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Distribution, abundance and persistence of species of *Orasema* (Hym: Eucharitidae) parasitic on fire ants in South America

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ABSTRACT

Parasitoid wasps of the genus *Orasema* Cameron have been considered as potential candidates for biological control of imported fire ants in the United States. Surveys were conducted for their occurrence in fire ant colonies across southern South America. In Argentina, 443 ant colonies were excavated at 57 sites and 11 positive sites were revisited to monitor the field persistence. In Paraguay, Bolivia and Uruguay, 288 colonies were examined in the field in 16 sites. *Orasema simplex* Heraty was the most abundant species, and found in 63.7% of the total parasitized colonies (*n* = 72). *Orasema xanthopus* (Cameron) and *Orasema salebrosa* Heraty were found at four sites in Argentina. In Bolivia, *Orasema pireta* Heraty was found at one site and parasitizing an unidentified *Solenopsis* species. Two new host species for *Orasema* aenea Gahan was found parasitizing fire ants for the first time. The parasitoids persisted at 36.4% of the positive sites, most of them in rural habitats.

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1. Introduction

The red and black imported fire ants, Solenopsis invicta Buren and Solenopsis richteri Forel, are important agricultural and urban pests in the United States (Lofgren et al., 1975; Jouvenaz, 1990; Vinson, 1997; Morrison, 2002). Fire ants were accidentally introduced from South America in the early 1900s (Loding, 1929), and apparently free of natural enemies present in their homeland (Porter et al., 1997). Since the 1970s, several surveys were carried out in South America to determine the diversity and abundance of fire ant natural enemies, in an effort to explore potential biocontrol agents for use in the United States. Over 35 natural enemies were found (Jouvenaz, 1983; Wojcik, 1990), including pathogens (Avery et al., 1977; Briano et al., 1995a,b), parasites (Jouvenaz and Wojcik, 1990; Jouvenaz et al., 1988), parasitoids (Porter and Pesquero, 2001; Porter et al., 1995a,b; Williams and Banks, 1987; Williams et al., 1973; Wojcik et al., 1987) and predators (Whitcomb et al., 1973; Wojcik and Naves, 1992; Wojcik et al., 1977). From them, two species of microsporidian pathogens (Briano et al., 1995a,b, 2002; Oi et al., 2005; Williams et al., 1999), several species of phorid flies (Calcaterra et al., 2005; Orr

parasitic ant (Briano et al., 1997; Calcaterra et al., 1999), and a mermithid nematode (Poinar et al., 2007, Porter and Varone unpublished data) have been under study as potential control agents. More recently, other entomopathogens have been discovered (Oi and Valles, 2009), including a neogregarine (Pereira et al., 2002), a fungus (Pereira, 2004), three viruses (Valles et al., 2004; Valles and Hashimoto, 2009; Valles et al., 2009), and a bacteria (Shoemaker et al., 2000). Eucharitid wasps in the genus *Orasema* Cameron (Oraseminae) belong to the complex of natural enemies attacking fire ants (Lof-

et al., 1995; Pesquero et al., 1995; Porter 1998, 2000), a congeneric

belong to the complex of natural enemies attacking fire ants (Lofgren et al., 1975; Jouvenaz, 1990; Williams and Whitcomb, 1974; Wojcik, 1990; Heraty, 1994b; Heraty et al., 1993). However, little is known about their occurrence, hosts, ecology, and perhaps most importantly, their impact on fire ants.

Species of *Orasema*, like other eucharitids, are small wasps that parasitize ant brood (Das, 1963; Johnson et al., 1986; Williams and Whitcomb, 1974; Heraty et al., 1993). Adult females lay their eggs into a wide range of host plants (Varone and Briano, 2009). The active emerging larvae (planidia) attach themselves to foraging ant hosts or to hemipteran or thysanopteran immatures (ant prey), which both allow them to be carried into the nest (Clausen, 1941; Heraty et al., 1993). Inside the nest, *Orasema* develops first as an endoparasitoid of the ant larva, and upon pupation of the





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ant host, completes development as an ectoparasitoid (Heraty 1994a, 2000; Heraty et al., 1993). While associated with the brood, larvae and pupae of *Orasema* either assimilate or produce compounds that mimic the cuticular hydrocarbon profile of their ant host, thus avoiding detection (Vander Meer et al., 1989). Pupation occurs within the brood pile, followed by adult emergence within the ant nest, and exiting for mating and oviposition (Clausen, 1941; Johnson, 1988).

Fifty-five species of *Orasema* have been described worldwide (Heraty, 1994a; Heraty, 2002). Neotropical *Orasema*, with more than 200 species estimated, are very poorly known (Heraty, unpublished). In Argentina, 11 species have been reported, 3 of which were found as parasitoids of fire ants at sites in Buenos Aires, La Pampa, and some of the northwestern provinces (Heraty et al., 1993; Heraty, 1994b). The occurrence of *Orasema* parasitizing *S. invicta* and *S. richteri* in Argentina has not been studied. The objective of this work was to determine the distribution and abundance of *Orasema* species attacking fire ants in southern South America and to evaluate their temporal prevalence in Argentina.

2. Materials and methods

2.1. Surveys

In Argentina, field surveys for *Orasema* were conducted from February 2005 to May 2007. Surveys followed the known distribution of *S. invicta* and *S. richteri* (Trager, 1991; Ross and Shoemaker, 2005), including eastcentral and northeastern Argentina (provinces of Buenos Aires, Entre Ríos, Corrientes, Misiones, Santa Fe, Formosa and Chaco). In addition, four localities in northcentral and northwestern Argentina were sampled (three in the province of Santiago del Estero and one in Salta). Most surveys were conducted every year from October to May, since brood production takes place only during warmer favorable conditions (Markin and Dillier, 1971). Additional samplings were carried out in Paraguay in August 2006, Bolivia in December 2007 and Uruguay in March 2008.

2.2. Collection method

In Argentina, 443 colonies of Solenopsis were excavated at 57 sites distributed every 50-100 km apart along paved or dirt roadsides, pastures, camping areas and parks. Only colonies with brood were sampled. When possible, eight colonies were collected at each site and placed in 8-l buckets dusted with talc to prevent ants from escaping. Geographic positions were recorded with a Garmin III GPS unit. Once in the laboratory, excavated colonies were separated from the soil by flotation (Banks et al., 1981) and the brood isolated using sorting sheets (Oi et al., 2008). Brood was examined under a dissecting scope for the presence of parasitoids. Any larvae or pupae of Orasema found inside the nests were transferred back to a fragment of the original host colony, consisting of 100-200 workers and a small amount of brood, held within a plastic vented container with food and humidity sources. The containers were kept at 30 ± 2 °C in rearing chambers and checked periodically until development of the brood was completed. Emerged adults of Orasema were separated from the host colony and kept in 96% ethanol for identification.

A different collection method was used in the surveys carried out in Paraguay, Uruguay and Bolivia. After excavating fire ant colonies, they were examined on site. Colonies were placed in talcdusted trays ($50 \times 40 \times 12$ cm), and were inspected by hand. The surveys involved sampling sixteen sites and examining 288 ant colonies. Adults found mixed with the brood were collected and preserved in 96% ethanol for identification.

2.3. Persistence of Orasema

In Argentina, 11 positive sites were revisited at least a second time to assess the parasitoid persistence. In Corrientes six sites were revisited, in Entre Ríos three, and in Buenos Aires, two. In addition, the Corrientes Biological Station (CBS) and Concepción del Uruguay (CDU) were chosen to repeatedly sample from February 2005 to April 2007 to determined the long-term field persistence. In all cases, more than five *Solenopsis* colonies were excavated per visit for laboratory examination.

Pearson correlation was performed between the proportion of parasitized colonies with *Orasema* and the number of individuals found inside the colonies for the periodical sampling of CBS and CDU. The proportion of parasitized colonies p and the number of individuals *i* were transformed using $\arcsin \sqrt{p}$ and \sqrt{i} , respectively.

2.4. Identification

Fire ant species identification was determined by gas chromatography analysis of cuticular hydrocarbon and venom alkaloids (Vander Meer et al., 1985) at the USDA-ARS-CMAVE Gainesville, FL. All adult Orasema parasitoids were identified by Heraty and Varone using Heraty et al. (1993), and compared to the original type material. Differences in species are very subtle and initial identifications based on morphology were confirmed by comparing sequence data obtained from one or more specimens at each site (Ortiz, Varone, Heraty and Hawks, unpublished). ITS2 sequence differences were used, with each species being fixed for a particular haplotype. Some specimens remained unidentified (Orasema sp.) because immature parasitoids failed to develop into adults. Vouchers specimens are maintained at the Entomology Research Museum (ERM), University of California, Riverside, CA, the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and the USDA-ARS Biological Control Laboratory, Hurlingham, Argentina.

3. Results and discussion

3.1. Surveys

In Argentina, Orasema was found parasitizing Solenopsis spp. in 60 colonies (13.5%), distributed over 24 (42.1%) sites (Fig. 1, Table 1). At positive sites, Orasema was found in 31.1% (range 12.5–100% per site) of the colonies. The number of Orasema individuals inside the ant colonies was very low, with a maximum of 96 specimens per nest, including unfed planidia, maturing larvae, pupae and newly emerged adults. In Uruguay, Paraguay and Bolivia, 3 (75%), 1 (50%) and 1 (9.1%) of the sites were positive for Orasema, with 3.3, 33.3 and 18.8% of the colonies parasitized at a positive site respectively (Table 2). Collections outside Argentina did not involve detailed brood examination, and low rates of within-colony parasitism might have been underestimated. On the other hand, Wojcik (1988) found Orasema in Brazil in approximately 40% of the colonies (*n* = 1502 colonies processed). However, comparisons are not valid since collection methods, collectors and sampling efforts differed from our study. The overall parasitism rate of Orasema (13.5% of the examined colonies) was intermediate relative to other arthropod parasites of fire ants surveyed in South America: the parasitic congeneric ant Solenopsis daguerrei (Santschi) was found in 1.4% of the colonies examined in the field (Briano et al., 1997) and the phorid flies Pseudacteon spp. were attracted to 51% of open and disturbed nests (Calcaterra et al., 2005).

In Argentina, the localities of Loreto (Sgo. del Estero) and Roldán (Santa Fe) had 100% of the colonies parasitized, but only four and three colonies were collected. Although *Orasema* was not found

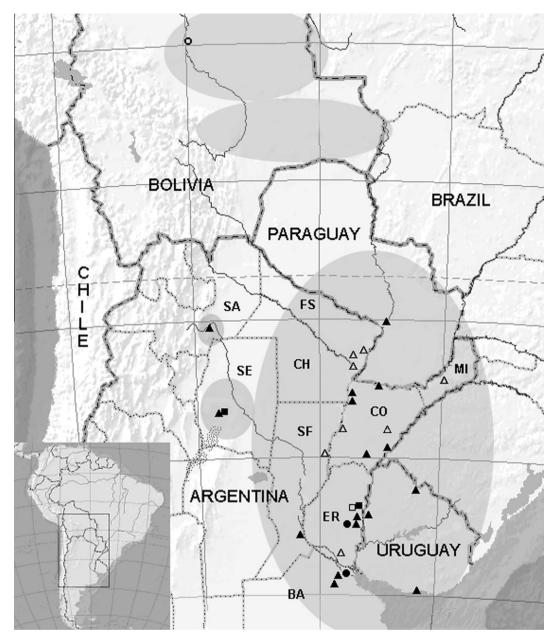


Fig. 1. Distribution of *Orasema simplex* (\blacktriangle), *O. xanthopus* (\blacksquare), *O. aenea* (\Box), *O. salebrosa* (\bullet), *O. pireta* (\bigcirc) and *Orasema* sp. (Δ) parasitizing *Solenopsis* spp. in Argentina, Bolivia, Paraguay and Uruguay. Shaded area was surveyed, including the provinces of Buenos Aires (BA), Entre Ríos (ER), Corrientes (CO), Misiones (MI), Formosa (FS), Salta (SA), Santiago del Estero (SE), Chaco (CH) and Santa Fe (SF) in Argentina.

in the Chaco province, it was collected in Villa Mansilla, very close to the border between Chaco and Formosa. The highest occurrences of *Orasema* were observed in the provinces of Entre Ríos, Buenos Aires, and Corrientes, being present in 62.5, 60.0 and 53.8% of the sites respectively. In contrast, Misiones province showed a low occurrence of positive sites (12.5%). The wide variety of habitats and geographic areas where *Orasema* occurs suggests that it is a common parasitoid of fire ants. In Argentina, it was found in three phylogeographic regions (Cabrera, 1971): the Pampas, with warm temperate climate and step grass as dominant vegetation; Chaco with a continental climate, summer precipitation, mostly shrublands; and Espinal with great temperature variations, high average precipitation and xerophytic forests as characteristic vegetation.

Five fire ant species hosted Orasema during the surveys: S. invicta, S. richteri, Solenopsis quinquecuspis Forel, Solenopsis macdonaghi Santschi, and an unidentified *Solenopsis* sp. (Tables 1 and 2). *S. invicta* was the most prevalent fire ant species in Argentina, and was therefore sampled the most. Of the 443 examined colonies, 350 (79.0%) were *S. invicta*, 66 (14.9%) were *S. richteri* and the remaining 27 (6.1%) *S. quinquecuspis.* The latter was found mainly in Entre Ríos and at one site in Corrientes (Table 1). Outside Argentina, the unidentified *Solenopsis* sp. was found parasitized in Bolivia and *S. invicta* in Paraguay. In Uruguay, from 151 checked colonies, 102 (67.6%) were *S. invicta*, 31 (20.5%) were *S. richteri* and 18 (11.9%) were *S. macdonaghi.*

In Argentina, four *Orasema* species were found parasitizing fire ants, *Orasema simplex* Heraty, *Orasema xanthopus* (Cameron), *Orasema salebrosa* Heraty, and *Orasema aenea* Gahan. In Paraguay and Uruguay, only *O. simplex* was present, and in Bolivia *Orasema pireta* Heraty was found inside colonies of an unidentified species of *Solenopsis* (Fig. 1, Tables 1 and 2).

Table 1

Positive sites with Orasema spp. in Argentina.

Province	Coordinates		No. collected colonies	No. parasitized colonies (%)	Orasema sp.	Host species	Total specimens collected
Locality	S	W					
Formosa							
Formosa	26° 08.425'	58° 09.367'	5	1 (20.0)	Orasema sp.	S. invicta	1
Herradura	26° 30.879′	58° 17.095'	11	4 (36.4)	Orasema sp.	S. invicta	8
Villa Mansilla	26° 39.194'	58° 37.824′	7	1 (14.3)	Orasema sp.	S .invicta	1
Salta							
J.V. Gonzalez	25° 14.612′	64° 23.738′	6	2 (30.3)	O. simplex	S. invicta	25
Misiones							
A. del Valle	27° 05.342′	54° 57.066′	8	1 (12.5)	Orasema sp.	S. invicta	5
Corrientes							
Yahape	27° 22.704′	57° 39.330'	8	1 (12.5)	O. simplex	S. invicta	11
Costa Paraiso	27° 27.304′	58° 40.820'	7	1 (14.3)	O. simplex	S. invicta	24
CBS	27° 33.173′	58° 40.771'	14	4 (28.6)	O. simplex	S. invicta	20
Santa Lucia	28° 54.902′	59° 05.352'	13	2 (15.4)	Orasema sp.	S. invicta	18
Torrent	28° 58.104′	57° 13.288'	7	1 (14.3)	Orasema sp.	S. invicta	1
P. de los Libres	29° 36.771′	57° 13.288'	8	3 (37.5)	O. simplex	S. invicta	89
Curuzu Cuatia	29° 51.679′	58° 04.165′	8	1 (12.5)	O. simplex	S. quinquecuspis	1
Sgo. del Estero							
Brea Pozo	28° 16.014′	63° 57.391′	9	5 (55.6)	O. simplex	S. invicta	106
Cdad. de Loreto	28° 19.365'	$64^{\circ} \ 08.018'$	4	4 (100.0)	O. xanthopus	S. invicta	115
Santa Fe							
Alejandra	29° 49.543′	59° 48.602'	11	3 (27.3)	Orasema sp.	S. invicta	3
Roldan	32° 48.666′	60° 51.345′	3	3 (100.0)	O. simplex	S. invicta	192
Entre Rios							
Concordia	31° 52.585′	58° 01.751'	5	2 (40.0)	O. simplex	S. invicta	7
			3	1 (33.3)	O. simplex	S. quinquecuspis	4
Palma Sola	31° 41.845′	58° 15.991'	12	5 (41.7)	O. xanthopus	S. quinquecuspis	18
				1 (8.3)	O. aenea	S. quinquecuspis	
Cnia. Hughes	32° 22.785′	58° 16.678'	8	5 (62.5)	O. simplex	S. invicta	65
C. del Uruguay	32° 27.761′	58° 14.196'	8	3 (37.5)	O. simplex &	S. invicta	8
					O. salebrosa		
Medanos	33° 25.507′	59° 05.202'	8	1 (12.5)	Orasema sp.	S. quinquecuspis	19
Buenos aires							
Mercedes	34° 34.330′	59° 21.296'	10	2 (20.0)	O. simplex	S. richteri	4
Otamendi	34° 10.848'	58° 52.247'	6	1 (16.7)	O. salebrosa	S. richteri	3
Capilla del Sr.	34° 22.154′	59° 14.582'	4	2 (50.0)	O. simplex	S. richteri	13
Total positive sites	24		193	60 (31.1)			761
Total surveyed sites	57		443	60 (13.5)			
Total positive sites	24	55 11.552	193	60 (31.1)	e. simplex	S. Henterr	

Table 2

Positive sites with Orasema spp. in Bolivia, Paraguay and Uruguay.

Country Locality	Coordinates		No. checked colonies	No. parasitized colonies (%)	Orasema sp.	Host species
	S	W				
Bolivia						
Trinidad	14° 49.985'	64° 54.235'	16	3 (18.8)	O. pireta	Solenopsis sp.
Paraguay					-	
Asuncion	25° 14.169'	57° 29.750'	12	4 (33.3)	O. simplex	S. invicta
Uruguay					-	
Atlantida	34° 41.084′	55° 48.066′	68	2 (2.9)	O. simplex	S. richteri
				1(1.5)	O. simplex	S. macdonaghi
Paysandu	32° 20.056'	58° 03.785'	52	1 (19)	O. simplex	S. invicta
Lunarejo	31° 11.176′	55° 54.260′	32	1 (3.1)	O. simplex	S. invicta
Subtotal			152	5 (3.3)		
Total positive sites	5		180	12 (6.7)		
Total surveyed sites	16		288	12 (4.2)		

O. simplex was the most abundant species parasitizing *Solenopsis* spp. in Argentina, Paraguay and Uruguay (44 from 69 parasitized colonies). *O. aenea* and *O. xanthopus* were found in Palma Sola (Entre Ríos), and the latter was also present in Loreto (Santiago del Estero). *O. salebrosa* was found in one *S. invicta* nest in Concepción del Uruguay (Entre Ríos), co-occurring with a second species (*O. simplex*), and in one colony in Otamendi, Buenos Aires. *O. pireta* was found parasitizing three fire ant colonies (*Solenopsis* sp.) in Trinidad, Bolivia.

So far, eleven species of *Orasema* have been described for Argentina, three of which are known to parasitize fire ants, *O. simplex*, O. xanthopus and O. salebrosa. O. simplex and O. salebrosa were described from S. richteri collected in Buenos Aires (Heraty et al., 1993). The data reported here extended the distribution of O. simplex in Argentina, Uruguay and Paraguay and revealed new associations with S. invicta, S. quinquecuspis and S. macdonaghi for O. simplex, with S. invicta for O. salebrosa and with an undescribed Solenopsis for O. pireta. Previously, O. xanthopus was found parasitizing S. invicta and other unidentified fire ant species of the Solenopsis saevissima complex in Brazil (Heraty, 1994b; Heraty et al., 1993; Vander Meer et al., 1989; Williams, 1980; Williams and Whitcomb, 1974; Wojcik, 1986, 1988, 1989, 1990; Wojcik et al., 1987) and *S. richteri* in Uruguay (Silveira-Guido et al., 1964) and Argentina (Williams, 1980). Ours are the first accurate records of *O. xanthopus* parasitizing *S. invicta* and *S. quinquecuspis* in Argentina. *O. aenea* was previously known to oviposit into the leaves of *Ilex paraguayensis* St. Hill (Aquifoliaceae) and *Olea europaea* L. (Oleaceae) (Nicolini, 1950 and Parker, 1942 respectively), but the ant host remained unknown; the current study is the first record for this species parasitizing fire ants.

3.2. Persistence of Orasema

The persistence of *O. simplex* in a second sampling of the Argentina sites was observed in four (36.4%) of the 11 revisited sites (Table 3). In nine of these sites, revisits were conducted between one and ten months later. The other two sites (CBS and CDU) were

sampled along 26 and 17 months respectively. In CBS, *O. simplex* was always present parasitizing fire ant colonies, with a parasitism ranging between 12.5 and 52.9% of the colonies. In CDU the parasitism was highly variable, and *Orasema* was even absent during some sampling periods (Fig. 2). The percentage of parasitized colonies and the number of specimens of *Orasema* inside the ant colonies was positively correlated in CBS (r = 0.56, P = 0.004), but not in CDU (r = 0.1, P = 0.5). In both sites, the abundance of *Orasema* was low between February and October/November 2005. From December 2005, the abundance increased and remained moderated with some oscillations at CBS but at CDU the presence of the parasitoid showed a cyclic occurrence.

O. simplex has a broad distribution across Argentina, but with variable field persistence. It was found parasitizing fire ants both in highly anthropic modified environments (roadsides and cities) and rural or unmanaged lands (pastures and abandoned fields).

Table 3

Persistence of Orasema simplex in positive sites in Argentina.

Province	Coordinates		Collection date	No. collected colonies	No. parasitized colonies (9
Locality	S	W			
Corrientes					
Curuzu Cuatia	29° 51.679′	58° 04.165′	29-Mar-05	8	1 (12.5)
			17-Oct-05	7	0
			4-Jan-06	11	0
Yahape	27° 22.704′57°	39.330′	5-Apr-05	8	1 (12.5)
			17-Oct-05	6	0
			3-May-06	5	0
P. de los Libres	29° 36.771′	57° 13.288'	20-Oct-05	8	3 (37.5)
			17-Nov-05	7	3 (42.8)
			4-Jan-06	7	0
CBS	27° 33.173'	58° 40.771'	24-Feb-05	14	4 (28.6)
			3-Mar-05	8	1 (12.5)
			30-Apr-05	7	1 (14.3)
			17-Oct-05	9	2 (22.2)
			12-Nov-05	7	1 (14.3)
			30-Nov-05	11	5 (45.4)
			4-Jan-06	15	6 (40.0)
			23-Feb-06	10	4 (40.0)
			28-Apr-06	17	9 (52.9)
			27-Aug-06	8	3 (37.5)
			8-Dic-06	11	6 (54.5)
			21-Apr-07	8	3 (37.5)
Costa Paraiso	27° 27.304′	58° 40.820'	6-Dec-05	7	1 (14.3)
Santa Lucia			4-Jan-06	7	0
			8-Dec-06	13	2 (15.4)
			24-Feb-07	8	1 (12.5)
Entre Rios					
Concordia	31° 41.845′	58° 15.991'	29-Mar-05	8	3 (37.5)
			7-May-05	7	0
			16-Nov-05	8	0
			5-Jan-06	10	0
CDU	32° 27.761′	58° 14.196'	4-Mar-05	8	3 (37.5)
			7-May-05	8	0
			16-Nov-05	8	0
			5-Jan-06	7	0
			24-Feb-06	8	4 (50.0)
			29-Apr-06	6	0
			27-Aug-06	7	3 (42.9)
			26-Sep-06	13	1 (7.79
Colonia Hughes			28-Aug-06	8	5 (62.5)
			25-Feb-07	10	10 (100.0)
Buenos Aires					
Otamendi	34° 10.848'	58° 52.247'	17-Mar-05	6	1 (16.7)
			15-Dec-05	9	0
Mercedes	34° 34.330′	59° 21.296′	24-Jan-06	8	0
			2-Mar-06	7	0
			8-Apr-06	10	2 (20.0)
			5-Jun-06	12	0
			21-Nov-06	11	0
Total				307	55 (17.9)

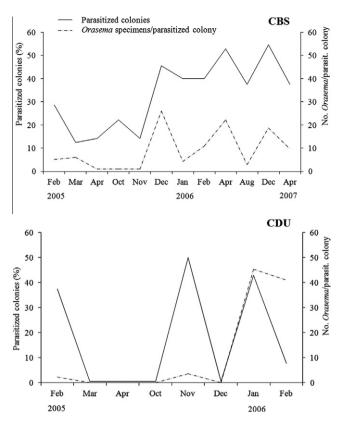


Fig. 2. Persistence of *O. simplex* in the Corrientes Biological Station, Corrientes (CBS) and Concepción del Uruguay, Entre Ríos (CDU), Argentina.

However, the proportion of positive sites in more rural environments was higher than in more anthropic sites. From 37 anthropic sampled sites, *Orasema* was found in 8 (21.6%), and from 20 rural collecting sites, it was present in 16 (80.0%). The differences in landscape vegetation between the anthropic and rural environments could explain the differences in the presence of *Orasema*. The parasitoid community structure could be related to the landscape complexity (Price, 1991). Thus, the abundance, diversity and persistence of plants suitable for oviposition present in more natural sites are likely to perpetuate and enhance the populations of *Orasema* in a particular place. Our findings would support the argument that landscape complexity associated with natural habitats, as opposed to more simplistic anthropic, supports a generally higher diversity and abundance of parasitoids (Bianchi et al., 2006; Heraty, 2009).

In summary, *Orasema* wasps occur over a broad geographic area, with a low to medium prevalence of parasitism, low rate of within-colony parasitism and cyclic persistence at most sites. *O. simplex* was the predominant parasitoid across both Argentina and Uruguay, and it does not appear to be host specific within the *S. saevissima* complex. *Orasema* appears to be more common in less modified areas possibly because of habitat complexity offering both a more diverse and more consistently available source of oviposition substrates. Additional work on the host range and impact on plants used for oviposition of *Orasema* females is needed to completely evaluate this parasitoid as a biological control agent against fire ants in the United States.

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