Survivorship of the Pupal Stages of the Mexican Fruit Fly *Anastrepha ludens* (Loew) (Diptera: Tephritidae) in an Agricultural and a Nonagricultural Situation[1]

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ABSTRACT Pupae of the Mexican fruit fly, *Anastrepha ludens* (Loew) (=mexfly), were placed outdoors at two localities in northeastern Mexico in order to measure mortality rates during this phase of the life cycle. Replicates were placed monthly in citrus orchards and in a montane canyon where native host plants supported wild mexfly populations. Replicates were placed in sheltered sites under trees and in exposed sites between trees. Adult flies emerged from 38% of these pupae. Deermice, *Peromyscus leucopus* (Rafinesque) and *P. boylii* (Baird), were found to destroy 34% of the total pupae. There was no difference in predation rates or adult eclosion between the orange grove and the montane canyon. There were significant ($P = 0.05$) differences in predation rates among months and in pupal survival between sheltered and exposed sites, with greatest survival of pupae in the sheltered sites during the summer months. Only weak correlations were found between monthly mortality rates and temperature and moisture extremes. The effects of weather variables were probably masked by the pattern of predation. In the native habitat variable predation rates seemed to result from natural cycles in the abundance of mice or from temporal shifts in their food supply. In the citrus orchard cultural practices such as irrigation and weed control displaced or reduced the rodent populations resulting in lower predation rates during some months.

KEY WORDS Mexfly, *Anastrepha, Peromyscus,* mortality, predation, citrus.

The Mexican fruit fly, *Anastrepha ludens* (Loew) (=mexfly), is a major pest of citrus and mangoes throughout the fruit-growing areas of Mexico. Alternate hosts include the fruits of indigenous trees, most notably the yellow chapote, *Sargentia greggi* (S. Wats.), an arborescent shrub native to northeastern Mexico. The yellow chapote is a member of the citrus family (Rutaceae) which occurs in submontane riparian environments. Thickets of chapote, "chapotales," dominate the canyon bottoms cutting the eastern escarpment of the Sierra Madre Oriental. The major citrus growing area of Mexico occurs on the upper alluvial slopes and foothills at the base of the Sierra Madre in the states of Veracruz, Tamaulipas, and Nuevo Leon. Thus, the citrus groves and the chapotales are in close proximity and it has long been suspected that the chapotales serve as sylvatic reservoirs of mexfly populations (Plummer et al. 1941).

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The phenology of mexfly populations in the sylvatic and the agricultural situation are quite different. Citrus groves have fruit on some of the trees practically year round. Before control procedures were implemented in citrus, Crawford (1927) reported four generations per year in Tamaulipas, with the most destructive generation occurring in January-February. On the other hand the yellow chapote produces fruit in the late spring-early summer, with some off-season fruit in the fall if there is sufficient rain (Plummer et al. 1941), thus, supporting one and sometimes two generations per year.

On completion of the feeding stage, the larvae egress the fruit to seek pupariation sites in the soil. Baker et al. (1944) observed that puparia were normally found within a half-inch of the surface and that, if the ground was hard or if there was a cover of leaf litter, they would not enter the soil at all, pupariating on the surface. Crawford (1927) observed that chickens and turkeys foraging in the orchards destroy many of the pupae. McPhail and Bliss (1933) studied adult emergence patterns in an outdoor, screened insectary using infested fruit brought in from local trees around Cuernavaca, Mexico. They found that the mexfly is parasitized in the larval stage by a braconid wasp and that pupae from parasitized larvae fail to produce adults. Pupal development was found to be from 19 to 36 d, depending on seasonal temperatures. Mortality of the pupal stage has not been studied quantitatively outside of the laboratory.

In order to better understand the dynamics of mexfly populations, I undertook a study of mortality rate in the pupal stage in both agricultural and sylvatic environments in northeastern Mexico. The experiment was designed with the idea of exposing known numbers of pupae to the rigors of the natural environment with simultaneous measurement of the climatic vicissitudes which were expected to influence survival. Additionally, the experiment was designed so that parasitism could be detected; however, predation by rodents interfered with this component of the study.

Materials and Methods

Two study areas were chosen on the basis of habitat (Fig. 1). One was a citrus orchard (oranges and grapefruit) 5 km N of the town of General Tehran, Nuevo Leon. This orchard (elev. 330 m) was surrounded by other citrus groves which are near the northernmost extent of an agricultural region dominated by citrus. This citrus growing area is localized along the upper alluvial plain facing the eastern slope of the Sierra Madre Oriental of the states of Nuevo Leon, Tamaulipas, and Veracruz. The soil of this orange grove was a dark, silty loam. The groves were separated by windbreaks of Mexican ash and pecan trees. The interstitial ground was intermittently disked for weed control.

The second site was a montane riparian habitat situated within the Sierra Madre Oriental at a point 30 km W of Linares, Nuevo Leon. The site chosen was a small family subsistence farm bordering the Rio Santa Rosa (elev. 1045 m). The margins of the river were dominated by thickets of the "chapote amarillo." Soils were riverine gravel overlain by a thin layer of humus and foliar litter. Nearby slopes were steep with a dense cover of native shrubs among them scattered pines and oaks.

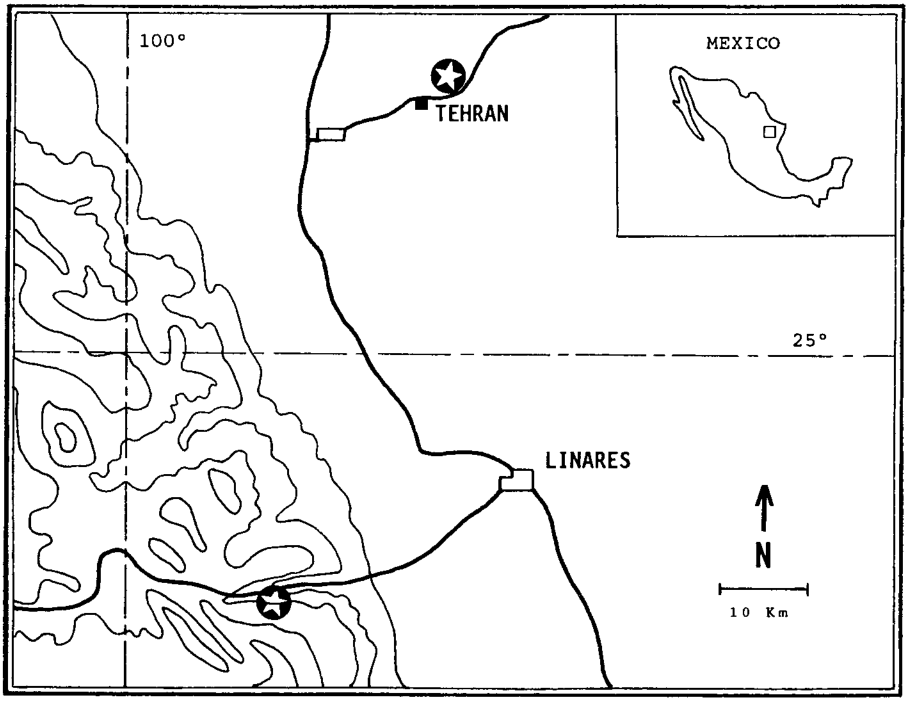

Fig. 1. Map showing location of two study sites in Nuevo Leon, Mexico (stars), and orange grove 5 km E of Tehran and a stand of yellow chapote in a mountain canyon 30 km W of Linares.

The study was begun in January and replicated monthly through December 1992. At the beginning of each month four test cohorts of 100 mexfly pupae each, were placed at each site. The insects used for this study were from a laboratory colony maintained by th USDA at Weslaco, Texas. Larvae were reared under a regime described by Rhode and Spishakoff (1965). Each test cohort was held in square, 11-liter capacity plastic tubs containing approximately 3 kg of loose, unpacked soil. On the morning of the first day of each replicate, 100 fully grown mexfly larvae (10 d old) were released on the surface of the soil of each tub. These larvae were allowed to seek their preferred depth for pupariation. The tubs were transported to the field that same day for enplacement in the afternoon. Two tubs of 100 pupae each were held in the laboratory as controls. Before the experiment was begun, trial runs established that the larvae pupariate within 24 h and that there was no adverse effect from transport to and from the field. At each site, two tubs were buried to the lip flush with the soil surface directly under the canopy of the trees and two tubs, likewise buried, were placed just outside the margin of the canopy. At the end of 19 d these tubs were retrieved. At room temperature the mexfly completes metamorphosis and emerges at 21 d post-pupariation. Metamorphic development is temperature dependent. Thus, the duration of the pupal stage in nature will vary with the season. A uniform exposure time was used in these experiments in order to standardize treatments to enable direct statistical comparisons. The pupae were recovered from the soil by flotation, counted, and held in an environmental chamber at 25°C for emergence.

At each site a weather monitoring station was established including a recording hygrothermograph, max-min thermometer, and rain gauge. On the afternoon of the day of retrieval, soil temperatures were measured at a depth of 3-4 cm both under the canopy and outside the canopy at both sites. A sample of soil from each tub was taken and soil moisture determined gravimetrically with oven-drying.

Rodents were captured with a Ketch-All™ automatic mouse trap (Kness Manufacturing). Live rodents were maintained in a 10-liter terrarium with a 7 cm layer of sand on the bottom. Live, radio-sterilized mexfly pupae were offered to the rodents by placing them on the surface or by burying them several centimeters deep in the sand. On succeeding days the sand was sifted for remaining pupae and broken puparia.

For statistical comparisons of mortality and predation rates between study areas, conditions of exposure and months, Model II Analysis of Variance was employed (Sokal and Rohlf 1973). For the relationship between soil moisture or temperatures and mortality or viability, the product-moment correlation coefficient (Sokal and Rohlf 1973) was calculated.

Results and Discussion

Climate. The 1992 weather data for the two study sites are shown in Table 1 (temperatures) and Table 2 (moisture). June through August were the warmest months at both sites with mean daily maximum temperatures in the range of 31° to 37°C, with the mountain canyon site typically about 2 degrees cooler than the lowland orange grove site. The highest ambient temperatures recorded occurred on 13 July, 38°C at the canyon site and 39°C at the orange grove site. The coolest months were November through January with mean daily minimum temperatures in the range of 9-11°C, with many days in the range of 3-6°C. Temperatures dropped below freezing (-1°C) at the orange grove for 1 h on the morning of 28 November.

Midday soil temperatures were uniformly higher for exposed ground between trees than for sheltered ground underneath the trees at both sites. The difference averaged 6-7°C (Table 1). Midday soil temperatures at the mountain canyon site averaged 3°C cooler than those at the orange grove site.

The pattern of rainfall was similar at both study locations, with dry summer and winter months, but rainy spring and fall weather. The major difference was in the amount of rainfall, with the mountain canyon site receiving nearly twice as much as the precipitation (600 mm) as the lowland orange grove site (333 mm) over the course of the year. Soil moisture levels tracked the rainfall pattern at the chapote canyon site, but because of irrigation, the orange grove soils were maintained at a high moisture level (11-12%) during the summer months despite the lack of rain. No consistent difference in soil moisture was found between exposed and sheltered ground at either location (Table 2).

Table 1. Ambient and soil temperatures (°C) at two study sites in Nuevo Leon, Mexico, 1992. Ambient temperatures were recorded continuously by a hygrothermograph. Soil temperatures were measured at midday; (in) under the canopy and (out) between the trees.

	ORANGE GROVE						CHAPOTE CANYON					
	MAX	MEAN MAX	MEAN MIN	MIN	SOIL OUT	SOIL IN	MAX	MEAN MAX	MEAN MIN	MIN	SOIL OUT	SOIL IN
Jan.	25	20	12	6	–	–	24	17	9	5	–	–
Feb.	30	25	14	4	–	–	33	24	11	4	–	–
Mar.	33	27	14	7	22	17	34	25	13	5	20	16
Apr.	38	31	17	9	25	16	37	27	14	9	25	14
May	36	30	19	17	25	20	31	25	16	13	21	16
Jun.	38	37	24	21	32	22	36	35	18	16	23	20
Jul.	39	36	23	22	32	25	38	33	21	18	33	23
Aug.	37	32	20	19	30	24	38	31	19	15	29	20
Sep.	37	30	19	16	28	21	34	30	17	14	21	18
Oct.	32	27	17	12	25	21	29	25	15	4	20	18
Nov.	26	21	11	-1	19	15	27	20	13	3	13	12
Dec.	18	19	9	6	28	14	25	21	8	6	18	12

Survival of Pupae. Mean survival to adult eclosion of control pupae held in the laboratory was 90% (90.08, ± 7.3 s.d., n = 24 × 100). Mean survival to adult eclosion of test pupae subjected to the vicissitudes of the environment was 38% (37.6, ± 29.9 s.d., n = 24 × 200) (Table 3). There was no significant (*P* = 0.05) difference in overall survival between the two study locations: 38% in the orange grove vs. 37% in the chapote canyon. However, the seasonal pattern between sites was quite different. At the orange grove, survival was highest in the early spring (February to April, 77%) and late fall (October, 79%). Winter survival (November-December) was quite poor, less than 1%. In contrast, the winter survival at the chapote canyon site was quite high, 72% for November-December with the highest survival rate in February, 88%. The lowest survival was during the late summer with only 2% of tested pupae surviving to adulthood during the period August-September.

A major source of variation in seasonal survival was the effect of shelter provided by the canopy of the trees. Mean survival of pupae placed underneath the canopy of the trees was 30% higher than pupae placed in exposed conditions between the trees; 43% vs. 33%. When the entire year's data were analyzed, that difference was not statistically significant (F = 2.33; df = 1,72; *P* = .131). However, the monthly variation in survival was statistically significant (F = 4.87; df = 11,72;

Table 2. Precipitation (mm) and soil moisture (percent water gravimetric), samples collected at midday; (in) under the canopy and (out) between the trees, at two study sites in Nuevo Leon, Mexico, 1992.

	ORANGE GROVE			CHAPOTE CANYON		
	RAIN (mm)	SOIL OUT	MOISTURE IN	RAIN (mm)	SOIL OUT	MOISTURE IN
Jan.	27	.11	.15	38	.11	.06
Feb.	62	.10	.15	5	.05	.03
Mar.	0	.01	.02	51	.05	.02
Apr.	0	.01	.02	3	.04	.03
May	98	.15	.18	85	.16	.16
Jun.	0	.12	.15	0	.02	.01
Jul.	2	.11	.07	0	.03	.05
Aug.	33	.20	.24	115	.23	.25
Sep.	49	.33	.33	140	.33	.26
Oct.	62	.26	.25	125	.27	.25
Nov.	0	.21	.20	38	.22	.15
Dec.	0	.12	.14	0	.14	.08

P = .0014E^{-2}). Examination of the monthly survival data (Table 3) revealed a seasonal effect of shelter on survival. During the spring, summer, and fall months (April-November) survival was highest in the sheltered sites, 43.4% vs. 24.3% in exposed sites, and this difference was significant (F = 20.71; df = 1,7; P = .0026). During the winter months (December-March) survival in the sheltered sites was equivalent to that of the summer months, 42.8%. Survival in the exposed sites rose to 51.0%, which was not significantly different from survival in the contemporaneous sheltered sites (F = 5.44; df = 1,3; P = .102). Soil moisture was not a determinant of pupal mortality. The correlation coefficient (r^2) was .025. A comparison of temperature extremes as identified by Darby and Kapp (1933) (using the sum of degrees from monthly minimum and maximum below 20°C and above 30°C) with monthly mortality produced a weak correlation, r^2 = .368. Clearly there were factors other than climate affecting pupal survival.

Rodent Predation. During the first two months of the experiment, virtually all test puparia were found to be intact when retrieved after 19 d exposure to the environment. Beginning in March, however, a large proportion of the puparia at the mountain canyon site were found to be broken with the edges gnawed and the body of the insect missing. The following month, closer inspection of the tubs containing the dirt and the pupae revealed evidence of

Table 3. Mean monthly survival (% adult eclosion) of mexfly pupae. Comparison of sheltered and exposed conditions at two study sites, an orange grove and a mountain canyon, in Neuvo Leon, Mexico.

	ORANGE GROVE			CHAPOTE CANYON			
	Shelter	Exposed	Both	Shelter	Exposed	Both	Controls
Jan.	.18	.32	.25	.12	.12	.12	.94
Feb.	.61	.87	.74	.83	.93	.88	.93
Mar.	.84	.70	.77	.05	.34	.19	.94
Apr.	.96	.62	.79	.27	.55	.41	.97
May	.11	.02	.06	.37	.26	.31	.81
Jun.	.59	.13	.29	.29	.22	.25	.95
Jul.	.02	.01	.02	.27	.02	.15	.90
Aug.	.85	.22	.54	.08	.00	.04	.87
Sep.	.67	.00	.33	.01	.00	.01	.77
Oct.	.65	.96	.79	.91	.36	.63	.97
Nov.	.01	.01	.01	.85	.46	.65	.82
Dec.	.00	.01	<.01	.78	.79	.78	.96
TOTALS	.46	.32	.38	.40	.34	.37	.90

excavation, or sifting, and considerable amounts of rodent feces. Again, a large proportion of the puparia were broken and gnawed (Fig. 2). On the first day of the May replicate, we placed rodent traps on the surface of the tubs on the first day of enplacement. The following morning, three of the four traps contained an individual of the Cricetid genus *Peromyscus.* Museum specimens were prepared from the skins and skulls of these animals for later identification. Stomach samples (4) were examined and although the bulk of material in the stomachs was green vegetation (probably chapote fruit) each contained insect parts (one mouse had eaten a tree snail). These individuals were undoubtedly trapped before having an opportunity to excavate the pupae in the tubs. When the tubs were retrieved at the end of this experiment, damaged puparia similar to those found at the mountain canyon site were also present in the orchard samples. Subsequent trapping at this site revealed that *Peromyscus* were indeed present in the Orange Grove. Specimens sent to Robert Bradley of Texas A&M University for identification were determined to be common white-footed mouse, *Peromyscus leucopus* (Rafinesque). The rodents at the mountain canyon site were a mixed population of *P. leucopus* and the brush mouse, *Peromyscus boylii* (Baird). Species of *Peromyscus* are usually the commonest mammals

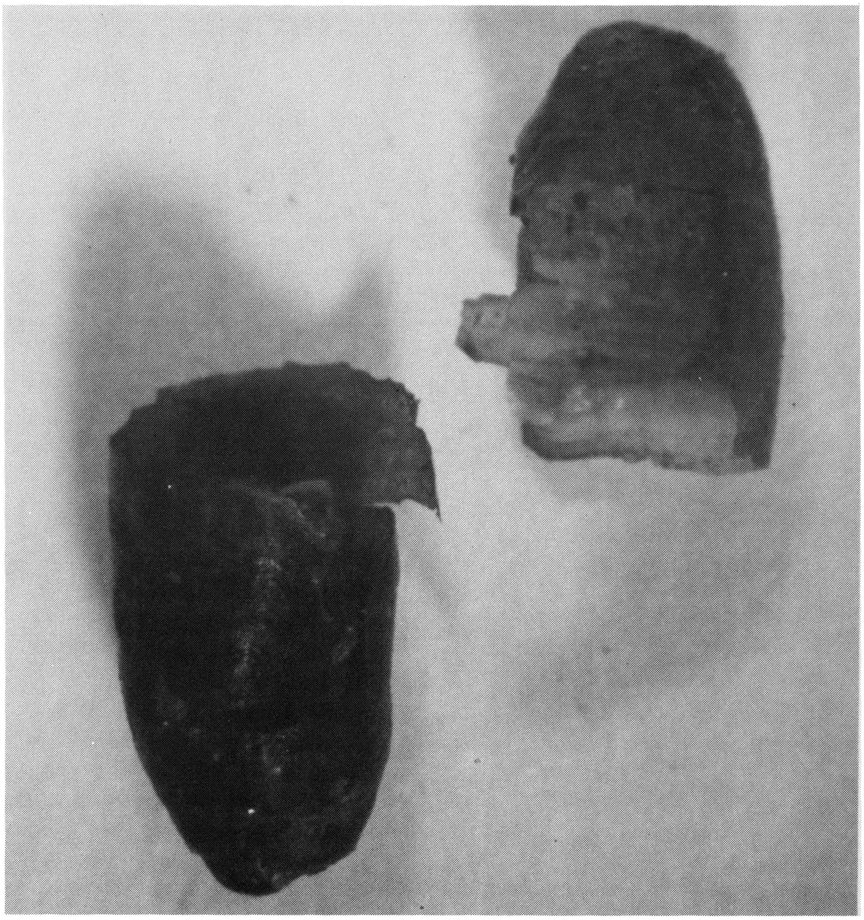

Fig. 2. Damage to mexfly puparia characteristic of rodent predation. Typically the puparium is bitten in half for easy removal of the pharate insect.

present in natural habitats in North America and multiple species frequently coexist (Baker 1968). The white-footed mouse is common in eastern North America, especially in disturbed habitats (Hamilton and Whitaker 1979). The brush mouse prefers rocky habitats and is found throughout the mountainous regions of Mexico and the western United States (Glazier 1980). *Peromyscus* mice are omnivorous with insects, fruit, and seeds of about equal importance (Eisenberg 1968). Jameson (1952) reported arthropods to be 27-28% by volume in a California study of *P. boylii* stomach contents. Hamilton (1941) found arthropods in three-quarters of all stomachs of white-footed mice in New York.

In order to confirm that the mice were the responsible predators, live individuals of both species were placed in a terrarium and offered mexfly pupae. In the initial test 15 live pupae were placed in the terrarium with a female *P. leucopus.* The following morning all puparia were found to be bitten in half and empty (*Peromyscus* are nocturnal). The next night 50 pupae were left in the terrarium, and the following morning, all were found to be eaten. On the succeeding night 100 pupae were left in the terrarium obtaining the same result. In the second experiment a pair of *P. boylii* (gender undetermined) were placed in a terrarium in which 150 pupae had been buried 2-3 cm below the surface. After two days one of the mice was discovered dead, apparently killed by the other. The remaining mouse was released and the sand sifted for pupae. All had been destroyed. The gnawed remnants of the puparia were compared to those recovered in our tubs and found to be essentially identical with respect to the character of the damage. Invariably, the puparium was ruptured through the middle segments leaving the case divided in half and devoid of its contents (Fig. 2).

In this study mice destroyed 34% of the pupae in the experiment (Table 4). There was no detectable difference in the predation rate at the two study areas, nor between exposed and sheltered situations. There were dramatic differences among months however. Cultural practices such as irrigation of the orchard in May and disc-plowing for weed control in September seems to have displaced the mice into surrounding field margins and reduced their depredations in those months. The mice destroyed nearly all of the pupae placed in the orchard in July (96%), November (99%), and December (99%). I presume that a paucity of dietary alternatives was an important determinant of predation rates during those months. Conversely, the low usage of pupae during the early summer may reflect the increased availability of seeds, or larger insects, as a food source. In the mountain canyon habitat, monthly predation rate was more uniform. Highest predation rates were in March (71%) and July (78%), perhaps reflecting peaks in the population cycle of these rodents.

Viability of Non-predated Pupae. Because 66% of the pupae escaped predation, the data were reanalyzed to determine the viability, e.g. adult eclosion rate, of the non-predated pupae and its relationship to weather variables. In total, 58% of the intact pupae were found to be viable (n = 3604/6228) (Tables 5, 6). No pupae were found to be parasitized. Viability was significantly higher in the sheltered situations than in the exposed situations, 69.3% vs 51.2% (F = 5.28; df = 1,11; *P* = .043). Monthly differences in viability were also significantly large, ranging from 18.5% in January to 95.5% in October (F = 4.13; df = 11,11; *P* = .013).

Nevertheless, viability was weakly correlated with soil moisture ($r^2 = 0.23$) and temperature ($r^2 = 0.31$). The effects of climate were probably skewed or masked by the pattern of predation. It seemed that those pupae which escaped predation tended to be either dead or hidden deeper in the soil. Those deep in the soil were probably less susceptible to temperature extremes. Thus, the viability of pupae which escape predation gives an invalid measurement of the effects of climate on pupal mortality.

Rodent Predation and Natural Control of the Mexfly. There have been suggestions that *Peromyscus* species exert some benefit against insect pests. Warnock and Grundmann (1963) found that during an outbreak of grasshoppers in Utah, the digestive tracts of *Peromyscus maniculatus* Wagner contained little else. During the study by Jameson (1952) there was an outbreak of the cutworm *Protorthodes rufula* (Boisduval). He calculated that for

Table 4. Rodent predation on mexfly pupae at two study sites in Nuevo Leon, Mexico in 1992. Numbers destroyed by month, study site and conditions of exposure. Test groups were 100 pupae with 2 replicates each (total n = 9600).

	ORANGE GROVE			CHAPOTE CANYON			
	Shelter	Exposed	Both	Shelter	Exposed	Both	Total
Jan.	5	5	10	8	6	14	24
Feb.	5	3	8	3	1	4	12
Mar.	15	3	18	181	104	285	303
Apr.	1	0	1	141	77	218	219
May	121	128	249	74	61	135	384
Jun.	0	4	4	46	62	108	112
Jul.	194	198	392	145	168	313	705
Aug.	2	55	57	136	82	118	275
Sep.	4	27	31	70	45	115	146
Oct.	64	27	91	11	45	56	202
Nov.	198	199	397	4	97	101	498
Dec.	200	199	399	9	10	19	418
TOTALS	809	848	1657	828	813	1641	3298
PERCENT	33.7	35.3	34.5	34.5	33.9	34.2	34.4

the month of June 1949 the cutworm provided 44% of the food supply of the *P. boylii* population.

It is difficult to assess the influence of rodent predation on mexfly abundance. Given the dynamics of pest populations a predation rate of 34% is significant but not sufficient to effect control. However, the foraging behavior of deer mice, as described by Jameson (1952) and Eisenberg (1968), indicates a "constancy" with regard to temporal resources. That is, upon "learning" of the availability of a temporal resource, they concentrate on that resource until it is exhausted. Thus, one can expect greater predation pressure at times when the concentration of prey is greater. Clearly, however, the concentration of pupae that existed under these experimental conditions was an artificial one being exploited by the mice. The difficulty then is to infer from the results of these experiments the potential for control in nature. The two situations that were studied were quite different as regards the temporal and spatial distribution of

Table 5. Viability of non-predated mexfly pupae from a mountain canyon site in Nuevo Leon, Mexico, under exposed and sheltered conditions, by month, 1992.

	Sheltered			Exposed			
	Pupae	Adults	Viable	Pupae	Adults	Viable	Both
Jan.	192	24	.12	194	23	.12	.12
Feb.	197	166	.84	199	186	.93	.89
Mar.	19	9	.47	96	68	.71	.67
Apr.	59	54	.92	123	109	.89	.90
May	126	74	.59	138	51	.37	.47
Jun.	154	57	.37	138	44	.32	.35
Jul.	55	54	.98	32	5	.16	.68
Aug.	64	16	.25	114	0	.00	.09
Sep.	130	1	.01	155	0	.00	<.01
Oct.	189	181	.96	82	72	.88	.93
Nov.	199	170	.85	103	91	.86	.88
Dec.	191	155	.81	190	158	.83	.82
TOTALS	1575	961	.61	1564	807	.52	.56

pupae. In the citrus orchards there are fruit hosts for the mexfly the entire year, and thus there are pupae to be found in the soil year round. In the chapotales, by contrast, there is normally production of fruit but once a year. Thus, there is a temporal concentration of pupae in the spring and early summer. The chapote fruits are dehiscent. They fall and roll, and with the aid of rainwater, they tend to concentrate along water channels in drift deposits. Thus, concentrations of pupae may be a natural phenomenon exploited by mice. In contrast, oranges remain on the trees until they are picked. In the orchard situation the larvae egress the fruit and pupate in the soil near where they fall. In this manner pupae tend to be scattered in the soil beneath the trees. This scattering may reduce the foraging constancy of the mice on pupae in the orchard situation. And, as noted, cultural practices such as irrigation and disking for weed control have an adverse effect on the rodent population. Future studies on the natural mortality of mexfly pupae are planned using a similar design but with rodent exclosures and without exclosures but at lower densities.

Table 6. Viability of non-predated mexfly pupae from an Orange Grove site in Nuevo Leon, Mexico, under exposed and sheltered conditions, by month, 1992.

	Sheltered			Exposed			
	Pupae	Adults	Viable	Pupae	Adults	Viable	Both
Jan.	195	35	.18	195	64	.33	.25
Feb.	195	122	.63	197	174	.88	.75
Mar.	185	169	.91	197	140	.71	.81
Apr.	199	191	.96	200	124	.62	.79
May	65	21	.32	28	3	.11	.26
Jun.	200	92	.46	196	25	.13	.29
Jul.	6	5	.83	2	2	1.00	.87
Aug.	198	171	.86	133	44	.33	.65
Sep.	197	133	.68	170	0	.00	.36
Oct.	136	129	.95	191	189	.99	.97
Nov.	2	1	.50	1	1	1.00	.67
Dec.	0	0	.00	1	1	1.00	1.00
TOTALS	1578	1069	.68	1511	767	.51	.59

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