Novel Analysis of Spatial and Temporal Patterns of Resource Use in a Group of Tephritid Flies of the Genus *Anastrepha*

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ABSTRACT   The spatial and temporal patterns of oviposition-resource use of various *Anastrepha* spp. fruit flies within the canopies of individual fruit trees were determined over periods of 4–6 yr in the state of Veracruz, Mexico. The flies examined were *Anastrepha obliqua* (Macquart), *Anastrepha striata* Schiner, *Anastrepha fraterculus* (Wiedemann), and *Anastrepha alveata* Stone, and their respective hosts were *Spondias mombin* L. (Anacardiaceae), *Psidium guajava* L., *Psidium sartorianum* (Berg.) Ndzu (Myrtaceae), and *Ximenia americana* L. (Olacaceae). The canopies were divided into six sectors: three strata (vertical planes of low, middle, and high canopy) and an exterior and interior component of the various heights. All ripe fruits produced by each tree species were individually harvested, weighed, and maintained until all larvae had exited and pupated. Because of the commonly positive correlation between fruit size and infestation, fly distributions were described using a novel technique, two-level hierarchal regression analysis, as deviations from the expected numbers of insects in a sector given the distributions of fruit weights within the canopy. Overall, there was a tendency for *A. alveata* to be more abundant in the lower portions of the tree, for *A. striata* to be more abundant in the upper, for *A. obliqua* to be less abundant in the upper, and for *A. fraterculus* to be uniformly distributed. The yearly densities of *A. striata* and *A. fraterculus* within the *P. guajava* tree were negatively correlated, and this seems to be due to annual changes in environment rather than to exploitive competition for oviposition resources. Along an altitudinal gradient (0–1,800 m), *A. striata* was more abundant than *A. fraterculus* at sea level and relatively less abundant at altitudes of 1000 m and higher. We suggest that habitat characteristics (oviposition-resource availability and quality, and microclimatic variables), intraspecific competition, and the behaviors of natural enemies and frugivores are potentially important interactive factors that influence the distribution of resource use to a different extent in each of the tephritid species.

KEY WORDS   resource use, spatial distribution, competition, habitat partitioning, altitudinal transect

THERE ARE TWO FORMS of ecological complexity (Earn and Rohani 1999): complexity due to interactions among species (ecosystem complexity) and that which arises from changing patterns of abundance over space and time (dynamical complexity). Descriptions of dynamical patterns of resource use are relatively rare because they often require detailed observations of habitat variance made over long periods. At the same time, they are critical for better understanding the distributions and abundances of organisms. In the case of *Anastrepha* spp. fruit flies, distributions and abundances can have considerable agricultural con-

sequences that in turn influence land use, insecticide use, and the conservation of biological diversity (Aluja 1999).

Dynamic patterns of resource use by herbivorous insects are influenced by variance in the distribution, availability, and quality of resources (Chew 1977). In fruit-infesting tephritids such as *Anastrepha* spp., high variance in oviposition-resources on spatial and temporal scales might lead to discontinuous ranges, genetic divergence among populations, and coarse-grained patterns of abundance within habitats. In terms of individual insects, variance and unpredictability may result in the evolution of behavioral plasticity, the capacity to monitor environmental changes, and competitive adaptations such as host-marking pheromones that help use occasional windfalls (Averill 1985, Aluja et al. 2000, Díaz-Fleischer et al. 2000, Díaz-Fleischer and Aluja 2004). The following are among the specific sources of resource variance confronting *Anastrepha* spp. fruit flies.

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First, there is the distribution of host fruits. Many species, particularly those with broad host ranges, will find oviposition resources in disparate habitats such as patches of tropical evergreen or deciduous forests, large monocrop orchards, and mixed orchards or backyard gardens. The distances among host patches can vary considerably as might the optimal foraging patterns that would best exploit the oviposition opportunities (Aluja and Prokopy 1992, Aluja and Birke 1993). On a smaller (micro) level, a fly must deal with variance within the tree itself given that the distributions of fruit and favorable microhabitats within the canopy may not be homogeneous. Uneven distributions of a number of frugivorous insects, including adult tephritids and the immature parasitoids of Tephritidae, within canopies sometimes reflect this variability (Strong and Levin 1979, Aluja and Birke 1993, Sivinski et al. 1997, Aluja et al. 2000). Some of the important components of microhabitat variance from an insect's perspective are temperature, solar radiation, and relative humidity (Hedström 1992). Similar factors may also influence the distribution of fruits, and hence the distribution of ovipositing females and their offspring (Messina 1989).

Host availability generates the second type of resource variance. Typically, fruit fly hosts have distinct fruiting seasons. The resource is only available for a short period, although the degree of ephemerality varies greatly among tree species (Aluja and Birke 1993). Wild hosts are often more ephemeral than cultivated species, which have been selected to bear fruits over an extended season (van Schaik et al. 1993). Further temporal variance in host availability is added by the unpredictability of the fruiting season and yearly differences in yield, which may be influenced by climate (Herrera 1998). For example, the fruiting of a highly seasonal fruit can be delayed by drought or low temperatures (Reuther 1973).

Finally, components of host quality, i.e., fruit size, color, and degree of ripeness, previous use by conspecifics and the concentration of deleterious allelochemicals, can all vary, some independently of the others (Díaz-Fleischer et al. 2000). Even though a fruit might be of optimal quality based on some physical character such as size, other factors such as stage of ripeness or previous use could be detrimental to larval development (Fitt 1983). Host-marking pheromones, such as used by a number of *Anastrepha* spp., may act to increase the uniformity of egg distribution (Averill 1985, Aluja et al. 2000).

Quantitative information related to resource use by fruit flies under natural conditions is rare, and as noted by Fitt (1989), few studies have considered the role of environmental heterogeneity in determining tephritid abundance. The spatial distribution of infestation in fruit trees has been previously studied in *Anastrepha striata* Schiner in Costa Rica (Hedström 1992), and to some extent, in *Anastrepha fraterculus* (Wiedemann) in Brazil (Salles 1995; adults were captured in food-baited traps). A more complete understanding of the effects of macro- and microenvironments upon the distributions of tephritid larvae would expand our

basic knowledge of insect–host interactions and interactions among competing species of fruit flies. From an agricultural perspective, it may help make better predictions of the potential range of invasive pests and improve sampling regimes for management programs (Averill 1985).

In this long-term study, we have begun to describe patterns of fruit fly resource use by determining spatial and temporal variation in the distributions of larvae of *Anastrepha obliqua* (Macquart), *A. striata, A. fraterculus,* and *Anastrepha alveata* Stone within the canopies of single representatives of their wild host trees in Veracruz, Mexico: *Spondias mombin* L. (Anacardiaceae), *Psidium guajava* L. and *Psidium sartorianum* (Berg.) Ndzu. (Myrtaceae), and *Ximenia americana* (Olacaceae), respectively. In the process we employ a novel statistical method, the two-level hierarchal regression model, to better ascertain the role that fruiting phenology considered here to be fruit availability and fruit size considered here to be host quality play in determining spatial distributions. Studies were carried out over 6 yr in the *P. guajava* tree, 5 yr in the *S. mombin* and *X. americana* trees, and 4 yr in *P. sartorianum* trees. *A. obliqua, A. striata,* and to some extent *A. fraterculus* are considered of economic importance in Mexico due to the damage they cause in mango, *Mangifera indica* L., and guava, *P. guajava* (Hernández-Ortíz and Aluja 1993, Aluja 1994). In contrast, *A. alveata* attacks the fruit of a single wild tree species, *X. americana,* and is of no agricultural significance (Piedra et al. 1993). In addition, the abundances of *A. striata* and *A. fraterculus* in *P. guajava* along an altitudinal transect (0–1,800 m above sea level) were determined, and the regional-scale patterns and their environmental correlates were used to help interpret the within-canopy distributions of the flies.

Materials and Methods

Study Sites. The study sites were in or near the villages of Tejería and Llano Grande in central Veracruz State, Mexico. Tejería is located at 19° 22′ N latitude and 96° 53′ W longitude, at a mean altitude of 1000 m above sea level. Llano Grande is situated at 19° 22′ N latitude and 96° 56′ W longitude, and a mean altitude of 950 m. Climates at both sites were semihot and humid (Soto 1986), and the environments were characterized by an abundance of wild fruits as well as various species of cultivated but insecticide-free trees (e.g., mango) (López 1996, López et al. 1999). The host trees *X. americana, P. sartorianum,* and *S. mombin* were located at Llano Grande, and the *P. guajava* tree at Tejería.

Samples of *Anastrepha* spp. infesting *P. gaujava* along an altitudinal transect were taken at 26 locations in Veracruz. These were grouped in nine categories according to altitude (200 m each) (see Sivinski et al. 2000) for a list of study sites.

Division of Tree Canopy. To systematically sample fruit, the tree canopies of a *P. guajava, P. sartorianum,* and *X. americana* were divided into six sectors formed by the combinations of three equal strata (low, middle

and high; vertical plane) and two zones establishing an interior area (around the trunk) and an exterior area (periphery of the tree canopy). Due to the limited foliage and the absence of fruit in the lower portion of its canopy, the *S. mombin* tree was only divided into two strata (mid and high). Subdivisions were accomplished using string and 6-m metal tubes. The height of each stratum was determined relative to tree height, starting with the point where the foliage first occurred and continuing to the top of the tree.

Process of Fruit Harvesting. The studies were carried out over 6 yr in a *P. guajava* tree, 5 yr in *X. americana* and *S. mombin*, and 4 yr in the *P. sartorianum* tree. Every day (or every third day, depending on the fruit tree species), all fully mature fruit, those of ripe color and that detached when lightly struck, were collected using a wooden pole, and placed individually in a plastic container with date and location data. Each fruit was transported to the laboratory and weighed the same day it was harvested. Vermiculite (Strong Lite Products Corp.; Seneca, IL) was then added to each container to provide a pupation medium for the larvae. Subsequently, the fruit was inspected every second day to ascertain whether the vermiculite needed to be moistened or whether the fruit was starting to rot. If a fruit was totally covered by mold or had disintegrated due to rotting, it was removed from the container and dissected to determine whether any larva or pupa remained in the pulp. All larvae and pupae were kept in vermiculite until either a fruit fly or parasitoid emerged, which were identified by species and sex. A more detailed description of this methodology can be found in Sivinski et al. (1997).

Climatic Information. The environmental conditions prevailing during a 14-h period (0500–19:00 hours) were periodically quantified in various sectors of the host trees. Temperature, relative humidity, and light intensity were recorded using sensors connected to an electronic data logger (Easy Logger R 900, Omnidata International, Logan, UT). For the purpose of statistical analyses, average daily values for temperature, relative humidity, and light intensity were calculated in the tree sectors during the fruit-collecting season each year other than 1998. No sensors were placed in the *X. americana* tree in 1993, and the low-external and high-external sectors were never sampled in *X. americana*, *P. guajava*, and *P. sartorianum*. Climatic factors in the external sections of the *S. mombin* were not monitored.

Altitudinal Transect. Because environmental changes on a regional level might parallel those that occur on a smaller scale among the microhabitats within a canopy, *P. guajava* fruit along an altitudinal transect (0–1,600 m) were collected in batches according to date, altitude, and collection site. For sample locations, altitudes, and environmental characteristics see Sivinski et al. (2000). Once adult insects had emerged, they were identified by species (see above).

Statistical Analyses. The primary spatial analysis was accomplished through a two-level, hierarchical regression analysis (Ojeda et al. 1999) in which level 1, "fruit," represented every single fruit harvested, and

level 2, "day," was sample date. Explanatory variables in the models were strata (height), zone (interior or exterior), sector (strata by zone), fruit weight, consecutive number of each sampled fruit, sampling date, and the response variable was number of pupae per fruit (adults per fruit for *Psidium* spp. because *A. striata* and *fraterculus* were not distinguishable as pupae). This analysis included a fixed effect part used to characterize the effects of tree sectors (i.e., strata by zone) and random effects to estimate the variance components for each level (Longford 1993, Goldstein 1995). Only the variability for fruit level (level 1) was studied, because the variances between days were not significant. The data from the *P. sartorianum* were insufficient to perform this analysis. Comparisons of fruit weights in various sectors were made through two-way analyses of variance (ANOVAs) (height by zone), followed when appropriate, by Tukey's honestly significant difference (HSD) test for the separation of means. One-way ANOVAs and Tukey's HSD test were used to compare mean environmental factors (temperature, relative humidity, and light intensity) in the various sectors of the tree species. The proportions of adults of *A. striata* and *A. fraterculus* that emerged from *P. guajava* fruits along an altitudinal gradient were compared assuming binomial distributions for each altitude.

Results

General Infestation Patterns. At the end of the study, a total of 23,483 fruits had been individually harvested and maintained. Of these, 52.1% were *S. mombin*, 18.2% *P. sartorianum*, 15% *X. americana*, and 14.7% *P. guajava*.

Environmental Patterns within Tree Canopies. The fruiting season distributions of mean temperature and relative humidity were relatively homogeneous within the canopies of *P. guava*, *P. sartorianum*, *X. americana*, and *S. mombin*, with only occasional and minor deviations. Light intensity showed greater variability, and in *X. americana* and *S. mombin* there was a consistent pattern of greater light falling on the higher portions of the foliage. There was greater annual variability in the light intensity patterns of *P. guajava* and *P. sartorianum*, presumably because of growth of the tree and/or the surrounding foliage.

Distributions of Fruit Weights within Canopies. There were several instances where the mean weights of fruits occurring at different heights or in the exteriors or interiors of the canopies differed significantly. However, these were inconsistent, and there was no obvious across-species pattern of particular fruit sizes occurring in certain areas of the canopies.

Relationship between Fruit Weight and Infestation. There was often a positive correlation between fruit weight and the numbers of larvae the fruits contained (Table 1). This may have been due to either females that increased their clutch sizes in larger fruits, and/or to females that were progressively more willing to lay eggs in previously attacked fruit as fruit size increased. Evidence that the later occurred can be
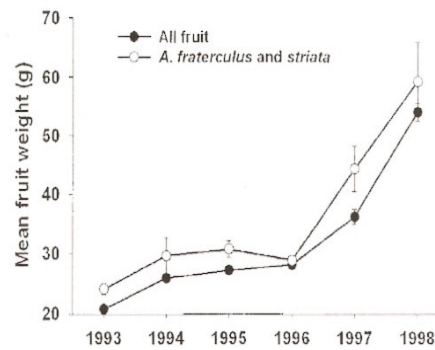
Table 1. Relationships between fruit weight and the number of pupae (adults for *Psidium* spp.) the fruits of various species contain as derived by the two-level hierarchal regression models

Year	P. guajava/ striata	P. guajava/ fraterculus	S. mombin/ obliqua	X. americana/ alveata
1993	0.25 (0.02)		0.80 (0.05)	
1994		0.07 (0.01)	0.13 (0.04)	
1995	0.06 (0.01)	0.03 (0.01)	0.67 (0.05)	0.02 (0.01)
1996		0.13 (0.01)	0.32 (0.04)	−0.10 (0.03)
1997		0.11 (0.03)	0.47 (0.08)	0.19 (0.07)
1998	0.07 (0.02)			

Only statistically significant correlation coefficients (r) are presented. Numbers in parentheses indicate standard errors of estimates. Fruit and fly species are paired at the top of the table. Years in which a particular fly and tree combination were not sampled are empty. For sample numbers, see Table 2.

Fig. 1. Relationship between sample year and mean (standard error) fruit weight in the *P. guajava* tree. Although the mean weight of the fruit increases steadily over the sample period, those fruits that contain both *A. striata* and *fraterculus* (i.e., must contain multiple clutches of eggs) are consistently heavier (Wilcoxon paired T test; T = 0, P < 0.05).

inferred from the sizes of the *P. guajava* fruits that contained both *A. striata* and *A. fraterculus*. These fruits must have received multiple clutches because at least one female of each species oviposited and were consistently larger than the mean sized fruit on the tree (Fig. 1). It was not possible to discriminate multiple from single clutches in fruits that contained only one fly species, but fruits that contained either *A. striata* or *A. fraterculus* alone over the years were not consistently larger than averages. The two tephritids are capable of recognizing each other's host-marking pheromones (M.A., unpublished data) and were presumably able to recognize previous ovipositions by both their own and the other species.

Spatial Distribution of Infestation. Statistically significant examples of heterogeneity in the spatial patterns of infestation are presented in Table 2. Time contributed significantly to the variability of the spa-

tial distributions in only a single instance (*A. fraterculus*, 1995; Table 3). That is, in general, the distributions of larvae within the canopy did not change over the fruiting season. As noted above, there was often a significant positive correlation between infestation and fruit size, and the two-level hierarchal regression models took these relationships into account. Thus, in a simple sense, the models predicted the numbers of larvae per fruit that should have been present in a sector given the weights of the fruit that occurred there and then compared that prediction to the actual numbers collected.

In all six sample years, *A. fraterculus* had a homogeneous distribution throughout the canopy of *P. gua-*

Table 2. Mean numbers of pupae per fruit (adults per fruit for *Psidium* spp.) in various host trees and the significant deviations from these overall means in various parts of the canopy as derived by the two-hierarchal regression models

Fly species	Year	n	Mean	CV	Interior			Exterior		
					Low	Mid	High	Low	Mid	High
A. P. guajava										
A. striata	1993	468	3.85 (0.17)	82	−1.21 (0.52)					
A. striata	1995	413	1.27 (0.09)	134	−1		0.74			
A. striata	1998	220	8.30 (0.43)	68					+5.27 (2.42)	
B. S. mombin										
A. obliqua	1993	1,432	2.80 (0.05)	65		−0.55 (0.21)	+0.35 (0.14)			
	1994	2,092	1.07 (0.03)	113						−0.25 (0.12)
	1995	3,811	2.80 (0.03)	69			−0.33 (0.09)			
	1996	2,418	2.10 (0.04)	83			−0.23 (0.12)			
	1997	2,486	2.45 (0.04)	64		+0.42 (0.18)				−0.21 (0.08)
C. X. americana										
	1996	970	0.53 (0.03)	195	+1.84 (0.36)		−1.05 (0.35)		−0.84 (0.35)	−1.19 (0.35)
	1997	929	1.29 (0.04)	93		+0.77 (0.34)		+0.76 (0.33)	+0.66 (0.33)	

These deviations are presented as either − or + numbers that can be compared directly to the overall means. That is, a deviation of +1 designates that, on average, there was one more pupae per fruit than the overall mean in that particular sector of the tree. If there was no significant difference from the overall mean in a particular sector of the canopy then the data were excluded. Numbers in parentheses are standard errors of estimates. CV refers to the coefficient of variation (s/mean *100) of the infestation of all of the fruit sampled, and n the numbers of fruit sampled. The canopies of different trees had different numbers of sectors (see descriptions of section location in the body of the table). Results for *P. guajava* refer only to the most abundant fly species for that year, except for 1995 when numbers of two *Anastrepha* spp. were similar. In 1993, in *X. americana*, the number of fruit sampled was too low to perform the analysis, but the mean and other values are still provided.

Table 3. Variability (σ^2_o) of pupae per fruit (adults per fruit for *Psidium* spp.) among days as derived by the two-level hierarchal regression models, i.e., the significance of time in explaining the spatial distribution of larvae

Anastrepha species	Year	Days	σ^2_o	t
A. *P. guajava*				
striata	1995	26	0.06 (0.06)	1
fraterculus	1995	26	0.46 (0.22)	2.1*
	1997	22	9.32 (8.50)	1.1
striata	1998	79	5.98 (8.56)	0.7
B. *S. mombin*				
obliqua	1994	20	0.11 (0.12)	0.92
obliqua	1995	22	0.43 (0.27)	1.6
obliqua	1997	25	0.12 (0.16)	0.75
C. *X. americana*				
alveata	1996	18	0.001 (0.15)	0.007

When σ^2_o equaled 0, i.e., when the spatial distribution of oviposition showed no temporal pattern, the data were excluded. A significant value means that the spatial distribution changed in a consistent manner over time. Significance is determined through the division of σ^2_o by its standard error of estimate resulting in a Student's t-value ($t > 1.9$ results in $P < 0.05$) and is represented in the table by *. In the *P. guajava* tree, only the most numerous *Anastrepha* species was considered, the exception being 1995 when both species had similar abundances. In 1993, the number of sampled fruit in the *X. americana* tree was too small to analyze.

java. However, in two sample years, A. *striata* was significantly less likely than expected to oviposit in fruits in the lower interior sectors of the same tree and was more likely to be in the upper interior and mid exterior sectors on one occasion each. A. *obliqua* was on two occasions less likely to infest fruits in the upper exterior of the tree, on two occasions (1994 and 1997) was less dense and once more dense in the upper interior, and once more dense and once less dense in the middle exterior. In *X. americana*, A. *alveata* was less likely to be found in fruits from the upper interior (1 yr), upper exterior (1 yr), and mid exterior sections (1 yr). However, it was more likely to infest fruits in the interior and exterior mid levels (1 yr each), and the lower exterior (1 yr).

Overall, there was a tendency for A. *alveata* to be more abundant than expected in the lower portions of the tree, for A. *striata* to be more abundant in the upper, for A. *obliqua* to be less abundant in the upper, and for A. *fraterculus* to be uniformly distributed.

Potential Competition and Distributions of A. fraterculus and A. striata. The relative numbers of adult A. *striata* and A. *fraterculus* obtained from the study tree fluctuate considerably over time (Fig. 2). The proportions of fruit infested by A. *striata* and A. *fraterculus* in *P. guajava* over the six sample years are negatively correlated (Fig. 3). This could reflect exploitive competition that favors one species and then the other because of yearly changes in some environmental variable, or be merely due to changes in environmental variables that would cause a particular
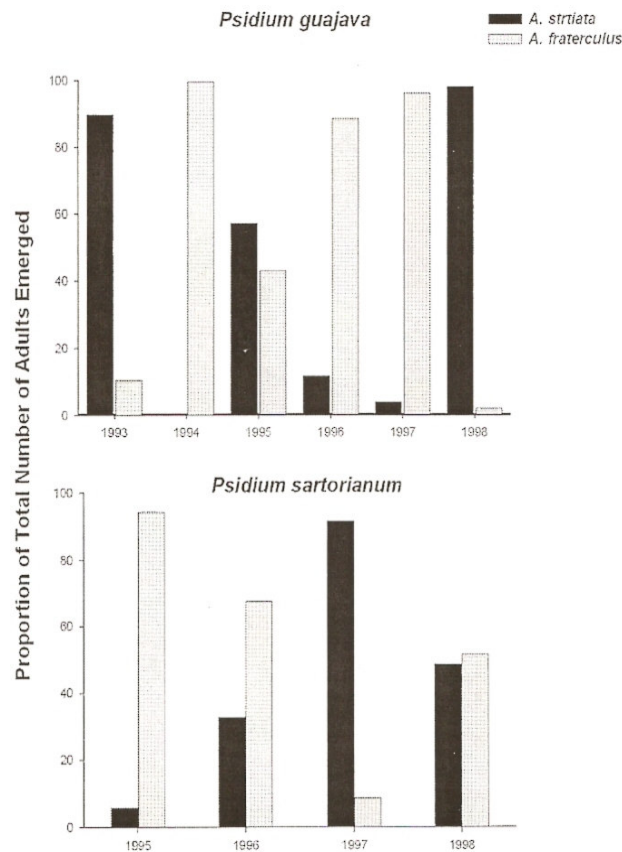

Fig. 2. Yearly proportions of A. *striata* and *fraterculus* obtained from the fruits of the *P. guajava* tree.
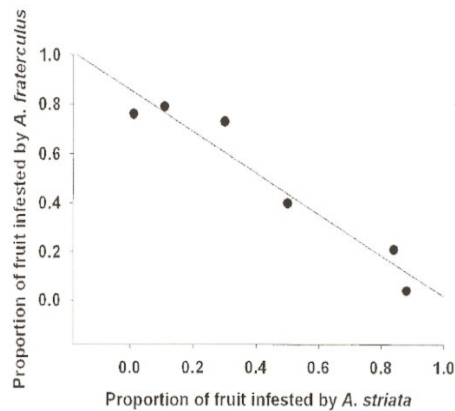
Fig. 3. Relationship between the proportions of *P. guajava* fruits infested by *A. striata* and *fraterculus* over a period of 6 yr.

species to flourish or not regardless of whether the other species was present. If competition were important to the pattern of relative abundance, and if there are situations (e.g., alternative hosts) where infestation levels are relatively low and the competition for oviposition sites is less, then the abundances of the two species should be less correlated in these less competitive environments. However, if there is still a negative relationship between the abundances of the two species regardless of the likelihood of competition, then some fluctuating environmental factor that favors one species over the other is more likely to account for the pattern. For example, in *P. sartorianum*, infestation levels were much lower than in *P. guajava*. Competition for oviposition sites was presumably much lower as well, and there is still a significantly negative correlation between the proportions of fruit infested by *A. striata* and *A. fraterculus* ($r = -0.99$, $P < 0.007$). This would suggest that some factor other than exploitive competition is responsible for the success of one species relative to the other.

However, there may be a curious relationship between the relative abundance of the two tephritid species and the relative weights of the fruit they infest that may indicate competition for larger fruits as oviposition sites. Although not significant ($r = 0.80$, $P = 0.20$; only 4 yr yielded relevant data and the sample size is small), as *A. fraterculus* becomes more numerous compared with *A. striata*, there is a tendency for *A. fraterculus* to be found in progressively larger fruits relative to those infested by *A. striata*. Should further collections confirm this relationship, it may be that both species prefer to lay eggs in larger fruits but that *A. striata* is somehow able to sequester these larger fruits to a greater extent.

Altitudinal and Climactic Factors Correlated to Relative Distributions of A. fraterculus and A. striata. What might be the environmental factors that seem to favor either *A. fraterculus* or *A. striata* in the focal tree? There may be some indication in the distributions of the two species along the altitudinal gradient. Mean annual temperature and precipitation had been pre-

viously obtained for 12 sites that occurred at altitudes ranging from 35 to 1, 400 m in the area under study (Aluja et al. 1998). These environmental factors could potentially effect fly distributions and were significantly correlated to altitude (Sivinski et al. 2000; $r[\text{temperature}] = -0.88$, $P < 0.0003$; $r[\text{percipitation}] = 0.73$, $P < 0.0007$); i.e., mean temperature decreased and rainfall increased with greater altitude.

Over both sampling years (1996 and 1997), *A. striata* predominated over *A. fraterculus* at lower altitudes (0–600 m; all altitudes refer to above sea level) and *A. fraterculus* was significantly more abundant than *A. striata* at altitudes higher than 1000 m. In 1996, *A. fraterculus* was equally as abundant as *A. striata* at sea level (0 m), and *A. striata* predominated over *A. fraterculus* at sites located between 200 and 600 m ($P < 0.001$), but *A. fraterculus* was predominant between 600 and 1,800 m (Fig. 4a). In 1997, *A. striata* was significantly more abundant from 0 to 600 m ($P < 0.001$), whereas between 600 and 800 m the proportion of species was similar ($P > 0.05$); and at 800 m or higher altitudes, the proportion of *A. fraterculus* was much higher than that of *A. striata* ($P < 0.001$) (Fig. 4b). In both years, *A. striata* was completely absent in *P. guajava* at altitudes >1,600 m. However, *A. fraterculus* was encountered, albeit in small numbers, at all sites.

Altitudinal distributions suggest that *A. striata* prefers warmer and drier environments than *A. fraterculus*. As noted earlier, in terms of expected numbers of flies, *A. striata* was twice underrepresented in the bottom interior of the focal tree and twice overrepresented in the top and mid-marginal sectors. The former locations correspond to the darker regions of the tree, whereas the later locations correspond to the brighter. *A. fraterculus* had a consistently homogeneous distribution within the canopy.

The yearly fluctuations in the proportions of *A. fraterculus* (Fig. 3) are correlated to the mean high temperatures recorded yearly in the host tree canopy (Fig. 1; $r = 0.97$, $n = 5$, $P < 0.006$). This is the opposite of what might be expected from the altitudinal transect.

Environmental Factors Correlated to Distributions of A. obliqua and A. alveata. There was a tendency for *A. obliqua* to be less abundant than expected in the upper portions of the canopy, and this region in *S. mombin* corresponded to brighter parts of the foliage. *A. alveata* was somewhat less likely than expected to be found in the upper portions of the canopy and more likely in the lower. In *X. americana*, these lower portions of the canopy tended to be darker. Temperature and relative humidity tended to be similar throughout the canopies of both trees.

Discussion

Because we sampled all the fruits of a single tree of each host species over long periods, there are certain conclusions about dynamic complexity in fruit fly distributions that we can reach with confidence and others that we cannot. We were not able to test
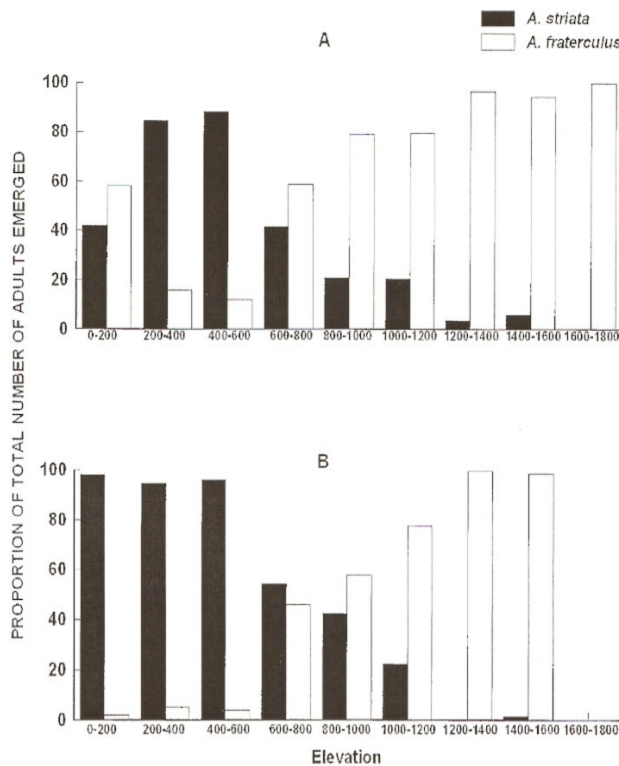
Fig. 4. Distributions of *A. striata* and *fraterculus* along an altitudinal gradient over two consecutive years, 1996 (a) and 1997 (b).

whether particular tephritid species prefer certain portions of the canopies of their different hosts; this would have required samples from multiple trees of each species. However, we were able to look in detail for repeated resource-use patterns in trees under relatively constant conditions, and this allows us address whether there are spatial and temporal components to oviposition site foraging by *Anastrepha* spp. and to speculate on what some of the factors influencing foraging might be.

Overall, there were repeated patterns that suggest that female oviposition was influenced by the canopy environment. There was a tendency for *A. alveata* to be more abundant than expected in the lower portions of the tree, for *A. striata* to be more abundant in the upper (but see Hedström 1992), for *A. obliqua* to be less abundant in the upper, and for *A. fraterculus* to be uniformly distributed. Typically, these spatial patterns of infestation did not change during the fruiting periods of the host trees, although the differences in fruit size within the canopy had a consistent effect on the numbers of fruit fly larvae within fruits. *A. striata* and *A. fraterculus* not only have different patterns of distribution within the canopy of their shared host but also have different distributions along an altitudinal gradient, with *striata* more abundant at low altitudes and *fraterculus* at high altitudes.

Any or all of three factors might result in nonrandom distributions of fruit fly larvae in the canopies of host trees: 1) environmental characteristics, abiotic

and those pertaining to fruit quality, that define optimal larval habitats may have spotty distributions and ultimately lead to heterogeneity of infested fruits either through female preference for better sites or larval mortality in less suitable locations; 2) potential competition among larvae may lead females to overdisperse their ovipositions over time leading to homogeneity; and 3) females may oviposit to minimize the risks posed by parasitoids and frugivores, in which case the numbers of eggs laid may be greatest in canopy areas that are least available to natural enemies.

Environmental Heterogeneity. There was suggestive evidence on a geographical scale that *A. striata* and *fraterculus* had different abiotic environmental requirements. *P. guajava* sampled at increasing altitudes contained progressively fewer *striata* and more *fraterculus*, and among the differences in the region associated with higher altitudes are decreasing mean temperatures and greater rainfall (Sivinski et al. 2000). Although there were occasionally greater numbers of *A. striata*/fruit in the upper portions of the *P. guajava* canopy, there was no evidence that this portion of the canopy was consistently warmer or drier than other sectors. However, in two instances there were fewer larvae per fruit in relatively dark portions of the canopy and in another instance more larvae per fruit in a bright part.

Environmental factors were also implicated in the strong negative relationship between the proportions of *P. guajava* fruits containing either *striata* or *frater-*

culus, i.e., when one was abundant the other tended to be proportionally rare. There was no evidence that this correlation was due to competition between the species; indeed a similar relationship occurred in the lightly infested *P. sartorianum* where the possibility of larval competition was much less (see below). Thus, the relatively minor environmental changes experienced in a single location over several years seemed to profoundly influence the composition of the local *Anastrepha* guild.

Intraspecific and Interspecific Competition. Although there were a number of instances of significant heterogeneity in the distributions of larvae per fruit within the tree canopies, there were many other cases, notably in *A. fraterculus*, where fruits throughout the tree contained similar numbers of larvae. This could either be the result of large numbers of randomly laid eggs, or of females avoiding the previously laid eggs of competitors that they were likely to recognize through "oviposition-deterring pheromones" (Averill and Prokopy 1989, Díaz-Fleischer et al. 2000).

There are circumstances where larval overdispersion through competition avoidance might be recognized. For instance, there may be preferred microhabitats within the canopy or females may initially lay their eggs at random. Regardless, if previous ovipositions force females to progressively lay their eggs in less desirable or less infested parts of the tree canopy, then the variance in the spatial pattern of infestation should change over time. That is, oviposition would be localized at first but spread over time through the canopy resulting in increasing homogeneity (Averill and Prokopy 1989). However, time was a significant factor in the larval distributions of only a single tree-year. Neither did exploitive competition seem to explain the yearly changes in abundance of *A. striata* and *A. fraterculus*, because their relative numbers are correlated regardless of larval density, which should influence the degree of competition.

Competition avoidance may have played a role in the common positive correlation between fruit size and the number of larvae per fruit. Several factors could explain the relationship, including large fruits being more visible to females, but if females on large fruits tend to increase the number of eggs in a clutch [e.g., as in *Anastrepha ludens* (Loew); Berrigan et al. 1988] or are more likely to lay in larger fruits that already contain eggs (Díaz-Fleischer et al. 2000), then minimizing competition among larvae might ultimately be the basis for the correlations.

Natural Enemies and Frugivores. In addition to environmental factors and competition, it is possible that females chose oviposition sites to avoid the local guild of braconid parasitoids that represents a considerable danger to the larvae. Parasitism in some Mexican host trees commonly exceeds 50% (Sivinski et al. 1997, 2000; López et al. 1999). If parasitoids have predictable environmental preferences or are less likely to forage in certain portions of the canopy, fruits in such locations might be particularly attractive to flies. For example, in all of the tree species examined in this study, fruits containing parasitoids tend to be smaller

on average than infested fruits in the same tree without parasitoids (Sivinski et al. 1997). This may be due to smaller fruits providing less shelter to larvae feeding in shallower pulp. Thus, the commonly observed pattern of more larvae in larger fruits might be either due to females avoiding larval competition or placing their offspring in a relatively safe location. Mexican fruit fly parasitoids only occasionally display heterogeneous within-canopy distributions, with a weak tendency be more common in the lower portions of the canopies (Sivinski et al. 1997; but see Sivinski et al. 1999).

In summary, there were some instances of spatial heterogeneity in the numbers of *Anastrepha* larvae per fruit in the canopies of host trees, and these greater or lesser abundances in different parts of the canopies seem to be consistent enough over time to be due to oviposition site preferences. The exact nature of these oviposition preferences are unknown, but the data suggest explanations. Environmental factors that change with altitude or on an annual basis seemed to be important in the abundance of at least some of the fly species considered, and perhaps scattered favorable microhabitats within canopies result in spotty patterns of oviposition. The possibility that females spatially organize their oviposition to minimize the competition faced by their larvae received less support, largely because patterns of infestation rarely changed over time and competition avoidance should generate increasing homogeneity of infestation over time. The importance of avoiding natural enemies and frugivores has seldom been considered in the discussion of *Anastrepha* oviposition patterns and its influence is unclear.

Finally, we offer a caveat concerning the scale of the sampling procedure, a caution about the overinterpretation of the data, and a proposal for further research. First, because of the effort involved in a project of this scope and duration, the canopies of the trees were divided into only four to six sectors, and biologically important phenomena might have occurred at a finer scale and gone unnoticed in comparisons among sectors. For example, suppose *A. fraterculus* had a hypothetical preference for relatively small, highly shaded microhabitats that occur sporadically throughout the canopy. What was actually a highly spotty distribution could seem in our analysis to be homogeneous. Thus, we are cautious about the overinterpretation of our negative results. However, it seems likely that broad differences between the tops and bottoms, and edges and interiors, of canopies are likely to be ecologically significant, and our positive results support the use of this scale of sampling. In the future, we suggest that the present work be used as a guide for the formation of hypotheses that can be tested at a finer scale, perhaps by observing individual *Anastrepha* females and examining their movements and oviposition decisions as they forage within the foliage of their host trees.

Acknowledgments

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