

THE SPATIAL PATTERNS OF PARASITISM OF EUMENID
WASPS, *ANTERHYNCHIUM FLAVOMARGINATUM* AND
ORANCISTROCERUS DREWSENI BY THE
MILTOGRAMMINE FLY
*AMOBIA DISTORTA*¹⁾

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INTRODUCTION

Theoretical host-parasitoid models (e.g. HASSELL and MAY, 1973; MAY, 1978; COMINS and HASSELL, 1979) have demonstrated that the aggregative behavioral response of parasitoids against a host population will contribute to the stability of the host population. The response of some parasitoid species to patchy host distributions are well known in the field (see HASSELL, 1982 for review). Most of these examples, however, deal with the spatial pattern of parasitism for only one generation and at only one study area. Only a few authors have shown that spatial distribution of percent parasitism changes between generations (HASSELL, 1968) or between habitats (HEADS and LAWTON, 1983). In these two cases, the basic spatial pattern did not change, but the slope of the density relationship changed. Both of them showed that the slopes of density dependent increase of the percent parasitism in relation to host density per patch were inversely correlated with the overall host density of the generation or of the habitat. Such a tendency is consistent with a model that assumes an optimally foraging parasitoid (COOK and HUBBARD, 1977). There have been, however, no field studies that analyze the effect of overall parasitoid density on spatial patterns of parasitism.

The goal of this study is to investigate the inter-generation difference of the spatial pattern of percent parasitism of two eumenid wasps, *Anterhynchium flavomarginatum* and *Orancistrocerus drewseni*, by the miltogrammine fly, *Amobia distorta*. Firstly, I show that the spatial pattern of percent parasitism is density dependent in generations of low and medium parasitism and density independent in generations of high parasitism in both species of host wasps. Secondly, to consider causes of this difference, I examined the spatial distribution of adult parasitoids among host patches. The miltogrammine fly avoided patches with many conspecifics. The severe mutual interference of mitogram-

1) Contribution to the ecological studies of the eumenid wasps. II.

mine flies at each host patch appeared to lead to such patch selection behavior. Finally, I discuss the role of such patch selection behavior in determining the spatial pattern of parasitism.

MATERIALS AND METHODS

Materials

Amobia distorta ALLEN is a miltogrammine fly that ranges widely in north temperate areas and is very common in Japan (KURAHASHI, 1970). In Kyoto, adult flies appear from June to October. The parasitizing behavior of female flies was studied by ITINO (1986). Seven host species were recorded by KURAHASHI (1973) (6 species of Eumenidae and 1 of Sphecidae). In addition, IWATA (1938) found that *Orancistrocerus drewseni* SAUSSURE was also parasitized by this fly. Of these 8 host species, eumenid wasps *Anterhynchium flavomarginatum* SMITH and *O. drewseni* were especially abundant in the study area. The general life histories of these two eumenid hosts have been discussed previously by ITINO (1986).

Study area

The study area (10 km × 10 km), located in the northern suburbs of Kyoto, contained about 150 small sheds each with 40–100 bamboo poles ($\phi > 2$ cm). The cut ends of the poles were available nest sites only for *O. drewseni*. Besides these sheds, there were about 30 small sheds lacking bamboo poles. I placed a bundle of 50–100 bamboo internodes ($\phi < 2$ cm) at each of 10–20 small sheds containing bamboo poles and at each of 10–20 small sheds lacking bamboo poles. These slender internodes were available for both *O. drewseni* and *A. flavomarginatum* (details in ITINO, 1986).

Census procedures

At the end of the breeding season of each generation (i.e., in early August for the first generations of *O. drewseni* and in the early winter for *A. flavomarginatum* and the second generations of *O. drewseni*), several sheds occupied by the wasps were chosen randomly for census. The number of sheds chosen for census is summarized in Table 1. At each shed, some of the nests of the two eumenids were collected. The mean number of total nests or that of total cells collected per shed was, respectively, 4.9 or 10.7 in *A. flavomarginatum* and 4.0 or 8.8 in *O. drewseni* (ITINO, 1986). Nests were then dissected to examine the number of cells and brood mortality factor at each cell.

Estimation of number of foraging trips

The miltogrammine fly finds the wasp nest by following the foraging wasp when the wasp returns to its nest. Once located, the miltogrammine fly attacks not only the nest of the returning wasp, but also neighboring nests. Thus, the probability that one nest in a small shed is found by the miltogrammine fly is thought to be a function of the

Table 1. Changes in percent parasitism of the two eumenid wasps, *Anterhynchium flavomarginatum* and *Orancistrocerus drewseni*, by the miltogrammine fly, *Amobia distorta*.

A. *flavomarginatum*

Generation	1980	1981	1982	1983
No. of censused sheds	4	16	7	21
No. of cells (total)	22	233	43	154
No. parasitized (total)	3	72	9	22
% parasitism	13.6	30.9	20.9	14.3
Standard error of % parasitism	19.8	7.3	7.6	4.9

O. *drewseni*

Year Generation	1980 2nd	1981 2nd	1982 2nd	1983		1984	
				1st	2nd	1st	2nd
No. of censused sheds	5	11	8	19	7	2	6
No. of cells (total)	115	45	82	87	84	24	55
No. parasitized (total)	25	10	1	2	14	3	8
% parasitism	21.7	22.2	1.2	2.3	16.7	12.5	14.5
Standard error of % parasitism	6.1	12.2	1.2	1.3	7.2	8.2	4.9

total number of foraging trips by wasps nesting in the shed.

The total number of foraging trips per shed during a generation period (F) is estimated by

$$F = f_a c_a n_a + f_o c_o n_o$$

where f is the average number of foraging trips to collect larval food into one cell, c the average number of cells per nest and n the number of nests made in the shed during the generation period. The subscripts a and o are used for *A. flavomarginatum* and *O. drewseni*, respectively. ITINO (1986) calculated the following estimates; $f_a = 9.25$, $f_o = 24.88$, $c_a = 2.17$ and $c_o = 2.60$. Thus F can be estimated from n_a and n_o in each shed. Since the two eumenids were followed at nearly equal probabilities by the miltogrammine fly per foraging trip (ITINO, unpub.), F is a good index of the shed being located by the parasitoid.

Spatial distribution of the miltogrammine fly

During 1982-1984, twenty to fifty sheds with nesting wasps were randomly selected in each year, and were censused at 1-10 day-intervals throughout their breeding season. At each of these sheds, the number of the wasp nests being con-

structed or provisioned was counted. The number of miltogrammine flies that flew or perched around the shed was also counted during a five minute observation.

Grouping of the data

Since the sample size (the number of censused sheds and nests dissected per shed) for each generation was rather small (cf. Table 1), the following analysis of spatial patterns of parasitism was done separately for three levels of percent parasitism by the miltogrammine fly. The generations of which the average percent parasitism by the miltogrammine fly was more than 20% is the high parasitism group (1981 and 1982 generations of *A. flavomarginatum* and 2nd of 1980 and 2nd of 1981 generations of *O. drewseni*); those of which the percent parasitism was less than 5% is the low parasitism group (2nd of 1982 and 1st of 1983 generations of *O. drewseni*); the remaining is the medium parasitism group (the other generations of the two eumenids, Table 1).

Considering the host searching behavior of the miltogrammine fly, it seems that we can analyze the data of several generations of the same level of percent parasitism as a group. As already shown, the miltogrammine fly, which emerges about half a month prior to the two eumenid wasps, disperses from the natal shed, and then, finds the host shed anew by following the foraging host (ITINO, unpub.). This behavior permits us to assume that the total number of adult miltogrammine flies emerging in each generation are distributed into each shed according to the host density there. Under such conditions, the spatial pattern of parasitism seems to be similar among generations of the same level of percent parasitism, and does not depend on the percent parasitism of the preceding generations in each shed.

RESULTS

Temporal changes in percent parasitism by the miltogrammine fly

The changes in percent parasitism of the two eumenid wasps by the miltogrammine fly are shown in Table 1. As the sample size of each generation (number of censused sheds and that of censused cells) was small, the standard error of the mean percent parasitism were throughout large. But there seemingly exist generations of relatively higher parasitism on one hand and generations of relatively lower parasitism on the other hand. I assume that the relative level of percent parasitism in each generation is the result of different density of adult parasitoid existing in the sheds at that period. That is, the more adult miltogrammine flies, the higher the rate of parasitism. As the changes in the host density between generations were rather small in the sheds (ITINO, unpub.), this assumption appears reasonable. This assumption is adopted in the following analysis of the spatial pattern of parasitism and I use 'higher parasitism' as synonymous with 'higher parasitoid density'. It was shown in Table 1 that the overall levels of percent parasitism of the two eumenids were similar in spite of the maternal defense of *O. drewseni* against the miltogrammine fly (ITINO, 1986). The

reason for this similarity will be discussed later in relation to the host density at each shed.

Spatial pattern of parasitism

Fig. 1 shows the spatial pattern of percent parasitism of *A. flavomarginatum* by the miltogrammine fly (*P*) in relation to total number of foraging trips per shed (patch) by the two eumenids (*F*). As already mentioned, data of several generations were combined according to whether the mean percent parasitism of the generation was high (>20%), medium (5-20%) or low (<5%). The data of sheds of similar *F* value are pooled (the ranges are shown at the top of each figure). In generations of medium parasitism (Fig. 1a), the percent parasitism per shed increased as *F* increased. On the

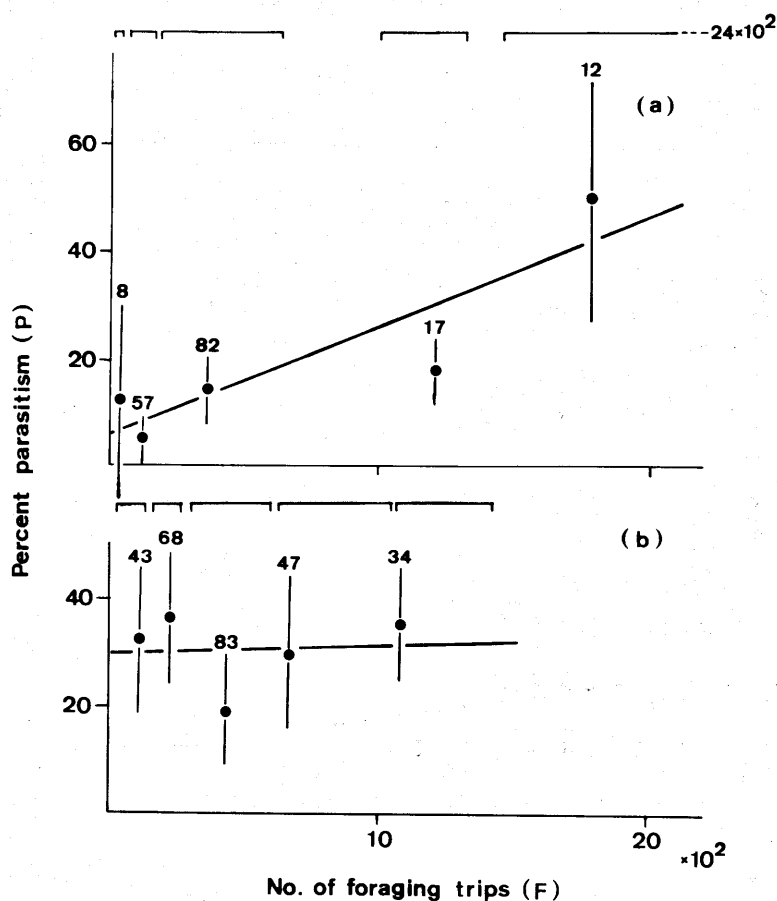


Fig. 1. The spatial patterns of percent parasitism of the eumenid wasp *Anterhynchium flavomarginatum* by the miltogrammine fly *Amobia distorta* (*P*) in relation to total number of foraging trips of the two eumenid wasps per shed (patch) (*F*). Vertical lines show standard error. The numbers of hosts inspected are shown above. The ranges of pooled data are shown at the top of each figure. (a): generations of medium parasitism ($P=2.00 \times 10^{-2}F + 6.01$, $r^2=0.776$, $p<0.05$), (b): generations of high parasitism ($P=1.51 \times 10^{-3}F + 30.0$, $r^2=0.0072$, $p>0.1$).

contrary, in generations of high parasitism (Fig. 1b), there was no positive relation between the percent parasitism and the number of foraging trips.

In *O. drewseni*, the pattern was similar to that of *A. flavomarginatum*. In generations of low and medium parasitism (Figs. 2a and 2b), the percent parasitism was spatially density dependent. On the other hand, in generations of high parasitism (Fig. 2c), there was no density relationship detected between *P* and *F*. The levels of the percent parasitism *P*, however, were lower in *O. drewseni* than in *A. flavomarginatum* if compared at the same *F* levels (see Figs. 1a vs. 2b and 1b vs. 2c). This is probably because *O. drewseni* defends the offspring against the attack of the miltogrammine fly

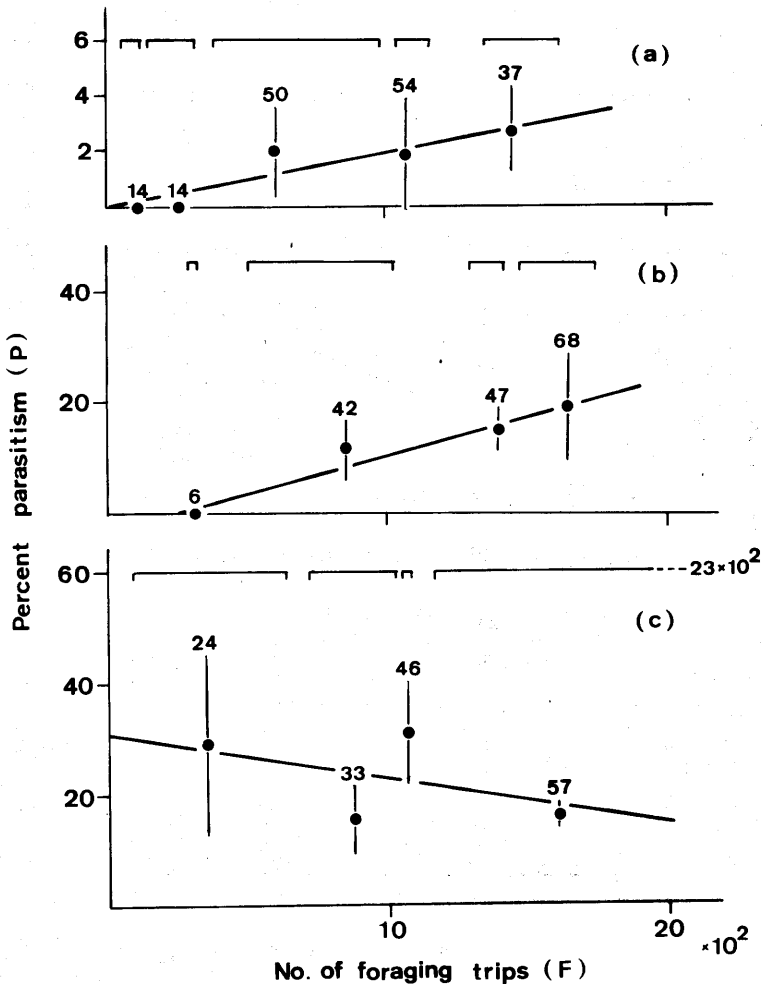


Fig. 2. The spatial patterns of percent parasitism of the eumenid wasp *Orancistrocerus drewseni* by the miltogrammine fly (*P*) in relation to total number of foraging trips of the two eumenid wasps per shed (patch) (*F*). (a): generations of low parasitism ($P=2.01 \times 10^{-3}F - 0.09$, $r^2=0.833$, $p<0.05$), (b): generations of medium parasitism ($P=1.34 \times 10^{-2}F - 2.51$, $r^2=0.929$, $p<0.05$), (c): generations of high parasitism ($P=-8.50 \times 10^{-3}F + 30.9$, $r^2=0.287$, $p>0.1$). See Fig. 1 for details.

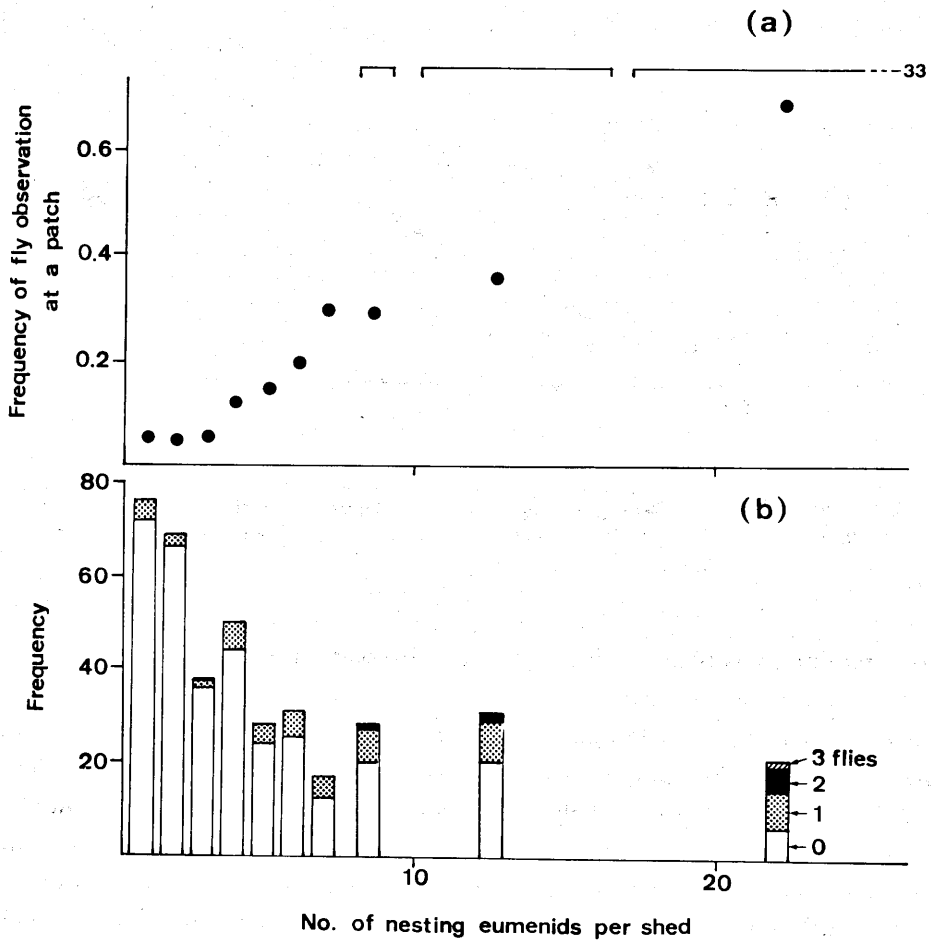


Fig. 3. (a) The frequency of cases in which the miltogrammine fly was recorded in a 5 minute observation plotted against the number of two eumenids nesting at the shed. The ranges of pooled data are shown at the top of the figure. (b) Frequency distribution of observed number of miltogrammine flies per shed.

with maternal care (ITINO, 1986).

The similarity of the spatial pattern of parasitism in these two host species indicates that there are some underlying mechanisms that determine the spatial parasitism pattern by the miltogrammine fly (e.g., the method of host shed selection by the parasitoid). To identify this mechanism, I will analyze the spatial distribution pattern of the adult miltogrammine fly among sheds. The following analysis is done only in generations of low and medium parasitism.

The behavioral response by the miltogrammine fly at generations of low and medium parasitism

Fig. 3a shows the relationship between the frequency of cases in which the

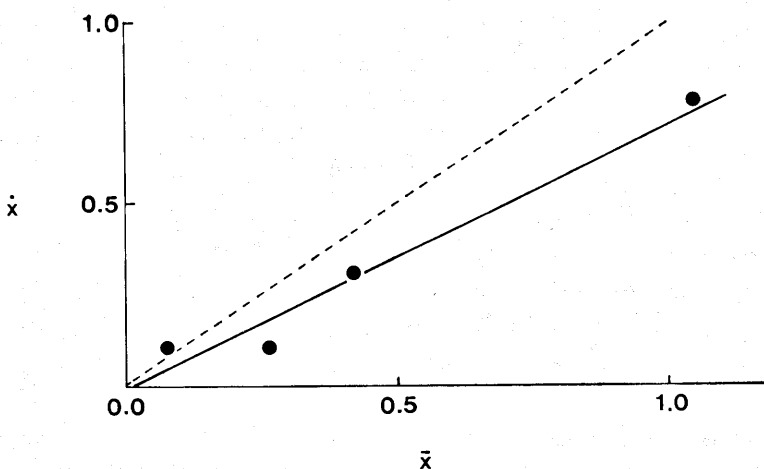


Fig. 4. The relation of mean crowding (\bar{x}^*) to mean density (\bar{x}) in the observed number of miltogrammine flies per shed. Dotted line shows expectation from Poisson series.
 $\bar{x}^* = -0.017 + 0.753\bar{x}$ ($r^2 = 0.967$, $p < 0.05$)

miltogrammine fly is recorded in a 5 minute observation and the number of the two eumenids nesting at the shed. The number of nesting eumenids is roughly proportional to daily number of foraging trips per shed because the two eumenids made similar numbers of foraging trips per day (ITINO, unpub.). The data of sheds of similar host density are grouped altogether in three cases (the ranges are shown at the top of the figure). The frequency observations of the miltogrammine fly was higher at sheds of higher host density (Fig. 3a). This indicates that miltogrammine flies aggregated at sheds of higher host density and/or they stayed longer there. Such an aggregative behavioral response is one of the reasons for the density dependent spatial pattern of parasitism at generations of low and medium parasitism (Figs. 1a, 2a and 2b).

As the host density per shed increased, the frequency of cases in which multiple miltogrammine flies were found increased as shown in Fig. 3b. This is the result of their aggregative behavioral response. But, from Fig. 3b, it seems that the frequency distribution of observed number of the miltogrammine fly at each host density level is more uniform than a Poisson distribution. I examined this by utilizing the mean-crowding index (IWA0, 1968). The \bar{x}^* - \bar{x} relationship of the number of miltogrammine flies observed per shed is shown in Fig. 4. Each plot represents pooled data according to 4 ranges of host densities per shed (i.e., sheds of 1-5, 6-9, 10-16, 17-33 hosts, from left to right). Judging from the values of the slope of the regression line and the intercept on the ordinate, the spatial distribution of the miltogrammine fly was the positive binomial distribution of which the maximum number of individuals per shed was 4.05 (IWA0, 1968). This means that the miltogrammine fly distribution is under-dispersed (or regular) among sheds.

DISCUSSION

There have been a few field examples in which the spatial pattern of parasitism differs between generations or between habitats (HASSELL, 1968; HEADS and LAWTON, 1983). Both of these two studies showed that the slopes of the density dependent increase of the percent parasitism in relation to host density per patch were inversely correlated with the mean host density of the generation or of the habitat. HASSELL (1980) showed that this was consistent with the prediction of the optimal foraging model of COOK and HUBBARD (1977). But in the present study, there was no significant relation between the mean host density of the generation and the slope of density dependence ($r^2 = 0.049$, $p > 0.1$ in *A. flavomarginatum* and $r^2 = 0.047$, $p > 0.1$ in *O. drewseni*). Rather than the mean host density of the generation, the mean percent parasitism of the generation was more crucial in determining the shape of density relationships. That is, the percent parasitism was spatially density dependent when the mean percent parasitism of the generation was high, and density independent when it was low. The host searching behavior of the parasitoid seems to cause such different spatial patterns of parasitism.

Fig. 4 suggests that there are some negative interferences between the miltogrammine flies at each shed. In practice, female mitogrammine flies approaching the same host interfered with each other so severely that they both nearly always failed to parasitize (ITINO, unpub.). Such mutual interference often occurred at sheds of higher parasitoid densities (ITINO, unpub.). ENDO (1980) also observed that mutual conspecific interference in the miltogrammine fly *Metopia sauteri*, which parasitizes the spider wasp *Episyron arrogans*, caused frequent failure in parasitism. In the present study, to avoid the adverse effect of the mutual interference, *A. distorta* seems to disperse from sheds of higher parasitoid density. Judging from the rather low maximum parasitoid density per shed (about 2, see Fig. 3b), the miltogrammine flies seemed to disperse before they interfered severely with each other. If they also use such a method of shed selection in generations of high parasitism, as sheds of high host density become filled with the miltogrammine flies, surplus flies tend to disperse to sheds with less hosts. As a result, more flies may come to sheds of low host density so that the percent parasitism at sheds of low host density would increase compared with those in generations of low parasitism. This is the most plausible reason for the spatially density independent relationship in generations of high parasitism.

HASSELL (1971) showed experimentally that the aggregative response of the parasitoid decreased as the total parasitoid density increased, i.e., the proportion of total time spent by the parasitoid at patches of higher host density reduced as the total number of searching parasitoid increased (analyzed in HASSELL, 1978). Such a tendency was consistent with the prediction of the optimal foraging model (COOK and HUBBARD, 1977). COOK and HUBBARD, however, assumed that a parasitoid forager maximized its rate of encounter with healthy hosts in a patchy environment. That is, the optimal

solution is affected only by the relative number of healthy hosts at each patch, and not by the spatial variation of parasitoid mutual interference. If accounts are taken of the reduction of patch fitness due to the mutual interference, such tendency of the optimal foraging model (lower aggregative response in situations of higher parasitoid total number) would be emphasized. Such an effect of mutual interference could be incorporated into the model by a positive correlation between the handling time and the parasitoid density per patch.

Although the basic spatial patterns of parasitism were similar in the two eumenids (Figs. 1 and 2), the percent parasitism was higher in *A. flavomarginatum* than in *O. drewseni* in the same range of the number of foraging trips (Figs. 1 and 2). This may be because the maternal care, which reduces the parasitoid attack rate, is lacking in *A. flavomarginatum* but is present in *O. drewseni*. A female of *O. drewseni* continues provisioning for about one week until the larva grows to instars 3-5. Her maternal behavior in this period contributes to reduce the mortality by the miltogrammine fly (ITINO, 1986). But, on the other hand, the percentage of parasitism per generation were, as a whole, at about the same level between the two eumenids (Table 1). This can be explained as follows. As *O. drewseni* was inhibited at sheds of relatively higher wasp densities (the mean number of foraging trips F was 1094.2 ± 502.8 (mean \pm SD, $N=58$) in *O. drewseni* and 450.5 ± 391.8 ($N=49$) in *A. flavomarginatum*, $p < 0.001$, two tailed t-test), the chances of host larvae being attacked by the miltogrammine fly were higher in *O. drewseni* than in *A. flavomarginatum*. However, because of the maternal care of *O. drewseni*, the percent parasitism of the two eumenids was roughly equivalent. Such an interspecific difference in the mean number of foraging trips per inhabited shed as shown above was the result of the pattern of shed use by the two eumenids. The emerged adults of *O. drewseni* often return to the natal shed and make their nest there. They, moreover, tend to make the second or third nest at the shed where they made the previous nest. As a result of this philopatry, *O. drewseni* tends to nest with a considerable number of conspecifics at a shed. On the other hand, *A. flavomarginatum* rarely returns to the natal shed nor makes the next nest at the same shed. So, *A. flavomarginatum* often makes its nest with a few conspecifics. Such shed utilization of the two eumenids will be published elsewhere in relation to pressures by various enemies including the miltogrammine fly.

SUMMARY

1. Spatial patterns of parasitism of eumenid wasps *Anterhynchium flavomarginatum* and *Orancistrocerus drewseni* by the miltogrammine fly *Amobia distorta* were studied in Kyoto, Japan during 1980-1984.
2. In generations of low (<5%) and medium (5-20%) parasitism, percent parasitism per shed (the habitat of the hosts) increased as a function of host density. Conversely, in generations of high (>20%) parasitism, percent parasitism was rather

constant over different host densities.

3. The spatial distributions of adult miltogrammine flies among sheds were censused in generations of low and medium parasitism. The frequency of observations of adult miltogrammine flies was higher at sheds of higher host density (aggregative behavioral response), but on the other hand, the adult miltogrammine flies distributed in an underdispersed (or regular) manner in relation to other conspecifics.

4. The spatially density independent relationship between host density and percent parasitism in generations of high parasitism was explained in relation to parasitoid dispersal from patches of high parasitoid density.

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オオフタオビドロバチとオオカバフスジドロバチに対する
ドロバチヤドリニクバエの寄生の空間的パターン

市野隆雄

寄生率の空間的密度依存性は、同じ寄主—寄生者の組み合わせであれば、場所や世代が違っていても基本的には同じパターンを示すという研究がこれまでなされてきた。本研究ではこの点について、世代によって寄生率の空間的パターンが異なっていた事例を示す。合わせて、異なる2種の寄主に対する寄生の空間的パターンが基本的には類似していたことも報告する。

京都市の広範囲にわたる地域 (10 km × 10 km) において1980年から1984年にかけて野外調査を行った。この地域にパッチ状に分布する2種のドロバチ、オオフタオビドロバチ (*Anterhynchium flavomarginatum*) とオオカバフスジドロバチ (*Orancistrocerus drewseni*) に対するドロバチヤドリニクバエ (*Amobia distorta*) の寄生率の空間的パターンをオオフタオビでは4世代、オオカバフでは7世代について調べた。

寄生率の空間的密度依存性は、両寄主とも世代によってそのパターンが変化した。平均寄生率が低い世代においては、寄主密度の高いパッチほど寄生率も高くなった。一方、平均寄生率が高い世代においては、寄生率はパッチ当たりの寄主密度の高低にかかわらずほぼ一定であった。これらの傾向は両寄主ともにみられ、寄生率の基本的な空間的パターンは2種の寄主間で類似していた。

世代によって寄生の空間的パターンが違っていった理由を理解するために、ニクバエ成虫がパッチ間でどのように空間分布しているかを、平均寄生率が低い世代について調べた。ニクバエが少なくとも1頭発見される確率は、寄主密度の高いパッチほど高く、寄主の多いパッチにニクバエが集まってくるのがわかった。しかし、Iwao (1968) の $m^* - m$ 法で解析するとニクバエ成虫は空間的に正の二項分布をしており、互いにある程度以上こみあわないようにパッチを選んでいることがわかった。パッチ当たり最大収容数は4.05頭と推定された。

平均寄生率の高い世代においては、寄主を探索するニクバエの個体数が多いため、寄主密度の高いパッチでニクバエ同士の相互干渉が頻繁におこると考えられる。この干渉を避けるためにニクバエが寄主密度の低いパッチへ分散することによって、寄生率がどのパッチでも同じレベルになったと結論づけた。