

Lekking and the Small-Scale Distribution of the Sexes in the Caribbean Fruit Fly, *Anastrepha suspensa* (Loew)

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Male and female *Anastrepha suspensa* (Loew) had a clumped distribution in the foliage of their guava host plants. Males were no closer to other males than they were to females or than females were to other females. Flies were often found in roughly the same locations over time. However, contemporaries (flies present at the same time) were closer to each other than subsequent flies were to their predecessors. Males were more likely to be found near spots previously occupied by males than they were to spots used previously by females. Some trees had more flies than others, but there was no regional (northwest, etc.) preference within trees. Females were no more likely to be found in the vicinity of clumped (lekking) males than they were by isolated males. About a third of the females taken from inside leks had sperm in their spermathecae, and it is not clear if their motive for being in these areas was sexual. In pairs of males (within 15 cm of each other), the larger fly tends to be in a position farther up the branch, suggesting that larger males may control preferred territories. It seems possible that males attempting to intercept females accumulate in favorable microhabitats where females are likely to be concentrated and that leks have evolved from such clumping.

KEY WORDS: *Anastrepha suspensa*; Caribbean fruit fly; behavior; distribution; leks; sexual selection.

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INTRODUCTION

Male tropical fruit flies often form leks, i.e., aggregated territories from which they broadcast acoustical, visual, and chemical displays and on which mating occurs (e.g., Burk, 1983; Sivinski and Burk, 1987). Such behavior is most likely due either to males clumping near "hot spots" (regions of female concentration) or to female preference for groups of suitors because their proximity facilitates mate choice (Bradbury and Gibson, 1983). A form of the latter argument has been proposed for the evolution of tephritid leks by Burk (1981) and Prokopy (1980). In the strictest sense of this classical female-choice model, aggregations would be limited to areas "that do not fill the habitat normally used by the species for other activities such as feeding, roosting, etc. . . . and . . . which contain no significant resources required by the females except the males themselves. This stipulation includes food, water, roosts, nest sites, egg deposition sites, etc." (Bradbury, 1981).

Evidence is presented here that there are female Caribbean fruit fly hot spots (in this case, regions without obvious resources, but perhaps favorable microenvironments) and that sexually active males may be accumulating where female density is likely to be high. That is, in accord with the first of Bradbury and Gibson's lek models, male interception of mates may have influenced the origin of tropical tephritids' mating aggregations. Also examined are other distribution features, including the influence of male body size on the distribution of males within the lek.

METHODS

Field observations of the distribution of flies on the foliage and fruit of host plants were made sporadically in the spring and autumn for 4 years. All data were gathered from flies on guava (*Psidium guajava* L.) in orchards in Dade County, Florida.

Distance Between Flies. A careful examination of the foliage within reach was made of two adjacent rows of 10 trees each over a period of five consecutive afternoons (1400-1800 EDT/DST; trees 4 m high; \bar{X} canopy circumference = 25.7 m, SD = 3.4 m). The location of flies marked with a piece of tape was placed on the branch (not the leaf), noting the sex of the fly and providing an individual number; 264 female and 159 male locations were so marked. The distances among flies within 1 m of each other, both on the same and from previous days, were measured. One meter was chosen, largely for convenience. Such measurements were used to determine clumping in the following manner. First, a simplifying assumption was made that the flies are distributed underneath the foliage in two dimensions, much as they would be on the inner surface of an inverted bowl. Then, it was supposed that flies are

distributed at random across the tree and so across the 1-m radius, 3.14-m² area zone surrounding a particular fly. If so, then 6% of all flies neighboring should fall by chance in the 0.2-m² circle that bears the original fly at its center and has a radius of 25 cm. Likewise, 19% of randomly located flies should inhabit the 0.59-m² doughnut that covers the area 25–50 cm from the center. Similarly, 31% will be found in the 0.98-m² area 50–75 cm from the fly, and 44% in the 1.37-m² area 75–100 cm away. These proportions are used to create the expected numbers of flies that should fall into the four distance categories and these are then compared to observations with a chi-square test.

The same procedure can be used in looking at spatial distributions over time, i. e., whether the locations used by flies on preceding days are distributed randomly about locations used by flies on subsequent days. Such an analysis cannot detect "loose" aggregations whose interfly distances exceed 1 m. Thus the null hypothesis, "flies are randomly distributed," can be rejected but not upheld. Another difficulty with such a method is that the area around a fly may not extend a full meter in all directions. For instance, a fly near the edge of the canopy would not have a meter of foliage extending in front of it. In this case, all the near-neighbor (0- to 25-cm) area might be present but up to half the far-neighbor area absent. Analysis of these data would exaggerate clumping. If I might anticipate results, I plead that the clumping is so extensive that not even an across-the-board halving of the far-neighbor area would rescue the null hypothesis of random distribution.

The distances between flies were also examined for sexual effects, i. e., if males were likely to be closer to other males or to females, etc. Such comparisons, between both contemporaries and noncontemporaries, were made through Friedman's nonparametric analysis of variance and, when appropriate, the non-parametric Wilcoxon two-sample test.

Also calculated was the sexual distribution of neighbors within 1 m, that is, whether males were more likely than randomly expected to be within 1 m of other males, as opposed to females, etc. This was done by taking the overall proportion of males and females and using an expanded binomial to calculate the expected proportions of male-male, male-female, and female-female neighboring pairs. These expected values were compared to the observed data using a chi-square test.

Distribution in a Field-Caged Host Tree. In support of fieldwork, the distributions of male and virgin female flies were observed in a 2.1-m-diameter, 2.4-m-high field cage surrounding a loquat tree [*Eriobotrya japonica* (Thunb.)] with no fruit present. The tree was divided into 55 numbered 15-cm-long branch sections. Fifty flies, either males or virgin females, were released into the cage, and at hourly intervals between 1000 and 1600 EST the flies located in the various sections were counted. Five replicates of each sex were performed. The tree was washed with water and allowed to stand unoccupied for at least 48 h

between replicates. Data from the hours with the greatest occupancy were compared through a chi-square test to a random distribution estimated from a Poisson distribution.

Position of Single Flies on Branches. The locations of single flies (those > 15 cm from another) of both sexes were noted and the distance from branch tips was estimated by counting how many leaves separated a fly from the branch tip. This was done in order to see if male and female flies, not influenced by nearby conspecifics, tended to inhabit similar parts of the canopy.

Male Size and Position. Trees were searched during the mid to late afternoon period of sexual activity. Males located 15 cm or less from each other were presumed to be lekking, their relative positions were noted, and their wet weights were measured.

Female Mating Status. To investigate the possible motives for female aggregation (for example, virgin females might accumulate in spots with conditions amenable for lek formation), females within 15 cm of other females, but in the absence of males, were captured, dissected, and examined for sperm in the spermathecae. Females taken from inside male aggregations were similarly treated.

RESULTS

Distance Between Flies. The interfly distances were, on average, much less than expected; the flies were highly aggregated (Table I, Fig. 1; $\chi^2 = 640.4$; $P < 0.0001$). There was no difference in mean distance among the various sexual categories of contemporary spatial relationship, i.e., male-male, female-female, male-female ($F = 0.6$; $P > 0.55$). Contemporary flies were closer to each other than they were to flies that previously occupied the area (\bar{X} 32.0 vs 46.2 cm; $Z = 4.5$; $P < 0.00001$); however, there was still considerable clumping over time ($\chi^2 = 35$; $P < 0.001$; Fig. 2). Males tended to be closer to spots previously occupied by other males than males were to spots previously occupied by females or subsequent females to previous males (Table II). The numbers of very intimate groups (flies less than 15 cm apart and usually on adjacent leaves) are shown in Table III.

Table I. The Mean Distance (cm) Between Contemporary Flies of Both Sexes

Type of relationship	N	Mean distance (cm)	SE
Male-male	29	35.3	4.6
Female-female	49	33.3	3.8
Male-female	89	30.2	2.5

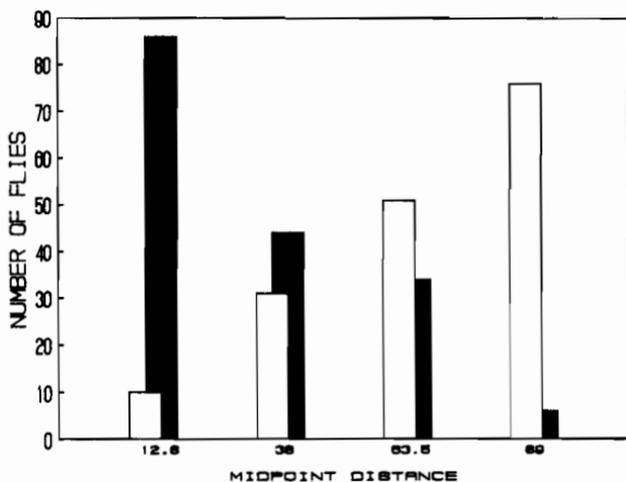


Fig. 1. The number of contemporaneous flies found in distance categories whose midpoints are 12.8, 38, 63.5, and 89 cm (filled bars). Open bars represent the expected numbers if the distribution of flies was random.

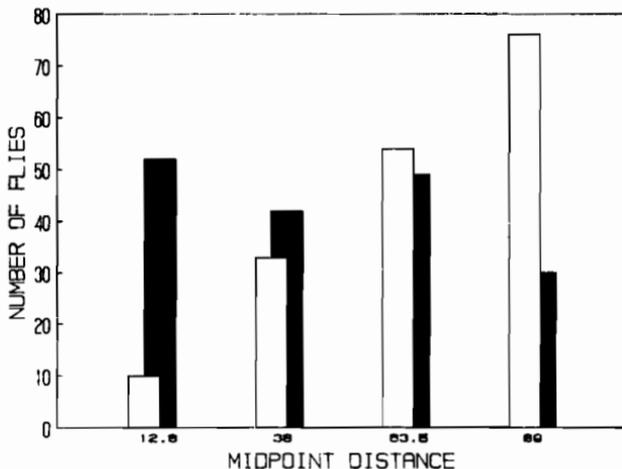


Fig. 2. The number of previous flies found in distance categories of 12.8, 38, 63.5, and 89 cm from subsequent flies (filled bars). Open bars represent the expectations of a random distribution.

Table II. The Mean Distances Between Previous and Subsequent Flies of Both Sexes^a

Type of relationship	<i>N</i>	Mean distance (cm)	SE	<i>P</i>
Male-male	32	38.4	5.3	A
Female-female	73	45.5	3.3	AB
Male-female	71	50.3	3.3	B

^aCategories sharing a letter under *P* are not significantly different (ANOVA/Duncan's multiple-range test).

Female-female neighbors (i.e., within 1 m) were less numerous than expected among flies occurring on the tree simultaneously, whereas male-male and male-female relationships were overrepresented ($\chi^2 = 11.6$; $P < 0.005$; Fig. 3A). Of the spatial relations among flies occupying an area on different days (i.e., subsequent/previous), male-male pairs were again more abundant than expected, as were, to a slight degree, female-female pairs. However, male-female neighbors were less frequent than expected ($\chi^2 = 9.5$; $P < 0.01$; Fig. 3B). These differences between contemporaneous flies and previous/subsequent flies are significant ($\chi^2 = 8.03$; $P < 0.025$).

All of the above calculations underestimate clumping because of the exclusion of a large aggregation found in an identical location on 3 consecutive days. The large numbers of flies, up to nine males and eight females, made interfly distance measurements difficult. Since its occurrence was atypical (it was the largest aggregation witnessed in 4 years of observation) and since its exclusion could only aid the acceptance of null hypotheses, it was removed from consideration. Data from this group are, however, considered in subsequent analyses (see, again, Table III).

Among the 20 observed trees, some acquired a great many more flies than others (6-56 fly observations per tree; $\chi^2 \gg 400$; $P < 0.0001$). Those in the

Table III. The Distribution of Highly Aggregated Flies into Female-Only, Male-Only, and Mixed-Sex Groups^a

Group size	1	2	3	4	> 10
All female	154	7	2	0	0
All male	87	2	0	1	0
Male-female		15	3	1	3

^aFor inclusion each member of the group must be within 15 cm of another member and none must be on a fruit (potential oviposition or feeding site). "Group" size refers to flies with no intimate neighbor.

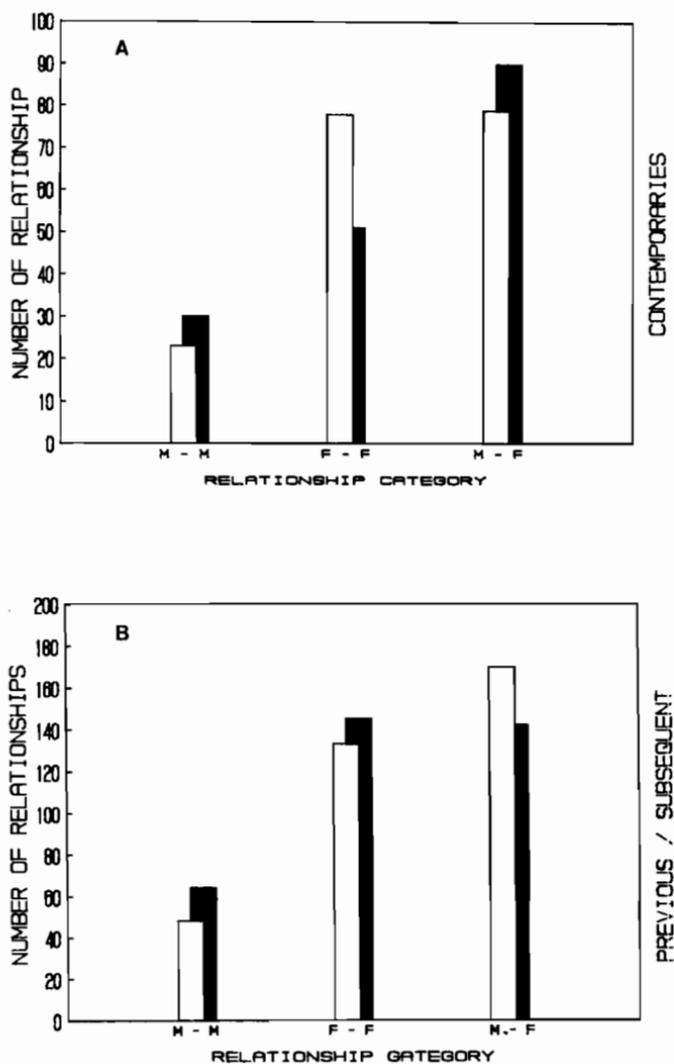


Fig. 3. (A) The numbers of different sexual combinations ("relationships") that occurred between contemporaneous neighboring flies (filled). The open bars represent the expectation of a random distribution. (B) The numbers of different sexual combinations that occurred between subsequent/previous occupants of a location (filled bars). The open bars represent the expectations of a random distribution.

westernmost portion of the study site were particularly densely inhabited. But when individual trees were divided into northwest, northeast, southwest, and southeast quadrants, they showed no significant pattern of regional abundance (Table IV).

Field cage studies support the conclusions from the field that both males and females are aggregated. In four of five cases for females and five of five instances for males, flies were nonrandomly distributed. In the case of this particularly heavily shaded tree, flies of both sexes tended to occupy the most illuminated sections (number of flies in an area correlated with illumination of the area in foot candles—males, $r = 0.45$, $P < 0.007$; females, $r = 0.56$, $P < 0.005$; male occupancy correlated with female occupancy— $r = 0.71$, $P < 0.0001$).

In order to test whether groups of males attracted a disproportionate number of females, the numbers of females within 1 m of clumped males 30 cm or less from each other was compared to the number of females in the vicinity of isolated males without nearby male neighbors. Both types of males had identical mean numbers of females per male (0.65) located within 1 m (46 grouped males near 30 females and 106 isolated males near 69 females). There was no difference in the mean distance between single and clumped males and their adjacent females (29.9 vs 30 cm; $Z = 0.28$; $P < 0.77$).

Position of Single Flies on Branches. Isolated male and female flies tend to occupy similar positions in the foliage: females 3.1 leaves from branch tips ($N = 44$; $SD = 3.1$) and males 3.7 leaves ($N = 22$; $SD = 2.6$; $P = 0.41$).

Male Size and Position. The structure of male aggregations was examined by comparing the weights of male flies that were within 15 cm of each other. Because of the greater ease in capturing two male groups and the greater abundance of this sized group, most of these data are from pairs of flies. In 24 of 33 cases, the innermost fly (i.e., the one occupying the leaf most proximal to the trunk) was larger than the outermost ($\chi^2 = 6.8$; $P < 0.01$). Four matings were observed in the process of collecting these pairs, all involving the innermost male (one case occurred in a four-male lek).

Female Mating Status. A total of 17 females were examined for sperm.

Table IV. The Mean Number of Flies Found in Each Region of Guava Trees After 4 Days of Observation

Region	<i>N</i>	Mean	SE
Northwest	20	2.5	0.6
Northeast	20	3.5	1.3
Southwest	20	2.9	0.6
Southeast	20	2.1	0.5

Eleven of these came from leks, i.e., males were within 15 cm of each other. Four had sperm present; seven had none (three of the four with sperm were taken from the very large lek mentioned previously). Of the six females from all-female aggregations (i.e., females within 15 cm of a neighbor), three had sperm and three were virgin.

DISCUSSION

Female preference for males in groups is one evolutionary force that could drive competing males together into leks (Alexander, 1975; Bradbury, 1981). As is the case in a number of vertebrates, there is little evidence of such a preference here [see Bradbury (1985) for a review of bird and mammal data]. Of the three matings seen during the 5-day mapping, two occurred outside leks. Isolated-male matings were often seen during lekking male collections, further indicating that matings can and do occur outside of leks. The number of females per male within a meter of isolated and grouped males was identical [aggregated calling male crickets also do not attract a higher average number of females/males (Cade, 1981)]. If one looks at intimate mixed-sex groups (flies within 15 cm of each other on adjacent leaves), those groups with a single male contained 1.3 females, and those with multiple males 0.65. Of course, the female sexual "value" may not be the same in both cases. Perhaps only females ready to mate visit leks. If receptive females are rare, this failure of females to be concentrated about leks is not unexpected. But then, why are multiple females found in some single-male groups? Either more than one female has approached a theoretically sexually unattractive single male or a male has come to visit a group of females. The latter possibility raises the intriguing case of all-female aggregations. How do these groups differ from their male counterparts? They might be simple accumulations of flies in favorable microhabitats, and there are two lines of support for this argument. First, in a field cage, virgin females clumped to virtually the same extent and in similar places as male flies. This repeated preference for certain parts of a tree, in the case of this one heavily shaded loquat but the most illuminated, suggests that lighting has an effect on choice of roosting site. Second, similarly, in the field, flies were found in the same location day after day. Sometimes, there would be a sequence of visits to the same leaf.

However, neighbors also appear to influence the locations of flies. The distance between contemporaneous flies is significantly shorter than that between previous and subsequent occupants of an area. That is, although flies often arrive at roughly the same locations time after time, they are closer together when they are at these spots at the same time. Neighboring flies also show a different sexual distribution during simultaneous occupancy. Males are more likely to be with contemporary females than they are to be where females were

on previous days. Taken together, these data suggest that some males may be searching for females that have accumulated at particularly favorable sites in the foliage. Leks may develop where several males have searched out either aggregated females or spots where females might soon arrive and have then set up territories and signaling posts. If so, this is somewhat parallel to the formation of vertebrate leks around female "hot spots" (Bradbury, 1985).

It is interesting from this hot-spot point of view that 4 of 11 females captured within mating aggregations had sperm present in their spermathecae. It is generally thought that remating is rare in tropical fruit flies (Prokopy and Roitberg, 1984). If so, then mated females in leks indicate a nonsexual purpose behind the presence of at least some females in an aggregation. *A. suspensa* females in the laboratory, however, remate several times when given oviposition opportunities (Sivinski, unpublished data), and Hendrichs (1986) noted that mated females remain in leks for a time after copulation. It is not clear, then, if sperm presence is a strong indication of sexual disinterest.

Even if leks are derived from concentrations of males in favorable microhabitats, simple accumulation appears insufficient to account for all the characteristics of the aggregation or the behavior of the males within them. Males are found closer to the locations of previous males than to spots previously occupied by females, and the elaborate male courtships suggest intense female choice (Burk, 1981). The structure size of pairs, with the larger males being more proximal to the trunk, suggests a pattern not likely to form at random around the regions of female location. It is reminiscent of the structure of vertebrate leks, where males in a particular location, often the center, are most likely to copulate (Bradbury and Gibson, 1983). It seems at least possible that males compete for prime positions relative to each other and that large males, being more successful in combat (see Burk, 1984; Burk and Webb, 1983), are more likely to hold the prime location (see Hendrichs, 1986). Recall that the four matings witnessed during male pair collections occurred with inner males. The importance of relative position may be supported simply by the existence of male aggression (see Burk, 1984). Why, after all, fight over a leaf? It would seem either that potentially attractive microhabitats are very small (leaf sized) or prior occupancy increases value, as when leaves become impregnated with pheromone, or that there is an advantage in being in some particular spot relative to sexual rivals. The value of certain sites to males has been demonstrated with captive *C. capitata* (Arita and Kaneshiro, 1985).

Small-scale Caribbean fruit fly distribution raises a number of questions about its mating system. One of the most intriguing, and one still not conclusively answered, is the relative importance of female choice in its origins and subsequent evolution.

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