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Forest Fragments as Barriers to Fruit Fly Dispersal: *Anastrepha* (Diptera: Tephritidae) Populations in Orchards and Adjacent Forest Fragments in Puerto Rico

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ABSTRACT McPhail-type traps baited with ammonium acetate and putrescine were used to monitor populations of *Anastrepha obliqua* (Macquart) and *Anastrepha suspensa* (Loew) in two orchards with hosts of these flies (mango, *Mangifera indica* L., and carambola, *Averrhoa carambola* L.), as well as in forest fragments bordering these orchards. Contour maps were constructed to measure population distributions in and around orchards. Our results indicate that *Anastrepha* populations are focused around host fruit in both space and time, that traps do not draw fruit flies away from hosts, even when placed within 15 m of the host, and that lures continue to function for 6 mo in the field. The contour mapping analyses reveal that populations of fruit flies are focused around ovipositional hosts. Although the trapping system does not have a very long effective sampling range, it is ideal, when used in combination with contour analyses, for assessing fine-scale (on the order of meters) population distributions, including identifying resources around which fly populations are focused or, conversely, assessing the effectiveness of management tools. The results are discussed as they pertain to monitoring and detecting *Anastrepha* spp. with the McPhail-type trap and ammonium acetate and putrescine baiting system and the dispersal of these flies within Puerto Rico.

KEY WORDS fruit fly, trapping, *Anastrepha obliqua*, *Anastrepha suspensa*, fruit fly-free zone

The genus *Anastrepha* (Diptera: Tephritidae) includes a number of economically important species (White & Elson-Harris 1992, Aluja 1994). The presence of these flies, including *Anastrepha obliqua* (MacQuart) and *Anastrepha suspensa* (Loew), can have direct consequences for fruit growers wanting to export their fruit. Fruits that are known hosts of these flies, such as mango (*Mangifera indica* L.: Anacardiaceae), cannot be exported to some countries, or must be subjected to expensive postharvest treatments, such as hot water immersion (Sharp et al. 1989). Fruit for which there are no data concerning their host status face the same restrictions until the host status is demonstrated unequivocally (see Jenkins and Goenaga 2007, 2008b; Aluja and Mangan 2008). Some localities maintain fruit fly-free zones that are certified not to have these flies, and orchards within the certified area are not subjected to the same restrictions as areas where these flies are known to occur (Simpson 1993). Among the

evidence used to demonstrate the absence of these fruit flies in an area is regimented trapping in and around the area. Regulatory agencies, such as APHIS-PPQ use traps to detect exotic fruit flies, including *Anastrepha* species (Anonymous 2010). As such, a premium is placed on the ability to monitor and detect these flies.

The McPhail-type trap (Great Lakes IPM, Vestaburg, MI) is the most widely used trap in operations that monitor and detect fruit flies (Steyskal 1977, Aluja et al. 1989, Anonymous 2010). Although the mechanics of this trap have changed little, much research has been conducted with the aim of improving its efficiency (see review in Epsky et al. 1993, 1995; Heath et al. 1993; Cruz-López et al. 2006; Kendra et al. 2008; Thomas et al. 2008). The most consistent factors of the trap are the yellow color and that liquid, usually water, is used to maintain and preserve the flies in the trap (Díaz-Fleischer et al. 2009). Various attractants are used in the trap, but the most commonly used are fruit juices (Kovaleski et al. 1999), or protein-based baits, including ammonium acetate in combination with putrescine, torula yeast, or corn protein hydrolysate (e.g., Thomas et al. 2001, Jenkins et al. 2011). Ammonium acetate in combination with putrescine is the standard for monitoring and detecting *Anastrepha* spp. (Anonymous 2010). The trap and lure combinations have many shortcomings, including low trap effi-

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ciency, illustrated best by Díaz-Fleischer et al. (2009). Recapture rates range from 0.5 to 37.1%, although between 1 and 10% is more typical (Thomas and Lora-Gallardo 1998, Kovaleski et al. 1999, Hernández et al. 2007, Díaz-Fleischer et al. 2009).

Most studies monitoring fruit fly abundance and biology are conducted in fruit orchards (Aluja et al. 1996, Pingel et al. 2006, Hernández et al. 2007, Kendra et al. 2010, Jenkins et al. 2011) for the simple reason that this is where the fruit flies are and where growers do not want them. These studies are useful in demonstrating trends for farmers wishing to monitor or control populations in a relatively homogenous landscape. For instance, the large-scale orchard study conducted by Aluja et al. (1996) demonstrated that flies are captured inordinately at the orchard edge. Similarly, Kendra et al. (2010) estimated the effective sampling range for McPhail-type traps baited with torula yeast and borax or ammonium acetate and putrescine, which they defined as the maximum distance at which relative trapping efficiency was still above 25%. They determined this distance to be between 20 and 30 m for *A. suspensa* in a guava orchard, with the wind playing an important role.

Such information is useful in planning a control program for orchards, but may not be applicable for regulatory agencies trying to detect exotic tephritid species in a landscape mosaic or for monitoring populations in an area-wide suppression and management program. In Puerto Rico, APHIS-PPQ deploys detection traps on naturalized host trees, including *Mangifera indica*, *Spondias mombin* L. (Anacardiaceae), *Psidium guajava* L. (Myrtaceae), and *Terminalia catappa* L. (Combretaceae) (Anonymous 2010). These trees usually are isolated from other hosts and always near roadways (to facilitate access to field technicians). Would the effective sampling range of these traps be the same in a natural area as in an orchard? Furthermore, treating orchards without considering the dynamics of fruit fly populations outside the orchard is to disregard important components of their biology, including their ability to disperse through and longevitate in natural areas.

Preliminary studies by our lab indicate that hosts of *A. obliqua* and *A. suspensa*, such as mango, *Spondias mombin*, *Spondias purpurea* L., (Anacardiaceae), *Psidium guajava*, *Syzygium malaccense* (L.), *S. jambos* L. (Myrtaceae), and *Terminalia catappa*, are rare in natural landscapes in the arid south of Puerto Rico and tend to be focused near homes and towns. These trees rarely are observed in natural areas (e.g., Guánica Dry Forest or Susua State Forest), except along rivers and roads, where all of these hosts can be common (D.A.J., unpublished data). Furthermore, fruit from trees in south Puerto Rico consistently harbor significantly fewer *Anastrepha* larvae than fruit from trees in western Puerto Rico and more humid parts of the island (D.A.J., unpublished data). The apparent lack of hosts in these natural areas and their low infestation rates led us to believe that these areas might be significant barriers to the dispersal of *Anastrepha* and could be

exploited in an area-wide management plan or eradication effort.

We trapped *Anastrepha* fruit flies in two orchards and two natural areas adjacent to these orchards. The primary goal of this study was to document the spatial and temporal distributions of *Anastrepha obliqua* and *A. suspensa* inside of orchards and in natural areas adjacent to the orchards.

Materials and Methods

Thirty plastic multilure traps were placed in orchards in a grid (six rows with traps on five trees per row on alternating host trees). Thirty traps also were placed at different distances from each orchard. Traps were hung ≈ 1.5 m above the ground and were placed within 15 m (± 5 m) of adjacent traps. Traps were baited with ammonium acetate and putrescine (Suterra, LLC, Bend, OR) and baits were refreshed every 6 mo (19 August 2010, 22 February 2011, and 18 August 2011). Water was used as a trap fluid and traps were filled two-thirds full (≈ 350 ml). Trap fluid was changed as needed, based on its clarity. Traps were checked weekly between 26 August 2010 and 27 December 2011. *Anastrepha* species were removed, identified, and counted and voucher specimens were deposited in the University of Puerto Rico, Mayaguez Campus, in the Department of Biology Arthropod Collection.

Sites. Global positioning system coordinates of both sites are given in Table 1 and the locations of the sites on the island of Puerto Rico are depicted in Fig. 1. Traps were placed in a carambola (*Averrhoa carambola* L.) orchard on the University of Puerto Rico's Agriculture Experimental Station in Juana Diaz, Puerto Rico, (see <http://goo.gl/maps/QIOR3> for an interactive satellite image of this site) and in a commercial mango orchard immediately adjacent to the Guánica dry forest in Guayanilla, Puerto Rico (see <http://goo.gl/maps/7hTaM> for an interactive satellite image of this site). Traps also were placed in a transect moving away from the orchards and into the forest (the Juana Diaz site) or along the forest border (the Guayanilla site) because cliffs prevented us from entering the forest.

Statistical Analyses. Spatial analysis with Surfer 8.05 (Golden Software, Inc. 2002) was used to generate contour maps of the *Anastrepha* populations in the two fruit orchards and their adjacent forest study sites. The radial basis (multiquadric) function was used as the interpolation algorithm with default values of the function parameters R^2 (smoothing) and h (anisotropy). Radial basis functions comprise a group of interpolation methods that attempt to faithfully honor data points (exact interpolators), and the multiquadric method has been shown previously to generate good representations of insect distributions based on discrete trapping data (Arbogast et al. 2000, 2003; Kendra et al. 2010).

Pearson's product-moment correlation was conducted for traps at each site to see whether the num-

Table 1. Total and mean number of *Anastrepha* spp. captured in orchards and adjacent forests, along with proportion females

Site/coordinates	Total flies captured		Mean flies captured per trap (± standard deviation)		Proportion females	
	<i>A. obliqua</i>	<i>A. suspensa</i>	<i>A. obliqua</i>	<i>A. suspensa</i>	<i>A. obliqua</i>	<i>A. suspensa</i>
Juana Diaz carambola orchard 18° 01'51" N 66° 31'41" W	1,826	372	61.9 ± 41.0	12.4 ± 11.0	0.81	0.78
JD forest 18° 01'52" N 66° 31'39" W	146	21	4.9 ± 14.0	0.7 ± 1.3	0.84	0.71
Guayanilla mango orchard 17° 58'24" N 66° 49'02" W	362	3	12.1 ± 14.0	NA	0.84	0
Guayanilla forest 17° 58'23" N 66° 49'03" W	13	0	0.4 ± 0.8	NA	0.69	0

ber of *A. suspensa* in a particular trap was correlated to the number of *A. obliqua* in that trap.

Results

Fruit fly abundance varied widely over time (Figs. 2, 3, and 4), between sites (Table 1), and within sites (Figs. 5, 6, and 7). High *Anastrepha* populations were correlated with the availability of hosts (Figs. 2 and 3). Lures continued to attract fruit flies 6 mo after deployment (Figs. 2–4).

Of the six species of *Anastrepha* reported from Puerto Rico (Norrbom 2004, Jenkins and Goenaga 2008a), we trapped two: *A. obliqua* and *A. suspensa*. We also captured seven male *Toxotrypana curvicauda* Gestaecker (Diptera: Tephritidae) from the forest adjacent to the mango orchard in Guayanilla. More *A. obliqua* and *A. suspensa* were caught in the carambola orchard in Juana Diaz than in the mango orchard or in either of the adjacent forest fragments. *Anastrepha obliqua* was common in the mango orchard in Guayanilla and adjacent to the carambola orchard in Juana Diaz.

In the mango orchard in Guayanilla, the number of flies captured was coincident to the availability of fruit, with 95% of all flies captured between July and October (Fig. 2), when mangoes were mature. The distribution of fruit flies over time in the carambola

orchard was also coincident to the availability of fruit (Fig. 3). The distribution of flies over time in the forest adjacent to the carambola orchard is broadly similar to the pattern within the orchard (Fig. 4).

The distribution of flies among traps in orchards and forest fragments was not equal, i.e., some traps caught more flies than would be predicted if flies were equally abundant throughout space (Figs. 5–7). To illustrate this, we list the percentage of flies captured in the five traps (16.7% of the total traps deployed at each site) capturing the most flies during the study:

- 1) In the mango orchard at Guayanilla, the five traps catching the most *A. obliqua* accounted for 67% ($n = 241$) of all of *A. obliqua* captured in the orchard (Fig. 5).
- 2) In the carambola orchard in Juana Diaz, five traps accounted for 35.7% ($n = 662$) and 41.7% ($n = 155$) of all *A. obliqua* and *A. suspensa*, respectively, captured in the orchard (Figs. 6 and 7).
- 3) In contrast, in the forest adjacent to the carambola orchard in Juana Diaz, one trap (3% of all traps deployed at that site) accounted for 50% of all *A. obliqua* captured, with a further 17% the total *A. obliqua* capture coming from a second trap. Both of these traps were on or in proximity to a host (*Spondias mombin* and mango, respectively). The five traps with the highest capture at this site

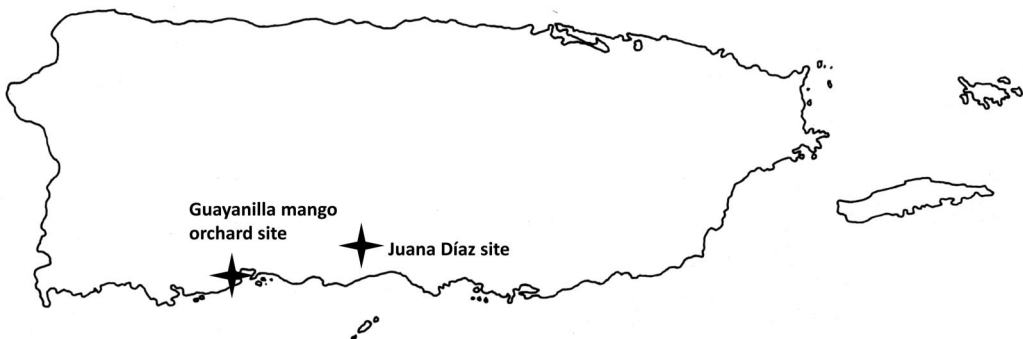


Fig. 1. Location of study sites on the island of Puerto Rico. The Guayanilla mango orchard consists of traps within the orchard and traps in the forest fragment adjacent to the orchard. The Juana Diaz site consists of traps within a carambola orchard and traps in the forest fragment adjacent to the orchard.

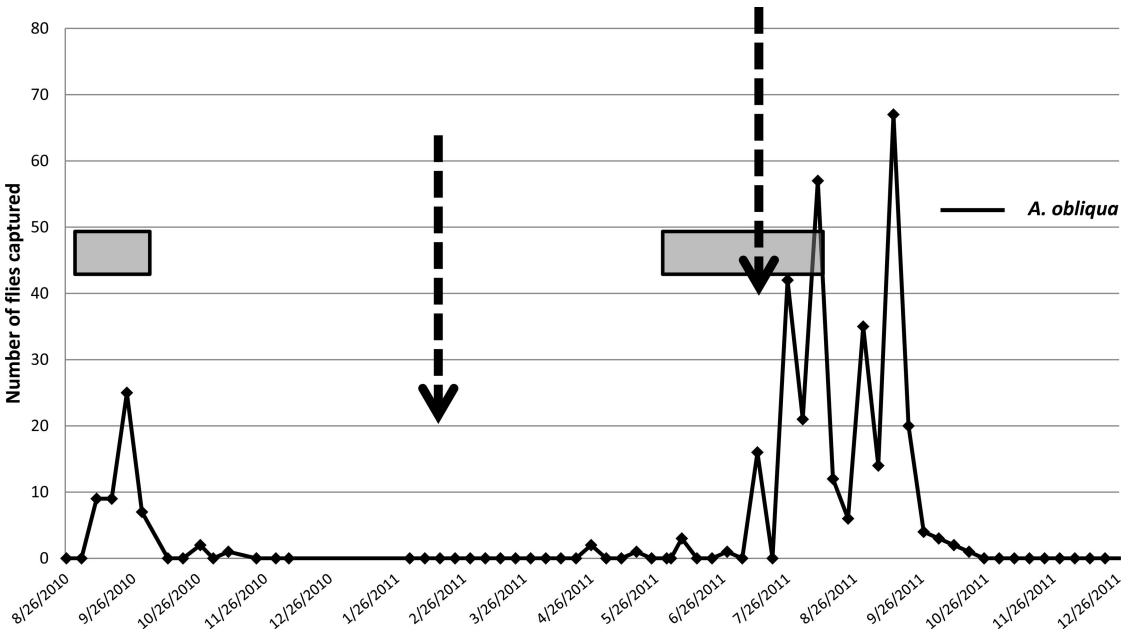


Fig. 2. The number of *A. obliqua* captured by date in the Guayanilla mango orchard. Arrows indicate dates baits were changed. Gray bars indicate availability of mature fruit in the orchard.

accounted for 82.8% ($n = 120$) of all *A. obliqua* captured. Five traps accounted for 66.7% ($n = 14$) of all *A. suspensa* captured in the forest adjacent to the Juana Diaz carambola orchard (Figs. 6 and 7).

The five traps capturing the most flies of a given species were never the same traps for other species at any site. However, the correlation between the num-

ber of *A. obliqua* caught in a given trap and the number of *A. suspensa* caught in that same trap was relatively high in the Juana Diaz carambola orchard ($r = 0.82$, $df = 29$, $P < 0.05$). In contrast, the correlation between the number of *A. obliqua* caught in a given trap and the number of *A. suspensa* caught in that same trap was lower ($r = 0.35$, $df = 29$, $P = 0.15$) for traps in the forest adjacent to the Juana Diaz carambola orchard. No

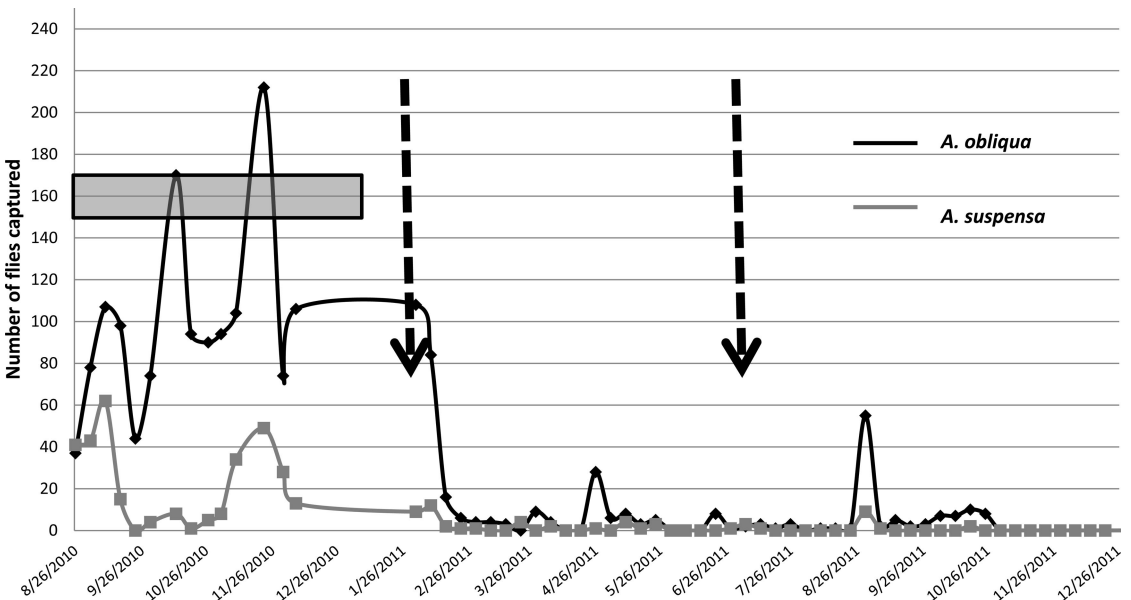


Fig. 3. Number of *A. obliqua* and *A. suspensa* captured by date in the Juana Diaz carambola orchard. Arrows indicate dates baits were changed. Gray bar indicates availability of fruit in the orchard.

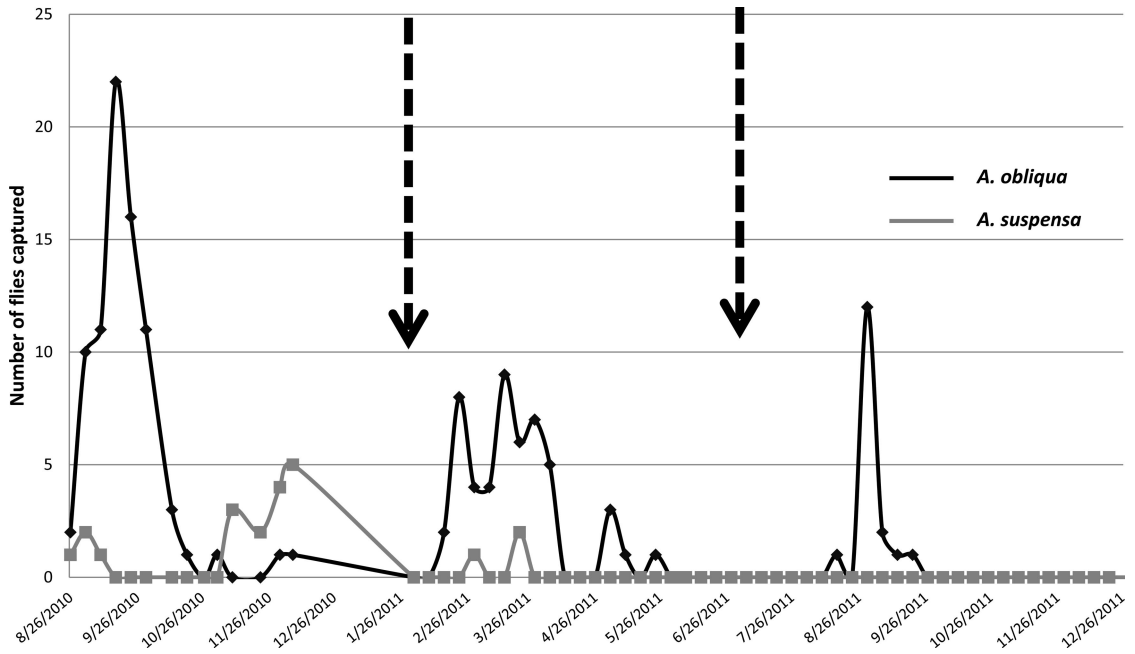


Fig. 4. Number of *A. obliqua* and *A. suspensa* captured by date in the Juana Diaz forest. Arrows indicate dates baits were changed.

such comparison could be made at the Guayanilla mango orchard because only three *A. suspensa* were captured there.

Discussion

Our results confirm the limited attractiveness of the McPhail-type trap baited with food attractants away from an orchard or host. This was most clearly illustrated by the distribution of flies among traps in the forest adjacent to the carambola orchard in Juana Diaz, where two traps, both attached to or near known *A. obliqua* hosts (*Spondias mombin* and mango, respectively), trapped large numbers of this fly species, with no or few flies trapped in adjacent traps (Fig. 6). There was no correlation between trap capture and proximity to the orchard in this case, as would be expected if the flies dispersed evenly from the orchard and all traps were equally attractive. Of the total number of flies captured at the Juana Diaz site, 92.5% were captured in the carambola orchard and 7.5% were captured in the adjacent forest. Of the total number of flies captured at the Guayanilla site, 96.4% were captured in the mango orchard and 3.6% were captured in the adjacent forest.

Several factors may explain the low numbers of fruit flies trapped in forests relative to orchards adjacent to these forests. First, the low numbers may accurately reflect populations in the forest, indicating lower populations in forest fragments. Second, the reduced numbers trapped may reflect a reduced sampling effort in the forests; a small number of inefficient traps relative to the size of the forest. Third, the existence

of unidentified food resources around which the flies are focused in the forest fragments would reduce an estimation of the number flies in that fragment. Lastly, flies may be abundant in the forest fragments, but because of environmental factors or internal physiological states do not respond to the lures used in these traps.

Given that traps near (within 15 m) host trees with relatively high fruit fly populations trapped negligible numbers of flies (Figs. 6 and 7), we infer that traps with relatively high numbers of flies are near (within 15 m) a host tree or other resource around which fruit fly populations are focused. Although this demonstrates that the trap system is not ideal for a detection application where a premium is placed on attraction of flies from great distances, it is ideal for mapping populations and potentially associating them with resources that are the foci of those populations or for assessing the effectiveness of suppression strategies, particularly when used to construct contour maps of fruit fly populations.

All trees with traps had fruit at the same time and of the same ripeness and, at least for the mango orchard, of the same variety. Nonetheless, the results from both the mango orchard and the carambola orchard demonstrate that fly capture is not evenly distributed among traps (Figs. 5–7). A previous study in carambola orchards obtained almost identical results with respect to distribution of flies among traps within an orchard (D.A.J., unpublished data). A notable result of these data are the revelation that *A. obliqua* and *A. suspensa* abundance are correlated within the carambola orchard at Juana Diaz ($r = 0.82$) ($n = 30$),

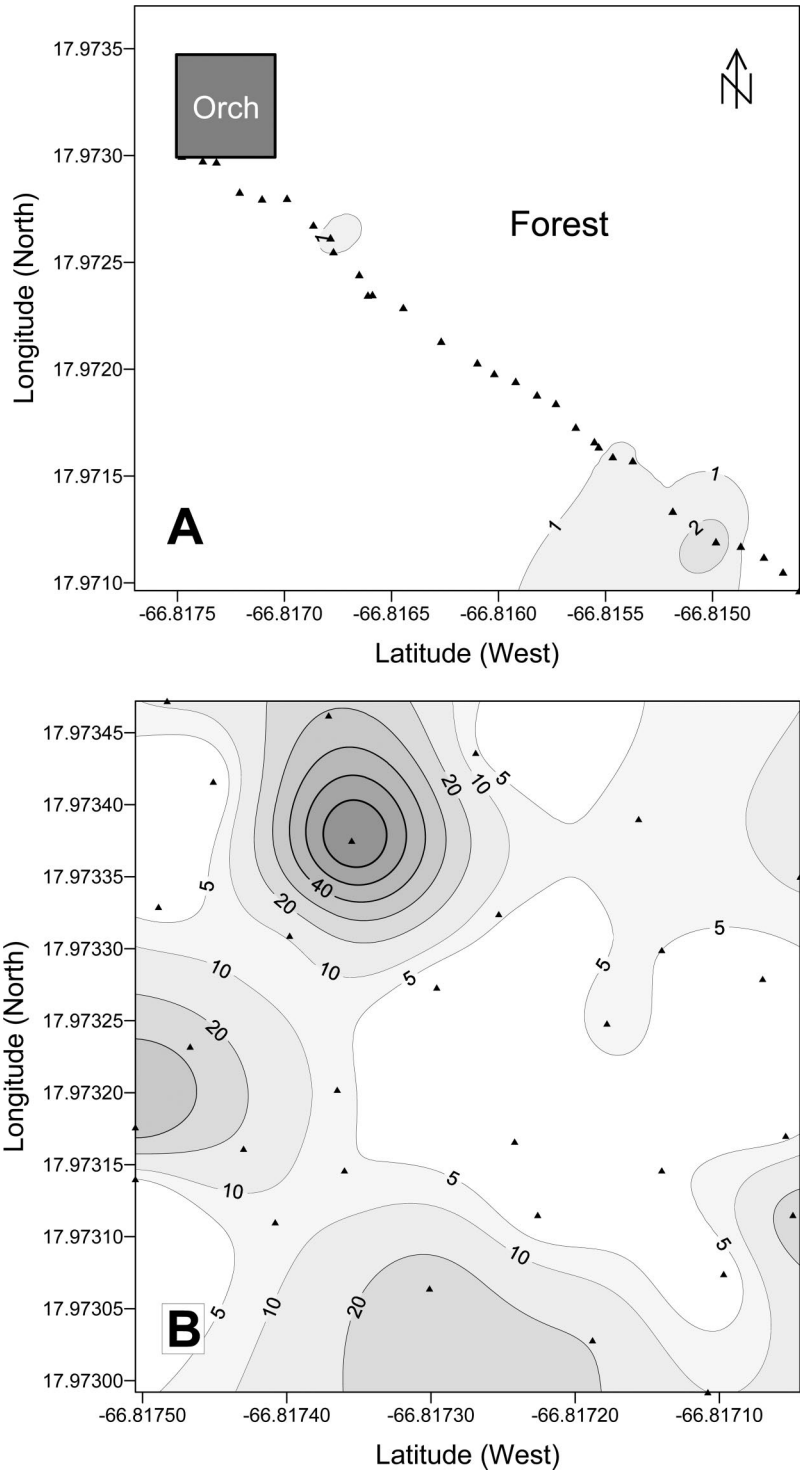


Fig. 5. Contour maps showing the distribution of *A. obliqua* captured in the Guayanilla forest fragment (A) and the adjacent Guayanilla mango orchard (B). Triangles represent traps.

indicating some intrinsic factor of the location that is attractive to both species of flies. This is confirmed by data from previous years in this same orchard ($r =$

0.83) ($n = 45$) and a carambola orchard located in Corozal, Puerto Rico, ($r = 0.77$) ($n = 45$) (D.A.J., unpublished data). An aggregated distribution of or-

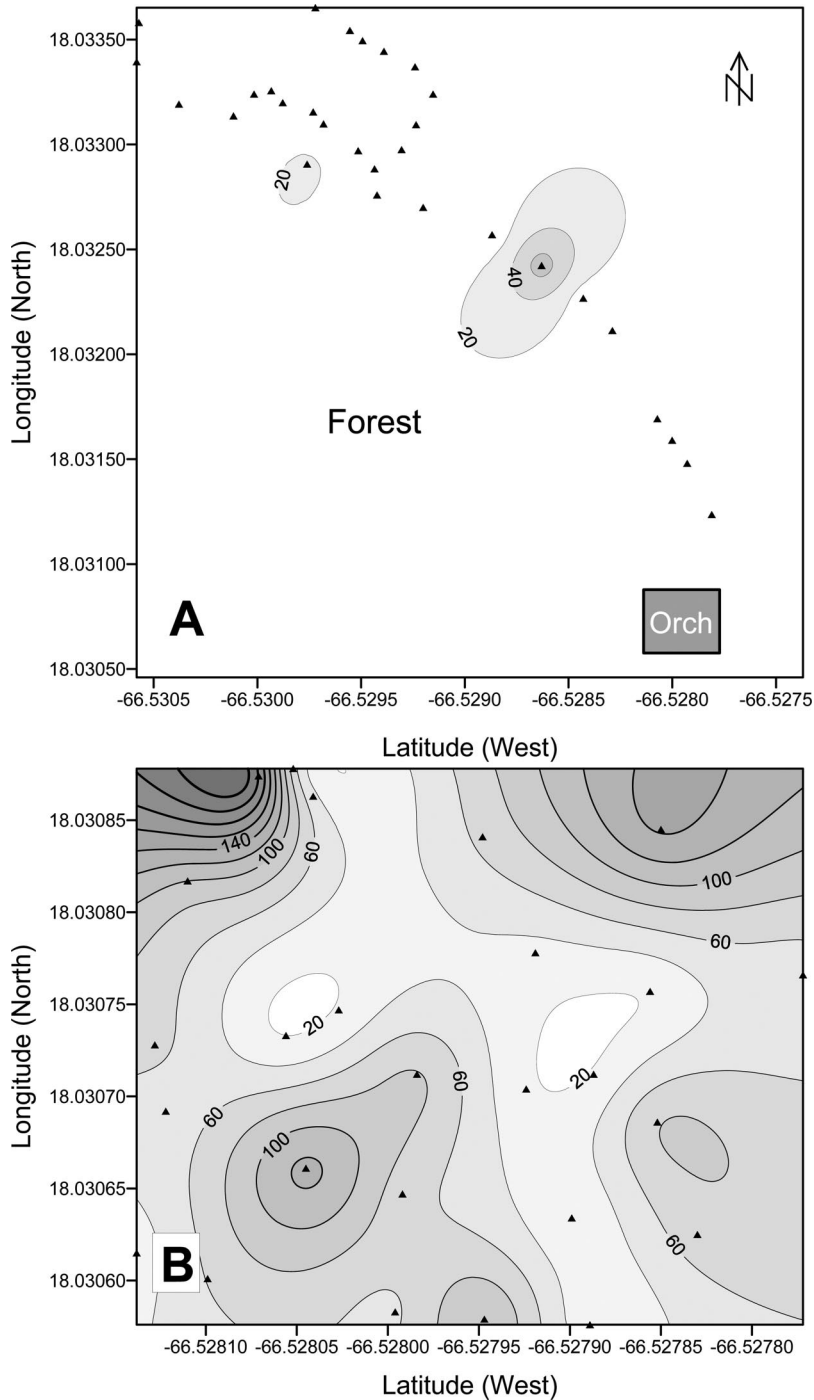


Fig. 6. Contour maps showing the distribution of *A. obliqua* captured in the Juana Diaz forest fragment (A) and the adjacent carambola orchard (B). Triangles represent traps.

ganisms in areas where resources are supposedly evenly distributed is a common phenomenon in insects, including fruit flies. In a study of the distribution of the olive fly, *Bactrocera oleae* (Gmelin) (Diptera: Tephritidae) in a Greek olive orchard, Dimou et al.

(2003) demonstrated these flies vary widely in their abundance in the orchard, although they conclude that fly abundance is related the number of fruit per tree. It is also a common phenomenon for immigrating insects to aggregate on the borders of orchards as they

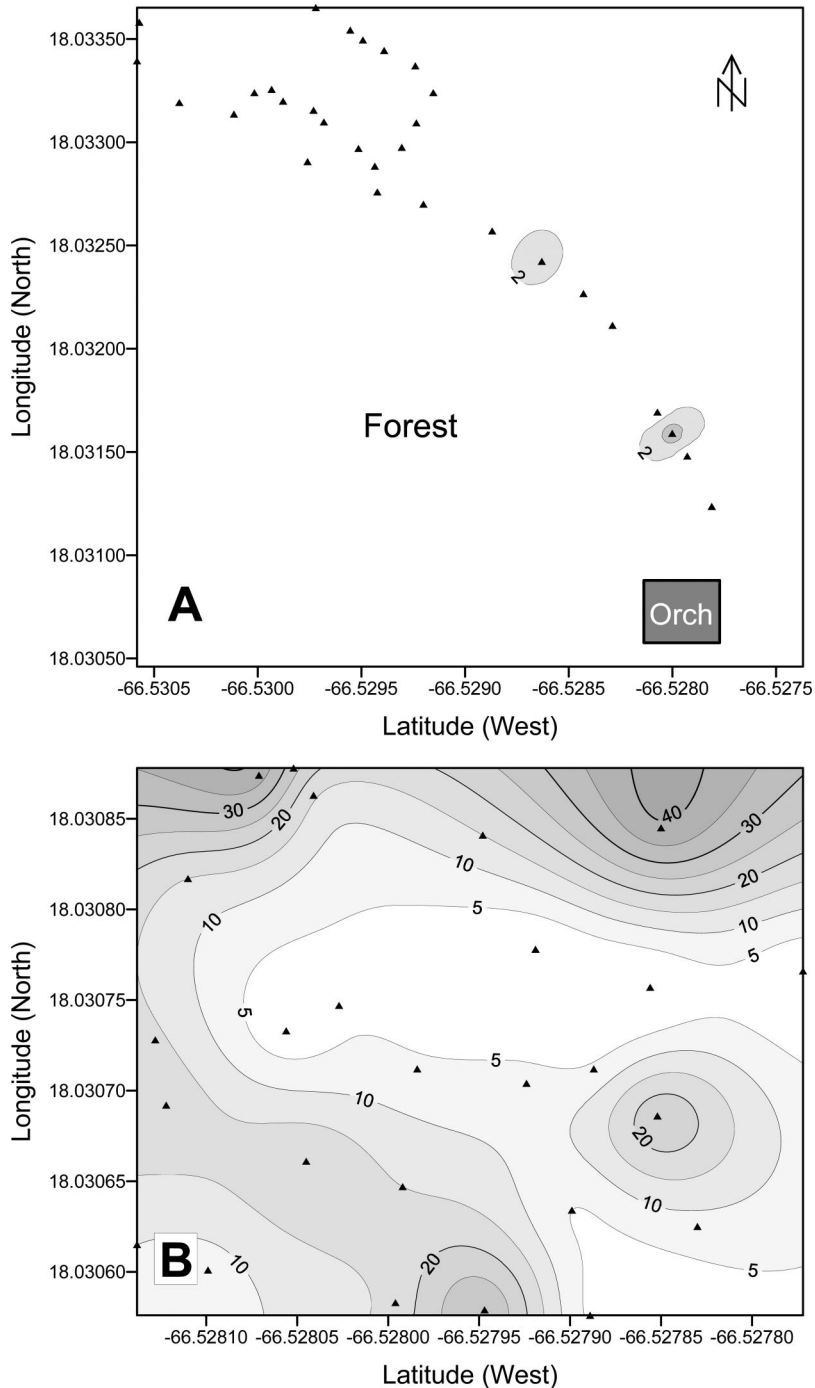


Fig. 7. Contour maps showing the distribution of *A. suspensa* captured in the Juana Diaz forest fragment (A) and the adjacent carambola orchard (B). Triangles represent traps.

move into the orchard, resulting in an aggregated distribution in a supposedly homogeneous environment (Nestel et al. 2004).

In a previous study (Jenkins and Goenaga 2008a), the authors never reared *A. suspensa* from carambola, even though many kilograms of this fruit were collected.

The current study, as well as a previous study in carambola orchards (Jenkins et al. 2011), suggest that *A. suspensa* are attracted to carambola, even though they have a low probability of reproducing in it. This may have a practical application in the management of *A. suspensa* populations and merits further investigation.

A reasonable model of fruit fly distribution in time and space would be that fly populations are large around fruiting hosts, immediately decreasing to negligible levels in a short radius of that host (on the order of meters), increasing again around another fruiting host. Similarly, fly populations are high when a host is fruiting and low when it is not fruiting (see Figs. 2 and 3; Aluja et al. 1996). Because hosts do not fruit all year round, flies can either wait for the tree to produce again or move to another host. No *Anastrepha* species that have been studied to date undergo diapause, though some of their parasitoids have this capacity (Aluja et al. 1998, Carvalho 2005). The length of time between emerging as an adult and ovipositing will depend on the availability of suitable hosts. It is likely that many females emerge from hosts under trees that are no longer yielding fruit and may not yield fruit for another 4–6 mo. The relative paucity of hosts in southern Puerto Rico means that fruit flies will have to travel farther than in other parts of the island to find a host and that host may not be fruiting. At this point, longevity and fertility of old flies becomes an important character in surviving this dearth of hosts and continuing the species. Joachim-Bravo et al. (2003) studied the longevity and fertility over time of four species of *Anastrepha* occurring in Brazil, including *A. obliqua*. They found that longevity differed by species, with 50% of *Anastrepha fraterculus* (Weidemann) females surviving to 115 d (maximum of 190 d), and 50% of *A. obliqua* females surviving to 80 d (maximum of 160 d) and that these two species had lower longevity than the other two species studied (*Anastrepha zenilldae* Zucchi and *Anastrepha sororcula* Zucchi). *Anastrepha obliqua* produced more eggs per female (an average of 80 total eggs over their lifetime) than the other species and produced eggs later in their lifetime than the other species (up to 160 d of age), although at much reduced levels (less than four eggs per female). These results are broadly similar to what Kendra et al. (2006) found regarding the fertility of *A. suspensa*, although they did not measure egg production beyond 30 d. We predict that female populations of *A. obliqua* and *A. suspensa* that have survived to find a host will be greatly reduced and with a reduced capacity to take advantage of that host (lower fertility). Despite these disadvantages, *A. suspensa* and *A. obliqua* have been able to persist in southern Puerto Rico.

Kovaleski et al. (1999) conducted a study of *A. fraterculus* dispersal from “native breeding” sites to an apple (*Malus domestica* Borkh.) orchard. Between 95 and 99% of their released flies were recaptured within 200 m of the release site. A small portion of the flies ($\approx 1\%$) dispersed >600 m. Kovaleski et al. (1999) captured very few flies ($<0.2\%$) in traps located in pastureland with herbaceous vegetation between the release site and the apple orchards where some marked flies were recaptured. This is similar to the distribution pattern of flies we recorded in the forest adjacent to the carambola orchard in Juana Diaz.

The trapping system studied herein (plastic trap baited with ammonium acetate and putrescine) has shortcomings with regard to detection programs

where a premium is set upon trap efficiency and long range effectiveness (the ability of the trap to draw target flies from great distances). However, the relative short effective sampling range (Kendra et al. 2010) of the trapping system means that the number of flies captured is an accurate measure of relative fruit fly populations near that trap. This makes it ideal for fine-scale population monitoring when used in conjunction with contour analysis. Such monitoring studies include identifying resources around which fly populations are focused or assessing the effectiveness and range of management tools to be used in area-wide suppression programs.

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