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## Life cycle of *Huarpea fallax* (Hymenoptera: Sapygidae) in a xeric forest in Argentina

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This study describes the life cycle of *Huarpea fallax* (Hymenoptera: Sapygidae) in a xeric forest in La Pampa province, Argentina. This cleptoparasitic wasp attacks the nests of two species of leaf-cutter bees: *Megachile catamarcensis* and *Anthidium vigintipunctatum*, both belonging to the family Megachilidae. Nests of these bee species were obtained during a trap-nesting programme. Adult emergence showed a unimodal pattern indicating a univoltine life cycle. The period from egg-laying to adult emergence lasted for 10–13 months; however, one female took about 2 years to emerge, suggesting parsivoltinism. Most females attack one cell per host nest, the outermost cells being the ones most parasitized. However, the position of the attacked cells was variable. In this paper, although there were insufficient data to prove a correlation, the data suggest a positive trend between body size of sapygid wasps and their host bees.

**Keywords:** *Anthidium vigintipunctatum*; host–parasite interaction; *Megachile catamarcensis*; Megachilidae; trap nest

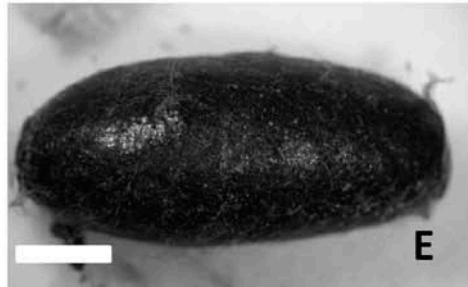
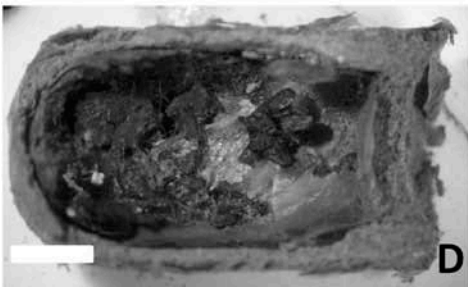
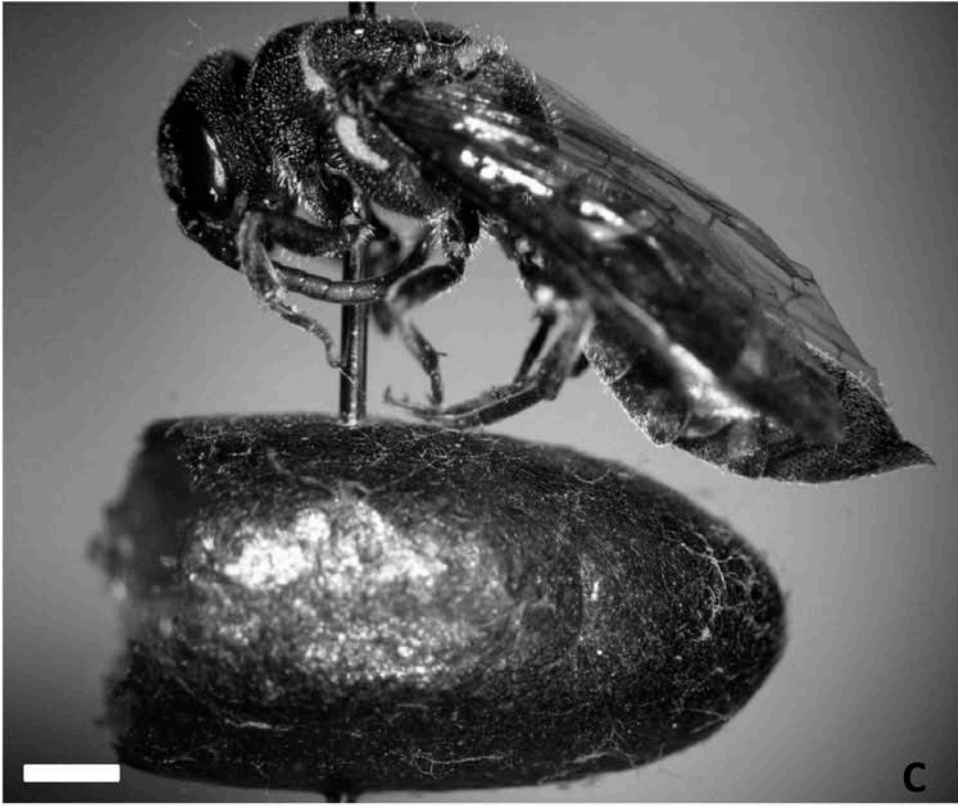
### Introduction

Sapygidae is a small, widely dispersed family, absent only in the Australian Region. This family comprises about 80–90 species, which are divided into two subfamilies: Fedtschenkiinae and Sapyginae (Pate 1947). All species are solitary and their larvae are cleptoparasitic on megachilid and apid bees (Pate 1947). In the Neotropical Region, Sapyginae are represented by three genera: *Araucania* Pate, *Huarpea* Pate and *Sapyga* Latreille (Brothers 2006). The genus *Huarpea* contains four species confined to southern South America. The strong, well-developed occipital carina and the peculiar conformation of the male antennal flagellum (Figure 1A) distinguish this genus from all other Sapyginae (Pate 1947).

There is relatively little information about the biology of the species of this genus. Individuals of *Huarpea wagneriella* (Buysson) have been reared from nests of *Megachile* sp. in Brazil, and *Huarpea fallax* (Gerstaecker) from nests of *Xylocopa augusti* Lepeletier and *Xylocopa brasiliatorum* (Linnaeus) in Argentina and Paraguay (Friese 1923). However, Pate (1947) believed that Friese's identifications were “questionable” and commented that “it is more likely that the Sapygid reared from nests of these *Xylocopae* were *Huarpea wagneriella* or perhaps a still undescribed South American species of Sapygid” (p.420). A century ago, Jörgensen (1912a) observed individuals of *H. fallax* (cited as *Sapyga fallax* Tasch.) in nests of *Xylocopa*

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*splendidula* Lepeletier and *X. brasilianorum* in Mendoza Province, Argentina, but Brèthes (1916) corrected the determination of the latter species to *Xylocopa ordinaria* Smith and/or *Xylocopa mendozana* Enderlein. Almost 50 years later, Hurd and Moure (1961) reported this sapygid wasp (cited as *Polochrum fallax* Burmeister) from nests of *X. brasilianorum* in Paraná (Brazil).

Currently, some authors are examining bees associated with trap nests in agroecosystems in the Pampean Region (Torretta and Durante 2011; Torretta et al. 2012, Torretta et al. forthcoming) and individuals of *H. fallax* have been reared from nests of native bees in a xeric forest in La Pampa province. Therefore, the objectives of this paper are to provide information about the life cycle of this cleptoparasitic wasp species, including host relationships, time of development, description and measurements of cocoons, and other associated organisms in trap nests.

## Material and methods

### Study site

The study was conducted in a xeric forest (*Caldenal*) on Estancia Anquilóo (36°25' S, 64°48' W), Toay, La Pampa province, Argentina. The *Caldenal* is an ecosystem located in central Argentina (biogeographic province of Espinal, Caldén district), primarily in La Pampa province (Cabrera 1994). This xerophytic open forest system is a transitional ecosystem between the Pampas grasslands, to the east, and the dry Monte shrublands, to the west. It is dominated by the caldén tree (*Prosopis caldenia*, Fabaceae) with an understorey of perennial grasses.

### Collection of parasitized nests

Trap nests were placed in the field during activity periods of bees and wasps (November 2010 to March 2011) and were inspected monthly thereafter. Each trap nest consisted of one hollow bamboo cane, which was cut so that a nodal septum closed one end (Aguiar and Garófalo 2004). Each cane was also cut longitudinally and taped closed, and measurements were taken of both its total length (from the entry to the node) and the inner diameter at the entry. In total, 280 bamboo canes were placed, arranged in 20 blocks of 14 canes. These blocks were located at two forest sites along four transects (two at each site) at intervals of 50–100 m, and 1–2 m above the ground in trees. At each monthly visit the traps with nests were removed and taken to the laboratory, where the cells were separated into plastic vials with cotton plugs, numbered from 1 to *n* (starting from the innermost) and kept in the laboratory at room temperature (c. 15–25°C) until adult eclosion. In those nests where *H. fallax* adults emerged, host species were determined, and sapygid wasps were sexed; the positions of the attacked cells in the trap nest and emergence dates were also registered. A comparison between the sexes (non-parametric Wilcoxon test) was

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Figure 1. *Huarpea fallax*: (A) detail of the male last antennal flagellum; (B) male in dorsal view, (C) female and open cocoon in lateral view; (D) close-up of the cleptoparasitized cell of *Megachile catamarcensis* showing faecal material of *H. fallax* larva (cell was longitudinally opened and cocoon was removed); (E) detail of closed cocoon. Scale lines: A: 0.5 mm, B, E: 2 mm, C: 1 mm, and D: 3 mm.

also performed to determine if differences in development time exist. Cocoons were described and measured.

The material studied is located at the Facultad de Agronomía, Universidad de Buenos Aires, Argentina (FAUBA), and at the Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN).

### *Relationship between body size of Huarpea fallax specimens and their host bees*

To determine if a relationship exists between the size of individual sapygid wasps and their hosts, the linear correlation between the body sizes of sapygids and bees reared from the same nest was calculated. For wasps and bees the intertegular span was used as an index of adult body size. Intertegular distance was measured as shortest linear distance between inner margins of wing tegulae across the thoracic dorsum (Cane 1987). Measurements were taken using a micrometer to the nearest 0.1 mm. For each nest, at least three adults, randomly chosen, were measured and the mean was used as a metric. If the number of emerged adults was less than three, all adults were measured (one or two). The sapygid which emerged with a perilampid wasp from the same cell (see below) was excluded from the analysis. In addition, a comparison between the sexes (non-parametric Wilcoxon test) was carried out, to determine if differences in body size exist.

### Results

In total, 11 individuals of *H. fallax* (Figure 1B, C) were obtained (eight females and three males) from 10 different nests. Only in one nest (#384) were two cells parasitized by *H. fallax* (Table 1). Nests were grouped in six different blocks of canes (Table 1). Eight nests were built by females of *Megachile catamarcensis* Schrottky (Figure 1D) and two by *Anthidium vigintipunctatum* Friese (Table 1). Most trap nests consisted of one nest, except for one in which two nests of *M. catamarcensis* had been built, separated by a space of 75 mm (#555 and #555B). Seven nests were obtained in December 2010, whereas the others were collected in January 2011. The positioning of parasitized cells by females of *H. fallax* was variable among nests, although the attacked cells were mainly the outermost ones in the traps (Table 1).

From each parasitized cell one *H. fallax* adult emerged, except for one cell of an *M. catamarcensis* nest (#740), which also led to the emergence of an adult of *Perilampus* sp. (Hymenoptera: Perilampidae) (Table 1). In another three nests, cells were attacked by other parasitic species. One nest of *A. vigintipunctatum* (#384) was attacked by *Chrysis saltana* Bohart (Hymenoptera: Chrysididae), one of *M. catamarcensis* (#498) was also parasitized by *Leucospis pulchriceps* Cameron (Hymenoptera: Leucospidae) and another (#555) by the bee fly *Anthrax oedipus* Fabricius (Diptera: Bombyliidae).

Emergence of *H. fallax* adults showed a clear unimodal pattern (Figure 2). However, one female took about 2 years to emerge. The period between egg laying and emergence of most adults lasted 290–390 days (10–13 months). Except for the female that emerged in the second year, the development time (females:  $337.4 \pm 16.3$  days,  $n = 7$ ; males:  $332.7 \pm 50.9$  days,  $n = 3$ ) did not differ between sexes ( $W = 14$ ,  $p = 0.63$ ,  $n = 10$ ).

Table 1. Individuals of *Huarpea fallax* reared from nests of native bees obtained in trap nests in a xeric forest in Argentina.

Block number	Trap nest number	Host species	No. of cells	Position of parasitized cell	No. of <i>H. fallax</i> emerged (% parasitism)	Sex of <i>H. fallax</i>	Other parasitic species in trap nest
28	384	<i>Anthidium vigintipunctatum</i>	4	1, 2	2 (50)	2f	<i>Chrysis saltana</i>
35	498	<i>Megachile catamarcensis</i>	5	5	1 (20)	f	<i>Leucospis pulchriceps</i>
	502	<i>M. catamarcensis</i>	3	2	1 (33.33)	f	
36	505	<i>A. vigintipunctatum</i>	11	8	1 (9.09)	m	
	513	<i>M. catamarcensis</i>	4	3	1 (25)	f	
39	554	<i>M. catamarcensis</i>	4	4	1 (25)	f	
	555	<i>M. catamarcensis</i>	4	4	1 (25)	f	<i>Anthrax oedipus</i>
	555B	<i>M. catamarcensis</i>	2	2	1 (50)	m	
50	702	<i>M. catamarcensis</i>	5	5	1 (20)	f	
52	740	<i>M. catamarcensis</i>	3	2	1 (33.33)	m	* <i>Perilampus</i> sp.

Note: f, female; m, male.

\*Emerged from same cell as *H. fallax*.

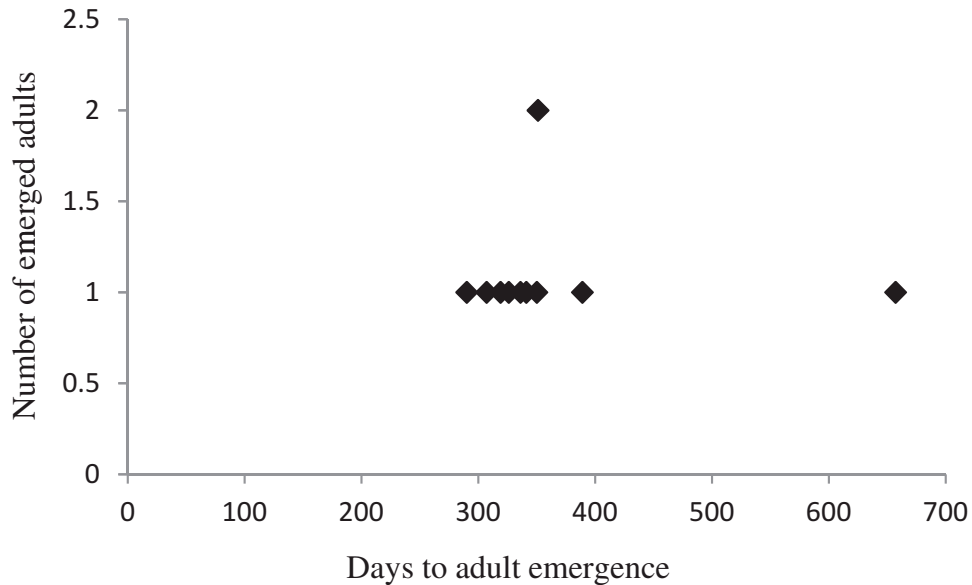


Figure 2. Emergence pattern of individuals of *Huarpea fallax* obtained from nests of wild bees collected in trap nests in a xeric forest of Argentina ( $n = 11$ ).

Cocoons ( $n = 5$ ) were  $9.2 \pm 0.3$  (range 8.9–9.6) mm long and  $3.9 \pm 0.2$  (range 3.7–4.1) mm in maximum width (Figure 1C, E). They were ovoid, shiny black, resistant to compression by touch, and thin-walled. Faeces were dark brown and ovoid ( $1.5\text{--}2.5 \times 1$  mm).

While the number of males studied is very low, body size (measured as intertegular distance; females:  $2.02 \pm 0.23$  mm,  $n = 8$ ; males:  $2.05 \pm 0.21$  mm,  $n = 2$ ) did not show significant differences between sexes ( $W = 11$ ,  $p > 0.99$ ,  $n = 10$ ). Wasp body size (measured as intertegular distance;  $2.00 \pm 0.11$  mm; range: 1.9–2.2 mm) was not linearly related ( $y = -0.42 + 0.8x$ ,  $p = 0.113$ ,  $n = 10$ , Figure 3) to body size of host bees (measured as intertegular distance;  $3.05 \pm 0.10$  mm; range: 2.9–3.2 mm).

## Discussion

This paper provides biological information about the poorly known cleptoparasitic wasp species *H. fallax* in relation to its life cycle, host–parasite relationships, other parasitic species associated, and development time. Biological information on species of Sapygidae is known mainly for species of the northern hemisphere. Parker (1926) described the egg and preimaginal stages of *Polochrum repandum* Spinola reared from nests of *Xylocopa violacea* L. Pate (1947) summarized the host species for numerous species of Sapyginae. Later, Krombein (1967) comprehensively described the life cycle of *Sapyga centrata* Say, and Torchio (1972, 1979) studied *Sapyga pumila* Cresson parasitizing two economically important bee species, the alfalfa pollinators *Megachile rotundata* (Fabricius) and *Megachile pacifica* (Panzer). Recently, Rozen and Kamel (2009) detailed the life cycle of *Sapyga luteomaculata* Pic, meticulously

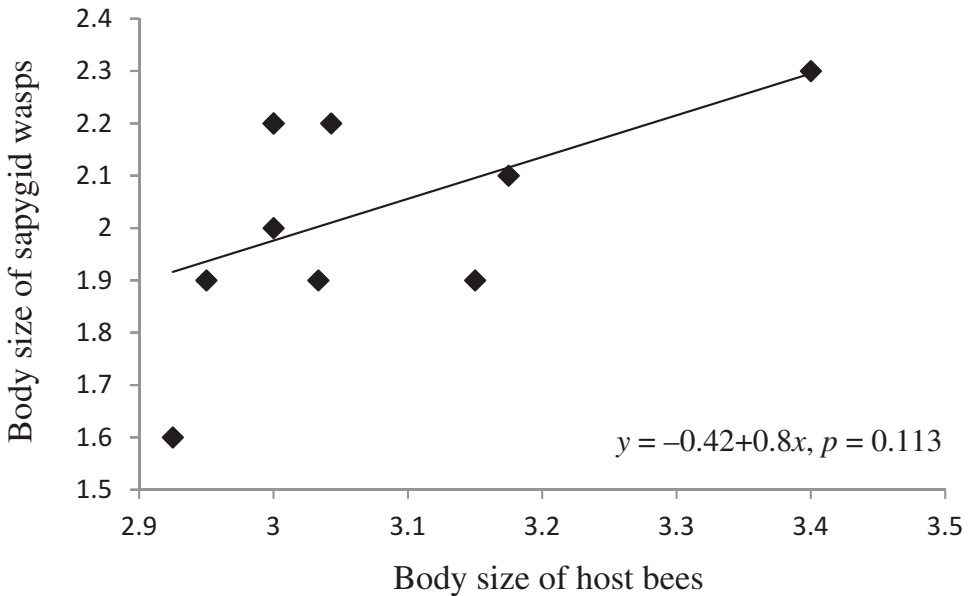


Figure 3. Regression between body size of individuals of *Huarpea fallax* and host bees obtained in same trap nests. The hyperparasitized nest was excluded from the analysis ( $n = 10$ ).

described the pre-imaginal stages, and discussed the behaviour and morphological adaptations of early larval stages to kill host larvae.

As mentioned above, there are few data for Neotropical species. Hurd and Moure (1961) reported on parasitism by *H. fallax* on different species of carpenter bees of the genus *Xylocopa* and reviewed the limited knowledge of the life cycle of this sapygid wasp. In this work, I reared adults of *H. fallax* from the nests of two species of Megachilidae bees, instead of carpenter bees. In our study site, *X. ordinaria* and *X. splendidula* were observed throughout the sampling period (November–March) foraging on flowers (Marrero 2013), but these carpenter bees did not use trap-nests. These two species of *Xylocopa* have been cited as hosts of *H. fallax* in Mendoza province (500 km northwest of our study site) (Jørgensen 1912a, 1912b). The current work is the first report of this species of Sapygidae attacking nests of Megachilidae.

Emergence of adults of *H. fallax* demonstrates a clear unimodal pattern, indicating a univoltine life cycle with adults emerging in late spring and parasitizing nests between late spring and early summer. The period between egg laying and adult emergence was similar between years and lasted for 10–13 months. At our study site, *M. catamarcensis* (host of *H. fallax*) is a specialist on the pollen of *Prosopis caldenia* (Torretta et al. forthcoming), flowering of which occurs in December–January (Burkart 1976). A high synchronicity between flowering of host plant and activity of specialist bee and cleptoparasitic wasp would be expected. One female took about 2 years to emerge, suggesting that *H. fallax* exhibits parsivoltinism. In several bee and wasp species, some individuals of each age cohort emerge in the following year (Torchio and Tepedino 1982; Wcislo and Cane 1996) and this may be a bet-hedging strategy related to unpredictable resources or to natural enemies or host availability (Neff and Simpson 1992; Wcislo and Cane 1996).



Sapygid cocoons studied in our population were similar in appearance to those reported by Jörgensen (1912a) from *X. brasiliatorum* and *X. splendidula* in Mendoza, but smaller ( $9.2 \pm 0.3 \times 3.9 \pm 0.2$  mm in the La Pampa population versus  $13 \times 7$  mm in the Mendoza population). The quantity of food supplied has been considered as an explanation for the variations in size that occur within the same species (Mickel 1924). Species of *Xylocopa* cited by Jörgensen (1912b) as hosts for *H. fallax* are bigger than *M. catamarcensis* and *A. vigintipunctatum*. If the provisioned pollen masses of females of *Xylocopa* spp. were larger than *Megachile/Anthidium*, the difference of body size in individuals of adults of *H. fallax* could be due to this fact. Within cleptoparasitic wasps, this phenomenon is well known in Mutillidae (Mickel 1924). In this study, although there were insufficient data to prove a correlation, the data suggest a positive trend between body size of sapygid wasps and their host bees. A greater number of individuals could help to confirm or reject this hypothesis. Another possible explanation could be differences in inherent body size among populations of *H. fallax*; obtaining individuals from nests of *Xylocopa* spp. and Megachilidae (or other possible host) in the same population could help to solve this issue.

In most nests attacked by *H. fallax* females, only one cell was parasitized. This is different for *Sapyga centrata* females, which have been shown to parasitize several cells in consecutive series in nests of *Osmia bucephala* Cresson and *Osmia pumila* Cresson (Krombein 1967). The same is apparently true for Brazilian populations of *H. fallax* according to Hurd and Moure (1961). Regarding the position within the nest, most attacked cells were the outermost ones, as reported for *S. centrata* (Krombein 1967) and the Brazilian population of *H. fallax*. The females of *H. fallax* parasitized nests that were also parasitized by other species (Hymenoptera and Diptera). The most remarkable fact is that in one cell of *M. catamarcensis* both a sapygid wasp and an individual of *Perilampus* sp. successfully developed. *Perilampus* species are very diverse in terms of their hosts, but with restrictions on particular species groups (Darling 2006); however, none is cited as a parasite of Megachilidae.

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