

Research Article

Prevalence of Stylopization of *Sphex ichneumoneus* (L.) (Hymenoptera: Sphecidae) by *Paraxenos westwoodi* (Templeton) (Strepsiptera: Xenidae)

Richard S. Miller, April M. Pearce, and Kevin M. O'Neill

Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, MT 5971, USA

Correspondence should be addressed to Kevin M. O'Neill, koneill@montana.edu

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On a seed production farm in southcentral Montana, USA, we found the strepsipteran *Paraxenos westwoodi* (Templeton) parasitizing adult *Sphex ichneumoneus* (L.), which were collected while they were foraging for nectar. Over a two-year period, 25% of males and 7% of female wasps were stylopized, as evidenced by the presence of puparia and empty puparial cases of male and female *P. westwoodi* exerted dorsally between abdominal segments. Our estimate is based on a sample size larger than those usually reported for strepsipterans attacking solitary aculeate wasps. We review the literature on strepsipteran prevalence in solitary aculeate wasps and provide an updated list of solitary wasps known to act of strepsipteran hosts in North America.

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1. Introduction

In North America, Strepsiptera of the families Stylopidae and Xenidae parasitize adult aculeate bees and wasps (Hymenoptera: Apoidea) [1–4]. Species of five genera of Stylopidae (*Crawfordia*, *Eurostylops*, *Halictoxenos*, *Hylecthrus*, *Stylops*) attack solitary bees of the families Andrenidae, Colletidae, and Halictidae. Species of two genera of Xenidae attack Vespidae, with *Polistes* (Polistinae) hosting *Xenos* and eumenine wasps of at least five genera *Pseudoxenos*. Finally, species of the xenid genus *Paraxenos* parasitize solitary wasps of the family Sphecidae. Strepsiptera that attack Hymenoptera have long been known to cause profound sublethal effects, including effective castration, but death of the adult host bee or wasp is delayed until late in the life cycle of the strepsipteran [4–7].

Salt [5, 6] described external morphological changes associated with stylopization in females of three species of *Ammophila* (Sphecidae). The most common modifications included altered patterns of pubescence on the head and thorax and reduced length of spines on the legs, with the result that those female characteristics had become more male-like. Recently, Tatsuta and Makino [8] found that

overwintering queens of *Vespa analis* (F.) parasitized by *Xenos moutoni* were unable to reproduce the following season. Kudô et al. [9] reported that *Xenos myrapetrus* (Trois) caused infected workers to be smaller than uninfected workers of *Polybia paulista*.

Hymenopteran host records for strepsipterans are often based on a few individual infected wasps found in samples collected for other purposes. As a result, little information exists on the prevalence of parasitism within host populations of solitary wasps. Here, we report on rates of parasitism by *Paraxenos westwoodi* (Templeton) in *Sphex ichneumoneus* in a sample of 182 wasps collected at one site over a two-year period in southcentral Montana, USA.

2. Materials and Methods

On nine days from 3 July to 11 August 2006 and three days from 17 July to 7 August 2007, we collected 182 *S. ichneumoneus* adults at the USDA-NRCS Bridger Plant Materials Center (BPMC), 4 km southeast of Bridger, Carbon Co, Montana. The vast majority of the wasps were collected either individually or within general sweep samples on flowers of slender white prairie clover (*Dalea candida* Michx.

TABLE 1: Prevalence of *Pseudoxenos westwoodi* parasitism of *S. ichneumoneus* at the Bridger Plant Materials Center, Bridger, MT.

		Sex of host	2006	2007	Both years
Number of wasps examined		both sexes	55	127	182
	Stylopized	male	4	6	10
female		0	10	10	
Not stylopized	male	11	19	30	
	female	40	92	132	
Prevalence of stylopization (%)	male	26.7	24.0	25.0	
	female	0	9.8	7.0	
	both sexes	7.3	12.6	11.0	

ex Willd.), which is grown in monoculture at BPMC for seed production. A few wasps were also taken in pan trap samples within stands of *D. candida*; several others were collected in nets on snowberry (*Symphoricarpos* sp.) or sowthistle (*Sonchus* sp.). All specimens were returned live under ice to Montana State University on the day of capture, and then either frozen or placed in vials for rearing of the strepsipterans in vials at room temperature. All wasps were examined under a stereomicroscope for the external presence of strepsipterans exserted between gastral segments; because we did not dissect hosts to check for the internal presence of triungulin larvae, it is possible that we have underestimated prevalence of stylopization. Voucher specimens of the host wasp and the strepsipterans have been placed in the Montana Entomology Collection, Montana State University, Bozeman.

3. Results and Discussion

Based on comparison to the species description, the strepsipterans parasitizing *Sphex ichneumoneus* were identified as *Paraxenos westwoodi* (Templeton); *Pseudoxenos smithii* (Heyden), previously recorded as a parasite of this wasp [2], is a synonym of *P. westwoodi*. Overall, 11% of *S. ichneumoneus* adults examined had evidence of stylopization (Table 1). On 16 wasps, one or more *P. westwoodi* were present as puparia or adults exserted from the host's gaster. On eight wasps, we found evidence that one ($N = 7$) or two males had exserted and then emerged from the host (Figure 1). Among the 20 parasitized wasps, seven males and seven females harbored one puparium, whereas three males and three females carried two puparia each. One of the 26 puparia or adult xenids protruded from the membrane following gastral segment III, 15 were positioned after segment IV, and 10 followed segment V. Twelve were located just left of the center of the longitudinal axis of the body, 13 were just to the right of center, and one was far to the right of center, though still between two tergal sclerites. On two wasps, triungulins (instar I larvae) were in the process of emerging from female puparia when they were preserved.

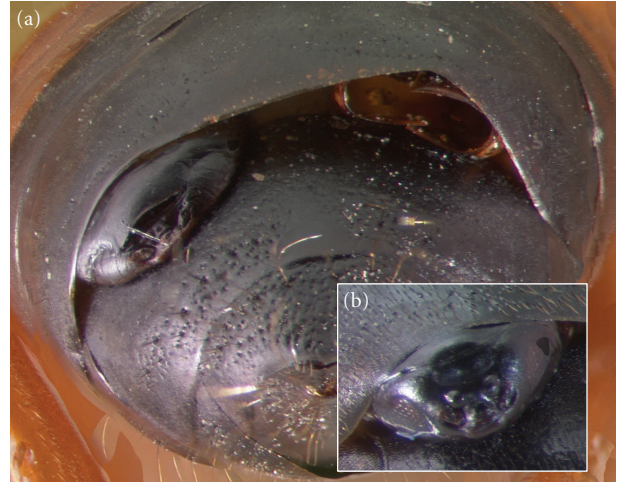


FIGURE 1: (a) Posterior dorsum of female *Sphex ichneumoneus* showing two *Paraxenos* exserted at posterior border of gastral tergum IV. On the left is a female puparium, and on the right is the remains of a male puparium following the adult's emergence. (b) Male puparium prior to emergence of adult on another host individual.

The sex ratio of the adult *P. westwoodi* (15 males:11 females) did not differ significantly from 1:1 (chi-square goodness-of-fit test, $\chi^2 = 0.34$, $P = .56$, d.f. = 1). However, the prevalence of parasitism among all *S. ichneumoneus* collected (independent of the number of parasites per wasp) was 3.5 times higher in host males than females (chi-square contingency table, $\chi^2 = 10.29$, $P = .0013$, d.f. = 1). Although this could be due to a real sex bias in rates of parasitism, our data cannot be used to falsify the alternative hypothesis that stylopized females were less likely than males to be collected foraging on flowers, where almost all of our samples were obtained. Salt [6] indicates that stylopized hymenopteran females have a lower propensity to forage. If this is the case for *S. ichneumoneus*, our sample may not only misrepresent sex bias in primary attack rates, but it may underestimate the overall rate of parasitism. On the other hand, if stylopized wasps are easier to collect than unparasitized individuals, if they are weaker fliers for example, then we may be overestimating the incidence of parasitism. Another potential source of bias could have occurred if parasitized *S. ichneumoneus* had longer life spans than unparasitized individuals, as can be the case for other species of insects [4].

Prevalence differed between years for females ($\chi^2 = 4.22$, $P = .04$, d.f. = 1), but not for males ($\chi^2 = 0.04$, $P = .85$, d.f. = 1). However, the overall prevalence did not change significantly from 2006 to 2007 ($\chi^2 = 1.11$, $P = .29$, d.f. = 1).

The range of previously reported rates of parasitism of solitary aculeate wasps by strepsipterans encompasses the overall value of 11% that we observed. Clausen [10] cites Piel [11] recording a 25% stylopization rate in *Isodontia nigella* (F. Smith) (= *Sphex nigellus* F. Smith); Kifune and Yamane [12] and Kifune [13] report that *I. nigella* is stylopized by *Paraxenos esakii* (Hirashima and Kifune). Evans and

TABLE 2: North American species of Sphecidae known to be parasitized by Strepsiptera (based on records from Krombein et al. [2] and Kathirithamby and Taylor [3]).

Strepsipteran species	Wasp host species
<i>Paraxenos lugubris</i> (Pierce)	<i>Ammophila aberti</i> Haldemann,
	<i>Ammophila breviceps</i> Smith,
	<i>Ammophila evansi</i> Menke,
	<i>Ammophila nasalis</i> Provancher,
	<i>Ammophila pictipennis</i> Walsh,
<i>Paraxenos auripedis</i> (Pierce)	<i>Ammophila pruinosa</i> Cresson,
	<i>Ammophila urnaria</i> Dahlbom,
	<i>Eremnophila aureonotata</i>
	(Cameron)
	<i>Isodontia auripes</i> (Fernald)
<i>Paraxenos luctuosae</i> (Pierce)	<i>Podalonia argentifrons</i> (Smith),
	<i>Podalonia luctuosa</i> (Smith), <i>Podalonia violaceipennis</i> (Smith)
<i>Paraxenos duryi</i> (Pierce)	<i>Prionyx atratus</i> Lepeletier
	<i>Sphex flavovestitus</i> Smith, <i>Sphex</i>
<i>Paraxenos westwoodi</i> (Heyden)	<i>habenus</i> Say, <i>Sphex ichneumoneus</i>
	L., <i>Sphex pensylvanicus</i> L.

Matthews [14] reported rates of stylopization of 8% in 250 *Bembix variabilis* Smith and 12% in 320 *Bembix littoralis* Turner in Australia. Krombein and Van der Vecht [15] found that 3 of 10 *Bembix orientalis* Handlirsch in Sri Lanka were stylopized by *Paraxenos krombeinii* Kifune and Hirashima.

Rates of strepsipteran parasitism have also been reported for several solitary Vespidae (Eumeninae). In Japan, Itino [16] documented an 8% stylopization rate in *Anterhynchium flavomarginatum* Smith; earlier, Iwata [17] had reported *Pseudoxenos iwati* Esaki as a parasite of this wasp. *Pseudoxenos hookeri* (Pierce) was present in 33% of nests and on 10% of individuals of *Euodynerus foraminatus apokensis* (Robertson) in the United States [18]. In Australia, 13% of 54 male and 25% of 24 female *Paragia decipiens* Shuckard (Vespidae: Masarinae) were stylopized, an overall prevalence of 17% [18]. It seems likely that even lower rates of strepsipteran parasitism than reported above are more typical of infected populations, but that they often remain unquantified or unreported. Therefore, we encourage all authors that report records of stylopization to include information on the number of hosts examined, the method by which they were collected, and the time period over which hosts were obtained.

In Table 2, we combine the information from previous sources [2, 3] to provide a list of sphecid host records for Xenidae in North America; the table includes updated taxonomic information on both hosts and parasites. In North America, *Paraxenos* species apparently specialize *P. lugubris* on *Ammophila* and the related genus *Eremnophila*, *P. luctuosae* on *Podalonia*, and *P. westwoodi* on *Sphex*. Outside of North America, species of *Paraxenos* attack sphecids, including *Sceliphron* [19], and crabronids (e.g., *Bembix*, *Tachytes*) [12, 14, 15, 20].

Despite the fact that the behavior and ecology of solitary wasps and their natural enemies are well studied in North

America (for reviews see [21, 22]), we actually know very little about the effects of Strepsiptera on individual host fitness or the population dynamics of host species in this region. Reports, such as that given here, at least provide some evidence that, in certain years and locations, *Paraxenos* can parasitize a significant proportion of a host population. However, long-term studies that include life-table analyses [23] of the host populations would be required to more fully explore the effect of *P. westwoodi* on *S. ichneumoneus*.

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