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LONGEVITY AND INDIVIDUAL ACTIVITY OF THE YUCCA MOTH, *TEGETICULA MACULATA EXTRANEA* (PRODOXIDAE), BASED ON MARK-RELEASE MONITORING

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ABSTRACT. The life history and pollination biology of *Tegeticula maculata* (Riley), the sole pollinator of *Hesperoyucca whipplei* (Agavaceae), have been studied extensively, but individual moth longevity and plant-to-plant movements have remained poorly known. I recorded activity by capture, mark-release, and recapture of adult moths over a 12-day period at two sites near San Diego, California. Moths lived 2-10 days at room temperatures, and, in the field, marked *Tegeticula* lived 2-9 days between captures. In total, 51 of 145 (35%) marked and released moths were sighted on one or more subsequent days (33% of males, 37% of females). Males tended to stay in one or two adjacent inflorescences: 18 of 29 (62%) recaptures were recorded at the same plant as previous release, whereas females usually relocated to another plant on a following day: 24 of 29 (83%) were found on plants distant (> 2m, avg. 53 m) from the preceding capture. The results help confirm long-held assumptions that cross pollination of yuccas is provided through purposeful behavior by yucca moths moving from plant to plant.

Additional key words: Pollination, Agavaceae, Incurvarioidea, moth longevity

Members of the genus *Tegeticula* (Lepidoptera: Incurvarioidea, Prodoxidae) represent perhaps the most widely acclaimed classic example of plant-insect mutualism. Employing uniquely specialized maxillae of the mouthparts, the female moth gathers pollen, moves to another yucca where she oviposits into a floral ovary, then purposefully transfers pollen to the floral stigma. The resultant larvae feed on the seeds; each consumes only a small number, so many seeds are left intact. This symbiotic interaction was first observed by the botanist George Engelmann (1872) at the Missouri Botanical Garden. C.V. Riley, then the State Entomologist for Missouri, carried out extensive studies on yucca moths (Riley 1872, 1881, 1892, 1893) and used the wonderful story to help promote the importance of insects in pollination when he became Chief of the Entomology Division of the U.S. Department of Agriculture as first entomologist in the USDA and founder of the American Association of Economic Entomologists.

This story of biological coevolution has been repeated in floras and biology and entomology text books, often almost unchanged from Riley's accounts, even becoming increasingly simplified (e.g., Trelease in Riley 1892, Jepson 1951, Webber, 1953), but in reality the relationships have been discovered to be much more complex. Included are species acting as "cheaters" in the system, which are not modified for pollen transfer, fly later, and oviposit into young seed capsules (Addicott et al. 1990). Olle Pellmyr and his students, in a series of elegant studies based on molecular and morphological evidence, demonstrated that cheater species are independently derived at least three times (Pellmyr et al. 1996). Ultimately, Pellmyr (1999) described a complex of 13 *Tegeticula* species in the western U.S. among populations formerly treated as *T. yuccasella* Riley, including two cheater species and 10 pollinators newly named.

Hesperoyucca (formerly *Yucca*) *whipplei* (Torrey) (Agavaceae) in California and Baja California (Fig. 1) harbors a distinctive pollinator, *Tegeticula maculata* (Riley), which was first collected by H. K. Morrison in Kern County in 1880. The typical moth in Sierra Nevada populations is white with evenly spaced black dots on the forewing distally (Fig. 2); there is a coastal phenotype (*apicella* Dyar) with apical, black blotch, that occurs from the Santa Monica Mountains northward; and south of the Transverse Ranges the moths' scaling is black (*T. m. extranea* H. Edwards; Fig. 3). Within *T. maculata*, Segraves and Pellmyr (2001) defined three distinct lineages based on cytochrome oxidase1 mtDNA sequences, one represented by the northernmost population in the Sierra Nevada (Kaweah, Tulare Co.); a second includes Kern (typical) and coastal (*apicella*) populations; and the third clade consists of the black southern California populations (*extranea*) plus a slate gray race in Baja California Norte. The last is a southern geographic isolate, located approximately equally distant from *extranea* at the Mexican border as the latter is from the northern race in Tulare Co. Diurnal activity and black scaling may be thermoregulatory adaptations in response to early spring (February– March) flowering of *H. whipplei*, when nocturnal temperatures may deter moth activity.

Yucca moth activity. Describing the pollination process of *Tegeticula yuccasella*, Riley (1892) stated, "After collecting the pollen . . . she usually runs about or flies to another plant; I have often noticed that oviposition as a rule is accomplished in some other

flower than that from which the pollen was gathered." There has been a general assumption this is the typical behavior of all *Tegeticula*.

For *Hesperoyucca whipplei*, Wimber (1958) made extensive observations of *T. maculata* behavior at the Rancho Santa Ana Botanic Garden, and found the moths active all day; dusk seemed to be the busiest time. She observed variation in female behavior, pollen collection, and searching for a suitable flower in which to oviposit. Consistently, upon withdrawal of the ovipositor, the female proceeded immediately to ascend the style to brush pollen over the stigma, then returned to oviposit in another groove of the same ovary, or more frequently, proceeded to another flower. Moths sometimes omitted the oviposition; one female consistently did so but pollinated many flowers, and one female was observed ovipositing and pollinating one day and replenishing her pollen load in the same inflorescence the following day. Wimber also carried out experiments with artificial pollination of *H. whipplei* and found that self-pollination generally is not as effective as cross-pollination. Aker and Udovic (1981) performed similar experiments at two localities in San Diego County, bagging individual branches of three inflorescences. Their results (0, 35, 0% capsules matured) supported Wimber's conclusion that *H. whipplei* is self-incompatible to a considerable extent. Because some other yuccas have been shown to be self incompatible, many authors have taken it for granted that the pollen-laden yucca moths regularly fly between separate plants, thus ensuring cross pollination. Powell & Mackie (1966) conducted studies of the interrelationships between *H. whipplei* and its moth guild. They described larval feeding habits, host partitioning, observed pollen collection, oviposition, and pollination.

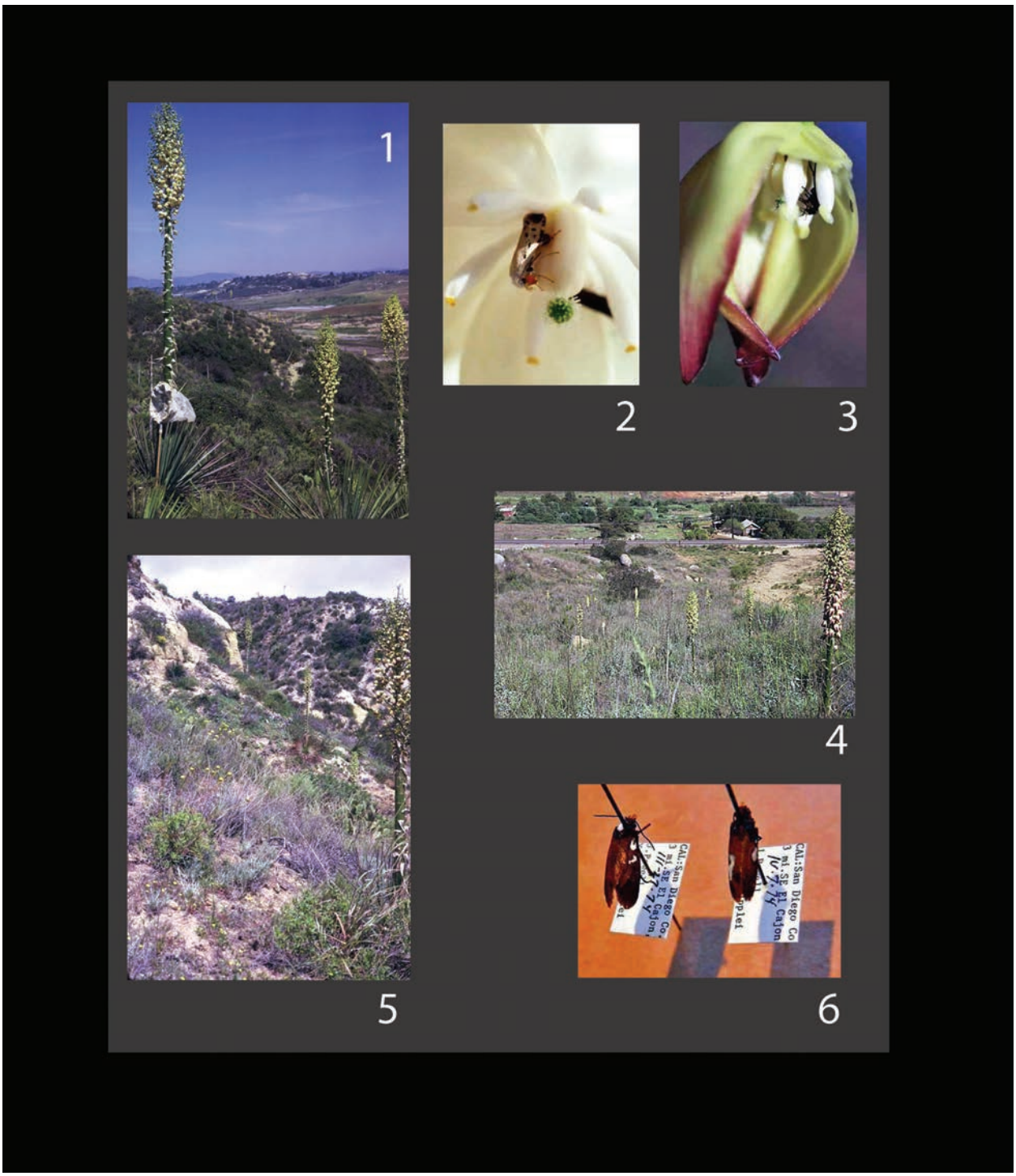
Subsequently, Aker and Udovic carried out detailed studies of *Tegeticula maculata* and *H. whipplei*, including oviposition, pollination, and regulation of fruit numbers (Aker & Udovic 1981, Udovic1981, Udovic & Aker 1981, Aker 1982,). They provided confirmation of Riley's reports on *T. yuccasella*; no female was seen ovipositing in the same inflorescence from which she collected pollen. They observed individuals of *T. maculata* in natural populations in Riverside and San Diego counties and concluded that females consistently disperse to another plant immediately after collecting pollen. In at least 9 of 12 instances the females crawled to branch tips, rested briefly, and then flew off. These flights were high, well above the surrounding vegetation, as are the yucca inflorescences, in a straight line, relatively long distances (i.e., "tens of meters"), often ignoring other yucca inflorescences closer by (Aker & Udovic 1981). None of these authors, however, documented longevity and individual moth movements among plants subsequent to the initial flight following pollen collection; i.e., if and when females carried pollen from one plant to another.

In 1972, during the first 10 days of flowering by *Yucca schottii* in southern Arizona, I attempted a mark-release-recapture study to monitor individuals in a population of *Tegeticula* (later named *T. maderae* Pellmyr, 1999) and a member of its sister genus, *Parategeticula pollenifera* Davis, at Cave Creek in the Chiricahua Mountains (Powell 1984). However, too few marked individuals were recovered to yield meaningful results; in 32 hours observation time during daily examination of 50 panicles, I found only 38 individual *Tegeticula*. I marked and released 24 (12♂, 12♀), and only 2 males were sighted on subsequent nights, one after 52 hours on the same plant where it had been released, and the other in an inflorescence 15 m from its release site after 3 and 4 days. *Parategeticula* outnumbered its *Tegeticula* competitor by 4:1 at Cave Creek, but although I released 99 marked *Parategeticula*, only 3 males were recovered, each in its original inflorescence, after 8, 8, and 24 hours. At the same time I caged two pairs each of marked and unmarked *Parategeticula*, and they survived only 2–4 days. I doubted that all the pollinator moths regularly dispersed long distances and concluded they were short lived, perhaps only 1–4 days (Powell 1984).

Despite minimal results in Arizona, in 1974 I elected to attempt a mark-release study of *Tegeticula maculata* in southern California, reasoning that monitoring should be more efficient because moths of this race are diurnal and black, more easily observed in the white flowers than are adults of the *T. yuccasella* complex. Goals of this study were to provide data on longevity of individuals, determine if females regularly move from plant to plant, and investigate differences between the sexes in daily movements.

METHODS

Study sites. Observations were conducted concurrently at two sites in San Diego Co., California: **A)** an inland locality off Jamacha Road, ca. 6 km SE of El Cajon. This was a gently sloping area of sparse chaparral vegetation that had been disturbed by recent construction of access roads to new home sites, building of which had not commenced (Fig. 4); and **B)** a coastal bluff at Manchester Road just east of Highway I-5. This was a steep sandstone slope supporting dense chaparral, and many of the yucca in bloom were difficult to access (Fig. 5). They were separated by about 43 airline km, with intervening urban development for many decades, industrial and agricultural plots, and the Miramar Naval Air Station, a region that included colonies of the yucca.



FIGS. 1–6. **1,** Upper Left, *Hesperoyucca whipplei* in bloom near Manchester Road (Study Site A), San Diego Co., California. Each inflorescence develops flowers during a period of 3–4 weeks or more. The net in foreground is 2.5 feet in height. **2,** female *tegeticula m. maculata*, typical form, in oviposition posture, head downward in pendant flower of *Hesperoyucca whipplei*, Tulare Co., Calif. **3,** female *T. maculata extranea* in oviposition posture in flower of *H. whipplei*, petals cut away, in San Diego Co., Calif. **4,** view downslope at the El Cajon Study Site A, with *Hesperoyucca* coming into bloom. **5,** View across the steep bluff near Manchester Road, Study Site B. **6,** Pinned specimens bearing white markings employed to distinguish individuals of *T. Maculata extranea*, captured on the first day of observations at Site A.

These two yucca populations had extensive colonies of *Hesperoyucca whipplei* flowering in similar density.

Site A included an observation area about 150 × 90 m, defined by a two-lane county road along its lower margin and by paved cul-de-sac roads along its northern and western border. Additional habitat with yucca occurred <20 m away, so moths readily could fly to plants outside the monitored area. By March 27, 15 yuccas had begun blooming, including one nearly finished, and others in bud stage began flowering during subsequent days. A total of 70 *Hesperoyucca* bloomed in Site A during the 12-day study period.

At Site B the observation area was arbitrarily defined within a much larger area supporting an enormous colony of *Hesperoyucca*, an estimated 150–200 plants in bloom across a wide sandstone cliff and its subtending talus slope. The study site was defined by two parallel ridges perpendicular to the slope, by the sandstone cliff on the north, and a graded road and agricultural field on the lower, south border. Thus defined, site B was similar in area to Site A, ca. 150 × 80m in right angle area, but most of the flowering yuccas were concentrated in a central zone ca. 80 × 60 m, with scattered clusters of plants to the east and west. In total, 43 inflorescences were sufficiently accessible to enable daily sampling, including two in late bloom at study onset, March 28, and three newly flowering on the last observation day, April 7.

Daily monitoring. I visited one or both sites daily during a12-day period: at site A from March 27 to April 7 (except March 31 and April 3); and at site B from March 29 to April 7 (except March 30 and April 3 and 6). Hence there were 9 and 6 days at the two sites respectively during which individually marked moths could be recovered. Typically, the inland San Diego area is warm early in the day, while at the coast fog persists until late morning or later. I visited Jamacha Road (A) for 2–3 hours starting ca. 1100 PDT, then drove to Manchester Road (B) for afternoon observations but not after 1800 PDT. Each inflorescence was numbered, mapped, and monitored daily as thoroughly as feasible for change in flowering sequence and for moth activity. At site A, I employed a 3-foot stepladder to access inflorescences on taller stalks, whereas at site B the steep terrain did not permit use of a stepladder, but taller inflorescences usually were reachable, at least by net, from the steep slope above the plant.

Each *Tegeticula* was captured into a plastic vial or netted, and its sex, time, pollen load, and yucca plant number recorded. New specimens were marked, and all the data and other observations were tape recorded. After marking, I attempted to reintroduce each moth into a flower in the same inflorescence where it had been captured. Nonetheless, about 14% of males and 25% of females flew off upon release, usually to nearby plants and were recaptured.

Marking technique. The southern California race of *Tegeticula maculata* has black forewing and thoracic scaling (Fig. 3). Therefore, marking individuals with felt-tipped pen, a technique favored by butterfly population biologists, was not feasible. Instead, I employed white Liquid Paper® typewriter correction fluid. I immobilized the captured specimen between layers of netting, without attempting to hold it by grasping with fingers or forceps; thus positioned, I applied 1, 2, or 3 small, white spots to left or right FW, either anteriorly or posteriorly, and/or on the prothorax (e.g., Fig. 6). I tape-recorded the Liquid Paper spot patterns and each evening reproduced them graphically on paper for field reference on subsequent days. After day 5 at Site A, with 47 moths marked, I began adding a red dot by felt-tipped marker to one of the white marks, on newly assigned moths #48–67, and later a green dot on #68–100. At Site B fewer *Tegeticula* were marked, and a red dot was added to moths #28–45. I assumed there was no chance that an individually marked moth would migrate 43 km to be found at the other site and did not try to maintain separate patterns or colors for individual moths at the two sites.

At the onset of study, I captured 6 *Tegeticula* (5♂, 1♀) and marked 3 with white spots of Liquid Paper to test its permanency and possible effects on longevity. These were confined in a small terrarium at household temperatures with a water source, although *Tegeticula* are not known to feed.

RESULTS

Abundance. There is enormous variation in relative abundance of *Tegeticula maculata* among different populations of *Hesperoyucca* and from year to year (Powell & Mackie 1966, Aker & Udovic 1981). Coastal *Hesperoyucca* are solitary—each plant dies after flowering once—and the number of inflorescences developing in a colony in any given year appears to be correlated with winter and spring rainfall. By contrast, desert populations consist of cespitose plants, vegetative clumps of many rosettes. As a result, hundreds of flowering stalks develop every year in a given colony, but the prodoxid moths are rare, in contrast to fewer inflorescences and more numerous *Tegeticula* in coastal solitary plant populations (Powell and Mackie 1966).

During the present study, in ca. 42.5 hr field observation time, I recorded 195 sighting events of *T. maculata* at Site A, including original capture and sighting of the same individuals on subsequent days, and 69 at Site B. This low frequency is in marked contrast to

TABLE 1. *Tegeticula maculata*: Movements by individual moths (site A = Jamacha Rd.; site B = Manchester Rd.)

Moths marked	Site	Moths resighted	Total resight events	Resight at same/ adjacent plant	Resight at distant plant
49 ♂	A	15 (31%)	29	18 (62%)	11 (38%)
20 ♂	B	8 (40%)	14	7 (50%)	7 (50%)
51 ♀	A	21 (41%)	30	5 (17%)	25 (83%)
25 ♀	B	7 (28%)	10	5 (50%)	5 (50%)
TOTAL					
69 ♂♂		23	43	25 (58%)	18 (42%)
76 ♀♀		28	40	10 (25%)	30 (75%)

my experience with some other populations of *T. maculata*, where several could be observed at any given inflorescence, including many females engaged in oviposition. My total number of sightings was meager compared to daily numbers recorded by Aker and Udovic (1981) in the Santa Rosa Mountains, Riverside Co., Calif. (i.e., daily peaks of 400–500+), but I monitored approximately the same number of inflorescences (ca. 113) as did Aker and Udovic (1981) at two sites in 6-day intervals during 1979. The abundance of *T. maculata* observed during my study (30–40/day) cannot be compared on an individuals per hour basis because the capture, marking, release, and recording appreciably slowed the process.

Recapture success. At Jamacha Road (A), 100 *Tegeticula* (49♂, 51♀) were successfully marked and released; 36 of them were sighted on at least one subsequent day. Of the marked moths released, 15 males (31%) and 21 females (41%) were recovered, and a total of 95 recaptures were recorded for the 36 moths (Table 1). Among those recovered, 4 males and 8 females were seen only on the following day. Moreover, 3♂, 8♀ (30%) were recorded on the last day, 4 of those (1♂, 3♀) only on the last two days of observation, so might well have been encountered again had the study continued. At Manchester Road (site B), 45 *T. maculata* were marked and released, 15 of which were sighted on one or more subsequent days. These included 8 males (40% and 7 females (28%) and 24 total recapture events (Table 1).

Mating, pollen collection, and oviposition. Considering the time devoted to field observations during the 10-day study, I encountered relatively few instances of mating and oviposition and none of pollen collection. Mating was observed only twice, both at Site A: 1) on March 29, 1430 PDT, female #22, which carried no visible pollen load, with male #11, which had been marked the previous day. 2) March 30 at ca. 1330, neither male nor female had been previously marked. The latter female was recaptured without pollen at 1210 on April 1 >110 m from the inflorescence where mating occurred two days previously. Females engaged in oviposition were recorded on 8 occasions, all but one at Site A, at various times, 1150 to 1645 PDT; 5 times (62%) between 1430 and 1520. All 5 carried pollen.

Longevity. Confined *Tegeticula* lived 2 to 10 days (avg. 5.5); unmarked individuals lived 5, 5, and 10 days, while marked specimens lived 2, 3, and 8 days; two were observed perched on cotton water wick but were not seen feeding. This trial suggested that the Liquid Paper applied to wings or thorax had minor adverse affect on longevity and indicated the markings were permanent for the duration of my study.

In the field, recaptured *T. maculata* that were marked during the first 4 days, March 27–30, provided the best estimate of longevity. At site A, recaptured males that were released March 27–30 (n = 7) lived 4–8 days (avg. 6.3), and females (n = 8) were recorded during 2–10 day spans (avg. 5.6). These are first to last dates observed, inclusive, and represent the minimum number of days individuals lived. Some may have eluded notice one or more days prior to first capture and/or after the last sighting. Moths marked and recaptured after March 30, with successively fewer observation days following marking, averaged shorter recapture spans. Statistical analyses of male-female relative abundance and longevity are subject to sampling error because males were active, easily seen moving from flower to flower, whereas females spent much of the time engaged in oviposition or resting deep in the flowers (Fig. 3). Moreover, temperatures were usually much lower and moth activity reduced at Site B.

Male movements. Males patrolled ceaselessly from one flower into another, not taking flight unless disturbed by the observer. They displayed a tendency to remain in the same or an adjacent (<2 m distant) inflorescence over several days—At site A, 15 marked

TABLE 2. *Tegeticula maculata*: ♂♂ movement documented by recapture (El Cajon site A)
+ = 1st mark-release; ● = same or adjacent yucca; ○ = distant yucca; – = no observation

Day:	1	2	3	4	5	6	7	8	9	10	11	12
Moth #												
4	+	●		○	–			–				
7		+	●	●,○	–		○	–				
11		+	●,○		–		●	–				
12			+	●	–	●	●	–	○			
25				+	–	●		–		○		
28				+	–		○	–	●			
30				+	–	○		–			○	
39					–	+	●	–				
41					–	+	●	–				
43					–	+	●	–				
54					–		+	–		●		
57					–			–	+	○	●	
64					–			–	+	●		
69					–			–		+	●	○
93					–			–			+	●

TABLE 3. *Tegeticula maculata*: ♀♀ movement documented by recapture (El Cajon site A)
+ = 1st mark-release; ● = same or adjacent yucca; ○ = distant yucca

Day:	1	2	3	4	5	6	7	8	9	10	11	12
Moth #												
5	+	○										
13			+						○		○	
17			+			○						
18			+	●								
19			+									○
22			+				○		○	○		
29				+		○	○					
32				+		○			○			
34						+	○		○			
35						+			○			
36						+,○						
37						+	●					
42						+	●					
47						+			○		○	●
73										+		○
77										+		○
82										+	○	
88											+	○
92											+	○
96											+	○,○
100											+	●

males were recovered 29 times, 18 (62%) in the same inflorescence as the preceding record, and 11 (38%) on more distant plants (Table 2). On average, the latter moved long distances (2–98 m, avg. 49 m).

Nine individual moths recorded on 3 or more dates were sighted 12 times in the same or 2 adjacent inflorescences. Male #12 was seen on the same plant on 4 dates spanning 5 days (Table 2). Three males flew off upon first release on March 30, and each was recovered on April 2 or 3, two from distant plants (25, 58 m), and one had returned to the original inflorescence of capture.

Female movements. Females at Site A. recorded two or more times usually had relocated to another plant each time (Tables 1, 3). Only 5 of 29 (17%) marked females were found in the previous inflorescence on a following day, a highly significant contrast to males (χ^2= 10.942, df = 1; p = 0.0009).

One female (#47) was found on the same plant 2 and 3 days after having flown from its original yucca upon release. Female #22 was observed on 4 different yucca plants over a 7-day period. Four females flew off upon first release, and all four were recovered in different plants on one or 2 later dates, 12–32 m distant (Tables 1, 3). Of the 21 marked females recorded again 29 times, 24 (83%) were recovered in different plants than the preceding capture, only 5 in the same inflorescence (Table 3). On average, females moved long distances (15–115 m, avg. 53.5 m), and their net average movement distance was 44.2 m, reflecting the more prevalent plant to plant movements by females.

Recaptures at Manchester Rd. (B) (14♂, 10♀) were too few to be significant, and equal numbers of each sex were recorded at the plant of preceding capture and at distant plants (Table 1). Overall, combined data from the two sites were 58% of 43 male recaptures had remained in the release inflorescences, whereas only 25% of 40 recaptured females had done so; 75% moved to a distant inflorescence, and the difference from males is highly significant (χ^2 = 8.023, df = 1; p = 0.0046) .

Discussion

The 4–10 days life span recorded in the field was longer than expected, based on reports for *Tegeticula yuccasella* and my experience with mark-release of *T. maderae* on *Yucca schotti* (Powell 1984). Rau (1945) studied *Yucca filamentosa–T. yuccasella* relationships during several seasons at Kirkwood, MO. He found males lived 2–3 days, females 3–5 days in the laboratory. That lifespan has been quoted by subsequent authors (Marr et al. 2000 based on Kingsolver 1984, Dodd and Linhart 1994), but evidently there has not been a study of yucca moth longevity in the field comparable to this one.

Marr et al. (2000) used fluorescent dyes to test the prediction that yucca moths primarily perform outcross pollination. They dusted different color dyes on the anthers of newly opened flowers of *Yucca filamentosa* at five sites in Ohio and Tennessee, then subjected all inflorescences within each local population to ultraviolet light later the same night. Although transfers occurred up to 50 m radius from the source plant, they found pollen was moved primarily among flowers within an inflorescence or between plants in close proximity; e. g., 80% of transfers occurred within 8 m and 50% of pollen collections were followed by oviposition and pollination on the same plant. This contrasts markedly to the behavioral sequence of *T. maculata* on *H. whipplei* observed by Aker and Udovic (1981) and indicated by results of the present study.

Based on DNA analysis of Agavaceae and related plants, Bogler et al. (1995) concluded that *Yucca sens. lat.* is polyphyletic, with *Hesperaloë* a sister to *Hesperoyucca* after divergence from the *Yucca* lineage. They suggested the yucca–yucca moth association therefore must have originated at least twice. The parsimony is based on characteristics of the Agavaceae. The conclusion that the yucca moth association must have evolved two or more times is not believable. The Bogler et al. proposal would require ignoring the numerous evolutionary steps during origin and development of the maxillary tentacles, together with correlated female moth behavior, which are without homologous development throughout Lepidoptera worldwide.

There are minor differences in pollination behavior between the *Tegeticula maculata-Hesperoyucca* association and those exhibited by other *Tegeticula* species and their host yuccas.

These involve differences in the plant; because the pollen of *Hesperoyucca* is glutinous, the female *T. maculata* drags several pollinia into a sticky ball that is carried in the same manner as the granulated pollen masses by other *Tegeticula*. *T. maculata* then scrapes the pollen across the capitate stigma of *H. whipplei*, contrasted with other *Tegeticula*, pushing it into the open stigmatic duct characteristic of other yuccas. The origin of the maxillary tentacles, their morphology, musculature, nervous system cues, and the elaborate female moth behavior are fundamentally the same and provide a uniquely derived character complex. Another evolutionary origin other than that indicated by the plants must have been the foundation of the complex. For example, during early radiation of Agavaceae,

ancestral *Parategeticula* may have adapted to seed feeding, although their oviposition occurs externally on the inflorescence stems (Davis 1967, Powell 1984). Adaptation to pollinating by a *Parategeticula* ancestor, which is effective in absence of *Tegeticula* (Powell 1984), may have developed later. Oviposition into the ovaries presumably evolved early in the *Tegeticula sens lat*. lineage prior to the *Hesperoyucca* + *Hesperaloë* split. Bogler et al. (1995) presumed yucca-yucca moth symbiosis probably arose when one of the seed-feeding prodoxid moths, precursor to the *Tegeticula* +*Parategeticula* lineage, evolved the ability to purposefully pollinate the plant upon which its larvae fed. They proposed two possible origins:

Scenario 1) yucca moth pollination evolved in the ancestor of *H. whipplei*+*Hesperaloë* and *Yucca* prior to evolution of the floral specialization of *Yucca sens. str*. The yucca moth pollination syndrome subsequently could have been lost from the *Hesperaloë* lineage and retained in *H. whipplei* without development of stylar and stigmatic specialization now seen in the *Yucca sens. str.* complex—i.e. distinctly recessed stigma, clavate and often bent filaments, outward pollen presentation, little or no nectar, and nocturnal blooming, all of which would have been developed later in the *Yucca sens. str.* clade. This scenario retains a single origin of yucca moth pollination and requires loss of dependence by *Hesperaloë* and associated morphological features of an early yucca association. *Hesperaloë* are arid habitat plants of the Chihuahuan Desert having tubular corollas. They are pollinated by hummingbirds (Pellmyr and Augenstein 1997) and possibly hawk moths, bees and bats, in horticultural situations, but not by prodoxid moths (Bogler et al. 1995).

In **Scenario 2**) Ancestors of *Hesperaloë* + *Hesperoyucca whipplei*, and *Yucca* had a presumably general zoophilous pollination system, which was retained by the *H. whiplei* + *Hesperaloë* clade, whereas the ancestors of *Yucca sens. str.* became adapted to yucca moth pollination. Selection to reduce the costs of resource-based pollination (small anthers loss of nectar production, perhaps recessed stigma) led to dependence on *Yucca* seen now. They suggest that a secondary yucca with mutualism apparently arose when an ancestor of *Hesperoyucca*. *whipplei* was colonized by a yucca moth as a pollinator. Reduction/loss of nectar production and elaboration of the large, cup-shaped white flowers would have resulted as convergent features evolved with increased dependency on yucca moths as pollinators. Other features would have been retained from a previous pollination system. Bolger et al. favor this scenario because it is more parsimonious than the single-origin hypothesis, and later authors have accepted this alternative (e.g. Smith et al. 2008).

Bogler et al.'s first scenario seems more plausible, requiring multiple losses in the *Hesperaloë* lineage but not a repeat origin of the yucca/yucca moth complex, in which several otherwise uniquely derived features would need to have evolved a second time: development of novel, movable, paired appendages on the base of the maxillae and their musculature; development of cues from the brain to direct purposeful collection of pollen and transfer of it to the stigma; oviposition into the immature yucca ovary. An alternative, more parsimonious scenario would be early origins of the yucca-moth association (e.g. during the Paleocene (Pellmyr and Leebens-Mack 1999), followed by separation of the *Hesperaloë* + *Tegeticula maculata* lineage. Later success of *Hesperaloë* would have been dependent upon evolving plant characteristics for attraction of pollinators, with concurrent loss of characteristics favorable to and dependent on yucca moths.

The phylogenetic relationships derived by Pellmyr et al. (2008), with the *T. maculata* lineage sister to the rest of the *Tegeticula*, best represent our current understanding of the pollinator genera but do not entirely reflect the phylogeny of Agavaceae. Certainly we do not have all pieces of the puzzle because there is a 20-million year discord between the age of Yucca (6–10 Myr) (Smith et al. 2008) and best estimates for the age of the pollinators (32–40 Myr) (Pellmyr and Leebens-Mack 1999).

CONCLUSIONS

Results of the present study support the beliefs by Riley in the 19th Century and numerous subsequent biologists for *Tegeticula* in general and *T. maculata* in particular: females mate prior to or following pollen collection, leave the pollen source and fly to distant plants (e.g. 20–100 m) for oviposition and purposeful pollen transfer. On subsequent days, each female usually moves to a different plant, whereas males in search of mates often remain in one or two adjacent inflorescences day after day. Individual moths live longer than had been supposed, up to least 9–10 days. Despite their conspicuous black color in the white flowers, no predator activity has been recorded. Their color may be a thermoregulatory adaptation favoring diurnal activity in early spring when temperatures are low contrasted with warm evenings prevalent in habitats occupied by other species of *Tegeticula*.

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