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Prevalence of the parasite Strepsiptera in adult *Polistes* wasps: field collections and literature overview

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The incidence of strepsipteran parasites in temperate *Polistes* wasps is recorded following the collection and dissection of adults from nests, foraging sites and hibernacula. The mean proportion of infected *P. dominulus* adults (i.e. parasite prevalence) on nests was around 7%, while wasps which were captured when hunting for prey or collecting water were rarely parasitized. Of the four *Polistes* species that were recovered from overwintering aggregations *(dominulus, gallicus, nimphus* and *associus*) only *P. gallicus* was uninfected. In *P. dominulus,* the most numerous host sampled, up to 25% of overwintering females were infected. We discuss our findings in the light of an extensive collation of records of *Polistes* parasitized by the strepsipteran genus *Xeno*s in old and recent literature.

KEY WORDS: *Polistes, Xenos,* Strepsiptera, parasitic castrators, social insects, overwintering groups.

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INTRODUCTION

Social insects are a valuable resource for exploitation by parasites, due to the aggregation of a large number of genetically related individuals in a central location (Schmid-Hempel 1998, Naug & Camazine 2002). Many examples of their effect have been collected to date such as: colony-level response (Hart et al. 2002, Mehdiabadi & Gilbert 2002), foraging (Schmid-Hempel & Schmid-Hempel 1990, Morrison 2000), colony growth (Currie 2001, Brown et al. 2003) and behavioural changes (Carney 1969, Müller & Schmid-Hempel 1993, Müller 1994). Due to the high diversity of parasites within colonies (Kistner 1982, Schmid-Hempel 1998), our knowledge of life histories of these parasites is limited for many taxa.

A prime example of this is the order Strepsiptera, which are obligate parasitic insects. Among the social insects, the family Stylopidae has been recorded as parasites of wasps (Vespidae of the genera *Provespa, Vespa, Vespula, Polistes, Mischocyttarus, Belanogaster, Brachygastra, Ropalidia, Apoica, Agelaia, Chartergus, Polybia*); the family Myrmecolacidae, if males, infect the ants (Formicidae belonging to genera *Camponotus, Crematogaster, Pheidole, Pseudomyrmex, Eciton, Solenopsis, Dolichoderus*), whereas females infect Orthoptera (see recent data in Kathirithamby & Johnston 2004). In most cases information on parasite abundance and behaviour is minimal.

Most information concerns wasps of the genus *Polistes*, which are popular study tools in their own right because of their tractability and accessibility (unenveloped nest and wide occurrence in temperate zones, see Reeve 1991, Turillazzi & West-Eberhard 1996). Indeed, the first record of an insect infected by Strepsiptera was from *P. dominulus* (Christ), parasitized, i.e. 'stylopized' by *Xenos vesparum* (Rossi 1793). In this species, as well as in other hymenopteran hosts, infection results in physiological castration (Brandenburg 1956, Strambi & Strambi 1973, Maeta & Kurihara 1999). A recent field and laboratory study on *P. dominulus* has shown a marked change in social behaviour of stylopized wasps, leading to nest desertion early in imaginal life and the formation of mid-season, extra-nidal aggregations (Hughes et al. 2004, Beani et al. in press).

In a previous study on Strepsiptera, we evaluated infection levels among different *Polistes* species from Old and New World sites through dissections of immatures and adults from nests (Hughes et al. 2003). The aim of the current work is to document the occurrence of Strepsiptera in *P. dominulus*, following collections and dissections of adult wasps. Particularly, we detail parasite prevalence (proportion of infected individuals), and parasite load (number of parasites/infected host) for various categories of adults: (1) on the nest; (2) foraging for prey on plants and collecting water; (3) in overwintering inter-specific groups, formed by *P. dominulus, P. gallicus, P. nimphus* and *P. associus*. Available information on Strepsiptera infecting *Polistes* in old and recent literature is briefly reviewed, focussing particularly on levels of parasitism across different host categories.

METHODS

Brief life-cycle of the strepsipteran genus Xenos parasitic in Polistes wasps

Infection occurs when the free-living, 1st instar larva enters a larval (or rarely egg) stage wasp. The parasite remains endoparasitic until the host ecloses from the cell as an adult. At which point both sexes of the parasite extrude the anterior region of the final instar through the intersegmental membranes of the host's abdominal cuticle. Thereafter, hosts become visibly stylopized. *Xenos* males form puparia, from which they later emerge as free-living adults for their short adult stage (< 5 hr). *Xenos* females, which are permanently neotenic endoparasites, extrude their cephalothorax through the intersegmental membranes of the host. Mating and emergence of 1st instar larvae occur through the brood canal opening in the cephalothorax (reviewed in KATHIRITHAMBY 1989).

The *Polistes* host is a primitively eusocial wasp, which in Italy begins nest foundation in March with the first workers emerging in May. Sexuals emerge in August-September, before colony decline. Only female wasps (and female *Xenos* inside their abdomen) overwinter in aggregations between November and March. After diapause, the female *Xenos* produce 1st instar larvae which infect all the larval stages of the host (in Tuscany from May to July-August). Emergence of stylopized workers and sexuals occurs from late May to August (see further details in HUGHES et al. 2003).

Host collections

All collections occurred within 20 km of Florence, Italy. Collection sites (the local names are given in Table 1) were old farmhouses, a greenhouse surrounded by fields and a cemetery. Three categories of adult host were collected: (1) on nests; (2) prey foraging or collecting water; (3) overwintering within hibernacula.

(1) *Adults on the nest*. Nests of *P. dominulus* (n = 21) were collected early in the morning under roof tiles of an abandoned property (henceforth Area 1) on 10th July (n = 7), 17th July (n = 7) and 3rd August 2000 (n = 7). The nest was frozen within 3 hr of collection and all adult dissected to check for signs of parasitism. Area 1 corresponds to Area C (HUGHES et al. 2003), and Area 1 (HUGHES et al. 2004).

(2) *Adults at foraging sites and water sources*. Wasps were captured as they flew around plants and a water point. All collections occurred at one site (henceforth Area 2), every 2 days between 13th July and 2nd August 2000. Flying wasps were collected as they visited a patch of non-flowering plants, i.e. without nectar and sugar sources at the time (approximately 10 m^2 area abutting an abandoned house where nests were numerous). Using a sweep net, wasps were captured if they flew very close (< 5 cm) around the stem and leaves of plants, presumably seeking for prey, such as caterpillars. Typically, individuals moved around a single plant for 5-10 sec before moving to another plant in the immediate vicinity. At the water point (1 m^2 container), at the margin of the 'foraging' area, a net was passed close to the surface to collect wasps as they visited the water. Wasps would alight on the water, or at the water's edge to drink. Collections on plants (n = 10) and at water (n = 11) lasted for 30 min, or until 10 wasps were caught. All wasps were sacrificed within 3 hr and later dissected.

(3) *Adults from hibernacula*. Wasps were collected between the 6-10th December 2000 from 5 sites (see Table 1): old farmhouses surrounded by fields (Area 1-4); greenhouse within ploughed field (Area 5). Between 15-18th December 2001, collections occurred in a cemetery (Area 6, corresponding to Area E in HUGHES et al. 2003). Overwintering sites (i.e. hibernacula) were commonly interstices of buildings, old nests under roof tiles, but also votive candleholders in the cemetery site. These wasps were not dissected for signs of parasitism as *X. vesparum* does not overwinter as a larval stage.

Statistical analyses

Data on parasite load (one parasite or ≥ two) and host species identity (4 species) was analysed using binary and multinomial logistic regression analyses with the enter method, respectively. Count data on the number of wasps on the nest or within hibernacula was analysed using ANOVA following log transformation to approximately normalize the data. All analyses were performed using SPSS 10 and all means are shown ± SE.

RESULTS

Adults on the nest

In total, *P. dominulus* nests contained 896 adults (840 females, 56 males, 21 nests). The mean number of adults per nest was 42.67 ± 5.30 and this did not significantly differ among the 3 sampling weeks (ANOVA $F_{2,20}$ = 0.80, P = 0.92). The proportion of female wasps did vary with week (ANOVA $F_{2,20}$ = 7.51, P = 0.04; proportion of females = 0.99 ± 0.01, 0.97 ± 0.01 and 0.87 ± 0.05 for week 1, 2 and 3 respectively). With the exception of one nest collected on 3rd August, all nests contained infected adults (20/21 or 0.95). The mean prevalence of infection among adult wasps was 0.07 ± 0.02, regardless of the week of collection (Fig. 1, ANOVA $F_{2,20}$ = 2.27, P = 0.15).

Of the 61 infected adults, 7 were parasitized by 2 or more *X. vesparum* (69 parasites of both sexes in total, max/host = 3). The probability of parasitism by more than one parasite was not influenced by week of collection (Binary Logistic Regression, Wald = 0.0015, 1 df, P = 0.97). The parasite load among infected wasps was 1.13 ± 0.05. Only 8 of 69 parasites extruded through the host cuticle, i.e. < 1% of the total number of adults on nests (n = 896) were visibly stylopized.

Adults at foraging sites and water sources

All wasps collected over non-flowering patches and water were female *P. dominulus*. Of the 63 adults captured while flying over vegetation, in manner suggestive of prey searching, only one was infected (with three larval *X. vesparum* males inside). Low levels of parasitism were also found among adults collected over water: only 4 of the 88 wasps were infected. All these wasps were singly infected by female *X. vesparum* releasing 1st instars at the time of capture. The degree of wing

Table 1.

The total number of wasps from overwintering aggregations according to the area of collection.

Area	*P. dominulus*	*P. gallicus*	*P. nimphus*	*P. associus*	Total wasps	Hibernacula composition (%)
1 (Peretola)	124 (22/0.17)	87 (0)	0	0	211	59/41/0/0
2 (Montoriolo)	143 (33/0.23)	6 (0)	0	0	149	96/4/0/0
3 (Impruneta)	97 (24/0.25)	16 (0)	0	23 (2/0.09)	136	71/12/0/17
4 (Ferrone)	105 (11/0.10)	135 (0)	0	34 (0)	274	39/49/0/12
5 (Mosciano)	47 (20/0.04)	4 (0)	12 (1/0.08)	117 (0)	180	26/2/7/65
6 (Trespiano)	377 (45/0.12)	73 (0)	0	30 (3/0.10)	480	79/15/0/6
Total	893 (137/0.15)	321 (0)	12 (1)	204 (5/0.02)	1430	63/22/1/14

The figures in parenthesis are the number and proportion of parasitized wasps. Hibernacula composition lists the relative percentages of wasps according to species in this order: *dominulus/gallicus/nimphus/associus*.

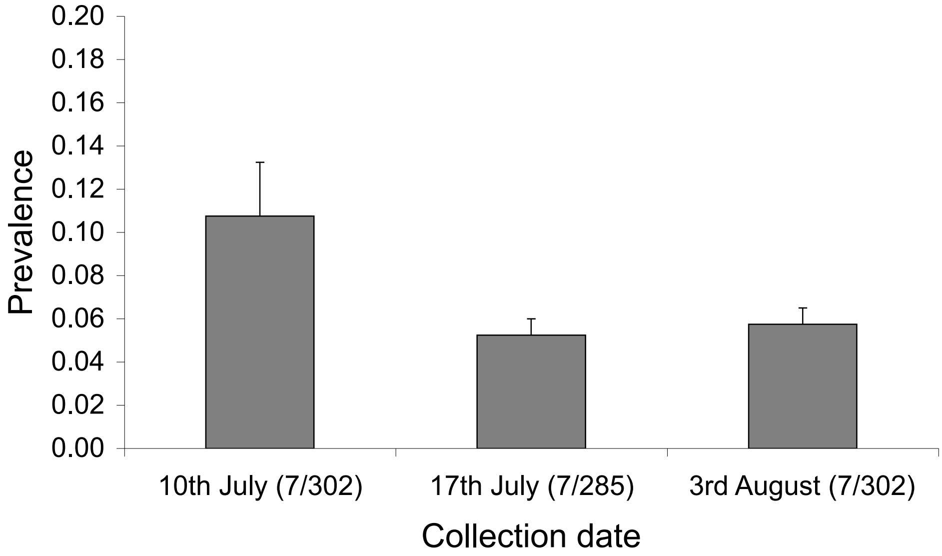

Fig. 1. — The mean prevalence (± SE) of infection of *P. dominulus* among adults on nests according to collection date. The values in parenthesis are number of nests and adults dissected respectively.

wear and tergite discoloration was extensive and suggested that these hosts were overwintered gynes from the previous season.

Adults from overwintering aggregations

Within hibernacula, 1430 wasps were recovered and all were female (Table 1). Between 6-10th December 2000, 33 separate overwintering aggregations (from Areas 1-5) contained 950 female *Polistes* of the following 4 species: *P. dominulus, gallicus* (L.)*, nimphus* (Christ) and *associus* Kohl. Between 15-18th December 2001, 480 female wasps (of *P. dominulus, gallicus* or *associus*) were collected from 23 overwintering aggregations (Area 6). The mean size of aggregations in hibernacula was 25.57 wasps ± 4.81 (n = 56). The largest aggregation was 250 wasps under a roof tile.

Table 1 shows the number and proportion of parasitized wasps for each species of wasp collected from 6 areas. Species were not randomly distributed among our collection sites (Multinomial Logistic regression $\chi^2 = 366.33$, 15 df, $P < 0.0001$). *Polistes gallicus* wasps (n = 321) were all uninfected, with only one *P. nimphus* wasp was parasitized (note we rarely found this species, n = 12).

In total, 143 parasitized wasps were collected from hibernacula. Parasite number and sex is presented here for 88 *P. dominulus* wasps: 70 wasps were singly parasitized by a female *X. vesparum*; 9 had 2, and 1 had 3 female *X. vesparum*. Unexpectedly, some wasps (n = 8) had male pupal stage *X. vesparum* or contained empty puparia co-occurring with female *X. vesparum*. Males within the puparia were dead, presumably they failed to emerge prior to host diapause. The mean parasite load in overwintering aggregations was 1.16, comparable to the parasite load in *P. dominulus* adults on nests.

DISCUSSION

Parasitism of adults on the nest

There is increasing evidence that Strepsiptera occur at high prevalence within populations and colonies of *Polistes* wasps. This study was focused on *P. dominulus* adults, and we found that all categories of hosts that were sampled were parasitized, but at different levels of infection and stages of the parasite.

We found a very high proportion of infected colonies in July (20/21 or 95%) and a relatively low parasite prevalence among adult wasps on nests (61/896, i.e. 7.1% regardless of collection date, Fig. 1). These data are in line with our previous findings in nests of *P. dominulus* collected in June and screened for endoparasitic stages by dissection (7/12 nests and 0/45 adults, HUGHES et al. 2003, see Table 2). Parasitized wasps leave the nest roughly one week after their emergence (HUGHES et al. 2004). The developmental stages of the parasite corroborates early nest desertion by infected wasps: 61 out of 69 *X. vesparum* in this sample were endoparasitic larvae (all at 3rd-4th stage, except one at 2nd stage). Thus, the temporal window to detect, by dissection, the infected larvae and pupae would be approximately 20 days compared to 7-10 days to discover infected adults before they desert the nest. The low proportion of infected colonies in *P. metricus* (approximately 18%, not based on dissection: HODGES et al. 2003, see Table 2) is attributable to this clear-cut methodological difference.

Nests containing parasitized adults have been previously recorded for *Polistes* from both Old and New World habitats (Table 2). Several samplings of stylopized wasps occurred during the terminal phase of the colony (BRUES 1905, PIERCE 1909, DUNKLE 1979, TURILLAZZI 1980), when nests may serve as a prediapause aggregation site from several colonies. Thus, in those cases high rates of infected wasps may be comparable to parasite prevalence in overwintering groups: stylopized individuals may come from a number of nests to aggregate on an abandoned colony.

On average, the parasite load among adults recovered from nests was approximately one *Xenos* per adult; which was less variable than the number of parasites earlier detected per brood member (> 40 HUGHES et al. 2003, see also BRUES 1903 in Table 2). Whilst another study (HUGHES & KATHIRITHAMBY submitted) showed no effect of single parasitism on the mortality of host larvae, it may be that superparasitized larvae either die, or are removed from the nest. This hypothesis is consistent with 81% of wasps in extra-nidal aggregations being singly infected (HUGHES et al. 2004); as well as the data presented here on parasite load among overwintering hosts (see below).

Parasitism among foraging and water collecting adults

A few studies, unfortunately, have assessed foraging ecology of *Polistes* (see NANNONI et al. 2001). Our collections have shown that stylopized *Polistes* are rarely

Table 2.

A survey of parasitized *Polistes* wasps from the literature, according to host category.

References	Host / Location	Notes on infected wasps	Method	Prevalence
		Collections of adults away from the nest		
Rossi 1793	*P. dominulus* / France	first account of a strepsipteran	[EP]	—
Horn 1871	*P. hebraeus* F. / India	superparasitism	[EP]	0.20
	P. stigma (F.) / India	'many' infected		—
Austin 1882	*P. metricus* Say / MA	2/14 ♂^{in} and 7/36 ♀^{in} (Aug)	[EP]	0.14, 0.19
Hubbard 1892	*P. fuscatus* (F.) / VA	1 ♀^{in} "hiding" under bark	[EP]	—
Brues 1903	*P. texanus** / TX	1 ♀^{in} with empty pupa	[EP]	—
Brues 1905	*P. annularis* (L.) / TX	7 ♀^{in} with empty pupae		—
	*P. rubiginosus** / TX	1 ♀^{in} with female releasing 1st instars (May)		—
Pierce 1909: 21	*P. pallipes* (Lep) / MA	6 ♀^{in}, 4 ♂^{in} with 30 *Xenos* (Sep)	[EP]	—
	P. metricus / OH	10 ♀^{in}; 4 ♂^{in} with 38 *Xenos* (Jun-Sep, over 5 years)		—
	*P. rubiginosus** / DC	1 ♀^{in} with 8 females and 1 ♀^{in} with empty puparia		—
	*P. rubiginosus** / TX	1 ♀^{in} with 6 empty pupae (Jul)		—
Wheeler 1910	*P. metricus* / CT	1000 wasps on flowers (14-29th Aug 1900)	[EP/D]	0.29
Pierce 1918: 393	*P. aurifer* Saussure / CA	1 ♀^{in} with larvipositing female (Aug)	[EP]	—
	*P. anaheimensis** / CA	1 ♀^{in} with female		—
	P. annularis / NE	7 ♀^{in} with 52 males and 6 females *Xenos* (Aug)		—
	P. bellicosus Cresson / AZ	1 ♀^{in} with 4 pupae (Aug)		—
	P. variatus Cresson / MD	5 ♀^{in} 4 with one female, 1 with pupa (Nov)		—
Brèthes 1923	*P. cavaptya* Saussure / Argentina	—	[EP]	—
	P. versicolor (Olivier) / Argentina			—
Richards & Richards 1951	*P. testaceicolor* Bequaert / Guiana	'heavily stylopized'	[EP]	—
	P. carnifex (F.) / Guiana			—

(*continued*)

Table 2. (*continued*)

References	Host/Location	Notes on infected wasps	Method	Prevalence
Oliveira & Kogan 1962	*P. canadensis* (L.) *P. melanosoma* Saussure *P. versicolor* *P.* spp. (?) / (all Southern Brazil)	10 ♀^{in} in total for 4 host species	[EP]	— — —
Riek 1970	*P. variabilis* (F.) / Australia *P. tepidus* (F.) / Australia	—	[EP]	— —
Kifune 1979	*P. lanio lanio* (F.) / Peru	4 ♀^{in} flying around building (Aug-Sep)	[EP/D]	—
Fowler & Parrish 1982	*P. fuscatus* / NJ	8 ♂^{in} aggregated on a eave (Jul)	[EP]	1.00
Kifune 1983	*P. crinitus* (Felton) / Virgin Islands	1 ♀^{in} and 1 ♂^{in} around buildings (Nov-Jun)	[EP]	—
Kifune & Maeta 1985	*P. rothneyi gressitti* Van der Vecht *P. gigas* (Kirby) / Taiwan	3 ♀^{in} 1 ♀^{in}	[EP/D]	— —
Polak 1993	*P. canadensis* / Costa Rica	several ♂^{in} at leks (May-Sep)	[EP]	0.05
Pickett & Wenzel 2000	*P. fuscatus* / NY	several ♀^{in} on flowers (K. Pickett pers. comm.)	[EP/LO]	0.16 (n=68), 0.18 (n=44)
Hughes et al. 2003	*P. carnifex* / Mexico	1 ♀^{in} with larvipositing female; 1 ♀^{in} with pupal males on vegetation (Apr)	[EP]	—
		Collections of adults on the nest		
Hubbard 1892	*P. americanus** / FL	1 nest: ♀^{in} were lethargic and did not forage. Some had 8 or 10 parasites. In lab >100 male *Xenos* bred out (Jun-Jul)	[EP/LO]	—
Brues 1903	*P. annularis* / TX	1 of 4 nests infected. 4 ♀^{in} reared out in lab	[EP/LO/D]	—
Skinner 1903	*P. texacanus** / TX	2 nests: 34/144 wasps parasitized (Sep)	[EP]	0.23
Brues 1905	*P. annularis* / TX	1 nest: 44/86 ♀^{in}; 91 *Xenos* (Jul) 1 nest: 36/42 ♀^{in}; 118 *Xenos* and some empty puparia (Oct)	[EP/D] [EP/LO/D]	0.51 0.85

(*continued*)

Table 2. (*continued*)

References	Host/Location	Notes on infected wasps	Method	Prevalence
Pierce 1909: 17	*P. annularis* / TX	2 large nests (84% males, Sep)		0.20
Pierce 1909: 16	*P. minor* Palisot de Beauvois / TX	2/4 nests: 1/26 and 5/191 wasps (Sep)	[EP]	0.04, 0.03
Pierce 1909: 21	*P. minor* / TX	1/2 nests: 1/17 wasps (Oct)		0.06
Fitzgerald 1938	*P. pacificus* (F.) / Trinidad	1 nest: all stylopized (12) and lethargic (no date)	[EP]	1.00
Dunkle 1979	*P. annularis* / FL	many nests, only males examined: 569/11542 ♂^{in} (Oct/ Nov)	[EP]	0.05
Turillazzi 1980	*P. gallicus* / Italy	♀^{in} by *Xenos* females Sep/Nov)	[EP]	0.19
Strassmann 1981	*P. exclamans* Viereck / TX	8 of "tens of thousands" examined were stylopized	[EP]	—
Hodges et al. 2003	*P. metricus* / GA	51 of 303 early season nests infected by *X. peckii*	[LO]	17.85
		Collections of overwintering females		
Pierce 1909: 20	*P. annularis* / FL	6/60 (Nov); 4/54 (Nov); 2/35 (Jan). ♀^{in}, plus 2 ♀^{in} with empty pupae	[EP]	0.10, 0.07, 0.05
Turillazzi 1980	*P. dominulus* / Italy	4 groups-on nests under tiles	[EP]	0.23
		Collections of immature wasps		
Brues 1903	*P. annularis* / TX	1 larva contained 31 parasites	[D]	
Brues 1905	*P. annularis* / TX	2 nests: 1/12 (Sept)	[D]	0.08
Hughes et al. 2003	*P. dominulus* / Italy *P. gallicus* / Italy *P. carnifex* / Mexico *P. stabilinus* / Mexico	7 of 12 nests: 44/261 immatures 4 of 10 nests: 45/154 immatures 4 of 8 nests: 9/77 immatures 2 of 15 nests: 5/400 immatures	[D]	0.17 0.29 0.12 0.01

Species names as supplied in original publication: * indicates possible invalid names. The list is not exhaustive (see Hughes 2003). Where possible, relevant notes are presented such as: host/parasite sex, proportion of infected wasps and nests, and date of collection. The abbreviations in 'method' refer to parasite detection: EP = Evidently Parasitized (without dissection); LO = Lab Observation, adults reared in cage; D = Dissection of at least some individuals to check for endoparasitic stages. The symbols ♀^{in} = infected female and ♂^{in} = infected male. The USA state names in Location column are abbreviated.

encountered around non-flowering vegetation, which were assumed to be foraging sites for proteinaceous food (e.g. caterpillars) to developing larvae: only one infected individual was recovered from 63 wasps sampled. This observation corroborates previous findings that infected wasps neither forage nor feed brood (HUGHES et al. 2004); but interestingly they do eat larval flies (maggots) brought to the nest by foragers, as well as sugar and honey (pers. obs.). In bumblebees, where infected workers may forage for their colony, the presence of parasites more subtly affects flower choice and pollen loads (SCHMID-HEMPEL & SCHMID-HEMPEL 1990, SCHMID-HEMPEL & MULLER 1991, SCHMID-HEMPEL & STAUFFER 1998).

Our study did not record the occurrence of stylopized wasps around sugar sources such as flowers, fruit or tree-sap, though they were often seen there (pers. obs.). A highly scattered distribution of flowering patches discouraged this approach in our study areas. Many records of stylopized wasps away from the nest do exist but in most cases no details have been furnished (Table 2). Special note should be made of the mammoth collection of 1,000 *P. metricus* over 10 days from flowers by WHEELER (1910) who recoded a 45% infection level in the first 4 days. This level was probably higher, as only a small number were dissected to check for endoparasitic stages. Stylopized individuals of a further North American species (*P. fuscatus*) were also collected from flowers at relatively high levels (16-18%) (PICKETT & WENZEL 2000, and pers. comm.). Both these records may reflect a similar occurrence of early nest desertion by stylopized individuals in these species as well as in *P. dominulus*.

Interestingly, all the stylopized wasps around a water container (4/88, i.e. 4.5%) were infected by a larvipositing female *X. vesparum*. Some morphological cues indicated that these wasps were old, overwintered females. The release of 1st instars at water could be a way to reduce desiccation of the primary stages whilst allowing encounters with phoretic agents (water-collecting workers).

Parasitism in overwintering aggregations of Polistes

Our data confirm previous observations that diapausing aggregations of *Polistes* may be multispecific and are composed principally of female wasps (BRIMLEY 1908, REED & LANDOLT 1991, HUNT et al. 1999). A strong area effect of the likelihood of belonging to a particular *Polistes* species (Table 1) suggests a patchy composition of species within Tuscan populations.

For *P. dominulus,* parasite prevalence was surprisingly high, ranging from 4 to 25% (Table 1). These data were in agreement with the few previous records which exist (see Table 2: 0.05-0.23 PIERCE 1909, TURILLAZZI 1980). This scarcity could reflect the cryptic nature of parasitism at this stage. That is, the visible portion (cephalothorax) of female strepsipterans is dorsoventrally flattened and hidden between the tergites. Thus, stylopization is less conspicuous than in case of large male puparia, which we rarely found in overwintering wasps (this study and PIERCE 1909).

Prevalence was very low in our limited sample of *P. nimphus* (1/12) as well as in the more regularly encountered species, *P. associus* (5/204). This is the first record, to our knowledge, of stylopized *P. associus* wasps. Unexpectedly, *P. gallicus* was not found to be parasitized although this species was collected in high numbers (n = 321) in these winter collections. This contrasts with a high proportion of nests and brood being infected (HUGHES et al. 2003). *P. gallicus* adults might represent a secondary and not suitable host for *X. vesparum*.

Because strepsipterans are parasitic castrators, the very high prevalence among hibernacula occupants means that up to 25% of overwintering *P. dominulus* wasps do not take part in nest foundation. In a recent report on the prevalence of strepsipteran parasitism among overwintering *Vespa analis*, the authors showed that between 8-15% of queens were infected but claimed that this level is not expected to have a serious effect on population dynamics of their hosts (Tatsuta & Makino 2003).

This study, and recent work, have revealed hitherto unappreciated levels of parasitism among *Polistes* by Strepsiptera. A review of the literature highlighted 31 known hosts among *Polistes* (32, including our first record for *P. associus*). Despite their wide distribution and high levels in some species, it remains difficult to make inferences on the effect of parasitism at the colony and population levels. Future work should attempt empirical investigations. Strepsiptera are useful tools with which to do this as they are: relatively easy and inexpensive to sample; tractable to laboratory manipulations; and found in wide range of social and non-social Hymenoptera, which permits inter-taxa comparison of their effects.

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