Anastrepha ludens and *Anastrepha serpentina* (Diptera: Tephritidae) Do Not Infest *Psidium guajava* (Myrtaceae), but *Anastrepha obliqua* Occasionally Shares This Resource With *Anastrepha striata* in Nature

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ABSTRACT This study examined whether economically important fruit fly species *Anastrepha ludens* (Loew), *Anastrepha serpentina* (Wiedemann), and *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae) may opportunistically exploit guavas, *Psidium guajava* L. (Myrtaceae), growing near preferred natural hosts. We collected 3,459 kg of guavas and 895 kg of other known host species [sour orange, *Citrus aurantium* L.; grapefruit, *Citrus paradisi* Macfadyen; mango, *Mangifera indica* L.; white sapote, *Casimiroa edulis* La Llave and Lex.; sapote, *Pouteria sapota* (Jacq.); sapodilla, *Manilkara zapota* L.; and wild plum, *Spondias purpurea* L. and *Spondias mombin* L.] along an altitudinal gradient over a 4-yr period (2006–2009). Plants were growing in sympatry in 23 localities where the guavas are usually infested in the state of Veracruz, México. The guava samples yielded 20,341 *Anastrepha* spp. pupae in total (overall mean, 5.88 pupae per kg of fruit). Confirming previous reports, *Anastrepha fraterculus* (Wiedemann) and *Anastrepha striata* (Schiner) were found heavily infesting guavas in Veracruz. Importantly, although we did not find evidence that *A. ludens* and *A. serpentina* are able to attack this valuable commodity, we document for the first time in the agriculturally important state of Veracruz that *P. guajava* is an alternative natural host plant of *A. obliqua*. We recovered two fruit in the mango-growing locality of la Víbora, Tlalixcoyan, that harbored larvae of *A. striata* and *A. obliqua*. This finding has important practical implications for management of *A. obliqua*. Over the entire altitudinal gradient, when individual fruit infestation was examined, a dynamic pattern of species dominance was unveiled with guavas growing below 800 m above sea level mainly attacked by *A. striata* and a progressive replacement with increasing altitude by *A. fraterculus*. Interestingly, most individual fruit examined (97%) harbored a single species of fruit fly, a finding that may be taken as evidence of competitive displacement among sympatric species of fruit flies. Based on this study and previously published work by us on this topic, we conclude that literature reports indicating that *A. ludens* and *A. serpentina* infest guavas under field conditions should be questioned.

KEY WORDS *Anastrepha*, *Psidium guajava*, competitive displacement, infestation patterns, host status

The correct status of a fruit as a host of pestiferous fruit fly species is critical in assessing the risk of introductions into importing countries (Aluja and Mangan 2008). Guava, *Psidium guajava* L. (Myrtaceae), is a tropical fruit of commercial value with a long history of local consumption in México and a significant export potential. During the past 4 yr, exports to the United States have increased by 45% with expected future yearly returns >US$350–400 million (http://sagarpa.gob.mx). In México, guavas are mainly attacked by *Anastrepha striata* (Schiner) and *Anastrepha fraterculus* (Wiedemann) (Aluja et al. 1987, 2000, 2003b,c; Sivinski et al. 2000, 2004); however, quarantine restrictions include Mexican fruit fly, *Anastrepha ludens* (Loew); *Anastrepha serpentina* (Wiedemann); and *Anastrepha obliqua* (Maquart) as species of concern in guava export protocols from México to the United States (http://www.senasica.gob.mx).

Guavas in Veracruz are widely distributed and can be found all the way from sea level to localities at altitudes of ≈1,600 m above sea level (Sivinski et al. 2000). There are no commercial plantations in Veracruz, mainly because of heavy damage inflicted by *A. fraterculus* and *A. striata.* Trees grow along rural roads and highways, in coffee (*Coffea* spp.) plantations, disturbed patches of native vegetation, parks, home gardens, backyards, or abandoned lots in urban areas often interspersed among natural hosts of economically important fruit fly species such as *A. ludens, A. serpentina,* and *A. obliqua.* In the lowlands, flowering begins in March and mature fruit is available between June and August. The latter time partially coincides with the fruiting period of *Spondias purpurea* L., a

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preferred host plant of *A. obliqua,* and with mango, *Mangifera indica* L. 'Manila', an exotic host plant of both *A. obliqua* and *A. ludens* (Aluja and Birke 1993). From ≈900 to 1,000 m above sea level, flowering begins between late April and early May, and mature fruit can be found between mid-August to late September, even though ripening of some fruit can be delayed until December. During this time, another *A. obliqua* preferred host plant, *Spondias mombin* L., is ripening (López et al. 1999, Aluja et al. 2000). Also, various species of *Citrus* and Sapotaceae, preferred hosts of *A. ludens* and *A. serpentina,* respectively, are abundant. Above 1,000 m above sea level, flowering begins in June, and mature fruit becomes available between mid-August and early October. Despite this altitudinal seasonality, one can find off-season fruit year-round in single trees, albeit in very small numbers.

A. ludens is one of the most economically important fruit pests in México. It is a polyphagous fruit fly species, whose geographical range spans from Central America to the southern United States (Thomas 2003, Aluja et al. 2009). Its main natural hosts are in the Rutaceae and include yellow chapote, *Casimiroa greggii* (S. Watson); white sapote, *Casimiroa edulis* La Llave & Lex.; and the exotic hosts bitter orange, *Citrus aurantium* L.; grapefruit, *Citrus paradisi* (Macfadyen); and orange, *Citrus sinensis* (L.) Osbeck. Other hosts include mango, *Mangifera indica* L. (Anacardiaceae); peach, *Prunus persica* L. (Rosaceae); and 'Manzano' pepper, *Capsicum pubescens* L. (Solanaceae) (Aluja et al. 2000, Norrbom 2004, Thomas 2004). Guava has been reported as a host of *A. ludens* (Hernández-Ortiz and Aluja 1993, White and Elson Harris 1992), but such reports are not based on field evidence but rather on questionable literature.

A. serpentina is distributed from the southern United States to Brazil and has been reported to exploit 22 plant species in seven families, with a marked preference for fruit in the Sapotaceae family (Robacker et al. 2009). Eskafi and Cunningham (1987) reported *P. guajava* as a host in Guatemala, but results of this survey are questionable because they were reported along with erroneous recoveries of *A. obliqua* and *A. striata* from *Citrus sinensis* (undoubtedly a mistake).

A. obliqua is distributed from México to southern Brazil and the Caribbean Islands (Aluja 1993, Hernández-Ortiz and Aluja 1993). It does not occur in the United States and is therefore considered a pest of quarantine significance for this country (Steck 2001). This species predominantly attacks fruit within the Anacardiaceae family; it is considered a major pest of mango and tropical plum (*S. purpurea*) across the Americas (Aluja and Birke 1993, Aluja et al. 1996, Niklaus-Ruiz and Basedow 1997, Rossetto et al. 2006), and it also inflicts significant damage to starfruit (carambola), *Averrhoa carambola* L. (Oxalidaceae) (Bressan and da Costa Teles 1991). In México, *A. obliqua* commonly infests *S. mombin, Spondias dulcis* L., *Spondias radlkoferi* Donn. Sm., *Tapirira mexicana* Marchand, *M. indica* (all Anacardiaceae), and *Ampelocera hottlei* (Standl.) Standl.(Ulmaceae) (Aluja et al. 1987; Aluja et al. 2000, 2003c).

There are at least 25 primary reports (sensu Aluja and Mangan 2008) indicating that *A. obliqua* is able to infest guava under field conditions (information summarized by Norrbom, 2004). Most credible reports stem from the Caribbean Islands (Dominican Republic and Puerto Rico; Jenkins and Goenaga 2008a) and some countries in Central and South America (Costa Rica, Colombia, Venezuela, Brazil, and Ecuador; (Malavasi and Morgante 1980, Malavasi et al. 1980, Caraballo 1981, Jirón and Hedström 1988, Ohashi et al. 1997, Katiyar et al. 2000, Zucchi 2000, Uchôa-Fernández et al. 2002, Araujo et al. 2005, Raga et al. 2006, Jenkins and Goenaga 2008b, Minzão and Uchôa-Fernández 2008). In México, *P. guajava* has only been recorded as a host of *A. obliqua* in the southern-most Soconusco region in the state of Chiapas (Aluja et al. 1987), despite extensive fruit collecting efforts in several areas throughout the country (e.g., Yucatán, Hernández-Ortíz et al. 2006; Veracruz, Hernández-Ortíz and Pérez-Alonso 1993, López et al. 1999, Aluja et al. 2000, Sivinski et al. 2000); northern Chiapas, Montes Azules, Aluja et al. 2003c; and Nayarit, Pérez-Staples and Aluja 2004).

Our null hypothesis was that in our study region guavas would only be naturally infested by *A. striata* and *A. fraterculus,* two fruit fly species with an unequivocally proven association to this host in México. Alternatively, we hypothesized that *A. ludens, A. serpentina,* and *A. obliqua* may opportunistically exploit guavas when growing in the vicinity(within flight range) of their preferred natural hosts. Hosts were considered to be in sympatry when found within 250 m of each other, which represents the mean daily flight distance for *Anastrepha* adults (Thomas and Loera-Gallardo 1998). To test these hypotheses, we conducted a 4-yr study in 23 different field sites along an elevation gradient in the agriculturally important state of Veracruz, México. The study was based on fruit collections in the field and follow-up quantification of infestation patterns.

Materials and Methods

Fruit Collection Sites. The study was carried out during the 2006–2007 and 2008–2009 fruiting seasons. Guavas were systematically collected along an altitudinal gradient (9–1,137 m above sea level) in central Veracruz, México. Nineteen localities were selected among those with the highest fruit fly infestation rates and greatest guava tree abundance (see Tables 1 and 2 for details; López et al. 1999, Sivinski et al. 2000). We also chose sites on the basis of the existence of natural *A. ludens, A. obliqua,* and *A. serpentina* hosts growing next or in proximity (<250 m) to guava trees (Table 3). To document the occurrence of these pestiferous fruit fly species in the experimental area, in addition to a literature review, we report infestation patterns on known hosts collected during the course of this study, in sites (or areas nearby) where we collected guavas. The fruiting period of the latter hosts broadly

Table 1. Sample sites, GPS records, sample size (kilograms of guavas), total number of pupae obtained, and number of pupae per kilogram of fruit in each of 18 locations along an altitudinal gradient (samples were collected during the fruiting season, 2006–2007)

Site	Municipality	Altitude (m above sea level)	Latitude (N)	Longitude (W)	Fruit (kg)	Total pupae	No. pupae/kg
Tlalixcoyan	Tlalixcoyan	9	18°47′	96°02′	199.6	110	0.55
Entronque Jamapa-Medellín	Jamapa	10	19°03′	96°09′	322.0	2,516	7.81
Parada Guayabos-Jamapa	Jamapa	13	19°02′	96°12′	48.5	145	2.99
Tierra Colorada	Paso de Ovejas	13	19°13′	96°22′	129.85	916	7.06
Tuzales	Tlalixcoyan	15	18°46′	96°05′	133.4	185	1.39
Javilla	Jamapa	15	19°02′	96°41′	21.9	20	0.92
Jamapa	Jamapa	19	19°02′	96°14′	496.3	2,842	5.73
Parada Cuajilote-Jamapa	Jamapa	19	19°02′	96°12′	98.2	858	8.74
Cempoala	Ursulo Galván	21	19°26′	96°24′	162.0	995	6.14
Salmoral	La Antigua	24	19°20′	96°20′	38.0	54	1.42
San Julián	Veracruz	26	19°15′	96°16′	90.4	567	6.27
La Víbora	Tlalixcoyan	35	18°55′	96°04′	41.6	135	3.25
Santa Fé	Veracruz	36	19°12′	96°16′	232.2	626	2.70
Coetzala	Tlaltetela	273	19°18′	96°41′	54.0	133	2.46
Carrizal	Carrizal	521	19°21′	96°42′	46.9	57	1.22
Carrizal-Chahuapan	Carrizal	528	19°21′	96°41′	46.9	73	1.56
Rancho Viejo	Emiliano Zapata	912	19°26′	96°46′	10.6	228	21.51
Entronque Xico-Teocelo	Xico	1,137	19°23′	96°57′	17.6	247	14.03

matched the one of guavas lending support to the assumption that all fruit species where present when guavas were ripening.

Fruit Sampling and Processing. Fallen fruit were recovered from the ground under trees and transported to the laboratory in Xalapa, Veracruz. Fruit was placed in plastic screened baskets, over plastic containers lined with a thin layer of vermiculite at the bottom as a pupation medium following methods outlined in Aluja et al. (1987). Total fruit weight for each collection site and date was recorded. Pupation medium was sieved every 3 d, pupae were recovered, and their number was recorded on a piece of masking tape glued on the side of the plastic container. All the pupae were kept in moist vermiculite until adult emergence.

Assessment of Infestation Level. Infestation levels were assessed because they can aid in establishing degree of host suitability (poor to good gradient in the flow chart presented in Aluja and Mangan 2008) and in the determination of host status (i.e., if a particular fruit species is unequivocally designated as a natural host, then it is useful to know whether it is commonly or only occasionally infested). In addition, to uncover possible fruit fly multispecific, simultaneous infestations in guavas, during the 2007 season (August 2007) 269 individual fruit from a 2,398.62-kg sample, recovered from six localities (four or five trees per locality) along the altitudinal gradient (see Table 5 for details), were separated and maintained individually. Fruit were individually weighed and kept in 0.25-liter plastic containers (Sivinski et al. 1997). Each container also was lined at the bottom with a thin layer of moist vermiculite as a pupation substrate. Pupae from each fruit were recovered, their number recorded and kept until adult emergence. When adults emerged they were identified and the sex ratio was recorded.

A. striata, *A. fraterculus*, and *A. obliqua* adults reared from guavas were identified by Larissa Guillén by using morphological characters detailed in Hernández-Ortíz (1992). *A. obliqua* specimens emerging from guava were placed as vouchers in the IEXA permanent Entomological Collection of the Instituto de Ecología, A.C. and in the collection of the Red de Manejo Biorracional de Plagas y Vectores, lnstituto de Ecología, A.C.

Statistical Analyses. All data were checked for normality and homogeneity of variances (Lilliefors and Kolmogorov–Smirnov test). Individual fruit infestation level was measured as the mean number of pupae per fruit, and data were rank transformed (Conover and Iman 1981) and analyzed by means of a one-way analysis of variance (ANOVA). Individual fruit weight also was analyzed by means of a one-way ANOVA. All statistical tests were run using STATISTICA (StatSoft, Inc. 2007).

Results

During the 2006–2007 fruiting season, 2,189.52 kg of guavas in total were collected from the 18 localities studied (Table 1). During the 2008–2009 season, 1,269.62 kg in total were collected across 10 localities (Table 2). During 2006–2009, we also collected 597.05 kg of sour oranges, 4.35 kg of grapefruit, 4.54 kg of mangoes, 112 kg of white sapote, 41 kg of sapote, 95.29 kg of sapodilla, and 40.95 kg of wild plums (*Spondias* spp.) (Table 3).

Overall, during the 4-yr study out of a total of 3,459.14 kg of guavas collected, 20,341 pupae in total were recovered (5.88 pupae per kg of fruit). Infestation rates varied widely according to collection site and year (Tables 1 and 2). Guava collections yielded mostly *A. striata* from samples collected below elevations of 900 m above sea level and *A. fraterculus* above elevations of 900 m (Table 4). Of the 269 individually kept fruit (Table 4), 84% of the specimens that emerged were *A. striata*, 15% *A. fraterculus*, and only 1% (n = 13) individuals were *A. obliqua*. *A. obliqua* were only recovered from fruit sampled at La Víbora, Tlalixcoyan, Veracruz. In this locality, tropical plums (*S. purpurea*) coexist with guavas, and on occasion fruit of both tree species ripen simultaneously. The

Table 2. Sample sites, GPS records, sample size (kilograms of guavas) and infestation level in each of 10 locations along an altitudinal gradient (samples were collected during the fruiting season, 2008–2009)

Site	Municipality	Altitude (m above sea level)	Latitude (N)	Longitude (W)	Fruit (kg)	Total pupae	No. pupae/kg
La Antigua	La Antigua	24	19°20′	96°20′	156.1	811	5.20
Entr. Piedras Negras	Tlalixcoyan	20	18°44′	96°08′	65.4	49	0.75
Jamapa	Jamapa	13	19°02′	96°12′	227.76	3451	15.16
La Mancha	Actopan	9	19°35′	96°22′	83.5	358	4.29
Catemaco	Catemaco	19	18°36′	95°54′	84.9	135	1.59
Tlalixcoyan	Tlalixcoyan	9	18°47′	96°02′	99.8	80	0.80
San Julián	Veracruz	26	19°15′	96°16′	123.4	769	6.23
La Víbora	Tlalixcoyan	35	18°55′	96°04′	128.7	557	4.33
Santa Fé	Veracruz	36	19°12′	96°16′	89.5	570	6.37
Entronque Xico-Teocelo	Xico	1,137	19°23′	96°57′	210.3	2,854	13.57

number of pupae per fruit varied between study sites (one-way ANOVA: $F = 20.58$; df = 5, 263; $P = 0.0001$) (Table 5). Guavas in la Víbora, Tlalixcoyan, Veracruz, were larger compared with those collected in all other sites (one-way ANOVA: $F = 14.56$; df = 5, 263; $P = 0.0001$). In this locality, fruit weighed 39.00 ± 2.62 g (data on all other localities in Table 5). Fruit in Santa Fé harbored the most pupae (Table 5). In 96% of the cases, individually kept fruit yielded a single *Anastrepha* species (either *A. striata*, *A. fraterculus*, or *A. obliqua*) and in 4.09% (11 fruit) of the samples two species emerged (*A. striata* and *A. obliqua* [two fruit]; see details in Table 4). In one case, we obtained seven *A. obliqua* (three females and four males) and three *A. striata* (three males) adults. In the remaining fruit that harbored larvae of these two species, we recorded two *A. obliqua* (one female and one male) and seven *A. striata* (five females and two males) adults, respectively. In the site at intermediate altitude (912 m above sea level, Rancho Viejo, Emiliano Zapata), we collected eight fruit that yielded two species (*A. striata* and *A. fraterculus*) and in the highlands (1,137 m) (entronque Xico-Teocelo, Xico), the only *A. striata* adult obtained was found in one guava that also yielded nine *A. fraterculus* adults. Importantly, no single fruit or sample from any of the 22 sites in which we collected fruit yielded a single *A. ludens* or *A. serpentina* adult.

From the additional hosts we collected, *A. ludens* was recovered from sour orange, grapefruit, mango, and white sapote; *A. obliqua* was recovered from mango and wild plums; and *A. serpentina* was recovered from sapodilla and sapote (Table 3). Such findings are consistent with previous published reports in

Table 3. Location, GPS records, recovered fruit fly species, host, sample size (kilograms of fruit), and number of pupae per kilogram of fruit at each of 17 locations along an altitudinal gradient where hosts are sympatric to guava (samples were collected during the fruiting season, 2006–2009)

Location	Municipality	Altitude (m above sea level)	Latitude (N)	Longitude (W)	Fruit fly species	Host	Fruit (kg)	No. pupae/kg
Apazapan[a-f]	Apazapan	291	19°18′	96°42′	*A. obliqua*	*Spondias* spp.	6.45	32
						M. ndica	2.8	24.3
El Aguaje[c,f]	Actopan	219	19°25′	96°36′	*A. obliqua*	*M. indica*	1.74	182.7
Entronque Piedras Negras	Tlalixcoyan	20	18°44′	96°08′	*A. obliqua*	*Spondias* spp.	0.8	2.5
La Camacha	Tlalixcoyan				*A. obliqua*	*Spondias* spp.	5	1,052.6
Carrizal[c]	Carrizal	521	19°21′	96°42′	*A. obliqua*	*Spondias* spp.	6.3	33.5
San Julián[c]	Veracruz	26	19°15′	96°16′	*A. obliqua*	*Spondias* spp.	6	1.3
Costa Rica[c,f]	Tuzamapan				*A. obliqua*	*Spondias* spp.	16.4	39.5
San Julián[c]	Veracruz	26	19°15′	96°16′	*A. serpentina*	*P. sapota*	12	28.6
Las Cuevas[c,d,f]	Teocelo	1,004	19°22′	96°57′	*A. serpentina*	*P. sapota*	3	40.6
Palo Gacho[f]	Emiliano Zapata	343	19°23′	96°38′	*A. serpentina*	*M. sapota*	38	5.26
Apazapan[c-f]	Apazapan	291	19°18′	96°42′	*A. serpentina*	*M. sapota*	57.29	3.96
El Aguaje[f]	Actopan	219	19°25′	96°36′	*A. serpentina*	*M. sapota*	26.0	43.42
Apazapan[c-f]	Apazapan	291	19°18′	96°42′	*A. ludens*	*C. aurantium*	262.45	16.01
Costa Rica[c,e,f]	Tuzampan	904	19°24′	96°52′	*A. ludens*	*C. aurantium*	292.8	21.46
Teocelo/Cosautlán[c-f]	Teocelo	1,229	19°23′	96°59′	*A. ludens*	*C. edulis*	112	10.6
Dos Ríos[f]	Emiliano Zapata	945	19°29′	96°47′	*A. ludens*	*C. aurantium*	13	16.46
Tlalixcoyan	Tlalixcoyan	9	18°47′	96°02′	*A. ludens*	*C. aurantium*	8	8.5
Entronque Xico-Teocelo[c,d,e]	Xico	1,137	19°23′	96°57′	*A. ludens*	*C. paradisi*	4.35	20.46
Rancho Viejo[c-f]	Emiliano Zapata	912	19°26′	96°46′	*A. ludens*	*C. aurantium*	20.8	9.03

[a] Infestations also reported by Aluja and Birke (1993).
[b] Infestations also reported by Aluja et al. (1998).
[c] Infestations also reported by Aluja et al. (2000).
[d] Infestations also reported by López et al. (1999).
[e] Infestations also reported by Sivinski et al. (1997).
[f] Infestations also reported by Sivinski et al. (2000).

Table 4. Proportion of *A. striata*, *A. fraterculus*, and *A. obliqua* specimens in guavas collected from six localities along an altitudinal gradient (San Julián, Veracruz; Jamapa, Medellín; Santa Fé, Veracruz; La Víbora, Tlalixcoyan;Rancho Viejo, Emiliano Zapata and Entronque Xico-Teocelo, and Xico)

Site	Municipality	Altitude (m above sea level)	Fruit fly species (%)		
			A. striata	*A. fraterculus*	*A. obliqua*
San Julián	Veracruz	26	100	0	0
La Víbora	Tlalixcoyan	35	87	0	13
Santa Fé	Veracruz	36	100	0	0
Jamapa	Jamapa	13	100	0	0
Rancho Viejo	Emiliano Zapata	912	90	10	0
Entronque Xico-Teocelo	Xico	1,137	1	99	0

the same study region (Sivinski et al. 1997, 2000; López et al. 1999; Aluja et al. 2000).

Discussion

Our survey confirmed previously documented patterns of guava infestation by *A. fraterculus* and *A. striata*, with the latter dominating at low elevations and being gradually replaced with increasing altitude by *A. fraterculus* (Sivinski et al. 2000). Despite that we sampled fruit over an altitudinal gradient in areas where natural hosts grew next or close to guavas, we were unable to record a single case of infestation by *A. ludens* or *A. serpentina* in this fruit in Veracruz. In contrast, we confirmed the fact that *A. obliqua* is indeed able to occasionally infest guavas in México (e.g., Aluja et al. 1987), albeit in very small numbers and in only one of the 23 sites considered in this study. We note that there are numerous reports of *A. obliqua* infesting guavas in the Caribbean Islands mainly in Dominican Republic and Puerto Rico (Jenkins and Goenaga 2008a,b), Central America (Jirón and Hedström 1988), and South American countries (Colombia, Venezuela, Brazil, and Ecuador; Malavasi and Morgante 1980, Malavasi et al. 1980, Caraballo 1981, Ohashi et al. 1997, Katiyar et al. 2000, Zucchi 2000, Uchôa-Fernández et al. 2002, Araujo et al. 2005, Raga et al. 2006, Minzão and Uchôa-Fernández 2008), confirming the notion that guavas are natural hosts of *A. obliqua*.

Despite the above-mentioned information, we consider that our report is important because 1) the locality where *A. obliqua* was recovered is found in the middle of a large mango-growing region (mainly 'Manila', but other cultivars such as 'Criollo', 'Kent', 'Piña', 'Paraiso', and 'Tommy Atkins' also can be found), and successful management of *A. obliqua* hinges on accurate identification of all hosts in which fly populations build up or are maintained when primary hosts are not available; 2) we had collected large amounts (>4.5 tons of fruit) of guavas within Veracruz since 1990 and had never recovered a single specimen of *A. obliqua* from any of the samples (Aluja et al. 1993, 1998, 2000, 2003c, 2005; Sivinski et al. 1997, 2000, 2004; López et al. 1999); and 3) we discovered that *A. obliqua* can occasionally share resources with *A. striata* (i.e., from a single fruit we recovered adults from both species), a finding that can shed light into patterns of niche partitioning and the nature of interactions among coexisting fruit fly species in the tropics.

To our knowledge, guavas being simultaneously infested by *A. obliqua* and *A. striata* had never been reported. Previously, López et al. (1999) and Sivinski et al. (2004) had reported that *A. striata* and *A. fraterculus* could simultaneously infest *P. guajava* in Central, Veracruz (1,000 m above sea level). Shared use of guava also has been found in several studies in South America. In Argentina, P. Schliserman et al. (personal communication) observed simultaneous infestations in guavas by *A. fraterculus* and *Anastrepha schultzi* (Blanchard), whereas in Brazil, Zucchi (2000) reported *A. fraterculus* and *Anastrepha sororcula* (Zucchi) exploiting this fruit together.

Our finding that only 4% of individual fruit examined yielded adults of more than one species indicates that competitive interactions are possibly at play. Coinfestation and scramble competition are often exhibited by polyphagous tephritids because of diet overlap (Duyck et al. 2004). Species dominance in tephritids depends on temperature, latitude and longitude, humidity, host fruit quality, and other factors that influence larval developmental time (Duyck et al. 2004,

Table 5. Individual fruit wt and mean number of pupae obtained per fruit in each of six locations along an altitudinal gradient

Site	Municipality	Altitude (m above sea level)	Latitude (N)	Longitude (W)	Fruit wt in g (mean ± SE)[a]	Pupae/fruit (mean ± SE)[a]
Jamapa	Jamapa	13	19°02′	96°12′	29.62 ± 1.49a	8.72 ± 1.13b
San Julián	Veracruz	26	19°15′	96°16′	28.22 ± 1.48ab	6.87 ± 0.92c
La Víbora	Tlalixcoyan	35	18°55′	96°04′	39.00 ± 2.62d	4.13 ± 0.70d
Santa Fé	Veracruz	36	19°12′	96°16′	22.41 ± 1.18ac	14.0 ± 1.26a
Rancho Viejo	Emiliano Zapata	912	19°26′	96°46′	22.55 ± 0.84ae	4.85 ± 0.47de
Entronque Xico-Teocelo	Xico	1137	19°23′	96°57′	27.57 ± 1.09abe	3.86 ± 0.36def

[a] Values followed by different lowercase letters indicate statistical differences.

2006; Rwomushana et al. 2009; Ekesi et al. 2009). It would be interesting to study which of these factors influences the outcome of species dominance in guava between *A. fraterculus* and *A. striata.*

Given that guava infestations at the same location (tree or patch) were not repeated the following 2 yr and that it has been reported that there is cross-recognition of host-marking pheromone within species of *Anastrepha* (Aluja et al. 2003a, Aluja and Díaz-Fleischer 2004), the only explanation we find for co-infestation by *A. obliqua* and *A. striata* during a single season is that the preferred hosts of *A. obliqua* were scarce or absent (*S. mombin* fruiting was delayed because of atypical weather patterns and only underdeveloped fruits were available when guavas were already ripening). Such circumstances have been documented to force egg-loaded females to dump eggs in alternative oviposition substrates Papaj (1993) and Aluja and Mangan (2008). We also could speculate that *A. obliqua* females could have been visually confused and attracted to guavas that display a lime-green, yellow color reflectance similar to other *A. obliqua* hosts (López-Guillén et al. 2009). It is unknown whether *A. obliqua* females actually recognized the volatiles emitted by ripening guava or if they landed by chance in guava trees and then responded to visual and tactile stimuli (see Aluja and Prokopy 1993 for further details on such a mechanism). We also do not know at this stage whether *A. obliqua* offspring performed well when larvae fed on guava pulp, because there is evidence in the case of *A. ludens* that guava pulp can be toxic or a very poor resource for larvae, resulting in significantly reduced adult fitness (Birke 2008).

In conclusion, guavas seem to be only an occasional host of *A. obliqua* in Veracruz, whereas this does not seem to be the case in other Neotropical areas (as documented herein) where this species is recovered regularly, and at times in large numbers (especially in the Caribbean). Such marked differences in host use patterns have been documented for a complex of cryptic species of *A. fraterculus* (Aluja et al. 2003b), and it would therefore be worthwhile to determine whether there is evidence for divergence within *A. obliqua.*

Finally, our results could have important practical implications for the management of *A. obliqua* populations in mango-growing regions in the lowlands of Veracruz and Chiapas (but also elsewhere in Latin America). In particular, we believe that it is important to consider the fact that guavas can serve as a bridging host in times when optimal or preferred hosts are scarce. *A. obliqua* populations could survive in guava and then build up again in early fruiting mango cultivars or in trees that have been treated with potassium nitrate to enhance early flowering (Salazar-Garcia et al. 2000). We also consider that more basic studies are needed to understanding interspecific co-infestations and should include how natural displacements among fruit fly pests (i.e., *A. striata, A. fraterculus,* and *A. obliqua*) occur and under which conditions. Finally, our results dispel the notion that guavas are natural hosts of *A. ludens* and *A. serpentina.*

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