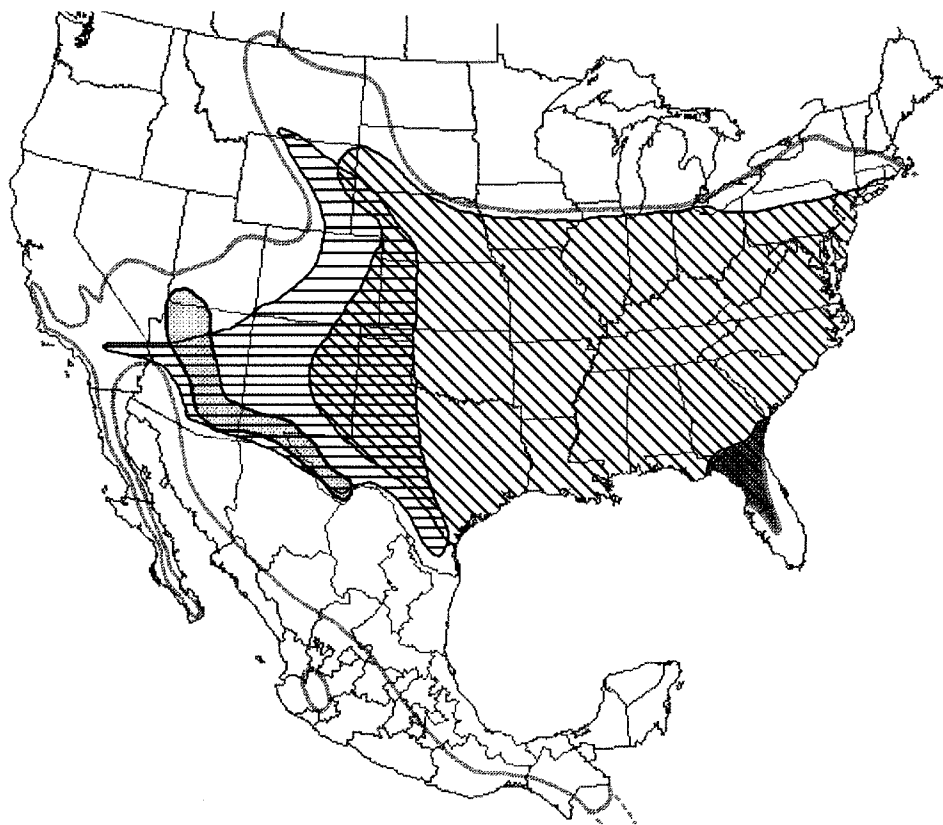


Figure 1: Composite range of all yucca species and their associated moths (gray line); dashed lines at bottom of figure indicate that yuccas are widely cultivated farther south but appear to lack pollinators. Patterns and shades give documented ranges of the cheater moth species (C) and their sister pollinator (P) taxa: dark gray = *Tegeticula cassandra* (P) and diagonal lines = *Tegeticula intermedia* (C); light gray = *Tegeticula elatella* and *Tegeticula superficiella* (P) and horizontal lines = *Tegeticula corruptrix* (C). Plant data compiled from Trelease (1902), McKelvey (1938–1947), and Matuda and Piña Lujan (1980); northern and interior portions of the United States east of the Great Plains have been colonized in historical time. Moth data compiled from Pellmyr (1999) and K. Segraves and D. Marr (unpublished data).

mtDNA, including most of the cytochrome oxidase I and II subunits and an intervening tRNA_{lys} region (positions 1,495–3,603 in the *Drosophila yakuba* genome; Clary and Wolstenholme 1985). The region was PCR amplified, and both strands were sequenced either manually with Sequenase T7 polymerase or with Amersham Dye-terminator chemistry on an ABI 377 automated sequencer following the manufacturer's protocols (Amersham Life Sciences, Arlington Heights, Ill.). Only two single-base length mutations were observed, and sequences were readily aligned by eye. All samples used for the analyses are listed in table 1 with GenBank accession numbers provided. For species with a wider host or geographic range, several individuals were sequenced yielding a total of 45 complete sequences. Following exploratory analyses, we limited the analysis to a total of 37 in-group sequences for computational reasons; this had no effect on species topology and only slight effect on robustness. Three species

of the sister genus *Prodoxus* were used as out-group taxa. Of the 2,103 bases in the sequenced region, 538 were variable, and 330 were phylogenetically informative.

Maximum-likelihood (ML) analysis was performed using Yang's modification of the Hasegawa-Kishino-Yano model of molecular evolution (Hasegawa et al. 1985; Yang 1994) as implemented in PAUP* (Swofford 1998). Maximum-likelihood estimates for the transition-transversion ratio and the gamma distribution parameter for rate variation among sites were 2.0 and 0.2, respectively. The resulting ML phylogeny is shown in figure 2. An unweighted parsimony analysis of the same data set also yielded one tree (confidence interval = 0.64, retention index = 0.74), that differed only in the placement of the [*Tegeticula elatella* + *Tegeticula superficiella*] + *Tegeticula corruptrix* clade. In the parsimony analysis, it was joined as sister to the *Tegeticula altiplanella* + *Tegeticula baccatella* + *Tegeticula rostratella* clade. Support for species

Table 1: Specimens used for phylogenetic analysis of *Parategeticula* and *Tegeticula*

Species	Locality	GenBank
<i>Tegeticula treculeanella</i> Pellmyr:		
<i>Yucca treculeana</i> Carrière	U.S.A., Cameron Co., Tex.	AY004292
<i>Yucca torreyi</i> Shafer	U.S.A., Brewster Co., Tex.	U49041
<i>Tegeticula carnerosanella</i> Pellmyr:		
<i>Yucca carnerosana</i> (Trel.) McKelvey	U.S.A., Brewster Co., Tex.	AY004293
<i>Tegeticula maderae</i> Pellmyr:		
<i>Yucca schottii</i> Engelmann	U.S.A., Santa Cruz Co., Ariz.	AY004294
<i>Tegeticula mojavelle</i> Pellmyr:		
<i>Yucca schidigera</i> Roehl ex Ortgies	U.S.A., San Bernardino Co., Calif.	U49039
<i>Tegeticula rostratella</i> Pellmyr:		
<i>Yucca rostrata</i> Engelmann ex Trelease	U.S.A., Brewster Co., Tex.	AY004295
<i>Y. rostrata</i>	Mexico, Coahuila	AY004296
<i>Tegeticula altiplanella</i> Pellmyr:		
<i>Yucca angustissima</i> var. <i>kanabensis</i> (McK.) Reveal	U.S.A., Kanab Co., Utah	AY004297
<i>Yucca baileyi</i> Wootton & Standley	U.S.A., Apache Co., Ariz.	AY004298
<i>Y. baileyi</i> var. <i>intermedia</i> (McK.) Reveal	U.S.A., Tarrant Co., N.Mex.	U49037
<i>Tegeticula baccatella</i> Pellmyr:		
<i>Yucca baccata</i> Torrey	U.S.A., Dona Ana Co., N.Mex.	U49026
<i>Yucca arizonica</i> McKelvey	Mexico, Sonora	AY004299
<i>Tegeticula superficiella</i> Pellmyr:		
<i>Yucca angustissima</i> var. <i>kanabensis</i>	U.S.A., Kanab Co., Utah	AY004300
<i>Yucca elata</i> var. <i>utahensis</i> (McK.) Reveal	U.S.A., Washington Co., Utah	U49042
<i>Tegeticula elatella</i> Pellmyr:		
<i>Y. elata</i> Engelmann	U.S.A., Cochise Co., Ariz.	U49028
<i>Tegeticula corruptrix</i> Pellmyr:		
<i>Y. arizonica</i>	U.S.A., Pima Co., Ariz.	AY004304
<i>Y. schidigera</i>	U.S.A., Riverside Co., Calif.	U49038
<i>Y. torreyi</i>	U.S.A., Brewster Co., Tex.	U49040
<i>Y. elata</i>	U.S.A., Cochise Co., Ariz.	U49027
<i>Yucca glauca</i> Nuttall	U.S.A., Crook Co., Wyo.	U49034
<i>Tegeticula intermedia</i> (Riley):		
<i>Yucca filamentosa</i> (L.)	U.S.A., Wilson Co., Tenn.	U49030
<i>Y. glauca</i>	U.S.A., Meade Co., Kans.	U49033
<i>Y. baileyi</i> var. <i>intermedia</i>	U.S.A., Valencia Co., N.Mex.	U49036
<i>Tegeticula cassandra</i> Pellmyr:		
<i>Y. filamentosa</i>	U.S.A., Clay Co., Fla.	AY004755
<i>Tegeticula yuccasella</i> (Riley):		
<i>Yucca campestris</i> McKelvey	U.S.A., Ward Co., Tex.	AY004301
<i>Y. glauca</i>	U.S.A., Meade Co., Kans.	U49043
<i>Y. filamentosa</i>	U.S.A., Wilson Co., Tenn.	U49032
<i>Y. glauca</i>	U.S.A., Crook Co., Wyo.	AY004302
<i>Y. reverchonii</i> Trelease	U.S.A., Sonora Co., Tex.	AY004303
<i>Tegeticula synthetica</i> (Riley):		
<i>Yucca brevifolia</i> Engelmann	U.S.A., Clark Co., Nev.	U49025
<i>Tegeticula maculata extranea</i> (Edwards):		
<i>Hesperoyucca whipplei</i> Torrey (Baker)	U.S.A., Riverside Co., Calif.	U49023
	Mexico, Baja California	AY004305
<i>T. maculata maculata</i> (Riley):		
<i>Hesperoyucca whipplei</i> Torrey (Baker)	U.S.A., Tulare Co., Calif.	U49024
<i>Parategeticula pollenifera</i> Davis:		
<i>Y. schottii</i> Engelmann	U.S.A., Santa Cruz Co., Ariz.	AF150921
<i>Parategeticula elephantipella</i> Pellmyr & Balcázar-Lara:		
<i>Yucca elephantipes</i> Regel	Mexico, Veracruz	AF150922

Table 1 (Continued)

Species	Locality	GenBank
<i>Parategeticula martella</i> Pellmyr & Balcázar-Lara: <i>Yucca endlichiana</i> Trelease	Mexico, Coahuila	AF150923
<i>Parategeticula tzoyatlilla</i> Pellmyr & Balcázar-Lara: <i>Y. rostrata</i>	Mexico, Coahuila	AF150924
<i>Prodoxus</i> n.sp.: <i>Y. schottii</i>	U.S.A., Pima Co., Ariz.	AY004306
<i>Prodoxus quinquepunctellus</i> (Riley): <i>Y. rostrata</i>	U.S.A., Brewster Co., Tex.	AY004307
<i>Prodoxus coloradensis</i> Riley: <i>Y. baccata</i>	U.S.A., Mohave Co., Ariz.	AF150917

Note: Specimens are listed from the top of the table, with individual moths listed by host within each moth species. Genbank accession number is given in right column.

relationships as measured by likelihood bootstraps is fairly strong, except in two sections of the tree. Monophyly of the two genera was supported, but the *Tegeticula maculata* lineage diverged shortly after the *Parategeticula-Tegeticula* split, leading to modest bootstrap support for the monophyly of *Tegeticula*. The *Tegeticula yuccasella* complex is also highly supported, but a rapid radiation event within the complex resulted in poor resolution of the relationships among four distinct clades (fig. 2; Pellmyr and Leebens-Mack 1999).

The Number of Origins of Cheating

As a first step to understanding the origin of cheating among pollinating moths, we used a phylogenetic approach to establish the number of lineages that had independently adopted this life-history strategy. In a previous analysis based on a far smaller set of taxa, three origins of cheating were obtained in a maximum-parsimony-based consensus tree (Pellmyr et al. 1996), but the Kishino-Hasegawa-Templeton test did not exclude the possibility of a single origin of cheating ($P > .05$). Using the expanded data set (fig. 2), we retested the hypothesis that cheating evolved once. Under this hypothesis, the cheaters, *Tegeticula intermedia* and *T. corruptrix*, are either monophyletic or paraphyletic if active pollination was regained. The results of the Kishino-Hasegawa-Templeton test comparing the likelihood (L) of the best tree constrained to join *T. intermedia* and *T. corruptrix* ($-\ln L = 8,807.5014$) against the ML tree shown in figure 2 forced us to reject the single-origin hypothesis ($P < .01$). There is now strong evidence for two origins of cheating.

Patterns of Oviposition and the Origin of Cheating

Next, we aimed to analyze character evolution in *Tegeticula* in order to determine whether changes in characters as-

sociated with oviposition behavior or ovipositor morphology were associated with the evolution of cheating. Mode of oviposition is quite variable among the pollinators but fixed within a species regardless of host (fig. 3). The basal, and most common, mode in *Tegeticula* is to place the egg inside a locule of the floral ovary. The locule is reached through different routes by different species (fig. 4). Two species cut into the style, and the ovipositor descends the open stylar tube to place eggs on top of the ovules in the locule (fig. 4,A). The most common route is to cut in at midovary, or, more rarely, near the top, to lay the eggs one at a time between the locule wall and the ovules (fig. 4,B). In *T. maculata*, the egg is inserted further to a position between ovules (O. Pellmyr, unpublished data). In all of these cases, the egg hatches inside the locule, and the larva can feed immediately on developing seeds. We refer to moths with these oviposition modes as "locule-ovipositing species." Another mode that is less common is for the female to oviposit very superficially in the ovary wall, about 0.1 mm below the surface, often at the base of the style (fig. 4,C). As the egg hatches, the first-instar larva tunnels in the wall to the locule where it eats seeds. We refer to moths with this oviposition habit as "superficially ovipositing species."

Flowers visited by moths of the two oviposition types are usually readily discerned by fruit shape because yuccas that have received ovipositions from locule-ovipositing species have a conspicuous constriction (Riley 1883) that is missing in others (fig. 5). This constriction occurs because females that oviposit into locules inevitably seem to injure a string of ovules. Ovules below an oviposition cut show an intense stress reaction within 12 h; development is slowed, and death occurs before significant size increase (D. Marr and O. Pellmyr, unpublished manuscript). As a consequence, the number of injured seeds increases with the number of ovipositions. This is important to the moth-plant interaction because yuccas are resource limited and only mature 5%–15% of their flowers to fruit (Aker 1982;

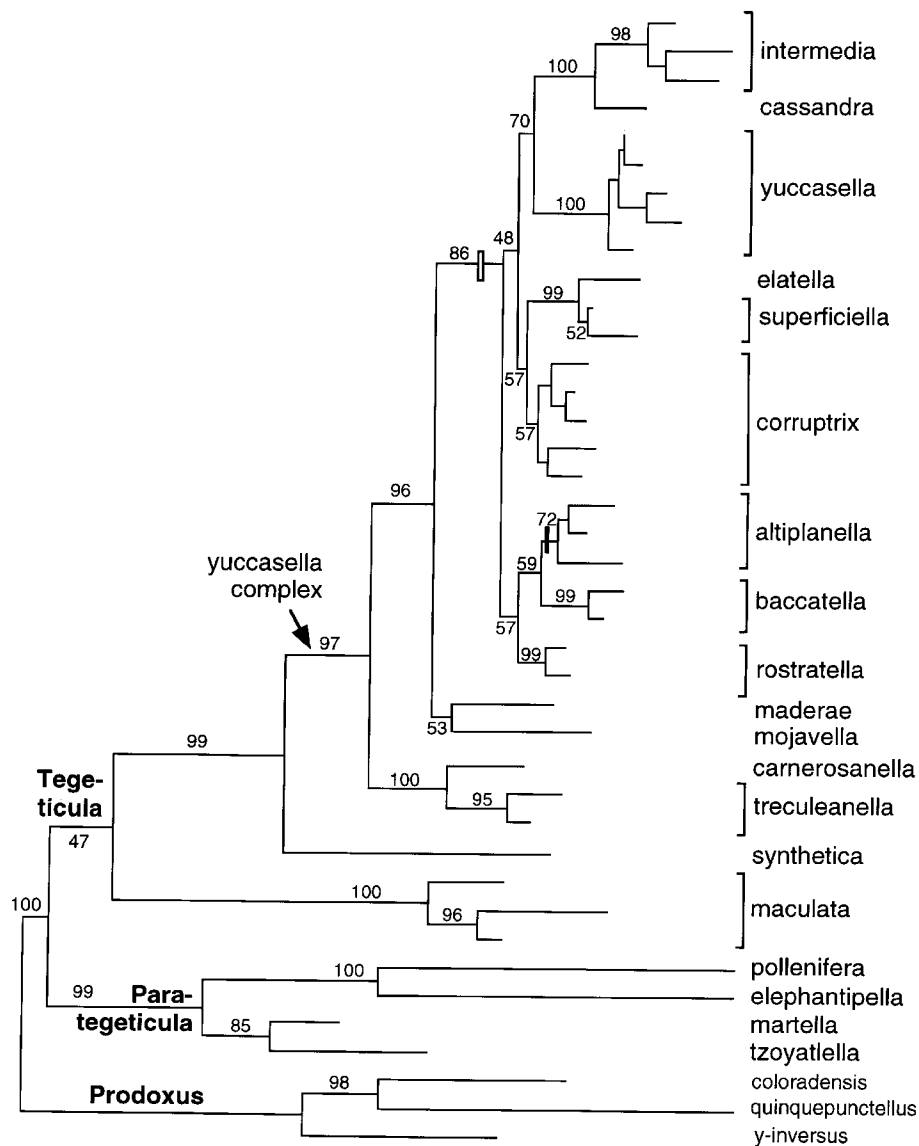


Figure 2: Maximum-likelihood-based phylogeny for all members of *Tegeticula* and *Parategeticula*. Three species of the sister group *Prodoxus* were used as outgroup. Brackets by species names (on right) indicate multisample taxa. Likelihood (L) bootstrap values were based on 100 iterations and are provided for all nodes except those within species. An open box on an internode indicates a single-base deletion; a solid bar indicates a single-base insertion. Both occurred at ends of the tRNA segment, and they were not used in the phylogenetic analysis. The single shortest tree had a $-\ln L = 8,767.3729$. Sample information is provided in table 1.

Keeley et al. 1984; Kingsolver 1984; Fuller 1990; James et al. 1993; Wilson and Addicott 1998), and there is selective abscission of fertilized flowers within a few days after pollination (Pellmyr and Huth 1994; Richter 1995). Such abscission kills all moth eggs in them. Flowers subjected to a higher number of locule ovipositions, and thus more ovule damage, are disproportionately often abscised (Huth and Pellmyr 2000; D. Marr and O. Pellmyr, unpublished

manuscript). There are now data for three different yuccas with different locule-ovipositing pollinator moths showing a negative relationship between moth egg number and the retention probability of the flower to mature fruit (Pellmyr and Huth 1994; Richter and Weis 1995; Wilson and Addicott 1998). Larval mortality is, therefore, density dependent. As a consequence, in yuccas exposed to seed consumption by locule-ovipositing pollinators alone, no more

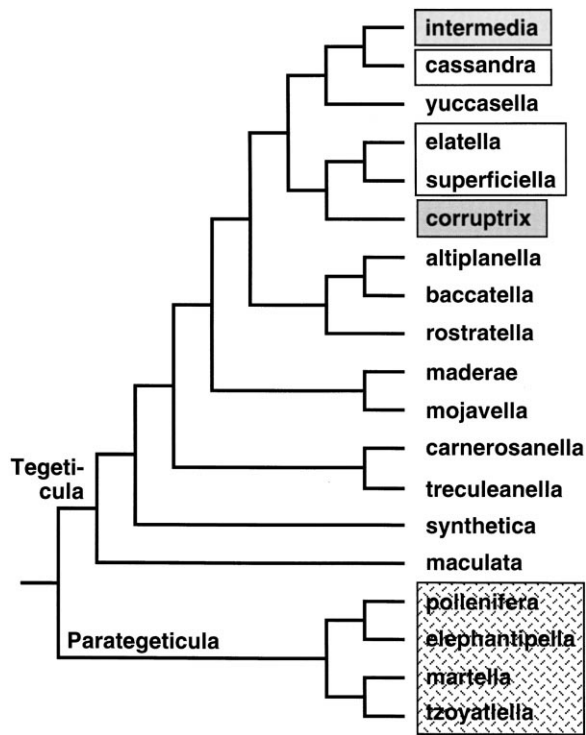


Figure 3: Species phylogeny for *Tegeticula* and *Parategeticula*, showing distribution of oviposition modes and of cheater species. *Nonboxed* = locule-ovipositing pollinator, *white box* = superficially ovipositing pollinator, *light grey box* = superficially ovipositing cheater (*intermedia*), *dark grey box* = seed-ovipositing cheater (*corruptrix*), and *hatched box* = pollinator laying egg away from ovary (larva enters; *pollenifera*, *elephantipella*, *martella*, and *tzoyatlilla*).

than 25%–35% of the seeds are destroyed (Keeley et al. 1984 for *Yucca brevifolia*; Keeley et al. 1986; Pellmyr and Huth 1994). Most published estimates of seed consumption may be composite values for two or more species of pollinators and/or cheaters (Keeley et al. 1984; Kingsolver 1984; Addicott 1986; Johnson 1988) and cannot be used for the present purpose. Flowers with larger egg loads that would produce more larvae and higher rates of seed destruction are selectively abscised. As a result, the remaining seeds are, in effect, out of reach for all locule-ovipositing yucca moths.

In contrast, the three superficially ovipositing pollinator species do not cause any ovule death, and there is no evidence that egg numbers affect the probability of abscission (Wilson and Addicott 1998). In principle, a sufficient number of larvae of such species could feed inside a developing fruit to destroy all seeds. High egg numbers per flower are common for these moth species, but larval counts in maturing fruit are usually low (Wilson and Addicott 1998; K. Seagraves, unpublished data). The mecha-

nism for egg or early instar mortality before they enter the locule is currently under investigation, but it is clear that the two oviposition modes observed in the pollinators trigger responses in the host plants that affect moth mortality differently. One of these, oviposition into the locule, affects moth mortality to abscission in a density-dependent manner, whereas the effect triggered by superficial oviposition is independent of egg density.

The distribution of the three superficially ovipositing species on the mtDNA phylogeny suggests that this mode of oviposition has two independent origins (fig. 3). The ML phylogeny, with the three superficially ovipositing pollinators found in two clades, is significantly more likely than the best phylogeny constrained to reflect a single origin of superficial oviposition (Kishino-Hasegawa-Templeton test [Felsenstein 1993], $P = .029$). Moreover, each of the two independent clades of superficially ovipositing pollinators comes out as a sister group to a cheater species (figs. 1, 2).

That both cheater species have distinct superficially ovipositing lineages as sister clades is an intriguing result, suggesting that the evolution of cheating is more likely among superficially ovipositing species. We performed a likelihood ratio test to assess the null hypothesis that cheating evolves independent of oviposition mode. Maximum likelihood estimates of instantaneous transition rates were made in TreeCalc (Milligan 1994) using the ML phylogeny shown in figure 2 and a continuous-time Markov model for evolution of traits with discrete character states (Milligan 1994; Pagel 1994, 1998). Two models of character evolution were considered. The independent change model assumed that transitions between pollination behavior states were independent of oviposition behavior and that

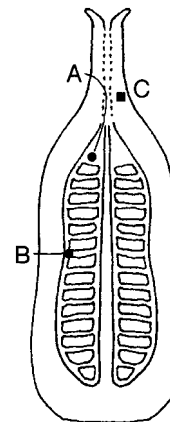


Figure 4: Vertical cross section through schematic yucca ovary, showing oviposition paths of locule (A, B) and superficially (C) ovipositing pollinator species. For further details, see text.

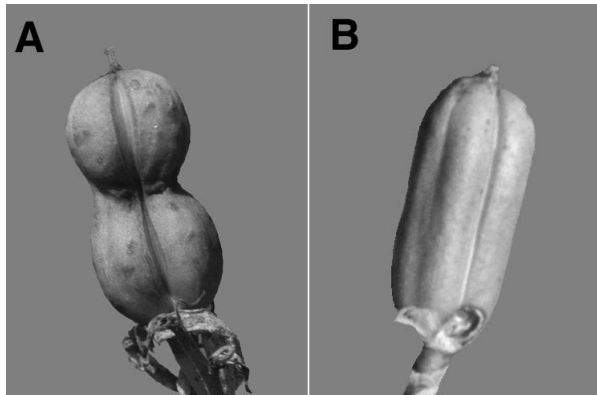


Figure 5: *Yucca* fruits with different shapes as a result of different modes of oviposition. A, *Yucca filamentosa* following oviposition by *Tegeticula yuccasella*. B, *Yucca elata* following oviposition by *Tegeticula elatella*.

transitions between oviposition behavior states were independent of pollination behavior (fig. 6A). This model was compared to a dependent change model in which transition rates between pollination behavior states were dependent on oviposition behavior and vice versa (fig. 6B). While the likelihood for the dependent rate model (fig. 6B) is greater than that for the independent rate model (fig. 6A), it is not significantly so ($P > .25$). However, with only two transitions to cheating and two transitions to superficial oviposition, failure to reject the null hypothesis may be due to lack of statistical power. In fact, the observation that the sister clades of both cheater species consist of superficially ovipositing species is perfectly consistent with the alternative hypothesis of evolutionary dependence between these characters. Under the dependent-change model, the estimated rate of change to cheating is nearly tenfold higher in superficially ovipositing pollinators than in locule-ovipositing pollinators (fig. 6B).

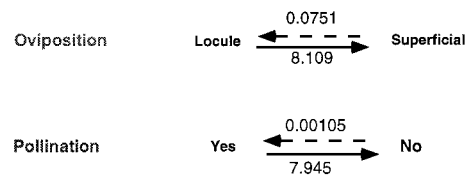
Life-History Evolution at the Pollinator-Cheater Transition

For purposes of developing hypotheses about the mechanisms that mediate the evolution of cheaters, we focus on the *Tegeticula cassandra*–*Tegeticula intermedia* pair because more data are available on the interactions between these species and their hosts and fewer trait changes are involved than in *Tegeticula corruptrix*. The sister-group relationship between *T. cassandra* and *T. intermedia* is very strong (fig. 2). Their divergence is relatively recent, estimated from a mitochondrial molecular clock as having happened 1.26 ± 0.96 million years ago (Pellmyr and Leebens-Mack 1999). In an analysis of all unique mitochondrial haplotypes from 230 moth individuals from the com-

posite ranges of the pollinator *T. cassandra*, the cheater *T. intermedia*, and their pollinating sister species *Tegeticula yuccasella*, *T. cassandra* and *T. intermedia* showed slight incomplete sorting in that one *T. cassandra* haplotype was nested with cheater haplotypes (J. Leebens-Mack and O. Pellmyr, unpublished manuscript). In contrast, a nuclear lysozyme intron marker for the same individuals indicated considerable intermixing of *T. cassandra* and *T. intermedia* alleles. This asymmetry is consistent with a model of ancestral polymorphism that is all but lost among mitochondrial markers but lingers in a nuclear marker because of the fourfold, larger effective population size for such markers (Avise 1989; Moore 1995; Palumbi and Cipriano 1998).

There are two major changes to be considered in looking at the transition from pollination to cheating. One is the loss of pollination; *T. cassandra* has fully developed tentacles and pollinates, whereas *T. intermedia* has rudimentary tentacles and does not pollinate (fig. 7). The other is the change in oviposition timing, with *T. cassandra* ovipositing into flowers on opening day (day 1), whereas *T. intermedia* uses fruit 5 d or more in age (day 6 onward; fig. 8). Meanwhile ovipositor characteristics such as tip thickness and size of a dorsal keel, which are highly divergent among yucca moths in general (Pellmyr 1999), do not differ between *T. cassandra* and *T. intermedia*, whereas both differ from *T. yuccasella* (fig. 9). It is evident that an

A. Independent change in oviposition and pollination behavior



B. Dependent change in oviposition and pollination behavior

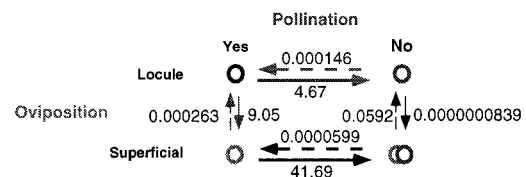


Figure 6: Maximum-likelihood estimates of instantaneous transition rates between modes of oviposition and pollinator/cheater habit. Transition rates were estimated assuming the relationships and branch lengths shown in figure 2 and a continuous-time Markov model of either independent (A) or dependent (B) character evolution. A likelihood ratio test fails to reject the four-parameter independent model of character evolution when compared to the eight-parameter dependent model of character evolution ($P > .25$).

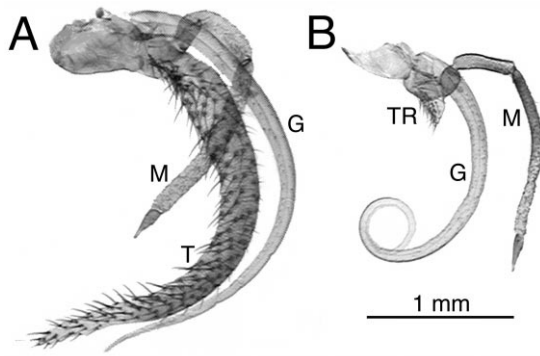


Figure 7: Maxillary palps of a pollinating yucca moth (A, *Tegeticula yuccasella*) and a cheater (B, *Tegeticula intermedia*) showing reduction of tentacle in the cheater. M = maxilla, G = galea, T = tentacle, TR = tentacle rudiment. Modified from Pellmyr (1999).

ovipositor tip that punctures the surface of a yucca ovary in flower stage to oviposit also punctures the surface of a young yucca fruit. Superficially ovipositing species thus are preadapted for cheating in this regard.

To erect a viable hypothesis for the evolution of cheating in the *T. intermedia* lineage, we must consider the costs and benefits of changes in the two traits that have evolved in this lineage: delay of oviposition and loss of pollination behavior. A stable first step to the cheater life habit is more likely if it is more beneficial than costly in terms of fitness. Analysis of correlates of ecological fitness have failed to unveil any significant benefits to be reaped from loss of pollination in the moths. Costs of pollination in terms of time budget (pollen collection and deposition) and biomass allocation (tentacles) are minor, so the cost of being a pollinator appears to be low (Pellmyr 1997). Meanwhile, cessation of pollination by a pollinator carries the cost that eggs laid in nonpollinated flowers will be lost. This is likely to be a heavy fitness cost, proportional to the frequency of pollinated flowers in the population. It could in part be reduced if the moth has the capability to assess pollination status of flowers and only oviposit in already pollinated flowers. We do not know whether *T. cassandra* can assess floral pollination status, but *T. yuccasella* makes a rough quantitative estimate of prior visitation and adjusts oviposition behavior in response (Huth and Pellmyr 1999). A behavioral response to pollination status has also been documented in a western *Tegeticula* species (Addicott and Tyre 1995). Such discrimination would reduce the cost of failure to pollinate but in turn increase potential costs in terms of mortality because of egg density-dependent selective abscission. By having to oviposit after another female, a nonpollinating female faces higher levels of flower abscission than females that can use virgin flowers because

distribution of total egg loads will be higher in flowers visited more than once (Pellmyr and Huth 1994; Huth and Pellmyr 1999). In conclusion, there are no evident fitness gains from ceasing pollination but potentially heavy costs. However, costs may be reduced if cheaters oviposit only in pollinated flowers.

Phenological delay of oviposition carries the benefit of avoiding selective flower abscission. Because abscission rate is very high, often causing the death of 60%–98% of all yucca moth eggs (calculated from Pellmyr and Huth 1994; Addicott 1998; Wilson and Addicott 1998), delayed oviposition into retained immature fruits is likely to make a large difference in frequency of egg survival. The cost of mortality because of abscission decreases with time throughout the abscission period, which lasts about 5 d in *Yucca filamentosa* (fig. 8). On the other hand, an increasing cost is the risk for competition with other larvae, particularly since larvae from eggs laid by a moth on the first day of flowering will have several days' advantage, but that cost would be reduced if females select fruits with few older larvae. Thus, whereas costs of delayed oviposition are currently uncertain, the avoidance of selective flower abscission can potentially lead to substantially higher fitness. This may argue in favor of a scenario of shifts first to oviposition in fruit, followed by loss of pollination. Such a shift in oviposition timing would only be adaptive when fruit set is ensured through the coexistence of pollinating moths.

Under some circumstances, obligate mutualisms are expected to be susceptible to cheater mutants that may sweep to fixation and drive the mutualism to extinction (Trivers 1971; Soberon Mainero and Martinez del Rio 1985; Bull and Rice 1991). A situation in which two mutualist pollinator species coexist on a host species reduces this risk, as it requires separate cheater mutants for each pollinator species to drive their shared host and consequently themselves to extinction (Compton et al. 1991; Pellmyr et al. 1996). There are at least five instances of two coexisting pollinator species on a yucca host (table 2). Available data

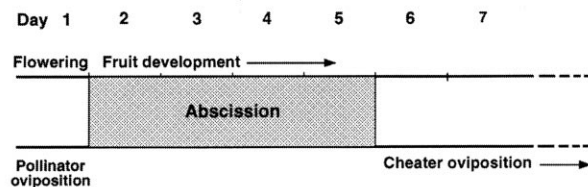


Figure 8: Temporal diagram of oviposition time on yucca flowers by *Tegeticula yuccasella* and *Tegeticula cassandra* (pollinators) and *Tegeticula intermedia* (cheater) on *Yucca filamentosa*.

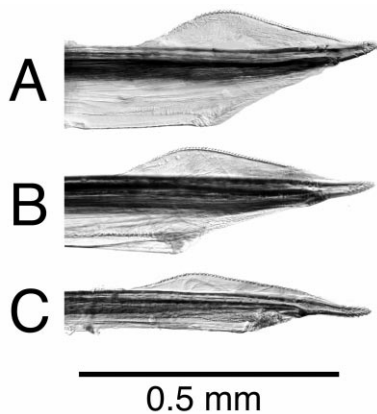


Figure 9: Ovipositor tips in left lateral view of *Tegeticula cassandra*, *Tegeticula intermedia*, and *Tegeticula yuccasella*. Note angular differences at tip. Modified from Pellmyr (1999).

suggest that one of those cases of coexistence, *T. cassandra* and *T. yuccasella*, may have been the site of origin of the early cheater, *T. intermedia*. The pollinator *T. cassandra* occurs exclusively in Florida and southeast Georgia (fig. 1; K. Segraves and D. Marr, unpublished data), a region that was connected to an area with a similar biota to the west from late Pliocene to mid-Pleistocene but has constituted a habitat island since that time (Webb 1990; Webb and Opdyke 1995; Walker and Avise 1998). Meanwhile, *T. yuccasella* is the pollinator of yuccas in all other portions of eastern and central United States. The two species now coexist in northern parts of Florida (Pellmyr 1999). The locule-ovipositing *T. yuccasella* can only oviposit into the youngest flowers because the closure of the intralocular space between wall and ovules where the egg is laid and ovary wall hardening restrict successful oviposition in older flowers. Meanwhile, the superficially ovipositing *T. cassandra*, while normally ovipositing into first-day flowers, also can oviposit into an older ovary. If *T. cassandra* oviposits side by side with *T. yuccasella*, it will suffer not only its ancestral mortality factor but also mortality because of the density-dependent flower abscission triggered by *T. yuccasella*. If *T. cassandra* instead oviposits into young fruits, then the elevated risk of mortality to egg-based selective flower abscission will decline quickly because a large proportion of all fruits that will abscise fall on day 2 and is >95% complete by day 5. Meanwhile, the risk of resource competition with older, larger *T. yuccasella* larvae is limited because of the density-dependent abscission mechanism triggered by *T. yuccasella*, which limits the number of *T. yuccasella* larvae and virtually guarantees that 65%–75% of the seeds will be available to a moth that can outwait the abscission period. *Tegeticula cassandra* can po-

tentially further increase its gains by selecting and ovipositing into fruits with few *T. yuccasella* larvae. The shift onto fruit may have been further facilitated by the relative phenology of coexisting *T. yuccasella* and *T. cassandra*. In areas for which we have preliminary data, the emergence period of *T. cassandra* is later than *T. yuccasella*, thus they are more likely to encounter young fruits. Addicott (1998) documented a similar phenological pattern in another pair of coexisting species, with the superficially ovipositing *Tegeticula superficiella* being late relative to the locule-ovipositing *Tegeticula altiplanella*. Related to this, behavioral plasticity has been reported in *Tegeticula maculata*, where Aker and Udovic (1981) showed how females that emerge at the tail of the flowering season attempt, likely in vain in that case, to oviposit into young host fruits.

Reversal of Mutualism as a Secondary Consequence of a Niche Shift

The phylogenetic and ecological data support the hypothesis that loss of pollination may have evolved secondarily to oviposition into fruit in the lineages that gave rise to cheaters. While direct measurements of fitness costs of pollination are needed, the available ecological correlates suggest that primary loss of pollination rarely would be a successful strategy in pollinator moths. If instead a phenological shift to later oviposition occurs first, pollination behavior and associated structural specializations become redundant. That coexistence of mutualist moths can allow evolutionary transition to cheating is not new (Pellmyr et al. 1996), but it is becoming apparent that the evolution of fruit-ovipositing cheaters may actually be facilitated by indirect effects between the two mutualists. The locule-ovipositing species indirectly cause increased egg mortality in superficially ovipositing pollinators whenever they come into coexistence because of the triggered selective abscission. This lowers the cost threshold to evolution of alternative life habits, including avoidance of flowers containing allospecific eggs or phenological shift to avoid the abscission mechanism. Whenever the latter occurs, retention of pollination behavior would be fitness neutral or negative.

Tegeticula corruptrix, the late cheater, differs from *Tegeticula intermedia* in having evolved further phenological delay to oviposit into full-sized fruit and oviposition into seeds. The proposed hypothesis for the origin of cheating is applicable in this case as well, given that the two traits are autapomorphies derived from a state of superficial oviposition. Available intraspecific phylogenetic information is insufficient to resolve the sequence of the two transitions. Resolution of this issue may be easier once the original host is identified through phylogeographic studies: *T. corruptrix* now has the widest host range of any western

Table 2: Recorded instances of coexistence between two yucca moth pollinators on yuccas

Moth species	Host yucca	Geographic area	Source
<i>Tegeticula yuccasella</i> / <i>Tegeticula cassandra</i>	<i>Yucca filamentosa</i>	North central Florida	Pellmyr 1999
<i>Tegeticula altiplanella</i> / <i>Tegeticula superficiella</i>	<i>Yucca angustissima</i> var. <i>kanabensis</i>	Southwest Utah	Tyre and Addicott 1993; Pellmyr 1999
<i>Tegeticula maderae</i> / <i>Parategeticula pollenifera</i>	<i>Yucca schottii</i>	Southeast Arizona	Davis 1967; Powell 1984
<i>Tegeticula rostratella</i> / <i>Parategeticula tzoyatlilla</i>	<i>Yucca rostrata</i>	Mapimi region of Chihuahuan Desert	Pellmyr 1999; Pellmyr and Balcázar-Lara 2000
<i>Tegeticula</i> sp. 1/ <i>Tegeticula</i> sp. 2	<i>Yucca filifera</i>	Southern Chihuahuan Desert	Villavicencio and Pérez-Escandón 1995

North American *Tegeticula*, coexisting with at least six pollinator species, and the host on which the radiation from pollinator to cheater took place may be any one of those species or a Mexican species.

Why Are There Only Young Species of Cheater Yucca Moths?

The pollinator life habit had evolved at least 40 million years ago, yet the two cheater species are estimated to have diverged from their respective pollinating ancestors about 1.25 ± 0.95 million years ago (Pellmyr and Leebens-Mack 1999). In addition to the possibility that unknown species of older age may exist in Mexico, where about half of all yucca diversity resides (Axelrod 1979a, 1979b; Matuda and Piña Lujan 1980; Clary 1997; García-Mendoza 1998) but the moth fauna is poorly known, there are at least three other hypotheses.

First, it is possible that cheater lineages may be more susceptible to extinction than pollinators. Both pollinators and cheaters need yucca seeds for larval development, and this resource is patchy and highly unpredictable because flowering frequency varies greatly between years and sites (McKelvey 1938–1947; Smith and Ludwig 1978; Fuller 1990; Addicott 1998). Pollinators that locate flowering hosts can always create larval substrate by pollination, whereas cheaters depend on pollinators for fruit production and thus are more likely to fail to find a suitable food patch. Preliminary studies suggest that small host patches are less likely to have resident cheaters (O. Pellmyr, unpublished data), a pattern consistent with occasional failure of fruit availability.

Second, both extant cheaters evolved from superficially ovipositing pollinators, and adaptive radiation from a locule-pollinating species may be far less probable because it requires ovipositor modification in addition to phenological shift. This begs the question of *Parategeticula*, however, which is functionally similar to superficially ovipositing *Tegeticula* species. Eggs are laid near the ovary, and

the larva bores into the young fruit, avoiding selective abscission (Powell 1984). This is the universal condition in the genus; thus pollinators with the type of host interaction inferred to have been critical to the origin of cheaters have been present since the origin of the mutualism (fig. 2). Two species of this almost exclusively Mexican genus coexist with locule ovipositing *Tegeticula* (table 2), and additional surveys in that part of the host range are needed to tell whether cheating *Parategeticula* species exist.

Third, the relatively recent, rapid radiation of species within the *Tegeticula yuccasella* complex (fig. 2; Pellmyr and Leebens-Mack 1999) particularly onto capsular-fruited yuccas show indications of elevated levels of host shifting, thus increasing the probability of pollinator coexistence. At least three of the five known instances of pollinator coexistence (table 2) involve at least one species more recent than this explosion, and thus coexistence must postdate this radiation. This hypothesis can be formally tested once a plant phylogeny becomes available.

Conclusion

Schluter (2000) asked in the introduction to this symposium whether ecological factors commonly mediate adaptive radiation. When applied to obligate mutualists, the answer remains uncertain for lack of needed data. For example, associations such as those between yuccas and yucca moths should be good candidates for pollinator-driven host diversification, but the lack of a robust plant phylogeny prevents us from testing such hypotheses at this time. Testing hypotheses of adaptive radiation in the moths by reversal of mutualism is possible, however, and the phylogenetic and ecological data point to quite specific circumstances facilitating the evolution of cheaters. This is to some extent an inevitable property of any one model system of complex, interacting organisms (Herre 1999). It may nonetheless be of use in comparative studies because reversals of obligate mutualism appear to be relatively uncommon and thus perhaps constrained by common fac-

tors. This analysis suggests, for example, that preadaptations have played a role in facilitating diversification, that mutualist species coexistence can make reversal more probable, and that coexistence directly or indirectly must carry fitness consequences for at least one of the species. If broadly applicable, we would predict that mutualists with intermediate ability of host shifting—that is, limited cospeciation with the host clade—may have a higher probability of evolving cheater habits than a strictly cospeciating lineage because the probability of mutualist coexistence is higher. This may be applicable to fig–fig wasp mutualisms, where a single documented reversal of mutualism involves wasp coexistence (Galil and Eisikowitch 1969; Compton et al. 1991; Wiebes 1994). Meanwhile, concordant phylogenies at various taxonomic levels indicate that host switching and mutualist coexistence are rare (Herre et al. 1996; but see Michaloud et al. 1996; Kerdelhue et al. 1997 for exceptions). Among other types of associations, parasitic fungi derived from lichen-forming ancestors (Winka et al. 1998) represent a scenario where loss of mutualism may have involved mutualist coexistence following horizontal transfer, that is, host shifting. Similarly, secondary prokaryotic endosymbionts of insects result from host shifting, but whether their relationship with the novel host remains a mutualism or not is unclear (Moran and Telang 1998).

In the specific case of evolution of a suite of nonpollinating yucca moths, such seemingly disparate ecological features as density-dependent selective fruit abscission, the versatility of a given ovipositor morphology, and developmental rates leading to offset emergence phenologies are traits of the plants and moths that may have facilitated the evolution of cheaters. The loss of pollination, which dramatically reverses the interaction between yucca and yucca moth from mutualism to antagonism, may be little more than an adaptively neutral secondary consequence of an adaptive radiation in the moths to utilize a previously inaccessible resource.

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