

Facultative non-mutualistic behaviour by an “Obligate” mutualist: “Cheating” by Yucca moths

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Abstract. The interaction between yucca moths (*Tegeticula* spp., Incurvariidae) and yuccas (*Yucca* spp., Agavaceae) is an obligate pollination/seed predation mutualism in which adult female yucca moths pollinate yuccas, and yucca moth larvae feed on yucca seeds. In this paper we document that individual yucca moths, which are capable of acting as mutualists, facultatively “cheat” by ovipositing in yucca pistils without attempting to transfer pollen. Additionally, a high proportion of flowers are unlikely to receive pollen even when pollination is attempted, because many yucca moths carry little or no pollen. The probability of occurrence of non-mutualistic behaviour is not affected by the amount of pollen a moth carries: moths with full pollen loads are just as likely to act non-mutualistically as moths carrying little or no pollen. We propose four hypotheses that could explain facultative non-mutualistic behaviour in yucca moths.

Key words: Cheating – Mutualism – Pollination – Yuccas – Yucca moths

Many mutualistic systems include species or individuals that utilize mutualistic resources or services without providing any benefits in return (Boucher et al. 1982). “Aprovechados” (sensu Soberon and Martinez 1985) are non-mutualistic species that take advantage of a mutualistic association. For example, some bees and birds utilize floral nectar without transferring pollen (Inouye 1983). “Cheaters” (sensu Soberon and Martinez 1985) are non-mutualistic individuals within a mutualistic species. For example, individuals of some plants produce little or no nectar but are still visited by pollinators (Feinsinger 1983).

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Yucca moths (*Tegeticula* spp., Incurvariidae) and yuccas (*Yucca* spp., Agavaceae) interact in an obligate mutualism (Riley 1892; Powell and Mackie 1966; Davis 1967). Yuccas rely exclusively on yucca moths for the transfer of pollen (but see Arrebola-Nacle 1991). Yucca moths gather a ball of pollen in specialized appendages known as maxillary tentacles (Riley 1892; Davis 1967), and actively transfer pollen to the stigmas of receptive flowers (Riley 1892). In return, yuccas are the only source of food for yucca moths, which lay their eggs on, or in, the ovaries of yuccas (Riley 1892). The developing yucca moth larvae eat about 15% of the developing seeds (Keeley et al. 1984; Addicott 1986).

In this paper we demonstrate that individual yucca moths facultatively “cheat” by ovipositing in yucca pistils without attempting to transfer pollen. We also demonstrate that many yucca moths carry little or no pollen resulting in a failure to transfer pollen, even though they attempt to pollinate.

Materials and methods

We observed the behaviour of *Tegeticula yuccasella* on *Yucca kanabensis* during the flowering season of 1991 at a study site 7.4 km south of US Highway 89 on the road to Coral Pink Sand Dunes State Park, Kane County, Utah, USA (112° 40' 45" W, 37° 7' 30" N 1800 m elevation).

Because *Tegeticula yuccasella* is actually a complex of relatively hostspecific species (Addicott unpublished data), we designate our study organism by its host plant and oviposition behaviour. Our observations relate to one of three members of the *T. yuccasella* complex that interact with *Y. kanabensis* in southwestern Utah. The moths we studied are “deeps”, as they lay their eggs in the intralocular cavity in the pistil of fresh flowers. The other two species are “shallows”, which oviposit in the carpel wall of fresh flowers, and “secondaries”, which oviposit into seeds of developing fruit. There is no possibility that our observations were made on either “shallow” or “secondary” moths: “shallows” do not occur at our study site, although they occur at study sites about 5 km away; and, although “secondaries” occur at our study site, their flight season began well after our observations were complete.

We observed the oviposition behaviour of “deeps” on 8 nights between June 8 and July 3, 1991. On each night we began our

observations at dusk (ca. 2100 h), when the moths became active, and continued our observations until approximately midnight, when the rate of occurrence of pollination and oviposition events diminished. In order to facilitate observation of moths within flowers, we occasionally removed one or two petals from flowers. We used headlamps covered with a red filter to illuminate the moths, because light from unfiltered headlamps noticeably affects the behaviour of moths (Kingsolver 1984; personal observations). We discarded any observations where a moth was noticeably disturbed either by another insect or by us.

We conducted sequence sampling (Altmann 1974; Lehner 1979) of the behaviour of individual female moths, recording the time at which a moth ended one behaviour and initiated the next. We began our observations with the entry of a moth into a flower and continued until one of the following events occurred: (1) the moth left the inflorescence; (2) we lost sight of it within an inflorescence; (3) we were unsure which of many moths within a flower was our focal animal; (4) the moth entered into prolonged copulation. We chose moths for observation haphazardly. Because of the small size of the moths, we were unable to mark moths without inflicting significant damage to them.

For each moth, we recorded the presence or absence of a pollen ball in its maxillary tentacles. A pollen ball is visible as a yellowish mass on the ventral surface of the head. Inspection of female yucca moths under a dissecting microscope shows that moths with no pollen ball visible to the naked eye carry little or no pollen (personal observations).

We refer to the oviposition, pollination, and movement behaviours of a single moth in a single flower as an oviposition/pollination bout (Lehner 1979). We observed a total of 56 oviposition/pollination bouts by a total of 37 different moths. We classified 27 bouts as complete, in that we observed the first oviposition in a flower by a moth. We observed 2–6 consecutive, complete bouts by 7 different moths. We were able to determine the pollen load carried by a moth for 32 bouts.

Results

In the context of the yucca-yucca moth interaction, the occurrence of non-mutualistic behaviour involves the failure of yucca moths to transfer pollen while ovipositing in flowers or fruit (Aker and Udovic 1981). Moths exhibited non-mutualistic behaviour in 25.6% of all bouts (Table 1). Furthermore, in 46.2% of bouts moths were carrying no detectable pollen, and were therefore ineffective in transferring pollen (Table 1). Overall, 59% of bouts were ineffective in pollen transfer, either because no pollination was attempted or because no pollen was carried, or both (Table 1).

Bouts in which no pollination occurred had less than half the number of oviposition events than bouts with at least one attempt to pollinate (Mann-Whitney $U = 21.0$, $n = 27$, $p = 0.001$) (Fig. 1a). This result suggests the

Table 1. Contingency table comparing pollination behaviour with the presence/absence of a pollen load. This table includes both complete bouts, and incomplete bouts that had at least one pollination attempt

		Pollination Attempted?	
		No	Yes
Pollen carried?	No	5	13
	Yes	5	16

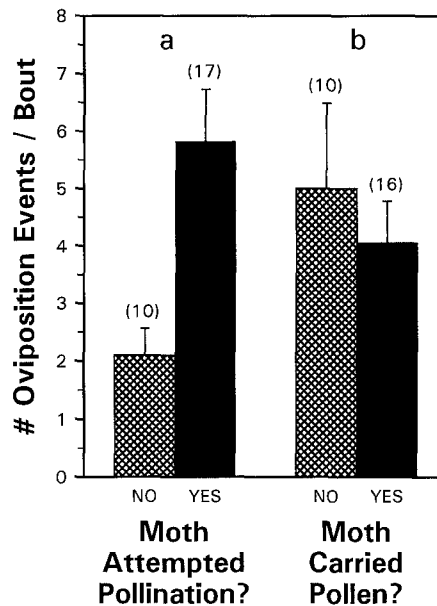


Fig. 1. Mean number of ovipositions per bout for complete bouts for (a) moths that did or did not attempt to pollinate the flower they oviposited in, and (b) moths that did or did not have visible amounts of pollen in their maxillary tentacles. Error bars represent standard errors, and numbers in parentheses represent sample size

hypothesis that failure to attempt to pollinate is simply an artifact of short bouts. However, we reject this hypothesis, because in bouts where pollination occurred at least once, the first pollination event occurred after the first or second oviposition event in 16 out of 17 cases, and never later than the third oviposition. Therefore, it is highly unlikely that the apparently non-mutualistic behaviour is an artifact of short bouts.

One possible explanation for the observed non-mutualistic behaviour is that moths which lack pollen do not attempt to pollinate. However, there was no relationship between the pollen load carried by a moth and the frequency of failure to attempt to transfer pollen ($\chi^2 = 0.08$, $p = 0.77$, $df = 1$, $n = 39$) (Table 1). Similarly, in bouts (both complete and incomplete) where at least one pollination attempt occurred, pollen load had no effect on the number of oviposition events in a bout (Mann-Whitney $U = 72.5$, $n = 26$, $p = 0.69$) (Fig. 1b). Therefore, oviposition/pollination behaviour appears to be independent of whether or not a female moth is carrying pollen.

Discussion

A number of aspects of our observations deserve emphasis. First, contrary to previous assumptions (Aker and Udovic 1981), yucca moths are not particularly efficient pollinators of yuccas. In more than half of the bouts, moths transferred no pollen, either because they were carrying none, or because they failed to attempt to pollinate. These observations are consistent with observations that between 5% and 25% of flowers do not receive pollen even though they have received ovipositions (Addicott unpublished data).

Second, the failure of moths to carry pollen could result from two distinct processes. Individual moths may choose not to collect pollen, even when pollen is available. Alternatively, pollen may simply be in short supply: there may be too many moths attempting to collect too little pollen. Although we cannot differentiate between these alternatives with the present data set, pollen limitation is probably not the sole cause. We saw very few attempts to collect pollen, despite the fact that many moths were not carrying pollen, and despite the fact that pollen was always available early each evening as fresh flowers opened.

Third, the failure to attempt to transfer pollen, particularly when a moth is carrying pollen, probably represents facultative "cheating" (sensu Soberon and Martinez 1985) by individuals of an obligate mutualistic species. This conclusion assumes that as more moths pollinate a flower the benefit to the plant increases. Under this assumption, moths that fail to pollinate increase the cost to the plant by laying more eggs without increasing the benefit, and therefore failure to pollinate can be considered cheating. We have no quantitative data on the validity of this assumption, but flowers sometimes fail to develop all ovules possibly indicating that insufficient pollen was transferred to the flower. Additionally, pollen from a variety of moths will increase the likelihood of outcrossing.

There are four hypotheses that could explain facultative cheating in yucca moths. First, bouts where pollination did not occur could be artifacts of bouts that were shortened by an outside influence. Second, moths without pollen may be more likely to fail to attempt to pollinate than moths with pollen. Third, the behaviour represents pollen conservation, in which case moths would fail to attempt to transfer pollen only in previously visited flowers that had already received sufficient pollen for fertilization of all ovules. Finally, moths may be following a mixed evolutionarily stable strategy where moths behave non-mutualistically in some fixed proportion of bouts. The first two hypotheses are inconsistent with our current observations. The remaining two hypotheses will be tested using future observations.

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