ECOLOGY, BEHAVIOR AND BIONOMICS

Reproductive Phenology of the Mexican Fruit Fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae) in the Sierra Madre Oriental, Northern Mexico

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Fenologia Reprodutiva de *Anastrepha ludens* (Loew) (Diptera: Tephritidae) na Serra Madre Oriental, Norte do México

RESUMO - Em seu hábitat nativo no Norte do México, *Anastrepha ludens* (Loew) é normalmente bivoltina, embora possa ocorrer uma terceira geração em alguns anos. As moscas entram em diapausa principalmente no estádio pupal, emergindo em janeiro-fevereiro. Essas moscas adultas ovipositam no cultivo de primavera do citrus selvagem *Sargentia greggii* (S. Wats.). O pico primário de população ocorre do final da primavera até o início do verão (em anos excepcionais, ocorrem picos separados na primavera e no verão). A dissecção das fêmeas demonstrou que a maioria das moscas que ocorrem no pico de primavera são imaturas reprodutivamente, indicando a emergência de novos adultos. A atividade se reduz ao final do verão, ou pelo menos poucas moscas são coletadas nessa fase. No outono ocorre a ressurgência da atividade dos adultos. Entretanto, ao contrário do que ocorre no pico de primavera, a dissecção das fêmeas revelou que a grande maioria das fêmeas adultas de outono já estão grávidas, indicando que elas permanecem na população do início do verão, ao invés de surgirem novas fêmeas. As fêmeas de outono ovipositam em outubro-novembro, produzindo a populacão que entra em diapausa e emerge em janeiro-fevereiro.

PALAVRAS-CHAVE: Reprodução, oviposição, bivoltino, citrus

ABSTRACT - In its native habitat in northern Mexico, *Anastrepha ludens* (Loew) is normally bivoltine although a third generation is achieved in some years. The flies overwinter mainly in the puparial stage, emerging in January-February. These flies oviposit in the spring crop of a wild citrus, *Sargentia greggii* (S. Wats.). The primary population peak follows in late spring to early summer (in exceptional years, separate peaks in spring and summer). Dissection of the females demonstrated that most of the flies in the spring peak are reproductively immature, indicating emergence of new adults. Activity subsides in late summer, or at least, few flies can be trapped at this time. Then in the fall there is a resurgence of adult activity. However, in contrast to the spring peak, dissection revealed that the great majority of the fall adult females are already gravid, indicating that they are carry-overs from the early summer population, rather than new recruits. The fall adults oviposit in October-November, producing the overwintering population that will emerge as adults in January-February.

KEY WORDS: Reproduction, egg-load, bivoltine, citrus

The Mexican fruit fly, *Anastrepha ludens* (Loew), is a pest of citrus, mangoes, and a variety of backyard tree fruits, from Mexico to Panama. It is thought to be native to the Sierra Madre of northeastern Mexico because it breeds there in a wild citrus, yellow chapote (*Sargentia greggi* (S. Wats.), Rutaceae) (Plummer *et al*. 1941). Because of the proximity of this wild population to the U.S. border area, a joint federal and state program maintains a surveillance grid of McPhail traps in the lower Rio Grande Valley of Texas, and every year in the spring, adults of the Mexican fruit fly are detected (Nilhake *et al*. 1991). At one time it was suspected that these captured flies might be introductions from the native populations or infested areas further south in Mexico (Shaw *et al*. 1967). However, the regularity of the appearance in the spring eventually led researchers to suspect that the Texas population, though at subliminal levels most of the year, might be a self replicating population (Thomas *et al*. 1999).

One possible explanation for the absence of the flies from the traps during the greater portion of the year in Texas would be that the insects enter diapause or aestivation. But, a study of larval and pupal development in the field failed to reveal evidence of a developmental arrest (Thomas 1997). Leyva-

Vazquez (1988) demonstrated that development is temperature driven in the laboratory and the field studies confirmed that the high temperatures prevailing from May to September shortens generation time to as little as five weeks, too short a time to allow the passage of the summer in a sheltered larval or pupal stage. Conversely, under the cool weather conditions that prevail in the winter, development is extended to approximately 12 weeks. Thus, oviposition in grapefruit in October and November should give rise to adult emergence in January and February, which timing coincides with the earliest annual detections in Texas. The conundrum is that adults are too short lived to carry the population over a full year from one spring to the next. Mark-recapture studies show that some adults can live as long as four months in the wild. But, the great majority have a much shorter life span, on average, only 5-10 days following release (flies were 3-4 days old at release) (Thomas & Loera-Gallardo 1998). The short life expectancy would seem to rule out the possibility that the Texas population is univoltine, yet, there is only evidence for breeding in the spring. Because of the quarantine issue the origin of the infestations is of some importance. There are 34,000 acres of commercial citrus on the Texas side of the Rio Grande, but less than 500 acres on the Mexican side. If the flies are breeding on the Mexican side of the river then they are depending on backyard fruit for hosts. But, if that is the case, then they are equally likely to be using backyard fruits on the Texas side.

There is ample data on reproductive behavior of this insect in captivity. Dickens *et al*. (1982) found that females are receptive to mating at an age of nine days, a time coordinate with the ovaries reaching full size. McPhail & Bliss (1933) found that most females begin laying eggs at 11 days age at constant 24-25°C. Moreover, at slightly lower temperatures, 20-21°C, McPhail & Bliss (1933) and Berrigan *et al.* (1988) found that the first oviposition was delayed out to 20-22 days age. Even under the optimal life expectancy of the laboratory, Liedo *et al*. (1993) calculated that females spend 52-64% of their life span in the pre-ovipositional stage. Once the female matures, oviposition is essentially continuous for as long as the fly lives. Berrigan *et al.* (1988) and Liedo *et al.* (1993) reported that females oviposit eggs in clutches of five to six eggs, laying an average of around three clutches per day when provided an ample supply of fruit.

The studies of reproduction in the laboratory provide context for studies of breeding in nature. The objective of the present study was to examine the phenology of egg production in the native habitat and its relationship to seasonal fluctuations in the adult population. The study was conducted in northern Mexico where the fly is indigenous and where populations were not under suppression by a control program.

Materials and Methods

McPhail traps baited with an aqueous slurry made by mixing 350 ml of water with three 5 gm pellets of torula yeast and preservative (2.25 gm yeast and 2.75 gm borax), were operated at two study areas approximately 75 km apart in Nuevo Leon, Mexico. The traps were in continuous operation from 1994 to 1998 in both areas. All traps were serviced weekly. All female flies captured in the traps were preserved in alcohol, transported to the laboratory, and dissected to determine fecundity. Aluja *et al.* (2001) are followed in defining egg load as the number of mature oocytes in the ovaries. Oocytes were counted as mature eggs when they were at least 1.0 mm in length, tapered at one end, with the surface shiny and translucent (Emmart 1933).

Study sites. The southern most study area was a steep sloped montane canyon west of the town of Linares where yellow chapote occurs in groves along the course of the Santa Rosa river. The groves of yellow chapote occur in riparian habitat bordering the intermittent streambed amongst a gallery forest of Mexican ash (*Fraxinus berlandieriana A. de Candolle*) and sycamores (*Platanus occidentalis* L.). Surrounding vegetation is classified as Tamaulipan scrub forest (Leopold 1950), consisting mainly of spiny leguminous trees with scattered oaks transitioning to pine with increasing elevation from the lowest site at 500 m to the highest at 1050 m. Traps were placed at nine locations about 2-3 km apart following the river course with five traps operated at each site. The sites were selected primarily for the density of yellow chapote trees but also for vehicular access.

The second area was located further north in the premontane foothills around the town of Allende. Here the yellow chapote occurs in scattered arroyos in the watershed of the Sierra Potrero. This area is more settled with a complex mosaic of small towns, subsistence farms, groves of fruit trees (mainly citrus), and secondary forest. In this piedmont area, five sites were selected for their density of yellow chapote trees and vehicular access. Five traps were operated at each site.

Two weather stations were operated during the study. One station was placed at a montane location near one of the trap sites in the Santa Rosa canyon at an elevation of 1045 m. The other station was located half-way between the two study areas on the grounds of the agricultural research station at General Teran, elevation 330 m. Each station included a recording hygrothermograph and a pluviometer.

Mean numbers of flies captured per unit time were compared by ANOVA. Probabilities of the F-values were calculated with the software program FPROB (Speakeasy Computing 1987).

Results

Population Trends. Numbers of flies trapped followed a seasonal pattern. Figs. 1 and 2 show the monthly captures of female flies trapped over a succession of five years at the two study areas. The trap results show that in their native habitat adults are present at all times of the year but with the captures greatly reduced in the late summer when hot, dry conditions prevail, and in mid-winter when frigid overnight temperatures are the norm. Peaks in abundance occurred at three times of the year: spring (March-April), early summer (June-July), and late fall (October-November). But, in any given year there were usually no more than two peaks, the one exception with three peaks being 1997 at the Allende site. The extra peak in fly numbers that year probably resulted from an exceptionally wet spring. The Teran station recorded 229 mm of precipitation in March and April that year. The mean for the same months in

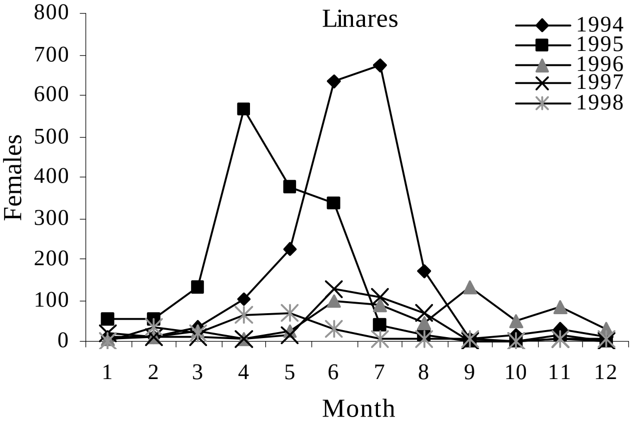

Figure 1. Captures of female Mexflies at Linares, N.L. by month, from 1994 to 1998. (totals from 45 McPhail traps)

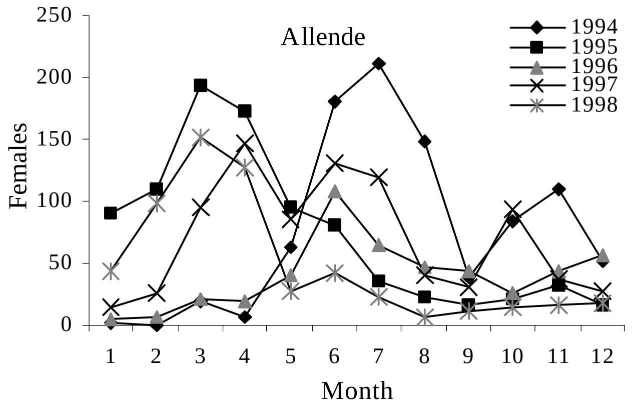

Figure 2. Captures of female Mexflies at Allende, N.L. by month, from 1994 to 1998. (totals from 25 McPhail traps)

the other four years of the study was only 49.3 ± 31.5 mm.

The phenology of the fly population seems to be linked to the host plant, yellow chapote. In a typical year fruit is present from March to May and the major peak in fly numbers occurs in June. The amplitude and timing of the major peak can vary and seems to be strongly influenced by weather. For example, in 1995 the peak occurred much earlier, in March-April, and this appears to have been generated by large numbers of flies that emerged from the overwintering stages in January and February. The winter of 1994-95 was the mildest winter during the study period with no freezing temperatures recorded. By contrast, in the winter of 1997-98 there were 14 dates with temperatures at or below freezing, seven on consecutive dates in mid-December. This could explain why the lowest numbers of flies were captured in the spring of 1998, following the severest winter during the study. The numbers of emerging adults detected at winter's end (Julian weeks 1-10) varied among years and these differences were statistically significant at both Linares (F = 6.772, P = 2.35 x 10^{-4}) and Allende (F = 13.8, P = 2.02 x 10^{-7}).

The amplitude of the springtime peak varied greatly among years and these differences were found to be significant by comparing mean weekly captures from weeks 21-30 at both Allende (F = 24.13, P = 1.04 x 10^{-10}) and Linares (F = 9.74, P = 9.19 x 10^{-6}). Regardless of when the springtime peak occurred, by late summer there was always a low level of activity. Then, with the moderation of temperatures and humidity in the autumn there is a marked increase in numbers trapped, although there were significant differences in the level of activity among years at both Allende (F = 10.95, P = 2.76 x 10^{-6}) and Linares (F = 25.75, P = 3.87 x 10^{-1}). Following the autumnal peak there was a depression in activity levels coincident with the onset of cold weather. Activity remained at minimal levels until the end of winter.

The autumnal increase in captures is enigmatic because although yellow chapote may produce some off-season fruit, abundant fruit are only produced in the spring. Thus a clarification of the origin of these fall flies would seem to be important for understanding the breeding cycle.

Fecundity. Figs. 3 and 4 show the numbers of mature eggs carried per gravid female at the two study areas, Linares and Allende, respectively. The mean number of mature eggs per female was 36.3 at Linares and 40.6 eggs at Allende. The maximum number of mature eggs carried by an individual female was 155 at Linares and 146 at Allende. Table 1 shows

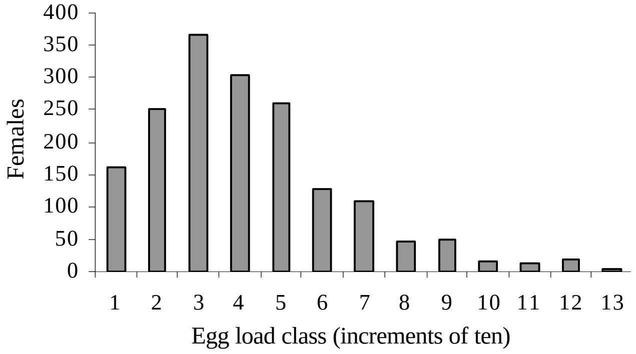

Figure 3. Mature eggs per gravid female captured at Linares expressed as frequency of females with egg load class in increments of ten, i.e., bin 1 = number of females with 1-10 eggs.

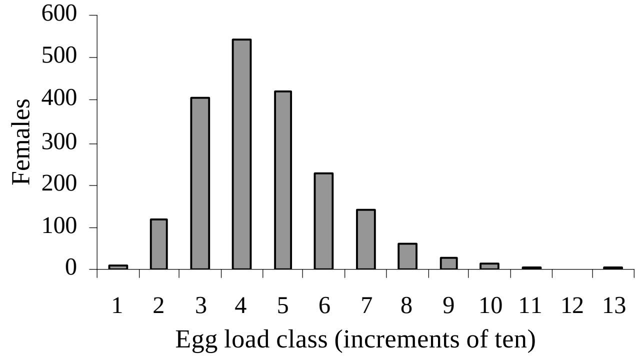

Figure 4. Mature eggs per gravid female captured at Allende expressed as frequency of females with egg load class in increments of ten, i.e., bin 13 = number of females with 121-130 eggs.

Table 1. Fecundity of Mexican fruit fly females: mean numbers of mature eggs per gravid female by site and year.

Site	Year	Gravid flies	Total eggs	Mean eggs/female
Linares	1994	478	17574	36.8
	1995	836	28034	33.5
	1996	158	6787	42.9
	1997	90	3583	39.8
	1998	160	6461	40.4
Total		1722	62439	36.3
Allende	1994	430	15328	35.6
	1995	444	17989	40.5
	1996	225	9772	45.0
	1997	496	21793	43.9
	1998	392	15722	40.1
Total		1987	80604	40.6
Grand Total		3709	143043	38.6

the annual variation in mean egg load at each site over the five year study period from a low of 33.5 eggs per gravid female in 1995, to a high of 45.0 eggs per female in 1996. The variation may be attributable to annual differences in environmental conditions, but there are confounding factors. Warm, wet, weather should enhance nutritional opportunities and promote fecundity in females, but the availability of oviposition sites will tend to reduce the egg load carried by individual flies. Berrigan *et al*. (1988), studying laboratory colonies, reported that females with continuous access to fruit would lay eggs in clutches with a mean of 6.5 eggs per clutch and at peak reproductive age would oviposit an average of three clutches per day. Under mass rearing conditions, Liedo *et al.* (1993) found that females matured eggs continuously at a mean rate of 10.8 eggs per day. Under laboratory conditions in which females were denied fruit, gravid females were found to carry a mean number of 74.7 eggs with a maximum of 233 eggs in one female (Thomas 1998). Therefore, egg load is only an index of fecundity. Conversely, Aluja *et al.* (2001) found no significant difference in egg loads betweenfemales with and without access to hosts and suggested that females may increase maturation rate of eggs to match the oviposition rate. Similarly, the present field study found much greater variation in egg load among females than was reported in the controlled laboratory experiments by Aluja *et al.* (2001).

The periodic changes in the numbers of gravid females in the population is the factor of interest for understanding the breeding phenology. Table 2 shows the proportion of gravid *vs* immature females at each site by year. Under optimal conditions, females do not become gravid until an age of 11 days. Yet, studies of longevity indicate that the half-life of a fly in the wild is only about 10 days (Thomas & Loera-Gallardo 1998). This means that about half of the females in the population never become gravid, and the other half spends the greater proportion of its life span in the pre-reproductive stage. That being so, much less than half of the females captured are expected to be reproductively mature. In three of the five years at the Linares site, the proportion of gravid females was in the range of 24% to 27%, commensurate with expectations. In the other two years though, and in all years at the Allende site, the proportion was much higher, in the 50-65% range. Either the life expectancy is much higher than the 10 day half-life measured in the study by Thomas & Loera-Gallardo (1998), or there was a bias in trapping that favored gravid females over immature females. The study of longevity by Thomas & Loera-Gallardo (1998) deployed the standard McPhail trap with aqueous torula yeast, as did the present study, but only looked at sterile flies.

Figs. 5 and 6 show the pattern of recruitment (new flies entering the population) by providing the numbers of immature flies trapped at each site by month over the five year study period. Sexually immature flies can be found at all times of the year but the peak normally occurs in the early summertime. This reflects emergence of adults from the spring crop of yellow chapote. In addition to the early summer peak, many years show a smaller impulse of activity early in the year at winter's end. This initial activity is attributable to the emergence of adults from the over-wintering puparia. The last year of the study was exceptional in that recruitment essentially failed that year at both sites, and as previously mentioned, this was probably due to the severe preceding winter. Importantly, the autumn peaks in population are not explained by the recruitment of new adults.

Phenology of Egg Production. Tables 3 to 12 track the changes in reproductive status of females over the course of the seasons at both sites. The tables provide the numbers of females captured by week, the proportion of those females that were gravid, and the mean number of eggs carried by gravid females. Because of annual differences in size and phenology of the populations, the results are discussed by year.

1994. In this, the first year of the study, there was a small pulse of activity at the end of February (weeks 9-10) at both study areas. By May (weeks 20-22) the numbers of flies had increased markedly and included a high percentage of gravid

Table 2. Number of gravid and immature females by year and by site

Year	Allende				Linares			
	Gravid	Immature	Total	% gravid	Gravid	Immature	Total	% gravid
1994	430	486	916	46.9	478	1344	1822[1]	26.2
1995	444	442	886	50.1	836	754	1590	52.6
1996	225	255	480	46.8	158	429	587	26.9
1997	496	351	847	58.6	90	285	375	24.0
1998	392	185	577	67.9	160	74	234	68.3

[1] Total includes only dissected flies.

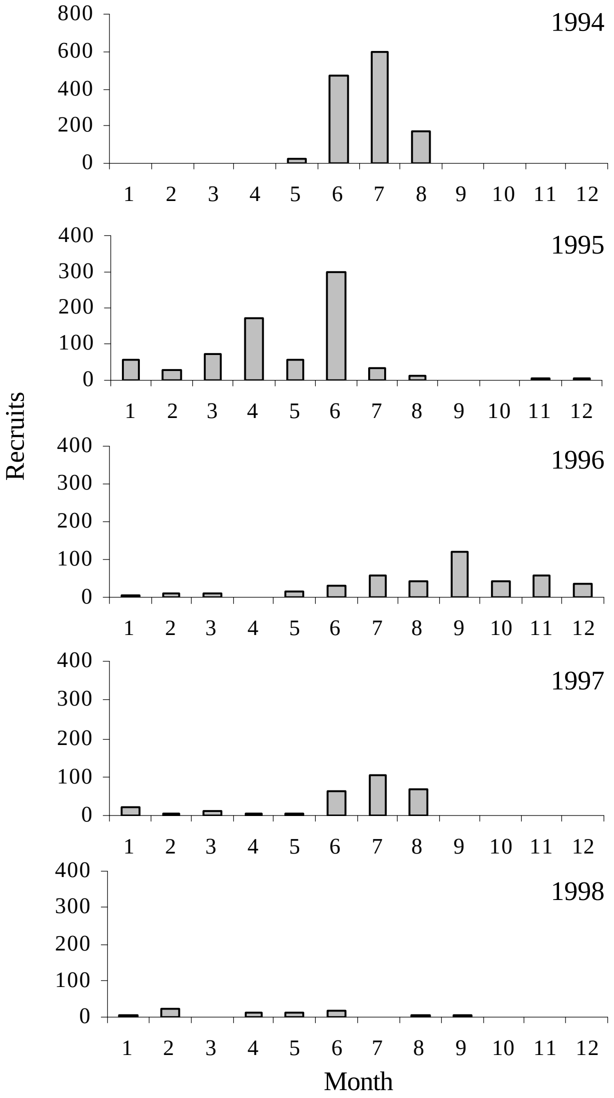

Figure 5. Recruitment of new females (captures of non-gravids) monthly at Linares, N.L. by year, 1994-1998. (totals from 45 traps)

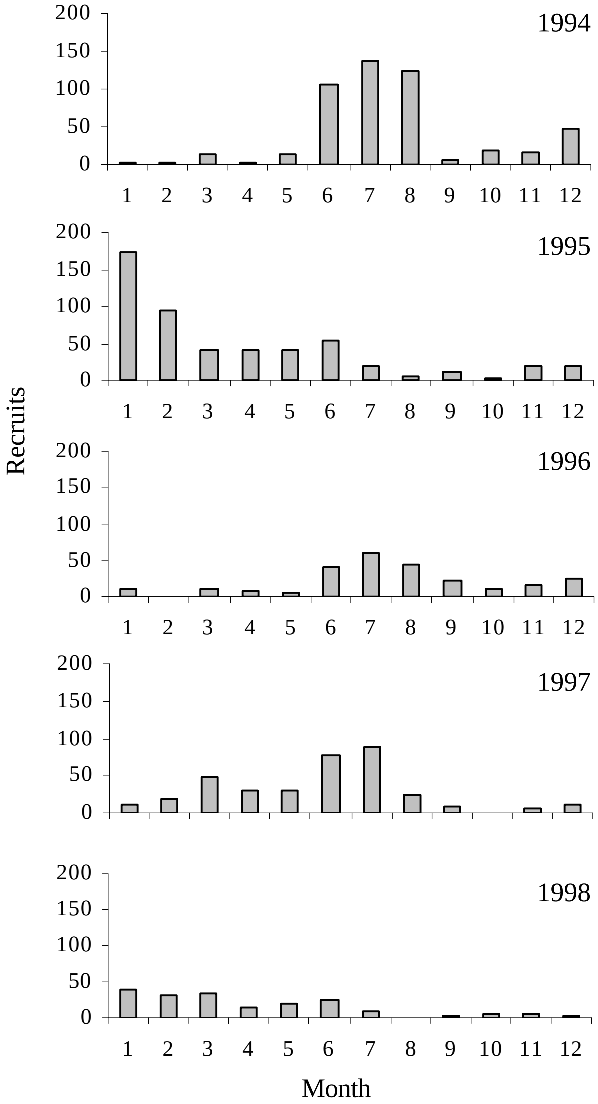

Figure 6. Recruitment of new females (captures of non-gravids) monthly at Allende, N.L. by year, 1994-1998. (totals from 25 traps)

females, around 60% at Linares and around 75% at Allende. Subsequently, there was a large summertime peak in numbers trapped at both sites (Tables 3 and 4). During this peak, weeks 26-30 (July), the percent gravidity was much reduced, in the range of 10-40%. The change in level indicates that the summertime peak was due mainly to recruitment of a new generation of adults.

A very different result was obtained in the makeup of the next peak in fly numbers that occurred in the fall. At both areas for a period of one month in the late summer almost no flies were captured. Then in October (weeks 41-45), flies began reappearing in the traps as the weather turned mild. When the females trapped in October were dissected, 70-90% were gravid. This result suggests that, unlike the summertime peak, the increase in numbers of flies in the traps in the fall resulted from an increase in activity, rather than from emergence. If so, then the fall peak must consist mainly of older flies that had carried over from the summer.

Thus, while capture rates indicate two peaks in abundance, actual recruitment of new flies was strongly restricted to one part of the year, the early summer. At Linares, 91.6% of the immature flies were captured in the three month period between weeks 22-34. Within that period, the majority, 64%, were taken in the four weeks encompassing June. Similarly, at Allende, 75.5% of the immature flies were captured during the three month period inclusive of weeks 23 to 35.

1995. The second year of the study began with a strong pulse of activity in January (weeks 2-6) at both sites (Tables 5 and 6). The percentage of gravid females was low (less than 30%) and even those gravid females were carrying small egg loads. This pattern suggests that the January flies were mostly newly emerged flies parented by the fall population that had overwintered in the puparial stage. The numbers of flies

Table 3. Number of females captured, percent with mature eggs, and mean number of eggs per gravid female, by week. Linares, 1994.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	1	-	-	27	347	10.1	41.5
02	3	-	-	28	134	14.2	39.0
03	1	-	-	29	107	11.2	56.1
04	3	-	-	30	86	8.1	47.0
05	0	-	-	31	27	0.0	0.0
06	4	-	-	32	74	1.4	27.0
07	4	-	-	33	36	0.0	0.0
08	4	-	-	34	33	3.0	40.0
09	10	-	-	35	2	0.0	0.0
10	3	-	-	36	1	0.0	0.0
11	5	-	-	37	0	-	-
12	8	-	-	38	0	-	-
13	9	-	-	39	4	0.0	0.0
14	20	-	-	40	1	100.0	29.0
15	34	-	-	41	5	60.0	25.7
16	21	-	-	42	7	71.4	46.8
17	26	-	-	43	3	66.7	78.0
18	14	-	-	44	4	75.0	48.0
19	17	64.7	35.5	45	6	83.3	58.8
20	15	46.7	35.3	46	9	88.9	31.4
21	19	63.2	31.3	47	5	80.0	32.7
22	161	64.0	31.4	48	3	100.0	35.0
23	114	57.0	31.5	49	7	71.4	34.4
24	88	53.4	33.4	50	3	33.3	66.0
25	77	39.0	37.3	51	0	-	-
26	356	24.7	41.7	52	1	0.0	0.0

Table 4. Number of females captured, percent with mature eggs, and mean number of eggs per gravid female (fecundity), by week. Allende, 1994.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	2	0.0	0.0	27	54	42.6	42.6
02	0	-	-	28	52	28.8	32.0
03	0	-	-	29	47	40.4	36.4
04	0	-	-	30	58	27.6	46.3
05	0	-	-	31	38	15.8	23.2
06	0	-	-	32	63	22.2	41.0
07	0	-	-	33	0	-	-
08	0	-	-	34	47	44.7	39.9
09	5	60.0	28.3	35	27	40.7	48.1
10	15	13.3	58.0	36	10	80.0	39.8
11	0	-	-	37	0	-	-
12	0	-	-	38	0	-	-
13	0	-	-	39	2	0.0	0.0
14	0	-	-	40	0	-	-
15	0	-	-	41	27	77.8	37.2
16	0	-	-	42	28	67.8	31.2
17	7	71.4	19.2	43	29	89.7	36.7
18	16	87.5	35.5	44	16	87.5	37.8
19	0	-	-	45	18	83.3	28.3
20	15	73.3	30.9	46	17	64.7	38.4
21	32	78.1	37.5	47	28	78.6	23.6
22	0	-	-	48	31	54.8	30.1
23	69	27.5	35.2	49	25	40.0	29.9
24	51	51.0	31.3	50	10	30.0	46.3
25	60	48.3	41.3	51	17	29.4	22.4
26	0	-	-	52	0	-	-

Table 5. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Linares 1995.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	3	0.0	0.0	27	17	0.0	0.0
02	16	25.0	28.0	28	10	10.0	46.0
03	21	9.5	26.0	29	11	27.3	43.7
04	14	21.4	29.7	30	2	0.0	0.0
05	19	15.8	48.0	31	5	20.0	24.0
06	10	30.0	19.3	32	2	0.0	0.0
07	4	25.0	49.0	33	4	0.0	0.0
08	20	25.0	23.8	34	2	0.0	0.0
09	5	60.0	42.7	35	0	-	-
10	6	66.7	39.2	36	0	-	-
11	15	46.7	41.7	37	0	-	-
12	43	39.5	28.3	38	0	-	-
13	61	36.1	28.6	39	0	-	-
14	110	58.2	36.8	40	0	-	-
15	118	62.7	36.4	41	0	-	-
16	204	72.1	36.6	42	0	-	-
17	136	82.3	36.8	43	2	0.0	0.0
18	193	93.8	32.3	44	1	100.0	76.0
19	95	84.2	26.5	45	1	0.0	0.0
20	32	75.0	17.4	46	6	33.3	39.5
21	27	66.7	18.0	47	2	0.0	0.0
22	29	55.1	29.3	48	5	20.0	26.0
23	43	14.0	36.6	49	0	-	-
24	61	9.8	50.2	50	0	-	-
25	67	20.9	42.5	51	0	-	-
26	167	6.6	44.9	52	1	0.0	0.0

Table 6. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Allende, 1995.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	8	0.0	0 .0	27	11	54.5	53.8
02	24	29.2	17.9	28	8	50.0	46.2
03	48	6.2	19.3	29	7	14.3	52.0
04	11	18.2	25.5	30	9	66.7	53.2
05	18	11.1	24.5	31	14	64.3	36.2
06	55	25.4	36.8	32	5	80.0	37.2
07	29	20.7	40.3	33	3	100.0	50.0
08	8	50.0	20.0	34	0	-	-
09	55	50.9	42.1	35	0	-	-
10	25	68.0	36.5	36	5	40.0	35.0
11	35	65.7	36.4	37	6	50.0	59.7
12	50	68.0	51.0	38	5	20.0	28.0
13	29	86.2	41.2	39	0	-	-
14	12	41.7	25.0	40	1	100.0	46.0
15	40	77.5	39.7	41	0	-	-
16	68	77.9	39.8	42	10	90.0	40.2
17	53	81.1	37.5	43	10	80.0	55.4
18	32	59.4	51.5	44	4	50.0	36.5
19	22	77.3	34.3	45	4	0 .0	0.0
20	14	78.6	45.1	46	13	30.8	41.8
21	6	83.3	24.4	47	6	33.3	31.0
22	21	14.3	45.3	48	6	16.7	62.0
23	17	17.6	25.3	49	11	0.0	0.0
24	36	11.1	31.0	50	2	0.0	0.0
25	12	50.0	39.7	51	0	-	-
26	15	80.0	47.8	52	3	33.3	64.0

Table 7. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by Week. Linares, 1996.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	0	-	-	27	23	73.9	35.4
02	0	-	-	28	27	25.9	42.7
03	3	0.0	0.0	29	30	6.7	36.5
04	0	-	-	30	6	0.0	0.0
05	1	0.0	0.0	31	4	0.0	0.0
06	1	0.0	0.0	32	2	100.0	23.5
07	2	0.0	0.0	33	8	0.0	0.0
08	6	33.3	14.0	34	7	28.6	32.5
09	4	25.0	101.0	35	25	8.0	32.5
10	4	25.0	57.0	36	40	2.5	18.0
11	5	40.0	60.0	37	37	8.1	43.3
12	5	60.0	62.7	38	39	7.7	32.0
13	4	50.0	40.5	39	17	17.6	41.7
14	0	-	-	40	5	0.0	0.0
15	3	66.7	73.0	41	5	0.0	0.0
16	2	100.0	27.0	42	15	6.7	37.0
17	0	-	-	43	23	17.4	69.7
18	0	-	-	44	23	0.0	0.0
19	2	100.0	37.5	45	16	25.0	29.0
20	2	100.0	50.5	46	19	36.8	48.9
21	8	12.5	39.0	47	16	18.8	29.7
22	11	36.4	38.0	48	10	10.0	36.0
23	21	57.1	43.4	49	6	0.0	0.0
24	50	82.0	48.6	50	14	28.6	58.8
25	16	68.8	34.4	51	4	25.0	35.0
26	9	33.3	22.3	52	7	0.0	0.0

Table 8. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Allende, 1996.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	0	-	-	27	19	21.0	21.8
02	1	0.0	0.0	28	16	6.3	97.0
03	2	0.0	0.0	29	12	0.0	0.0
04	2	0.0	0.0	30	17	0.0	0.0
05	5	0.0	0.0	31	14	7.1	32.0
06	0	-	-	32	8	0.0	0.0
07	1	100.0	40.0	33	14	7.1	69.0
08	0	-	-	34	7	0.0	0.0
09	4	75.0	46.0	35	3	0.0	0.0
10	6	33.3	20.5	36	12	16.7	36.0
11	2	0.0	0.0	37	7	85.7	34.8
12	4	25.0	78.0	38	10	50.0	58.8
13	5	80.0	55.7	39	15	60.0	39.0
14	5	60.0	62.0	40	7	85.7	35.5
15	7	71.4	60.0	41	1	100.0	83.0
16	5	40.0	45.0	42	13	38.5	73.4
17	2	0.0	0.0	43	5	40.0	40.5
18	1	100.0	64.0	44	6	66.7	35.5
19	5	100.0	47.4	45	9	55.5	37.4
20	7	71.4	53.6	46	12	41.7	52.8
21	6	66.7	42.5	47	7	57.1	42.3
22	22	90.9	39.5	48	10	60.0	59.3
23	27	81.5	52.5	49	0	-	-
24	41	68.3	36.2	50	42	59.5	36.7
25	20	50.0	29.3	51	14	71.4	42.4
26	20	35.0	38.4	52	0	-	-

Table 9. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Linares, 1997.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	5	0.0	0.0	27	13	23.1	29.0
02	14	14.3	53.0	28	33	0.0	0.0
03	0	-	-	29	25	0.0	0.0
04	0	-	-	30	37	0.0	0.0
05	2	0.0	0.0	31	20	0.0	0.0
06	0	-	-	32	47	0.0	0.0
07	0	-	-	33	3	0.0	0.0
08	6	0.0	0.0	34	0	-	-
09	0	-	-	35	0	-	-
10	4	0.0	0.0	36	1	0.0	0.0
11	5	20.0	36.0	37	0	-	-
12	3	0.0	0.0	38	0	-	-
13	0	-	-	39	0	-	-
14	2	50.0	74.0	40	0	-	-
15	2	100.0	67.0	41	0	-	-
16	0	-	-	42	1	0.0	0.0
17	2	0.0	0.0	43	1	100.0	31.0
18	0	-	-	44	1	100.0	82.0
19	6	100.0	46.8	45	0	-	-
20	0	-	-	46	1	100.0	71.0
21	11	36.4	32.8	47	1	100.0	54.0
22	0	-	-	48	0	-	-
23	22	27.3	38.3	49	1	100.0	25.0
24	63	50.8	36.6	50	1	100.0	22.0
25	4	75.0	30.7	51	0	-	-
26	38	63.2	39.9	52	0	-	-

Table 10. Number of females captured, percent with mature eggs, and mean number of eggs per gravid female (fecundity) by week. Allende, 1997.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	0	-	-	27	33	33.3	40.2
02	13	69.2	44.8	28	0	-	-
03	1	0.0	0.0	29	64	6.2	41.7
04	0	-	-	30	22	68.2	40.9
05	5	0.0	0.0	31	20	50.0	38.8
06	7	0.0	0.0	32	11	54.4	35.5
07	0	-	-	33	0	-	-
08	14	7.1	58.0	34	10	20.0	39.0
09	1	100.0	74.0	35	1	0.0	-
10	14	57.1	43.5	36	5	60.0	32.3
11	17	47.1	37.2	37	0	-	-
12	0	-	-	38	13	76.9	39.1
13	63	49.2	48.0	39	13	76.9	43.2
14	30	63.3	57.5	40	23	100.0	37.3
15	43	93.0	47.1	41	17	100.0	42.4
16	39	84.6	46.3	42	25	96.0	43.3
17	35	74.3	57.2	43	28	100.0	44.4
18	23	65.2	26.0	44	9	100.0	39.7
19	2	50.0	72.0	45	16	68.7	44.6
20	18	61.1	34.3	46	7	85.7	37.7
21	17	52.9	39.8	47	1	100.0	39.0
22	25	80.0	52.7	48	4	75.0	40.3
23	28	32.1	37.2	49	12	58.3	34.4
24	41	56.1	33.7	50	4	100.0	40.2
25	29	27.6	58.6	51	2	50.0	61.0
26	33	39.4	42.8	52	10	60.0	35.2

Table 11. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Linares, 1998.

Week	Females	% gravid	Fecundity	Week	Females	% gravid	Fecundity
01	0	-	-	27	0	-	-
02	0	-	-	28	0	-	-
03	1	0.0	0.0	29	0	-	-
04	1	0.0	0.0	30	3	33.3	30.0
05	1	0.0	0.0	31	0	-	-
06	18	55.5	34.0	32	1	0.0	0.0
07	10	30.0	44.3	33	2	0.0	0.0
08	4	75.0	32.3	34	1	0.0	0.0
09	6	33.3	34.0	35	0	-	-
10	5	100.0	31.6	36	3	0.0	0.0
11	9	100.0	44.4	37	0	-	-
12	0	-	-	38	0	-	-
13	0	-	-	39	0	-	-
14	6	83.3	39.0	40	0	-	-
15	17	100.0	46.1	41	0	-	-
16	23	91.3	44.3	42	0	-	-
17	17	41.2	42.1	43	1	0.0	0.0
18	17	100.0	42.5	44	0	-	-
19	8	100.0	42.9	45	0	-	-
20	15	93.3	43.8	46	1	100.0	36.0
21	17	94.1	38.1	47	2	100.0	34.5
22	12	41.7	38.8	48	0	-	-
23	11	63.6	29.0	49	3	100.0	40.7
24	7	28.6	30.5	50	0	-	-
25	4	50.0	27.5	51	2	0.0	0.0
26	7	0.0	0.0	52	0	-	-

Table 12. Number of females captured, percent with mature eggs, and mean number of mature eggs per gravid female (fecundity) by week. Allende, 1998.

Week	Females	%gravid	Fecundity	Week	Females	%gravid	Fecundity
01	6	33.3	31.5	27	4	25.0	20.0
02	9	33.3	50.3	28	6	66.7	30.0
03	19	47.4	40.4	29	3	100.0	76.3
04	10	40.0	42.5	30	9	77.8	44.0
05	25	52.0	32.6	31	2	100.0	35.5
06	32	59.4	41.7	32	0	-	-
07	13	61.5	35.1	33	0	-	-
08	28	78.6	40.5	34	2	50.0	34.0
09	24	70.8	41.9	35	3	100.0	43.0
10	33	75.8	41.6	36	4	50.0	30.5
11	27	59.3	40.2	37	4	75.0	42.3
12	37	78.4	42.2	38	2	100.0	33.0
13	30	80.0	39.6	39	1	100.0	32.0
14	38	89.5	42.3	40	5	80.0	41.0
15	32	81.2	39.7	41	4	50.0	40.5
16	30	93.3	40.0	42	1	100.0	48.0
17	27	92.6	38.8	43	4	25.0	2.0
18	21	23.8	31.0	44	4	75.0	54.3
19	0	-	-	45	6	50.0	44.3
20	5	80.0	49.5	46	1	0.0	0.0
21	0	-	-	47	5	80.0	42.5
22	2	0.0	0.0	48	6	83.3	37.0
23	6	50.0	35.3	49	7	85.7	38.2
24	11	72.7	36.3	50	3	100.0	42.0
25	9	33.3	28.0	51	0	-	-
26	16	25.0	29.5	52	1	0.0	0.0

trapped decreased through February, but the percent gravidity increased as the population aged, reaching 67-68% by week 10. At that point the numbers of flies began to increase dramatically with a concomitant dip in the proportion of gravid flies, down to 30-40% at Linares (weeks 12-13), as immature females entered the population. Thereafter, the gravid rate increased to reach 80-90% at the backside of the peak in May. This was followed by a pulse of fly numbers in June (weeks 22-24 at Allende, weeks 23-28 at Linares) where the proportion of gravid flies dropped again to only 10-20%, indicating the emergence of a new generation at the start of the summer, just as in the previous year.

The number of flies trapped was sharply reduced during the late summer (weeks 30-40). But when fly numbers increased again in the autumn (weeks 42-43), the females trapped were 80-90% gravid. Again, the pattern suggests that the fall pulse is due to increased activity, rather than recruitment, and that these are primarily females that have carried over from the peak in the early summer.

1996. The year 1996 was an unusual year, but instructive. Population levels were low at both sites, much lower than in the previous two years, with a small summer peak (weeks 22-30) in fly numbers. Recruitment followed in September (weeks 35-39) with a small pulse of immature flies. Clearly, recruitment was poor at both sites and this is reflected in the maintenance of relatively high rates of gravidity over most of the year (Tables 7 and 8). In other words, the populations were small with a large proportion of mature flies.

This pattern suggests that adult longevity is crucial for carrying the population through seasons when conditions for breeding are unfavorable.

1997. Although the population remained low in 1997 at Linares (Table 9), it rebounded strongly at Allende (Table 10), achieving three population peaks that year. The initial pulse of flies in January were 70% gravid, suggesting that some adults had overwintered. In February the picture was different. Only one of 26 females captured was gravid, indicating emergence of new flies from overwintering puparia. The spring peak followed in March with 50% of the females gravid, which proportion increased to 93% two weeks later. The population ebbed until the next peak in July (week 29) with only 6% of the captured females gravid. As before, this population peak must have resulted from breeding by the March generation. The population ebbed again as usual for the late summer. When the numbers trapped rose in late September-October, weeks 38 to 43, the females captured in those weeks were already 80% to 100% gravid. As in the previous years, the autumn population seems to consist mainly of mature flies which have carried over from the early summer peak.

1998. In the final year of the study, numbers captured were low because of the severe winter. Nonetheless, springtime peaks were achieved at both areas. At both areas there was a gradual increase in numbers trapped and a gradual increase in gravidity (Tables 11 and 12). For example, at Allende, the percent gravidity was 33% in weeks 1 and 2, but this increased to 93% gravid by weeks 16 and 17. Recruitment was at best sporadic during the rest of the year at both areas. Only small numbers of flies were captured over the course of the year with the larger proportion of females captured being mature with eggs.

Discussion

The results of this study indicate that the Mexican fruit fly population is functionally bivoltine in its native habitat in the piedmont of the Mexican Sierra Madre Oriental. In this respect the findings are similar to trapping studies in more tropical regions. In Belize, Houston (1981) reported a major annual population peak in February- March with a minor peak in October-November. The only known host for *A. ludens* was commercial citrus and Houston found no evidence that seasonal changes in the population were attributable to climate or natural enemies. In Chiapas, Mexico, Celedonio-Hurtado *et al.* (1995) similarly found that peak populations followed host fruit availability with little correlation to rainfall or other biotic factors. Weather factors seem to be more influential in northern Mexico.

Breeding occurs mainly in the spring and fall producing a major peak in fly numbers around May-June with a secondary minor peak in October-November. In exceptional years an additional peak can occur in the early spring if the winter is mild and the spring is rainy. Breeding is asynchronous so there is noise in the data. As many as five to six generations may be occurring in isolated patches where microclimates are favorable. But over most of the range the dearth of hosts and inclement seasonal weather restrict activity and effective breeding to the spring and fall. Adults first appear following the winter months leading to oviposition in the spring crop of the primary host plant, yellow chapote. Dissection of females shows that the succeeding late spring peak in numbers consists of new adults entering the population. The great majority of recruitment occurs at this time of year. By contrast, the autumn peak seems to result from an increase in adult activity following the summer nadir rather than from recruitment. Because the developmental rate of the immatures is shortened by high temperatures, very little of the over-summering can be attributable to the preimaginal stages. Eggs oviposited in the early summer would give rise to emerging adults in the mid- to late summer. But, no such generation is seen, rather, at this time practically no flies are caught. Thus, over-summering must be accomplished primarily by the adult stage. There appears to be two possibilities. One can hypothesize that the adults are quiescent to explain why there is so little trap activity in the late summer. Alternatively, perhaps under unfavorable conditions the fly population is sequestral; that is, with survival limited to patches of microhabitats where shade, water and food remain available. Under this scenario, when temperatures and humidity moderate in the fall, the surviving flies disperse, seeking reproductive sites. Both scenarios are consistent with the dissection data from this study which show that the fall adults are already reproductively mature when trap numbers increase.

It can also be inferred that the Mexfly population must use secondary hosts to breed in the fall. At the Allende site a variety of domesticated citrus trees are fructescent at this season and we have found abundant larvae in December, especially in sour orange. However, the Linares study site was located in native vegetation. Here, the autumnal host is unknown to us. The Mexican fruit fly has one of the broadest host ranges of any species of fruit fly, so it is likely that more than one host is involved. Gonzalez-Hernandez & Tejada (1979) found that there can be as many as three generations per year in yellow chapote because of erratic fructification. But in most years there is only a single spring crop and carry-over must be occurring in a secondary host.

The fall peak in activity is crucial because it gives rise to the overwintering brood. Field cage studies have shown that oviposition in October and November will give rise to adults emerging in January and February. This coincides with the first appearance of flies in south Texas and is consistent with our dissection studies showing a pulse of reproductively immature flies early in the year in Mexico.

These studies suggest that the immature stages form the primary over-wintering population, whereas the adults form the primary over-summering population. Some opportunistic breeding in offseason fruit and alternate hosts is undoubtedly occurring at all times of the year, just as there are adults captured in the traps at all times of the year. The longevity of the adults and ability to breed in a wide range of hosts is important for carrying over the population during extended periods of limited breeding opportunities. These are the very characteristics which make the Mexican fruit fly so difficult to eradicate from commercial fruit growing regions.

In its native habitat, the montane canyons and riparian piedmont of the Sierra Madre, the topographic variation provides a patchwork of vegetational and microclimatic diversity. In Texas, California and northern Mexico, the citrus orchards surround and interdigitate with urban residential areas. Backyards would seem to provide the sort of microclimates and off-season hosts that could allow a sequestral population to carry through periods of unfavorable weather.

Because the target of a sterile release program is the breeding population, these studies have implications for the efficient application of an SIT program. If the over-summering population consists of quiescent adults, then virtually all control procedures, including the sterile insect releases, toxic bait sprays, kill stations, fruit stripping and classical biological control will be ineffective at this time, and thus a waste of resources. Conversely, if the over-summering population is sequestral (intuitively the more likely scenario), then bait sprays or kill stations could be effective at this time, but only if focused in those patches where the flies are located, which is probably in urban backyards, rather than commercial groves. Similarly, because most of the fall adults are already gravid, the sterile releases at this time may be inconsequential. Bait sprays in the groves and kill stations targeting the backyards would be more likely to impact the pest population at this time. Canonically, SIT is most effective when the target population is at its low ebb and Holler *et al.* (1984) found that suppression of the Mexfly population in south Texas improved when releases were extended to include summer, even though no adults are trapped at that time.

When resources are limited, control procedures need be deployed in a manner that obtains the greatest efficacy. Our understanding of the breeding cycle of this insect is still at the stage of first approximation. The present data suggest that there could be opportunities to adjust the suppression program as this knowledge becomes refined.

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