

AN ABSTRACT OF THE THESIS OF

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Title: Preliminary Investigation into Aspects of the
Population Biology of the Yucca Moth, *Tegeticula yuccasella*
and the Plant *Yucca filamentosa*.

Abstract approved: *John Richard Shrank*

During the summer of 1990, population studies were conducted on the yucca moth confined to the cultivated yuccas constituting an island population in Emporia, Kansas. Mark-recapture of adults allowed estimations of the total population, sex ratios, flight range, and life span. By sampling pods and counting emergence holes, this allowed an estimation of the total larval population. Comparisons of female moths and emergence holes provided a moth-to-larvae ratio. Results suggest the moths remain on site, are active less than five days, and few of their larvae survive in mature pods. With additional studies that would complete a life-table, it might be possible to determine what prevents "cheating." (A "cheater" is a moth that lays too many eggs and decimates yucca seed production).

PRELIMINARY INVESTIGATION INTO ASPECTS OF THE POPULATION
BIOLOGY OF THE YUCCA MOTH, Tegeticula yuccasella,
AND THE PLANT Yucca filamentosa

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INTRODUCTION

Species of the yucca moth in the genus Tegeticula and yucca plants (Yucca spp.) have long existed in a state of mutualism (Baker, 1986; Miles, 1983). The yucca moth cannot reproduce without the yucca because there are no alternate host plants (Johnson, 1988). Yucca plants are able to reproduce vegetatively, but no cross pollination or genetic variability occurs without Tegeticula. It is the only pollinator of Yucca spp. (Baker, 1986; Kingsolver, 1984; Miles, 1983). Since Riley's 1892 exhaustive (by 19th century standards) descriptive work, few additional studies have been done and little is known about Tegeticula's complete life cycle from a modern population biology standpoint.

If the biology of the moth were better known, the moth-Yucca system would provide an excellent opportunity to research population biology questions. Because it is a very transparent system in which the life stages of the moth and seed production of the yucca are visible and easily manipulated, research including testing for inbreeding in a patchy system and DNA variation among populations would be possible. A fine balance in which the moth larvae eat only a certain portion of the developing yucca seeds currently exists within this system (Addicott, 1986; Johnson, 1988; Kingsolver, 1984), and the most plausible suggestion to the existing arrangement seems to be group selection which is considered by most biologists to be a nonfunctional theory.

Group selection in this case brings about self-regulation of the moth populations by destroying those whole populations that destroy all of their resources. The moth larvae that do not eat all of the developing yucca seeds are selected for because they allow the plant to continue to procreate through mature seeds which provides more plants for the moths. The question that undermines such group selection is: What prevents a "cheater?" That is, what prevents a moth from laying twice as many eggs, therefore producing larvae that in turn eat more than their share of seeds? In this system, this question might be answered and could possibly provide clues as to why this is a balanced, dependent, mutualistic system. Before such studies on Tegeticula can be conducted, aspects of the moth's life history must be quantified. Do the larvae travel to pupate, and if so how far? How deep in the soil or yucca whorl are the larvae found? Do the larvae overwinter more than one year? How many seeds do the larvae consume during development? What is the survival rate at each stage in the life table?

This study was designed to examine just two different areas in the Tegeticula moth life cycle to confirm or shift perceptions on the many factors involving the yucca moth's participation in this mutualistic relationship.

The first part of the study estimates the number of adult moths on city yucca using a mark-recapture method.

This also reveals both adult moth movements and sex ratios. The second portion estimates larval numbers by counting emergence holes.

Tegeticula yuccasella is a small, white Lepidopteran approximately a centimeter in length. The males tend to be slightly smaller (Riley, 1892). This species is the only yucca moth found east of the Rocky Mountains and is responsible for pollinating all eastern species as well as most western species of yuccas, except Yucca whipplei and Yucca brevifolia (Baker, 1986).

The adult moths usually emerge from the ground (Baker, 1986), presumably near a yucca plant, in conjunction with the flowering of the plant. Males have been observed to emerge earlier (Davis, 1967; Kingsolver, 1984), as is common with many insects. The males and females then mate in a flower after which the male plays no part in the pollination process (Baker, 1986). During the evening, the female gathers pollen with specially adapted mouthparts and forms it into a ball which she then carries between tentacles and her thorax to another flower. She deposits an egg in one or more of the six locules comprising the ovary of the yucca flower, and stuffs her pollen load into the stigmatic groove (Baker, 1986; Davis, 1967; Kingsolver, 1984). Without her help, the yucca cannot be pollinated and produce seeds. Not only are the yucca stamens bent away from the stigma and reach only two-thirds the length of the pistil, but the

pollen is sticky, and remains so throughout the season (Riley, 1892).

The adult moths themselves do not feed at all on either the nectar or the flowers (Miles, 1983; Riley, 1892), but the larvae can consume up to one-half of the total seeds in a given yucca population (Johnson, 1988). The fruit usually shows a constriction in the vicinity where the larvae fed (Baker, 1986). Before the larvae are ready to exit the pods, they excavate an exit burrow, but leave it capped with a thin outer layer. They then continue feeding (Davis, 1967). When they reach a certain state of maturity, they chew completely through the seed pod, leaving a hole or scar, and apparently descend to the ground either by use of a silken thread (Riley, 1892) or by simply dropping (Davis, 1967). At the soil level they form cocoons, overwinter, pupate approximately a week before emergence, then emerge as adults (Davis, 1967). This length of time is assumed to be one year, although Riley observed one larvae unchanged and still living in a cocoon after two and one-half years (Davis, 1967). It is not known whether the overwintering and pupation occurs in the yucca whorl or in the surrounding soil a distance from the plant.

By observing the yucca moth emergence in May-June, and using a capture-recapture method (Southwood, 1978), the first part of this research focuses on estimating the adult yucca moth population. This is in association with Yucca

filamentosa, a common, small, narrow-leafed ornamental yucca in Emporia, found in yards and cemeteries only where planted. Because eastern Kansas lacks other yuccas, this is an isolated population of both moths and plants.

First, the mark-recapture method provides an estimate of the adult moth population in Emporia. Because all moths are marked and a date recorded for each marked animal, sex ratios and differential emergence can be measured. Additionally, the moths' flight range may be estimated by keeping site records of marked moths.

The second part of the research involves a count of larval emergence holes in the yucca seed pods to determine larvae numbers per pod as well as estimating total larvae numbers. Additionally, a comparison of larval numbers with adult female estimates will show approximate numbers of eggs laid per female. This will help to provide a data base for a future life table and will also allow for the detection of possible "cheaters."

MATERIALS AND METHODS

Research locations

Because the moths emerge in late May to early June, suitable sites throughout the city of Emporia were chosen in the spring by surveying north-south streets and examining known sites where moths were previously found. Suitable sites were determined by the presence of last year's seed pods, and would ideally consist of clusters of yucca plants with neighboring plants within a distance of a city block. Six sites were originally chosen, two of which were excluded later because of lack of moths. As the season progressed, two additional sites were added when they showed evidence of yucca moths, bringing the total number of sites back to six (Fig. 1).

Site Descriptions

Site 1 was an open site located on Peyton Street near 12th Avenue in the northeast corner of Emporia. A row of yucca plants bordered a yard and driveway on the north side of the house, and received sunlight throughout the day.

Site 2 was located on Lincoln Street slightly north from the junction of Briarcliff and Lane Streets. The plants, found along the west side of the street, occurred in two separate clumps on either side of a driveway. They were shaded by large elm trees and received very little direct sun in the morning. This particular site was located in the north-northwest portion of Emporia.

Figure 1. Map of Emporia, Kansas; study sites indicated by numbered circles: 1-Peyton south of 12th, 2-Lincoln north of 18th, 3-East north of South, 4-22nd near I-35, 5-Turner west of Exchange, 6-Exchange south of 12th.

The third site, on East Street, just north of South Street consisted of several clumps of yuccas in approximately a half-block area. Most of these plants were near houses or larger shrubs and in the shade, although some received late afternoon sun. They were on the east side of the street in the central portion of the east side of Emporia.

Site 4 was located in the northwest corner of Emporia near I-35 on 22nd Street. Again, these plants occurred along a half-block area, but occurred on both sides of the street. Most received full or nearly full sunlight throughout the day.

Site 5 was located on Turner Road west of the junction with College Street. The line of yuccas bordered the street on the south side, and were being grown alternately with an ornamental grass. The neighborhood was located at the base of a bowl-shaped depression, and the plants were partially shaded during the day. This site was located in the northeast portion of Emporia.

The final site, Site 6, was located a few blocks south of Site 5 on Exchange Street south of 12th Avenue. The clump of yuccas bordered the northwest corner of a house and the plants received only afternoon and evening sunlight.

Because the moths are not thought to travel long distances, I considered I-35 Interstate as my northern boundary. Industrial Road made up the western boundary as

Y. filamentosa is an ornamental and not found in the industrialized portion of the city. The Cottonwood River set the south boundary, and Weaver Street the east boundary. All living areas east of Weaver Street consisted of newer trailer courts which generally did not have yucca plants.

Methodology and Procedure

The mark-recapture method was used on adult moths to collect data on the adult populations. According to this procedure, adult moths are captured, marked, and released back into the population. A tally of marked moths that are recaptured is kept which allows an estimation of the population. According to the mathematics behind the mark-recapture method, a ratio is formed where the total number marked in relation to the total (unknown) population equals the total number recaptured in relation to the number captured. This resultant estimation is considered a minimal population estimate because certain factors prevent capturing and marking all involved organisms; thus we gain a conservative estimate of the population.

At each site, the flowers on each inflorescence were examined for moths daily. Because the moths rest during the day in the yucca flowers, a small net, originally designed by Kingsolver and resembling a yucca flower, was used to capture the moths by shaking or coaxing them into the net from the flower. This net consisted of a granulated-drink-mix scoop with the bottom removed and

insect netting attached in the form of a small tapering cylinder, much like an airport windsock. Once they were captured, non-toxic, luminous, acrylic, water-based biological paint was used to mark each moth. The orange, red, and blue paint was obtained from BioQuip Products Company. Each wing was divided into three sections. The left wing represented the particular study site, and the right wing portions allowed each moth to be marked and distinguished individually (Fig. 2).

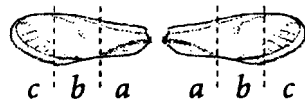
Marking began at the first-noticed emergence and ended when no more moths were available. Previously-marked moths as well as new moths, were tallied daily, along with their sex and location. This procedure was followed at each site beginning with the first day a moth was actually found, and continued for three days after no moths were found.

In August, after the larvae emerged from the pods and had fallen to the ground, a survey of all accessible yucca plants in the Emporia "island" was conducted. One of every 10 pods was harvested throughout the city. At study sites, all of the pods were harvested. From these pods, mature larvae numbers were determined by counting the number of emergence holes per pod.

Mathematical Analysis

The mark-recapture method used in this research is based on the Lincoln Index, which was developed by Petersen and Lincoln in studying plaice and waterfowl populations

Wing Regions



Site 1 — Day 1



Site 1 — Day 2



Site 2 — Day 1



Figure 2. Examples of markings: left forewing, site location; right forewing indicating individuals by marking either basal (a), medial (b), apical (c) regions with up to three colors.

(Southwood, 1978). This index can be expressed as:

$$\hat{N} = \frac{an}{r}$$

in which: \hat{N} = estimate
 a = total number marked individuals
 (four-day cumulative)
 n = total number of individuals in second sample
 (marked and unmarked)
 r = total recaptured individuals

This formula was used to calculate a daily population estimation for each site.

The adult life expectancy was assumed to be four days because no moths were recaptured after a four day time period. Kingsolver's (1984) data also showed this to be true, and individuals of T. maculata were active only a few days (Aker and Udovic, 1982). Therefore a running total of marked specimens was maintained on a four day shelf. At each site, specimens marked five days earlier "fell" off the shelf. The running total was used to provide a daily adult moth population estimation. An overall estimation from each site was obtained by adding each different column (total moths, marked moths, recaptured moths) and inserting the totals into the formula. Sex ratios were obtained by comparing males to females at each site.

Larval estimations involved a direct count of emergence holes. Pods at each site were harvested and emergence holes per pod were tallied. One of every 10 pods was collected at all accessible yuccas throughout the rest of town, and also

tallied. The overall larval estimation involved multiplying the town totals by 10 and adding the site totals. An estimated female-moth-to-emergence-hole ratio was obtained by comparing estimated female moths to estimated larval numbers.

RESULTS AND DISCUSSION

Sex Ratio

Sex ratios varied among sites, although females dominated at all sites. There were at least twice as many females as males at any of the given sites throughout the research period even though males of many insects often emerge first and overlap the female's emergence period. My results showed nearly continuous overlap at all sites with the exception of site 2, where no males were found, and site 1, where a single female was found several days after no moths were found (Fig. 3). Site 5 shows male and female emergence peaking at the same time, although the number of females was still twice that of males. Looking at sex ratios per site takes into account possible microclimates and their effect on differential emergence. A comparison of male and female moths at all sites was made according to rank day, which compiles all site populations based on first day of adult emergence noted at each site (Fig. 4). This shows a much smaller, spread-out male population compared to females, which implies that male moths are on the decline. However, when examining male and female ratios according to calendar day (Fig. 5), males and females proportionally follow the same curve. This goes against accepted literature stating male moths emerge earlier (Davis, 1967) and peak while females begin to emerge; sex ratios then cross at 1:1 with males declining as females reach their

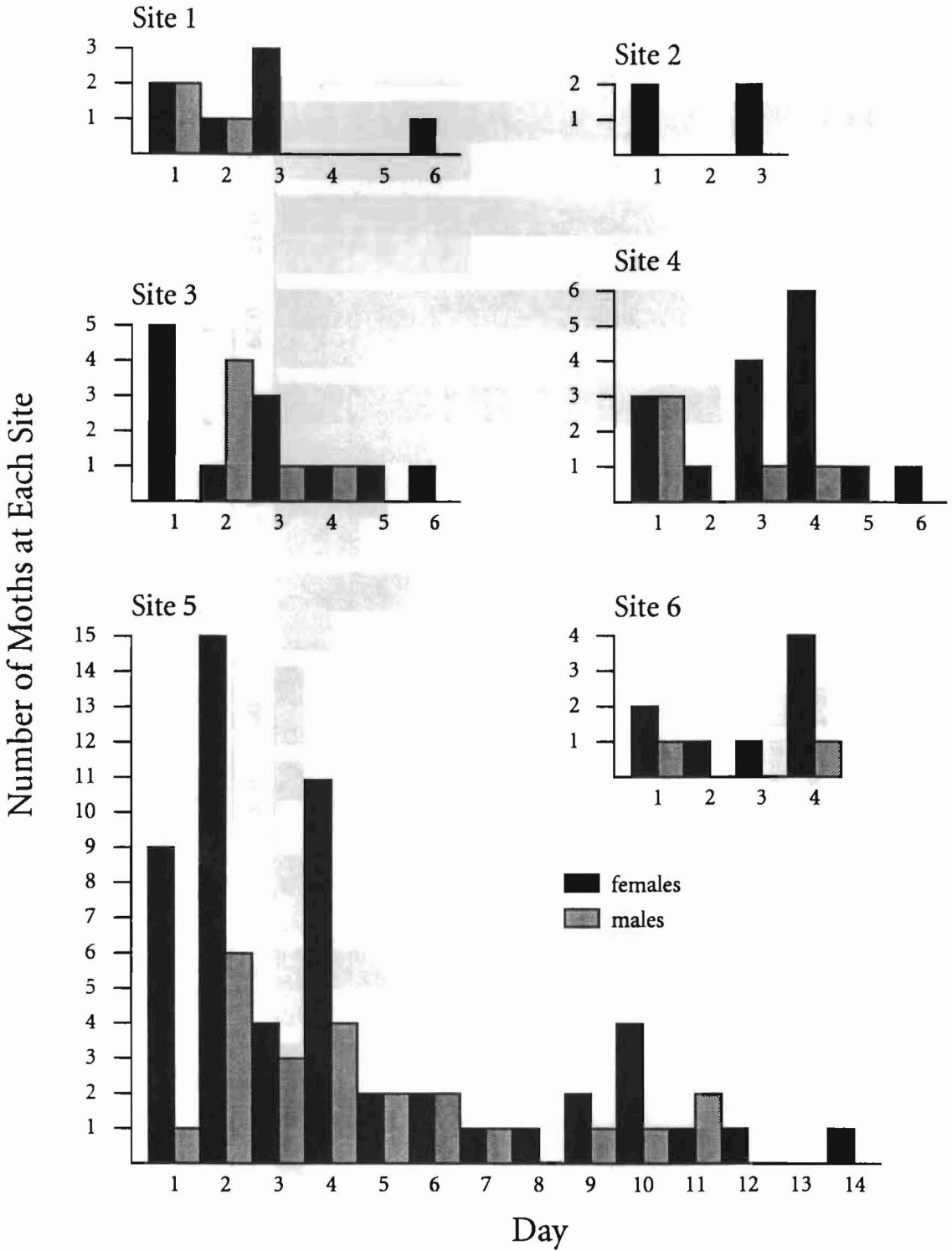


Figure 3. Number of male and female moths found per day at each site.

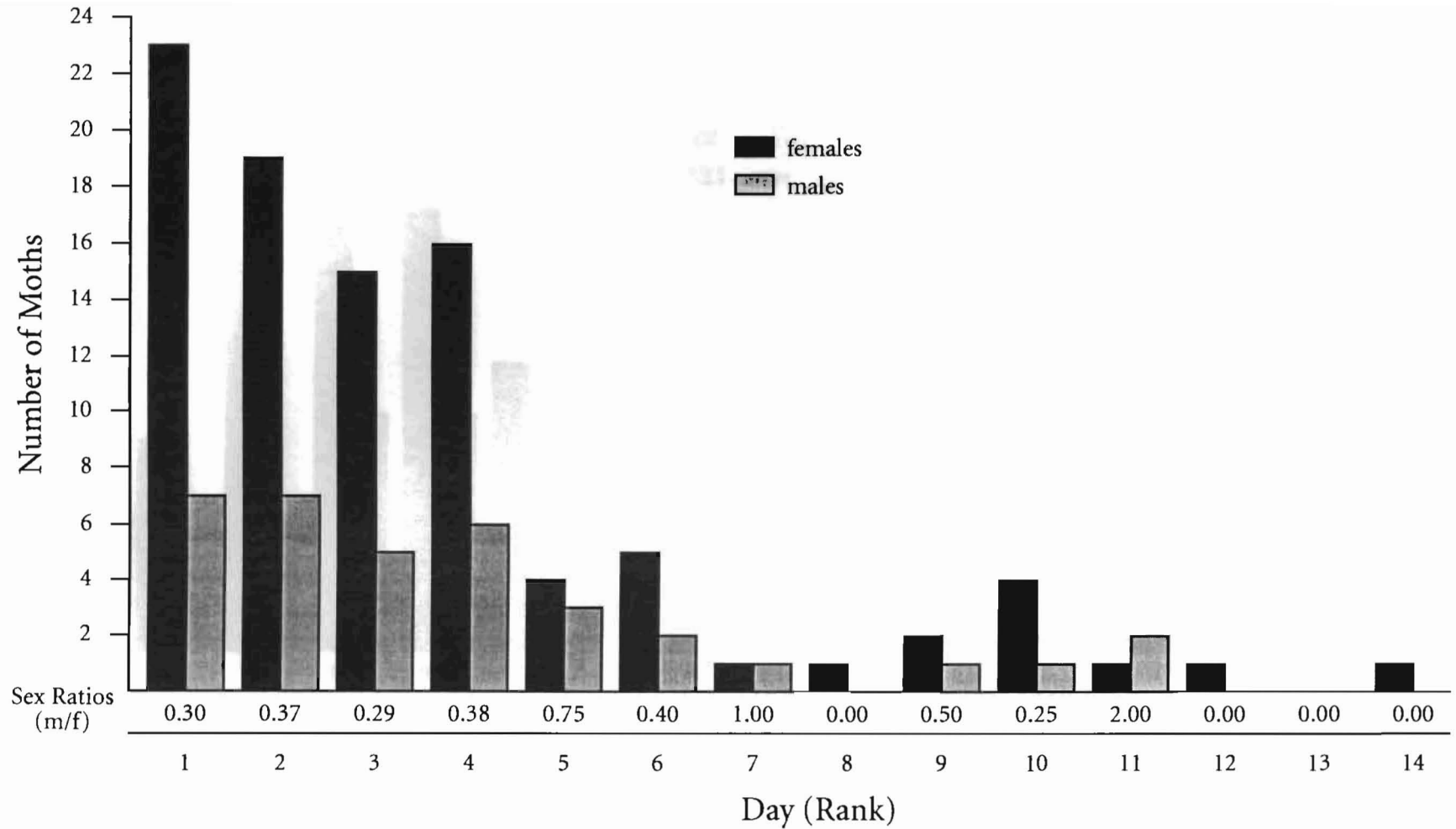


Figure 4. Total number of moths and sex ratios (male and female) found per rank day at all sites.

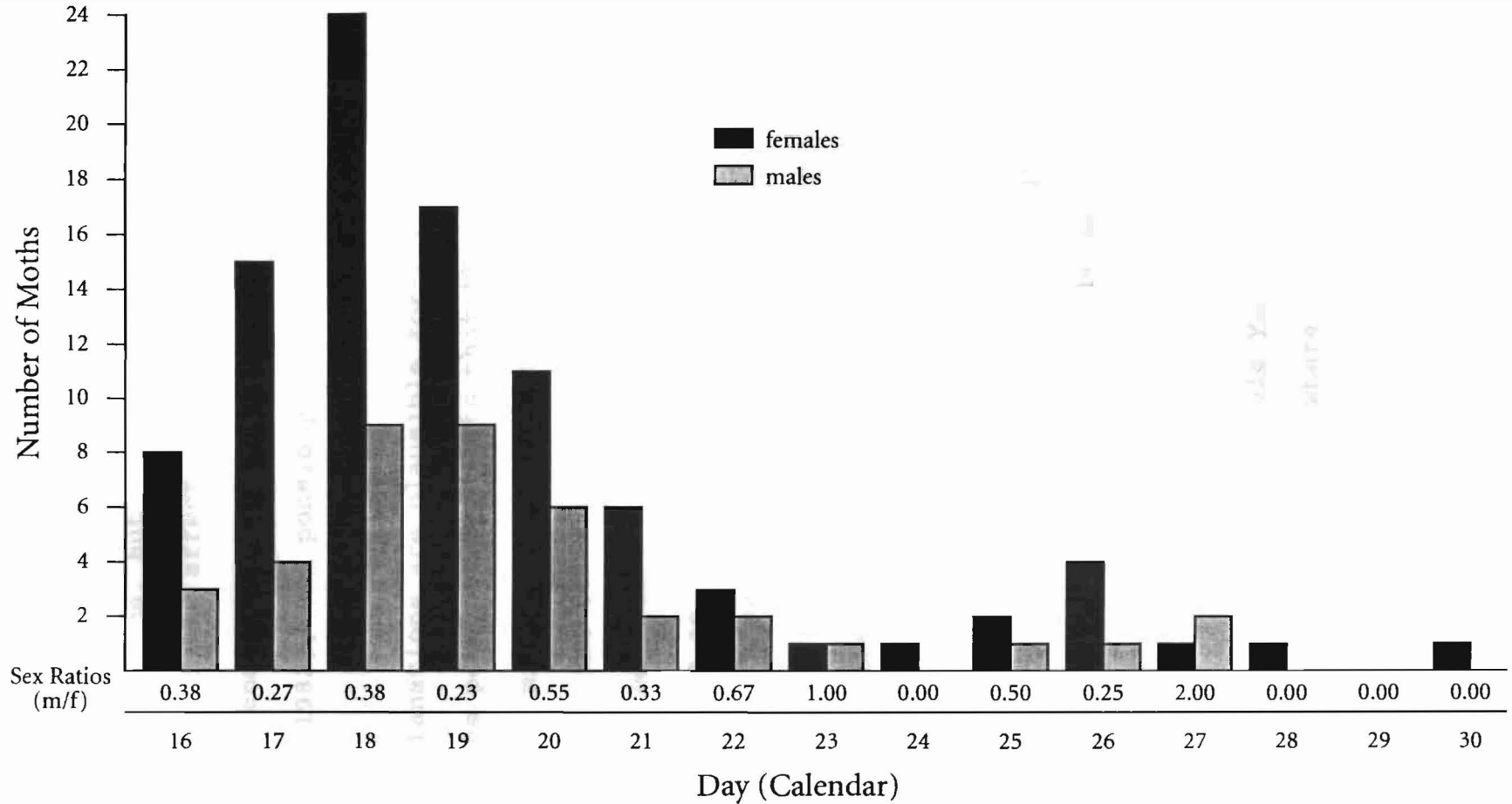


Figure 5. Total number of moths and sex ratios (male and female) found per calendar day at all sites.

peak (Kingsolver, 1984). Little is known of the effect of weather on moth emergence, but this study suggests that microclimates have little affect on emergence timing. However, rainfall and temperature have been shown to affect flowering (Aker, 1982), and possibly moth emergence (Baker, 1986).

Several explanations are plausible for the lack of males. First, the possibility exists that the beginning of male emergence was missed, especially in light of site 1 and site 2 results. On the other hand, males might be hiding in non-flower environments during the day, whereas females remain in the flowers as was previously observed. If males don't remain in the flowers, male predation could be higher. Still another possibility is a lower survival rate for male yucca moths because they are only needed for female fertilization. In many insects, males emerge early and the weak males are culled. All these explanations assume a 1:1 male-to-female primary sex ratio, the accepted norm for most organisms (Fisher, 1930), which could also be an incorrect assumption for this species.

Flight Range

It is not known how far Tegeticula yuccasella travels from it's emergence site to flowers where it gathers pollen. Previous research on T. maculata suggests "tens of meters" (Aker and Udovic, 1981). However, Baker's (1986) review of literature regarding flight range shows inconclusive data on

the subject. Kingsolver (1984) reported an incidence of one female T. yuccasella traveling more than 100 meters. Only one moth, a female, traveled any distance during this study; from site 5 to site 6, a distance of approximately two and one-half blocks. All other recaptured moths stayed at their original sites. Many marked moths disappeared for several days before being recaptured. Several of the sites had other yuccas in the area, so the moths could have traveled to these other plants and returned later. Riley (1892) and Aker and Udovic (1981) have noted that female moths (T. yuccasella and T. maculata) generally carry their pollen to another flower or inflorescence which allows for cross-pollination. One moth flew away from the flowers when she was released after marking and landed in the grass. She was recaptured the next day in a flower.

Population Estimation

Adult moths--the estimated adult moth population for the city of Emporia was a minimum of 2320 adult moths. If the sex ratios from the sample population holds for the whole population, there would roughly be 1696 females and 624 males.

Larvae--The estimated larval population for the city of Emporia (including study sites) was 6370 larvae.

Addicott (1986) reports that an average of 30% of total seeds per pod are destroyed by Tegeticula larvae. He also states that the system is highly variable with losses of

viable seeds ranging from 0% to 100% per pod. In an entire population, approximately half the seeds are eaten (Johnson, 1988). In order for Yucca to have an adequate amount of seeds available for reproduction, ideally, a maximum of only six larvae must exist in a single pod. Emergence hole numbers varied from none to 11 per pod (Fig. 6), although the peak number of larva per pod was three, well within acceptable levels. Female moths tend to frequent newly opened flowers (Davis, 1967) which would help spread the larvae over the entire inflorescence; however, Riley reported a pod with 21 larvae in it (Davis, 1967). Other research has shown larvae in excess of 18 (Addicott, 1986), the optimum number for total seed consumption within a pod. Excess larvae in a pod could destroy too many seeds, thus decreasing the yucca's chances for sexual reproduction and weakening the mutualistic relationship. However, Kingsolver (1984) discovered that the larvae in an over-populated pod don't consume as many seeds as in a pod with only two or three larvae. This would, in turn, reduce larvae fitness. If these larvae survive, they would be weak adults and less likely to reproduce. The pods with no emergence holes suggest that either the larvae died, or the female was interrupted before she laid her eggs, but after pollination. Aker and Udovic (1981) observed female moths mistake the pistil for a stamen and consequently draw their tentacles across the stigmatic surface as if they were collecting

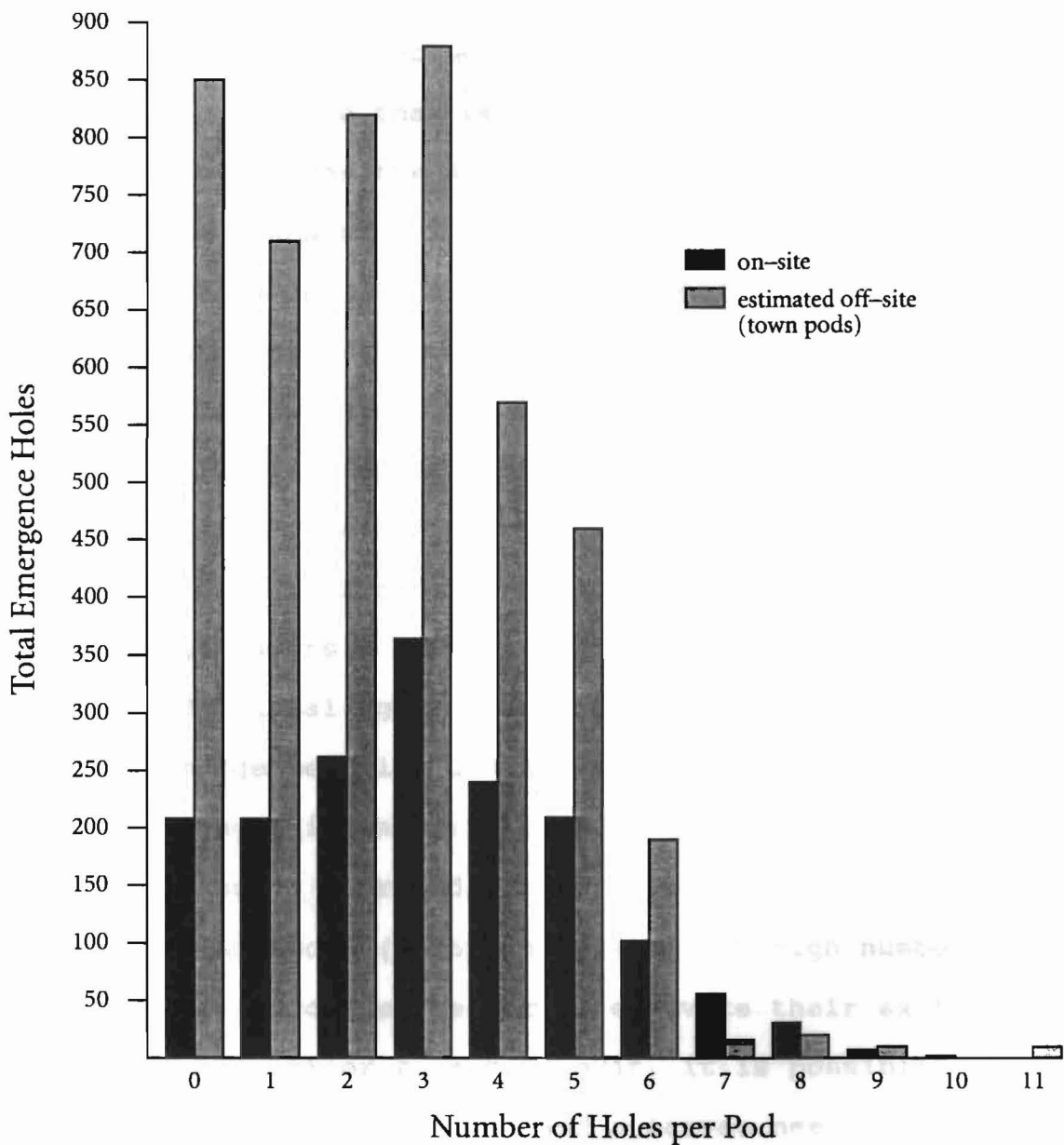


Figure 6. Total number of emergence holes according to the number of holes per pod based on 100% pods on-site and 10% pods off-site.

pollen. This "misdirected behavior" could result in accidental pollination without oviposition, resulting in pods without emergence holes. Excessive holes suggest fertilization by more than one moth, or a "cheater," although this reduces the mutualistic benefit as more seeds than half are consumed. These superfluous holes could also result from chemical signal failure. Tegeticula maculata secretes a drop of liquid after oviposition (Aker and Udovic, 1981) which could act as a signal to other moths. Kingsolver (1984) observed female moths rubbing their ovipositor and abdomen on the pistil as they move toward the stigma, followed by avoidance of that flower by other potential egg-layers. Moths who don't find chemical signals might lay additional eggs in an already egg-bearing ovary. Excessive emergence holes could also be the result of female moths laying eggs in maturing pods toward the end of the flowering season. Aker and Udovic (1981) observed such behavior and Addicott (1986) theorizes that high numbers of larvae result. Because the larvae excavate their exit burrow some time prior to actual exit, it is possible in some cases orientation is lost and a larvae needs to create a new exit burrow. When emergence holes were counted on still-green pods, extra holes might appear if the outer covering was broken. This occurrence would most likely be minimal, but it is a possibility.

Adult/Larval Comparison

Comparisons of emergence holes per site with the estimated female population show much lower ratios than expected (Table 1). The ratio for the entire "island" population was only one female to every 2.76 eggs. These data suggest several interesting implications.

Most insects lay far more eggs and have a much higher female-to-larvae ratio. In this particular system, each pod has room for only six larvae. A low female-to-larvae ratio could be part of a system that prevents "cheaters" if the moths are limited in the number of eggs they can lay. Female moths tend to experience difficult ovipositor withdrawal (Davis, 1967) which could be a mechanism by the yucca plant to prevent the moth from laying too many eggs by producing flower ovaries with a tough skin. Furthermore, as a defense mechanism, the yucca plant might prematurely dehisce a certain percentage of its pollinated flowers to control the moth population. This would result in a high proportion of the larvae dying-off. No research has been done on premature pod abortion in Y. filamentosa, but Aker and Udovic (1981) found that Y. whipplei does regulate its seed set by aborting developing immature pods (up to a 50% abortion rate) with most abortions occurring near the top of the stalk. Kingsolver (1984) reported 90% random flower abortion in Y. glauca. He states that this could be a key factor in controlling moth populations, which would provide

Table 1. Comparison of emergence holes per site, estimated moth population per site, and estimated female-moth-to-emergence-hole ratios.

Site	Estimated moth pop.	Estimated female pop.	Emergence holes per site	Ratio
1	121.0	84.7	159	1:1.88
2	12.0	12.0	119	1:9.92
3	79.3	68.2	397	1:5.82
4	86.7	65.9	418	1:6.34
5	431.1	293.1	480	1:1.64
6	100.0	80.0	117	1:1.46
Town*	2298.7	1679.8	4680	1:2.79
Total	3128.8	2283.7	6370	1:2.79

*Based on a sample of one of every ten pods.

an explanation for the rarity of hyperoviposition or "cheating." Most likely, the moth would evolve to reduce the number of eggs laid; this would spread her offspring out among as many pods as possible (Kingsolver, 1984). Addicott (1986) suggests that yucca plants might selectively abort pods with too many larvae.

CONCLUSIONS

Much research has been conducted on different species of both Tegeticula and Yucca and some research has been done on T. yuccasella in relation to Y. glauca, which is a wild species of yucca. The system involving T. yuccasella and Y. filamentosa needs to be more closely examined. Too little is known about each stage in the moth's life history. What is the actual sex ratio between male and female moths? When do the males emerge? How far do these moths travel? Do they stay near the plants where they emerge? If so, how does genetic inbreeding affect such a closed mutualistic system? What controls the number of eggs laid and is there a chemical signal at work to discourage other potential egg-layers? Does the plant control the moth population entirely, or does the moth regulate itself? How many larvae can a pod support and still produce sufficient viable seeds? Where are the larvae pupating? Are there "failsafe" mechanisms the system uses such as larvae overwintering more than one year in case of poor emergence timing? What are the mortality rates at each stage of the moths' life? Because of its easy accessibility, domesticity, and transparency of the system, the yucca and yucca moth has great potential for study of questions in population biology and mutualism. Further studies must be done on the basic biology of Tegeticula yuccasella before this system can be used for researching more complex population biology questions.

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LITERATURE CITED

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APPENDICES

Appendix 1. Raw mark-recapture data used for calculating daily site population estimates and town population estimates (Da = total number marked; Ra = running total number marked with four-day shelf; n = total number individuals in 2nd sample [marked and unmarked]; r = total recaptured).

	<u>Day</u>	<u>Da</u>	<u>Ra</u>	<u>n</u>	<u>r</u>	<u>Daily est.</u>
Site 1	1	5	5	5	0	
	2	2	7	2	0(1)*	>10
	3	3	10	3	0(1)	>21
	4	0	10	0(1)	0(1)	>10
	5	0	5	0(1)	0(1)	>10
	6	1	4	1	0(1)	>5
Site 2	1	2	2	2	0	
	2	0	2	1	1	2
	3	2	4	3	1	>6
	4	0	4	0	0(1)	>4
Site 3	1	5	5	5	0	
	2	1	6	1	0(1)	>5
	3	4	10	4	0(1)	>24
	4	2	12	4	2	20
	5	1	8	2	1	24
	6	1	8	1	0(1)	>8

*Any recorded data of zero in the n or r column is calculated using one (in parenthesis). I assume moths are present as evident from the Ra data with a shelf life of four days. The resulting estimates are a minimum estimate of the daily moth populations at each site. These are indicated by a greater than (>) sign.

Appendix 1 con't.

	<u>Day</u>	<u>Da</u>	<u>Ra</u>	<u>n</u>	<u>r</u>	<u>Daily est.</u>
Site 4	1	6(5)**	6(5)	6(5)	0	
	2	1	6	3	2	7.5
	3	5	11	6	1	36
	4	6	17	7	1	77
	5	2	14	4	2	34
	6	1	14	1	0(1)	>14
Site 5	1	10	10	10	0	
	2	21	31	23	2	115
	3	7	38	9	2	139.5
	4	9	47	12	3	152
	5	4	41	5	1	235
	6	4	24	4	0(1)	>164
	7	2	19	2	0(1)	>48
	8	1	11	3	2	>28.5
	9	3	10	5	2	27.5
	10	5	11	6	1	60
	11	3	12	4	1	44
	12	1	12	1	0(1)	>12
	13	0	9	0(1)	0(1)	>12
	14	1	5	1	0(1)	>9

**One marked moth killed; therefore population reduced by one.

Appendix 1 con't.

	<u>Day</u>	<u>Da</u>	<u>Ra</u>	<u>n</u>	<u>r</u>	<u>Daily est.</u>
Site 6	1	5	5	5	0(1)	
	2	3	8	3	0(1)	>15
	3	1	9	1	0(1)	>8
	4	0	9	0(1)	0(1)	>9
	5	1	5	1	0(1)	>9

Appendix 2. Total number of male and female Tegeticula at each study site. (See Figure 1 for site locations.)

Site	Males	Females
1	3	7
2	0	4
3	2	12
4	5	16
5	23	48
6	2	8
Total	35	95

Appendix 3. Raw data of emergence hole counts by on-site or off-site and by number of holes per pod. Site data include all pods and off-site data (town) is based on one of every 10 pods collected.

Site	Emergence holes per pod											Total holes per site	
	0	1	2	3	4	5	6	7	8	9	10		11
1	40	25	32	32	13	8	5	1	3	-	-	-	159
2	3	10	10	29	24	18	14	6	5	-	-	-	119
3	107	52	39	67	42	45	30	12	3	-	-	-	397
4	17	48	69	114	79	53	19	10	5	3	-	1	418
5	34	48	79	97	71	74	29	27	15	4	2	-	480
6	7	25	33	25	11	11	5	-	-	-	-	-	117
Total holes	208	208	262	364	240	209	102	56	31	7	2	1	1690
Town	85	71	82	88	57	46	19	16	2	1		1	468

Marylee A Ramsay
Signature of Graduate Student

John Richard Schrock
Signature of Major Advisor

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Marylee A Ramsay
Signature of Author

15 Mar 94
Date

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PLANT Yucca filamentosa
Title of Thesis

Dorey Cooper
Signature of Graduate Office Staff Member

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