

Oviposition and Pollination Behavior of the Yucca Moth, *Tegeticula maculata* (Lepidoptera: Prodoxidae), and its Relation to the Reproductive Biology of *Yucca whipplei* (Agavaceae)

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Summary. The adult behavior of the yucca moth, *Tegeticula maculata* Riley, is finely tuned to the reproductive biology of its specific host plant, *Yucca whipplei* Torr. The female moths oviposit in the ovaries of the yucca flowers and actively pollinate the same flowers with pollen which they have collected previously. The selective pressures imposed on the moths by 1) the plant's need for pollen transfer via an insect pollinating agent, 2) its partial self-incompatibility, and 3) its ability to regulate seed set by aborting excess fruits, have molded the pollinator's behavior in such a way that its offspring have the greatest possible chance of surviving through the early larval stages. The evolutionary responses of the pollinator include the following: 1) the female moths consistently fly to a different plant after collecting pollen, thus insuring cross-fertilization of the flowers, 2) they always pollinate after depositing the first egg in a flower, but not necessarily after subsequent ovipositions, and 3) females emerging near the end of the flowering season frequently oviposit in developing seed pods, as opposed to open flowers which are more likely to be aborted by the plants.

Introduction

Population biologists have recognized the need to study the behavior of individual animals in order to understand the dynamics of populations (Holling 1966; Gilbert et al. 1976) and to analyse behavioral traits in terms of the selective pressures responsible for their evolution (Krebs and Davies 1978). In this paper we describe several aspects of the oviposition and pollination behavior of the yucca moth, *Tegeticula maculata* Riley, and show how they are related to the reproductive biology of its host plant, *Yucca whipplei* Torr. The plant's requirement for pollen transfer via an insect pollinating agent, the constraints imposed by its genetic system, and its capacity to regulate seed set by aborting excess fruits (Udovic and Aker 1981) constitute selective pressures on the behavior of the pollinator, which, in this case, also utilizes the seeds of the plant as a source of food for its offspring. Since the yucca moth larvae grow and develop within the maturing yucca fruits, their fate is inextricably bound up with that of the fruits themselves. We provide evidence which suggests that the oviposition, pollination and dispersal behavior of *T. maculata* serve to enhance the reproductive success of the adults by increasing the likelihood that their offspring are placed in situations in which they have the greatest chance of surviving through the early larval stages.

The obligate mutualistic interaction between the approximately 40 species of *Yucca* (Munz 1959) and their pollinators,

the yucca moths, has attracted considerable attention since its discovery by Engelmann (Engelmann 1872a, b; Riley 1872, 1881, 1892a, 1893; Coquillett 1893; Trelease 1893; Rau 1945; Powell and Mackie 1966; Davis 1967). Although the general outlines of the behavior of the adult moths have been known for some time, our observations have helped to clarify some of the confusion which exists in the literature and have revealed even further the extent to which one species, *T. maculata*, has coevolved with its host.

Yucca whipplei is native to southern California and the Baja Peninsula (Munz 1959) and grows as a monocarpic perennial in the portion of its range where our study was conducted. Individual plants grow as rosettes for several years and then bloom in the spring, sending up a single, large, paniculate inflorescence. The flower stalks may bear up to several thousand flowers, which open progressively from the bottom to the top of the stalk. Each flower remains open for several days, and an individual plant may continue to open flowers for as long as seven weeks. Flowering is somewhat asynchronous within a local population, and the flowering season at the site where most of our observations were made lasts about ten weeks.

The flowers are pollinated by *Tegeticula maculata*, which is responsible for most, if not all, of the seed set by this species (Wimber 1958; Powell and Mackie 1966). The life history of *T. maculata* has been described by Powell and Mackie (1966), and it is known to be restricted to *Y. whipplei*. The female moths use a piercing ovipositor to insert their eggs into the ovaries of open yucca flowers and then actively pollinate the same flowers, using pollen which they carry about with them in a ball held against the thorax. The larvae then hatch out inside the fruits and feed on the developing seeds.

Methods

In this paper we attempt to integrate what are essentially two separate sets of data, one consisting of direct observations of behavior recorded in the field, and the other derived from a broader study of the population interaction, which we use to test hypotheses relating to the adaptive significance of that behavior.

The field observations of adult female moth behavior were made between 11 April and 27 May 1978 and between 31 March and 29 May 1979. Most of the observations were made at Pinyon Flat (elev. 1,200 m) in the Santa Rosa Mountains (Riverside Co., California); additional observations were made at three sites in San Diego County: the Elliot and Ryan Oak Glen Reserves and a site just north of the San Elijo Lagoon. Unlike the other species of *Tegeticula*, *T. maculata* is diurnal (Trelease 1893; Wimber 1958; Powell and Mackie 1966), and all of our observations were made between sunrise and approxi-

mately one hour after sunset. Individual moths were observed for varying lengths of time, while they were on the inflorescences. The presence of an observer appeared to have little or no effect on their behavior. Behavioral events and the times at which they occurred were recorded, as well as wind conditions and the ambient temperature. Unfortunately, we were not able to follow individual moths when they moved from one inflorescence to another.

The following information, collected in connection with the other study, is used to show the distribution of adult moths in time and the survival probabilities of maturing fruits. During the 1979 flowering season, a total of 108 flowering plants at two sites at Pinyon Flat were checked at approximately six-day intervals. Both the number of open flowers and the number of adult moths (both male and female) present on each inflorescence were recorded. At the end of the flowering season, the total number of flowers produced and the number of seed pods matured by each plant were counted. In addition, we were able to count the number of pods which had been aborted by the plants by counting the number of enlarged flower pedicels remaining on the stalks after the abscission of the pods (Udovic and Aker 1981)

Wimber (1958) carried out a series of artificial pollination experiments on *Y. whipplei* and concluded that self-pollination was probably not as effective as cross-pollination. We performed similar experiments on several plants to determine whether they were self-compatible. Individual branches on two inflorescences at the Ryan Oak Glen Reserve and one at the Elliot Reserve were bagged with nylon mesh before the flower buds had opened. Flowers on approximately half of the bagged branches were pollinated with pollen taken from a different inflorescence, while the other half were pollinated with pollen taken from the same plant. The pollinated flowers were checked periodically for pod formation and abortion.

Results and Discussion

Summary of Adult Tegeticula maculata Behavior

The overall sequence of adult *T. maculata* behaviors, as determined by our general observations and those of other investigators, is as follows. The adult moths emerge from overwintering sites in the soil throughout the period in which *Y. whipplei* flowers are present and available (Aker in prep.) Mating generally takes place inside the open flowers, and it appears that the males are more active in searching for mates. After mating, the females apparently require a preoviposition period of at least several hours, during which they rest inside the flowers and reject any further attempts at mating by other males. The initial gathering of pollen can occur either before or after mating, since females were observed *in copulo* both with and without pollen. Oviposition in open flowers commences after the initial pollen gathering event. Flowers in which eggs have been deposited are actively pollinated by the females, which use the pollen they have collected and carried about with them for that purpose. Females have also been observed to replenish their pollen supply after ovipositing and pollinating, but it is not known how often this occurs during the life of an individual moth. Individuals are probably active for no more than a few days. Details of the various components of female behavior are described below, along with data suggesting their adaptive significance.

Pollen Gathering and Between-Plant Movements

Several earlier authors have witnessed and described the pollen gathering behavior of *T. maculata* (Coquillett 1893; Trelease 1893; Wimber 1958). Our observations of 12 different individuals engaged in pollen gathering activity were basically similar to theirs; however, we were also able to observe other behaviors associated with pollen collection which were not previously reported. The most notable of these is that female moths con-

sistently disperse immediately after collecting pollen, which we interpret as an adaptation to the plant's genetic system.

When collecting pollen, the female moths climb up on the stamens and use their highly specialized maxillary tentacles (Davis 1967) to remove the pollinia from the anthers. Pollinia may be collected from more than one flower. The time and effort required can be considerable if there are relatively few pollinia available on the inflorescence at that time. One female, apparently collecting pollen for the first time, spent several hours attempting to pull pollinia from the stamens, with little success. In most cases the process probably requires no more than a few minutes. Once collected, the pollinia are packed into a ball, which is held against the thorax with the tentacles and other mouth parts, and carried by the moth as she moves from flower to flower. The moths do not feed at all as adults (Riley 1892b), and the pollen collected is used exclusively for pollination.

One phenomenon not reported by the previous investigators is the frequent occurrence of pollination during pollen collection. Females collecting pollen make no attempt to oviposit, but they do commonly draw their tentacles back and forth across the stigmatic surface of the flowers as though they were pollinating. Their behavior appears to be identical to the pollination behavior described in the next section, but it seems likely that what we are observing is a case of misdirected behavior and that the moths are simply mistaking the pistil for a stamen. Any pollen transferred to the stigma as a result of such behavior would most likely have come from the same inflorescence, if not the same flower.

In at least nine of the twelve cases observed, female moths which had been collecting pollen flew away from the inflorescence immediately afterwards. In no case was a female seen ovipositing on the same inflorescence after collecting pollen. Having collected a full load of pollen, the females typically crawl out onto the branches or unopened flower buds, rest briefly, and then fly off. In those cases where it was possible to observe them in flight, they either flew away in a straight line, if there was no wind, or else spiraled out from the inflorescence until they were heading downwind and then flew straight. The flights were generally high, well above the surrounding vegetation, and the moths often ignored other inflorescences nearby. Females also fly between plants at other times, but we lack sufficient data to comment on the frequency or stimuli for such flights.

Riley (1892a) recognized that dispersal to a different inflorescence after pollen collection would result in cross-fertilization of the flowers (xenogamy). However, he did not state clearly whether dispersal always followed pollen collection in the species he studied, *Tegeticula yuccasella*. Our artificial pollination experiments support Wimber's (1958) conclusion that *Y. whipplei* is to some extent self-incompatible (Table 1). A female moth pollinating a flower in which she has just placed an egg will likely suffer a decrease in fitness if she uses pollen taken from the same plant, due to the lower probability of maturation of selfed fruits. Any degree of self-incompatibility would be expected to select for the kind of obligate dispersal behavior we observe. Also, the fact that dispersing females fly relatively long distances (i.e., tens of meters) suggests that they are minimizing the likelihood that they will ever return to the same plant from which they have collected pollen or visit other closely related individuals in the vicinity of the pollen donor.

Oviposition and Pollination in Flowers

The oviposition and pollination behavior of *T. maculata* has also been described by several authors (Trelease 1893; Wimber

Table 1. Results of artificial pollination experiments performed on *Yucca whipplei* during spring 1979

Site	Plant	Treatment	Flowers pollinated		% Pods matured	χ^2 ^c
			Pods matured	Pods aborted		
ROG ^a	20	crossed	10	32	23.8	10.9
		selfed	0	40	0.0	
ROG	37	crossed	39	17	69.6	12.5
		selfed	19	34	35.8	
ERES ^b	138	crossed	11	17	39.3	13.3
		selfed	0	27	0.0	

^a ROG = Ryan Oak Glen Reserve

^b ERES = Elliot Reserve

^c χ^2 calculated using the number of pods matured and the number of pods aborted for the two treatments. All values are significant ($p < 0.005$)

1958; Powell and Mackie 1966); however, their reports are sometimes conflicting and the extent of their observations relatively limited. In the course of our study, we were able to collect sufficient data to resolve most of the problems of interpretation raised by the earlier investigations. Our analysis supports the hypothesis that the behavior of the female moths tends to maximize the efficiency with which they utilize pollen and distribute their eggs among the available flowers.

During the two field seasons, we recorded observations of a total of 48 different females which we found ovipositing in open flowers. In several cases it was possible to follow individuals for several hours at a time and thus record extended sequences of oviposition and pollination events. The following descriptions attempt to summarize the behavior we observed.

The female moths are generally selective in their choice of oviposition sites; they often spend a considerable amount of time crawling in and out of flowers before choosing one in which to oviposit. Most seem to prefer fresh or recently opened flowers, and they are commonly found ovipositing in newly opened flowers in which the anthers have not yet dehisced. They typically tap with their antennae against the base of the ovary of the flower before inserting the ovipositor in the ovary wall. Females will also frequently insert their ovipositor only to withdraw within one or two minutes. These brief insertions are always followed by continued searching or probing but never by pollination. Some observers have interpreted these as oviposition events, but the short amount of time involved and the absence of pollination suggest that the moths are simply rejecting unsuitable oviposition sites.

Rothschild and Schoonhoven (1977) reported on the ability of another lepidopteran, *Pieris brassicae*, to avoid ovipositing on leaves containing eggs or larvae of the same species. They concluded that the cabbage butterflies were responding to both visual and chemical cues associated with the presence of the eggs and the larvae. Similar behavior has been reported for the cherry fruit fly, *Rhagoletis fausta* (Prokopy 1975). Withdrawal of the ovipositor by *T. maculata* is often accompanied by the exudation of a small drop of fluid from the flower ovary at the point of insertion. It is possible that other moths are able to detect this or some chemical marker left by the ovipositing females and thus avoid placing their eggs in the same place. This kind of avoidance behavior would clearly be adaptive since each *Tegeticula* larva requires several seeds in order to complete

its development, and larval competition would almost certainly be deleterious.

Having located a suitable oviposition site, a female will insert her ovipositor in the ovary and assume an upright position on the pistil. The average time required to deposit an egg, that is, the time between insertion and withdrawal of the ovipositor, was 34.4 min, although the actual time was found to be inversely related to the ambient temperature ($\text{Time} = 59.3 - 1.2 \times ^\circ\text{C}$, $p < 0.01$). By carefully sectioning the flower ovary and tracing the path of the ovipositor, Riley (1892a) was able to determine that *T. yuccasella* deposits only one egg at a time. We could not perform such an operation for *T. maculata* in the field, but we assume that this species behaves in a similar manner. The fact that we rarely find more than one larva in a single row of seeds lends support to this assumption.

Pollination, when it occurs, always follows directly after oviposition. Flower bagging experiments at Pinyon Flat and other locations indicate that the plants rarely, if ever, produce fruits in the absence of pollinators (Wimber 1958, Aker in prep.). Thus, survival of the larval offspring is dependent on the pollinating activity of the parents. That pollination always follows, rather than precedes oviposition, is explained by the relatively high frequency of unsuccessful oviposition attempts (i.e., brief ovipositor insertions). Considerable wastage of pollen would occur if the sequence were reversed. Shortly before withdrawal of the ovipositor, the ovipositing female begins to move her maxillary tentacles over the pollen ball held against her thorax. This behavior apparently always occurs, regardless of whether pollination will actually follow, and it may be stimulated by some event associated with the passage of the egg through the oviduct. Immediately after withdrawing the ovipositor, the female will either move to the top of the pistil and begin to pollinate by drawing her tentacles back and forth over the stigma, or else turn away without pollinating.

Most females will generally attempt to oviposit more than once in the same flower. Each flower contains six vertical rows of ovules, and the feeding activity of each larva is normally restricted to one row. A female ovipositing in the same flower a second or third time will generally do so in different locules. In 13 out of the 17 cases in which it was known that a particular female was ovipositing in a given flower for the first time, oviposition was immediately followed by pollination. In two of the cases where it was not, the flower had recently been pollinated by a different female. In only 7 out of 18 cases in which females were observed ovipositing a second or third time in a flower, was oviposition followed by pollination. A test for association between pollination and oviposition events, depending on whether the female was ovipositing in a flower for the first time or not, revealed a significant difference between first and subsequent oviposition events ($\chi^2 = 5.04$, $p < 0.05$). This suggests that the moths are able to recognize when a flower has been pollinated and thus avoid wasting more pollen on the same flower. Individuals carrying relatively large pollen loads seemed to have a greater tendency to pollinate after every oviposition event.

The tendency to be conservative in the use of pollen for pollination has presumably evolved in response to the need to minimize the time, energy and risk involved in pollen gathering and subsequent dispersal. A female which uses up her pollen supply must interrupt oviposition activity to gather more pollen, and, because of the need for out-crossing, she must then fly to a different inflorescence. Since the adult moths do not feed, flight uses up non-replenishable energy reserves, which could possibly be used for additional egg production, and also exposes



Fig. 1. Female *T. maculata* ovipositing in a developing *Yucca whipplei* seed pod

the moths to predation or accidental death. There may also be circumstances in which the dispersing moths are unable to locate another inflorescence and are thus prevented from reproducing any further.

Oviposition in Developing Seed Pods

In May 1978 we discovered several female *Tegeticula* apparently ovipositing in green, developing seed pods on inflorescences on which most of the flowers had already wilted (Fig. 1). None of the earlier authors reported having witnessed this behavior, which is not surprising, since it is necessarily restricted to the latter portion of the flowering season. The significance of this behavior did not become apparent to us until the end of the following season, when we were able to observe the extensive abortion of fruits by the plants.

During our periodic censuses in the spring of 1979, we were careful to note the presence of moths on developing pods, as well as in open flowers. Females were seen ovipositing in pods only during the final two weeks of the flowering season, i.e., 15 May through 27 May (Fig. 2). Of the 22 females found on pods, all but two were on inflorescences on which most of the flowers had wilted; the other two were on plants on which the last flowers had just wilted. No moths were found on flower stalks which had no open or recently open flowers, suggesting that the presence of at least some flowers is necessary in order for the moths to locate the stalks. Most of the females carried pollen, although none were observed attempting to pollinate the wilted stigmas. No one individual was observed ovipositing in both flowers and pods, but we presently lack sufficient evidence to determine whether we are observing a case of behavioral polymorphism or behavioral plasticity.

One female discovered while ovipositing on a developing pod was observed continuously for 183 min on the afternoon of 24 May 1979. During that period she appeared to oviposit a total of six times on different pods; the average time between ovipositor insertion and withdrawal was 11.5 min. The same female also made more than 37 short insertions lasting less than two minutes, which we interpreted as rejections of unsuitable

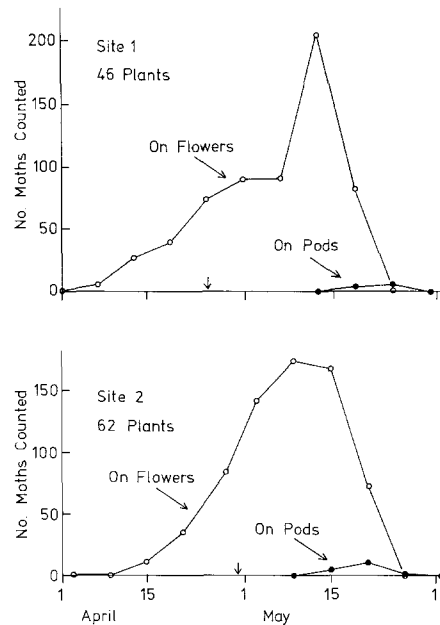


Fig. 2. Seasonal distribution of *Tegeticula maculata* adults (both male and female) counted in open flowers and on developing seed pods at two sites at Pinyon Flat in 1979. All adults counted on pods were females. The vertical arrows (↓) indicate the date on which green, developing pods were first observed on inflorescences at the site

oviposition sites. She consistently selected pods between 2 and 2.5 cm in length, even though both smaller and larger pods, as well as flowers, were available on the same inflorescence.

Our subsequent observations of pod abortion by the plants and our analysis of the pod abortion data (Udovic and Aker 1981) suggest a probable explanation for the pod oviposition behavior. Developing pods start to become noticeable on the inflorescences a few weeks after the first flowers have wilted (about 25 April at Pinyon Flat in 1979). Individual plants begin to drop small (<2 cm long), partially developed pods at about the same time the last flowers are wilting. In 1979, plants at Pinyon Flat aborted on the average slightly more than half of the pods which had been initiated or fertilized (Udovic and Aker 1981). To determine whether flowers fertilized later in the season had a greater probability of being aborted than those fertilized earlier, we chose ten plants at random from one of the Pinyon Flat sites and divided the initiated pods into three classes, according to their vertical position on the flower stalks (Table 2). For the sample taken as a whole, the survivorship of pods initiated on the lower third of an inflorescence was found to be significantly greater ($p < 0.001$) than that of pods initiated on the upper third. Note that the differences within individual plants become more significant as the total number of flowers produced increases. This may be due to the fact that larger inflorescences bear open flowers for a longer period of time, and pods initiated near the bottom of the stalk will have developed almost to full size before the flowers near the top have even opened. Also, the divisions based on the vertical position on the stalk do not correspond exactly to the temporal pattern of flower opening, and this lack of correspondence will tend to be more pronounced in the smaller inflorescences.

Tegeticula larvae feeding in seed pods which are subsequently aborted do not survive. Thus, an egg placed in a flower near the top of an inflorescence, when most of the flowers below have already wilted, will have a lower probability of surviving than one deposited earlier and further down on the inflorescence.

Table 2. Differences in the probability of maturation of *Y. whipplei* seed pods as a function of their vertical position on an inflorescence

Plant ^a	Position on inflorescence	Number of flowers	Pods initiated		% pods matured	χ^2 ^{b,c}	Plant ^a	Position on inflorescence	Number of flowers	Pods initiated		% pods matured	χ^2 ^{b,c}
			Pods matured	Pods aborted						Pods matured	Pods aborted		
1	Bottom	386	15	29	34.1	0.803 ($p > 0.05$)	6	Bottom	568	50	7	87.7	15.8 ($p < 0.005$)
	Middle	386	35	58	37.6			Middle	564	44	11	80.0	
	Top	372	34	92	27.0			Top	553	57	43	57.0	
	Total	1144	84	179	31.9			Total	1685	151	61	71.2	
2	Bottom	444	23	57	28.8	0.798 ($p > 0.05$)	7	Bottom	625	63	73	46.3	18.7 ($p < 0.005$)
	Middle	451	48	106	31.2			Middle	623	95	178	34.8	
	Top	441	20	68	22.7			Top	642	75	220	25.4	
	Total	1336	91	231	28.3			Total	1890	233	471	33.1	
3	Bottom	440	60	49	55.0	3.68 ($p > 0.05$)	8	Bottom	855	131	7	94.9	108 ($p < 0.005$)
	Middle	451	59	87	40.4			Middle	847	220	46	82.7	
	Top	451	35	50	41.2			Top	846	124	170	42.2	
	Total	1342	154	186	45.3			Total	2548	475	223	68.1	
4	Bottom	472	30	29	50.8	2.56 ($p > 0.05$)	9	Bottom	881	91	13	87.5	43.5 ($p < 0.005$)
	Middle	466	51	87	37.0			Middle	878	86	33	72.3	
	Top	472	31	52	37.3			Top	896	26	40	39.4	
	Total	1410	112	168	40.0			Total	2655	203	86	70.2	
5	Bottom	551	31	0	100.0	24.3 ($p < 0.005$)	10	Bottom	919	78	80	49.4	21.7 ($p < 0.005$)
	Middle	555	74	29	71.8			Middle	928	125	250	33.3	
	Top	564	56	53	51.4			Top	906	68	186	26.8	
	Total	1670	161	82	66.3			Total	2753	271	516	34.4	

^a Ten plants chosen at random from one site at Pinyon Flat, 1979

^b χ^2 calculated using the number of pods matured and the number aborted from the bottom and top thirds of the flower stalks. The middle third was excluded from the analysis because of problems with overlap between the classes

^c For the pooled data, the abortion rate for pods on the bottom third of an inflorescence was significantly different from the top third

$$\left(\chi = \sum_{i=1}^{10} \chi_i / \sqrt{10} = 12.7; \quad p \ll 0.001 \right).$$

According to the null hypothesis (i.e., no difference in abortion rates), χ should be a standard normal deviate (Snedecor and Cochran 1967; p. 254)

If a female moth which finds herself on an inflorescence with very few open flowers remaining can deposit her eggs in pods which have reached a size at which the likelihood of being aborted is minimal, and if those eggs can hatch and develop normally within the pods, then that female is likely to have a greater fitness relative to one which places her eggs in the remaining open flowers. Such behavior would be selected for near the end of the season when most of the flowers have relatively little chance of producing mature pods. Similar behavior has been observed in the pink bollworm, *Pectinophora gossypiella* Saunders, which preferentially oviposits on flower buds and cotton bolls of intermediate size, as opposed to small bolls which are most likely to be shed when the plants are stressed (McLaughlin 1974; Gutierrez et al. 1977).

At this time we do not know how the survival rate of eggs placed in pods compares with that of eggs placed in flowers which then develop into mature pods, and it is not likely that we will be able to determine this. It is also not clear whether the moths switch to ovipositing on pods as soon as they become available in the population or whether there is a point in the

flowering season at which pod oviposition becomes more advantageous than flower oviposition, because of the increased likelihood of pods aborting as the season progresses. This second question should be more amenable to further investigation.

Other alternative hypotheses to explain this behavior should also be mentioned. One possibility is that year to year variation in the length of the flowering season has selected for oviposition in pods by females which emerge in the latter half of May. Moisture stress will be more severe in some years than others, and flowers may not always be available to the moths at the end of the season, whereas pods will always be present. Another related hypothesis is that competition for oviposition sites among females near the end of the season may be intense in some years for the same reason as that just given. Natural selection would then be expected to result in the broadening of the potential range of acceptable oviposition sites.

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