Aphid Parasitoids (Hymenoptera: Braconidae: Aphidiinae) on Citrus: Seasonal Abundance, Association with the Species of Host Plant, and Sampling Indices

Nickolas G. Kavallieratos,[*,1] Christos G. Athanassiou,[1] George J. Stathas[2] and Željko Tomanović[3]

Samples were collected from southern Greece during 1996–2000 in order to investigate the presence of parasitoids on *Aphis gossypii* Glover infesting several citrus species. The species of aphidiines found to have a significantly different preference for *A. gossypii* were *Aphidius colemani* Viereck, *Aphidius matricariae* Haliday, *Diaeretiella rapae* (M'Intosh), *Ephedrus persicae* Froggat, *Lysiphlebus testaceipes* (Cresson), *Binodoxys acalephae* (Marshall) and *Binodoxys angelicae* (Haliday). In another sampling experiment, the relative abundance of aphidiine parasitoids on aphids infesting orange and tangerine trees was studied in southern Greece (Nea Kios) in 1996 and 1997. *A. gossypii* constituted the largest part of the aphid population and was the only species parasitized. *B. angelicae* and *A. colemani* were the most abundant parasitoid species. The parasitization rate differed among the parasitoid species. *B. angelicae* had the highest colonization rate in centrally located and large host (*A. gossypii*) groups, whereas *A. colemani* was found in more isolated and relatively small host groups. The percentage of parasitism by *B. angelicae* was high mainly in large host groups, when *B. angelicae* was the only parasitoid present. However, in cases of coexistence of *B. angelicae* with *A. colemani* with hyperparasitoids, in the same sampling unit, the percentage of parasitism was relatively low.
KEY WORDS: *Aphis gossypii*; Aphidiinae; hyperparasitoids; density dependence; isolation; citrus species.

INTRODUCTION

Aphids are very important citrus pests in several citrus-growing areas of the world, causing great damage both directly and indirectly (leaf deformation, flower and very young fruit drop, underdeveloped shoots, honey residues causing sooty mold, virus transmission) (1,2,11,22). In Greece, nine aphid species have been reported to infest citrus trees: *Aphis craccivora* Koch, *Aphis gossypii* Glover, *Aphis spiraecola* Patch, *Aulacorthum solani* (Kaltenbach), *Brachycaudus helichrysi* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas), *Myzus persicae* (Sulzer), *Rhopalosiphum maidis* (Fitch) and *Toxoptera aurantii* (Boyer de Fonscolombe) (11). However, aphids have several natural enemies that can affect their numbers, among them being aphidiine parasitoids which are potential control agents (34).

In Greece, the aphidiine parasitoids *Aphidius colemani* Viereck, *Aphidius matricariae* Haliday, *Aphidius urticae* Haliday, *Diaeretiella rapae* (M'Intosh), *Ephedrus persicae* Froggat, *Lysiphlebus confusus* Tremblay and Eady, *Lysiphlebus fabarum* (Marshall), *Lysiphlebus testaceipes* (Cresson), *Praon volucre* (Haliday), *Binodoxys acalephae* (Marshall) and *Binodoxys angelicae* (Haliday) have been reported to parasitize aphids on citrus such as *A. craccivora, A. gossypii, A. spiraecola, A. solani, B. helichrysi, M. euphorbiae, M. persicae, R. maidis* and *T. aurantii* (11,12,13). Furthermore, *Alloxysta* spp., *Asaphes vulgaris* Walker, *Asaphes* spp., *Dendrocerus* spp., *Pachyneuron aphidis* (Bouché), *Pachyneuron* spp., *Phaenoglyphis* spp. and *Syrphophagus aphidivorus* (Mayr) have been reported as hyperparasitoids that attack primary parasitoids of aphids infesting citrus (11,30).

Although there are well established data concerning the occurrence of parasitoids in citrus, very little information is available for estimating parasitoid populations, data that might be useful in assessing their efficiency as biological control agents. When assessing and interpreting parasitoid populations, apart from actual population densities, interactions between species must be taken into account (8,23,43). Although the colonization rate of a given parasitoid species is likely to be positively influenced at high aphid densities (9), the simultaneous activity of another parasitoid species can lead to uncertain outcomes for biological control (8,24). This problem is more complex when several species of parasitoids coexist (8,16,24,39,44), which is the most usual case.

This study was conducted to obtain information concerning the abundance and the patterns of host utilization of aphid parasitoids on citrus. Additionally, consideration was given to interactions between parasitoid species and density-dependent responses.

MATERIALS AND METHODS

In 1996 and 1997, samples were taken every 10 days from an untreated citrus orchard in southern Greece (Nea Kios) covering an area of 20,000 m^2, planted with approximately 10-year-old orange and tangerine trees. Forty young shoots, 20 cm long, were randomly collected on each sampling date: two shoots from each of ten orange trees and ten tangerine trees. Some trees were chosen to be located centrally while others to be more isolated.

Leaf samples bearing mummified aphids were also collected from orange, sour orange and tangerine trees in southern Greece, which is a primary citrus-growing area, during 1996–2000. The relative abundance (percentage of occurrence of the different parasitoid species per aphid species [36]) of *A. gossypii* parasitoids for each citrus species was estimated during the period of the study.

Each sample was placed separately in a plastic bag, which was brought to the laboratory where aphids were identified to species. Live aphids were preserved in 90% ethyl alcohol and 75% lactic acid (2:1) (4). Mummies, each attached on a small leaf piece, were placed separately in small plastic boxes inside a growth cabinet. On the lid of each box there was a circular opening covered with muslin for ventilation in order to maintain conditions inside the boxes similar to those existing in the growth cabinet (22.5°C, 65% r.h., 16L:8D). The percentage of parasitization was estimated by calculating the number of mummified aphids (emerged and non-emerged) to the total number of aphids (40).

Data were analyzed by one-way ANOVA using the statistical package JMP (29). Means were compared by the Tukey - Kramer (HSD) test (at $P=0.05$). The percentages of parasitoids on orange, sour orange and tangerine trees were compared in pairs, with the z test (at $P=0.05$) (42), using the statistical package Statgraphics (37).

N.G. Kavallieratos *et al.*

In order to classify density dependence, which measures the ability of a parasitoid species to respond numerically to changes in host densities (3), the percentage of parasitism was plotted against the host population size (total number of aphids per sampling unit). Finally, the effect of isolation (repulsion) on spatial distribution among parasitoid species was classified using the "Isolation index" (7,16,23), which is calculated as:

$$S_i = \sum g_j e^{-\alpha dij}, j \neq i$$

where α is a constant setting the distance-dependent migration rate, d_{ij} is the distance between host groups/populations i and j (shoots in our case), and g_j denotes the size of the host group/population. The index is scaled for different groups/populations, so that it varied from 0 to 1. In general, isolation increases with decreasing S value. Thus, the maximum value indicates that a group is centrally located in the population and is surrounded by large host groups (16).

RESULTS

Occurrence of parasitoids and hyperparasitoids The infestation of orange and tangerine trees by aphids in southern Greece (Nea Kios) in 1996 and 1997 varied markedly among sampling dates (Figs. 1, 2). ANOVA showed significant differences among the species of aphids that infested orange and tangerine trees (F=4.65, d.f.=4, 497, P=0.0011 in 1996, F=7.09, d.f.=2, 537, P=0.0009 in 1997 for orange trees; and F=5.15, d.f.=4, 495, P=0.0004 in 1996, F=11.11, d.f.=3, 716, P<0.0001 in 1997 for tangerine trees). In the case of orange trees, there were significantly more *A. gossypii* ($\bar{X}$=23.00 in 1996, $\bar{X}$=15.70 in 1997) than *A. solani* ($\bar{X}$=1.63 in 1996, $\bar{X}$=0.14 in 1997), *T. aurantii* ($\bar{X}$=0.47 in 1996, $\bar{X}$=0.64 in 1997), *A. spiraecola* ($\bar{X}$=0.04 in 1996) or *M. persicae* ($\bar{X}$=0.20). Similarly, in the case of tangerine trees, the mean number of *A. gossypii* ($\bar{X}$=18.37 in 1996, $\bar{X}$=50.26 in 1997) was significantly higher than that of *A. spiraecola* ($\bar{X}$=3.51 in 1996, $\bar{X}$=2.49 in 1997), *T. aurantii* ($\bar{X}$=4.21 in 1996, $\bar{X}$=5.81 in 1997), *A. craccivora* ($\bar{X}$=0.03 in 1996), *M. euphorbiae* ($\bar{X}$=0.14 in 1996) or *M. persicae* ($\bar{X}$=0.006 in 1997).

Furthermore, although in 1996 the mean numbers of *A. gossypii* infesting citrus species did not differ significantly (F=0.15, d.f.=1, 198, P=0.70), in 1997 these numbers were significantly different (F=5.39, d.f.=1, 358, P=0.02). The mean number of *A. gossypii* was higher in orange trees ($\bar{X}$=23.00) than in tangerine ($\bar{X}$=18.37) in 1996, but it was significantly higher in tangerine trees ($\bar{X}$=50.26) than in orange ($\bar{X}$=15.70) in 1997. No significant differences were recorded between citrus species for *A. spiraecola* (F=1.42, d.f.=1, 198, P=0.24 in 1996) and *T. aurantii* (F=0.97, d.f.=1, 198, P=0.33 in 1996; F=2.62, d.f.=1, 358, P = 0.11 in 1997).

Only *A. gossypii*, among the aphid species infesting orange and tangerine trees, was found to be parasitized. The percentages of parasitized *A. gossypii* individuals and the percentages of parasitism by hyperparasitoids as well as the numbers of parasitoids and hyperparasitoids of *A. gossypii* on orange and tangerine trees are presented in Figures 3 and 4. ANOVA showed significant differences among the species of aphidiines that parasitized *A. gossypii* on orange and tangerine trees (F=4.28, d.f.=2, 297, P=0.0147 in 1996, F=3.06, d.f.=3, 716, P=0.028 in 1997 for orange trees; and F=6.43, d.f.=3, 396, P=0.0003 in 1996, F=5.86, d.f.=4, 895, P=0.0001 in 1997 for tangerine trees). In the case of orange trees, there were significantly more *B. angelicae* ($\bar{X}$=0.94 in 1996, $\bar{X}$=0.94 in
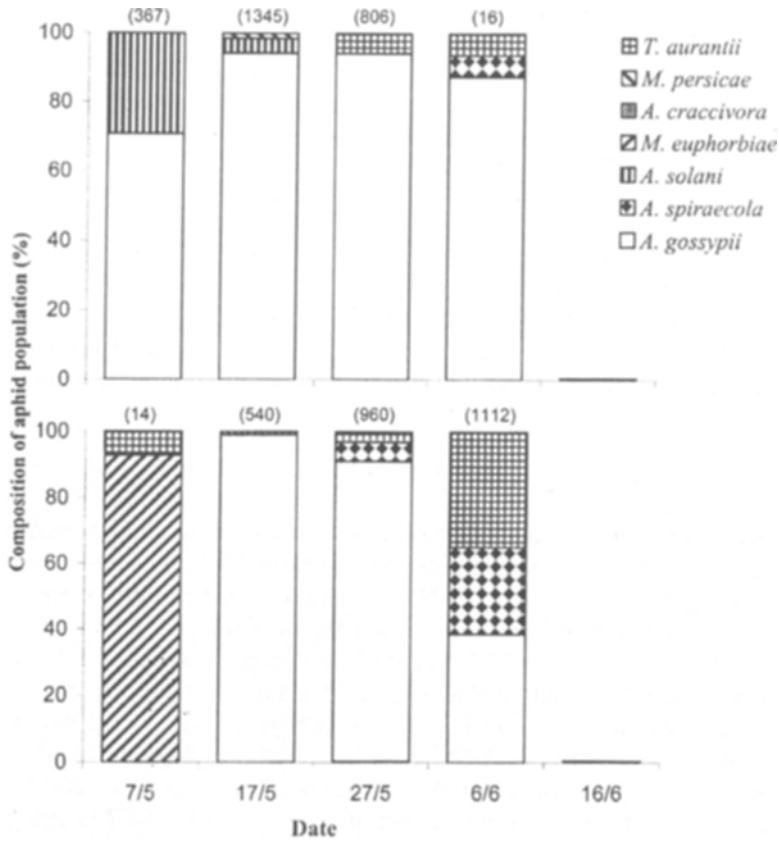
Fig. 1. Numbers of aphids and composition of aphid species (%) found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1996.

1997) than *A. matricariae* ($\bar{X}$=0.01 in 1996, $\bar{X}$=0.05 in 1997) or *L. testaceipes* ($\bar{X}$=0.03 in 1997). However, the mean number of *A. colemani* was not significantly different from that of *B. angelicae*, although lower numbers were recorded ($\bar{X}$=0.53 in 1996, $\bar{X}$=0.32 in 1997). In the case of tangerine trees, there were significantly more *B. angelicae* ($\bar{X}$=1.21 in 1996, $\bar{X}$=1.17 in 1997) than *A. colemani* ($\bar{X}$=0.24 in 1996), *L. testaceipes* ($\bar{X}$=0.11 in 1996, $\bar{X}$=0.02 in 1997), *A. matricariae* ($\bar{X}$=0.06 in 1996, $\bar{X}$=0.09 in 1997) or *E. persicae* ($\bar{X}$=0.01 in 1997). However, the mean number of *A. colemani* was not significantly different from that of *B. angelicae* in 1997, although lower numbers of the former were recorded ($\bar{X}$=1.03).

No significant differences were noted between citrus species for any of the parasitoid species found in both years of the study (F=0.29, d.f.=1, 198, *P*=0.59 in 1996, F=0.14, d.f.=1, 358, *P*=0.71 in 1997 for *B. angelicae*; F=1.16, d.f.=1, 198, *P*=0.28 in 1996, F=3.05, d.f.=1, 358, *P*=0.08 in 1997 for *A. colemani*; F=1.20, d.f.=1, 198, *P*=0.27 in 1996, F=0.71, d.f.=1,358, *P*=0.40 in 1997 for *A. matricariae*; F=0.20, d.f.=1, 358, *P*=0.65 in 1997 for *L. testaceipes*).

The hyperparasitoid spectrum was composed mainly of *Asaphes* spp. and *S. aphidi-*
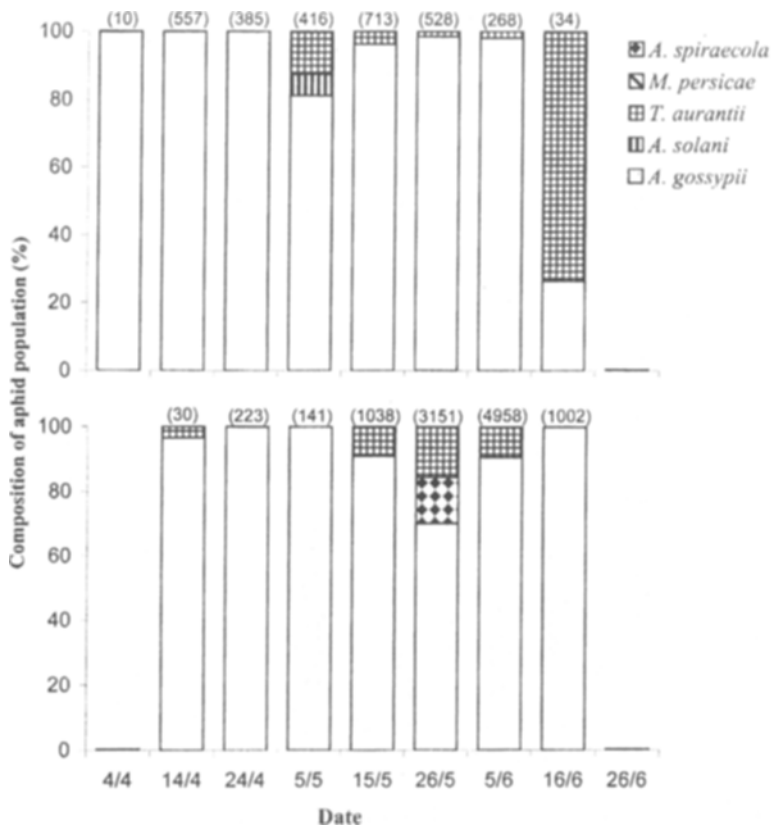
N.G. Kavallieratos *et al.*

Fig. 2. Numbers of aphids and composition of aphid species (%) found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1997.

vorus for both citrus species in 1996 (Fig. 5), whereas *S. aphidivorus* was the most abundant in 1997 (Fig. 6).

The examination of orange, sour orange and tangerine samples resulted in the collection of 9,321 individuals of aphidiine parasitoids from *A. gossypii* mummies (Table 1). Significant differences in the percentages of various *A. gossypii* aphidiine parasitoids found on the above samples are shown in Table 2.

Sampling indices   Examination of the samples showed that only a relatively small fraction of the sampling units was occupied by aphids or parasitoid individuals. *A. gossypii* individuals were found in approximately 23.1% of the sampling units examined, while the corresponding figure for *B. angelicae* and *S. aphidivorus* was 13.2% and 5.4%, respectively. These numbers, combined with the data presented in Figures 1–6, are indicative of the high range of variation among sampling units.

The parasitism of *A. gossypii* tended to be density-dependent (host group size-dependent). In the case of *B. angelicae*, a high parasitism rate was recorded mainly in large aphid colonies (host groups) when these colonies were occupied by this species (Fig. 7). On the other hand, a noticeable reduction in the rate of parasitism was found in cases of coexistence of *B. angelicae* and *A. colemani*. Furthermore, this coexistence
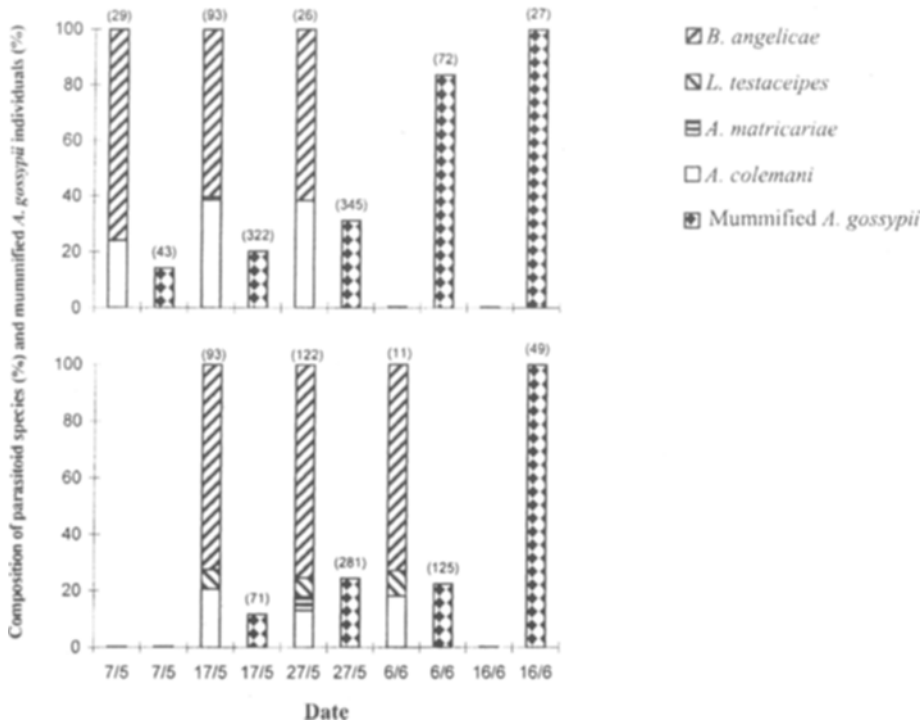
Fig. 3. Numbers of parasitoids and composition of parasitoid species (%) on *Aphis gossypii*, and percent parasitized *A. gossypii* individuals, found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1996.

TABLE 1. Relative abundance (% of the total) of *Aphis gossypii* aphidiine parasitoids found on sour orange, orange and tangerine trees (1996–2000)

Host plant	A.c.	A.m.	D.r.	E.p.	L.c.	L.f.	L.t.	P.v.	B.ac.	B.an.	Total number
Sour orange	35.92	4.47	1.46	0.72	1.83	0.46	0.31	0.53	4.44	49.86	3221
Orange	31.45	2.77			1.64		0.87		0.39	62.88	3106
Tangerine	16.53	3.64	0.80	0.07	1.23		1.74	0.30	0.57	75.12	2994

A.c., Aphidus colemani; A.m., Aphidus matricariae; D.r., Diaeretiella rapae; E.p., Ephedrus persicae; L.c., Lysiphlebus confusus; L.f., Lysiphlebus fabarun; L.t., Lysiphlebus testaceipes; P.v., Praon volucre; B.ac., Binodoxys acalephae; B.an., Binodoxys angelicae

was observed in relatively small host groups (as compared with those occupied by only *B. angelicae*), whereas in larger host groups (more than 200 aphids per sampling unit) the rate of parasitism did not exceed 19%. Similar observations were recorded in the cases of coexistence of *B. angelicae* with hyperparasitoids; most hyperparasitism occurred in small host groups and appeared negatively correlated with percentage of parasitism by primary parasitoids.
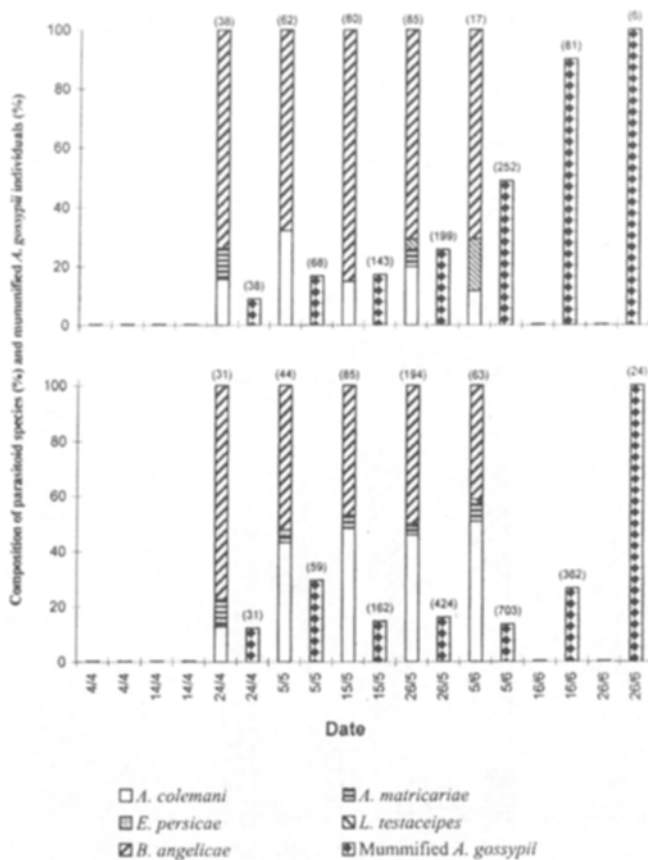
N.G. Kavallieratos *et al.*

Fig. 4. Numbers of parasitoids and composition of parasitoid species (%) on *Aphis gossypii*, and percent parasitized *A. gossypii* individuals, found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1997.

TABLE 2. Significant differences in the percentages of various *Aphis gossypii* aphidiine parasitoids found on different host plants

| Host plants	Aphidiines	Computed z statistic
Sour orange *vs* Orange	*A. colemani*	3.77, $P=0.0002$
	A. matricariae	3.63, $P=0.0003$
	L. testaceipes	-2.90, $P=0.004$
	B. acalephae	10.66, $P<0.0001$
	B. angelicae	-10.53, $P<0.0001$
Sour orange *vs* Tangerine	*A. colemani*	17.88, $P<0.0001$
	D. rapae	2.47, $P=0.0134$
	E. persicae	4.15, $P<0.0001$
	L. testaceipes	-5.54, $P<0.0001$
	B. acalephae	9.97, $P<0.0001$
	B. angelicae	-21.35, $P<0.0001$
Orange *vs* Tangerine	*A. colemani*	13.88, $P<0.0001$
	L. testaceipes	-2.99, $P=0.0282$
	B. angelicae	-10.44, $P<0.0001$
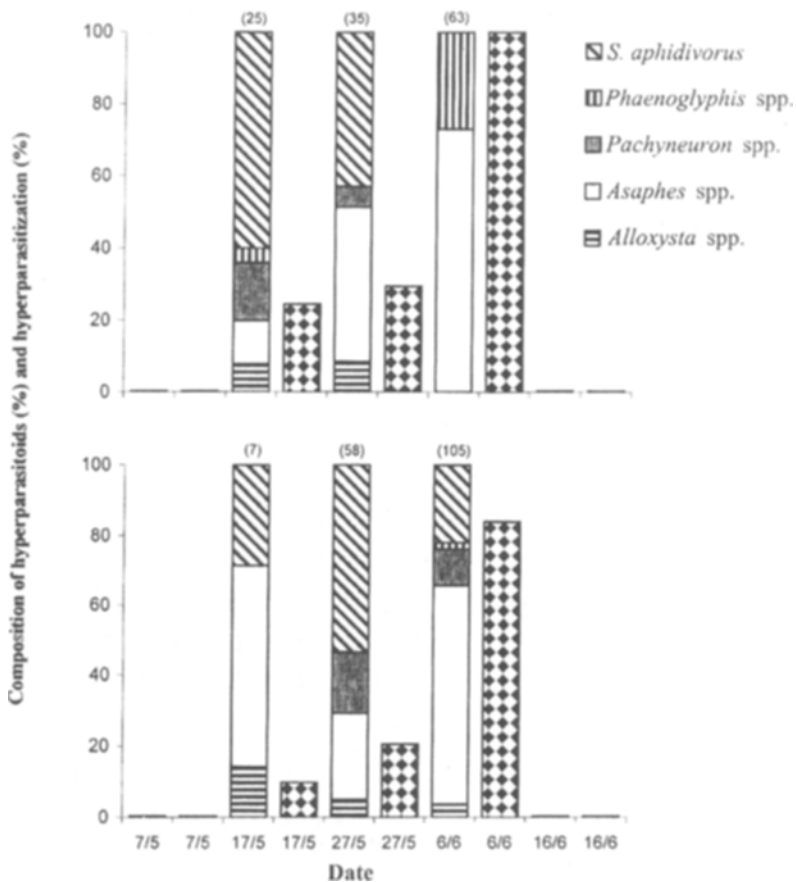
Fig. 5. Numbers of hyperparasitoids and composition of hyperparasitoids (%) on *Aphis gossypii*, and percent hyperparasitization, found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1996.

Isolation had a considerable effect on the spatial distribution of the parasitoids among sampling units. The average value of the isolation index for host groups occupied by *A. colemani* was much lower, as compared with groups occupied by *B. angelicae* (Fig. 8). Also, the highest *S* values for *B. angelicae* were recorded for large host groups. In the case of groups occupied by the two species, *S* values were low, especially in large groups.

DISCUSSION

Aphis gossypii did not 'prefer' orange or tangerine trees since its population showed different patterns in 1996 and 1997. This is in accord with Barbagallo and Patti (1), who mention that this aphid species appears mainly on orange or tangerine trees.

Parasitoids were a mortality factor only for *A. gossypii* during both years. The other aphid species were not found to be parasitized, despite the presence of various parasitoid species of which they have been reported as potential hosts (11,13,18-21,27,28,33,41). It
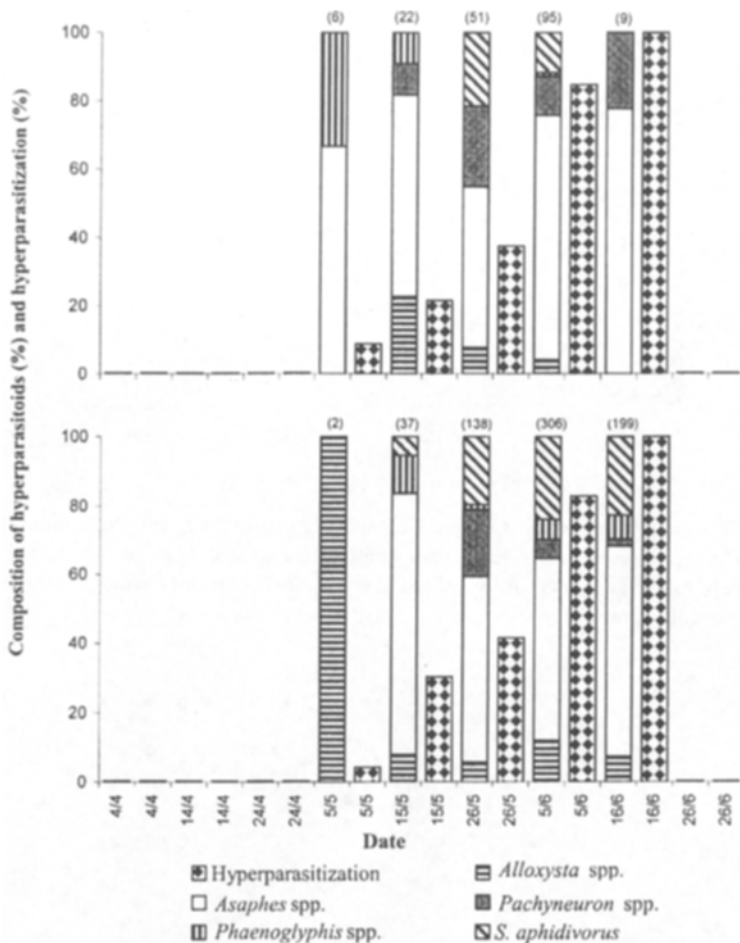
N.G. Kavallieratos *et al.*

Fig. 6. Numbers of hyperparasitoids and composition of hyperparasitoids (%) on *Aphis gossypii*, and percent hyperparasitization, found on orange (top) and tangerine (bottom) trees in southern Greece (Nea Kios) in 1997.

is possible that the significantly higher populations of *A. gossypii* compared with those of other aphids, account for this species preference in parasitization, as it was the easiest to be found and parasitized. Similar observations regarding the parasitization of the most abundant aphid species have been made by Pimentel (26) and Starý (34).

The findings of the present study may suggest that parasitoids did not suppress aphid densities in either of the years tested, given that the aphid presence was high for most of the sampling period. This could be attributed to the parasitoids' delayed action since, in agreement with Starý (36), the first mummies appeared generally after the development of aphid populations at high levels. Furthermore, the strong presence of the hyperparasitoids appeared to limit the numbers of the primary parasitoids, mainly by appearing later seasonally and increasing in numbers later on in both years. Similar observations regarding the appearance of hyperparasitoids and their effect on primary parasitoids have been made
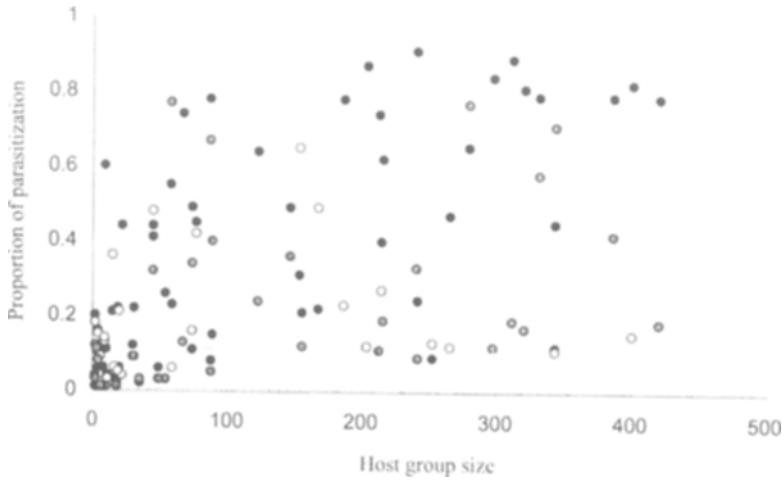
Fig. 7. Relationship between host group size and parasitism rate, for the combined sampling seasons and citrus species data. Each data point refers to one host group, occupied by only *Binodoxys angelicae* (black dots), *B. angelicae* and *Aphidius colemani* (white dots) or *B. angelicae* and hyperparasitoids (gray dots).
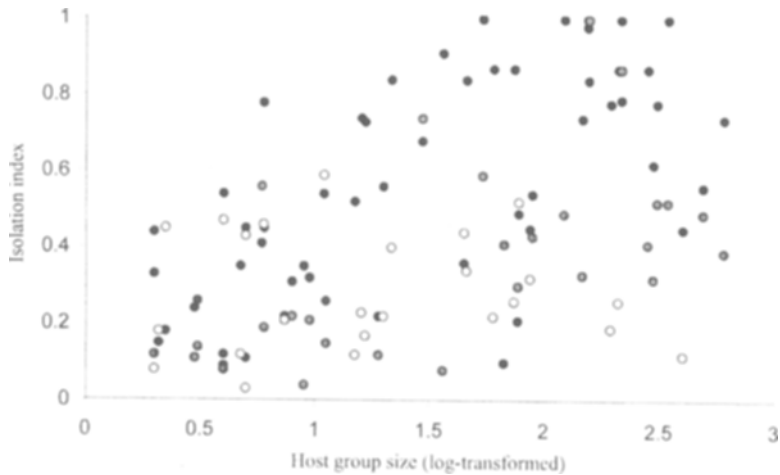

Fig. 8. Relationship between isolation index and host group size, for the combined sampling seasons and citrus species data. Each data point refers to one host group, occupied by only *Binodoxys angelicae* (black dots), or only *Aphidius colemani* (gray dots), or by *B. angelicae* and *Aphidius colemani* (white dots).

by Evenhuis (5), Latteur (14) and Starý (34,36) as well. However, the percentage of parasitization was relatively high towards the end of the period (June). At that time *A. gossypii* migrates to alternative host plants, since citrus trees are unsuitable for infestation during summer due to their lack of new growth (2), resulting in population decline unrelated to parasitization.

The findings of the present study suggest that different citrus species may markedly affect the parasitism preference of aphidiine species. However, the fact that no significant differences were found between citrus species for any of the parasitoids in the first part of the study could be attributed to the small number of specimens collected during the 2-year period in relation to the number collected during 1996–2000. This stands in accordance with Starý (36), who mentions that relative abundance is the most constant parameter if it is determined from a large number of samples taken over the course of several years in a defined geographical area. The effect of plant species on the host selection of aphid parasites is mentioned in other studies as well. Sekhar (31) reported that *L. testaceipes* preferred to attack *A. gossypii* on squash (Cucurbitaceae) rather than on hibiscus (Malvaceae), and *M. persicae* on tobacco (Solanaceae) rather than on radish (Cruciferae). According to Starý (32,34), the parasitization of *Aphis fabae* Scopoli by *B. angelicae* varied between the host plants *Euonymus europea* L. (Celastraceae) and *Philadelphus coronarius* L. (Saxifragaceae). There are also reports on differences in the rate of aphid parasitization between plant species of the same genus. Mackauer *et al.* (17) report that the percentage of parasitization of *Aphis fabae* ssp. *cirsiiacanthoidis* Scopoli by *Lysiphlebus cardui* (Marshall) was greater on *Cirsium arvense* Scopoli (Asteraceae) than on *C. palustre* Scopoli (Asteraceae).

The clumping of *A. gossypii* and its parasitoids on a relatively small proportion of shoots is indicative of an aggregated distribution among sampling units. However, the density dependence noted in this study (at least for *B. angelicae*) suggests that the aggregation of the parasitoids is apparently a secondary consequence of the host's aggregation (7,10,15,38).

Parasitism by *B. angelicae* showed a positive trend against group size. In addition, *B. angelicae* was found mainly in centrally located large host groups as indicated by S values. These facts signify the high colonization rate of this species, when it is not 'disturbed' by competition, or low host densities. Hence, *B. angelicae* was the prevalent parasitoid species when *(a)* it was the only parasitoid species in a host group, *(b)* the host group was large and centrally located and *(c)* the host colony was surrounded by other large host colonies. However, when *B. angelicae* was not the only parasitoid species, its parasitism rate was negatively influenced by the presence of other aphidiines (we examined the case of *A. colemani*) and by the activity of hyperparasitoids. These facts resulted in the reduced efficiency of parasitism in the *A. gossypii* populations. Moreover, *A. colemani* is likely to have a more random dispersal; our results showed that it was present mainly in isolated and relatively small host groups (Figs. 7, 8). However, a locally weaker competitor with higher dispersal activity can easily become the most abundant under conditions of low host density (3,6,8,24,25,39). Nevertheless, in our case, the coexistence of parasitoids is likely to have a negative influence on rates of colony discovery and may be associated with lower levels of parasitism within colonies. Similar observations implicating interspecific competition between aphid parasitoids have been made by Starý (35).

The connection between the seasonal occurrence and the effectiveness of parasitoids must be assessed on the basis of the variables affecting their spatial dynamics. Unless these parameters are taken into account, any evaluation of the presence of the parasitoids as control agents may be inaccurate. On the other hand, apart from the interspecific competition itself, the patchily structured patterns of parasitism are directly related to plant characteristics, aphid colony size and hyperparasitoid densities (9). Our results

indicate that, when developing sampling protocols for assessing these patterns, parasitoid coexistence and host-group density dependence must be taken into account. This coexistence, although of much interest from an ecological viewpoint, in practice is one of the main factors in applying biological control strategies for pest management in citrus. The interpretation of these variables with additional data over a broader range of cases, is needed before development of a program in which the parasitoids could be one of the main components.

REFERENCES

1. Barbagallo, S. and Patti, I. (1983) Citrus aphids and their entomophagous in Italy. *in*: Cavalloro, R. [Ed.] *Proc. Meeting EC Experts' Group* (Portici, Italy). A.A. Balkema, Rotterdam, the Netherlands. pp. 116-119.
2. Barbagallo, S. and Patti, I. (1986) The citrus aphids: Behaviour, damages and integrated control. *in*: Cavalloro, R. and Di Martino, E. [Eds.] *Proc. Meeting EC Experts' Group* (Acireale, Italy). A.A. Balkema, Rotterdam, the Netherlands. pp. 67-75.
3. Brodmann, P.A., Wilcox, C.V. and Harrison, S. (1997) Mobile parasitoids may restrict the spatial spread of an insect outbreak. *J. Anim. Ecol.* 66:65-72.
4. Eastop, V.F. and van Emden, V.F. (1972) The insect material. *in*: van Emden, H.F. [Ed.] Aphid Technology. Academic Press, London, UK. pp. 1-45.
5. Evenhuis, H.H. (1964) The interrelations between apple aphids and their parasites and hyperparasites. *Entomophaga* 9:227-231.
6. Hanski, I. (1983) Coexistence of competitors in patchy environment. *Ecology* 64:493-500.
7. Hanski, I. (1994) A practical model of metapopulation dynamics. *J. Anim. Ecol.* 63:51-62.
8. Hanski, I. (1999) Metapopulation Ecology. Oxford University Press, Oxford, UK.
9. Hassel, M.P. (2000) The Spatial and Temporal Dynamics of Host–Parasitoid Interactions. Oxford University Press, Oxford, UK.
10. Hassel, M.P., Comins, H.N. and May, R.M. (1994) Species coexistence and self-organizing spatial dynamics. *Nature (Lond.)* 370:290-292.
11. Kavallieratos, N. and Lykouressis, D. (1999) Parasitoids (Hymenoptera: Braconidae) emerged from aphids (Homoptera: Aphidoidea) on citrus and their frequency in Greece. *Boll. Lab. Entomol. Agrar. Portici* 55:93-104.
12. Kavallieratos, N.G. and Lykouressis, D.P. (2000) The coloration of mummies of *Aphis gossypii* Glover on citrus and other plants as a useful tool for parasitoid identification. *Isr. J. Entomol.* 34 (in press).
13. Kavallieratos, N.G., Lykouressis, D.P., Sarlis, G.P., Stathas, G.J., Sanchis Segovia, A. and Athanassiou, C.G. (2001) The Aphidiinae (Hymenoptera: Ichneumonoidea: Braconidae) of Greece. *Phytoparasitica* 29:306-340.
14. Latteur, G. (1973) Étude de la dynamique des populations des pucerons des céréales. Premières données relatives aux organismes aphidiphages en trois localités différentes. *Parasitica* 29:134-151.
15. Lei, G. and Hanski, I. (1997) Metapopulation structure of *Cotesia melitaearum* (Wilkinson) (Lepidoptera: Nymphalidae), a specialist parasitoid of the butterfly *Melitaea cinxia* (Linnaeus) (Hymenoptera: Braconidae). *Oikos* 78:91-100.
16. Lei, G. and Hanski, I. (1998) Spatial dynamics of two competing specialist parasitoids in a host metapopulation. *J. Anim. Ecol.* 67:422-433.
17. Mackauer, M., Michaud, J.P. and Völkl, W. (1996) Host choice by aphidiid parasitoids (Hymenoptera: Aphidiidae): host recognition, host quality and host value. *Can. Entomol.* 128:959-980.
18. Mescheloff, E. and Rosen, D. (1988) Biosystematic studies on the Aphidiidae of Israel (Hymenoptera: Ichneumonoidea). 2. The genera *Ephedrus* and *Praon. Isr. J. Entomol.* 22:75-100.
19. Mescheloff, E. and Rosen, D. (1990) Biosystematic studies on the Aphidiidae of Israel (Hymenoptera: Ichneumonoidea). 3. The genera *Adialytus* and *Lysiphlebus. Isr. J. Entomol.* 24:35-50.
20. Mescheloff, E. and Rosen, D. (1990) Biosystematic studies on the Aphidiidae of Israel (Hymenoptera: Ichneumonoidea). 4. The genera *Pauesia, Diaeretus, Aphidius* and *Diaeretiela. Isr. J. Entomol.* 24:51-91.

21. Mescheloff, E. and Rosen, D. (1993) Biosystematic studies on the Aphidiidae of Israel (Hymenoptera: Ichneumonoidea). 5. The genera *Trioxys* and *Binodoxys*. *Isr. J. Entomol.* 27:31-47.

22. Michaud, J.P. (1998) A review of the literature on *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Fla. Entomol.* 81:37-61.

23. Moilanen, A. and Hanski, I. (1995) Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model. *J. Anim. Ecol.* 64:141-144.

24. Nee, S. and May, R.M. (1992) Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecol.* 61:37-40.

25. Nee, S., May, R.M. and Hassel, M.P. (1997) Two-species metapopulation models. *in*: Hanski, I. and Gilpin, M. [Eds.] Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, San Diego, CA, USA. pp. 123-147.

26. Pimentel, D. (1961) Competition and the species per genus structure of communities. *Ann. Entomol. Soc. Am.* 54:323-333.

27. Rosen, D. (1967) The hymenopterous parasites and hyperparasites of aphids on citrus in Israel. *Ann. Entomol. Soc. Am.* 60:394-399.

28. Rosen, D. (1969) The parasites of coccids, aphids and aleurodids on citrus in Israel: some zoogeographical considerations. *Isr. J. Entomol.* 4:45-53.

29. Sall, J., Lehman, A. and Creighton, L. (2001) JMP Start Statistics. A Guide to Statistics and Data Analysis using JMP and JMP IN Software. Duxbury Press, Belmont, CA, USA.

30. Santas, L.A. (1979) Distribution of aphids of citrus and cotton and their parasites in Greece. *Biol. Gallo-Hell.* 9:315-319.

31. Sekhar, P.S. (1960) Host relationships of *Aphidius testaceipes* (Cresson) and *Praon aguti* (Smith), primary parasites of aphids. *Can. J. Zool.* 38:593-603.

32. Starý, P. (1966) Aphid Parasites of Czechoslovakia. A review of the Czechoslovak Aphidiidae (Hymenoptera). Academia, Publishing House of the Czechoslovak Academy of Sciences, Prague, Czech Republic.

33. Starý, P. (1967) A review of hymenopterous parasites of citrus pest aphids of the world and biological control projects (Hymenoptera: Aphidiidae, Homoptera: Aphidoidea). *Acta Entomol. Bohemoslov.* 64:37-61.

34. Starý, P. (1970) Biology of Aphid Parasites (Hymenoptera: Aphidiidae) with Respect to Integrated Control. Dr. W. Junk, the Hague, the Netherlands.

35. Starý, P. (1973) Relative abundance of parasite species as an area dependent phenomenon and its possible significance in biological control (Hymenoptera: Aphidiidae). *Boll. Lab. Entomol. Agrar. Portici* 30:19-27.

36. Starý, P. (1988) Aphidiidae. *in*: Minks, A.K. and Harrewijn, P. [Eds.] Aphids, Their Biology, Natural Enemies and Control. Elsevier, Amsterdam, the Netherlands. pp. 171-184.

37. Statgraphics Plus (1995) Statgraphics Plus Version 2. Manugistics Inc., Rockville, MD, USA.

38. Stiling, P., Throckmorton, A., Silvanima, J. and Strong, D.R. (1991) Does spatial scale affect the incidence of density dependence? A field test with insect parasitoids. *Ecology* 72:2143-2154.

39. Tilman, D. (1994) Competition and biodiversity of spatially structured habitats. *Ecology* 75:2-16.

40. Tomanović, Ž., Brajković, M., Krunić, M. and Stanisavljević, L. (1996) Seasonal dynamics, parasitization and colour polymorphism of the pea aphid, *Acyrthosiphon pisum* (Harris) (Aphididae: Homoptera) on alfalfa in the south part of the Pannonian area. *Tiscia* 30:45-58.

41. Tremblay, E. (1984) The parasitoid complex (Hymenoptera: Ichneumonoidea) of *Toxoptera aurantii* (Homoptera: Aphidoidea) in the Mediterranean area. *Entomophaga* 29:203-209.

42. Wayne, W.D. (1999) Biostatistics: A Foundation for Analysis in the Health Sciences. John Wiley and Sons, New York, NY.

43. Weisser, W.W. (2000) Metapopulation dynamics in an aphid-parasitoid system. *Entomol. Exp. Appl.* 97:83-92.

44. Weisser, W.W. and Hassel, M.P. (1996) Animals "on the move" stabilize host–parasitoid systems. *Proc. R. Entomol. Soc. Lond. B* 263:749-754.