

SEASONAL ABUNDANCE OF THE BROWN CITRUS APHID,  
*TOXOPTERA CITRICIDA*, (HOMOPTERA: APHIDIDAE)  
AND ITS NATURAL ENEMIES IN PUERTO RICO

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ABSTRACT

Populations of the brown citrus aphid (BCA), *Toxoptera citricida* (Kirkaldy), and associated insects were monitored in citrus groves in western Puerto Rico in 1996 and 1997. Peak populations of the aphid were observed in spring and fall of both years. A total of 6,737 infested citrus terminals were examined and categorized by growth stage and BCA colony size. Natural enemies, primarily coccinellids, syrphids, chrysopids, and aphidiids, were recorded when present in BCA colonies and a list of species is presented. A complex of large coccinellid species was inferred to have the greatest potential for impact on BCA populations in Puerto Rico. Predation by syrphid larvae was another important source of BCA mortality. The parasitoid, *Lysiphlebus testaceipes* (Cresson), was abundant in some samples, but usually parasitized only a small percentage of aphids within colonies. The fungus, *Verticillium lecanii* (Zimm.), infected BCA colonies sporadically. The red imported fire ant, *Solenopsis invicta* Burren, was often observed harvesting honeydew from BCA colonies and interfering with natural enemies.

RESUMEN

Durante 1996 y 1997 se realizó un monitoreo del áfido pardo de los cítricos (BCA) *Toxoptera citricida* (Kirkaldy) e insectos asociados en huertos de cítricos ubicados en el occidente de Puerto Rico. En ambos años, las poblaciones máximas del áfido ocurrieron durante la primavera y el otoño. Se examinó un total de 6,737 brotes infestados, los cuales se clasificaron por etapa de desarrollo y el tamaño de la colonia de BCA. Se presenta una lista de enemigos naturales encontrados en las colonias de BCA, principalmente Coccinellidae, Syrphidae, Chrysopidae y Aphidiidae. Se dedujo que un complejo de especies grandes Coccinellidae tienen el mayor potencial para el control

de BCA en Puerto Rico. Otra causa importante de mortalidad de BCA fue la predación por larvas de Syrphidae. En algunas muestras se encontraron poblaciones altas del parasitoide *Lysiphlebus testaceipes* (Cresson), pero éstos solamente parasitaron pocos áfidos dentro de las colonias. El hongo *Verticillium lecanii* (Zimm.) se encontró infectando colonias de BCA de manera esporádica. Con frecuencia se observó a la hormiga de fuego roja importada, *Solenopsis invicta* Buren, cosechando secreciones en colonias de BCA e interfiriendo con los enemigos naturales.

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The discovery of the brown citrus aphid (BCA) in Ft. Lauderdale and Miami, Florida in 1995 caused widespread concern among citrus growers due to the potential impact of this pest on citrus production (Halbert & Brown 1996). The primary concern is the efficiency of this aphid in vectoring citrus tristeza virus (CTV) (Meneghini 1948), a serious disease of citrus worldwide (Lee & Rocha-Peña 1992). There are many strains of CTV that range from benign to virulent, and most are presumed to have entered the country on infected budwood that was subsequently propagated. The strain commonly referred to as "quick decline" is widespread throughout Florida and induces a hypersensitivity reaction in sweet orange and grapefruit scions on sour orange rootstock, resulting in the death of the tree within two or three years. Although trees are now being planted on CTV-tolerant or resistant rootstocks, it is estimated there are as many as 20 million producing trees rooted on sour orange in Florida (Garnsey 1995). Of equal concern are the various "stem-pitting" strains which, although presently rare, may become more common with the introduction of BCA. Although these strains do not directly cause tree death, they reduce fruit size and yield. Furthermore, stem-pitting strains are capable of infecting most citrus cultivars independent of rootstock. For reasons not yet understood, the BCA is capable of transmitting CTV, and the severe strains in particular, with far greater efficiency than all other aphid species found in citrus (Balaraman & Ramakrishnan 1979, Yokomi et al. 1994). In addition to viral transmission, large infestations of BCA have been implicated in stunting the growth of young trees and reducing fruit set (Symes 1924, Hall 1930, Smit 1934, Hely 1968).

Literature on the BCA has recently been summarized (Michaud 1998). In anticipation of the need to develop an integrated management program for the BCA in Florida, we monitored BCA populations and their associated natural enemies in Puerto Rico where the insect has been present since at least 1992 (Roche-Peña et al. 1995). Here we summarize our findings of two years observations on the seasonal abundance of the BCA and its natural enemies in Puerto Rico.

#### MATERIALS AND METHODS

We monitored BCA populations regularly at three sites in western Puerto Rico throughout 1996 and 1997 and sampled five additional sites intermittently. The Enseñat and Muñoz sites were located in the mountainous interior of western Puerto Rico in the heart of the citrus-growing region. Both sites receive plentiful rainfall from spring to fall and experience moderate evening temperatures due to their elevation (300-400 m above sea level). The Enseñat site is a research station of the University of Puerto Rico (Recinto Universitario de Mayagüez) located at km 10.5, Carretera 124 and bordered on all sides by natural forests. The two groves sampled at this site both were budwood foundation blocks; one was a 6-10 yr-old grove of Tahiti lime, the other a 12-20 yr-old block of mixed sweet orange, mostly Valencia.

The Muñoz site is a private plantation located at km 1 on Carretera 124 on the outskirts of the city of Lares, consisting of ca. 80 hectares of mixed commercial citrus on the slope of a mountain, interplanted mostly with coffee but with some plantain and banana at lower elevations. The grove borders semi-riparian land (mostly forest) on two sides, and urban development on the outskirts of the town of Lares on the other two.

The Cancell site is a privately owned plantation located 2 km off Carretera 358 at km 2.5 in San Germán at the southwestern edge of the citrus growing region, about 8 km from the coast, in somewhat drier climate than the other two sites. The site, at an elevation of 100-150 m. ASL, was bordered primarily by grazing pastures and mountain forests and was interplanted with plantain and banana.

Other sites sampled intermittently included Corozál, a research substation of the University of Puerto Rico located at the intersection of Carretera 647 and Carretera 159 in the district of Corozál; Neuva Era, a private plantation located at km 5 of Carretera 124 in the district of Las Marias; Limaní, a research substation of the University of Puerto Rico located at km 6.5 of Carretera 525 in the district of Adjuntas; and La Baleár, a private plantation located 2 km off Carretera 135 at km 63.5 near the town of Castañer.

We defined an aphid colony as the aggregate of aphids infesting a single citrus terminal. Flushing citrus terminals expand new leaves at the rate of about one per day and remain suitable for aphid growth and reproduction for a period of 20 to 30 days. Infested terminals were categorized according to their stage of growth as follows: F = Feather (most leaves still folded); F/NE = Feather/Newly Expanded (some leaves folded, others newly expanded); NE = Newly Expanded (most leaves newly expanded); NE/NH = Newly Expanded/Newly Hardened (some leaves newly expanded, others newly hardened); NH = Newly Hardened (most leaves newly hardened). BCA colonies were classified into 6 size categories: 1 (1-10 aphids); 2 (11-50); 3 (51-150); 4 (151-500); 5 (501-1000); 6 (> 1000).

Alate adults were also tallied when present in colonies and, during the second season, we recorded the presence of nymphs with wing buds as an indication of colony maturation. This enabled us to examine the distribution of immigrant alates by tallying the numbers of alates present on non-maturing colonies, i.e. colonies without alate nymphs present.

The numbers of natural enemies present at each BCA colony were recorded by life stage and family, e.g. "1 syrphid egg" "2 coccinellid larvae" etc. Syrphid adults were occasionally observed ovipositing on aphid colonies but their incidence was too low to permit statistical analysis. Adult coccinellids were frequently collected in the field and samples of coccinellid, chrysopid, and syrphid larvae were collected periodically, brought back to the laboratory, and reared through to adult stages for identification and detection of parasitism. We tallied the number of *Lysiphlebus testaceipes* (Cresson) mummies in BCA colonies, as well as the number of discernibly parasitized aphids. The latter are distinguishable by their swollen and discolored appearance when the parasitoid larva is in the later stages of development.

To test for discrimination by predators against parasitized aphids as prey, we exposed mixtures of parasitized and unparasitized BCA to late instar larvae of *Pseudodorous clavatus* (F.) (n = 8) and *Cycloneda sanguinea* ssp. *limbifer* (L.) (n = 5) in plastic petri dishes in the laboratory. A number of ant species were observed tending BCA colonies and these were noted when present. In particular, the red imported fire ant, *Solenopsis invicta* Buren, was frequently observed. At certain times and locations, aphid corpses were observed with fungal hyphae growing out of them and, with some experience, we were able to distinguish saprophytic fungi consuming deceased aphids from the entomopathogenic form, *Verticillium lecanii* (Zimm.).

## Statistical Analyses

Site-to-site and year-to-year comparisons were made using a one-way ANOVA design followed by Fisher's LSD when more than 2 groups were compared (SPSS® 1995), and comparisons between dates within years and sites using ANOVA for repeated measures (Systat® 1989). The distributions of natural enemy life stages across BCA colonies of different size classes were compared with those expected by chance using a Chi-Square Goodness-of-Fit Test with 5 df. Similarly, the frequencies with which different insects occurred together on BCA colonies (e.g. predatory larvae and fire ants) were compared to expected values (calculated from their independent frequencies) using a Chi-Square Goodness-of-Fit Test with 2 df.

## RESULTS

The Enseñat site averaged a higher percentage of shoots infested in 1996 than in 1997, (mean = 43.1% vs. 15.5%,  $F = 9.360$ ,  $P < 0.01$ ) and the same trend was evident, though not significant, at Muñoz (mean = 30% vs. 11.4%,  $F = 2.540$ ,  $P = 0.13$ ). Cancell displayed an opposite, though non-significant, trend to higher percentage of shoots infested in 1997 than in 1996 (mean = 17.5% vs. 28.5%,  $F = 1.980$ ,  $P = 0.17$ ). Pooling data from all 3 sites yielded a mean of 31.6% shoots infested in 1996 and 18.7% in 1997 ( $F = 5.100$ ,  $P = 0.03$ ).

Colonies in smaller size classes were invariably more abundant than those in larger size categories (Table 1), and had a higher frequency of occurrence on terminals in early, rather than late, developmental stages (Table 2). Many colonies appeared to be founded by multiple alate foundresses (Fig. 1). The mean number of alate foundresses per non-maturing colony in 1997 was calculated to be  $1.85 \pm 0.06$  (SEM), almost certainly an underestimate given that a significant proportion of founding alates would have already died and gone undetected.

We examined 3,667 BCA colonies in 1996 and 3,070 in 1997, for a total of 6,737. Summary data for the three primary sites in both years are shown in Figs. 2-7, and for secondary sites, in Table 3. The following differences between primary sites were significant (Fisher's LSD,  $P < 0.05$ ) in 1996: Enseñat had fewer coccinellid adults than either Cancell or Muñoz ( $F = 18.459$ ); Cancell had more coccinellid eggs than Enseñat ( $F = 4.185$ ) and more coccinellid larvae and syrphid eggs than either Enseñat or Muñoz ( $F = 20.087$  and  $F = 16.308$ , respectively); Muñoz had more mummies than Cancell, which had more than Enseñat ( $F = 18.329$ ); Cancell had fewer colonies tended by fire ants than either Enseñat or Muñoz ( $F = 18.123$ ) and; Enseñat had more colonies mixed with *Aphis spiraecola* Patch than either Cancell or Muñoz ( $F = 19.660$ ). No other differences between sites in 1996 were significant.

In 1997, the following differences between sites were significant: Cancell had more coccinellid adults, eggs and larvae than either Enseñat or Muñoz ( $F = 11.111$ ,  $F = 17.100$ , and  $F = 20.512$ , respectively); Cancell had more mummies than Enseñat ( $F = 8.571$ ) and fewer colonies tended by fire ants than either Enseñat or Muñoz ( $F = 19.355$ ); Enseñat had more colonies infected with *V. lecanii* than either Cancell or Muñoz ( $F = 55.996$ ) and; Cancell had more colonies mixed with *A. spiraecola* than Enseñat, which had more than Muñoz ( $F = 13.026$ ). Our estimate of the percentage of colonies maturing was not significantly different among sites in 1997 ( $F = 3.126$ ,  $P = 0.058$ ); Cancell: Mean =  $15.4 \pm 4.6\%$ ; Enseñat: Mean =  $7.9 \pm 2.1\%$ ; Muñoz: Mean =  $4.4 \pm 2.1\%$ .

There were significant differences between years at all 3 sites. In 1997 the Enseñat site had significantly more coccinellid adults ( $F = 14.730$ ,  $P < 0.001$ ), coccinellid larvae ( $F = 12.176$ ,  $P < 0.001$ ), syrphid eggs ( $F = 6.061$ ,  $P < 0.05$ ) and syrphid larvae ( $F =$

TABLE 1. DISTRIBUTION OF COLONY SIZE CLASSES BY SAMPLING SITE.

Location	Total no. samples	Percent of BCA colonies in various size classes					
		1-10	11-50	51-150	151-500	500-1000	>1000
Cancél	2415	31.7	40.4	18.6	5.7	2.0	0.8
Enseñat	1617	29.4	31.2	24.3	10.6	3.6	0.9
Muñoz	832	36.0	36.3	18.9	7.5	1.0	0.1

TABLE 2. NUMBERS OF BCA COLONIES IN DIFFERENT SIZE CLASSES OBSERVED ON CITRUS TERMINALS IN VARIOUS GROWTH STAGES. F = FEATHER, F/NE = FEATHER/NEWLY EXPANDING, NE = NEWLY EXPANDING, NE/NH = NEWLY EXPANDING/NEWLY HARDENING, NH = NEWLY HARDENING.

Colony Size	Terminal Stage					Totals
	F	F/NE	NE	NE/NH	NH	
1-10	554	464	753	160	137	2068
11-50	444	422	942	293	266	2367
51-150	127	237	602	278	239	1483
151-500	16	78	242	142	134	612
500-1000	0	14	61	53	37	165
>1000	0	7	7	19	9	21
Totals	1141	1222	2607	945	822	6737

4.311,  $P < 0.05$ ) than in 1996, and more colonies attended by *L. testaceipes* ( $F = 9.286$ ,  $P < 0.01$ ), but fewer colonies mixed with *A. spiraecola* ( $F = 26.130$ ,  $P < 0.001$ ). The Cancél site had significantly more coccinellid larvae ( $F = 16.669$ ,  $P < 0.001$ ) in 1997 than in 1996, more colonies attended by *L. testaceipes* ( $F = 17.033$ ,  $P < 0.001$ ), more colonies mixed with *A. spiraecola* ( $F = 9.839$ ,  $P < 0.01$ ), but fewer syrphid eggs ( $F = 6.727$ ,  $P < 0.01$ ). The Muñoz site also had more coccinellid larvae in 1997 than in 1996 ( $F = 17.747$ ,  $P < 0.001$ ) but fewer colonies mixed with *A. spiraecola* ( $F = 7.778$ ,  $P < 0.01$ ).

The following species of natural enemies were observed feeding on the BCA during the study. Coleoptera, Coccinellidae: *Chilocorus cacti* (L.), *Cladis nitidula* (F.), *Coelophora inaequalis* (F.), *Curinus coeruleus* Mulsant, *Coleomegilla innotata* (Mulsant), *C. sanguinea* ssp. *limbifer*, *Diomus* sp., *Egius platycephalus* Mulsant, *Hippodamia convergens* (Guerin), *Hyperaspis festiva* Mulsant, *Olla v-nigrum* (Mulsant), *Procula feruuginea* (Oliver), *Scymnus (Schymnus) floralis* (F.); Diptera, Chamaemyiidae: *Leucopis* sp. Diptera, Syrphidae: *Allograpta radiata* (Bigot), *Allograpta exotica* (Wiedmann), *Ocyptamus cubanus* (Hull), *Ocyptamus fuscipennis* Say, *P. clavatus*; Hymenoptera, Aphidiidae: *L. testaceipes*; Neuroptera, Chrysopidae: *Cereaochrysa* sp.

One particular set of observations (March 12, 1997, Limaní) revealed an interesting difference in the distribution of coccinellids and syrphids between two adjacent blocks. The first block was a mixed citrus collection of mature trees surrounded by tall weeds ( $n = 76$  BCA colonies), whereas the second was a block of recently top-worked

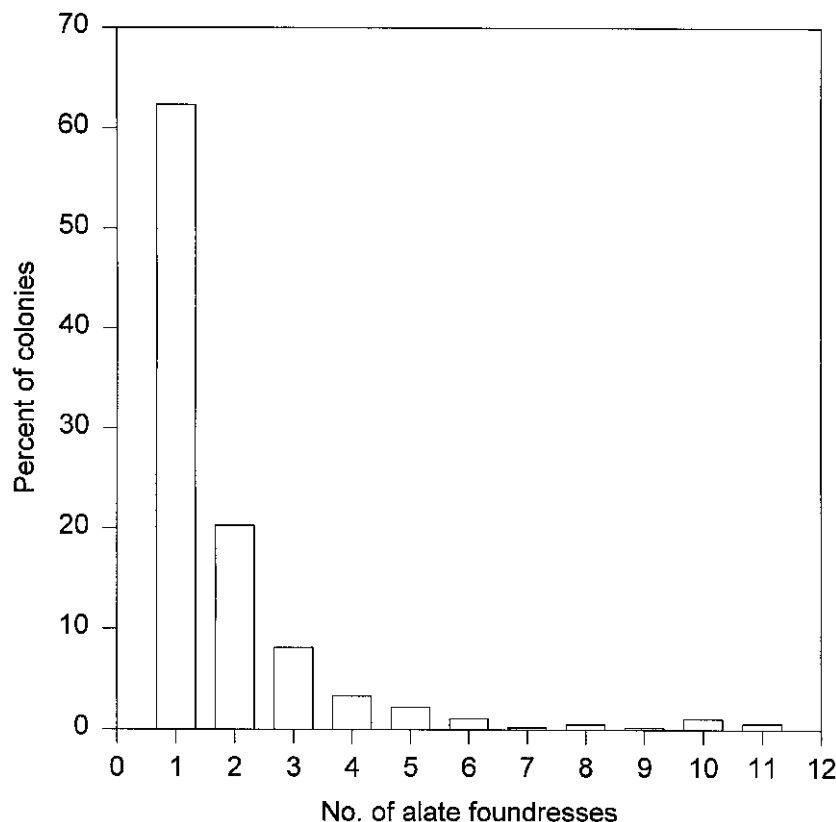


Fig. 1. Frequency distribution of BCA colonies with different numbers of alate foundresses.

trees with virtually no canopy structure and very little ground cover ( $n = 81$ ). The first block had significantly more coccinellid adults per colony (mean  $\pm$  SE =  $0.20 \pm 0.05$ ) compared with the second block ( $0.02 \pm 0.02$ ) ( $F = 11.333$ ,  $P = 0.001$ ) and significantly more coccinellid larvae ( $0.29 \pm 0.06$  vs.  $0.00 \pm 0.00$ ,  $F = 23.543$ ,  $P < 0.001$ ). On the other hand, the second block had significantly more syrphid eggs per colony than did the first block ( $0.61 \pm 0.12$  vs.  $0.01 \pm 0.01$ ,  $F = 21.720$ ,  $P < 0.001$ ), although the numbers of syrphid larvae were not significantly different ( $F = 1.156$ ,  $P = 0.284$ ). Block one also had significantly more mummies per colony than block two ( $1.92 \pm 0.61$  vs.  $0.02 \pm 0.02$ ,  $F = 10.293$ ,  $P = 0.002$ ), although the numbers of parasitized aphids was not different ( $F = 0.896$ ,  $P = 0.345$ ).

A total of 821 coccinellid adults were observed on 653 BCA colonies, 969 coccinellid eggs on 85 colonies, and 1427 larvae on 759 colonies. The egg data represent only the large coccinellid species (primarily *C. sanguinea* ssp. *limbifer* and *C. inaequalis*) which oviposit in exposed locations. The fact that coccinellid eggs are usually laid in masses of 5 to 25 accounts for their highly clumped distribution. However, most eggs of these species appear to be laid outside aphid colonies on older, hardened leaves, which likely

accounts for their relatively low numbers in this study (we recorded only eggs associated with BCA colonies). The eggs of smaller coccinellid species (*Diomus*, *Hyperaspis* and *Scymnus* spp.) were never detected during our observations; eggs of these species are very small and usually laid in concealed locations. Coccinellid pupae were sometimes observed on the undersides of hardened leaves below aphid colonies, but almost never within a colony. On several occasions we observed newly eclosed coccinellid larvae feeding on eggs of their own species in the field. The distribution of coccinellid eggs and larvae across BCA colonies of different size classes is depicted in Fig. 8.

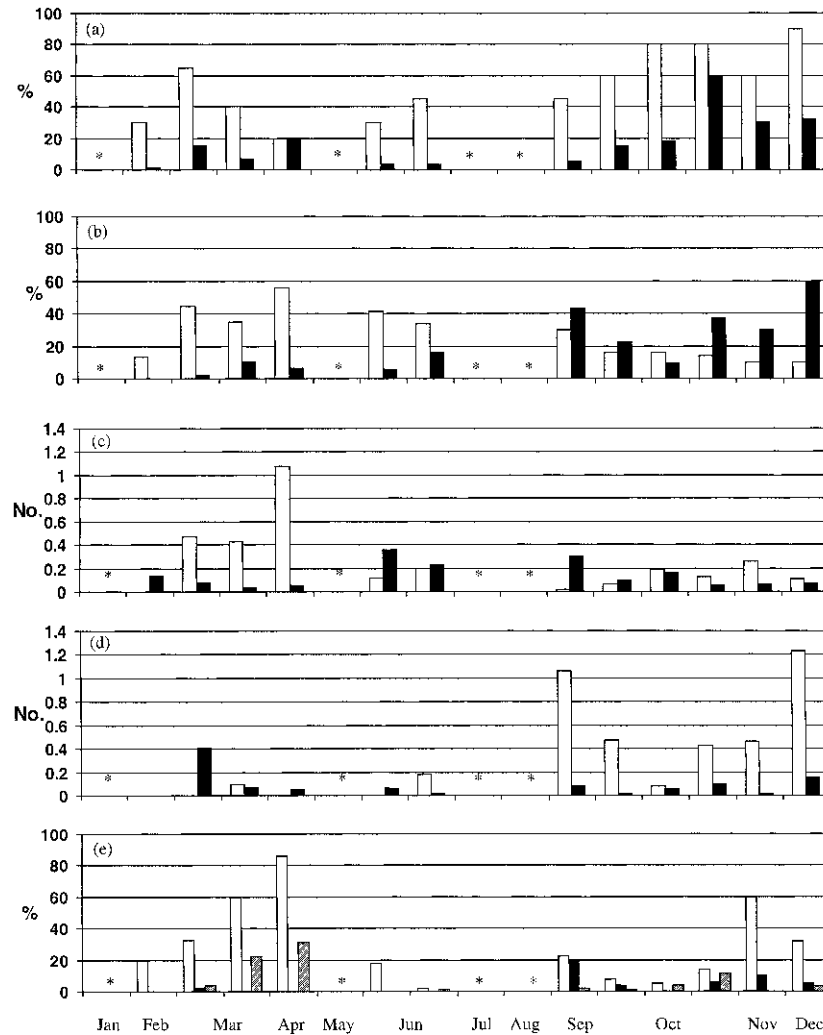
A total of 1,676 syrphid eggs were counted on 842 BCA colonies, and 533 larvae on 432 colonies. The vast majority (>85%) appeared to be eggs and larvae of *P. clavatus*, although *O. fuscipennis* comprised up to 25% of specimens in samples of larvae collected in late summer and fall. Syrphid pupae were occasionally recorded on BCA colonies, but most mature larvae appeared to leave aphid colonies before pupation. When syrphid larvae (*P. clavatus*) were confined together with coccinellid larvae (*C. sanguinea* ssp. *limbifer*) in petri dishes (n = 16) we did not observe any evidence of attacks by one on the other, even when larval size was asymmetric and no aphids were provided as food. As many as 30% of syrphid larvae in some samples were parasitized by a gregarious parasitoid, *Syrphophagus* nr. *aphidivorus* (Hymenoptera: Encyrtidae). The distribution of syrphid eggs and larvae across BCA colonies of different size classes is depicted in Fig. 9.

The only aphidiid collected in our samples was *L. testaceipes*. We observed 20,645 parasitized aphids in 1,299 BCA colonies and 8,939 mummies in 892 colonies. We collected 23 samples of mummies from various sites and the emergence of adult wasps varied from 0 to 33% between samples, with an overall average of 4.2%. The hyperparasitoid *Pachyneuron* nr. *siphonophorae* (Ashmead) (Hymenoptera: Pteromalidae) emerged from 2.6% of mummies. We also collected several specimens of another hyperparasitoid, *Alloxysta* sp., that we observed probing aphids on a number of occasions, although this species never emerged from any of our mummy samples. Late instar larvae of *P. clavatus* and *C. sanguinea* ssp. *limbifer* did not appear to discriminate against parasitized aphids as prey; both species readily consumed parasitized aphids in our petri dish trials, even with unparasitized aphids present.

The red imported fire ant, *S. invicta*, was the ant species most frequently observed tending BCA colonies in Puerto Rico. Other ant species collected at BCA colonies included *Brachymyrmex obscurion* Ford, *Monomorium ebeninum* Ford, *Paratrechina longicornis* (Latrielle), *Pheidole fallax*, *Solenopsis glogularia*, and *Wasmannia auropunctata* (Roger). We found that both syrphid and coccinellid larvae occurred on fire ant-tended BCA colonies at significantly lower frequencies than expected by chance (Chi-square = 11.4, 2df, P < 0.005 & Chi-square = 35.7, 2df, P < 0.005, respectively).

#### DISCUSSION

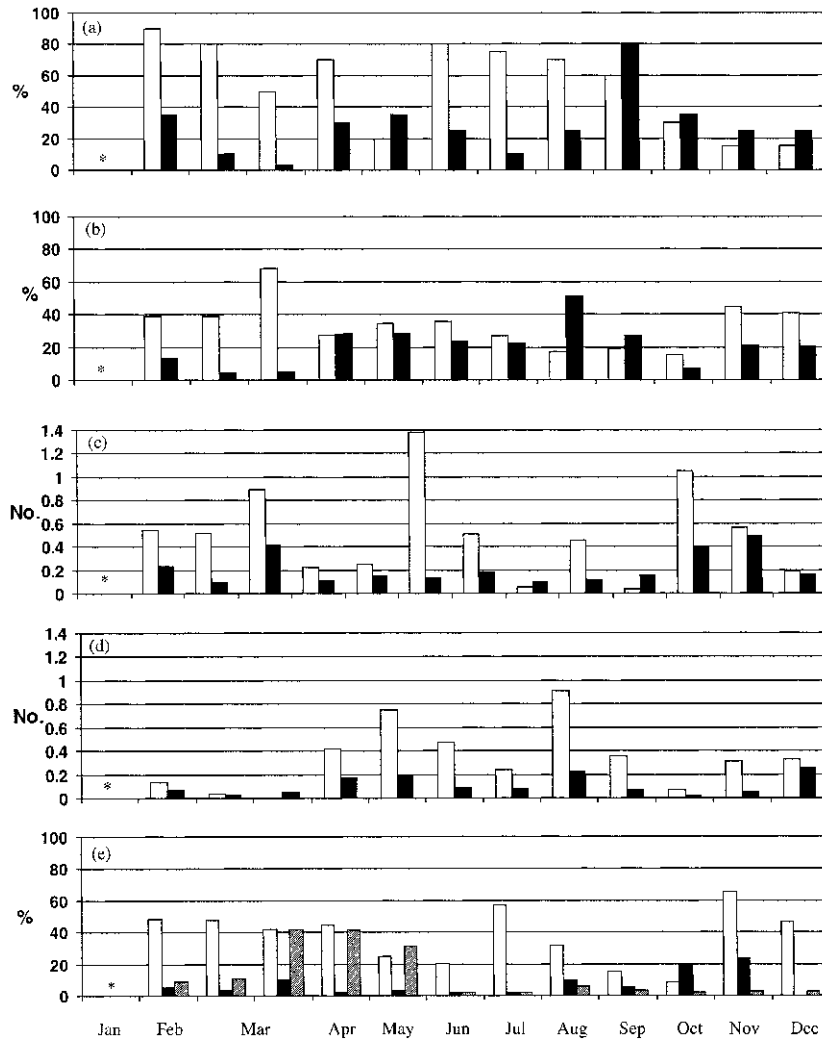
BCA abundance in Puerto Rico typically peaks twice a year, once in early spring and again in mid fall, coinciding with peak periods of flush availability during these seasons. A large proportion of available terminals may be infested during these periods and a significant number of large colonies are typically present. A third population peak may sometimes occur in mid-summer (e.g. Cancél, 1997, Fig. 3), but infestation of summer flush is usually low. Mean daily temperatures above 25°C have adverse effects on BCA reproduction and survival (Komazaki 1982, Michaud unpublished). Mean daily temperatures in summer frequently exceed 25°C in Puerto Rico and this may be a key factor limiting population growth during this season. However, the primary coccinellid species reside in groves throughout the summer, even when



Cancél, 1996

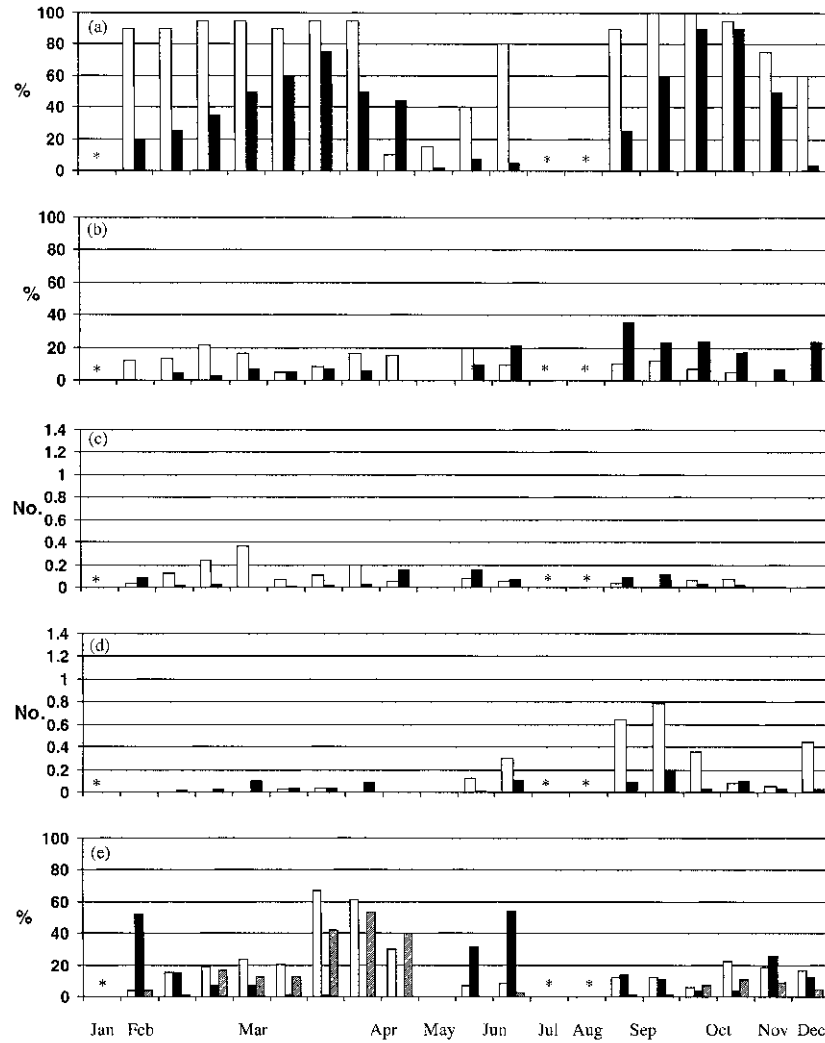
Fig. 2. Summary data for Cancél site, 1996; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (e) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraecola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.





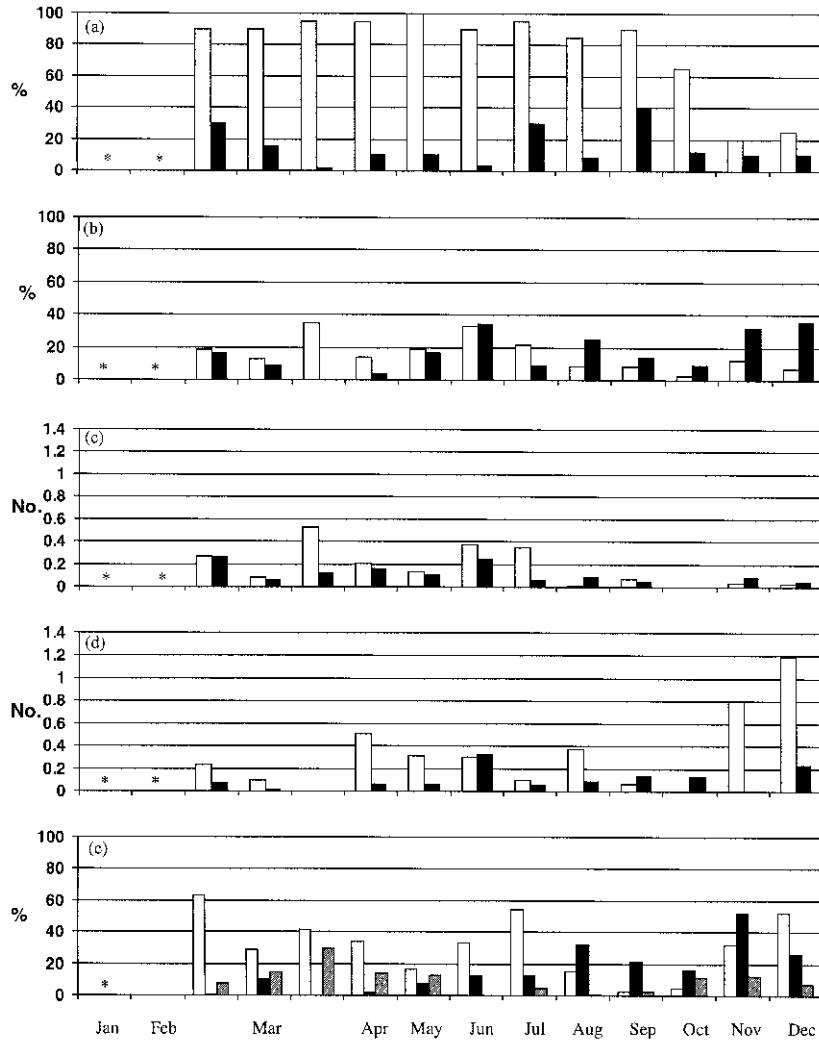
Cancél, 1997

Fig. 3. Summary data for Cancél site, 1997; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (d) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraecola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.



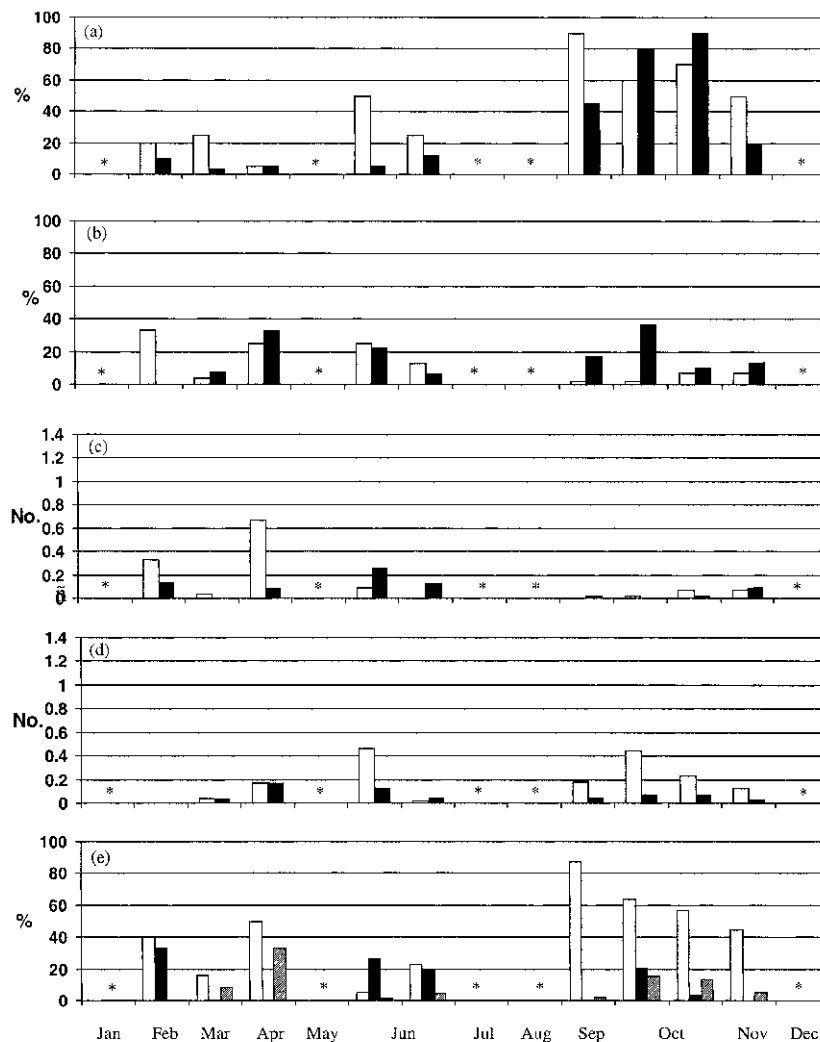
Ensañat, 1996

Fig. 4. Summary data for Ensañat site, 1996; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (e) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraecola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.



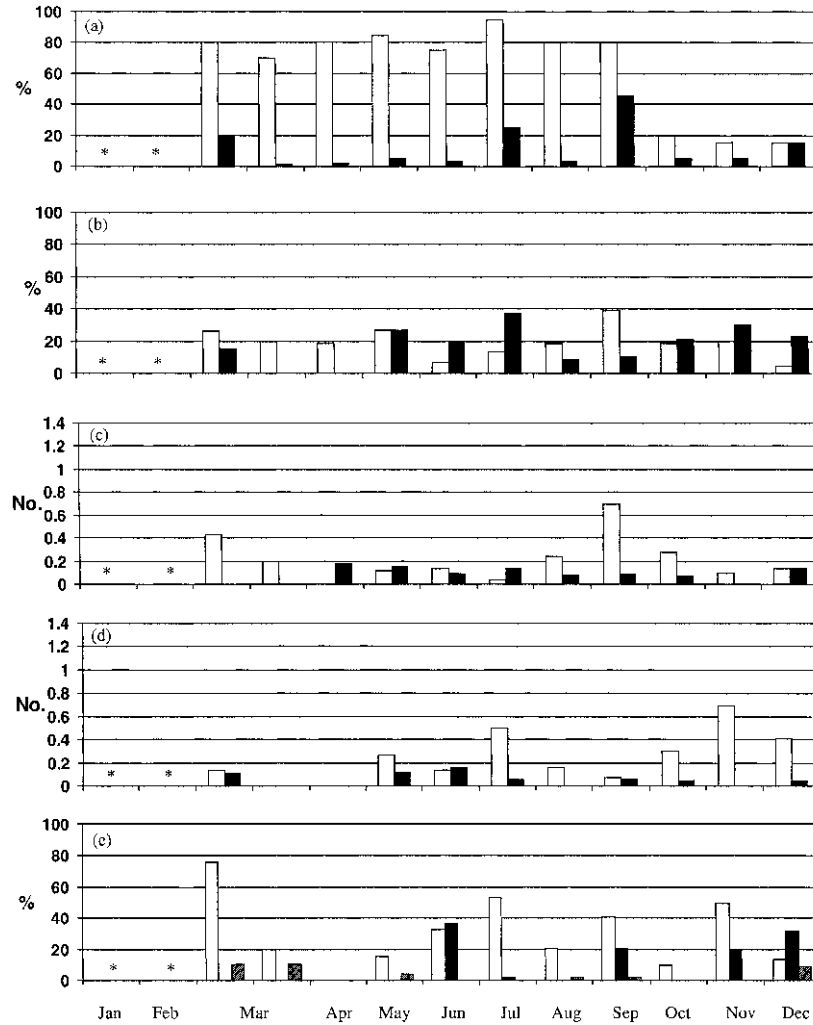
Ensañat, 1997

Fig. 5. Summary data for Ensañat site, 1997; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (d) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraeicola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.



Muñoz, 1996

Fig. 6. Summary data for Muñoz site, 1996; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (d) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (e) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraeicola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.



Muñez, 1997

Fig. 7. Summary data for Muñez site, 1997; (a) Percentage of trees with flush (open bars) and percentage of flushed terminals infested (solid bars); (b) Percentage of BCA colonies under attack by coccinellids (open bars) and syrphids (solid bars); (c) Mean no of coccinellid larvae (open bars) and adults (solid bars) per BCA colony; (e) Percentage of BCA colonies with mummies and or aphids parasitized by *L. testaceipes* (open bars), attended by *S. invicta* (solid bars), and mixed with *A. spiraecola* (hatched bars). Asterisks indicate months for which data was not available, all other gaps represent '0' values.

TABLE 3. SUMMARY DATA FOR SECONDARY SITES. VALUES BEARING THE SAME LETTER WERE NOT SIGNIFICANTLY DIFFERENT AMONG DATES WITHIN SITES.

Date	% trees w/flush	% flush infested	n	Coccinellidae			Syrphidae			Percent of colonies with:			
				% colonies maturing	% colonies present	Larvae/ colony	Adults/ colony	% colonies present	Eggs/ colony	Larvae/ colony	<i>Lysiphlebus testaceipes</i>	<i>Solenopsis invicta</i>	<i>Aphis spiraeola</i>
Feb. 26, '96	95.0	30.0	23	NA	43.5	0.44 <sup>b</sup>	0.48 <sup>d</sup>	0.0	0.00 <sup>a</sup>	0.00 <sup>a</sup>	8.7 <sup>ab</sup>	4.4 <sup>ab</sup>	0.0 <sup>a</sup>
Mar. 14, '96	95.0	45.0	50	NA	32.0	0.18 <sup>a</sup>	0.20 <sup>b</sup>	14.0	0.00 <sup>a</sup>	0.18 <sup>c</sup>	6.0 <sup>ab</sup>	0.0 <sup>a</sup>	0.0 <sup>a</sup>
Mar. 19, '96	100.0	65.0	192	NA	7.3	0.08 <sup>a</sup>	0.01 <sup>a</sup>	13.0	0.00 <sup>a</sup>	0.14 <sup>bc</sup>	15.6 <sup>b</sup>	0.0 <sup>a</sup>	4.7 <sup>a</sup>
Mar. 26, '96	70.0	50.0	150	NA	11.3	0.14 <sup>a</sup>	0.06 <sup>ab</sup>	10.7	0.00 <sup>a</sup>	0.12 <sup>abc</sup>	30.4 <sup>c</sup>	0.0 <sup>a</sup>	14.8 <sup>b</sup>
Sept. 20, '96	50.0	5.0	92	NA	19.6	0.08 <sup>a</sup>	0.27 <sup>c</sup>	14.1	0.14 <sup>ab</sup>	0.05 <sup>a</sup>	2.2 <sup>a</sup>	20.7 <sup>b</sup>	3.3 <sup>a</sup>
Mar. 24, '97	80.0	2.0	94	8.5	34.0	0.19 <sup>a</sup>	0.19 <sup>a</sup>	28.7	0.67 <sup>c</sup>	0.06 <sup>ab</sup>	6.4 <sup>a</sup>	0.0 <sup>a</sup>	13.8 <sup>b</sup>
Oct. 24, '97	50.0	45.0	72	9.7	27.8	0.13 <sup>a</sup>	0.21 <sup>c</sup>	16.7	0.17 <sup>b</sup>	0.03 <sup>a</sup>	2.8 <sup>a</sup>	9.7 <sup>b</sup>	22.2 <sup>b</sup>
Apr. 2, '96	40.0	30.0	82	NA	25.6	0.18 <sup>a</sup>	0.15 <sup>a</sup>	12.2	0.12 <sup>a</sup>	0.13 <sup>bc</sup>	47.6 <sup>b</sup>	0.0 <sup>a</sup>	53.7 <sup>c</sup>
June 4, '96	30.0	7.0	35	NA	20.0	0.00 <sup>a</sup>	0.20 <sup>b</sup>	34.3	0.51 <sup>c</sup>	0.11 <sup>ab</sup>	11.4 <sup>a</sup>	0.0 <sup>a</sup>	0.0 <sup>a</sup>
June 11, '96	60.0	4.0	130	NA	18.5	0.11 <sup>a</sup>	0.11 <sup>a</sup>	16.9	0.12 <sup>a</sup>	0.16 <sup>c</sup>	3.9 <sup>a</sup>	2.3 <sup>a</sup>	0.8 <sup>a</sup>
Sept. 13, '96	20.0	3.0	75	NA	46.2	0.08 <sup>a</sup>	0.75 <sup>b</sup>	3.8	0.08 <sup>a</sup>	0.00 <sup>a</sup>	7.7 <sup>a</sup>	23.1 <sup>b</sup>	7.7 <sup>a</sup>
Mar. 12, '97	95.0	50.0	158	13.9	20.3	0.14 <sup>a</sup>	0.10 <sup>a</sup>	20.3	0.33 <sup>bc</sup>	0.03 <sup>a</sup>	46.9 <sup>b</sup>	18.6 <sup>b</sup>	24.4 <sup>b</sup>
Oct. 17, '97	60.0	20.0	45	4.4	55.5	0.62 <sup>b</sup>	0.96 <sup>b</sup>	20.0	0.20 <sup>ab</sup>	0.04 <sup>ab</sup>	0.0 <sup>a</sup>	24.4 <sup>b</sup>	0.0 <sup>a</sup>
June 6, '96	40.0	4.0	36	NA	38.9	0.14 <sup>a</sup>	0.36 <sup>ab</sup>	30.5	0.36 <sup>b</sup>	0.08 <sup>a</sup>	5.5 <sup>a</sup>	2.8 <sup>a</sup>	2.8 <sup>a</sup>
June 13, '96	90.0	3.0	46	NA	58.7	0.28 <sup>a</sup>	0.67 <sup>c</sup>	10.9	0.22 <sup>b</sup>	0.00 <sup>a</sup>	2.2 <sup>a</sup>	0.0 <sup>a</sup>	4.4 <sup>a</sup>
Apr. 10, '97	90.0	50.0	137	12.4	42.3	0.37 <sup>a</sup>	0.19 <sup>a</sup>	7.3	0.02 <sup>a</sup>	0.06 <sup>a</sup>	15.3 <sup>b</sup>	4.4 <sup>a</sup>	39.4 <sup>b</sup>
Oct. 23, '97	90.0	3.0	44	9.1	40.9	0.295 <sup>a</sup>	0.43 <sup>bc</sup>	11.4	0.18 <sup>b</sup>	0.05 <sup>a</sup>	0.0 <sup>a</sup>	15.9 <sup>b</sup>	18.2 <sup>a</sup>

TABLE 3. (CONTINUED) SUMMARY DATA FOR SECONDARY SITES. VALUES BEARING THE SAME LETTER WERE NOT SIGNIFICANTLY DIFFERENT AMONG DATES WITHIN SITES.

Date	% trees w/flush	% flush infested	n	% colonies maturing	Coccinellidae				Syrphidae				Percent of colonies with:		
					% colonies present	Larvae/colony	Adults/colony	% colonies present	Eggs/colony	Larvae/colony	<i>Lysiphlebus testaceipes</i>	<i>Solenopsis invicta</i>	<i>Aphis spiraeicola</i>		
June 6, '96	40.0	20.0	56	NA	13.0	0.00	0.13	8.9	0.04 <sup>a</sup>	0.05 <sup>a</sup>	0.0 <sup>a</sup>	30.4 <sup>b</sup>	0.0 <sup>a</sup>		
June 12, '96	50.0	50.0	82	NA	10.0	0.11	0.04	43.9	0.39 <sup>b</sup>	0.24 <sup>b</sup>	1.2 <sup>a</sup>	28.0 <sup>b</sup>	1.2 <sup>a</sup>		
Sept. 19, '96	60.0	12.0	42	NA	14.0	0.24	0.05	50.0	0.55 <sup>b</sup>	0.29 <sup>c</sup>	4.8 <sup>a</sup>	9.5 <sup>a</sup>	2.4 <sup>a</sup>		
Mar. 14, '97	70.0	2.0	15	0.0	7.0	0.07	0.00	6.7	0.07 <sup>a</sup>	0.00 <sup>a</sup>	6.7 <sup>a</sup>	0.0 <sup>a</sup>	40.0 <sup>b</sup>		
Oct. 19, '97	8.0	30.0	40	10.0	5.0	0.00	0.05	12.5	0.03 <sup>a</sup>	0.15 <sup>a</sup>	0.0 <sup>a</sup>	0.0 <sup>a</sup>	2.5 <sup>a</sup>		

Nueva Era

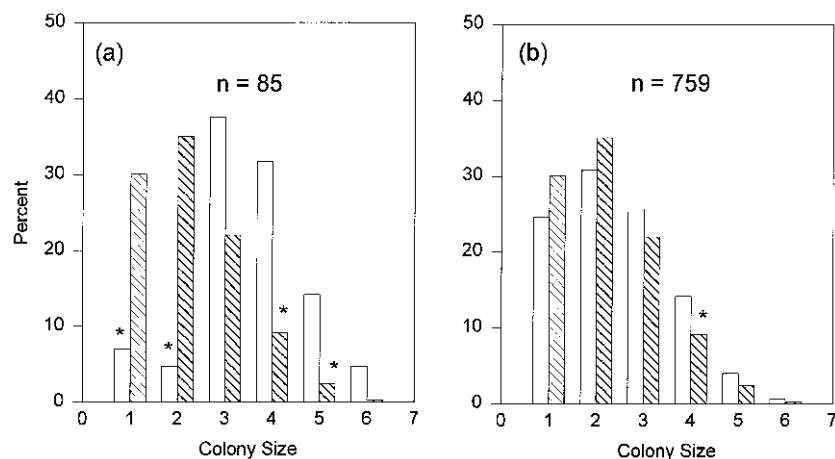


Fig. 8. Distribution of observed (open bars) vs. expected (hatched bars) percentage of BCA colonies of different size classes with coccinellid (a) eggs and (b) larvae. Asterisks indicate significant differences between observed and expected values,  $P < 0.05$ . Chi-square Goodness of Fit test.

BCA density is low, and eliminate many aphid colonies in their early stages. Adult coccinellids were sometimes observed feeding on soft scales or whitefly larvae when very few aphids were present.

Year to year variation in BCA infestation intensity was evident. The BCA was apparently more abundant in 1996 than in 1997, especially in the Lares district where the Enseñat site averaged a larger proportion of terminals infested across all sampling dates. The same trend was evident, though not significant, at the Muñoz site which is only 12 km from Enseñat, but was not evident at the Cancél site which is relatively distant from the other two. We conclude that regional differences exist with respect to various ecological parameters that influence BCA populations in particular years.

There were also consistent differences between sites with respect to natural enemies. The Cancél site had a consistently higher rate of coccinellid attendance at BCA colonies than either of the other two sites in both years. It is not clear whether this difference is due to more successful reproduction of coccinellid populations within the Cancél grove, or to higher rates of immigration from surrounding habitats, but both these parameters are likely important determinants of coccinellid impact on BCA populations.

#### BCA Colony Structure

Small colonies were more often observed on terminals in earlier growth stages, whereas large colonies were more frequently encountered on mature terminals. This result is expected if younger terminals are the preferred sites for colonization. A number of small colonies were observed on relatively mature terminals but many of these were in decline, i.e. they had been decimated by predation and/or other mortality factors. Newly expanded terminals can be rare toward the end of a flush cycle and a significant number of small colonies may form on older terminals, despite a low probability of colony maturation prior to shoot hardening.



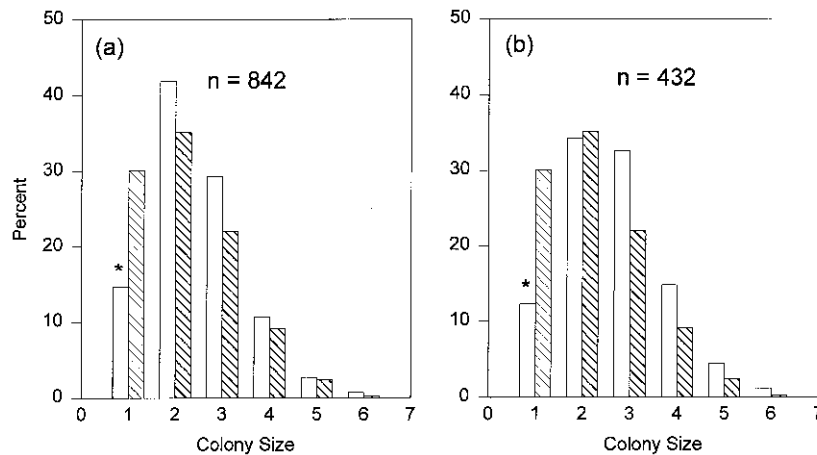


Fig. 9. Distribution of observed (open bars) vs. expected (hatched bars) percentage of BCA colonies of different size classes with syrphid (a) eggs and (b) larvae. Asterisks indicate significant differences between observed and expected values,  $P < 0.05$ . Chi-square Goodness of Fit test.

On heavily infested trees, large colonies could be found on shoots in relatively early developmental stages, probably founded by apterous migrants from adjacent mature colonies. Apterous adults have a significantly higher age-specific fecundity and net reproductive rate than their alate counterparts, together with a shorter pre-reproductive period (Takanashi 1989). Therefore, colonies founded by multiple apterous migrants grow much faster than alate-founded colonies.

The data in Fig. 1 suggest that a large proportion of immigrant alates join colonies already in progress as opposed to initiating colonies of their own. Recent laboratory investigations (Michaud 1999) have confirmed that alate BCA have an intrinsic aggregation tendency. It seems likely that multiple foundresses would increase colony growth rate, although whether this would lead to an increased probability of colony maturation remains to be shown. We suspect that small colonies are more vulnerable to elimination by predation events that would have little impact on larger colonies, leading to individual fitness benefits for foundresses that pool their reproductive efforts to produce faster-growing/larger colonies.

#### Coccinellidae

We concur with Frazer & Gilbert (1976) that current methods for counting adult coccinellids in the field greatly underestimate their true numbers. At any given time, only a proportion of the population may be actively feeding on aphid colonies. This proportion may be even lower following heavy rain or inclement weather when many adults tend to seek shelter in secluded sites. We are confident, therefore, that our data tend to underestimate the true numbers of coccinellid adults present in these citrus groves. *C. sanguinea* ssp. *limbifer* was the most abundant and ubiquitous coccinellid species in the study, closely followed by *C. inaequalis*. *C. sanguinea* is also the most common coccinellid on BCA in the Dominican Republic (Borbón et al. 1992) and Cuba (Zeleny 1969, Batista et al. 1995) and one of the prominent species in Venezuela (Morales & Burandt 1985) and Brazil (Lara et al. 1977, Bartoszeck 1980, Santos & Pinto 1981).

It is evident from Fig. 8a that established BCA colonies in the larger size classes were the preferred oviposition sites of the large coccinellid species and that small, newly formed colonies were less preferred. However, coccinellid larvae occurred on the smaller colony size classes at close to expected frequencies (Fig. 8b), indicating that the larvae search for, and effectively locate, aphid colonies. We sometimes observed egg masses laid on leaves adjacent to infested terminals, rather than on the terminals/colonies themselves. The tendency for a significant amount of oviposition to occur outside the actual colonies may account for the relatively low incidence of coccinellid eggs within colonies. Hemptinne et al. (1992) presented evidence that oviposition by gravid females of *Adalia bipunctata* (L.) was inhibited as a result of exposure to conspecific larvae or other females. Given the cannibalistic habits of the larvae of many coccinellids, it may be adaptive for females to place their egg masses near, but not on, the infested terminals that are likely to attract conspecific larvae. Alternatively, the survival and/or fecundity of some coccinellid species may be reduced when feeding on the BCA, as reported by Tao & Shui (1971) and Morales & Burandt (1985). We successfully reared larvae of *C. sanguinea* ssp. *limbifer* and *C. inaequalis* to adulthood in the laboratory on an exclusive diet of BCA, but did not assess the fertility of adults.

The difference in distribution of coccinellid adults and larvae observed between the two adjacent blocks at Limaní on March 12, 1997 could be explained by a foraging preference among adult coccinellids for habitats with substantial ground cover. Distinct habitat preferences are known to influence the local abundance of many coccinellid species (Honek & Rejmanek 1982, Honek 1985). The generalized escape response of coccinellid adults is to fall to the ground when a threat is perceived, a behavior which may be less effective in the absence of ground cover. We observed the assassin bug *Zelus longipes* (L.) (Hemiptera: Reduviidae) preying on both adult and larval coccinellids and this species may be an important source of mortality when it becomes abundant in summer months. However, the most vulnerable coccinellid life stage appears to be the pupa; we observed high rates of pupal predation but never observed the predatory agent.

#### Syrphidae

Colonies in the smallest size class had fewer syrphid eggs than would be expected by chance (Fig. 9a), a result that appears to conflict with accounts of syrphid preference for ovipositing on small colonies (e.g. Firempong & Kumar 1975, Kan 1988). However, syrphid preference for aphid colonies of particular sizes varies among species and some are known to prefer larger colonies for oviposition (Dixon 1959, Chandler 1968). There was a tendency for large BCA colonies to receive multiple ovipositions, which may partially account for the higher than expected proportion of class 3 and 4 colonies with syrphid eggs (Fig. 9a). Syrphid larvae have lower vagility than coccinellid larvae and, presumably, a lower probability of locating another aphid colony should they completely consume their nascent colony. Consequently, the selection of oviposition sites by adult female syrphids is probably a more important determinant of larval survival than it is for coccinellids. Newly initiated BCA colonies may be avoided as oviposition sites because their establishment, and their ability to provide sufficient food for larval development, is uncertain. The largest number of syrphid eggs were laid on class 2 and 3 colonies, which presumably have greater survival probability than class 1 colonies. These data are consistent with those for syrphid larvae which show the largest number appearing on class 3 and 4 colonies (Fig. 9b). Overall, these data are remarkably similar to those presented by White (1995) for *P. clavatus* on BCA colonies of different size classes in Trinidad. Adult syrphids may prefer to forage in open habitats rather than among closely-spaced trees with full cano-

pies. Spider predation is an important mortality risk for adult syrphids and spider webs are abundant within and between trees in mature citrus groves. Such a habitat preference could explain the dramatic difference in numbers of syrphid eggs on colonies in block 1 vs. block two observed on March 12, 1997 at Limaní.

#### Chrysopidae

Chrysopids are relatively rare in Puerto Rican citrus groves, despite generally low pesticide use and an abundance of alternate prey species. We collected a total of nine larvae and three adults of *Ceraochrysa* sp. The larvae are trash-carriers and one reared out in the laboratory yielded a parasitoid, *Brachycyrtus* sp. (Hymenoptera: Ichneumonidae).

#### Aphidiidae

Incomplete development of *L. testaceipes* in *A. spiraecola* has been observed in Italy (Tremblay & Barbagallo 1983), France (Stary et al. 1988), and Florida (J. P. Michaud, unpublished), although Costa and Stary (1989) found a strain in Portugal which did complete development in BCA. The low emergence rate of *L. testaceipes* from mummies of BCA in Puerto Rico was very similar to that reported by Yokomi & Tang (1996) and Carver (1978, 1984) in Australia. On several occasions we tried, and failed, to initiate laboratory colonies using wasps from samples of mummies with high percentage emergence. We suspect that local populations of *L. testaceipes* express additive genetic variance for survival in BCA, which would account for the high variability in emergence rates among samples and across generations.

Despite the low emergence rate, *L. testaceipes* females readily oviposit in the BCA, causing the aphid to act as an 'egg trap' for the parasitoid, as previously noted by Carver (1984). Considering the paucity of alternate host aphids for *L. testaceipes* in citrus (both *Toxoptera aurantii* Boyer de Fonscolombe and *Aphis gossypii* Glover are scarce and *A. spiraecola* is an unsuitable host), it is doubtful that the parasitoid population is self-maintaining within the citrus ecosystem in Puerto Rico. Nevertheless, the high floral diversity of the region apparently affords many suitable hosts for *L. testaceipes*, and citrus groves receive periodic waves of immigration. We suspect that the variation in abundance of *L. testaceipes* in BCA populations, both seasonally and between sites, largely reflects variation in its emergence rate from alternative hosts in the vicinity of citrus groves.

Rosenheim et al. (1995) have recently drawn attention to the importance of identifying intra-guild predation as a potential impediment to biological control programs. We observed no intra-guild predation under laboratory conditions when *C. sanguinea* and *P. clavatus* larvae were placed in petri dishes together, even when larval size was asymmetric. Consumption of parasitized prey has been previously recorded for coccinellids (Quezada & Debach 1973; Hoelmer et al. 1994, Colfer & Rosenheim 1995) and syrphids (Kindlmann & Ruzicka 1992). Both the syrphid and coccinellid larvae we tested readily consumed BCA parasitized by *L. testaceipes*, and it is therefore likely that predation of larvae within aphids is a source of mortality for *L. testaceipes* in addition to hyperparasitism by *Pachyneuron* and *Alloxysta* spp.

#### Myrmicinae

The red imported fire ant, *S. invicta*, is a ubiquitous resident of citrus groves in Puerto Rico and was the most common ant species in attendance at BCA colonies. It has

been reported that ants in general (Shindo 1972), and *S. invicta* in particular, can have negative effects on aphid predators (El-Ziady & Kennedy, 1956; Vinson & Scarborough 1989) and parasitoids (Frazer & van den Bosch 1973). The fact that syrphid eggs were observed on fire ant-tended colonies at close to expected frequencies suggests that syrphid adults do not discriminate against fire ant-tended aphid colonies for oviposition. However, significantly fewer syrphid larvae were observed on fire ant-tended colonies than would be expected by chance, and the same was true for coccinellid larvae, suggesting a negative impact of fire ants on the beneficial activities of both these important natural enemies groups. Vinson & Scarborough (1991) showed that fire ants remove *L. testaceipes*-parasitized aphids and mummies from *Rhopalosiphum maidis* (Fitch) colonies growing on sorghum. We observed fire ants carrying mummies away from BCA colonies on occasion, although mummies and aphids parasitized by *L. testaceipes* were both encountered on fire ant-tended colonies at close-to-expected frequencies.

Vinson & Scarborough (1991) also reported that fire ants carried aphids to uninfested leaves and we observed live aphids being transported by fire ants on several occasions. This behavior could potentially lead to amplification of BCA infestations within trees if fire ants frequently initiate new colonies on uninfested terminals. We also observed fire ants removing dead aphids from BCA colonies, a behavior which could conceivably interfere with disease dynamics in the aphid population.

#### Other Aphididae

The green citrus aphid, *A. spiraecola*, was frequently observed to form mixed colonies with the BCA, even when many uninfested terminals were available for colonization. The percentage of mixed colonies seemed to peak in April at most sites (see Enseñat, 1996, Fig. 4; Cancél 1996 & 1997, Figs. 2 & 3; Muñoz 1996, Fig. 6; Limaní and La Baleár, Table 3) when 50% or more of BCA colonies may be mixed with *A. spiraecola*. This appears to be the period of peak flight activity for *A. spiraecola*, when alates are migrating into citrus in large numbers from maturing colonies on other hosts. Why *A. spiraecola* alates select terminals already occupied by BCA (or vice versa) remains to be explored. Both species are attacked by the same guild of natural enemies and there may be a 'safety in numbers' advantage to the association. *A. spiraecola* could benefit from dilution of predation pressure when in association with BCA, since the latter is a larger aphid with a higher reproductive rate. Possible benefits for the BCA include the protected microenvironment created by the cupped and twisted leaves produced by citrus in response to *A. spiraecola* feeding.

#### Implications for biological control

Assuming that only alate aphids usually move from tree to tree, only those BCA colonies which mature and export alates are of economic importance with regard to the transmission of CTV. We suspect that colony resilience to predation increases with colony size, simply because larger colonies are more likely to leave survivors. Based on the high reproductive potential of the BCA (Komazaki 1988), we suspect that only colonies discovered by natural enemies in relatively early stages have a high probability of being completely eliminated. Nevertheless, predation appears the most likely reason that only a relatively small proportion of BCA colonies were observed in mature stages, i.e. producing migratory alatae.

The BCA is notorious as an aphid species with few effective parasitoids (Carver 1978, Carver & Woolcock 1985, Murakami et al. 1984). In Japan, *Lysiphlebia japonica* is reported to attack the BCA (Takanashi 1990, 1991). Flanders & Fisher (1959) at-

tributed some control of BCA to parasitism by *Trioxys* and *Aphelinus* spp in Kwangtung Province, China but relatively little information is available on other potential parasitoids of BCA in China which is presumably its country of origin. In Puerto Rico, the relatively low survival of *L. testaceipes* in the BCA essentially negates any numerical response of this parasitoid within BCA infestations. Furthermore, the tendency of females to parasitize only a small fraction of the aphids in each colony means that colonies are rarely eliminated by parasitism alone.

The pathogenic fungus *V. lecanii* was observed in BCA colonies only sporadically, but was occasionally a significant mortality factor at the Enseñat site, particularly in 1997. This fungus has been reported to cause significant mortality to BCA populations in Venezuela (Rondón et al. 1981) and Argentina (Yasem de Romero 1985) although epizootics are contingent on environmental conditions conducive to infection, specifically prolonged periods of leaf wetness.

The most important natural enemies of the BCA in Puerto Rico appear to be the complex of larger coccinellid species which apparently eliminate large numbers of colonies in their earliest stages. Syrphids are another important natural enemy group probably contributing to the elimination of many BCA colonies, and to a reduction in the number of alates exported from others. The conditions influencing production of alatae in the BCA have not been studied, but one important factor appears to be crowding. We suspect that predation within colonies can delay the production of alates, both through direct reductions in aphid density and by the disturbance and scattering of aphids within colonies. The potential exists for an additive impact of syrphids and coccinellids on BCA populations, in that intra-guild predation does not appear to occur between the primary species. On the other hand, our observations indicate that these two predator guilds may express disparate habitat preferences under some circumstances. It is notable that other guilds of aphidophagous predators such as the Staphylinidae (Coleoptera), Anthocoridae, Miridae and Nabidae (Hemiptera) were not recorded from BCA colonies in this study. However, since our observations were restricted to daylight hours, nocturnal predators would not have been observed. Our observations also indicate that red imported fire ants have a measurable negative impact on natural enemies when they tend BCA colonies, and may therefore warrant consideration in integrated management of the BCA.

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