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Levels of Parasitism *by Xenos moutoni* du Buysson (Strepsiptera, Stylopidae) and their Seasonal Changes in Hornets (Hymenoptera: Vespidae, *Vespa*) Caught with Bait Traps

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Abstract. Parasitism by *Xenos moutoni* was studied in four *Vespa* species collected with bait (fruit juice and liquor) traps in forests in Miyazaki Prefecture, southern Japan. Stylopized hornets were seen between May and mid October. The overall rate of stylopized female hornets (queens or workers) was largest in *V. analis insularis* (11.2%), followed by *V. mandarinia japonica* (4.3), *V. ducalis pulchra* (4.2), and *V. simillima xanthoptera* (1.7). Male hornets were also stylopized in *V. analis* (6.4%) and *V. ducalis* (1.7). The number of parasites per host varied from one to five, though 60% of hosts were singly parasitized. Male parasites did not occur before late July, but they outnumbered females in September and early October. Female parasites were almost always found between the 5th and 6th gastral tergites of hosts, and most males between the 4th and 5th or the 3rd and 4th. Cephalothorax widths of female parasites were positively correlated with head widths of female hosts in *V. analis, V. mandarinia* and *V. ducalis.* Multiple parasitism on single females decreased the average size of female parasites in *V. analis.* The percentage of stylopized individuals among overwintered queens was estimated at 15% in *V. analis* and 4% in *V. mandarinia* and *V. ducalis.* Stylopized workers that had overwintered were found: they accounted for 24 to 44% of overwintered stylopized females. Workers were most frequently stylopized in August in *V. mandarinia* and in September in *V. analis* and *V. ducalis.*

Key words: *Xenos moutoni, Vespa simillima, Vespa mandarinia, Vespa analis, Vespa ducallis,* stylopization, bait trap.

Introduction

Seven hornet (*Vespa*) species occur in Japan. They are not only notorious for stinging humans, but are potentially effective predators of insect pests in forests and other environments (Matsuura & Yamane, 1984). Natural enemies possibly affect their populations or colonial adult productivities. However, biologies of the natural enemies, including their roles in changing hornet densities or colonial productivities, largely remain unknown.

Xenos moutoni du Buysson is a strepsipterous parasite of hornets and is distributed in China, Taiwan, Vietnam, and Japan (Kifune, 1992). In Japan, it parasitizes six *Vespa* species (Kifune, 1992; Matsuura, 1995), and has been recorded from all the main islands (Kifune, 1992; Kifune & Arakawa, 1996; Kifune & Makino, 1996). Stylopized adults do not show foraging activities if they are workers and lose reproductive abilities if males or new queens (Matsuura & Yamane, 1984). Although the impact of *X. moutoni* on host colonies is usually minimal, it can stop the development of colonies, or cause their premature dissolution when all workers are infected early in the post-emergence period (Matsuura, 1995).

It is usually difficult to find stylopized hornets in the field (Matsuura & Yamane, 1984). This may be because they are generally rare, and because stylopized workers do not usually carry out extranidal activities (Matsuura & Yamane, 1984). This makes studies

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difficult that are concerned with, for instance, levels of parasitism, sex ratios of the parasite, or their seasonal changes on a population basis. There have only been a few records on levels of parasitism by *Xenos* in vespines (Kifune & Maeta, 1975; Matsuura & Yamane, 1984; Maeta & Kifune, 1990).

When monitoring populations and species compositions of social wasps in forests in Miyazaki, southern Japan, we found that stylopized workers and reproductives of four *Vespa* species were often attracted to bait traps. This allowed us to collect stylopized individuals throughout the nesting season. Here we describe levels of parasitism and the sex ratio of *Xenos moutoni,* and how they change during the season. We also give the number and locations of parasites on the body of the hosts, and show how sizes of parasites correlated with those of their hosts.

Materials and Methods

Hornets were collected using bait traps in national forests (31°N, 131°E; 200–400 m a.s.l.) in Takaoka, Miyazaki Prefecture, southern Japan in 1997. Bait was comprised of clear liquor (made from sweet potato) and an equal amount of orange juice, both available from stores or supermarkets. We used beverage bottles of clear plastic (about 30 cm high, 10 cm in diameter, and 1500 to 2000 m*l* in capacity) as bait containers. A small square hole (3×3 cm) was made in the upper part of the bottle, which allowed the odor to attract insects. Thirty traps, each with 150 to 200 m*l* bait, were set in four plantations of Japanese cedar and two natural woods mainly composed of evergreen broad-leaved trees. Two of the four cedar plantations were young (5 years old), and the other two were old (ca. 40 years old). The traps were strung from trees between 1.0 and 1.5 m above the ground. The traps were visited every week from early May to mid December to collect trapped insects and replenish the containers with bait. Additional 50 traps were set in various places near the regularly monitored areas from May to July. Trapped hornets were preserved in 70% ethanol. Some stylopized individuals, after being pinned as dried specimens, were measured using the ocular micrometer of a dissecting microscope for the head width and cephalothorax width of their female parasites. Measurements were made at the greatest width in dorsal view. Gastral tergites of the hosts were partly removed to expose and measure the cephalothoraces of the parasites.

Results

1. *Stylopized hornets*

From May 2 to December 22, 3,457 hornets of four species were collected: *Vespa mandarinia japonica* Radoszkowski, *V. analis insularis* Fabricius, *V. ducalis pulchra* Buysson, and *V. simillima xanthoptera* Cameron. In all species, individuals were parasitized by female and/or male *Xenos moutoni.* The overall level of parasitism during the trapping period was highest in *V. analis,* followed by *V. mandarinia* and *V. ducalis,* and was least in *V. simillima* (Table 1). Females were more frequently parasitized than males in all species; no males were parasitized in *V. mandarinia* or *V. simillima.*

Many triungulin larvae were visible through the skin in 25% of female parasites, including those occurring on overwintered female hosts. Almost all (92%) male parasites had already emerged, only leaving empty puparia in the hosts.

Symptom of stylopization was most pronounced in

Table 1. Percentage parasitism by *Xenos moutoni* in female and male hornets caught with bait traps from May to December, 1997. Figures in parentheses show the numbers of hornets examined. Female hosts include both queens and workers.

Host	Female host	Male host	Total
Vespa analis	11.2 (829)	6.4 (110)	10.6 (939)
V. mandarinia	4.3 (835)	0 (101)	3.8 (936)
V. ducalis	4.2 (1073)	1.7 (230)	3.8 (1303)
V. simillima	1.7 (238)	0 (41)	1.4 (279)
Total	6.0 (2975)	2.3 (482)	6.6 (3457)

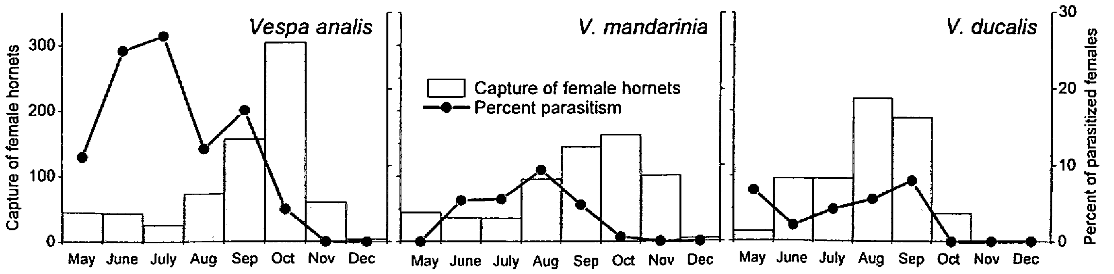

Fig. 1. Seasonal changes in rates of stylopized females in the three host species. Columns show the monthly capture of female hornets, and lines show percentage ratios of stylopized individuals among them.

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V. simillima: yellowish orange areas of stylopized individuals became wider and somewhat paler and hairs were much reduced on the dorsal surface of the gaster and, less frequently, on the head or thorax, as noted by Maeta & Kifune (1990). In the other species, similar changes occurred to usually weaker extents. Dried specimens of those individuals that extensively lost body hairs had rather lustrous appearance.

Besides the four *Vespa* species, we also collected 44 workers of *Vespula flaviceps lewisii* Cameron with the bait traps. From *Vl. flaviceps* another strepsipteran, *Xenos vespularum* Kifune et Maeta, has been recorded in Honshu, Japan (Kifune & Maeta, 1975). However, there were no stylopized individuals in the collection of *Vl. flaviceps.*

2. *Seasonal changes in levels of parasitism*

Changes in monthly catches of female hornets and percentage of parasitized individuals are shown in Fig. 1 for the three main hosts, *V. analis, V. mandarinia,* and *V. ducalis,* collected with the regularly visited 30 traps. *V. simillima* was not included in the following analysis because the parasitism level was too small.

The females were, in general, overwintered queens collected early in the season and workers collected in the summer and fall. Fig. 1 shows that the parasitic level of overwintered queens in *V. analis* was much higher than in the other two species. However, because stylopized workers can go into hibernation as new queens do (Matsuura & Yamane, 1984), it is possible that the parasitized females caught in the spring included not only queens but workers of the previous year. We estimated the number of stylopized individuals of each caste as follows.

In *V. mandarinia,* queens and workers are easily distinguished by external morphology (Matsuura, 1995). A total of 160 spring queens were collected from May 2 to July 11. Of these, five (3.1%) were parasitized by a female *Xenos.* Four workers with a female parasite were collected in May and early June. These were probably workers which had overwintered because of stylopization, as workers free of *Xenos* did not occur before early June in the study sites. Then, about half (4/9) of stylopized females that had overwintered were workers from the previous year (1996). Almost all stylopized workers caught in and after July were considered as parasitized in 1997. Stylopized workers were most frequent in August, and ceased to occur after October (Fig. 3). Pre-overwintering queens were not caught with the traps.

In *V. analis* and *V. ducalis,* morphological caste differentiation is much weaker than in *V. mandarinia,* and it is often difficult to distinguish new queens from workers by external appearance alone, especially late in the nesting season when workers are increasing in size (Vecht, 1957; Matsuura, 1995). As reference material, the head widths of non-parasitized females collected in Takaoka before June 20 in 1995 were measured (those hornets were collected by Mr. Motokurumada using the same method as above). Because the first workers of colonies usually appear around mid June in *V. analis* and mid July in *V. ducalis* (Matsuura & Yamane, 1984), those females that occurred before June 20 should have been spring queens unless they were parasitized. If females caught in that period were parasitized and smaller than the smallest queen, they were considered to be overwintered workers. This procedure may underestimate the number of overwintered workers because of the difficulty of separating larger workers from queens.

The head width of *V. analis* varied from 6.90 to 7.88 mm ($\bar{x}=7.50\pm$SD 0.21; N=22) in the non-parasitized spring queens. Between early May and late June in 1997, we collected 86 queens, of which 13 (15%) were parasitized, and four overwintered parasitized workers. Almost all stylopized females collected from July onwards were workers produced in the current year. The parasitic level varied between 4% and 26% from July to October (Fig. 1). In *V. ducalis,* head widths varied from 6.75 to 7.96 mm ($\bar{x}=7.55\pm$ 0.29; N=45) in parasite-free 1995 spring queens in Takaoka. Six of 162 queens (3.7%) with head widths within this range collected between May and late July were parasitized. In the same period, another three parasitized females were found with head widths smaller than 6.75 mm, the minimum in the non-parasitized queens. They were possibly overwintered workers. We could not exclude the possibility that new queens occurred among the fall collection of *V. ducalis* or *V. analis,* though it seems unlikely, judging from the result of *V. mandarinia.*

Males of *V. analis* were caught from late August to early December, and those of *V. ducalis* from late August to late October. Eight stylopized males were caught from late August to mid October in the former, and four from late September to mid October in the latter.

3. *Number and positions of parasites on hosts*

The number of parasites per host varied from one to five in female hosts and one to three in males, though most hosts had only a single parasite (Table 2). Female or male hosts with a single parasite accounted

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Table 2. Numbers and positions of *Xenos moutoni* on hosts.

Host species	Sex of host	Number and Sex of parasites	Number of hosts	
Vespa analis	female	1♀	49	5–6
		1♂	24	4–5 (16); 3–4 (8)
		2♀♀	3	5–6
		2♂♂	2	3–4 & 4–5
		1♂+1♀	7	3–4 & 5–6 (4)2); 4–5 & 5–6 (3)2)
		3♀♀	1	5–6
		2♂♂+1♀	3	3–4 & 5–62)
		1♂+2♀♀	2	3–4 & 5–6 (1)2); 4–5 & 5–6 (1)2)
		2♂♂+2♀♀	3	3–4 & 4–5 & 5–6 (1)2); 3–4 & 5–6 (2)2)
	male	1♀	2	5–6
		1♂	5	3–4 (2); 4–5 (3)
		1♂+2♀♀	1	3–4 & 4–5 & 6–73)
V. mandarinia	female	1♀	28	5–6
		2♀♀	2	5–6
		1♂+1♀	2	3–4 & 5–6 (1)2); 4–5 & 5–6 (1)2)
V. ducalis	female	1♀	26	5–6
		1♂	8	3–4 (1); 4–5 (7)
		2♀♀	3	5–6 (1); 4–5 (1); 4–5 & 5–6 (1)
		2♂♂	2	4–5 (1); 4–5 & 5–6 (1)
		1♂+1♀	1	4–5 & 5–62)
		3♂♂	3	3–4 & 4–54)
		5♂♂	2	2–3 & 3–4 & 5–6 & 4–5 & (1)5); 2–3 & 3–4 & 5–6 (1)6)
	male	1♀	1	5–6
		1♂	3	3–4 (1); 4–5 (2)
		2♂♂	1	4–5
V. simillima	female	1♀	1	5–6
		1♂+1♀	1	4–5 & 5–62)

1) Positions of parasites are indicated by the numbers of two terga (e.g. 5–6) between which parasites were found. Figures in parentheses are the numbers of hosts which had parasites in the positions. 2) Females between the terga 5 and 6, and males in the other positions. 3) One female between the terga 3 and 4, the other between 6 and 7, and a male between 5 and 6. 4) Two males between the terga 4 and 5, and one between 3 and 4. 5) The terga 4 and 5 had two males, and the other positions one male each. 6) The terga 3 and 4 had three males, and the other positions one male each.

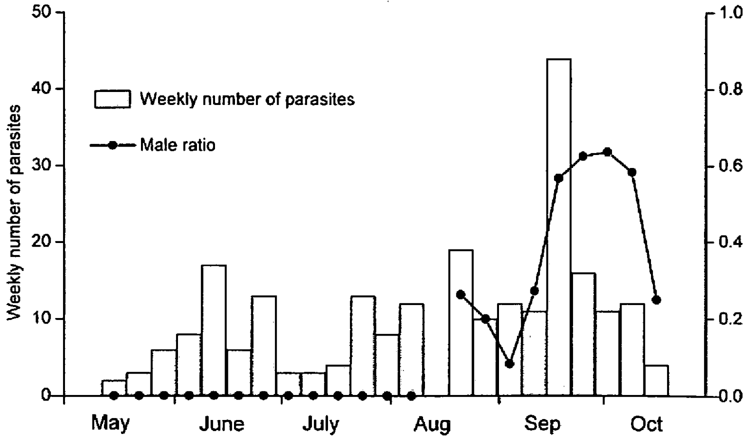

Fig. 2. Seasonal changes in the weekly number of *Xenos moutoni* and male ratio in them. Pooled data from *V. analis*, *V. mandarinia* and *V. ducalis*.

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for 78%, 84%, and 87% of stylopized individuals in *V. analis, V. ducalis,* and *V. mandarinia,* respectively. Overwintered female hosts, queens or workers (see above), almost always had only one female parasite. The only exceptions were two overwintered females of *V. ducalis* collected in early and late June, each with two female parasites.

The parasites always occurred between the terga of their hosts. Irrespective of the species or sex of hosts, female parasites were always situated between the 5th and 6th terga of the hosts, while male pupae or puparia were found between the 4th and 5th terga or, less frequently, between the 3rd and 4th (Table 2). This was also the case when more than one parasite of either sex or both occurred on a single host: females were nearly always between the 5th and 6th terga, never coexisting with males there in the positions. An exception was found in a single male of *V. analis* on which one female parasite occurred between the 3rd and 4th terga and another female between the 6th and 7th, with a male between the 4th and 5th.

The sex ratio of the parasite was not constant but greatly varied during the season. Fig. 2 shows changes in the weekly number and sex ratio (male ratio to total) of parasites found on the three main hosts collected with the regularly visited 30 traps. Only female parasites were found from May to mid August. Male parasites were first recorded on August 22 on a worker of *V. ducalis.* Male ratio increased thereafter and peaked at 0.63 in late September. The last stylopized hosts (*V. analis* and *V. ducalis*) were caught on October 16, though many unparasitized hornets were trapped after this date.

4. *Sizes of hosts and parasites*

Females of *Xenos moutoni,* as usual in strepsipterans, spend their whole life in the bodies of hosts after parasitizing them as 1st instar larvae. This suggests that the sizes of adult parasites are, at least partly, determined by the sizes of their hosts. However, this correlation has not hitherto been studied. We compared sizes of hosts and parasites within and among the host species. Only female hornets (queens or workers) that were parasitized by a single female were measured to exclude effects of multiple parasitism (see below).

The average head width of female hosts was 8.63±SD 0.77 mm ($N=27$), 6.80±0.33 ($N=44$) and 6.77±0.29 ($N=25$) in *V. mandarinia, V. analis,* and *V. ducalis,* respectively. These interspecific differences in host sizes were partially reflected in the sizes of the parasites: female *Xenos moutoni* had the widest average cephalothorax (3.04±0.29 mm; $N=27$) when parasitizing *V. mandarinia* and were smaller when parasitizing *V. ducalis* (2.69±0.12; $N=26$) or *V. analis* (2.33±0.11; $N=49$). The average sizes of parasites were significantly different between all three pairs of the hosts ($P<0.001$; Spjøtvoll and Stoline test for multiple comparison).

Also, there was a positive correlation between the head widths of their hosts and the cephalothorax widths of parasites within each species of the hosts: $r=0.86$ ($P<0.001$) in *V. mandarinia,* 0.76 ($P<0.001$) in *V. ducalis,* and 0.42 ($P=0.002$) in *V. analis* (Fig. 3). Thus, females of *Xenos moutoni* increase in size as they parasitize larger hosts.

There is another possible factor that affects parasite sizes: the number of parasites per host. Maeta (1963) mentioned that the cephalothorax sizes of *Pseudoxenos iwatai* females that parasitize eumenid wasps vary with the number of conspecifics on a host. So, we compared sizes of female parasites in singly parasitized and multiply parasitized female hosts of *V. analis* caught in July and later. These female hosts did not differ in the head width between the two groups [6.53±SD 0.42 ($N=20$) vs. 6.55±0.36 ($N=18$) mm; $t=$

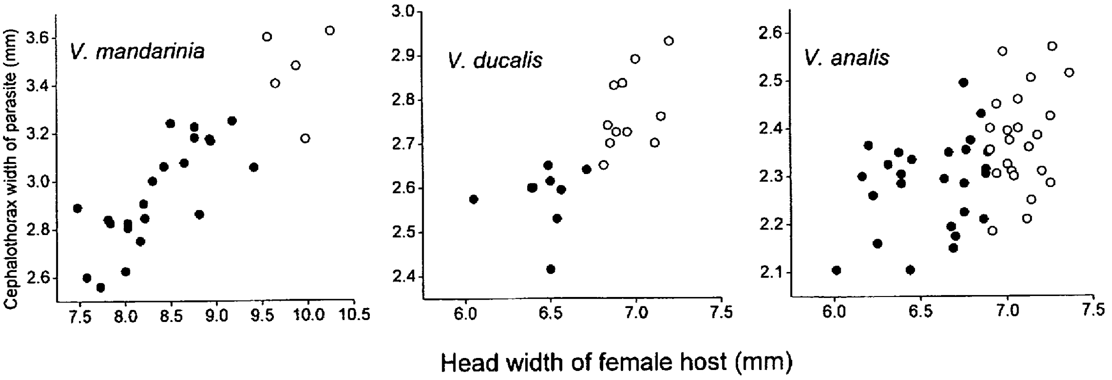

Fig. 3. Relationships between head widths of hornet females and cephalothorax widths of *Xenos moutoni* parasitizing them. Open and solid circles respectively stand for queens and workers of the hosts. For criteria dividing the castes, see text.

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0.15; $P>0.05$). The widths of the cephalothoraces, however, were significantly larger in female parasites which occurred singly on hosts when compared with those which cohabited with at least one parasite [2.29±0.10 (N=20) vs. 2.12±0.14 (N=21) mm; $t=3.94$, $P<0.001$).

Discussion

Matsuura & Yamane (1984) reports the percentage of stylopized hornets collected for ten years in Wakayama Pref., southwestern Japan: 2.2% in *V. ducalis*, 1.1% in *V. analis*, and 0.8% in *V. mandarinia* and *V. simillima*. These figures are much smaller than those in the present study (Table 1). One possible reason for the generally high proportions of stylopization in our study is that we selectively collected those hornets that were attracted to the bait traps. The bait, orange juice mixed with liquor, may have attractive components (odors) similar to those in fermented tree sap, a highly preferred food source of carbohydrate for adult hornets (Matsuura & Yamane, 1984). Holes or scars on tree trunks producing abundant tree sap are visited by many hornets (Matsuura, 1969). Such spots frequented by hornets are suitable places for triungulin (1st instar) larvae of *Xenos moutoni* to wait for new hosts after emerging from the mother's body (Matsuura, 1995). Therefore, the adult female parasite may manipulate the host into visiting those spots producing attractive odor in order to facilitate the dispersal of their offspring. This will result in higher rates of stylopization in hornets collected with attractant traps than in those otherwise collected.

The above explanation, however, does not apply to the hornets with male parasites. Emerged male adults of *Xenos vespularum* live only for 4 to 12 hours in captivity (Kifune & Maeta, 1975), and Kifune & Maeta suppose that the males mate with females within nests of the host, *Vespula flaviceps lewisii*. Although we do not know where *X. moutoni* mates, the fact that almost all male parasites had already emerged when collected suggests that mating also occurs in the host nest in this species. Stylopized males deprived of reproductive ability may spend the rest of the lifetime largely in visiting food places after leaving the nest.

The frequency of stylopized hornets was largest in *V. analis*. In particular, females caught from May to July, mostly consisting of overwintered hornets, were much more frequently parasitized in *V. analis* than in the other species (Fig. 1). Because parasitism levels can vary greatly among localities or years, as Matsuura & Yamane (1984) pointed out, we have to be cautious about generalization from the results. However, similarly high levels of parasitism have been found in spring females of *V. analis* at widely separated localities. In Tsukuba, Ibaraki Pref., stylopized females (overwintered queens and workers) accounted for 16% of all females caught with bait traps from April to June, 1998, while not a single female was parasitized in other *Vespa* species (S. Makino & K. Sayama, unpublished). In Nagoya, Aichi Pref., 40% of females collected with bait traps from April to June, 1997, were parasitized (H. Yamauchi, pers. com.). The high parasitic levels in the spring females suggest either that new queens and workers of *V. analis* are more prone to stylopization late in the nesting season, or that parasitized females are more likely to be attracted to the bait than in the other species. At present, it is unknown what actually occurs.

Parasitism in overwintered queens is of special interest from the viewpoint of hornet population dynamics. Stylopized queens can neither mate nor found colonies (Matsuura & Yamane, 1984), thus decreasing the number of initiated nests in a population. We can not determine if the parasitism in the spring queens has any adverse effect on *Vespa* populations, because there is only scanty information on factors regulating them. It is even possible that decrease in the number of reproductive spring queens results in an increase in the number of productive nests by weakening spring competition over nest sites among the queens, especially of those species that nest in closed spaces (Archer, 1980). It seems, however, that the effects of 3 to 15% parasitism among spring queens on *Vespa* populations may be negligible as compared with other possible factors that reduce the number of initiated nests.

Parasitism levels in workers (overwintered workers excluded) were largest in August and September in the three host species. This is partly compatible with the observation by Matsuura & Yamane (1994) that nests containing stylopized hornets become more frequent as the season proceeds. The declines of parasitic levels in females after September or October may be a result of the adult production schedule of host colonies. The number of worker pupae peaks in August (*V. analis* and *V. ducalis*) or September (*V. mandarinia*), greatly decreasing thereafter (Matsuura & Yamane, 1984). Decrease in the number of worker larvae naturally begins earlier. Because strepsipterans parasitizing social wasps invade larval hosts (Maeta & Kifune, 1990), the decrease in worker larvae in the summer may lead to fewer adult workers found stylopized in the fall. It may be that reproductive larvae are the main hosts for *X. moutoni* larvae after summer.

The nearly complete monopoly of the position between the 5th and 6th terga of the host by female parasites, also reported by Kifune & Arakawa (1996) in *V. analis insularis,* is the opposite of what is observed in *X. vespularum.* Females of *X. vespularum* occur between the 4th and 5th terga and males between the 5th and 6th terga in the host *Vespula lewisii* (Kifune & Maeta, 1975). Maeta & Kifune (1990) reported the same difference in positions between these two parasites. Its biological meaning is unknown.

The correlation in size between hosts and parasites is not surprising, though it was demonstrated for the first time with *Xenos moutoni* in this study. It can be reasonably assumed that larger female parasites produce more larvae than smaller ones do, and that female parasites which occur in larger hosts will produce more offspring, as long as there are no other parasites on the host. Because spring queens are generally larger than workers or males, female parasites in spring queens will have the largest fecundity on average.

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