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Trophic Relationships of Aphid Hyperparasitoids (Hymenoptera) in Costa Rica

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ABSTRACT

Aphids are attacked by primary parasitoids (mostly Braconidae: Aphidiinae), which in turn are parasitized by hyperparasitoids (secondary parasitoids). We report for the first time in Costa Rica some trophic relationships between host plants, aphids, primary parasitoids and hyperparasitoids. Twenty nine species of aphids yielded 2832 primary parasitoids and 173 hyperparasitoids, the latter from just 12 of the aphid species. Five species of hyperparasitoids were obtained but three of these accounted for 98 % of all indviduals: *Asaphes californicus, Pachyneuron aphidis* (Pteromalidae) and *Syrphophagus aphidivorus* (Encyrtidae). The altitudinal and geographical distribution of each hyperparasitoid taxon is discussed within the context of the Costa Rican fauna.

Key words: Hymenoptera, hyperparasitoids, Costa Rica, trophic associations.

INTRODUCTION

One of the most important issues in biological control using parasitoids is to evaluate the effectiveness of parasitoid species in controlling the target pest. In some cases the effectiveness of a parasitoid can be diminished by mortality due to hyperparasitoids (Gómez-Marco *et al.*, 2014), although other factors such as dispersal of the primary parasitoids may also play a role (Holler *et al.*,1993). Hyperparasitoids, also known as secondary parasitoids (parasitoids of parasitoids), have evolved numerous times in the order Hymenoptera (Hanson and Gauld, 2006; Sullivan and Völkl, 1999).

Aphids are an important group of plant pests and harbor a species rich and taxonomically diverse group of hyperparasitoids. For example, a study in southern England found that 25 species of aphids were parasitized by 18 species of primary parasitoids, and the latter were attacked by 28 species of hyperparasitoids (Müller *et al.*, 1999). The most frequently encountered hyperparasitoids of aphids belong to four families in three superfamilies of Hymenoptera: Megaspilidae (Ceraphronoidea), Figitidae (Cynipoidea), Encyrtidae and Pteromalidae (Chalcidoidea) (Sullivan, 1987; Sullivan and Völkl, 1999).

Hyperparasitoids of aphids vary with respect to time of oviposition and mode of larval development. *Alloxysta* species (Figitidae: Charipinae) oviposit into primary

parasitoid larvae residing in living aphids, but the egg does not hatch until the primary parasitoid mummifies the host aphid and the larva develops as an endoparasitic koinobiont within the primary parasitoid (Sullivan, 1987; Grasswitz and Reese, 1998). In contrast, *Asaphes* and presumably *Pachyneuron* (Pteromalidae) attack primary parasitoids residing in mummified aphids; the female injects a paralyzing venom into the primary parasitoid larva, deposits an egg on the surface of the latter, and the larva develops as an ectoparasitic idiobiont (Keller and Sullivan, 1976; Sullivan, 1987). Unlike most other hyperparsitoids of aphids, *Pachyneuron aphidis* females locate potential hosts during slow and prolonged flights (Hübner, 2001). The biology of *Dendrocerus* (Megaspilidae) is similar to the preceding two genera but its venom does not cause paralysis (Bocchino and Sullivan, 1981) and thus its ectoparasitic larva shows incipient koinobiosis. *Syrphophagus aphidivorus* (Encyrtidae) prefers to oviposit in host pupae residing in mummified aphids and the larva develops as an idiobiont, but it sometimes oviposits into living aphids and develops as a koinobiont (delaying development until the aphid mummifies); the egg is deposited inside the primary parasitoid and the larva begins as an endoparasitoid and finishes as an ectoparasitoid (Kanuck and Sullivan, 1992; Buitenhuis *et al.*, 2004).

Relatively few studies have been carried out on the primary and hyperparasitoids of aphids in tropical countries and what few exist for tropical America are mostly from South America (e.g., Vaz *et al.*, 2004). Long-term sampling of the aphid fauna of Costa Rica has yielded a current total of 91 species (Voegtlin *et al.*, 2003; Pérez Hidalgo *et al.*, 2009; Zamora Mejías *et al.*, 2010a; Zamora Mejías *et al.*, 2010b; Villalobos Muller *et al.*, 2010; Sánchez-Monge *et al.*, 2010; Zamora Mejías *et al.*, 2012), the vast majority of which appear to be introduced species. Ten species of primary parasitoids have been found thus far in the country and several of these also appear to be introduced species, in particular *Aphidius colemani* and *Lysiphlebus testaceipes*, which accounted for nearly 90% of all the specimens (Zamora Mejías *et al.*, 2010). There are few studies of the hyperparasitoids of aphids in Costa Rica (Ferrer-Suay *et al.*, 2011; Ferrer-Suay *et al.*, 2013) and therefore the objective of the present investigation is to provide, for the first time, an inventory of the aphid hyperparasitoids found in the country, as well as their relationships with the third, second, and first trophic levels (i.e., primary parasitoids, aphids, and plants).

MATERIALS AND METHODS

Hyperparasitoids were obtained by collecting and rearing different species of aphids from their host plants at various locations in Costa Rica from 2008 to 2010. GPS Garmin Etrex was used for recording the geographic coordinates and altitude above sea level at each collecting locality. Sampling locations (Table 1) cover the complete altitudinal range of the country and were chosen for suitable characteristics for aphid infestation, especially crop plantations, ornamental plants in urban areas, but also gardens and forests.

Aphid colonies, whether containing mummies or not, were collected by cutting plant parts with scissors, which were then placed in plastic containers covered with nylon mesh, and transferred to the laboratory. The number of aphids and mummies collected on a particular plant in the field varied between approximately 25 and 200. A subsample of 5-70 aphids was preserved in 70% ethanol for later identification.

Plant parts with aphids were placed in square plastic containers 10cm wide on each side and 10cm in height. The containers were maintained for 25-30 days for formation of mummies and emergence of primary and secondary parasitoids under a temperature range of 24°- 28°C and ambient light conditions in the laboratory. Boxes containing the samples were checked daily. After emergence, the parasitoids were placed in 70% ethanol for identification. Specimens of primary parasitoids and hyperparasitoids are deposited in the Museum of Zoology at the University of Costa Rica.

Field sampling was done by the first author who also identified the aphids with the help of Nicolas Perez Hidalgo. The primary parasitoids were identified by P. Starý (Institute of Entomology, Biology Centre, Academy of Sciences of the Czech Republic) and the first author. Encyrtidae were identified by John Noyes (Natural History Museum, London) and the other hyperparasitoids by the authors.

Table 1. Sampling locations of aphids in Costa Rica. * Hyperparasitoids present.

Locality code	Province	Location	Elevation in meters		Locality code	Province	Location	Elevation in meters
1	Alajuela	Grecia	1963		21	Guanacaste	Liberia	133
2	Alajuela	La Garita	857		22	Guanacaste	Tilarán	548
3	Alajuela	Palmares	1100		23	Heredia	Cariblanco	848
4	Alajuela	Poás	1588		24	Heredia	San Miguel	1165*
5	Alajuela	San Ramón	1098*		25	Heredia	Sarapiquí	172
7	Alajuela	Zarcero	1648*		26	Limón	Colorado	86
8	Alajuela	Volcán Arenal	532		27	Puntarenas	Buenos Aires	150
9	Cartago	Cervantes	1513		28	Puntarenas	Coto Brus	1311*
10	Cartago	Coris	1424		29	Puntarenas	Esparza	160
11	Cartago	Cot	1895		30	Puntarenas	Garabito	60
12	Cartago	La Unión	1843		31	Puntarenas	Monteverde	1382
13	Cartago	Oreamuno	1946		32	Puntarenas	Osa	10
14	Cartago	Paraíso	1079		33	Puntarenas	Sardinal	161
15	Cartago	Taras	1598		34	San José	Cerro Buena Vista	3161*
16	Cartago	Tierra Blanca	2380*		35	San José	Coronado	1758*
17	Cartago	Turrialba	680		36	San José	Desamparados	1199
18	Cartago	Volcán Irazú	3203		37	San José	Montes de Oca	1214*
19	Guanacaste	Cañas	26		38	San José	Mora	1016
20	Guanacaste	La Cruz	2		39	San José	Pérez Zeledón	1706*

RESULTS

During the study period 48 aphid species were identified from 230 samples associated with 62 families and 111 species of plants; we obtained primary parasitoids (Aphidiinae) from 29 aphid species (60% of the aphid species) and hyperparasitoids from 11 aphid species (23%), from a total of 10 host plant species (9 %). Hyperparasitoids emerged from just 14 (6%) samples, from 9 out of 39 sampling localities (Table 2). In total, 3005 parasitoids were reared from aphids, 2832 (94%) Aphidiinae and 173 (6%) hyperparasitoids. In addition, one specimen of *Tamarixia* sp. (Eulophidae) was reared from *Myzus ornatus* on *Rubus urticifolius* (Cartago, Cerro Buena Vista, 9° 33.736´N, 83° 44.421´W, 3161 m, 02.05.2009), presumably as a primary parasitoid.

The most commonly reared hyperparasitoids were *Asaphes californicus, Pachyneuron aphidis* (Pteromalidae) and *Syrphophagus aphidivorus* (Encyrtidae), accounting for 45%, 40% and 13%, respectively, of the total number of hyperparasitoids that emerged from the samples. The remaining 2% consisted of *Signiphora* sp. (Signiphoridae) and *Alloxysta* sp. (Figitidae).

Hyperparasitoids were reared mainly from two primary parasitoids, *Aphidius colemani* and *Lysiphlebus testaceipes*. Their effect on primary parasitoid emergence was occasionally substantial, in one case reaching 100% of emerged Hymenoptera from aphid mummies. In seven of the fourteen samples hyperparasitoids accounted for 30% to 100% of emerged hymenopterans (Fig. 1).

Below, the data are arranged in the following sequence for each hyperparasitoid: primary parasitoid species, aphid species, host plant, province, locality, geographic coordinates, meters above sea level (m), date, number of specimens reared (spn.). Abbreviations used for Costa Rican provinces are: Al-Alajuela, Ca-Cartago, Gu-Guanacaste, He-Heredia, Pu-Puntarenas, SJ-San José.

Alloxysta sp. (Figitidae)

Diaeretiella rapae in *Brevicoryne brassicae*, on *Rubus urticifolius*: SJ, Cerro Buena Vista, 9° 33.736´N, 83° 44.421´W, 3161 m, 02.05.2009, 1 spn.

Asaphes californicus Girault (Pteromalidae)

Aphidius colemani in *Aphis nerii* on *Tabernaemontana alba*: He, San Miguel, 9°58.600´N, 84°04.600´W, 1165 m, 03.08.2008, 1 spn. In *Myzus ornatus* on *Rubus urticifolius*: Ca, Cerro Buena Vista, 9° 33.736´N, 83° 44.421´W, 3161 m, 02.05.2009, 1 spn. In *Brachycaudus helichrysi* (mixed with *Myzus ornatus*) on *Solanum* sp.: SJ, Cerro Buena Vista, 9° 40.727´N, 83° 52.755´W, 2465 m, 29.09.2009, 4 spns.

Aphidius sp. nr. *colemani* in *Macrosiphum salviae* on *Morella pubecens*: Ca, Cerro Buena Vista, 9° 44.491´N, 83° 57.038´W, 2123 m, 20.05.2009, 1 spn. In *Illinoia morrisoni* on *Cupresus lusitanica*: SJ, Coronado, 10° 00.220´N, 83° 57.563´W, 1724 m, 12.07.2009, 3 spns.

Lysiphlebus testaceipes in *Aphis gossypii* (mixed with *Aulacorthum solani*) on *Cyphomandra betaceae*: Al, Zarcero, 10° 11.058´N, 84° 23.472´W, 1648 m, 14.05.2009, 66 spns.

Unknown primary parasitoid in *Aphis nerii* on *Tabernaemontana alba*: SJ, Montes de Oca, 9° 55.694´N, 84° 03.211´W, 1183 m, 09.05.2009, 1 spn.

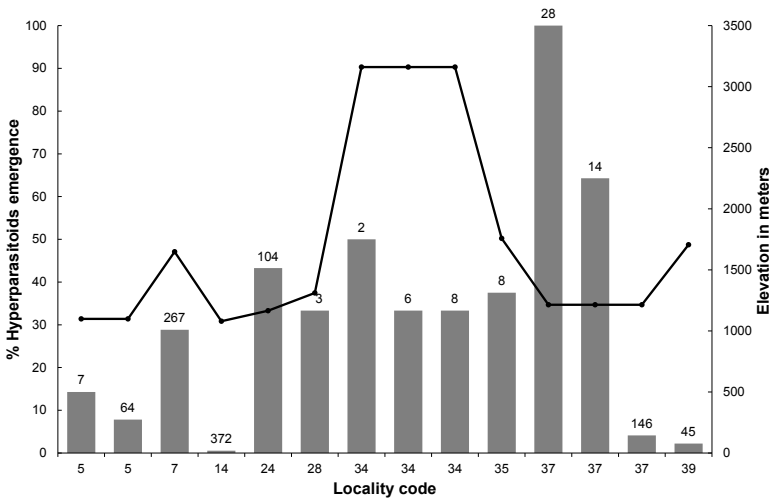

Fig. 1. Samples with hyperparasitoids (n=14) and the percentage of hyperparasitoids (n=172) emerged from aphid mummies and their respective elevation in meters (numbers over bars represent the total number of emerged parasitoids, n=1375).

***Pachyneuron aphidis* (Bouché) (Pteromalidae)**

Aphidius colemani in *Aphis nerii* on *Tabernaemontana alba*: He, San Miguel, 9°58.600´N, 84°04.600´W, 1165 m, 03.08.2008, 30 spns. In *Uroleucon (Lambersius) gravicorne* on *Coniza canadensis*: SJ, Montes de Oca, 9° 55.953´N, 84° 02.786´W, 1214 m, 05.09.2009, 7 spns. In *Aphis gossypii* on *Cyphomandra betaceae*: Ca, Tierra Blanca, 9° 56.120´N, 83° 52.963´W, 2382 m, 04.09.2009, 2 spns.

Aphidiusurantium: Al, San Ramon, 1055 m, 10° 07.086´ N, 84° 32.164´ W, 10.09.2009, 4 spns. In *Aphis gossypii* (mixed with *Aulacorthum solani*) on *Cyphomandra betaceae*: Al, Zarcero, 10° 11.058´N, 84° 23.472´W, 1648 m, 14.05.2009, 1 spn.

Unknown primary parasitoid in *Aphis nerii* on *Tabernaemontana alba*: SJ, Montes de Oca, 9° 55.694´N, 84° 03.211´W, 1183 m, 09.05.2009, 23 spns.

***Signiphora* sp. (Signiphoridae)**

Lipolexis oregmae and *Lysiphlebus testaceipes* in *Aphis illinoisensis* on *Vitis tiliifolia*: Pu, Coto Brus, 8° 46.978´N, 82° 58.294´W, 1311 m, 21.03.2009, 1 spn.

Lysiphlebus testaceipes in *Toxoptera citricidus* on *Citrus aurantium*: Al, San Ramon, 10° 07.086´ N, 84° 32.164´ W, 1055 m, 10.09.2009, 1 spn.

***Syrphophagus aphidivorus* (Mayr) (Encyrtidae)**

Aphidius colemani and *Aphis nerii* on *Tabernaemontana alba*: He, San Miguel, 9°58.600´N, 84°04.600´W, 1165 m, 03.08.2008, 14 spns. In *Uroleucon (Lambersius) gravicorne* on *Coniza canadensis*: SJ, Montes de Oca, 9° 55.953´N, 84° 02.786´W, 1214 m, 05.04.2009, 2 spns.

Lysiphlebus testaceipes and *Lipolexis oregmae* in *Toxoptera citricidus* on *Citrus aurantium*: Al, San Ramon, 10° 04.676´N, 84° 32.447´W, 916 m, 24.05.2009, 1 spn.

Lysiphlebus testaceipes, *Aphidius colemani* and *Binodoxys* sp. in *Aphis gossypii* on *Cyphomandra betaceae*: SJ, Perez Zeledon, 9° 29.914´N, 83° 36.781´W, 1706 m, 20.09.2009, 1 spn.

Unknown primary parasitoid in *Aphis nerii* on *Tabernaemontana alba*: SJ, Montes de Oca, 9° 55.694´N, 84° 03.211´W, 1183 m, 09.05.2009, 4 spns.

DISCUSSION

Emergence of primary parasitoids from 60% of the aphid species sampled and hyperparasitoids from only 23% suggests that many aphid species were not reared in sufficient numbers. Since only 6% of the total number of parasitoids emerging from aphid mummies were hyperparasitoids, it would appear that the latter do not generally represent a limiting factor for primary parasitoid populations. However, in one sample all of the parasitoids were hyperparasitoids and so it is possible that they occasionally have a substantial impact. More detailed studies of particular aphid-Aphidiinae-hyerparasitoid systems are required to examine in greater detail the impact of hyperparasitoids on populations of primary parasitoids in Costa Rica.

Asaphes californicus, Pachyneuron aphidis, and *Syrphophagus aphidivorus* were the most abundant hyperparasitoids reared from aphid mummies, together accounting for 98% of all the hyperparasitoids. In Túcuman, Argentina, *Alloxysta brassicae* and *Pachyneuron aphidis* were the most common hyperparasitoids reared from aphids on tomato; *Asaphes vulgaris* and *Dendrocerus* sp. were also found (Berta *et al.*, 2002). In Minas Gerais, Brazil, the most common hyperparasitoids reared from Aphidiinae (mostly *Diaeretiella rapae*) attacking the aphid *Brevicoryne brassicae* were, in order of decreasing frequency, *Alloxysta fuscicornis*, *Syrphophagus aphidivorus*, and *Pachyneuron* sp.; the most common hyperparasitoids from Aphidiinae (mostly *Lysiphlebus testaceipes*) attacking *Aphis nerii* were *Pachyneuron* sp. and *Syrphophagus aphidivorus* (Vaz *et al.*, 2004). While there are many similarities between our results and those from these two previous studies, the most notable differences are the greater frequency of *Asaphes* in Costa Rica and the lesser frequency of *Alloxysta*.

All *Asaphes* species are hyperparasitoids of aphids whereas the biology of *Pachyneuron* and *Syrphophagus* is more variable. Of the 17 described species of *Pachyneuron* reported from the New World (Noyes, 2014), *P. aphidis* is the only one having 3 anelli and 5 funicular segments in the antenna; the other 16 species all have 2 anelli and 6 funicular segments. In Costa Rica the only other *Pachyneuron* known

to have 3 anneli is what appears to be an undescribed species that was reared from Psylloidea, probably as a hyperparasitoid; all those reared as primary parasitoids from syrphid (Diptera) larvae have 2 anelli (Hanson, unpublished data). Of the three principal genera obtained in our study, *Syrphophagus* is by far the most species-rich; there are about 70 species of this genus in Costa Rica, nearly all undescribed, and the vast majority of which are probably parasitoids of syrphid larvae (J. Noyes, pers. comm.).

Table 2. Trophic interactions of hyperparasitoid species in Costa Rica.

Hyperparasitoid	Family	Abundance	Parasitoid	Aphid Host	Host Plant	Locality code
Alloxysta sp.	Figitidae	1	*Diaeretiella rapae*	*Brevicoryne brassicae*	*Rubus urticifolius*	34
Asaphes californicus	Pteromalidae	1	*Aphidius colemani*	*Aphis nerii*	*Tabernaemontana alba*	24
		1		*Myzus ornatus*	*Rubus urticifolius*	34
		4		*Brachycaudus helichrysi*	*Solanum* sp.:	34
		1	*Aphidius* sp. nr. *colemani*	*Macrosiphum salviae*	*Morella pubecens*	34
		3		*Illinoia morrisoni*	*Cupresus lusitanica*	35
		66	*Lysiphlebus testaceipes*	*Aphis gossypii*	*Cyphomandra betaceae*	7
		1	Unknown primary parasitoid	*Aphis nerii*	*Tabernaemontana alba*	37
Pachyneuron aphidis		30	*Aphidius colemani*	*Aphis nerii*		24
		7		*Uroleucon (Lambersius) gravicorne*	*Coniza canadensis*	37
		2		*Aphis gossypii*	*Cyphomandra betaceae*	16
		3	*Aphidius colemani* and *Lysiphlebus testaceipes*	*Pentalonia nigronervosa*	*Costus pulverulentus*	37
		4	*Lysiphlebus testaceipes*	*Toxoptera citricidus*	*Citrus aurantium*	5
		1		*Aphis gossypii*	*Cyphomandra betaceae*	7
		23	Unknown primary parasitoid	*Aphis nerii*	*Tabernaemontana alba*	37
Signiphora sp.	Signiphoridae	1	*Lipolexis oregmae* and *Lysiphlebus testaceipes*	*Aphis illinoisensis*	*Vitis tiliifolia*	28
		1	*Lysiphlebus testaceipes*	*Toxoptera citricidus*	*Citrus aurantium*	5
Syrphophagus aphidivorus	Encyrtidae	14	*Aphidius colemani*	*Aphis nerii*	*Tabernaemontana alba*	24
		2		*Uroleucon (Lambersius) gravicorne*	*Coniza canadensis*	37
		1	*Lysiphlebus testaceipes* and *Lipolexis oregmae*	*Toxoptera citricidus*	*Citrus aurantium*	5
		1	*Lysiphlebus testaceipes*, *Aphidius colemani* and *Binodoxys* sp.	*Aphis gossypii*	*Cyphomandra betaceae*	39
		4	Unknown primary parasitoid	*Aphis nerii*	*Tabernaemontana alba*	37

Two other genera were reared in very small numbers: *Alloxysta* (1 specimen) and *Signiphora* (2 specimens). All *Alloxysta* species are hyperparasitoids of aphids whereas *Signiphora* are primary parasitoids or hyperparasitoids of various Sternorrhyncha (Hanson and Gauld, 2006). After concluding the present study 2 specimens of *Dendrocerus* sp. (Megaspilidae) were reared from *Sitobium avenae* on the grass *Pennisetum purpureum* (Heredia, Universidad Nacional Campus, 20.11.2014).

With respect to altitudinal distribution, it is worth noting that all hyperparasitoids reported here were obtained from sites above 900 m.a.s.l., which is in contrast to the primary parasitoides which were obtained from all altitudes (Zamora Mejías *et al.*, 2010). *Syrphophagus aphidivorus* occurs from 900 to 1700 m.a.s.l., *Pachyneuron aphidis* from 1000 to 2400 m.a.s.l., and *Asaphes californicus* from 1000 to 3200 m.a.s.l. The vast majority of *Alloxysta* that have been collected in Costa Rica occur at high altitudes (1600 m.a.s.l. and higher), although *A. luismii* was collected from yellow pan traps in a coffee plantation at 1200 m.a.s.l. (Ferrer-Suay *et al.*, 2011, 2013). The surprisingly low number of *Alloxysta* obtained in our study might be due to rather limited rearing of aphids from very high altitudes.

As noted in the introduction, the majority of Costa Rican aphids are probably exotic species, as are several of the primary parasitoids. With respect to the hyperparasitoids, it is possible that *Pachyneuron aphidis* and *Syrphophagus aphidivorus* are introduced species since both have cosmopolitan distributions (Noyes, 2014), but additional information is required to confirm this suggestion. *Asaphes californicus* is restricted to the New World (Gibson and Vikberg, 1998) and is possibly a native species. Eleven species of *Alloxysta* have been reported from Costa Rica and nine of these are known only from the neotropical region (Ferrer-Suay *et al.*, 2013), and thus nine out of eleven species are probably native. Further rearing of aphids from high altitudes is required to obtain host information for these *Alloxysta* species and to determine whether they are associated primarily with native species of aphids.

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