Relative Abundance of *Ceratitis capitata* and *Anastrepha fraterculus* (Diptera: Tephritidae) in Diverse Host Species and Localities of Argentina

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ABSTRACT Two fruit fly species (Diptera: Tephritidae) of economic importance occur in Argentina, the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and *Anastrepha fraterculus* (Wiedemann). Here, we compared the relative abundance of these fruit pests in 26 fruit species sampled from 62 localities of Argentina in regions where *C. capitata* and *A. fraterculus* coexist. In general, *C. capitata* was predominant over *A. fraterculus* (97.46% of the emerged adults were *C. capitata*), but not always. Using the number of emerged adults of each species, we calculated a relative abundance index (RAI) for each host in each locality. RAI is the abundance of *C. capitata* relative to the combined abundance of *A. fraterculus* and *C. capitata*. Some families of fruit species were more prone to show high (Rutaceae and Rosaceae) or low (Myrtaceae) RAI values, and also native plants showed lower RAI values than introduced plants. RAI showed high variation among host species in different localities, suggesting a differential use of these hosts by the two flies. There were localities where *A. fraterculus* was not found in spite of suitable temperature and the presence of hosts. Most host species showed little variation in RAI among localities, usually favoring *C. capitata*, but peach, grapefruit, and guava showed high variation. This suggests that these fruit species are suitable for both fruit flies but more favorable to one or the other, depending on local environmental conditions (e.g., relative humidity and degree of disturbance) of each locality.

KEY WORDS Tephritidae, relative abundance index, geographical distribution, Mediterranean fruit fly

The family Tephritidae includes some of the most important fruit pests worldwide (White and Elson-Harris 1992). The economic damage caused by these flies is two-fold: direct damage to the fruit (larval activity) and limited access to potential markets because of quarantine restrictions imposed by countries that are free of these pests (Malavasi et al. 1994). In the American Continent, flies within *Anastrepha, Ceratitis, Rhagoletis,* and *Toxotrypana* cause the most economic damage (Landolt 1985, Enkerlin et al. 1989, Aluja 1994).

In Argentina, there are two quarantine species of fruit flies: the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), and *Anastrepha fraterculus* (Wiedemann) (Aruani et al. 1996). *C. capitata* is native to Africa and has a wide distribution, covering many tropical, subtropical, and temperate regions of the world (Copeland et al. 2002). This species shows a high adaptability to diverse climates as well as a large number of host fruit species (>350; Liquido et al. 1991). Its presence in Argentina was first recorded at the beginning of the 20th century in orchards located in the vicinity of Buenos Aires city (Vergani 1952). Later, it was reported in commercial orchards of northeastern and northwestern regions of the country. The last region in which it was reported was northern Patagonia (southern Argentina), where *C. capitata* was first detected in 1952 (Rial 1997). *A. fraterculus* is native to South America and is distributed from Mexico to Argentina, but there is morphological and genetic evidence indicating that there are many cryptic species (Steck 1991, Hernández-Ortíz et al. 2004) and that not all the species within this species complex are pests (Aluja et al. 2003). In Argentina, *A. fraterculus* is mainly distributed in regions with tropical and subtropical climate (Ovruski et al. 2003). It is also a polyphagous species that attacks different families of fruit species, but the number of hosts cited is smaller than that for *C. capitata* (≈80 species; Norrbom 2004). Both species cause significant annual losses to the fruit

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production of Argentina and constitute a major barrier to the expansion of this market (Ovruski et al. 1999).

In spite of the importance of these fruit fly species, there is little information published on the relative abundance of *C. capitata* and *A. fraterculus* in areas of Argentina where they coexist. Other than Vergani (1956), the only map available showing the distribution of the two species at the national level is hypothetical (Ortiz 1999). Variability in the relative abundance of the two species among different regions was reported by Vattuone et al. (1995) based on average values among different hosts, but the relationship between the two species strongly depended on the fruit considered. Comparisons based on trapping data (FAO 1989, Segade and Polack 1999, Vattuone et al. 1999) are biased by the degree of attraction that adult flies of the two species show to the bait used in the traps. Some local studies provide data based on fruit sampling (Costilla 1967, FAO 1989, Putruele 1993, Vattuone et al. 1999). In Tucumán province, Costilla (1967) found a greater proportion of *C. capitata* than *A. fraterculus* in citrus orchards of grapefruit, *Citrus paradisi* L., and orange, *Citrus sinensis* (L.) Osbeck. Schliserman and Ovruski (2004), working in areas of the same province with much native vegetation, found mainly *C. capitata* in bitter orange, *Citrus aurantium* L. Ovruski et al. (2003) also reported proportions of *C. capitata* and *A. fraterculus* adults and larval infestation levels in wild or commercially grown plants, both native and introduced, and emphasized the importance of *Citrus* spp. as hosts of *C. capitata* and native fruit species as hosts of *A. fraterculus.* In Entre Ríos province, Putruele (1993) recovered both species from grapefruit; peach, *Prunus persica* L.; fig, *Ficus carica* L.; and mandarin, *Citrus reticulata* Blanco; but only in grapefruit was *A. fraterculus* more abundant than *C. capitata.* In the same province, apple, *Malus domestica* Borkh, and pear, *Pyrus communis* L., were infested only by *C. capitata,* whereas pomegranate, *Punica granatum* L., and quince, *Cydonia oblonga* Mill, were attacked only by *A. fraterculus* (Putruele 1993). In Catamarca province, Vattuone et al. (1999) reported that orange, peach, grapefruit, mandarin, and kumquat, *Citrus aurantium* variety *myrtifolia* Ker-Gawl, were infested only by *C. capitata.* In La Rioja province, Nasca et al. (1996) recorded greater infestation of *C. capitata* than *A. fraterculus* in fig; persimmon, *Diospyros kaki* L.; quince; pomegranate; plum, *Prunus domestica* L.; and apricot, *Prunus armeniaca* L. Although these studies are valuable, there has been no comprehensive study comparing the relative abundances of both species along the variety of hosts and regions present in Argentina.

The aim of this study was to provide these comparative data for *C. capitata* and *A. fraterculus.* We describe the relative abundance of these flies through the analysis of data obtained from fruit samplings of many different host species. Specifically, we were interested in comparing the possible variability in the abundances of the two fly species 1) among different host species from the same locality and 2) among different localities for the same host. We also examined the influence of plant taxonomy and origin (native or introduced) as well as variations in the climate on the relative abundance of these two species.

Materials and Methods

Sampling. Fruit sampling was carried out in those political provinces of Argentina where the two fruit flies are reported to coexist (see *Appendix* 1). The localities ranged from undisturbed areas with most of the vegetation being native to very disturbed systems, such as suburban areas or agricultural landscapes. The climatic characteristics, specifically rainfall and relative humidity, also varied widely.

Sampling was performed mainly during the fruiting season of 1999–2000. Nevertheless, because of inherent logistical complexities faced in a study covering such a large geographical area, sampling data derived from the 2000–2001 season in some localities (e.g., Concordia), and from the 1998–1999 fruiting season in others (e.g., Posadas). To include as much area as possible, we also present fruit-collecting data from 1993 for three localities in the province of Catamarca. For the localities that were sampled during more than one fruiting season, no substantial differences between years were found in the relative abundance index (RAI) values (not shown), so these data were pooled. Descriptions of each locality are provided in *Appendix* 1.

All fruit species sampled have been previously cited as hosts for both fruit fly species (Liquido et al. 1991, Norrbom 2004), and they included native and introduced plants. In each locality, at least 10 fruit were sampled for each host species. Only fruit with evident signs of infestation by fruit flies was collected. The sampled fruit was placed in plastic trays over a layer of sand (or vermiculite), which was used by larvae as a pupation substrate after leaving the fruit. Pupae were separated from the sand using a sieve and then transferred to new containers, where they were maintained until emergence. Adults were identified, and the number of individuals of each fruit fly species was recorded. For inclusion in the analysis, at least 10 adults were required for a given host species and locality.

Data Analysis. To describe the relationship between the abundances of the two fruit fly species, a relative abundance index (RAI) was calculated for each host species in each locality according to the following formula: $RAI_{xy} = Cc/(Cc + Af)$, where Cc and Af are the number of emerged adults of *C. capitata* and *A. fraterculus,* respectively, for host X in locality Y. RAI ranges from 0 (exclusive presence of *A. fraterculus*) to 1 (exclusive presence of *C. capitata*). The RAI value for a given host (RAI_X) was estimated as the mean value for all of the localities, where that particular host was sampled. According to the RAI value obtained, hosts and localities were assigned to one of five categories: exclusive presence of one or the other species (RAI = 0 or RAI = 1), both species present but higher abundance of one or the other ($0 < RAI < 0.33$ or $0.66 < RAI < 1$), and intermediate cases ($0.33 \leq RAI \leq 0.66$).

Table 1. Host species sampled

Common name	Scientific name	Family	Native/exotic
Albarillo	*Ximenia americana* L.	Olacaceae	N
Apple	*Malus domestica* Borkh	Rosaceae	E
Asian pear	*Pyrus pyrifolia* (Burn. F.) Nakai	Rosaceae	E
Bitter orange	*Citrus aurantium* L.	Rutaceae	E
Feijoa	*Feijoa sellowiana* Berg	Myrtaceae	N
Fig	*Ficus carica* L.	Moraceae	E
Grapefruit	*Citrus paradisi* L.	Rutaceae	E
Guava	*Psidium guajaba* L.	Myrtaceae	N
Kiwi fruit	*Actinidia chinensis* Planch.	Actinidiaceae	E
Kumquat	*Citrus aurantium var. myrtifolia* Ker-Gawl	Rutaceae	E
Loquat	*Eriobotrya japonica* (Thunb.) Lindl	Rosaceae	E
Mandarine	*Citrus reticulata* Blanco	Rutaceae	E
Orange	*Citrus sinensis* (L.) Osbeck	Rutaceae	E
Papaya	*Carica papaya* L.	Caricaceae	N
Peach	*Prunus persica* L.	Rosaceae	E
Pear	*Pyrus communis* L.	Rosaceae	E
Persimmon	*Dyospiros kaki* L.f.	Ebenaceae	E
Plum	*Prunus insititia* L	Rosaceae	E
Quince	*Cydonia oblonga* Mill	Rosaceae	E
Ubajay	*Hexachlamys edulis* (O. Berg)	Myrtaceae	N

For every host–locality combination, we compared the observed frequencies with expected frequencies estimated multiplying the number of cases by the probability that in a random sample of 10 pupae: all of them were *C. capitata;* all of them were *A. fraterculus;* seven to nine pupae were of one of the two flies (and three to one of the other); and four to six pupae were of either of them. A chi-square goodness-of-fit test was performed to compare observed and expected frequencies (StatSoft, Inc. 2000).

A Mann–Whitney test was performed to compare the RAI values recorded for native and introduced fruit species (StatSoft, Inc. 2000). To compare the RAI values found for the main taxonomic families of fruit species (Myrtaceae, Rosaceae, and Rutaceae), a nonparametric analysis of variance (ANOVA) (Kruskal–Wallis test) was performed. When this analysis showed significant differences, nonparametric multiple comparison tests were performed (Analytical Software 2000).

Results

We obtained fruit samples from 62 localities in 12 of the 24 political provinces of Argentina, covering six ecological regions (see *Appendix* 1) and representing the complete area shared by both species of fruit flies in the country. In total, 30,354 fruit were collected, belonging to 20 host species from eight families of plants. Three of these families are native to South America (Myrtaceae, Caricaceae, and Olaceae), and five are introduced (Actinidiaceae, Ebenaceae, Moraceae, Rosaceae, and Rutaceae) (Table 1). Of 43,142 pupae recovered from the fruit, a total of 27,301 adults emerged: 23,608 (97.46%) were *C. capitata*, and 3,693 (2.54%) were *A. fraterculus.* We recovered parasitoids in only seven sampling sites, and in those cases the percentage of parasitism was never higher than 5%.

Thirty-two localities and 12 host species were sampled in northwestern Argentina (NWA) (Fig. 1; *Appendix* 1), and 30 localities and 18 host species were sampled in northeastern Argentina (NEA) (Fig. 2; *Appendix* 1). A general predominance of *C. capitata* was observed, which was higher in NWA than in NEA ($U = 1096.5$, $P = 0.042$; Mann–Whitney test). The proportion of samples in which RAI = 1 was 72% in the NWA and 50% in NEA (Table 2).

In some cases, RAI showed a marked variation among hosts in the same locality, e.g., in Yuto from NWA and in Posadas and Concordia from NEA (Figs. 1 and 2; Table 2). In those cases, some hosts had a RAI that was very high (mandarin from Yuto; persimmon from Posadas; and peach, guava, and orange from Concordia) or very low (guava, *Psidium guajava* L., from Yuto; grapefruit and guava from Posadas; and feijoa from Concordia), whereas other hosts showed intermediate values. In other localities, the variation among hosts was considerably lower. For example, in Chilecito (Fig. 1) and in Saenz Peña and San Pedro (Fig. 2), *C. capitata* was the main fruit fly species found, whereas in Montecarlo (Fig. 2) *A. fraterculus* was more abundant than *C. capitata* in almost all host species.

Irrespective of locality, many fruit species showed values of RAI closer to 1 than to 0, e.g., orange and fig. No host species consistently had values of RAI near 0 (Table 3). Other fruit species, such as grapefruit, peach, and guava showed a wide range of RAI values (Table 3).

Native host plants showed significantly lower values of RAI than introduced hosts (Table 4). Significant differences were also found among the three most abundant families of host species (Table 4). Nonparametric multiple comparisons showed differences between Myrtaceae and Rutaceae (df = 1, $P < 0.05$), whereas host species belonging to the family Rosaceae gave intermediate values of RAI that did not differ statistically from the other two.

The number of cases in which the two species of fruit flies shared a host in equal abundance (Fig. 3) was

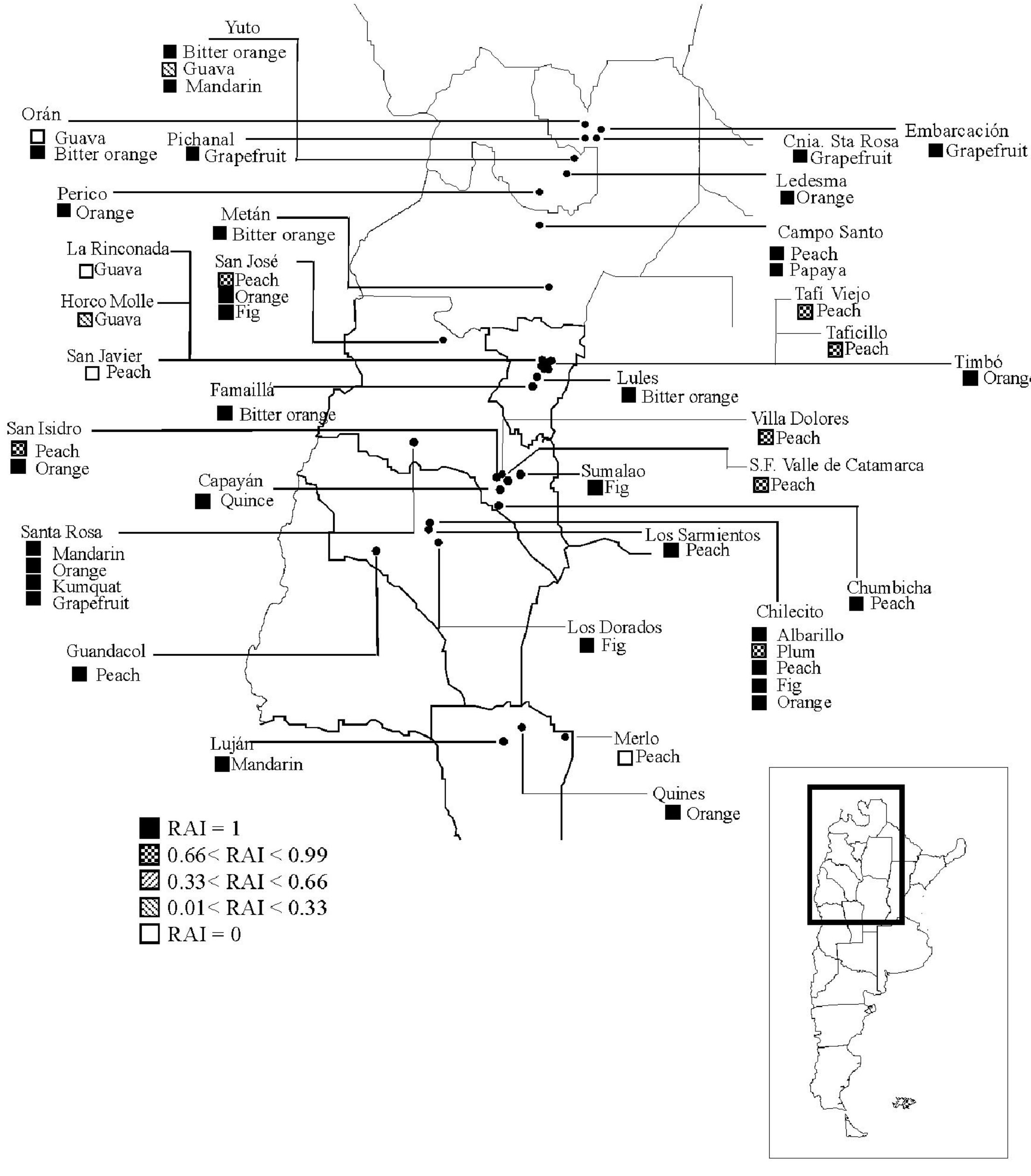

Fig. 1. RAI for each locality and host species sampled in NWA.

lower than expected, whereas the cases in which only one fruit fly species was recovered from a host was much higher than expected ($\chi^2 = 326.39$, $P < 0.001$).

Discussion

In some localities, we sampled fruit suitable for both *C. capitata* and *A. fraterculus*, and only one fruit fly species was recovered, or one of them occurred in extremely low abundance (Sáenz Peña, Monte Caseros, Montecarlo, San Pedro, and Bella Vista in Fig. 2; Chilecito and Campo Santo in Fig. 1). This fact suggests that factors other than availability of suitable hosts are limiting the establishment of one fruit fly species and not the other. Among these factors, we can postulate abiotic factors, such as temperature, humidity, or rainfall, and biotic factors, such as the duration of periods without mature suitable fruit, the competition between the two fruit fly species (Celedonio-Hurtado et al. 1995, and references

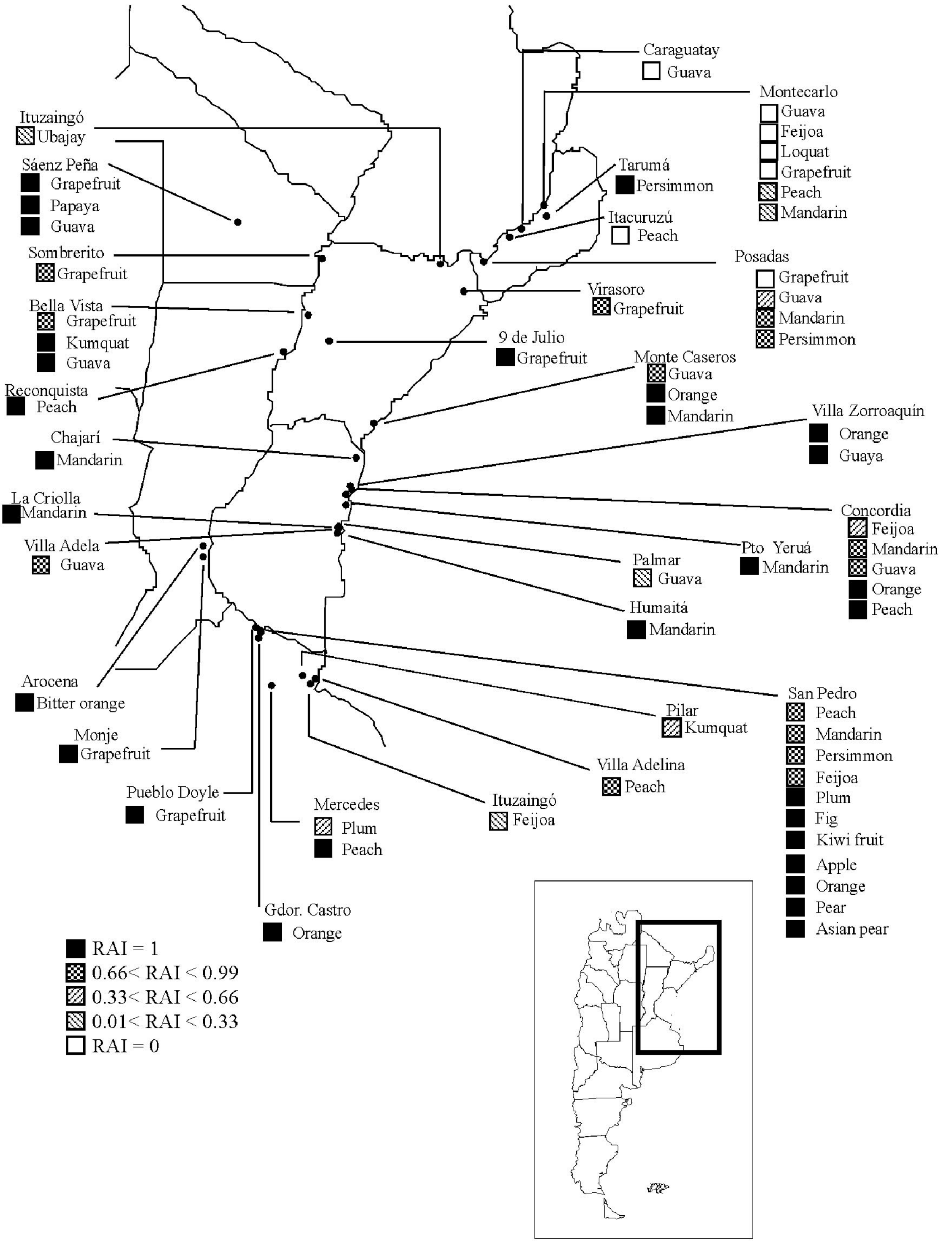

Fig. 2. RAI for each locality and host species sampled in NEA.

therein), and the degree of environmental disturbance. Parasitism could bias the relative abundances of these fruit fly species favoring one of the two species (Ovruski et al. 2004); however, the numbers recovered were so low that parasitism did not significantly affect the RAI values obtained here.

Table 2. RAI values per localities and hosts

Province	Locality	Host	Sampled fruit	Infestation level[a]	RAI
Buenos Aires	Mercedes	Plum	500	1.31	0.33
		Peach	41	2.66	1.00
	Pilar	Kumquat	181	1.15	0.36
	Gob. Castro	Orange	265	0.72	1.00
	Doyle	Grapefruit	676	0.14	1.00
	San Pedro	Orange	211	1.76	1.00
		Peach	1425	3.64	0.99
		Mandarin	1685	0.57	0.99
		Plum	791	0.51	1.00
		Apple	120	0.60	1.00
		Asian pear	150	2.20	1.00
		Fig	1457	2.90	1.00
		Pear	30	1.67	1.00
		Persimmon	495	2.13	0.99
		Kiwi fruit	230	0.73	1.00
		Feijoa	143	1.92	0.97
	Villa Adelina	Peach	15	3.00	0.79
	Ituzaingó	Feijoa	50	2.92	0.03
Catamarca	S. F. V. Catamarca	Peach	103	1.77	0.83
	Capayan	Quince	151	1.09	1.00
	Chumbicha	Peach	91	1.16	1.00
	San José	Orange	36	1.36	1.00
		Fig	88	0.68	1.00
		Peach	41	1.56	0.88
	Sta. Rosa	Mandarin	27	1.96	1.00
		Orange	30	1.27	1.00
		Grapefruit	30	1.37	1.00
		Kumquat	41	2.15	1.00
	Sumalao	Fig	50	6.04	1.00
	San Isidro	Orange	35	0.69	1.00
		Peach	57	1.79	0.93
	Villa Dolores	Peach	30	4.13	0.90
Corrientes	9 de Julio	Grapefruit	38	1.24	1.00
	Bella Vista	Grapefruit	31	3.35	0.86
		Kumquat	123	0.66	1.00
		Guava	286	1.11	1.00
	Ituzaingó	Ubajay	70	5.03	0.01
	Monte Caseros	Orange	129	1.25	1.00
		Mandarin	108	0.99	1.00
		Guava	101	2.18	0.98
	Sombrerito	Grapefruit	60	1.18	0.97
	Virasoro	Grapefruit	59	1.93	0.92
Chaco	Saenz Peña	Papaya	26	1.54	1.00
		Guava	87	1.64	1.00
		Grapefruit	12	1.25	1.00
Entre Ríos	Palmar	Guava	375	4.77	0.06
	Concordia	Peach	567	2.76	1.00
		Feijoa	1468	0.60	0.50
		Guava	987	1.18	0.99
		Mandarin	743	0.58	0.95
		Orange	568	0.17	1.00
	Chajarí	Mandarin	252	0.43	1.00
	Humaitá	Mandarin	153	1.40	1.00
	La Criolla	Mandarin	80	1.46	1.00
	Pto Yeruá	Mandarin	21	6.57	1.00
	Villa Adela	Guava	33	6.00	0.99
	Villa Zorraquín	Guava	173	5.85	1.00
		Orange	219	0.49	1.00
Jujuy	Yuto	Guava	461	3.36	0.28
		Mandarin	53	0.68	1.00
		Bitter orange	36	3.47	1.00
	Ledesma	Orange	76	1.04	1.00
	Perico	Orange	195	0.75	1.00
La Rioja	Chilecito	Albarillo	31	0.81	1.00
		Plum	23	3.17	0.96
		Peach	1296	0.89	1.00
		Fig	183	4.91	1.00
		Orange	36	1.69	1.00
	Los Dorados	Fig	25	3.72	1.00
	Guandacol	Peach	170	0.92	1.00
	Los Sarmientos	Peach	25	2.68	1.00

(continued)

Table 2. Continued

Province	Locality	Host	Sampled fruit	Infestation level[a]	RAI
Misiones	Caraguatay	Guava	79	1.85	0.00
	Itacuruzú	Peach	28	2.36	0.00
	Montecarlo	Guava	106	3.01	0.00
		Mandarin	591	0.36	0.35
		Grapefruit	45	0.49	0.00
		Peach	64	0.95	0.07
		Feijoa	377	3.00	0.00
		Loquat	761	0.19	0.00
	Posadas	Persimmon	80	2.46	0.99
		Guava	3272	0.99	0.46
		Mandarin	153	0.78	0.85
		Grapefruit	169	0.83	0.00
	Taruma	Persimmon	26	2.88	1.00
Salta	Campo Santo	Peach	31	5.52	1.00
		Papaya	14	1.93	1.00
	Cnia. Santa Rosa	Grapefruit	22	1.18	1.00
	Embarcación	Grapefruit	131	1.36	1.00
	Metán	Bitter orange	18	0.72	1.00
	Orán	Guava	225	0.40	0.00
		Bitter orange	55	2.24	1.00
	Pichanal	Grapefruit	31	1.77	1.00
San Luis	Lujan	Mandarin	11	3.73	1.00
	Merlo	Peach	23	3.43	0.00
	Quines	Orange	16	2.25	1.00
Santa Fé	Arocena	Bitter orange	32	1.38	1.00
	Reconquista	Peach	405	1.46	1.00
	Monje	Grapefruit	103	1.50	1.00
Tucumán	Famailla	Bitter orange	57	1.79	1.00
	Horco-Molle	Guava	3371	0.53	0.06
	La Rinconada	Guava	106	2.54	0.00
	Lules	Bitter orange	12	3.25	1.00
	San Javier	Peach	186	4.06	0.01
	Tafi Viejo	Peach	160	3.86	0.98
	Taficillo	Peach	325	5.38	0.95
	Timbó	Orange	615	0.52	1.00

[a] Infestation level is the number of pupae per fruit.

Consideration of specific localities offers some insight into the factors affecting fly distribution. For example, in Saenz Peña, *A. fraterculus* was absent from all the host species sampled, including guavas, one of the primary host for this species (Putruele 1993, Aluja et al. 2000, Selivon 2000). The thermal regime of Saenz Peña is suitable for this species, but the annual relative humidity is close to 50%, suggesting that this site is too

Table 3. Number of localities in each RAI categories for each host species

Host species	RAI = 0	0 < RAI < 0.33	0.33 < RAI < 0.66	0.66 < RAI < 1	RAI = 1	n	RAI range
Albarillo	0	0	0	0	1	1	1.00–1.00
Apple	0	0	0	0	1	1	1.00–1.00
Asian Pear	0	0	0	0	1	1	1.00–1.00
Bitter orange	0	0	0	0	6	6	1.00–1.00
Feijoa	1	1	1	1	0	4	0.00–0.97
Fig	0	0	0	0	5	5	1.00–1.00
Grapefruit	2	0	0	3	8	13	0.00–1.00
Guava	4	3	1	3	3	14	0.00–1.00
Kiwi fruit	0	0	0	0	1	1	1.00–1.00
Kumquat	0	0	1	0	2	3	0.36–1.00
Loquat	1	0	0	0	0	1	0.00–0.00
Mandarin	0	0	1	3	8	12	0.35–1.00
Orange	0	0	0	0	13	13	1.00–1.00
Papaya	0	0	0	0	2	2	1.00–1.00
Peach	3	1	0	7	9	20	0.00–1.00
Pear	0	0	0	0	1	1	1.00–1.00
Persimmon	0	0	0	2	1	3	0.99–1.00
Plum	0	1	0	1	1	3	0.33–1.00
Quince	0	0	0	0	1	1	1.00–1.00
Ubajay	0	1	0	0	0	1	0.01–0.01

RAI = 0 indicates only AF found; 0.01 < RAI < 0.33 indicates more AF than CC; 0.33 < RAI < 0.66 indicates same amt of AF as CC; 0.66 < RAI < 0.99 indicates more CC than AF; RAI = 1 indicates only CC present.

Table 4. RAI values by origin and botanic family of host plants

Classification by	RAI[a]	Q25[b]	Q75[c]	*n*	Nonparametric test
Origin					
Introduced	1.000	0.974	1.000	84	Mann–Whitney test: $U = 490.00$, $P < 0.001$
Native	0.370	0.004	1.000	22	
Host family					
Myrtaceae	0.060a	0.000	0.982	19	Kruskal–Wallis test: $H = 24.11$, df = 2, $P < 0.001$, $n = 94$
Rosaceae	0.986ab	0.810	1.00	28	
Rutaceae	1.000b	1.000	1.000	47	

[a] Medians followed by a different letter differed statistically ($P < 0.05$; multiple comparison Dunn's test).
[b] First quartile.
[c] Third quartile.

dry for *A. fraterculus.* Orán, by contrast, has a similar thermal regime but a higher annual relative humidity, and here guavas were heavily infested by *A. fraterculus.* Environmental disturbance supposedly favors *C. capitata* (Putruele 1997, Malavasi et al. 2000, Ovruski et al. 2003). This seems to be the case for Saenz Peña with a very extensive agricultural landscape and very little native vegetation, but not for Orán [although currently there is a heavy trend to deforest the Yungas and start soybean, *Glycine max* (L.) Merr., plantations]. However, in Montecarlo, where the original environment also has been disturbed, there is high abundance of *A. fraterculus,* indicating that the local environment may have a stronger impact than the disturbance on the relative abundance of this fruit fly. Montecarlo, in Misiones province, with subtropical climate and high relative humidity exhibits a landscape with dense vegetation and backyards with fruit fly host plants, many of them native, that provide excellent refuges for *A. fraterculus.* In San Pedro, the thermal regime and the relative humidity seem appropriate for the development of *A. fraterculus;* however, RAI values for this locality are high because this species is present in a small number of hosts and in low abundance. The absence of suitable hosts for *A. fraterculus* from late autumn to middle spring (Segura et al. 2004) is the most likely explanation for this pattern.

The great variation in RAI among hosts (see Posadas, Concordia, and others) indicates a pattern of differential use of the available hosts. The possible explanations are 1) a different pattern of host preference in adults of each fruit fly species; 2) asymmetric interspecific competition (the result of which depends on the fruit species; Fitt 1989); 3) differential mortality of eggs, larvae, or both in each host species (Carey 1984); or 4) differential ability of each fruit fly species to find and infest different fruit species.

Citrus spp. were found to be better hosts for *C. capitata* than for *A. fraterculus,* regardless of the inter-locality variation in biotic and abiotic factors that may favor one of the other species, at least in Argentina (Tables 2 and 3). Mandarin, orange, and bitter orange showed lower variation in RAI than the other fruit, and the most abundant species was always *C. capitata.* In agreement with other observations (Malavasi and Morgante 1980, Putruele 1993, Nasca et al. 1996, Vaccaro 2000, Ovruski et al. 2003) we found that grapefruit was the only *Citrus* with values of RAI favoring *A. fraterculus.* Several studies (Nascimiento et al. 1984, da Silva-Branco et al. 2000, Aluja et al. 2003) have shown the low suitability of *Citrus* spp. as host for *Anastrepha* spp., but in the laboratory, forced development on grapefruit, orange, and lemon, *Citrus limon* L., showed better recovery of *A. fraterculus* pupae in the case of grapefruit (Gramajo 2004). Ovruski et al. (2003) proposed a stronger attraction of *C. capitata* toward infochemicals (sensu Dicke and Sabelis 1988) produced by *Citrus* as another explanation for the high RAI values found in these host species (for example, Howse and Knapp (1996) suggested that some components of male *C. capitata* pheromone are similar to

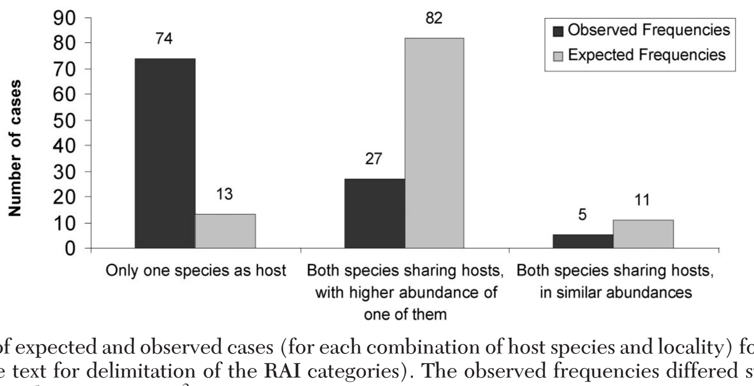

Fig. 3. Number of expected and observed cases (for each combination of host species and locality) for each classification category of RAI (see text for delimitation of the RAI categories). The observed frequencies differed statistically from the expected frequencies (chi-square test: $\chi^2 = 326.39$, $P < 0.001$).

volatiles emitted by *Citrus* trees and fruit). Asymmetrical larval competition favoring *C. capitata* also could be postulated (but then, it is not clear why this asymmetry would be reversed for grapefruit).

From apple and pear, we recovered pupae of *C. capitata* in San Pedro (Buenos Aires province), as did previous studies in the neighboring province of Entre Ríos (FAO 1989, Putruele 1996). Nasca et al. (1996) recorded *A. fraterculus* pupae from pear collected in Antinaco-Los Colorados Valley (La Rioja province). Several studies carried out in Brazil report the presence of *A. fraterculus* in these two fruit species (Malavasi et al. 1980, Kovaleski et al. 2000, Nora et al. 2000). However, Ovruski et al. (2003) did not find infestation by any fruit fly in apple and pear (157 and 196 fruit sampled, respectively) in NWA, questioning the status of these fruit species as hosts for the two fly species. Surveys of these two fruit species should be expanded, with emphasis in NWA.

C. capitata was more abundant in plant species belonging to the family Rutaceae, whereas *A. fraterculus* was predominant in plants of the family Myrtaceae. Species belonging to the family Rosaceae showed intermediate values of RAI, roughly corresponding to the comparison of RAI between introduced and native species: *C. capitata* dominates in introduced plants (Rutaceae and Rosaceae, among others), whereas in native plants (Myrtaceae among others) *A. fraterculus* shows higher abundance (Table 4). Various Brazilian authors also found this (Malavasi and Morgante 1980, de Souza Filho et al. 2000, Malavasi et al. 2000, Veloso et al. 2000). Eskafi and Kolbe (1990) described the same pattern in Guatemala, although their samplings also included different *Anastrepha* species. Ovruski et al. (2003) also reported that the introduced fruit species favor *C. capitata* and that the native species serve as a reservoir for *A. fraterculus* (with two exceptions discussed below). The fact that almost 85% of all fruit species sampled are exotic in Argentina could be responsible, at least to some extent, for the high predominance of *C. capitata* in our samplings.

As noted above, *A. fraterculus* showed better yields in native plants, probably because of their common evolutionary history. *C. capitata,* being such a polyphagous species with such high reproductive capacity (Liquido et al. 1991), may gain advantage in introduced hosts with which *A. fraterculus* has had less contact in its evolutionary history. Moreover, plant species introduced to the Americas from the same region as *C. capitata,* for example, coffee, *Coffea arabica* L., constitute good hosts for this fly (Harris and Lee 1989, Malavasi et al. 2000). Interestingly, Copeland et al. (2002) did not find *C. capitata* in guavas sampled in Kenya (in a sample of 84 fruit), where this fly is native, and *P. guajava* is an introduced species. In our study, *C. capitata* was found infesting guavas in 10 of 14 localities sampled (Table 2; Figs. 1 and 2). Another exception, mentioned by Ovruski et al. (2003), might be peach and plum (both introduced species). But, if we calculate the RAIs from their published data (0.16 and 0.25, respectively) they differ markedly from those found in the current study (average RAI of 0.77 and 0.76 for peach and plum, respectively). In Ovruski et al. (2003), however, the sampling of these two host species occurred in forest areas, scattered among native vegetation, whereas in our study, they occurred in highly disturbed areas, illustrating the strong influence of the environment on the RAI values. RAI values lower than 0.10 for peach, in Itacuruzú, Montecarlo, and San Javier, located in areas with native vegetation and subtropical climate are good examples supporting our explanation.

We found that both species tended to occur alone many more times than they occurred together sharing one host in one locality. We could interpret this pattern as competitive exclusion of one species by the other. It has been suggested that, when two or more fruit fly species coexist, some form of competition for hosts could arise (Duyck et al. 2004). Most examples of interspecific competition among tephritids derive from situations in which a new species has been introduced into a given environment (Duyck et al. 2004). For example, interspecific competition was proposed to explain the displacement of *C. capitata* by *Bactrocera dorsalis* (Hendel) (Fitt 1989) in Hawaii and by *Bactrocera tryoni* (Froggatt) in Australia (Allman 1939, Andrewartha and Birch 1954, Christenson and Foote 1960, Bateman 1971, Fitt 1989). Owing to the short period of coexistence ($\approx$100 yr), mechanisms that tend to minimize the competition for resources ("avoidance" sensu Díaz-Fleischer et al. 2000, Duyck et al. 2004, Sivinski et al. 2004) have probably not yet evolved. However, the patterns of relative abundance give only indirect evidence for the existence of interspecific competition. Fitt (1989) suggests looking for direct evidence of competition, as a modification in the abundance of one species after manipulating the abundance of the other.

In conclusion, this first attempt to analyze the relative abundance of *C. capitata* and *A. fraterculus* covering different regions and different hosts in Argentina proved that both species coexist here in several areas and exhibit similar ecological requirements. Therefore, we should expect strong competition between them in habitats where the resources are scarce, as in wild or urban habitats where the density of host plants is usually low. These habitats serve as refuges for small populations that are usually neglected by traditional pest control efforts and may be *foci* where reinfestation starts. Future studies of interspecific competition between *C. capitata* and *A. fraterculus* should focus on these habitats to produce valuable information for area-wide management of these pests. *C. capitata* is the major fruit fly pest in almost all regions in Argentina. The sterile insect technique (Knipling 1955), successfully implemented in La Rioja, Mendoza, and San Juan provinces, and the Patagonia region (De Longo et al. 2000, Frissolo et al. 2001, Sánchez et al. 2001), aims at the eradication of *C. capitata.* It would be very useful to be able to predict the response of *A. fraterculus* populations to a marked decrease in the density of *C. capitata* and identify areas likely to experience an increase in the *A. fraterculus* population, thereby avoiding outbreaks of this pest.

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Appendix 1. Ecological regions (Cabrera and Willink 1973, Cabrera 1976, Anonymous 1992), geographical coordinates, and altitude for each locality sampled.

Ecological region			Geographic coordinates			
Domain	Province	Localities	Latitude (S)	Longitude (W)	Altitude (m)	Climatic and ecological conditions
Amazonico	Las Yungas	Famaillá	27.03	65.25	363	Hot and wet climate; rainfall in summer and frosts during winter; 2,500–3,000 mm per year; 19.1–29.8°C mean maximum temperature; 10.1–15.6°C mean minimum temperature; vegetation of subtropical cloud forest, rich in Lauraceae and Myrtaceae.
		Horco Molle	26.91	65.08	466	
		La Rinconada	26.85	65.31	425	
		Lules	26.93	65.35	415	
		San Javier	26.85	65.33	514	
		Tafi Viejo	26.75	65.35	592	
		Taficillo	26.73	65.27	619	
		Timbó	26.70	65.13	531	
		Colonia Santa Rosa	23.45	64.36	322	
		Metán	25.48	64.95	803	
		Orán	23.13	64.33	337	
		Pichanal	23.33	64.23	303	
		Yuto	23.63	64.47	346	
		Ledesma	23.83	64.77	413	
		Perico	24.38	65.10	897	
	Paranaense	Caraguatay	26.66	54.75	193	Hot and rainy climate; rainfall throughout the year, 1,600–2,000 mm per year; 27.4–28.5°C mean maximum temperature; 13.0–15.3°C mean minimum temperature; vegetation of subtropical rainforest, rich in Leguminosae, Lauraceae, Meliaceae, and Myrtaceae.
		Itacuruzú	26.90	55.13	96	
		Montecarlo	26.57	54.78	161	
		Posadas	27.38	55.88	133	
		Taruma	26.70	54.66	150	
		Ituzaingó (Corrientes)	27.60	56.66	63	
		Sombrerito	27.70	58.70	65	
Chaqueño	Chaqueña	Embarcación	23.22	64.10	274	Hot continental climate; summer rainfalls, varying between 200 mm annually in the east to 500 mm in the west; 20.5°C–28.6°C mean maximum temperature; 13.6°C–16.1°C mean minimum temperature; vegetation characteristic of deciduous xerophytic forests, with an herbaceous stratum compose by Gramineae, Cactaceae and terrestrial Bromeliaceae; also palm trees, savannahs and bushy steppes.
		Campo Santo	24.70	65.08	850	
		Saenz Peña	26.80	60.45	60	
		S.F. Valle de Catamarca	28.50	65.78	505	
		Capayń	28.77	66.07	358	
		Chumbicha	28.87	66.23	377	
		San José	26.78	66.06	984	
		Santa Rosa	28.45	65.71	512	
		Sumalao	28.45	65.62	518	
		San Isidro	28.45	65.76	514	
		Villa Dolores	28.43	65.73	530	
		Lujń	32.37	65.95	589	
		Merlo	32.35	65.03	808	
		Quines	32.23	65.80	482	
		de Julio	28.83	58.83	55	
		Bella Vista	28.52	59.05	58	
		Reconquista	29.11	59.42	53	
	Espinal	Monte Caseros	30.28	57.63	35	Hot and wet climate in the north, temperate and dry in the south; summer ranfall, 340–1,170 mm per year; 21.9–25.7°C mean maximum temperature; 6.7–14.0°C mean minimum temperature; vegetation characteristic of deciduous xerophytic forests, palm trees, savannahs, and grassy steppes.
		Chajarí	30.77	57.98	55	
		Virasoro	28.50	56.17	112	

Monte	Chilecito	29.17	67.50	1080	Hot and dry climate in the north, dry and coller in the south; summery rainfalls in the north and winter rainfalls in teh south, varying from 80 to 200 mm per year; 20.4–27.0°C mean maximum temperature; 5.7–10.4°C mean minimum temperature; vegetation characteristic of deciduous xerophytic forests, palm groves, grassy savannahs, grassy steppes, and bushy steppes.
	Los Dorados	29.35	67.47	1063	
	Guandacol	29.56	68.56	1053	
	Los Sarmientos	29.15	67.52	1072	
Pampeana	Palmar	32.16	58.28	44	Hot-temperate climate; rainfall throughout the year, diminishing from north to south and from east to west, varying from 600 to 1,200 mm per year; 20.1–24.2°C mean maximum temperature; 6.9–11.8°C mean minimum temperature; vegetation of grassy steppe and xeric woodland.
	Concordia	31.38	58.02	22	
	Humaitá	31.78	58.30	44	
	La Criolla	31.15	58.06	38	
	Pto. Yeruá	31.53	58.03	35	
	Villa Adela	31.10	58.20	40	
	Villa Zorraquín	31.32	58.05	47	
	Arocena	32.08	60.97	14	
	Monje	32.38	60.93	15	
	Mercedes	34.65	59.43	117	
	Pilar	34.45	58.90	19	
	Gob. Castro	33.76	59.88	52	
	Doyle	33.46	60.10	20	
	San Pedro	33.66	59.72	15	
	Villa Adelina	34.53	58.55	24	
	Ituzaingó (Buenos Aires)	34.67	58.67	31	