Lek Distribution in the Mediterranean Fruit Fly (Diptera: Tephritidae): Influence of Tree Size, Foliage Density, and Neighborhood

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ABSTRACT. Based on censuses of a wild population of the Mediterranean fruit fly, *Ceratitis capitata*, this study describes differences in lek numbers among individual persimmon trees and attempts to determine associations between lek number and certain physical and positional characteristics of the trees. Multiple regression was performed using lek number as the dependent variable, and tree height, tree volume, foliage density, distance to nearest eastern neighbor, average distance to 2 nearest neighbors, and total lek number on the 2 nearest neighbors as independent variables. Only tree volume and total lek number on the 2 nearest neighbors showed a positive association with lek number. This finding resulted primarily from an avoidance of the smallest trees and the clustering of 5 trees that harbored the greatest numbers of leks. Factors affecting the distribution of male *C. capitata* are discussed.

INTRODUCTION

The Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), exhibits a lek mating system (Prokopy & Hendrichs 1979, Arita & Kaneshiro 1989, Hendrichs & Hendrichs 1990, Whittier et al. 1992, Shelly et al. 1993). Males aggregate during midday in the canopies of host trees and defend individual leaves as mating territories. While resting on a leaf underside, a male may adopt a "calling" posture by curling his abdomen upward and everting the rectal epithelium, thus releasing a sex pheromone attractive to females (Feron 1962). Following the arrival of a female, the male performs a brief courtship, and (if the female is receptive) mating occurs directly on the territory.

In *C. capitata*, the locations of leks are fairly stable through time and, as a result, leks occur on only a small subset of the available trees. In a Hawaiian fruit orchard, Whittier et al. (1992) found that only about 10% of the available trees harbored leks over a 1-month period and that 80% of all male sightings were on these trees. Similarly, Hendrichs et al. (1991) recorded leks only from 1 tree species (orange, *Citrus sinensis* Ob.) on a fruit and vegetable farm in Greece. It also appears that the great majority of matings in *C. capitata* occur within leks. Isolated males achieved only 2 of the 55 matings observed in the Hawaiian population studied (Whittier et al. 1992). For the Greek population studied, male calling and matings were restricted to the orange trees containing leks (Hendrichs et al. 1991).

While the aggregative tendency of *C. capitata* males is now widely recognized, few data specifically address the question of why leks form on certain trees over others. Existing information focuses primarily on the importance of tree species on lek location. As noted above, Hendrichs et al. (1991) found leks only on orange trees despite the presence of other host and non-host trees and bushes. Studying *C. capitata* in Egypt, Hendrichs & Hendrichs (1990) found similarly that, though leks were not restricted to a single tree species, the incidence of sexual activities varied greatly among different tree species.

While species identity is clearly important, other tree characteristics, such as size, foliage density, and location relative to other trees, probably also influence lek formation by *C. capitata* males. For example, Whittier et al. (1992) described large variation in male

distribution among available persimmon trees (*Diospyros kaki* L.): in censuses conducted over 22 days, more than half of the persimmon trees did not harbor even a single male, whereas a few trees had more than 100 male sightings.

In the course of a previous study (Shelly et al. 1994), we made regular censuses of a natural population of *C. capitata*, noting male and female abundance on individual host trees. As described below, persimmons were the dominant host tree in the study area and also contained the majority of leks. Subsequently, for each persimmon tree we made several measurements regarding its size, foliage density and location relative to other host trees. Here, we describe differences in lek distribution among individual persimmon trees and attempt to identify which of the tree characteristic(s) measured accounted for this variation.

MATERIALS AND METHODS

Study site

Field work was conducted during July–August, 1992, in a fruit orchard near Kula, Maui, Hawai'i (elevation 1150 m). This same site was used in our previous work on reproductive behavior in *C. capitata* (Whittier et al. 1992, Shelly et al. 1993, 1994). The orchard, approximately 0.50 ha in area, was isolated from any other suitable host plants by a minimum of 200–300 m. During the study period, the orchard contained 74 trees with sufficient foliage to serve as potential lek sites. These trees, which were individually numbered with small aluminum tags, included 48 persimmon, 14 Kelsey plum (*Prunus* sp.), 4 lemon (*Citrus limon* L.), 3 peach (*Prunus persica* L.), 2 red plum (*Prunus* sp.), 2 loquat (*Eriobotrya japonica* (Thunb.)), and 1 avocado (*Persea americana* Mill.). All species bore fruit during the study period except persimmon and loquat trees.

Census protocol

Censuses were conducted on 5 days between 12–19 July and 4 days between 12–17 August. On 22 July, we released 7,000 marked sterile flies of both sexes at the study site, but subsequent censuses revealed that these individuals departed the study area within 10 days of release (Shelly et al. 1994). Thus, we are confident that the distributional patterns noted in mid-August were "natural" and were not affected by the release.

Two censuses, 1 starting at 0830 h and the other at 1200 h, were conducted daily. During a census, 2–3 observers examined every tree on the farm and recorded the numbers of calling and non-calling males, females, and matings. Individuals whose sex could not be determined comprised only 0%–8% of the total count and were omitted from the analyses. Leaves and fruit (where present) of each tree were surveyed for 2–3 min by crouching or standing near the trunk as well as walking around the perimeter of the canopy. Based on previous results (Whittier et al. 1992), searching was concentrated on the eastern (i.e., sunlit) portion of the trees. With the exception of the avocado and loquat trees, all trees were less than 3 m high and were easily examined. The avocado and both loquat trees were 6–8 m high and, owing to their larger size, were examined for longer periods (6–8 min each). Even on these trees, however, it appeared that most flies perched on the lower portion of the canopy and were therefore included in the censuses.

Definition of lek

In the present study, a lek was defined as an aggregation of males that included at least 1 actively calling individual. We associated leks with entire trees rather than specific volumes or distances within tree canopies (Prokopy & Hendrichs 1979, Sivinsky 1989, Hendrichs & Hendrichs 1990), because there was always only 1 male aggregation per tree, and males readily moved between leaves within the canopy of a single tree (making it difficult to delimit exactly the boundaries of an aggregation).

Thus, a given tree could harbor only 1 lek per census, but since leks were identified anew each census, a tree could have contained as many as 18 leks (= number of censuses conducted) over the entire study ("lek number" hereafter represents the total number of leks observed on a given tree). This method assumes that, for statistical purposes, censuses conducted on the same day were independent. While the distribution and signaling activity of males in the morning probably had some influence on the afternoon census, we observed males entering and departing leks, indicating turnover in male composition at a lek site, as well as the formation of "new" leks in the afternoon at sites that were unoccupied in the morning of the same day. Based on these observations, we conclude that the assumption of independent censuses, though not strictly upheld, was valid.

Measurements of persimmon trees

Eight tree parameters (height, volume, foliage density, distance to nearest eastern neighbor, distance to 2 nearest neighbors & lek number on 2 nearest neighbors) were measured for each of the 48 persimmon trees for inclusion in multiple regression analysis (see below). All linear measurements were made to the nearest 0.1 m. Height equaled the distance from the base of the trunk to the top of the canopy measured using a long piece of PVC tubing. Volume was estimated as $4/3\pi r^3$ (sphere), where r equalled the average value of 4 horizontal radii plus height/2. Horizontal radii represented distances from the trunk to the edge of the canopy along east/west and north/south axes, respectively. Foliage density equaled total number of leaves between 1–2.5 m in contact with a PVC tube held vertically through the canopy at 10 evenly spaced positions on the eastern half of the tree. At each position, the tube was held 0.75 m (TES arm length) from the outer edge of the
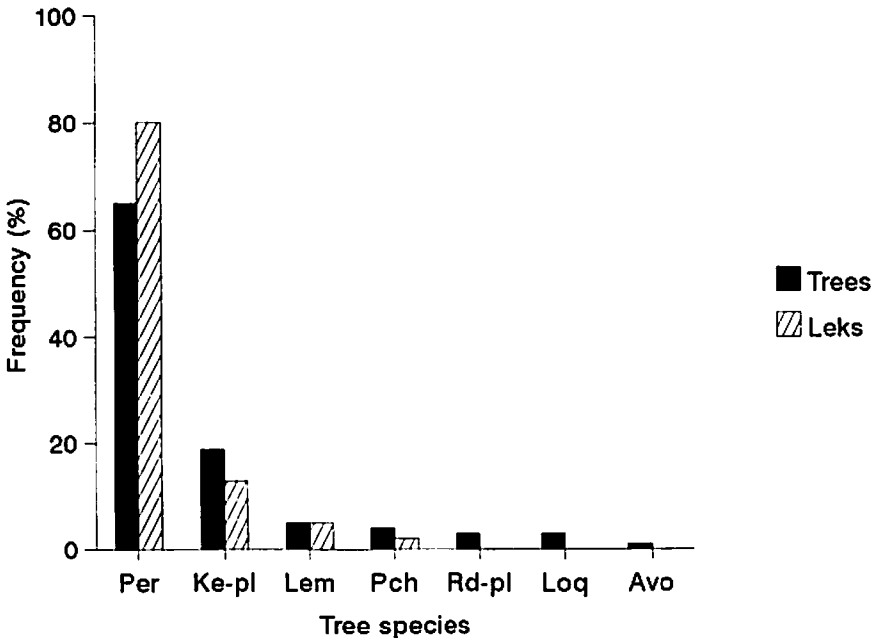

Fig. 1. Frequency distributions of tree and lek abundance. Solid bars represent relative abundance of different tree species at the study site. Hatched bars represent proportion of all leks observed on the different tree species. Abbreviations: Per = persimmon; Ke-pl = Kelsey plum; Lem = lemon; Pch = peach; Rd-pl = Red plum; Loq = loquat; Avo = avocado.
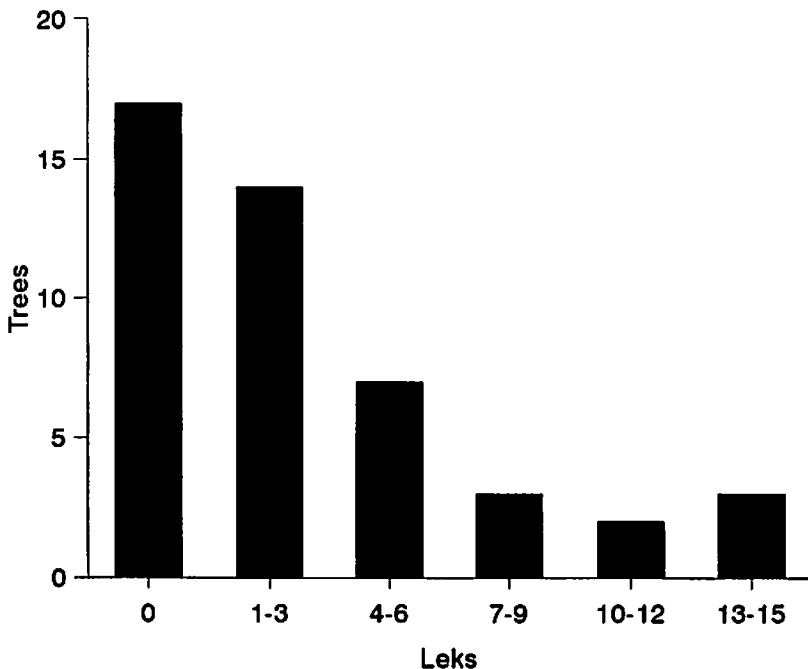
Fig. 2. Frequency distribution of leks among persimmon trees. Abscissa represents total number of leks observed during both censusing periods. Ordinate represents number of persimmon trees that harbored a particular number of leks.

canopy. Distance to nearest eastern neighbor was measured as edge-to-edge distance to nearest tree (regardless of species) in eastern direction. This measure was made to include possible effects of shading (particularly in the early morning) by eastward trees on lek formation on the focal tree. Distance of 2 nearest neighbors equaled average of the edge-to-edge distances to the 2 nearest trees (regardless of species) in any direction. Lek number on 2 nearest neighbors was the total number of leks recorded for the 2 nearest trees (regardless of species).

Data analysis

Multiple regression was performed using the above measurements as independent variables and lek number as the dependent variable. A backward selection was accomplished using the backward selection option of PROC REG in SAS (SAS Institute 1988). Variables were removed if their type II sums of squares had an F statistic with $P > 0.05$. Diagnostic procedures were conducted after model selection. Colinearity was not present, and there were no significant jackknife residuals, leverage or influence. Visual inspection of residuals and normal quantile-quantile plots showed no serious deviations from normality.

RESULTS
Lek distribution among different tree species

Leks were observed on 4 species of host trees, namely persimmon, Kelsey plum, lemon, and peach (Fig. 1). Relative to their abundance at the study site, persimmons harbored a disproportionately large number of leks: though comprising 65% (48/74) of the available host trees, persimmons contained 80% (146/183) of all leks observed ($G = 5.4$, $P < 0.05$, G test with Yates correction).
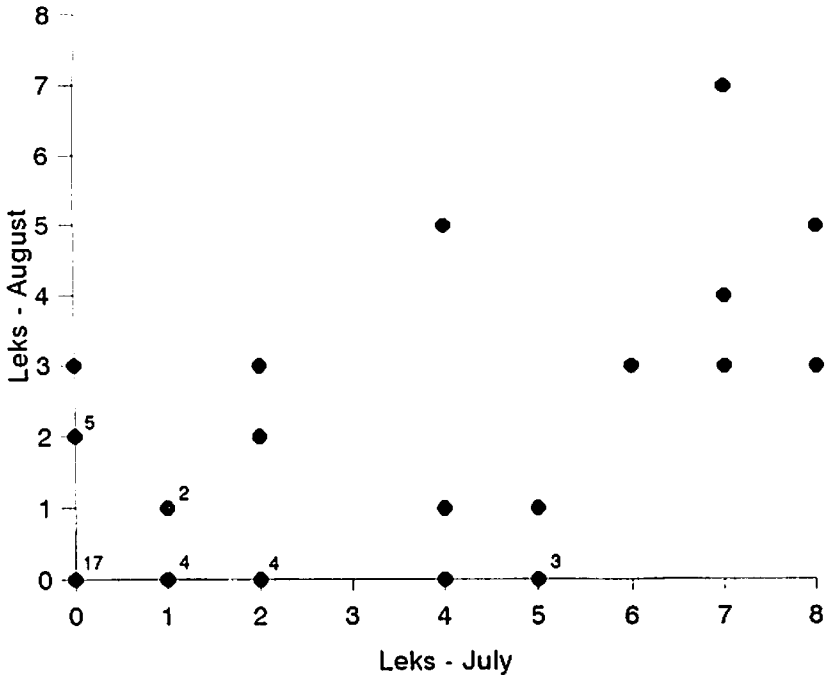
Fig. 3. Number of leks observed on individual persimmon trees during the July and August census periods, respectively. Where 2 or more trees have the same coordinates, the number is given next to the point.

Lek distribution among persimmon trees

Leks were distributed nonrandomly among individual persimmon trees ($C^2 = 31.7$, $P < 0.001$, df = 2, Poisson distribution, Fig. 2). This result derived primarily from the large number of persimmon trees (17/48 = 35%) that contained no leks at all during any census. Among the persimmon trees, lek distribution was relatively stable over time as a positive correlation was found between the numbers of leks present on individual trees during the first and second censusing periods, respectively ($r_s = 0.58$, $P < 0.001$, Spearman rank, Fig. 3).

After model selection in the multiple regression analysis, only tree volume and total number of leks on the 2 nearest trees showed significant association with lek location (Table 1). Perhaps the simplest possible explanation for this result is that males preferentially settled on the largest persimmon trees, which were aggregated at the study site. In other words, male distribution may have simply reflected the distribution of large persimmon trees in the orchard. However, 2 observations suggest that this explanation, though plausible, was not valid. First, males did not preferentially settle in the largest trees: among the 8 most voluminous persimmon trees (top 17% = 8/48), only 1 was ranked in the top 8 trees with respect to the number of leks present. Additionally, the largest trees were not clustered. We compared the average nearest neighbor distance among the 8 most voluminous persimmon trees with average nearest neighbor distances obtained for 100 sets of 8 randomly selected persimmon trees and found that nearly 20% (18/100) of the values obtained for the random sets were lower than that observed for the set of the largest persimmon trees, indicating that the largest trees were not aggregated.

Table 1. Results of multiple regression using backward selection of tree height, tree volume, foliage density, distance to nearest eastern neighbor, average distance of 2 nearest neighbors, and total number of leks on 2 nearest neighbors on lek location (final model: df 2, 44; $r^2 = 0.41$, $F = 15.4$, $P < 0.001$).

Variable	Parameter Estimate	Standard Error	F	P
Intercept	-1.01	0.97	1.1	0.30
Lek number of 2 nearest neighbors	0.37	0.06	28.5	0.001
Tree volume	0.04	0.01	4.7	0.035

Alternatively, rather than being attracted to the largest trees, males may have avoided trees below a certain critical threshold volume and at the same time settled on trees that were close to trees harboring male aggregations. Our data support the notion of a size threshold for tree suitability. The critical size range appeared to be 16–25 m³ as only 20% of the persimmon trees below this size harbored 1 or more leks compared to 75%–100% of persimmon trees above this size (Fig. 4). Although tree size affected the presence/absence of leks, it did not appear to have a marked effect on lek size: the average number of males in a lek varied independently of tree volume ($r_s = 0.10$, $P > 0.05$, $n = 19$, Spearman rank; only trees that contained a minimum of 3 leks were considered).

The apparent clustering of leks, suggested by the positive relationship between the lek number of a given tree and the combined lek number of its 2 nearest neighbors, resulted primarily from the fact that the 5 most frequently used persimmon trees (accounting for 64/146 = 44% of all leks observed on this species) were aggregated. We compared the mean nearest neighbor distance among these 5 trees with mean nearest neighbor distances obtained from 100 sets of 5 randomly selected trees and found that only 1 of the randomly derived values was smaller than the value for the heavily used trees. As a result of this clumping, the 2 nearest neighbors for each of the 5 most frequently used trees were likewise members of this small set of heavily used trees. Spatial clustering of leks was detected only for this set of 5 trees, and similar analyses performed on a larger sets of trees (including the 7 and 10 most frequently used trees, respectively) failed to reveal significant departures from random spacing.

DISCUSSION

The tendency of *C. ceratitis* males to aggregate presumably reflects a way of simultaneously maximizing encounter rates with receptive females and minimizing predation risks associated with sexual signaling. Hendrichs & Hendrichs (1990) and Hendrichs et al. (1991) proposed that these selective pressures are, in large part, responsible for the evolution of lek behavior in *C. capitata*: males attempting to mate on or near fruit would encounter a high proportion of already mated (nonreceptive) females as well as a large number of predators. In addition to shaping the basic "structure" of the mating system, these selective forces might also influence the specific locations of leks in the habitat. That is, leks might be expected to form on trees that are visited frequently by receptive females but infrequently by predators.

The present study does not offer an explicit test of this expectation, since no data on female arrival rates or predation risks were gathered. Nonetheless, the differences observed in lek occurrence between and within tree species allow 3 tentative conclusions
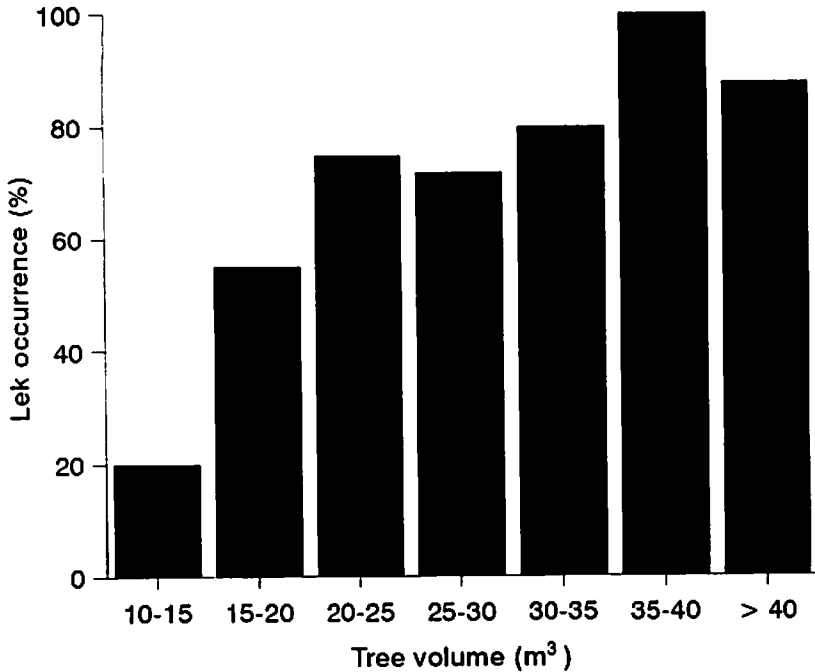
Fig. 4. Incidence of leks on persimmon trees as a function of tree volume. Ordinate represents the proportion of trees within a given size interval that contained at least 1 lek. Numbers above bars represent sample sizes for the different size categories.

regarding the factors influencing male distribution. First, lek sites did not appear to coincide closely with either female egg-laying or feeding sites (see also Hendrichs et al. 1991). Although males settled preferentially on persimmon trees over other available tree species, the persimmon trees bore only green fruit that was not utilized by *C. capitata* females for either oviposition or feeding. The role of female feeding sites in affecting lek distribution requires further investigation, however, as food items other than fruit, such as bird droppings, honeydew and leaf surface microbes, may represent important nutritional sources (Hendrichs & Hendrichs 1990, Hendrichs et al. 1991, Prokopy et al. 1992). Secondly, tree size affected lek distribution in that males appeared to avoid trees below some threshold volume. It is not known why males avoided the smallest trees, but it possibly reflected size-related differences in canopy structure. Among the smallest trees, leaves appeared to be concentrated primarily in the outer portion of the canopy and relatively scarce near the trunk. An open central area possibly allowed greater maneuverability or visibility for aerial predators, such as wasps or birds (e.g., the Japanese white eye, *Zosterops japonica* Temminck & Schlegel) or was a preferred microhabitat for web-building spiders (which were abundant at the study site), thus increasing predation risks on *C. capitata*. In contrast, leaf density appeared similar between the central and peripheral parts of the canopy of larger trees, and aerial predators may have had less success at detecting or capturing prey. Though lek distribution was not related to foliage density in the multiple regression analysis, our measurements were restricted to vertical transects at the edge of the canopy, and cross-sectional transects are needed to compare horizontal leaf distributions of large vs. small trees. Thirdly, lek sites were not formed independently of one another but tended to be aggregated in the habitat. Significant clustering was detect-

ed among 5 persimmon trees that harbored over 40% of all leks observed. As with the formation of individual leks, the aggregation of leks presumably results from male attraction to male-produced sex pheromones (Ohinata et al. 1977). Clustering of leks suggests that male reproductive success is enhanced, not only by signaling on the same tree as other males (i.e., forming leks), but also by signaling on trees adjacent to other lek-bearing trees. Data on the distribution of females among persimmon trees are consistent with this interpretation: female/male ratios averaged 0.79 (SD = 0.51) for leks found on the 5 most heavily used trees compared to only 0.55 (SD = 0.05) for leks occurring on other trees (Z = 2.35, $P < 0.01$; normal approximation to the Mann Whitney test). As noted above, however, significant clumping of leks was restricted to the set of the 5 most heavily used trees and was not detected when the set of trees considered was expanded slightly ($n = 8$). Thus, it appears that other factors may offset the increase in mating opportunities conferred by grouping and thereby limit the tendency for leks to be clustered.

In conclusion, because only a few variables were included in the analysis, this study represents only a first step toward identifying key factors influencing the distribution of *C. capitata* in a natural environment. In particular, additional data should be gathered on the availability of non-fruit food sources, such as bird droppings and leaf surface microbes, which may greatly influence movement patterns in both sexes. Similarly, future studies should attempt to assess predation risks even if indirectly via counts of potential predators in different trees. Inclusion of these and other variables will presumably increase our ability to predict the specific location of leks of *C. capitata*. By placing trimedlure-baited traps in probable lek sites, investigators may improve the effectiveness of control/eradication programs via more rapid detection of incipient infestations.

ACKNOWLEDGEMENTS

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