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Pollination ecology of *Yucca elata*

An experimental study of a mutualistic association

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Abstract. The pollination biology of a population of 250 *Yucca elata* (Liliaceae) plants was studied in southern New Mexico. *Yucca elata* and the prodoxid yucca moth *Tegeticula yuccasella* have a mutualistic association that is essential for the successful sexual reproduction of both species. However, a wide range of other invertebrate species visit flowers during the day and at night. Our aim was to quantify the role of yucca moths and other invertebrate visitors in pollination and fruit set, using manipulative field experiments. Inflorescences were bagged during the day or night ($N=12$ inflorescences) to restrict flower visitors to either nocturnal or diurnal groups. Yucca moths were active exclusively nocturnally during the flowering period and thus did not visit inflorescences that were unbagged during the day. None of the 4022 flowers exposed only to diurnal visitors set fruit, whereas 4.6% of the 4974 flowers exposed only to nocturnal visitors (including yucca moths) produced mature fruit. The proportion of flowers producing fruit in the latter treatment was not significantly different from unbagged control inflorescences. In a series of experimental manipulations we also determined that: (1) flowers opened at dusk and were open for two days on average, but were only receptive to pollen on the first night of opening; (2) pollen must be pushed down the stigmatic tube to affect pollination; and (3) most plants require out-cross pollination to produce fruit. The combination of these results strongly suggests that yucca moths are the only species affecting pollination in *Y. elata*, and that if another species was to affect pollination, it would be a rare event.

Key words: *Yucca elata* – *Tegeticula yuccasella* – Mutualism – Pollination – Fruit set

The association between yucca plants (Liliaceae) and yucca moths (*Tegeticula* and *Parategeticula:* Prodoxidae) was first documented over a century ago and still stands as one of the classic cases of obligate monophilic mutualism (Baker 1986). In this system, the yucca flower is deliberately pollinated by a female yucca moth after she has laid an egg in the ovary of the flower. As a result, yucca flowers are fertilized and have the potential to produce seeds, while the larvae of the moth develop inside the seed pod where they feed on some of the seeds. Both the moth and the yucca plant are reliant on each other for the realisation of sexual reproduction. Engelmann (1872) and Riley (1872) were the first to publish an account of the pollination of *Yucca* by yucca moths. They observed that flowers were pollinated solely by yucca moths, citing evidence that the structure of the flower prevented self-fertilization, and that insect visitors other than yucca moths did not behave in a way that would lead to pollination (Riley 1873a). Some debate ensued over the necessity of yucca moths for pollination of yucca flowers (Barstow 1872a, b; Milligan 1874; Riley 1892, 1893) following reports of fruit production from flowers that were bagged before anthesis to exclude moths. These cases appear to be restricted to the species *Y. whipplei* and *Y. aliofolia* (Riley 1893; Galil 1973). For most species of *Yucca*, pollination by vectors other than yucca moths appears to be rare (Aker and Udovic 1981; Baker 1986), and the necessity of yucca moths for most of the pollination and fruit production in yuccas is undisputed. However, the role of other invertebrate visitors in pollination and fruit set of *Yucca* flowers is unclear (Wimber 1958; Powell and Mackie 1966; Aker and Udovic 1981; Baker 1986).

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Uncertainty over the pollination of *Yucca* flowers by vectors other than yucca moths stems from a number of possible sources. First, there are some records of self-compatibility of yucca flowers resulting in fruit production in the absence of a pollinating vector (Milligan 1874; McKelvey 1947; Wimber 1958; Powell and Mackie 1966; Galil 1973; Baker 1986). Second, a number of authors have recorded fruits that do not contain yucca-moth larvae, and fruits that do not have the deformities characteristic of fruits that have been affected by yucca moths (Trelease 1893; Rau 1945; Webber 1953). One interpretation to account for these fruits is that pollination is occurring without yucca moths. A third cause for uncertainty about the exclusive role of yucca moths is the multitude of invertebrates (and vertebrates) that visit *Yucca* inflorescences during the day and night (Riley 1873b; Coquillett 1893; Powell and Mackie 1966; Wiggins 1980; Powell 1984 pp 46–50). Some of these flower visitors may be responsible for fruit set when it apparently occurs without yucca moths, or when fruit have no larvae in them. There have been no attempts to quantify the role of various flower visitors in the pollination of yuccas. Thus, the first aim of this study was to document invertebrate visitors to *Y. elata* Engelm., and to experimentally examine the potential role of flower visitors in pollination. Our second aim was to describe the pollination behavior of *T. yuccasella,* and the pollination ecology of *Y. elata,* neither of which has been studied since brief notes by Trelease (1893).

Yucca elata is widely distributed in western Texas, southern New Mexico, southern Arizona, and the northern states of Mexico (Campbell and Keller 1932). The pollination ecology of a number of species of *Yucca* has been studied in detail (*Y. filamentosa* – Riley 1892; Trelease 1893; Rau 1945; *Y. glauca* – Kingsolver 1984; *Y. schotti* – Powell 1984; and *Y. whipplei* – Powell and Mackie 1966; Aker and Udovic 1981; Udovic 1981; Aker 1982), but *Y. elata* is relatively little studied compared with other members of the infra-generic section Chaenocarpa (Baker 1986). *Yucca elata* is closely allied to *Y. filamentosa* and *Y. glauca,* and its pollination ecology is likely to be similar to these species. Other studies of the biology of *Y. elata* deal with aspects of growth, reproduction, and fruit production (Campbell and Keller 1932; Smith and Ludwig 1976, 1978; Laslei and Ludwig 1985). The morphology of the yucca moths that pollinate *Y. elata* in southern New Mexico has also been studied (Trelease 1893; Miles 1983).

Materials and methods

The study was conducted during one flowering season (May–June 1990) of a *Y. elata* population 2 km east of the New Mexico State University, Las Cruces, on the southwest side of Tortugas Mountain (106°42′ W, 32°17′ N). The study site was located on a sandy ridge-crest flanked by drainage channels. The surrounding areas had relatively coarse-grained gravelly soils compared with the ridge-crest, and the density of *Y. elata* was much higher on the sandy ridge crest than in the surrounding area. The study site of 2.3 ha supported approximately 250 *Y. elata* plants which produced about 500 inflorescences in the 1990 season. In this study we define an "individual" as a unit comprising a caudex (stem) and a rosette (crown). A "clone" was defined as a clump of individuals that were contiguous in space and at least 3 m from another clump (clone). A clone had from 1–10 individual *Y. elata* caudexes and rosettes. Individuals produce only one inflorescence, but not all individuals produced an inflorescence.

In mid May, when flowering stems were developing, 100 inflorescences were chosen and randomly assigned to the various bagging and hand-pollination experiments. The first inflorescence chosen was at the approximate center of the population. Thereafter, inflorescences were chosen by moving a random distance (in m) and a random direction (compass bearing) to the next clone. Flowering began on May 14, and finished by June 24.

We documented the invertebrate visitors to *Y. elata* inflorescences by bagging and collecting five inflorescences during the day and five inflorescences during the night, at three times during the flowering period. Collections were made at 1100 h and 2200 h on May 17 (night 4 of flowering), May 27 (night 14), and June 7 (night 25). We selected inflorescences of an average size, about midway through flowering, 20–700 m away from the main study site. These inflorescences were rapidly covered with large plastic garbage bags, sealed, cut from the rosette, and placed in cold storage. The invertebrates on each inflorescence were counted and identified to species where possible. We also collected large mobile insects such as wasps, that evaded our bagging technique by sweep-netting at inflorescences during the day and night.

Pollination and oviposition behavior of *T. yuccasella* was quantified by observations of individual flowers and moths. Observations began before yucca moths began to fly at about 2030 h. A small pocket flashlight, shining obliquely onto an inflorescence, was used to observe moths. Although we did not determine the effect of the light on the moths' behavior, we were confident that the disturbance to the moths caused by our presence was minimal. Records were kept of the number of moths visiting, the duration of visits, the number of ovipositions made, the number of times a flower was pollinated, and the number of different female moths that oviposited and pollinated a flower.

Four manipulative experiments were conducted to study the pollination ecology of *Y. elata.*

1. Nocturnal and diurnal flower visitors. We used nylon mesh bags (1.5 × 0.5 m) to experimentally limit insect visitors to inflorescences. Observations during the first week of flowering suggested that *T. yuccasella* was active only at night. We attempted to prevent *T. yuccasella* from pollinating flowers on 12 inflorescences by manually guarding the inflorescences. This technique proved ineffective because moths were too numerous and too quick at pollinating. Therefore, we manipulated the time of day that invertebrates could access inflorescences. Inflorescences left unbagged during the night (bagged during the day) only received nocturnal visitors (including *T. yuccasella*), whereas inflorescences left unbagged during the day (bagged during the night) only received diurnal visitors. Diurnal treatments were unlikely to be visited by *T. yucasella.* We reasoned that fruit produced in either treatment could be examined for yucca moth larvae or constrictions indicative of oviposition by yucca moths. However, we were also aware that a fruit may develop after being pollinated by a yucca moth, but not contain a larvae (Addicott 1986), thereby appearing not to have been pollinated by *Tegeticula.*

Six clones, each with at least two inflorescences, were assigned to the bagging study. Two inflorescences on a clone ($N = 12$) were bagged either during the day or during the night throughout their flowering period, and a third inflorescence when present, was used as an unbagged control. The diurnal treatment was open to flower visitors from 0800–1800 h (two hours after sunrise until two hours before sunset). The nocturnal treatment was open to flower visitors from 2000–0600 h (sunset to sunrise).

After all flowers on an inflorescence had finished flowering, the bags were removed. The number of mature fruits and the total number of flowers were counted on each treatment and control inflorescence (the number of flowers was estimated by counting the pedicels which remain after the flowers have abscised).

2. Pollen position on stigma. We used two treatments to test the hypothesis that invertebrate visitors other than *T. yuccasella* may pollinate *Y. elata* by incidentally leaving pollen on top of the stigmatic tube. Fifteen flower buds that were to open on the same night (night 20) on each of three inflorescences were chosen. Three treatments of five flowers each, were performed on each inflorescence: (a) a control group which was untouched; (b) a group in which pollen was scraped across the top of the stigmatic tube, simulating an insect brushing pollen off its body onto the stigma; and (c) a group in which pollen was pushed down the stigmatic tube to a depth of 2–3 mm. Inflorescences were bagged after the hand pollinations and the number of mature fruit resulting from these pollinations were counted.

In all hand pollination experiments, we collected pollen from anthesis flowers of at least three separate (non-clonal) inflorescences 50–500 m from the study population. The flowers were placed in a plastic bag and mixed before being selected. Pollen was scraped from two anthers of two different flowers with a fine pair of forceps or a fine lachrymal probe, and gently pushed into the opening of the stigmatic tube, or scraped onto the stigma with the probe or fine paint brush.

3. Stigma receptivity. Flowers were hand pollinated at different times after anthesis to determine the duration of receptivity of stigmas to pollination. Twentyfive buds on five inflorescences that were all due to open on the same evening (night 14) were chosen, and five flowers on each inflorescence were hand pollinated with out-cross pollen at each of the following times: (a) anthesis (≈2000 h, May 27); (b) four h after anthesis (≈2400 h); (c) 10 h after anthesis (≈0600 h, May 28); (d) 24 h after anthesis (≈1930 h, May 28); and (e) 48 h after anthesis (≈1930 h, May 29). Inflorescences were bagged before and after treatment, and the number of mature fruit that developed were counted.

4. Breeding system. The breeding system of *Y. elata* was determined by a series of hand pollination treatments. Five treatments were executed on 25 buds of each of five separate clonal inflorescences, all of which were to open on the same night (night 16): (a) an untreated control; (b) an out-cross treatment in which flowers were pollinated with pollen from flowers on other clones; (c) a clonal-cross treatment in which pollen from flowers of another inflorescence on the same clone was used; (d) a geitonogamous treatment in which pollen from flowers of the same inflorescence was used; and (e) a self-pollination treatment in which the flower's own pollen was used. Inflorescences were bagged after the hand pollinations and the number of mature fruit that developed were counted.

The results of hand-pollinations were recorded as the proportion of flowers pollinated that developed into mature fruit. These data were arcsine transformed before being analyzed with analyses of variance. A Cochran's test was used to ensure that the assumption of homogeneity of variances in the ANOVA tests was not violated.

Results

Invertebrate visitors to Yucca elata

Invertebrate taxa collected from *Y. elata* inflorescences by bagging and sweep samples are listed in Table 1. There were more taxa of invertebrates and individuals visiting inflorescences during the day than at night. Some of the diurnal visitors were large and may have been capable of transporting pollen between flowers, if the pollen were to stick to the insect. For example, sphecid wasps (e.g., *Bembix* spp.), vespid wasps (e.g., *Stenodynerus apache* Bohart), pompilid wasps (e.g., *Pepsis formosa* (Say)), and cerambycid beetles (*Tragidion armatum* Lec.) were frequently observed crawling through the flowers during the day. Similarly, some of the nocturnal visitors apart from yucca moths were potentially capable of incidental transfer of pollen from anther to stigma. These include tettigoniid katydids (*Eremopedes scudderi* Cock.) and noctuiid moths.

Behavior of Tegeticula yuccasella

During the day *T. yuccasella* moths were observed motionless, head toward the base of the ovary in old flowers (> 1 day) that had partially closed. None of the moths observed in flowers during the day was active. Examination of female moths ($N=6$) collected from flowers at three times during the day (0700, 1130 and 1500 h)

Table 1. Invertebrates visiting *Y. elata* inflorescences during the day and at night, during the flowering period of a population near Las Cruces, New Mexico. The totals for day and night are from 15 inflorescences sampled at the beginning, middle and end of the flowering season (May 17 to June 24 – see Methods). Plus signs after a number indicate the possibility that one or two more species may be present in the samples

Order	Day		Night	
	species	individuals	species	individuals
Lepidoptera	3	52	3	19
Tegeticula yuccasella	1	37	1	15
Prodoxus quinquenpunctellis	1	14	1	2
Homoptera[a]	2	–	2	–
Hymenoptera	12^+	93	7^+	245
Diptera	9^+	230	6^+	184
Coleoptera	18^+	216	9^+	35
Hemiptera	5	35	4	10
Thysanoptera[b]	2	–	1	–
Neuroptera	1	5	2	24
Araneida	2	31	2	7
Orthoptera	2	2	1	2
Totals	56^+	663	37^+	526

[a] One species of Aphididae was abundant on flowers late during the flowering period but was too numerous to count

[b] Two species of thrips were very abundant in flowers but were too numerous to count

Table 2. Results of bagging experiment to manipulate diurnal and nocturnal visitors to *Y. elata* flowers (means ± 2 SE and extremes). Inflorescences were open to invertebrate visitors either during the day (0800–1800 h) or at night (2000–0600 h). Control inflorescences were exposed to both diurnal and nocturnal invertebrate visitors and were on the same clone as the treatment inflorescences

	Diurnal access ($n=12$)	Diurnal control ($n=5$)	Nocturnal access ($n=12$)	Nocturnal control ($n=3$)
No. flowers	335.2 ± 64.6 (210–562)	332.4 ± 66.7 (179–529)	414.5 ± 84.6 (114–672)	393.7 ± 315.6 (212–708)
No. fruit	0.0 ± 0.0	19.6 ± 3.5 (14–33)	18.3 ± 5.0 (2–35)	15.3 ± 6.0 (11–21)
% fruit	0.0 ± 0.0	6.4 ± 0.8 (3.2–7.8)	4.6 ± 1.1 (0.5–7.1)	4.6 ± 2.0 (3.1–7.2)

showed that 33% had pollen in their mouthparts. About 15 min after sunset, moths became active in the flowers that had served as their diurnal retreats, but they did not began flying until 40 min after sunset (2040 h) when it was dark. Peak yucca moth activity occurred in the first hour after dark and tapered off thereafter. The mean air temperature at 2100 h (around the time most of the observations were made) was 28.0 ± 3.1° C ($\bar{x} \pm$ SD; $N=34$).

Male yucca moths flew to an inflorescence, ran rapidly around the flowers with no obvious pattern, and often departed within a few minutes, having searched many flowers. If a female was encountered the male would attempt copulation. Often two or three males were found crowded into a flower in which a female was copulating with another male. Female moths arriving at a flower would rapidly circle the stamens and ovary near the base for 5–25 s ($\bar{x}=10.7$, $N=15$). Three females of 34 observed left flowers after circling the base of the stamens, without inserting their ovipositor into the flower or pollinating. After circling the base of the ovary, females aligned themselves with the long axis of the ovary and inserted their ovipositors. Sometimes a female would probe around with her ovipositor in different places in the ovary before appearing to settle down. We assumed oviposition to have occurred when a female had inserted her ovipositor deep into an ovary and remained stationary for a while. We only recorded this behavior as oviposition if the moth pollinated the flower immediately afterward, and we did not dissect flowers to determine if an egg had been laid. By these criteria we recorded oviposition times from 10–35 s ($\bar{x}=22.5$ s, $N=15$), and pollination times from 4–12 s ($\bar{x}=6.9$ s, $N=15$). We never observed a female moth to pollinate without first appearing to oviposit, but did observe oviposition behavior which was not followed by pollination (3 of 53 observation). However, in each of these cases, the yucca moth had previously oviposited in another locule of the same flower and had already pollinated the flower. Female moths only oviposited in and pollinated flowers that had opened the same evening.

A flower received on average 1.3 female yucca moth visitors (extremes 1–5, $N=33$) in the two hours after dark (2100–2300 h) of the first night of opening. This resulted in an average of 2.3 ovipositions per flower (extremes 1–5, $N=33$). Usually a female oviposited in one or two locules and departed; however, one female oviposited in five of the six locules. Eight of 33 flowers (24%) were oviposited in and pollinated by more than one female *T. yuccasella.*

Table 3. Results of the hand-pollination experiment to determine the period of stigma receptivity to pollen. Flowers were pollinated at anthesis (≈2000 h), four h after anthesis, 10 h after anthesis, 24 h after anthesis, and 48 h after anthesis. Control inflorescences were not pollinated. Each mean for the number of fruit set and the proportion of fruit set is for five flowers on five plants

Pollination treatment	Number of fruit $\bar{x} \pm 2$ SE (extremes)	Proportion of fruit $\bar{x} \pm 2$ SE (extremes)
Anthesis	1.0 ± 1.5 (0–4)	0.20 ± 0.31 (0.0–0.8)
+4 h	1.2 ± 1.6 (0–4)	0.24 ± 0.32 (0.0–0.8)
+10 h	0.6 ± 1.2 (0–3)	0.12 ± 0.24 (0.0–0.6)
+24 h	0.0 ± 0.0	0.0 ± 0.0
+48 h	0.0 ± 0.0	0.0 ± 0.0
Control	0.0 ± 0.0	0.0 ± 0.0

Nocturnal and diurnal flower visitors

None of the inflorescences that were exposed to only diurnal invertebrates produced mature fruit, whereas inflorescences that were exposed to only nocturnal invertebrates did produce fruit (Table 2). The proportion of flowers producing mature fruit was not significantly different among unbagged control inflorescences and inflorescences that were open at night ($F_{2,16}=0.93$, $P=0.41$). These results suggest that none of the diurnal visitors pollinates *Y. elata,* and that bagging had little effect on the proportion of flowers becoming fruit.

Pollen position on stigma

None of the flowers on which pollen was scraped across the top of the stigmatic tube either initiated fruit or produced mature fruit ($N=15$). In contrast, 93% ± 1.4% ($\bar{x} \pm 2$ SE) of flowers pollinated by pushing the pollen down the stigmatic tube produced mature fruit (extremes 80–100%). Although invertebrates may brush pollen onto the stigmatic surface, it seems unlikely that this will result in pollination. Our results suggest that pollen must be pushed into the stigmatic tube to cause pollination.

Stigma receptivity

Some flowers that were pollinated at anthesis, 4 h after anthesis, and 10 h after anthesis developed mature fruit, whereas none of the flowers pollinated after the first night of opening set fruit (Table 3). There was no significant

Table 4. Result of the hand-pollination experiment to determine the receptivity of flowers to pollen from different sources. Each mean for the number of fruit set and proportion of fruit set is for five flowers on five plants. Out-crosses were with pollen from another clone; self-crosses were with pollen from the same flower; geitonogamous-crosses were with pollen from another flower on the same inflorescence; clonal-crosses were with pollen from another inflorescence on the same plant; and controls were not pollinated

Pollination treatment	Number of fruit $\bar{x} \pm 2$ SE (extremes)	Proportion of fruit $\bar{x} \pm 2$ SE (extremes)
Out-cross	3.8 ± 1.4 (1–5)	0.76 ± 0.30 (0.2–1.0)
Self-cross	1.0 ± 2.0 (0–5)	0.20 ± 0.40 (0.0–1.0)
Geitonogamous	1.0 ± 2.0 (0–5)	0.20 ± 0.40 (0.0–1.0)
Clonal-cross	0.8 ± 1.6 (0–4)	0.80 ± 1.60 (0.0–0.8)
Control	0.0 ± 0.0	0.0 ± 0.0

difference in fruit set between the treatments ($F_{5,24} = 1.14$, $P = 0.37$), possibly because of the low and variable proportion of fruit set in the treatments that did respond to pollination.

Breeding system

Four of five clones set fruit only when cross-pollinated (Table 4). However, one clone (#77) set fruit from 80–100% of flowers pollinated in every treatment. Despite this aberrant clone, there was a significant difference in the proportion of fruit set between out-crossed flowers and all other pollination treatments ($F_{4,20} = 3.43$, $P = 0.027$). Most clones, therefore, require out-cross pollination to produce fruit but some individuals are capable of self pollination.

Discussion

The pollination behavior reported in this study is similar to that reported by Trelease (1893) for *T. yuccasella* on *Y. elata* in southern Arizona. The speed of oviposition and pollination reported in this study (< 1 min) is considerably less than that reported for other populations of *T. yuccasella,* and other species of yucca moth. Trelease (1893, pg 204) also remarked on the rapid oviposition rate for *T. yuccasella* on *Y. elata* and mentioned a time of "rather less than a minute". Ovipositions have been reported to take from one min in *T. yuccasella* on *Y. filamentosa* (Riley 1892), to 34 mins in *T. maculata* on *Y. whipplei* (Aker and Udovic 1981). Aker and Udovic (1981) suggest that some of the observations of short oviposition times may be aborted attempts in which females did not find suitable oviposition sites. Our criteria for judging a genuine oviposition was that the female pollinated immediately afterward. The coupling of the behavior of pollination and oviposition is apparently so tight that we are confident our observations reflect genuine oviposition times for this population of *T. yuccasella.*

The bagging studies indicate that visits by diurnal invertebrates to *Y. elata* flowers rarely, if ever, result in pollination. Of 4022 flowers on 12 inflorescences that were open only to diurnal visitors, none initiated fruit or produced mature fruit. The 4974 flowers on 12 inflorescences that had only nocturnal visitors produced fruit at a similar rate to the inflorescences in the natural population. Most of these fruits had obvious constrictions indicating that they had been oviposited in by *T. yuccasella,* and therefore pollinated by *T. yuccasella* (Riley 1892; Trelease 1893; Powell and Mackie 1966; Kingsolver 1984).

There are at least four hypotheses to account for the lack of pollination in *Y. elata* by invertebrate visitors other than *T. yuccasella:* (1) other invertebrates are incapable, by virtue of their morphology, behavior, or mobility, of carrying pollen between anther and stigma; (2) the pollen cannot be transported unless deliberately collected (as is done by *Tegeticula*); (3) the pollen may be transported but is not deposited in the appropriate place (within the stigmatic tube) for pollination; and (4) the pollen be may be transported but is not placed in the stigmatic tube at the appropriate time for pollination. Our data allow us to analyze all of these hypotheses. First, many of the invertebrates observed on the flowers were too small (e.g., thrips) or immobile (e.g., aphids) to pollinate flowers. Other invertebrates such as carpenter bees (*Xylocopa californica* Cr.) and noctuiid moths approached flowers from the rear and behaved in such a way that they rarely came into contact with the anthers or the open stigmatic tube. Second, casual examination of insects collected at inflorescences suggested that *Y. elata* pollen rarely sticks to these visitors. The glutinous nature of the pollen may prevent it from incidentally adhering to an insect. Third, our pollen-placement experiment indicates that pollination is only successful if the pollen is pushed down the stigmatic tube, where the receptive stigmatic surface is located (Trelease 1893). Such an accomplishment appears to be executed only by yucca moths. Similar experiments to our pollen-placement experiment have been conducted in the past on other *Yucca* species with lobed stigmatic tubes, producing similar results (Milligan 1874; Webber 1892). If diurnal visitors such as sphecid or pompilid wasps happen to scrape pollen from their bodies onto the top of the stigmatic tube in *Y. elata,* it is unlikely to result in pollination.

Finally, the results of the stigma receptivity study suggest that the stigmatic surface is receptive to pollen during the first night of flowering, up until at least the following dawn. We do not know precisely when stigmas cease to be receptive to pollen but it seems to be sometime between 10 and 24 h after anthesis. Hence, the lack of fruit production in inflorescences left open during the day is because *T. yuccasella* is not active during the day, and the flowers are not receptive to pollination after their first night.

Fruits produced on inflorescences open to visitors only at night usually had constrictions indicative of oviposition by yucca moths (Aker and Udovic 1981), but some did not. This does not mean that these fruits were the result of pollination by a nocturnal vector other than *T. yuccasella.* Most studies of *Yucca* and its pollination have recorded instances of developing fruit without larvae or constrictions of the pod (Riley 1892; Rau 1945; Keeley et al. 1984; Laslei and Ludwig 1985; Addicott 1986; Hoffman et al., unpubl. data), and have often concluded that the egg, or the early stage of the larva had died or was parasitized. Alternatively, Rau (1945) suggested that moths may exhaust their ovaries and yet continue to insert their ovipositors and pollinate flowers, or that they pollinated without ovipositing. Addicott (1986) confirmed that insertion of the ovipositor is nearly always accompanied by oviposition, and we found that *T. yuccasella* nearly always pollinated a flower after having inserted the ovipositor into an ovary for more than a few seconds. Parasitism of the eggs and larvae of *T. yuccasella* also appears to be uncommon (Rau 1945; Force and Thompson 1984; Hoffman et al., unpubl. data). Thus, we concur with Addicott (1986) that egg or larval mortality are the most likely sources of the high rates of *Y. elata* fruits without *Tegeticula* larvae. We cannot confirm that all fruits produced in the nocturnal treatment (unbagged at night) were exclusively pollinated by *T. yuccasella,* but the evidence from our experiments strongly suggests that only an invertebrate mimicking the pollinating behavior of *T. yuccasella* could pollinate *Y. elata.*

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References

Addicott JF (1986) Variation in the costs and benefits of mutualism: the interaction between yuccas and yucca moths. Oecologia 70:486–494

Aker CL (1982) Regulation of flower, fruit and seed production by a monocarpic perennial, *Yucca whipplei.* J Ecol 70:357–372

Aker CL, Udovic D (1981) Oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its relation to the reproductive biology of *Yucca whipplei* (Agavaceae). Oecologia 49:96–101

Baker HG (1986) Yuccas and yucca moths – a historical commentary. Ann Missouri Bot Gard 73:556–564

Barstow JW (1872a) Yucca. Bull Torrey Bot Club 3:37

Barstow JW (1872b) *Yucca filamentosa.* Bull Torrey Bot Club 3:52

Campbell RS, Keller JG (1932) Growth and reproduction of *Yucca elata.* Ecology 13:364–374

Coquillett DW (1893) On the pollination of *Yucca whipplei* in California. Insect Life 5:311–314

Engelmann G (1872) The flower of yucca and its fertilization. Bull Torrey Bot Club 3:33

Force DC, Thompson ML (1984) Parasitoids of the immature stages of several southwestern yucca moths. Southwest Nat 29:45–56

Galil J (1973) Topocentric and ethnodynamic pollination. In: Brantges NBM, Linskens HF (eds) Pollination and dispersal. Botany Dept University Nijmegen Holland, pp 85–100

Keeley JE, Keeley SC, Swift CC, Lee J (1984) Seed predation due to yucca-moth symbiosis. Am Midl Nat 112:187–191

Kingsolver RW (1984) Population biology of a mutualistic association: *Yucca glauca* and *Tegeticula yuccasella.* PhD Thesis University of Kansas, Lawrence, Kansas USA

Laslei RJG, Ludwig JA (1985) Fruit production by *Yucca elata* Engelm. (Liliaceae) in four Chihuahuan desert habitats. Southwest Nat 30:321–322

McKelvey SD (1947) Yuccas of the southwestern United States, Part 2. Arnold Arboretum, Harvard University, Massachusetts, USA

Miles NJ (1983) Variation and host specificity in the yucca moth, *Tegeticula yuccasella* (Incurvariidae): a morphometric approach. J Lepidopt Soc 37:207–216

Milligan JM (1874) *Yucca filamentosa.* Am Nat 8:749–752

Powell JA (1984) Biological interrelationships of moths and *Yucca schottii.* Univ California Publ Entomol 100:1–93

Powell JA, Mackie RA (1966) Biological interrelationships of moths and *Yucca whipplei.* Univ California Publ Entomol 42:1–59

Rau P (1945) The yucca plant, *Yucca filamentosa,* and the yucca moth, *Tegeticula (Pronuba) yuccasella* Riley: an ecological study. Ann Missouri Bot Gard 32:373–394

Riley CV (1872) Insects shaped by the needs of flowers. Nature 6:444

Riley CV (1873a) On the oviposition of the yucca moth. Am Nat 7:619–623

Riley CV (1873b) On a new genus in the Lepidopterous family Tineidae, with remarks on the fertilization of *Yucca.* Trans St Louis Acad Sci 3:55–59

Riley CV (1892) The yucca moth and *Yucca* pollination. Ann Rep Missouri Bot Gard 3:99–158

Riley CV (1893) Further notes on yucca insects and *Yucca* pollination. Proc Biol Soc Wash 8:41–54

Smith SD, Ludwig JA (1976) Reproductive and vegetative growth patterns in *Yucca elata* Engelm. (Liliaceae). Southwest Nat 21:177–184

Smith SD, Ludwig JA (1978) Further studies on growth patterns in *Yucca elata* Engelm. (Liliaceae). Southwest Nat 23:145–150

Trelease W (1893) Further studies of yuccas and their pollination. Ann Rep Missouri Bot Gard 4:181–226

Udovic D (1981) Determinants of fruit set in *Yucca whipplei:* reproductive expenditure vs. pollinator availability. Oecologia 48:389–399

Webber HJ (1892) *Yucca* pollination. Am Nat 26:774–778

Webber JM (1953) Yuccas of the southwest. U. S. Department of Agriculture, Agric. Monogr. 17:1–93

Wiggins IL (1980) Flora of Baja California. Stanford University Press, Stanford, USA

Wimber DR (1958) Pollination of *Yucca whipplei* Torr. Masters Thesis, Claremont Graduate School, Claremont, California