Native and Introduced Host Plants of *Anastrepha fraterculus* and *Ceratitis capitata* (Diptera: Tephritidae) in Northwestern Argentina

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ABSTRACT Wild or commercially grown, native and exotic fruit were collected in 30 localities in the Tucumán province (NW Argentina) from January 1990 to December 1995 to determine their status as hosts of *Anastrepha fraterculus* (Wiedemann) and/or *Ceratitis capitata* (Wiedemann), the only two fruit fly species of economic and quarantine importance in Argentina. A total of 84,094 fruit (3,466.1 kg) representing 33 species (7 native and 26 exotic) in 15 plant families were sampled. We determined the following 17 host plant associations: *Annona cherimola* Miller (Annonaceae), *Citrus paradisi* Macfadyn (Rutaceae), *Diospyros kaki* L. (Ebenaceae), *Eugenia uniflora* L., *Psidium guajava* L., *Myrcianthes pungens* (Berg) Legrand (Myrtaceae), *Ficus carica* L. (Moraceae), *Juglans australis* Grisebach (Juglandaceae), *Mangifera indica* L. (Anacardiaceae), *Eriobotrya japonica* (Thunb.) Lindl., *Prunus armeniaca* L., *P. domestica* L., and *P. persica* (L.) Batsch (Rosaceae) were infested by both *A. fraterculus* and *C. capitata*. *Citrus aurantium* L., *Citrus reticulata* Blanco, *Citrus sinensis* (L.) Osbeck (Rutaceae), and *Passiflora caerulea* L. (Passifloraceae) were only infested by *Ceratitis capitata*. Out of a total of 99,627 adults that emerged from pupae, 69,180 (≈69.5%) were *Anastrepha fraterculus*, 30,138 (≈30.2%) were *C. capitata*, and 309 (≈0.3%) were an unidentified *Anastrepha* species. *Anastrepha fraterculus* predominated in native plant species while *C. capitata* did so in introduced species. Infestation rates (number of larvae/kg of fruit) varied sharply from year to year and between host plant species (overall there was a significant negative correlation between fruit size and infestation level). We provide information on fruiting phenology of all the reported hosts and discuss our findings in light of their practical (e.g., management of *A. fraterculus* and *C. capitata* in citrus groves) implications.

KEY WORDS Tephritidae, *Anastrepha fraterculus*, *Ceratitis capitata*, host plants, Argentina

THE ACCURATE AND RELIABLE determination of the status of a particular plant species as a host of a given fruit fly species (Diptera: Tephritidae) has become critical because of intensive international trade and the expansion of fruit growing regions in many parts of the world. Unfortunately, the literature on fruit fly host plants is marred with methodological flaws and inaccuracies so pervasive that they have even generated long-standing commercial disputes between trade partners (Aluja 1999). According to Norrbom and Kim (1988) and Aluja (1999), a host record should only be validated if the plant and fly species was identified by an expert taxonomist (and the author cites the name and affiliation of the person performing the identification) and if the infestation occurred under natural conditions (i.e., field). Host records should also be accompanied by information on the part of the fruit being used by larvae for development (i.e., seed or pulp), levels of infestation (i.e., larvae per fruit or kg of fruit), fruiting phenology and accurate information on cultivar type. Further, and as indicated by Cowley et al. (1992), one has to consider the fact that host status can change over time and is influenced by environmental conditions such as drought (and the concomitant effect on primary and secondary host availability). Considering the latter, Cowley et al. (1992) proposed a strict experimental procedure to unequivocally ascertain host status in the case of multivoltine fruit flies that includes laboratory and field cage trials in addition to field collection of fruit.

Anastrepha fraterculus (Wiedemann) (South American Fruit Fly) and *Ceratitis capitata* (Wiedemann) (Mediterranean Fruit Fly) are the only two economically important fruit fly species found in Argentina (Aruani et al. 1996). *Ceratitis capitata* was introduced to Argentina either unnaturally via Buenos Aires, where it was found infesting peaches in 1905 (Vergani 1952) or naturally from Brazil (González 1978). Both tephritid species are serious pests of a wide range of commercial fruit crops and severely limit the export of fruit as a result of quarantine restrictions in countries such as the United States and Japan (SENASA 1998). Although *C. capitata* is widely distributed throughout Argentina, the native *A. fraterculus* is mainly restricted to the northwestern provinces of Tucumán, Salta, Jujuy, and Catamarca and the northeastern provinces of

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Misiones, Corrientes, and Entre Ríos. In the latter provinces, there are important citrus-growing regions in which *A. fraterculus* and *C. capitata* apparently coexist in wild and commercially grown native and exotic fruit. With respect to citrus, *A. fraterculus* mainly has been reported infesting *Citrus paradisi* Macfadyn (grapefruit) in several provinces of Argentina (Vaccaro 2000). There are other occasional reports of infestation in *Citrus aurantium* L. (sour orange), *Citrus sinensis* L. (Osbeck) (sweet orange), and *Citrus reticulata* Blanco (tangerine) in the provinces of Misiones and Entre Ríos (Ogloblin 1937, Putruele 1996). *Ceratitis capitata* infests grapefruit, sour orange, sweet orange, tangerine, and *Citrus deliciosa* Tenore (Mediterranean tangerine), *Citrus unshiu* Marcovitch (satsuma tangerine), *Citrus aurantifolia* (Christm.) Swingle (lime), and *Citrus limetta* Risso (sweet lemon) (Putruele 1996, Nasca et al. 1996).

In addition to these citrus species, other purported (see below) *C. capitata* and *A. fraterculus* host plants of commercial value in Argentina are figs (*Ficus carica* L.), apples (*Malus domestica* Borkh), pears (*Pyrus communis* L.), plums (*Prunus domestica* L.), peaches (*Prunus persica* (L.) Batsch), apricots (*Prunus armeniaca* L.), cherimoya (*Annona cherimola* Miller), Japanese persimmons (*Diospyros kaki* L.), quinces (*Cydonia oblonga* Miller), loquats (*Eriobotrya japonica* [Thunb.] Lindley), avocados (*Persea americana* Miller), pomegranates (*Punica granatum* L.), and grapes (*Vitis vinifera* L.) (Lahille 1915; Rust 1916, 1918; Hayward 1944, 1960; Domato and Aramayo 1947; Vergani 1952; Ratkovich and Nasca 1953; Rosillo 1953; Blanchard 1961; Costilla 1967; Nasca 1970; Turica et al. 1971; Nasca et al. 1981). Nevertheless, many of these host records are anecdotal and have not been confirmed since their first publication or are based on reports of adult flies captured in traps placed in fruiting trees (Table 1). For example, Rust (1918), writing on the status of *A. fraterculus* as a "menace" to the United States, mentions (p. 462) avocado (*P. americana*) as a host plant in NW Argentina. Despite the fact that Rust (1918) provides no hard data ("the writer knows"), his publication has been used as evidence of the status of *P. americana* (unknown cultivar) as a host of flies in the genus *Anastrepha.*

Wild native hosts of *A. fraterculus* and *C. capitata* in Argentina have been poorly studied. Species such as *Eugenia uniflora* L., *Myrcianthes pungens* (Berg.) Legrand (cited as "mato"), and *Juglans australis* Grisebach have been reported in Tucumán (Nasca 1973, Nasca et al. 1981, Fernández de Araoz and Nasca 1984), *Hexachlamys edulis* (Berg.) Krausel et Legrand in Entre Ríos (Putruele 1996), and *H. edulis* (cited as *Eugenia myrcianthes* Berg), *Campomanesia crenta* Berg, and *Eugenia retusa* Berg in Misiones (Ogloblin 1937, Turica and Mallo 1961). Unfortunately, most of these host records also lack the rigor needed to consider them fully valid for the reasons cited in the preceding paragraph (also see Table 1).

Our aim in this study was to unequivocally establish the host status of as many of the wild or commercially grown native and introduced fruit species found in the citrus growing province of Tucumán, Argentina. We wanted to establish which fruit were infested by *A. fraterculus* and *C. capitata* larvae, and we also were interested in determining infestation levels (larvae/kg fruit) over a long period of time (6 yr). As noted by Aluja (1996, 1999) and Aluja and Liedo (1986), short term studies of this nature shed little light into the dynamics of long-term fly population fluctuations and provide information of little value when trying to design biorational fruit fly management schemes. Given the fact that the Argentinean government is making efforts to establish low fruit fly prevalence areas in NW and NE citrus-producing regions (SENASA 1998), we also wanted to determine periods of alternative host availability.

Materials and Methods

Study Area. We collected fruit in 30 sites located in central and western portions of the Tucumán province (NW Argentina). Details on the exact location (latitude and longitude) and altitude of each site are provided in Table 2. The Tucumán province is an important citrus-growing region located between 64°28′ – 66° 13′W longitude and 26°05′ – 28° 01′S latitude, with elevations ranging between 250 and 5,500 m above sea level (Guido et al. 1998). According to Köppen's climatic classification (Torres-Bruchmann 1976), the climate in central and western portions of the province varies between *Cwa* (temperate-calid humid with a summer rainy season and winter dry season, temperature of warmest month >22°C) at elevations of 300 – 1,000 m and *Cwb* (temperate-calid humid with a summer rainy season and winter dry season, temperature of warmest month <22°C) at elevations of 1,000 –2,000 m (Sesma et al. 1998). The native vegetation of this region at elevations of 300 – 600 m was totally removed to establish sugar cane plantations and citrus groves. At higher elevations (600 –1,500 m) stands of native subtropical forest (locally known as "Yungas") are still common, even though cattle ranching and logging are causing widespread devastation.

Sampling and Insect Processing Procedures. We collected any available wild or commercially grown fruit in the study sites (Tables 2 and 3) between January 1990 and December 1995 for two consecutive months in each year (period for each plant species identified in Table 3). Based on Aluja et al. (1996) and Cowley et al. (1992), who pointed out marked yearly variations in fly populations and the effect environmental factors such as drought can have on host availability, we decided that, instead of collecting fruit over the entire fruiting season in a particular year, to collect during the peak fruiting season (2 mo) over a 6-yr period. Consequently, we would enhance the chances of finding infestations in at least 1 of the 6 yr during which we sampled. Having done otherwise (i.e., intensive sampling in one or two seasons), would have enhanced the risk of reporting lack of infestation when infestations did not occur every year. The only exception to the latter sampling scheme involved *Passiflora caerulea* L., *Mangifera indica* L., and *J. australis,*

Table 1. Historical review of host plant records for *Anastrepha fraterculus (A.f.)* and *Ceratitis capitata (C.c.)* in Argentina

Source	Plant species code (complete name in Table 3)	Fruit fly species		Larvae reared from fruit	Sexual maturity of adult flies determined	Infestation rates recorded	Name of expert fly taxonomist provided	Name of expert plant taxonomist provided	Comments
		C.c.	*A.f.*						
Lahille (1915)	2	No	Yes	Yes	No	No	No	No	
Rust (1916)	2, 4, 25, 26, 27	No	Yes	No	No	No	No	No	Undocumented list of host plants
Rust (1918)	2, 6, 7, 18, 25, 26	No	Yes	No	No	No	No	No	
Ogloblin (1937)	2, 4, 7, 11, 13, 16, 17, 18, 20, 21, 24, 25, 26, 27	No	Yes	?	No	No	No	No	Not clear if larvae were reared
Hayward (1944)	2, 4, 7, 13, 16, 18, 20, 24, 25, 26, 27	No	Yes	No	No	No	No	No	Undocumented list of host plants
Domato and Aramayo (1947)	17, 20, 21, 27	Yes	Yes	No	No	No	Yes	No	Information based on adult flies captured in traps
Vergani (1952)	4, 6, 7, 13, 16, 17, 18, 20, 21, 23, 24, 25, 27, 33	Yes	No	No	No	No	No	No	Undocumented list of host plants
Rosillo (1953)	17, 18, 19, 20, 21, 33	Yes	Yes	No	No	No	Yes	Yes	Information based on adult flies captured in traps
Hayward (1960)	2, 4, 13, 16, 17, 18, 19, 20, 21, 25, 27	No	Yes	No	No	No	No	No	Undocumented list of host plants
Blanchard (1961)	2, 4, 13, 16, 17, 18, 19, 20, 21, 25, 27	No	Yes	No	No	No	No	No	Undocumented list of host plants
Turica and Mallo (1961)	4, 7, 20, 24, 25, 27	Yes	No	Yes	Yes	No	Yes	No	
Costilla (1967)	20, 25, 27	Yes	No	Yes	Yes	No	No	No	
Nasca (1970)	5, 12, 13, 20, 25, 27	No	Yes	No	No	No	No	No	Undocumented list of host plants
Turica et al. (1971)	4, 6, 7, 17, 18, 20, 21, 23, 24, 25, 27	Yes	Yes	No	No	No	No	No	Undocumented list of host plants
Nasca (1973)	5, 13, 20, 25, 27	Yes	Yes	Yes	Yes	No	Yes	No	
Nasca et al. (1981)	4, 7, 11, 12, 13, 14, 16, 18, 20, 23, 25, 26, 27	Yes	Yes	No	No	No	No	No	Undocumented list of host plants
Fernandez de Araoz and Nasca (1984)	1, 5, 6, 11, 13, 19, 25, 27	Yes	No	Yes	Yes	No	No	No	
Putruelle (1996)	1, 3, 6, 7, 12, 13, 14, 16, 17, 18, 20, 21, 24, 25, 26, 27	Yes	Yes	Yes	No	No	No	No	
Nasca et al. (1996)	4, 6, 7, 16, 18, 19, 20, 21, 23, 24, 25, 26, 27, 33	Yes	No	Yes	Yes	Yes	No	No	
Nasca et al. (1996)	4, 7, 15, 18, 19, 20, 21, 25, 33	No	Yes	Yes	Yes	Yes	No	No	
Vaccaro (2000)	1, 16, 17, 19, 24, 25, 27	Yes	No	Yes	Yes	No	Yes	No	
Vaccaro (2000)	4, 13, 25, 26	No	Yes	Yes	Yes	No	Yes	No	

Table 2. Description of collection sites in the Tucumán Province, Argentina

Collection sites	Altitude (meters above sea level)	Southern latitude	Western longitude
Alpachiri (Al)	540	27° 20′	65° 46′
Concepción (Co)	405	27° 21′	65° 36′
El Siambón (ES)	1185	26° 43′	65° 27′
El Timbó (ET)	590	26° 42′	65° 08′
Famaillá (Fa.)	361	27° 03′	65° 25′
La Cocha (LC)	444	27° 47′	65° 34′
La Florida (LF)	430	27° 14′	65° 34′
Los Nogales (LN)	600	26° 42′	65° 16′
La Ramada (LRa)	570	26° 42′	64° 57′
La Reducción (LRe)	510	26° 58′	65° 22′
La Rinconada (LRi)	550	26° 51′	65° 19′
Los Sosa (LS)	420	27° 09′	65° 34′
Lules (Lu)	425	26° 56′	65° 21′
Malvinas (Ma)	550	26° 55′	65° 17′
Potrero Las Tablas (PT)	850	26° 54′	65° 25′
Pueblo Viejo (PV)	371	27° 13′	65° 35′
Raco (Ra)	1172	26° 39′	65° 26′
Rumi Punco (RP)	440	28° 01′	65° 34′
San Javier (SJ)	936	26° 45′	65° 20′
San Felipe (SF)	600	26° 45′	65° 16′
San Miguel de Tucumán (SMT)	426	26° 50′	65° 13′
San Pablo (SP)	412	26° 53′	65° 19′
San Pedro de Colalao (SPC)	1080	26° 14′	65° 30′
Sauce Guascho (SG)	470	27° 55′	65° 24′
Tafí Viejo (TV)	609	26° 44′	65° 16′
Taruca Pampa (TP)	548	26° 35′	64° 50′
Villa Alberdi (VA)	390	27° 36′	65° 37′
Villa Carmela (VC)	609	26° 45′	65° 17′
Villa Padre Monti (VPM)	770	26° 30′	64° 57′
Villa Quinteros (VQ)	371	27° 15′	65° 33′

which were only collected during one month every year because of fruit scarcity (exact timing specified in Table 4). Importantly, not all fruit species were sampled in every collection site (listed in Table 2) because in some localities they were absent (details in Table 5).

Fruit were collected in areas covered with wild native vegetation, such as the protected area known as "Parque Sierra de San Javier" (administered by the Universidad Nacional de Tucumán), in backyard gardens in rural areas, untreated semicommercial orchards, public gardens and parks in urban areas, and in patches of wild vegetation adjacent to commercial citrus groves or sugarcane plantations. Individual samples consisted of fallen ripe fruit or ripe fruit still on the tree, and ranged in number from 50 to 2,000 fruit, depending on availability and fruit size. Each sample was individually placed in cloth bags and transported to our laboratory in plastic crates. All fruit in the sample were counted, weighed, rinsed with a 20% solution of sodium benzoate, and placed in closed Styrofoam boxes with damp sand in the bottom as a pupation substrate for fly larvae (fruit were placed on a metal screen [10 mm mesh] fitted ≈10 cm from the bottom of each box). All fruit samples were kept inside a room at 25 ± 1°C and 65 ± 10% RH during 1 mo. During this period, the sand in each box was sifted once per week to collect fly puparia. Pupae were counted and placed in plastic cups filled with sterilized moist sand. These cups were inspected daily and any emerging adult fly removed. If fruit showed signs of decomposition, they were dissected to remove all larvae. The latter were handled as described above.

Once adults emerged, they were transferred to a cage and provided with water and food until wing coloration was fully attained and we could determine whether sexual maturity was reached. To ascertain the latter, we dissected 13-d-old adults and determined ovary and testicle development. We also selected 25 females and 25 males per fruit sample, placed them in screened cages and provided them with food (hydrolyzed protein and sugar) and water. These cages were kept inside a growth chamber (26 ± 1°C, 75 ± 5% HR, 14:10 h (L:D) photoperiod). Once reaching 13 d of age, we introduced ripe peaches as an oviposition substrate (fruit were thoroughly rinsed with tap water). After 48 h of exposure to ovipositing flies, we removed the fruit from the cage and handled it as described in the preceding paragraph to determine whether larvae and pupae developed.

Fly and Plant Identification. All fruit fly adults were identified by S. Ovruski. Keiko Uramoto (Instituto de Biociências, Universidade de São Paulo, Brazil) confirmed the validity of the identifications from a sample of *A. fraterculus*, *Anastrepha* sp., and *C. capitata* adults preserved in alcohol. Allen Norrbom (Systematic Entomology Laboratory, PSI, USDA–ARS, Washington, D.C.) tried to identify *Anastrepha* sp. but concluded that a DNA analysis was needed before rendering an accurate determination. Voucher specimens were deposited in the Fundación Miguel Lillo (FML) entomological collection in San Miguel de Tucumán, Argentina. Dried plants were compared with herbarium specimens at the FML and formally identified by Alejandra Roldán (Facultad de Ciencias Naturales e Instituto Miguel Lillo, Universidad Nacional de Tucumán – FCNeIML, UNT) and Hugo Ayarde (FML). *Persea americana* specimens were checked by Prof. María Inés Figueroa de Orell (Cátedra de Fruticultura, Facultad de Agronomía y Zootecnia, Universidad Nacional de Tucumán) in an effort to determine the cultivar. Nomenclature employed for native plant identification was based on Morales et al. (1995), and for exotic plant species was based on Boelcke (1992).

Data Analysis. All infestation values reported here are based on the number of fruit fly larvae (*A. fraterculus* plus *Anastrepha* sp. plus *C. capitata*) per kg of fruit. The relationship between fruit size (measured as individual fruit weight) and infestation level was analyzed by correlation analysis using log-transformed data.

Results

A total of 84,094 fruit (3,466.1 kg) representing 33 plant species (7 native and 26 exotic) in 15 plant families were collected during this study (Table 3). Only 17 (51.5%) of the plant species sampled were infested. The fruiting phenology of the latter is described in Table 4. Notably, 14,225 fruit (328.3 kg), representing 16 fruit species (4 native and 12 exotic)

Table 3. Plant species sampled between January 1990 and December 1995 in Tucumán, Argentina

Plant family	Plant species code	Scientific name	Spanish common name	English common name	Status
Anacardiaceae	1	*Mangifera indica* L.	Mango	Mango	Exotic
Annonaceae	2	*Annona cherimola* Mill.	Chirimoya	Cherimoya	Exotic
Caricaceae	3	*Carica papaya* L.	Papaya	Papaya	Exotic
Ebenaceae	4	*Diospyros kaki* L.	Caqui	Japanese persimmon	Exotic
Juglandaceae	5	*Juglans australis* Grisebach	Nogal criollo	Wild walnut	Native
Lauraceae	6	*Persea americana* Miller Rootstock of probable Mexican origin	Palta	Avocado	Exotic
Moraceae	7	*Ficus carica* L.	Higo	Fig	Exotic
	8	*Broussonetia papyrifera* L.	Mora turca	?	Exotic
	9	*Morus alba* L.	Mora blanca	White mulberry	Exotic
	10	*Morus nigra* L.	Mora negra	Black mulberry	Exotic
Myrtaceae	11	*Eugenia uniflora* L.	Arrayán	Surinam Cherry	Native
	12	*Myrcianthes pungens* (Berg) Legrand	Mato	?	Native
	13	*Psydium guajava* L.	Guayaba	Guava	Exotic
Passifloraceae	14	*Passiflora caerulea* L.	Pasionaria	Blue Passion Fruit	Exotic
Punicaceae	15	*Punica granatum* L.	Granado	Pomegranate	Exotic
Rosaceae	16	*Eriobotrya japonica* (Thunb.) Lindley	Níspero	Loquat	Exotic
	17	*Malus domestica* Borkh	Manzano	Apple	Exotic
	18	*Prunus armeniaca* L.	Damasco	Apricot	Exotic
	19	*Prunus domestica* L.	Ciruela	Cultivated plum	Exotic
	20	*Prunus persica* (L.) Batsch	Durazno	Peach	Exotic
	21	*Pyrus communis* L.	Pera	Pear	Exotic
	22	*Rubus boliviensis* Focke	Zarzamora	?	Exotic
Rutaceae	23	*Citrus aurantifolia* (Christm.) Swingle (unknown cultivar)	Lima	Lime	Exotic
	24	*Citrus aurantium* L. (Rootstock)	Naranja agria	Sour Orange	Exotic
	25	*Citrus paradisi* Macfadyn ('Marsh' cultivar)	Pomelo	Grapefruit	Exotic
	26	*Citrus reticulata* Blanco (unknown cultivar)	Mandarina	Tangerine	Exotic
	27	*Citrus sinensis* (L.) Osbeck ('Valencia' cultivar)	Naranja dulce	Sweet Orange	Exotic
	28	*Citrus limon* (L.) Burman (unknown cultivar)	Limón	Lemon	Exotic
Sapindaceae	29	*Allophylus edulis* (St.Hil.) Radlkofer	Chalchal	?	Native
Solanaceae	30	*Cyphomandra crassicaulis* (Ortega) Kuntze	Tomate árbol	TreeTomate	Native
	31	*Lycium cestroides* Schlecht	Chivil	?	Native
	32	*Psychotria carthagenesis* Jac.	Moradillo	?	Native
Vitaceae	33	*Vitis vinifera* L.	Uva	Grape	Exotic

did not yield any fruit fly larvae during the 6-yr study period (Table 5).

Although *C. capitata* was recovered from all infested samples, *A. fraterculus* was only present in 76% of them. *Anastrepha* sp. was only reared from *J. australis* and *Psidium guajava* L. Of the 13 plant species from which *A. fraterculus* was recovered, only *E. uniflora, M. pungens* (Myrtaceae), and *J. australis* (Juglandaceae) are native plants in the study region.

The total number of adult flies recovered from the 69,869 infested fruit (3,137.8 kg) was 99,627. Of this total, 69,180 (≈69.5%) were *A. fraterculus*, 30,138 (≈30.2%) were *C. capitata*, and 309 (≈0.3%) were *Anastrepha* sp. The proportion of adults of each fly species emerging in each of the infested fruit species is shown on a yearly basis in Table 6 and averaging all 6 yr in Fig. 1. Note that the proportion of *A. fraterculus* in *F. carica, D. kaki, E. japonica, C. paradisi* ('Marsh' cultivar), and *M. indica* (all exotic fruit species) was low (between 2.0 and 34.9%). *Citrus aurantium* (used in the region as rootstock), *C. reticulata* (unknown cultivar), *C. sinensis* ('Valencia' cultivar), and *P. caerulea* (all exotic) were only infested by *C. capitata.* Therefore, these four plants were not included in Fig. 1.

As shown in Table 6, infestation rates (number of larvae/kg of fruit) varied sharply from year to year and between host plant species. For example, in *M. pungens, P. guajava,* and *E. uniflora* (all Myrtaceae), there were 2.5-, 3.0-, and 3.5-fold differences in the infestation levels when comparing years 1994–1995, 1991–1995, and 1990–1993, respectively. Marked yearly variations also were registered in *F. carica.* In contrast, infestation rates were relatively stable in the remaining fruit species (Table 6). Overall, there was a significant negative correlation ($r = -0.6733189$) between fruit size and infestation level (Fig. 2). Fruit weighing between 1 and 60 g were the most infested. High levels of infestation were recorded in the native *Eugenia uniflora, M. pungens* and *J. australis* and the introduced *Psidium guajava, Prunus persica, P. domestica, P. armeniaca,* and *Eryobotria japonica* (Table 6).

Table 4. Fruiting phenology of *C. capitata* and *A. fraterculus* host plants in Tucumán, Argentina

Fruit fly host plant species	Months											
	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
A. cherimola		◧	◧	■								
C. aurantium	■				■	■	■	■	■	◧	◧	■
C. paradisi			■	◧	◧	■						
C. reticulata					◧	◧	■	■				
C. sinensis					■	■	■	■	◧	◧	■	
D. kaki	■										◧	◧
E. japónica							■	■	◧	◧		
E. uniflora	■									■	◧	◧
F. carica	◧	■									■	◧
J. australis	◧	■									■	■
M. indica	■	◧	■									
M. pungens	◧	■	■								■	◧
P. caerulea	◧	■										■
P. armeniaca										■	◧	◧
P. domestica	■										◧	◧
P. persica	■										◧	◧
P. guajava		■	◧	◧	■							

■ = fruit available ◧ = when fruit were sampled.

Lowest infestation values were recorded in the introduced *F. caraica* and *P. caerulea*, *D. kaki*, *A. cherimola*, *M. indica*, and the four commercially grown citrus species sampled in the study (Table 6).

Discussion

Two hosts discovered here for *A. fraterculus* and *C. capitata* (*J. australis* and *M. pungens*) had been previously reported in local Argentinean journals or technical reports (Table 1), but do not appear in the most updated host lists for these fly species (Norrbom 2000 and Liquido et al. 1991, for *Anastrepha* and *Ceratitis*, respectively). Our results confirm the previous records and the plants should, therefore, be included as hosts of *A. fraterculus* and *C. capitata.* We note that *J. australis* and *M. pungens* belong to the plant families Juglandaceae and Myrtaceae, respectively, which contain other species also identified as hosts for both fly species. Fruit in the family Myrtaceae are the principal hosts of *A. fraterculus* (Aluja et al. 2000a, Norrbom 2000) and are also commonly infested by *C. capitata* (Liquido et al. 1991). In the case of the Juglandaceae, *Juglans regia* L. had been reported as a host of both *A. fraterculus* and *C. capitata* (Korytkowski and Ojeda-Peña 1968, Liquido et al. 1991) and for *C. capitata* (Nasca et al. 1996), and *J. neotropica* Diels and *J. nigra* L. as hosts of *A. fraterculus* and *C. capitata*, respectively (Korytkowski and Ojeda-Peña 1969 and Liquido et al. 1991, respectively). We also note that many species within the Juglandaceae are commonly infested by flies in the genus *Rhagoletis* of Central or South American origin (species within the *suavis* group [e.g., *R. boycei* Cresson, *R. completa* Cresson, *R. juglandis* Cresson, *R. ramosae* Hernández-Ortíz, *R. suavis* (Loew), *and R. zoqui* Bush]; Bush 1966, Hernández-Ortíz 1985, Aluja et al. 2000a).

When comparing the proportion of *A. fraterculus* and *C. capitata* in the fruit species that were infested, it becomes apparent that *C. capitata* is much more abundant, or on occasion, the single species present in exotic cultivated fruit such as *F. carica*, *D. kaki*,

Table 5. Plant species not found infested by *Anastrepha fraterculus* and *Ceratitis capitata* between January 1990 and December 1993 in Tucumán, Argentina

Collecting years	Host plant species	No. of samples	Total no. of fruit sampled	Total wt (kg)	Collecting sites (complete name in Table 2)
1990–1993	*Allophylus edulis*	10	2572	1.4	LRi, SJ, TV
1992	*Broussonetia papyrifera*	1	15	0.08	Lri
1990–1992	*Carica papaya*	5	38	19.9	SMT, VC
1990–1993	*Citrus aurantifolia*	11	349	13.4	LRi, TP, TV
1990–1993	*Citrus limon*	12	426	19.8	LRi, SMT, SP, TP, TV, VC
1991–1993	*Cyphomandra crassicaulis*	14	496	9.2	LRi, Lu, SF, TP, TV, VC
1990–1993	*Lycium cestroides*	13	1258	1.4	LRi, TP, TV, VC
1990–1993	*Malus domestica*	6	157	9.7	LRi, SMT, TV
1990–1992	*Morus alba*	4	515	0.3	LRi, Lu
1990–1992	*Morus nigra*	17	3108	1.6	LRi, SMT, TV, VC
1990–1993	*Persea americana*	8	1027	227.4	LRi, Lu, SMT, TV, VC
1991–1993	*Psychotria carthagenesis*	8	1450	1.1	LRi, SJ, TV
1990–1993	*Punica granatum*	7	178	7.8	LRi, SMT
1990–1993	*Pyrus communis*	6	196	6.9	TV, SMT
1990–1993	*Rubus boliviensis*	9	686	0.4	LRi, TV, VC
1990–1993	*Vitis vinifera*	10	1754	7.9	LRa, Lre, LRi, Lu, TV

Table 6. Infestation levels of *Anastrepha fraterculus* (*A. f.*), *Anastrepha* sp., and *Ceratitis capitata* (*C. c.*) in fruit samples of host plants collected in Tucumán, Argentina, between January 1990 and December 1995

Host plant species	Total no. of fruit sampled (no. of samples)	kg of fruit	Degree of infestation (larvae/kg fruit) per collecting year						Total no. of pupae	Fruit flies		Collecting sites (complete name in Table 2)
			1990	1991	1992	1993	1994	1995		Fly sp.	Total no. adults	
					Small (<30 g)							
E. japónica	3,930 (61)	32.9	44.9	37.1	28.2	38.5	73.2	60.5	1,505	*A. f.*	194	LRi, Lu, SMT, SP, TV, VC
										C. c.	543	
E. uniflora	12,288 (46)	56.6	179.7	76.8	84.4	52.7	86.7	92.1	5,924	*A. f.*	1,969	Lu, SF, SJ, SMT, TV, VC
										C. c.	1,294	
F. carica	1,411 (62)	34.9	40.1	44.5	14.1	13.1	21.7	–	765	*A. f.*	4	Fa, LRe, LRi, Lu, SP, SMT, TP, TV, VC
										C. c.	309	
M. pungens	3,418 (31)	41.7	–	69.3	59.3	40.1	35.9	83.7	2,379	*A. f.*	1,214	Lu, TV
										C. c.	167	
P. caerulea	187 (12)	2.4	23.3	21.6	10.5	–	–	–	46	*A. f.*	0	LRi, SMT
										C. c.	25	
					Medium (30–100 g)							
C. reticulata	2,195 (73)	161.2	5.7	3.6	3.4	4.1	2.8	4.6	187	*A. f.*	0	ET, LRi, Lu, TV, SF, SMT, SP, TP, VC
										C. c.	289	
D. kaki	546 (23)	48.6	15.8	20.3	13.3	–	–	–	784	*A. f.*	58	ES, LRi, SMT
										C. c.	296	
J. australis	2,005 (21)	69.5	55.0	57.1	63.1	72.8	65.4	54.8	4,131	*A. f.*	1,435	Lu, LRi, SMT, TV
										A. sp.	276	
										C. c.	392	
P. armeniaca	1,784 (20)	60.6	–	53.9	56.3	42.5	39.7	44.1	2,853	*A. f.*	1,239	Ra
										C. c.	534	
P. domestica	2,541 (27)	101.4	–	62.7	54.3	72.0	63.6	57.4	6,437	*A. f.*	2,638	ES, Ra, SPC
										C. c.	871	
P. persica	26,189 (156)	788.6	53.3	111.9	91.6	69.9	75.2	59.9	73,526	*A. f.*	20,359	Al, Co, ES, ET, Fa, LF, LN, LS, LRe, LRi, Lu, PV, Ra, SF, SG, SJ, SMT, SP, SPC, TP, TV, VA, VC, VPM, VQ
										C. c.	3,916	
P. guajava	11,075 (117)	555.3	122.1	94.6	126.7	169.3	260.5	122.3	88,540	*A. f.*	9,771	Co, ET, LS, LRa, LRe, LRi, Lu, Ma, PT, SF, SG, SJ, SP, TV
										A. sp.	33	
										C. c.	3,999	
					Large (100–500 g)							
A. cherimola	157 (20)	26.9	29.0	21.8	12.5	–	–	–	601	*A. f.*	266	LRi, SMT, SP, TV
										C. c.	75	
C. aurantium	2,401 (84)	376.6	8.8	12.6	17.4	14.8	19.1	18.2	5,610	*A. f.*	0	Co, ET, Fa, LN, LRe, LRi, Lu, SF, SMT, SP, TP, TV
										C. c.	2,704	
C. paradisi	1,153 (71)	270.6	18.7	15.1	11.3	10.7	8.9	12.5	3,463	*A. f.*	657	Al, ET, Fa, LC, LF, LS, LRa, LRe, LRi, Lu, RP, SF, SP, TP, TV, VC, VQ
										C. c.	1,537	
C. sinensis	2,276 (96)	297.5	11.3	21.6	16.5	23.1	20.9	13.1	5,192	*A. f.*	0	Al, Co, ET, Fa, LC, LF, LS, LRe, LRi, Lu, PV, RP, SF, SMT, SP, TP, TV, VA
										C. c.	2,239	
M. indica	350 (27)	127.2	16.3	25.3	18.1	21.2	17.8	33.1	2,606	*A. f.*	593	Lu, LRi, SMT, TV, VA, VC
										C. c.	1,002	

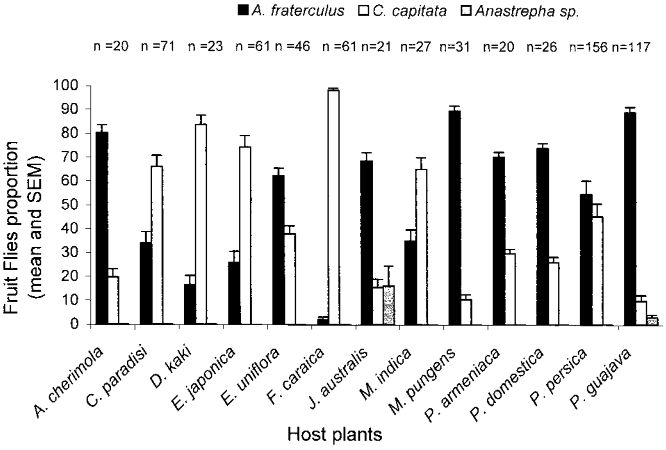

Fig. 1. Mean (±SE) proportion of *Anastrepha fraterculus*, *Ceratitis capitata*, and *Anastrepha* sp. in fruit samples collected in Tucumán, Argentina between 1990 and 1995. N = number of samples.

E. japonica, and several *Citrus* species. Furthermore, the presence of *C. capitata* was much more common in backyard gardens in urban and rural houses and in semicommercial orchards in all sampled localities. A similar phenomenon has been recorded in Brazil, where *C. capitata* is mainly found in urban areas associated with *Terminalia catappa* L., an exotic ornamental tree (Malavasi et al. 2000). In contrast, native species such as *M. pungens, E. uniflora,* and *J. australis,* and exotic "feral" species such as *P. guajava* and *Prunus* species, which form part of the vegetation in perturbed Yungas forests of Tucumán, serve as important reservoirs of high *A. fraterculus* populations. Similar observations were made by Malavasi and Morgante (1981) and Veloso et al. (2000) in Brazil. These authors showed that *A. fraterculus* mainly occurred in local native fruit species belonging to the Myrtaceae and Anacardiaceae. In sum, it becomes clear that *C. capitata* appears to adapt well to highly perturbed environments were the native vegetation has been replaced by exotic plants.

Several previous reports (see Table 1 for details) cite all *Citrus* species sampled during this study, with the exception of *C. limon* (L.) Burman, as hosts of *C. capitata.* In contrast, there are fewer reports of *A. fraterculus* infesting citrus in Argentina and none of the existing reports provide information on levels of infestation (Table 1). Basically, *A. fraterculus* only commonly infests *C. paradisi* in Argentina. We note, however, that in a recent survey in Tucumán, *C. aurantium* (used as rootstock) was sporadically infested by this fruit fly species and when such was the case, infestation levels were extremely low (P.S., unpublished data). Why is *C. capitata* so common and *A. fraterculus* so rare in citrus? A possible explanation is that these host plants emit infochemicals attractive to *C. capitata* (Jang and Light 1996). For example, Howse and Knapp (1996) suggested that citrus trees and fruit emit volatiles that are similar to the male pheromone of *C. capitata.* Another plausible explanation is that environmental conditions in citrus groves are more suitable for *C. capitata* than for *A. fraterculus.* Furthermore, Aluja et al. (2000b) mention that it is likely that many species of *Anastrepha* have not yet developed the ability to metabolize the toxic allelochemicals that some recently (in evolutionary time) introduced exotic fruit contain. As a result, there is low egg viability and high larval mortality in these types of hosts (M.A., unpublished data).

We note that some of the plant species that we found to be free of *A. fraterculus* or *C. capitata* infestations, such as *V. vinifera, Pyrus communis, Persea americana,* and *Malus domestica* (cited as *Malus sylvestris* Miller), have either been previously reported as hosts of these tephritid species in Tucumán and other Argentinean provinces or have been included in listings of fruit fly host plants in Argentina (Table 1). We therefore recommend that the host status of these plants be confirmed following the methodology of Cowley et al. (1992). However, we note too that apple (*M. pumila*) cultivars 'Gala', 'Fuji', and Golden Delicious' are heavily infested by *A. fraterculus* in Caçador, Santa Catarina, Brazil (Sugayama et al. 1997). In the case of *P. americana, C. capitata* has been reported

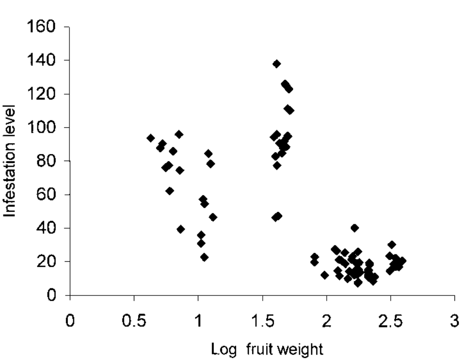

Fig. 2. Relationship between infestation level (mean number of larvae per kg of fruit) and fruit size (mean individual weight of fruit).

infesting cultivars such as 'Chabil', 'Itzamná', 'Kashlan', 'MacDonald' in Guatemala (Willard et al. 1929), and 'Sharwil' in Hawaii (Oi and Mau 1989). Natural (orchard) infestation levels in Guatemala were extremely low (e.g., one fruit out of 66 and two fruit out of 180 in 'Chabil' and 'Itzamná' cultivars, respectively) (Willard et al. 1929). Reports from Hawaii stem from caged fruit hanging naturally from branches that were artificially exposed to gravid *C. capitata* females (1 fruit/35 females). Under these circumstances, only 15.8% of the fruit were infested (Oi and Mau 1989). In the case of *Anastrepha,* virtually all purported records of infestations in *P. americana* are questionable, and none provide information on the cultivar, infestation levels (i.e., larvae per kg of fruit or per individual fruit), or the expert taxonomist performing the plant identification (M.A., unpublished data). Based on the above, we recommend that any future record of *P. americana* infestations in Argentina by *A. fraterculus* or *C. capitata* be expertly confirmed.

Overall, we were able to detect two patterns of infestation over time, depending on the fruit species. In fruit such as *M. pungens, P. guajava,* and *E. uniflora* there were up to 3.5-fold differences between years, whereas in species such as *J. australis* and *P. armeniaca,* yearly variations in infestation levels (i.e., larvae/kg of fruit) were more stable and consistently high. This discovery underscores the importance of conducting these types of studies over long periods (Aluja 1996, 1999; Aluja et al. 2000a). Had our study only encompassed one or two fruiting seasons, these yearly fluctuations in fruit infestation patterns would have gone undetected. The polyphagy observed in *A. fraterculus* and *C. capitata,* added to host availability, allows these two species to be present almost year-round in NW Argentina. In the case of *A. fraterculus, C. paradisi* and *E. japonica* seem to play a critical role as alternative hosts between May and September, which is the time of the year when the preferred hosts *E. uniflora, P. guajava, M. pungens, J. australis,* and *Prunus* spp. are not available. In the case of *C. capitata,* several citrus species serve as bridges between the fruiting periods of *F. carica, D. kaki,* and the various myrtaceous and rosaceous hosts that fruit between October and April.

We believe that the information yielded by this study can aid the efforts by the Argentinean government to determine the location and feasibility of establishing fly-free areas in certain fruit-producing regions of N Argentina and to better structure the quarantine protocols needed when exporting fruit. However, we believe that the numerous alternative host plants in this part of the country will represent a hurdle. If our information on fruiting phenology is used to program mass releases of sterile flies or parasitoids, it might be possible to suppress fly populations in key hosts such as *Prunus armeniaca, P. domestica, P. persica, J. australis, E. uniflora,* and *Psidium guajava.* These hosts seem to play a key role in the increase of fly populations and targeting them could prove highly profitable. Our results also allow us to conclude that eradication or suppression strategies have to be tailored to the "idiosyncrasy" of each fly species. We have shown that *C. capitata* is able to infest all citrus species grown in the region, whereas *A. fraterculus* can really only be considered a pest of *C. paradisi.* Further, we have shown that *C. capitata* seems to thrive in highly perturbed environments, whereas *A. fraterculus* does better in areas with vast remnants of native vegetation or where native hosts are more common than introduced ones. Thus, management strategies will have to entail area-wide approaches that take into account the biogeographic characteristics of the region (Aluja and Liedo 1986). In other cases, when resource poor farmers are involved, methods such as fruit bagging may represent the only feasible alternative (Aluja 1996).

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