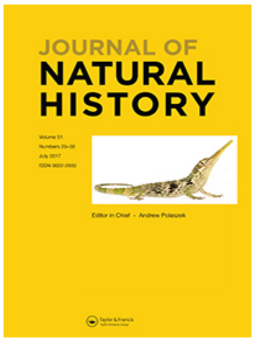

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Life cycles and host–parasitoid relationships of five species of Leucospis wasps in Argentina (Hymenoptera: Leucospidae)

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ABSTRACT
The genus *Leucospis* Fabricius is comprised of parasitoid wasps relatively uncommon in nature. Their immature stages develop on aculeate Hymenoptera, in particular solitary bees, but hosts are known for only around 25 *Leucospis* species (about 20% of 115–120 world species), so the true relationship of this family with bees is largely unknown. Here we report on individuals of five species of *Leucospis* wasps which emerged from nests of different bee and wasp species during distinct sampling periods during a trap-nesting programme, in two contrasting areas: agro-ecosystems and natural habitats in the Pampean region. Some of these nests were parasitised by *L. cayennensis* Westwood, *L. coxalis* Kirby, *L. egaia* Walker, *L. pulchriceps* Cameron and *L. signifera* Bouček. Our results expand the available information of host species for *L. cayennensis, L. coxalis, L. egaia* and *L. pulchriceps* and represent the first record of hosts associated with *L. signifera*. The hosts were only bee species of the genera *Centris, Tetrapedia* (family Apidae) and *Megachile* (Megachilidae). These species were more abundant in the natural reserve than in agro-ecosystems, suggesting that anthropogenic activities could negatively affect their populations. Most nests were attacked in one (43.7%) or two (40.7%) cells, but the remaining nests (16.5%) had more (up to seven cells). However, the position of the attacked cells was variable, suggesting that females of *Leucospis* species oviposit in recently built cells, and that the hatching of larvae is delayed, or that the first larval stage waits until the host larva reaches a sufficient size to attack.

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Introduction

The genus *Leucospis* Fabricius is comprised of large parasitoid wasps (8–12 mm). These species mimic wasps or bees (Bouček 1974), and are relatively uncommon. These wasps are larval parasitoids of aculeate Hymenoptera, and they attack, in particular, solitary

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bees (Apidae and Megachilidae), and less frequently solitary wasps (Sphecidae and Vespidae: Eumeninae) (Bouček 1974; Grissell 2007; Noyes 2016). One species was reported as an ectoparasitoid of an ichneumonid attacking a cerambycid beetle (Hesami et al. 2005). However, hosts are known for only around 25 *Leucospis* species (about 20% of 115–120 world species), so the true relationship of this family with bees is largely unknown (Grissell 2007). To attack the brood cell of their hosts, the females drill through the hardened cell walls with their atypical ovipositors, and the preimaginal instars develop as ectoparasitoids (Cooperband et al. 1999).

Bouček (1974) revised the world fauna of *Leucospis* and designated species-groups based on morphological characteristics. In the Neotropical Region, there are 44 species of *Leucospis*, and there are known hosts for 14 species (Hanson 2006). In Argentina only 13 are present (Loiácono et al. 2006), and there are records of host–parasitoid relationships for only 4 species, either in local populations or in other countries (Table 1).

Trap-nests are a very effective tool for studying activity and getting biological information on bees and wasps that nest in pre-existing cavities, and provide good evidence about associated parasitoids and/or cleptoparasites (Krombein 1967; Cooperband et al. 1999). A few studies have examined bees and wasps found in trap-nests in the Pampean region (Torretta and Durante 2011; Torretta et al. 2012, 2014), and their host–parasitoid interactions (Torretta 2014; Martinez & Torretta 2015). In this work, we present results of investigations carried out in two contrasting areas: agro-ecosystems and natural habitats. In the Pampas region, agriculture expanded quickly during the 20th century, transforming the landscape into a mosaic dominated by agricultural fields (de la Fuente et al. 2010; Medan et al. 2011). In the last decades, intensification of agricultural management imposed harsher constraints to the persistence of insect species (Medan et al. 2011). Thus, the studies in natural habitats can provide some data about species susceptible to anthropogenic disturbance.

Here, we report on individuals of five species of *Leucopis* wasps which emerged from nests of different bee and wasp species during distinct sampling periods. Specifically, the objective of this paper is to provide information about the life cycle of these five parasitoid wasp species in Argentina including (i) description of the host–parasitoid relationships, (ii) life cycles and emergence patterns, and (iii) provision of data about sex ratio and parasitism percentage.

Materials and methods

Study sites

The Río de la Plata grasslands are part of the most extensive biogeographic unit of the prairie biome in South America, and constitute one of the most important grasslands in the world (Medan et al. 2011). Currently, the landscape reveals an intense use of the land, annual crops being the predominant land-use (over 70%; Molina et al. 2014). Surveys were concentrated in two contrasting areas of the Pampas region: agro-ecosystems and a Natural Reserve (Figure 1). Within agro-ecosystems we placed trap-nests in 'San Claudio' farm (S 35°56′ W 61°12′), Carlos Casares, Buenos Aires province (hereafter SC) and in 'Anquilòo' farm (S 36°24′ W 64°48′), Toay, La Pampa province (hereafter AN, Figure 1). The landscape in SC is a mosaic of crop fields, sown pastures, and semi-natural grasslands used

Table 1. Argentine species of *Leucospis* with published reports of host species in local populations or in other countries.

		Hosts			
Species	Group-species	Species	Family	Reference	Country
L. cayennensis	*cayennensis*	*Centris analis*	Apidae	Cooperband et al. (1999)	Costa Rica
				Gazola and Garófalo (2003)	Brazil
		Centris bicornuta	Apidae	Cooperband et al. (1999)	Costa Rica
		Centris nitida	Apidae	Cooperband et al. (1999)	Costa Rica
		Centris vittata	Apidae	Cooperband et al. (1999)	Costa Rica
		Eualema meriana	Apidae	Cameron and Ramírez (2001)	Ecuador
		Tetrapedia curvitarsis	Apidae	Gazola and Garófalo (2009)	Brazil
		Tetrapedia diversipes	Apidae	Camillo (2005); Gazola and Garófalo (2009)	Brazil
L. egaia	*egaia*	*Centris bicornuta*	Apidae	Cooperband et al. (1999)	Costa Rica
L. hopei	*hopei*	*Megachile rancaguensis*	Megachilidae	Bouček (1974)	Argentina
		Trichothurgus laticeps	Megachilidae	Vitale and Vázquez (2017)	Argentina
L. pulchriceps	*egaia*	*Anthidium vigintipunctatum*	Megachilidae	Torretta (2015)	Argentina
		Megachile catamarcensis	Megachilidae	Torretta et al. (2014)	Argentina

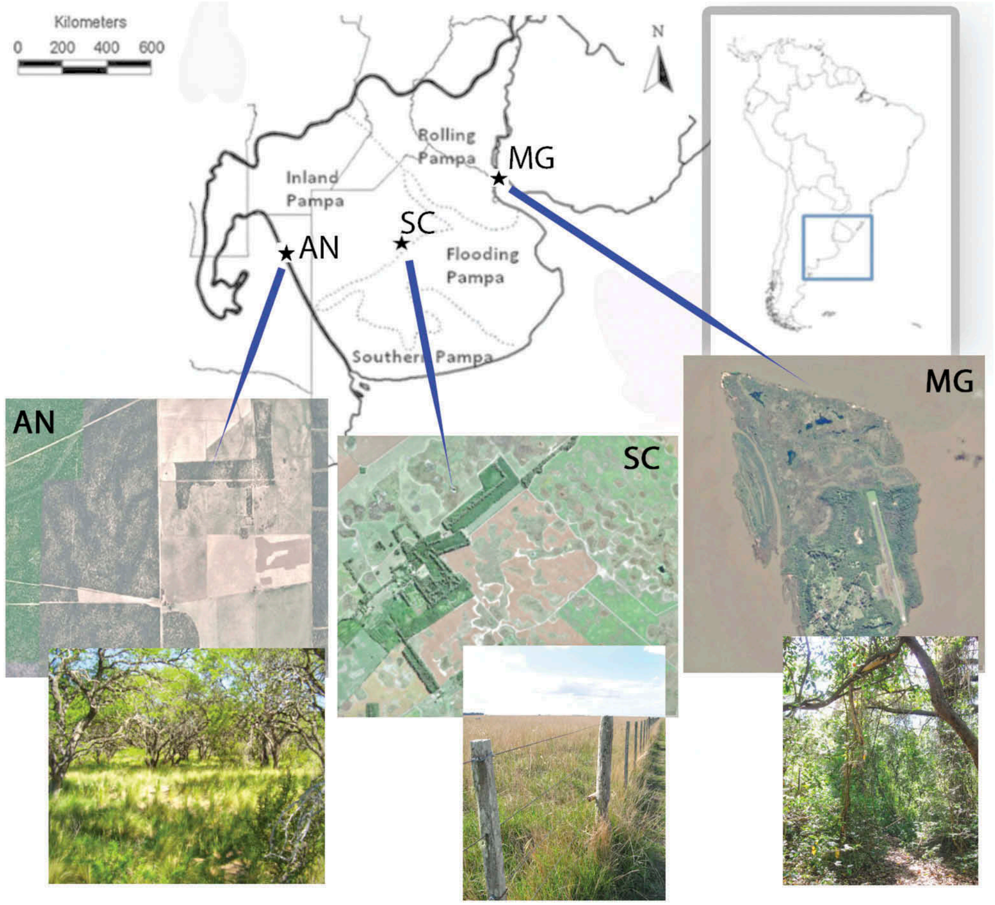

Figure 1. Location of the sampling sites (SC: San Claudio, AN: Anquilóo and MG: Martín García reserve) within the grasslands of Río de la Plata (the area surrounded by a thick line), with satellite images (altitude 5km), and representative photographs of the different vegetation structure at each site (Satellite images copyright Google Inc. 2013).

for livestock grazing. The main summer crops in this area are soybean (*Glycine max*), maize (*Zea mays*) and, to a lesser extent, sunflower (*Helianthus annuus*) and alfalfa (*Medicago sativa*) (Torretta et al. 2012). The climate is temperate sub-humid, with a mean annual precipitation of 1022 mm for the last 25 years. Mean monthly temperatures vary from 7.2° C in July to 23.8°C in January (Tognetti et al. 2010). The site AN is located in a transition zone between the Pampean grassland and the Espinal region, characterized by woodland dominated by 'Caldén' (*Prosopis caldenia*) with a perennial grass understory. The climate is dry-temperate, with a mean annual temperature of 15.5°C, the annual precipitation ranging between 500 and 600 mm (Cano 1998; González-Roglich et al. 2012). Production in AN is mixed farming with a predominance of extensive cattle production and controlled grazing. Here, the agricultural fragments were sown with alfalfa (*M. sativa*) and weeping lovegrass (*Eragrostis curvula*) as forage (Marrero et al. 2014).

We also worked in the multi-purpose 'Martín García' Natural Reserve island (S 34°11 W 58°14), Buenos Aires province. Martín García Island (hereafter MG) is located in the

Upper Rio de la Plata, south of the Uruguay River Delta. The island is slightly elliptical, elongated in a north-south direction, with a maximum length of 3380 m and average width of 1700 m (Lahitte and Hurrell 1994). The climate is temperate and humid, with an average annual temperature of 17ºC. The precipitation is around 1000 mm per year, and high humidity reaches an average of 81% in June and July (Núñez Bustos 2007). The particular geographical location of this multi-purpose Nature Reserve, and the possibility of exploitation for touristic purposes both make the island an important study area. According to Ringuelet (1981) MG is located in 'subtropical-Pampean ecotone', in zoogeographical terms. Eight green vegetation units can be distinguished: marginal jungle, xeromorphic forests, interior dunes, peri-urban forests, riparian forests, shrubberies and riparian grasses, mixed scrublands and reed beds (Lahitte and Hurrell 1994).

Collection of parasitised nests

Trap-nests used in this study consisted of hollow bamboo canes, which were cut so that a nodal septum closed one end of the cane (Aguiar and Garófalo 2004). Previously, each cane had been cut longitudinally and taped, and measured in total length (from the entry to the node), and outer and inner diameters in the entry (Torretta et al. 2012). Trap-nests were placed between November and March during four periods (Table 2), and were visited monthly. The number of trap-nests varied among sites and sampling periods (Table 2). In agro-ecosystems the trap-nests were arranged in bundles of 14 canes and the bundles were placed at intervals of 50–100 m on fence posts in field margins associated with diverse crops, semi-natural grassland and/or sown pasture. In MG, trap-nests were arranged in bundles of 15 canes (Table 2), and were placed in three different habitats: marginal jungle, interior dunes and peri-urban forests.

Each trap-nest was numbered and identified as to location, and date of placement. At each monthly visit, trap-nests with completed nests were removed, taken to the laboratory, and then replaced with a new bamboo cane of the same diameter. In the laboratory, the cells of each removed nest were separated in different plastic vials with cotton plugs and numbered from 1 to n (starting from the innermost). The cells were kept at room

Table 2. Description of the study sites in Argentina.

	Agro-ecosystems		Natural Reserve Martín García
Sites	Toay	Hortensia	
Geographic provinces	La Pampa	Buenos Aires	Buenos Aires
Geographic coordinates	S 36º 22′ W 64º 50′	S 35º 56′ W 61º 11′	S 34º 11′ W 58°14
Phytogeographic provinces	Ecotone Pampean grasslands and xeric forest	Inland Pampa	Subtropical-Pampean ecotone
Altitude (m asl)	310	90	10
Sampling dates /Number of trap-nest placed (bundles)	Nov-09 to Mar-10 /140(20) Nov-10 to Mar-11 /350(25)	Nov-09 to Mar-10 /140(20) Nov-10 to Mar-11 /350(25)	Nov-13 to Mar-14 /1080(72) Nov-14 to Mar-15 /1080(72)
Main economic activity	Cattle ranching	Agriculture	Touristic activity
Neighboring crops	pasture, alfalfa	Soybean, wheat, maize	none

temperature (ca. 15-25ºC) and observed weekly until the adults emerged. Since trap-nests were collected at monthly intervals, development time can only be estimated with an error of ± 15 days (Thiele 2005). In those nests where *Leucospis* spp. adults emerged, host species were determined. The total number of host cells, the position of attacked cells by *Leucospis* in each nest, and the emergence dates were also registered. For each host species, we calculated the percentage of parasitism as the number of parasitised host cells divided by the total number of host(s) cells (for each studied period). For each *Leucospis* species, we report the number and sex of emerged adults, estimated developmental time, host/s, material used by female host for nest construction, the percentage of parasitism and other parasitic species associated to bundle of trap-nests (Table 2).

Identification of *Leucospis* species

In order to determine *Leucospis* species we used Bouček (1974). In addition, we also had the opportunity to compare our specimens with those deposited at the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN) and at the Museo de La Plata (some identified by Bouček). Emerged specimens of *Leucospis* wasps and their bee hosts are deposited in the Entomological Collections of the Department of Botánica General of the Facultad de Agronomía, Universidad de Buenos Aires (FAUBA), and of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN).

Results

During the four sampling periods, a total of 1376 trap-nests (n = 69 in 2009–2010, n = 288 in 2010–2011; n = 424 in 2013–2014 and n = 595 in 2014–2015) were colonised by different bee species of the families Apidae and Megachilidae, and wasps of the families Crabronidae, Pompilidae, Sphecidae, and Vespidae (Eumeninae). Of these, only 32 nests (n = 1 in 2009–2010, n = 9 in 2010–2011, n = 14 in 2013–2014 and n = 8 in 2014–2015; Table 2) were parasitised by five species of *Leucospis* wasps: *L. cayennensis* Westwood, *L. coxalis* Kirby, *L. egaia* Walker, *L. pulchriceps* Cameron and *L. signifera* Bouček. The only hosts were bee species of the families Apidae and Megachilidae (Table 3).

Most nests had only 1 (43.7%) or 2 (40.7%) attacked cells, while the remaining nests (16.5%) had more (Table 3, 4). The species with the highest attack rate (i.e., with more attacked nests) were *L. cayennensis* and *L. egaia* (Table 3, 4). Moreover, females of most species attacked only one nest of each block, except one female (or possibly more females) of *L. cayennensis* that parasitized seven nests of *Centris tarsata* Smith in block no. 70, all of them in January 2014 (Table 4). On the other hand, the positioning of parasitized cells by females of different species of *Leucospis* was variable among nests (Table 4).

In the agro-ecosystems:in SC farm, seven individuals of *L. coxalis* emerged from one nest of *Megachile* (*Dactylomegachile*) sp. 1, two nests of *M.* (*Dactylomegachile*) *jenseni* Friese and two nests of *M.* (*Pseudocentron*) *gomphrenoides* Vachal (2010–2011). The estimated emergence time occurred in a range of around 7–10 months. The sex ratio was slightly higher for males (0.75/1).

Table 3. Species of *Leucospis* wasps rearing from nests of wasps and bees obtained in trap-nests in agro-ecosystems in Argentina, during several years of study.

Species	Nest number	Date Nest Collection	Host cells / *Leucopis* emerged (sex)	Date *Leucospis* emerged (range)	Estimated developmental range (months)	Hosts	Host cell partition	Percentage parasitism: parasitized cells /total cells of host species	Other parasitic species associated	Site
L. cayennensis Westwood	410	15 January 2014	2/2 (2 f)	30 January 2014 2 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance	10 (17/170)		MG
	1039	14 January 2014	4/2 (2 m)	31 January 2014 2 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1041	14 January 2014	4/1(f)	08 February14	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1043	14 January 2014	5/1 (m)	29 January 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1044	14 January 2014	6/3 (3 f)	26 January 2014 28 January 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1046	14 January 2014	7/3 (1 m, 2 f)	31 January 2014 5 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1047	14 January 2014	5/2 (2 m)	31 January 2014 5 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1049	14 January 2014	8/1 (f)	5 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
	1288	15 January 2014	7/2 (2 f)	30 January 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance			MG
L. coxalis Kirby	216	13 January 2011	6/1 (m)	2 December 2011	7 – 8	*Megachile* (*Dactylomegachile*) *jenseni*	Petals and mud	2.9 (4/135)		SC

(*Continued*)

Table 3. (Continued).

Species	Nest number	Date Nest Collection	Host cells / *Leucopis* emerged (sex)	Date *Leucospis* emerged (range)	Estimated developmental range (months)	Hosts	Host cell partition	Percentage parasitism: parasitized cells /total cells of host species	Other parasitic species associated	Site
	219	13 January 2011	5/2 (2 f)	9 December 2011 11 December 2011	10	*Megachile* (*Dactylomegachile*) sp. 1	Petals and mud		*Mellitobia* sp. (Hym. Eulophidae) *Coelioxys remissa* (Hym. Megachilidae)	SC
	238	24 February 2011	5/1 (m)	2 December 2011	7 – 8	*Megachile* (*Pseudocentron*) *gomphrenoides*	Petals and mud			SC
	296	13 April 2011	6/2 (1 f, 1 m)	11 December 2011 13 December 2011	8	*Megachile* (*Pseudocentron*) *gomphrenoides*	Leaves	1.7 (2/117)		SC
	349	24 February 2011	5/1 (m)	11 December 2011	9 – 10	*Megachile* (*Dactylomegachile*) *jenseni*	Petals and mud	1.3 (1/75)	*Mellitobia* sp. (Hym. Eulophidae)	SC
L. egaia Walker (2013–14)	170	16 April 2014	10/2 (2 f)	29 November 2014	7 – 8	*Megachile* (*Dactylomegachile*) sp. 2	Leaves	1.9 (4/204)		MG
	195	16 January 2014	6/2 (2 f)	31 January 2014 5 February 2014	0 – 1	*Megachile* (*Dactylomegachile*) sp. 2	Leaves			MG
	846	25 February 2014	7/5 (5 f)	25 March 2014 31 March 2014	0 – 1	*Megachile* (*Pseudocentron*) sp. 1	Leaves	5.4 (6/110)		MG
	976	25 February 2014	8/1 (f)	17 March 2014	0 – 1	*Megachile* (*Pseudocentron*) sp. 1	Leaves			MG
L. egaia Walker (2014–15)	5	19 April 2015	8/2 (2 f)	2 December 2015	7 – 8	*Megachile* (*Austromegachile*) sp. 1	Leaves	5.1 (2/39)		MG

(*Continued*)

Table 3. (Continued).

Species	Nest number	Date Nest Collection	Host cells / *Leucopis* emerged (sex)	Date *Leucospis* emerged (range)	Estimated developmental range (months)	Hosts	Host cell partition	Percentage parasitism: parasitized cells /total cells of host species	Other parasitic species associated	Site
	116	14 February 2015	10/2 (2 f)	30 November 2015 5 December 2015	9 – 10	*Megachile* (*Acentron*) sp. 1	Leaves	18.4 (9/49)		MG
	1129	19 April 2015	9/1 (f)	21 December 2015	7	*Megachile* (*Acentron*) sp. 1	Leaves			MG
	1209	19 April 2015	8/7 (6 f, 1 m)	11 November 2015 22 November 2015	7 – 8	*Megachile* (*Acentron*) sp. 1	Leaves			MG
	1377	19 April 2015	7/1 (f)	2 December 2015	7 – 8	*Megachile* (*Acentron*) sp. 1	Leaves			MG
	1243	19 April 2015	10/7 (6 f, 1 m)	2 December 2015 5 December 2015	7 – 8	*Megachile* (*Pseudocentron*) sp. 1	Leaves	5.4 (6/112)		MG
L. pulchriceps Cameron (2009–10)	145	14 January 2010	16/2 (2 m)	2 February 2010 3 February 2010	0 – 1	*Anthidium vigintipunctatum*	Trichomes	0.4 (2/482)		AN
L. pulchriceps Cameron (2010–11)	463	22 January 2011	9/2 (2 f)	15 November 2011 11 November 2011	9 – 10	*Anthidium vigintipunctatum*	Trichome	0.8 (1/131)	*Chrysis saltana* (Hym. Chrysididae) Eupelmidae (Hym.)	AN
	498	10 December /10	5/1 (f)	5 January 2011	0 – 1	*Megachile* (*Chrysosarus*) *catamarcensis*	Leaves and mud	3.4 (3/89)	*Huarpea fallax* (Hym. Sapygidae)	AN
	554	10 December 2010	5/1 (f)	27 December 2010	0 – 1	*Megachile* (*Chrysosarus*) *catamarcensis*	Leaves and mud		*Chrysis boutheryi* (Hym. Chrysididae) *Huarpea fallax* (Hym. Sapygidae)	AN

(*Continued*)

Table 3. (Continued).

Species	Nest number	Date Nest Collection	Host cells / *Leucopis* emerged (sex)	Date *Leucospis* emerged (range)	Estimated developmental range (months)	Hosts	Host cell partition	Percentage parasitism: parasitized cells /total cells of host species	Other parasitic species associated	Site
	581	4 April 2011	3/1 (f)	12 November 2011	7 – 8	*Megachile* (*Chrysosarus*) *catamarcensis*	Leaves and mud		*Anthrax oedipus* (Dip. Bombyliidae)	AN
L. signifera Bouček (2013–14)	506	15 January 2014	8/1 (f)	6 February 2014	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance	0.6 (1/170)		MG
L. signifera Bouček (2014–15)	973	16 December 2014	5/1 (f)	17 January 2015	0 – 1	*Centris tarsata*	Sand and oily agglutinating substance	0.3 (1/372)		MG
	976	19 April 2015	3/2 (2 f)	5 December 2015 7 December 2015	7 – 8	*Tetrapedia* sp.	Sand and oily agglutinating substance	12.5 (1/8)		MG

Abb.: f: female, m: male. Hym.: Hymenoptera, Dip.: Diptera; MG: Martin Garcia reserve, SC: San Claudio farm, and AN: Anquilóo.

Table 4. Positions of attacked cells in host nests.

Species	No. nest	No. block	Position of attacked cells	Total number of host cells
L. cayennensis Westwood	410	28	3, 4	5
	1039	70	1, 4	6
	1041	70	2	6
	1043	70	5	5
	1044	70	4, 5, 6	6
	1046	70	2, 4, 7	7
	1047	70	2, 5	5
	1049	70	6	8
	1288	28	3, 7	7
L. coxalis Kirby	216	16	6	6
	219	16	4, 5	5
	238	17	3	10
	296	21	4,5	5
	349	27	5	7
L. egaia Walker (2013–14)	170	12	1, 2	10
	195	13	5, 6	6
	846	57	1, 3, 5,6,7	7
	976	66	1	8
L. egaia Walker (2014–15)	5	1	1, 3	8
	116	8	1, 2	10
	1129	72	9	9
	1209	4	1, 2, 3, 4, 5, 6, 7	8
	1377	33	1, 2, 3, 4, 5, 7, 10	10
	1243	27	1	7
L. pulchriceps Cameron (2009–10)	145	11	7, 9	16
L. pulchriceps Cameron (2010–11)	463	33	3, 4	9
	498	35	3	5
	554	39	5	5
	581	41	1	5
L. signifera Bouček (2013–14)	506	34	3	8
L. signifera Bouček (2014–15)	973	65	1	7
	976	66	1, 3	5

In AN farm, during two consecutive years (2009–2010 and 2010–2011) we reared seven individuals of *L. pulchriceps* from two nests of *Anthidium vigintipunctatum* Friese (n = 1 in 2009–2010 and n = 1 in 2010–2011) and three nests of *Megachile* (*Chrysosarus*) *catamarcensis* Schrottky (all in 2010–2011). The estimated emergence time showed a bimodal pattern with a first peak within one month and a second one occurring in a range of around 7–10 months. The sex ratio was female-biased (2.5/1; Table 3).

In the period 2014–2015 in MG, we reared 17 individuals of *L. cayennensis* from 9 nests of *Centris tarsata*. All the nests were collected during early summer (January), when seven nests were grouped in one block, and the remaining nests in another/a different block (Table 4). These data could suggest either that one female was capable of ovipositing a large quantity of eggs, or that different females were attracted to the *Centris* nests (note that the percentage parasitism was 10%). Most nests attacked by females of this species exhibit two or more parasitized cells (Table 3). The sex ratio was higher for females (1.83/1).

Also in MG, during two consecutive seasons of study, 30 individuals of *Leucospis egaia* (n = 10 in 2013–2014 and n = 20 in 2014–2015) were reared from nests of *Megachile* (*Acentron*) sp. 1 (n = 4), *M.* (*Pseudocentron*) sp. 1 (n = 3), *M.* (*Dactylomegachile*) sp. 2, (n = 2) and *M.* (*Austromegachile*) sp. 1 (n = 1). One nest was collected in January, three others during February and the remainder six during April (Table 3). Estimated emergence time showed a bimodal pattern, although most individuals needed 7–10 months of development (Table 3). In both sampled periods, the sex ratio was strongly female-biased, all the adults emerged in the season 2013–2014 being females, and in a ratio of 9:1 during the season 2014–2015 (Table 3).

In MG we registered the first record for hosts of *Leucospis signifera* during two consecutive years (2013–2014 and 2014–2015). Four individuals of *L. signifera* (n = 1 in 2013–2014 and n = 3 in 2014–2015) were reared from two nests of *Centris tarsata*, and one *Tetrapedia* sp. nest. Although the number of obtained specimens was low, the estimated emergence time showed a bimodal pattern with 50% emerged within one month and other 50% in 7–8 months. All the emerged adults were females (Table 3).

Discussion

This study is the first report about host–parasitoid relationships and life-cycle data for these five species of *Leucospis* in the Pampean region. Our results expand the available information of host species for *L. cayennensis, L. coxalis, L. egaia* and *L. pulchriceps* and represent the first record of hosts associated with *L. signifera*. These species were more abundant in the natural reserve (MG) than in agro-ecosystems (SC and AN), suggesting that anthropogenic activities could negatively affect their populations.

For *L. egaia* and *L. cayennensis*, the number of emerged adults and attacked nests provide good information about their biological traits. Both species were reared from collected nests in Martín García reserve. The females of *L. cayennensis* only parasited cells of the oil-collecting bee *Centris tarsata* (Apidae: Centridini). Fritz and Genise (1980) were the first to record *Centris tarsata* as a host of *L. cayennensis*. However, several hosts have been recorded for this species in other studies: the oil-collecting bees *Centris bicornuta* Mocsáry, *C. nitida* Smith, *C. vittata* Lepeletier (Cooperband et al. 1999), *C. analis* (Fabricius) (Cooperband et al. 1999; Gazola and Garófalo 2003), and *Tetrapedia curvitarsis* Friese (Gazola and Garófalo 2009) and *T. diversipes* Klug (Camillo 2005; Gazola and Garófalo 2009), and the orchid bee *Eulaema meriana* (Olivier) (Cameron and Ramírez 2001). In our studied site, the adults of *L. cayennensis* emerged rapidly (within the first month) after collecting the nests in the early summer (January). This fact suggests a univoltine life cycle. Gazola and Garófalo (2003) reared adults of this species from *Centris analis* nests, and also reported a similar development time. Regarding the sex ratio, our results show a female-biased proportion (3.25:1), agreeing with Cooperband et al. (1999), who reported that only one third of the obtained specimens were male. *Leucospis cayennensis* has a wide distribution (from México to Argentina) and much is known of its life cycles and host–parasitoid relationships (Cooperband et al. 1999; Cameron and Ramírez 2001; Gazola and Garófalo 2003, 2009; Camillo 2005).

In our study, the females of *Leucospis egaia* attacked several species of *Megachile* bees, whose females used different materials (petals and mud or pieces of leaves) for building the brood cells. In another study in the Neotropical Region, *L. egaia* attacked *Centris bicornuta* (Apidae: Centridini) and an unidentified megachilid species in Costa Rica (Cooperband et al. 1999). Remarkably, the females can attack cells built with different materials, with consequent differences in texture and hardness. The studied population of this species shows a bimodal pattern of adult emergence (Table 3). In previous work carried out on *Leucospis egaia*, information on hosts is available, but there are no data on life cycles, due to the low number of specimens collected (Cooperband et al. 1999). We also reared individuals of *Leucospis signifera* in Martín García reserve. Because of the low number of specimens collected (n = 4) for this species, the life cycle data are not conclusive, but still provide novel information. The nests were collected in different months (January, February and April) and the development range for those specimens during the summer was less than a month, while for the nest collected in early autumn (April) the development range was 7–8 months, which shows a bivoltine life cycle in MG. This work represents the first published data of hosts and development times for *L. signifera*. The hosts of this species were oil-collecting bees of two different tribes (Centridini and Tetrapediini) in the family Apidae.

From the two agro-ecosystems studied we obtained a few individuals of *L. coxalis* (n = 7) and *L. pulchriceps* (n = 7). The literature review on *L. coxalis* reports data about their development on an unidentified species of megachilid (Bouček 1974). In our study, we found nests of three species of *Megachile* were attacked. The development period to adult emergence was between 7–10 months, regardless of the period of nests collection (January, February or April), suggesting that this species has a unimodal pattern of emergence. Here we found that the sex ratio is inclined slightly towards the males, and females of *L. coxalis* were able to attack nests built with petals/mud and leaves. Furthermore, we found other parasitoid species associated with nests attacked by *L. coxalis: Mellitobia* sp. (Eulophidae) associated with *M. jenseni*, and *M.* sp. 1 and *Coelioxys remissa* Holmberg (Megachilidae) with *Megachile* sp. 1.

Finally, the *Leucospis pulchripes* individuals were obtained from nests of *Anthidium vigintipunctatum* and *Megachile catamarcensis*, whose brood cells were built with different materials (trichomes and petals/leaves mixed with mud, respectively). The development time to adult emergence shows a bimodal pattern of emergence, the first peak within the nests collection month, and the second 7–10 months later. These periods of time seem to be related to the period in which the nest was built and collected, with one generation with adults emerging in summer (December-January), and the second one with adults emerging during the following spring, having spent the winter as post-defecating larvae or prepupae, from nests collected in April. These data suggests a bivoltine life cycle of *L. pulchripes* in our study site. The sex ratio was female-biased. We also found other parasitoid species associated with nests attacked by females of *L. pulchripes*: the wasps *Chrysis saltana* Bohart (Chrysididae) and one species of Eupelmidae in nests of *A. vigintipunctatum*; and the wasps *Huarpea fallax* (Gerstaecker) (Sapygidae), and *Chrysis boutheryi* Brèthes (Chrysididae), and the bee fly *Anthrax oedipus* Fabricius (Bombyliidae) in nests of *M. catamarcensis*. Strikingly, one female of *L. pulchripes* and one female *C. boutheryi* emerged from a single cell of *M. catamarcensis* (Torretta 2015).

Very little is known about sex ratio in many parasitoid species (Yokoi et al. 2012) and sex ratio may vary between sites and years (Krombein 1967). Therefore, more data should be obtained to clarify sex-ratio dynamics in these species.

When it comes to quantity and positioning of cells attacked by these *Leucospsis* species, our results do not show a clear pattern. Based on dissections of marked cells in which *Leucospis* were observed ovipositing, Cooperband et al. (1999) comments that 'the females only attack cells in which the mature larvae had at least begun to spin a cocoon' and 'leucospid eggs were always located inside the cocoons, either on the surface of a host larva still finishing its cocoon, a prepupa, or a pupa'. Also, they mention that 'in other randomly dissected nests, all (larvae or pupae) were within the cocoon of a bee' and suggests that due to 'the failure of finding *Leucospis* larvae on younger stages of bee larvae' these parasitoid wasps do not attack early stages of their hosts. Nevertheless, Gazola and Garófalo (2003) observed that attacks of *L. cayennensis* on host species nesting in cardboard trap-nests varied, and comments that 'the eggs were placed inside the host cocoons attached to lateral wall of cocoon, to cellular partition, or on surface of the host'. Our observations were made on nests with lineal series of cells, and we believe that females of *Leucospis* spp. oviposit in recently built cells, and that the hatching of larvae is delayed, or that the first larval stage waits until the host larvae reaches a sufficient size to attack. More detailed observations will support or reject our suggestion.

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