SEASONAL CHANGES IN LEVELS OF PARASITISM AND SEX RATIO OF XENOS MOUTONI DU BUYSSON (STREPSIPTERA, STYLOPIDAE) IN THE JAPANESE HORNET, VESPA ANALIS INSURALIS DALLA TORRE (HYMENOPTERA, VESPIDAE), COLLECTED WITH ATTRACTANT TRAPS


The percentage of parasitism by Xenos moutoni du Buysson in individuals of Vespa analis insularis Dalla Torre collected with traps containing an attractant in central Japan from 1998 to 2000 was 15-20%. The percentage in overwintered female hornets was 9-23% in May, and 30-48% in June. Parasitism levels decreased to 3-13% in September and 0-7% in October, when workers and males were collected instead of overwintered females. Overwintered female hornets that were parasitised had only one or two strepsipterans, while workers and males harboured more: one to five. The overwintered female hornets were always parasitised by female strepsipterans, while the workers and male hornets were more frequently parasitised by male rather than female Strepsiptera.

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_Xenos moutoni_ du Buysson is a strepsipteran parasite of hornets and is distributed in China, Taiwan, Vietnam, and Japan (Kifune 1992). In Japan, it is reported to parasitise six species of *Vespa* (Kifune 1992, Matsuura 1995). When parasitised, workers of the host do not work, and reproductive individuals (males and new queens) do not mate or show nesting behaviour (Matsuura 1984). Therefore, high levels of parasitism in the colonies, especially in their early stages, may lead to serious loss in fecundity of the host. In this respect, _X. moutoni_ is a potentially important natural enemy.

Stylopized hornets are encountered only rarely in the field. Makino & Yamashita (1998), however, found that many hornets collected with an attractant trap harboured _X. moutoni_. They showed that _Vespa analis insularis_ Dalla Torre was the most frequent host of the strepsipteran among the trap-collected hornets, and that levels of parasitism and the sex ratio of the parasite greatly fluctuated throughout the season. However, their results are based on a single-year study in a locality in southern Japan, so it remains unknown how general their results are through time and regions. In this paper, I give the results of a three-year monitoring study of stylopized hornets in central Japan between 1998 and 2000.

MATERIAL AND METHODS

Hornets were collected with bait traps from April through November in Ushiku City and Kukizaki Town (36°N, 140°E), Ibaraki Prefecture, from 1998 to 2000. These localities are located in the Kanto Plane, central Japan. The traps were of the same type as that described by Makino & Yamashita (1998): bait was comprised of clear liquor and an equal amount of orange juice, and beverage bottles of clear plastic (about 30 cm high, 10 cm in diameter, and 1500 to 2000 cm$^3$ in capacity) with a small square hole (3x3 cm) were used as bait containers. Ten bait traps were set in a small copse (Oak plot) mainly composed of de-
Fig. 1. Total number of hornets of the five *Vespa* species collected with attractant traps from April through November, 1998 to 2000. For each species, the total catch is divided into females (overwintered queens and workers) and males.

Fig. 2. Percent of individuals parasitised by *Xenos moutoni* in the total number of female or male hornets of the five *Vespa* species collected in the three years.
ciduous oaks, *Quercus serrata* Thunb. and *Q. acutissima* Carruth., and another ten in a part of a nursery (Willow plot) where hundreds of willows (*Salix* spp.), less than 10 cm in diameter, were planted. The two plots were 1 km away from each other. The traps, strung from trees between 1.0 and 1.5 m above the ground, were set at intervals of about 10 m. Additional traps (12 in 1998 and 16 in 1999 and 2000) were set in an outdoor apiary of the National Institute of Animal Industry (Honeybee plot), 1.5 km apart from the Willow plot. These traps used a mixture of apple juice, liquor and vinegar as bait instead of liquor and orange juice, and were also hung from trees surrounding the apiary at intervals of less than 10 m. In general, trapped hornets were collected every day, though sometimes at longer intervals up to seven days. Bait was renewed every two weeks in the Oak and Willow plots and once a week in the Honeybee plot. Collected vespine wasps were preserved in 70% ethanol and later examined.

RESULTS

Species compositions of hornets collected with bait traps

The total numbers of hornets collected in the three plots from May through December were 990, 1,334 and 1,587 in 1998, 1999 and 2000, respectively. Yearly catch per trap was largest in the honeybee plot in all three years (about 40 to 50 hornets per trap). The collected hornet species were *Vespa analis insularis* Dalla Torre, *V. mandarinia japonica* Radoszkowski, *V. ducalis pulchra* Buysson, *V. simillima xanthoptera* Cameron and *V. crabro flavofasciata* Cameron, of which the first three species predominated, accounting for about 90% of the total capture in all of the three years. Other collected vespid wasps were *Vespula flaviceps lewissii* (Cameron), *Polistes chinesis antennalis* Peréz, *P. melleni* de Saussure, *P. jadwigae* Dalla Torre, *P. nipponensis* Peréz, and *Parapolybia indica* (de Saussure), of which *Vespula flaviceps* and *Parapolybia indica* accounted for more than 80% of these wasps.

Both female and male hornets were collected from the above five *Vespa* species, though male catches were much smaller than female (fig. 1). Principally, females that were collected from May through June were overwintered individuals. Females collected from August onwards were workers produced in the current year (hereafter called ‘new workers’ to distinguish them from overwintered workers). Some females collected in July were overwintered individuals, and the others were new workers. Males usually occurred in and after September along with workers; male ratios in the annual catch in the three years were relatively high in *V. ducalis* (0.17 to 0.20), and *V. crabro* (0.04 to 0.17), while only 0.02 to 0.07 in the other species. New queens before their hibernation were not collected except in *V. ducalis*, in which queen-size females were often collected in autumn.

Levels of parasitism by *Xenos moutoni*

Stylopized individuals occurred in all *Vespa* species except for *V. mandarinia* at least in one of the three years (fig. 2). However, the levels of parasitism greatly differed among the species and between sexes of the host: it was fairly high and constant in female *V. analis*, where 15-20% individuals were parasitised every year, whereas it was quite low in the other three species, only 2% at largest. Levels of parasitism in males were usually much lower than in females; the relatively high levels in *V. simillima* and *V. crabro* males in 1999 (fig. 2) seem to be sampling errors because of the small sample sizes of male (fig. 1). Because stylopized individuals were very rare in the three hornet species other than *V. analis*, these species were omitted from the following description.

Seasonal changes in level of parasitism and sex ratio of *X. moutoni*

Seasonal changes in the proportion of stylopized insects of *V. analis* are shown in fig. 3. In the three years, the percentage of parasitism was 9-23% and 30-48% in May and June, respectively, when almost all wasps that were collected were females that had overwintered. In all three years, the parasitism level was significantly higher in June than in May (*P*<0.001 in all years; χ² test). Because stylopized workers often overwinter as new queens (Matsuura & Yamane 1990), a part of these overwintered females were supposed to have been produced as workers, judging from their apparent small sizes (Makino & Yamashita 1998, Tatsuta &
Fig. 3. Monthly changes in percent of parasitised hornets (lines) and the number of collected hornets (columns) in the three years in *Vespa analis*. Overwintered females, new workers of the current year, and males are distinguished in the columns by patterns of hatching.

Fig. 4. Monthly changes in the number of female and male *Xenos moutoni* (columns) harbored by trapped hornets of *Vespa analis* and in the male ratio of *X. moutoni* (lines) in three years. Male ratio is the number of males divided by the total number of parasites in each month.
Makino, submitted).

In July and August, collected hornets mainly comprised of new workers, and the level of parasitism was comparable to that in June, though catches were generally small in these months. The level of parasitism in new workers was 3-13% in September, and 0-7% in October.

Monthly changes in the sex ratio (male ratio to total) of the strepsipterans on *V. analis* are depicted in fig. 4. Only female strepsipterans were found in May and June, while the male ratio increased after August onwards in 1998 and 1999. A similar change was seen in 2000, though a small number of males occurred in July.

**Numbers and positions of strepsipterans on hosts**

The number of adult *X. moutoni* per host varied from one to five (table 1). More than 90% of overwintered females that were stylopidized had a single female strepsipteran, and the rest had two. Superparasitism was more common in new workers or males, and male and female strepsipterans often occurred in the same host. There is a significant difference in the number of parasites per host between overwintered and new workers in the three years (*P*<0.05 in all years; Mann-Whitney U-test).

In both female and male hosts, female strepsipterans almost always occurred between the gastral tergites 5 and 6, protruding the anterior part of the cephalothorax. Males, on the other hand, occurred between the tergites 4 and 5, or 3 and 4. Nearly all male parasites on the hosts had already emerged, leaving only their empty puparia in the host metasoma.

**Discussion**

The study established the dominance of *V. analis* as a host of *X. moutoni* among the five species of hornets attracted to the bait trap. This result agrees with those reported for southern Japan (Makino & Yamashita 1998). The dominance of *V. analis* as a host was not caused by collection bias: as many *V. ducalis* and *V. mandarina* were collected as *V. analis*. The high rate of parasitism in trapped *V. analis* suggests either that hornets of the species are more prone to be parasitised by *X. moutoni*, or that parasitised hornets are more likely to be attracted to the bait as compared with those of *V. mandarina* or *V. ducalis*. These three species naturally have different bionomic characteristics in terms of colony cycle and size, or prey preference (Matsuura & Yamane 1990). However, it is unknown what makes *V. analis* the most frequently parasitised host. A detailed study of the biology of the hornet host and that of the strepsipteran has to be carried out.

The difference in levels of parasitism between May and June is interesting from the viewpoint of the tactics of the strepsipteran. First instar larvae of *X. moutoni* are transferred by a hornet (foundress) to the nest and they parasite the larval hosts (Maeta & Kifune 1990). Because first instars are generally short-lived (Maeta & Kifune 1990), they would perish unless the nest contains larvae of the host. Nests of *Vespula* spp. are usually initiated from early to mid May in central to southern Japan, except for *V. ducalis* whose nesting activity starts in June (Matsuura & Yamane 1990). Host larvae appear after mid to late May because the eggs require four to six days to hatch (Matsuura & Yamane 1990). Therefore, it is advantageous for the strepsipteran to produce first instars in late May or later when nests of the hornets contain larvae. It is possible that the strepsipteran makes the female host hornets come out from hibernation a little later than non-parasitised females. This will enable the first instars to emerge at the right time to invade the hornets’ nest. This would result in a higher proportion of stylopidized females in June than in May, as was observed.

*X. moutoni* that were found on overwintered hornets were always female, thus the sex ratios are female-biased in the early part of the season. This is possibly because hornets parasitised by male *Xenos* die in autumn after the emergence of the strepsipteran without entering hibernation. However, female hornets parasitised only by female *Xenos* are considered to go into hibernation, even if they are workers and are small in size compared with new queens (Matsuura & Yamane 1990, Makino & Yamashita 1998). There is another possibility of the female-biased sex ratio of the parasite among the overwintered females: these overwintered females may be somehow parasitised more frequently by female *Xenos* than by males. Kifune & Maeta (1975) found that in autumn colonies of another social wasp, *Vespula flaviceps lewisi* (Cameron), sex ratio of *Xenos vesparium* was female-biased among new queens, while male-biased among workers. They suggested that this is advantageous for female parasites, because they can safely overwinter if parasitising new queens which have the ability to hibernate. It is unknown whether the sex ratio of *X. moutoni* is also female-biased in new queens of *V. analis* before hibernation. Further study is needed to examine the sex ratio of the strepsipteran among different casts of the host. On the other hand, female *X. moutoni* seems to be able to manipulate workers to go into hibernation (Matsuura & Yamane 1990, Makino & Yamashita 1998). Therefore, parasitising new queens is not the only way the strepsipteran overwinters, although its fecundity is expected to be higher when parasitising new queens than when parasitising workers. This is because new queens are usually larger than workers and because larger hosts tend to be parasitised by larger females of strepsipteran (Makino & Yamashita 1998, Maeta et al. 1998).

The ratio of male strepsipteran was 0.5 or higher.
after September. This roughly agrees with sex ratios of *X. moutoni* in infested nests: seven *V. analis* nests collected near the study plots in September, 1998 and 1999, contained 5-40 workers or males parasitised with *X. moutoni*; the ratio of male strepsipteran in these individuals was 0.4-1.0, averaging at 0.7 (Makino unpublished).

Male puparia of *X. moutoni* found in nests of *V. analis* nearly always had pupae (Makino unpublished), while almost all puparia in the baited hornets were empty. This suggests that hosts of male *X. moutoni* leave their nests immediately after the parasites emerge, or that male parasites emerge after the hosts leave the nests. Although Kifune & Maeta (1975) and Makino & Yamashita (1998) mention the possibility that mating in *X. vesparum* and *X. moutoni* occurs in nests of the hosts, it is also possible that mating occurs outside the nests, especially in places where hornets visit frequently such as sap-rich apertures of trees (Matsuura & Yamane 1990).

In order to understand why the level of parasitism and the sex ratio fluctuate seasonally, we need information on the number of generations of *X. moutoni* in one year. Though voltinism of the species is not clear, Matsuura & Yamane (1990) said there are at least three generations a year because adult hornets with *X. moutoni* are continuously found in nests from mid to late June through late November. First instars of *X. moutoni* invade the hornets’ larvae and emerge after the host larvae develop into adults (Maeta & Kifune 1990). Hornet larvae take 25-35 days to develop into adults (Matsuura & Yamane 1990), and parasitised workers of *V. crabro* leave their nests nine to 12 days after emergence (Matsuura & Yamane 1990), when the strepsipterans already emerged or are ready to emerge. The duration from first instar to adult in *X. moutoni* is estimated at 35-50 days. If this estimation is correct, at least three generations are possible in one year, as supposed by Matsuura & Yamane (1990).

This study shows that the attractant trap is useful in collecting stylopized hornets away from the nests. By combining it with examination of stylopized nests, this method will provide us with a useful way of studying the biology of *X. moutoni* in much more detail.

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**REFERENCES**


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