Some Colony Factors Influencing the Hunting Activity of
Polistes chinensis antennalis PÉREZ
(Hymenoptera : Vespidae)

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Field examinations were made to determine the more important colony factors influencing the hunting activity of *Polistes chinensis antennalis* PÉREZ. The degree of hunting activity was directly proportional to the number of workers. Low hunting activity before emergence of the first workers was due partly to solitariness of foundresses and partly to their low hunting efficiency as compared with that of workers. Hunting activity increased with an increase in the number of the 3rd to 5th instar larvae after the first workers emerged. Age polyethism among workers was observed. Rapid increase of the hunting activity was due partly to their high hunting efficiency enhanced by the age polyethism until the emergence of the first males. The hunting activity decreased after the emergence of the first males partly because the number of larvae decreased owing to cannibalism by adults and partly because workers devoted more labor to collecting liquid food than to hunting. It is concluded that the number of larvae has a great effect on the hunting activity of workers, but that the number of reproductives also has an effect on it.

INTRODUCTION

Polistes wasps are known to be important natural enemies of some lepidopterous pests (RABB and LAWSON, 1957; FURUTA, 1968; ITÔ and MIYASHITA, 1968; YAMANAKA et al., 1972; HASUI, 1977). In order to evaluate the role of predatory wasps in the natural control of pests, it is necessary to investigate various factors influencing their hunting activities.

Since *Polistes* wasps are social insects, the groups of adults cooperate in caring for larvae and in nesting a colony. Thus adults of *Polistes* expend time and energy for various nesting activities other than hunting. Therefore, some colony factors, such as the amount of labor in the colony, requirements of the nest-building program and demands of the broods, are supposed to be important in influencing their hunting activity. Hunting activities of *Polistes* wasps have been studied (RABB, 1960; MORIMOTO, 1960a, b, c; NAKASUJI et al., 1976; SUZUKI, 1978; YAMANAKA et al., 1979; KASUYA, 1980; YAMASAKI et al., 1980), but the more important colony factors influencing the hunting activities remain to be determined.

P. chinensis antennalis PÉREZ is one of the most common *Polistes* species in Japan. Its nests are initiated from April to May by a single overwintered foundress and the

first workers of the species emerge in early to mid-June. Then the nests grow rapidly with an increase in the number of workers emerging successively throughout the summer. During this period, *P. c. antennalis* preys heavily on lepidopterous larvae, e.g. *Pieris rapae crucivora* (MORIMOTO, 1960b; HASUI, 1977) and *Spodoptera litura* (YAMANAKA et al., 1972; NAKASUJI et al., 1976). The present study was undertaken to determine the more important colony factors influencing the hunting activity of *P. c. antennalis*.

MATERIALS AND METHODS

Observation of hunting and other foraging activities. The hunting activity of five natural nesting colonies was observed on the campus of Kyushu University, Fukuoka in 1977. It was measured in terms of the number of flesh pellets brought to a colony per hour. The foraging activities for liquid food and pulp were also observed to know the allocation of labor for each foraging task. They were measured in terms of the number of foraging trips for liquid food and pulp per colony per hour. These hunting and other foraging activities were observed for a total of 37 days (mean 2.7 hours per day) at irregular intervals (maximum 20 days, minimum one day) during the period 3 May–1 August. In 1978 four natural nesting colonies were transferred to two wooden screens (Fig. 1) placed on the campus of Kyushu University. Flesh pellets and other loads brought to a colony per hour were counted in two of the four colonies for a total of 38 days (mean 1.8 hours per day) at irregular intervals (maximum 6 days, minimum one day) during the period 8 July–14 September.

Observation of nesting behavior. Observations of the nesting behavior of foundresses before the emergence of the first workers were carried out for the five colonies where foraging activities were observed in 1977. These colonies were observed for a total of 17 days (mean 2.8 hours per day) at irregular intervals (maximum 20 days,

Fig. 1. Scene of a field observation on *P. chinensis antennalis* colonies transferred onto wooden screens.

minimum one day) from 3 May to 6 July.

Observations of the nesting behavior of workers were also made on the above-mentioned colonies in 1977 and on the two colonies transferred in 1978. The workers were individually marked with color paint for identification.

Census of broods and estimation of cannibalism. Cell maps were drawn for the five colonies in 1977 and for the four in 1978. The broods of these nine colonies were examined at three-day intervals for the period from mid-April to mid-September in both years. When the eggs changed in their positions on the cell walls or disappeared from the cell walls between two consecutive census dates, they were counted as cannibalized eggs. Larvae and cocoons replaced by eggs or empty cells were also counted as cannibalized.

Census of reproductives. The number of males and new queens in a transferred colony were counted at five-day intervals during the period August-September in 1978.

Census of workers and examination of their longevity. The number of workers in the five colonies where foraging activities were observed were counted daily from June to August in 1977. In order to determine the longevity of adult workers in the field, newly emerged workers in the colonies were individually marked with colored paint without anaesthetization and their disappearance from the nests was recorded daily. Workers absent from the nests for one day or more were considered to have died.

In order to determine the physiological longevity of adult workers, two field-collected colonies were reared in the laboratory from mid-May to late July in 1978, and the emergence and death of all the wasps in these two colonies was recorded daily. The colonies were kept in cages ($20 \times 25 \times 25$ cm) at 25°C under long daylength (L:D=16:8) and provided with filter paper as nest material. Honey and water were supplied to them every day. Nymphs of *Acrida turrita* and *Gampsocleis buergeri*, larvae of *Pieris rapae crucivora*, and pupae of *Bombyx mori* were also given to them every day as prey.

RESULTS

Hunting activity in relation to colony development.

Fig. 2 shows the change in hunting activity of a colony as it developed. The activity was low in the larval and pupal substages and increased gradually during the first 30 days of pre-male substage. In the second half of this substage, it increased quickly and reached a maximum, decreasing rapidly in the postmale substage.

Number of workers in relation to colony development.

Fig. 3 shows the change in the mean number of workers per colony as it developed. Workers increased in number during the 20 days following emergence of the first workers; there was no increase in their number in the period 20 to 60 days after that. Following this, however, the number again increased rapidly. There was a positive correlation ($r=0.64$, $p<0.01$) between the number of workers in a colony and the number of flesh pellets brought to a colony per hour.

Longevity of workers.

The mean life span of workers that emerged in June and July under field con-

Fig. 2. Hunting activity of *P. chinensis antennalis* in relation to its colony development. Activity is shown in terms of the mean number of flesh pellets brought by wasps per colony per hour. After JEANNE (1972), the colony stages are classified as follows: PrES, Pre-emergence stage; PoES, Postemergence stage; ES, Egg substage; LS, Larval substage; PS, Pupal substage; PrMS, Pre-male substage; PoMS, Postmale substage. Mean number of flesh pellets per colony per hour is calculated for each of the seven 25-day periods of observation and plotted in the middle of each period.

Fig. 3. Number of workers of *P. chinensis antennalis* in relation to its colony development. See legend of Fig. 2 for colony stage.

Table 1. LIFE SPAN OF ADULT WORKERS OF *P. chinensis antennalis* UNDER FIELD AND LABORATORY CONDITIONS

Conditions	Month of emergence	Life span (days)
Field	June	27.9 $\pm$ 5.4 ^a (56 ^b)
	July	15.0 $\pm$ 2.1 (147)
Laboratory	June	48.5 ^c $\pm$ 2.5 (30)

^a Mean $\pm$ 2 S.E.

^b Number of workers examined.

^c This value was underestimated because the workers alive were assumed to die on 1 August when colony growth stopped and brood population decreased rapidly due to cannibalism by adults.

ditions was rather short as compared with that of workers under laboratory conditions (Table 1).

Foraging activities for liquid food and pulp in relation to colony development.

Fig. 4 presents changes in the foraging activities for liquid food and pulp per colony as it developed. Foraging activity for liquid food was low in the pre-emergence stage and during the first 40 days of pre-male substage. It increased rapidly after these periods and reached a maximum when the first males emerged, then decreased quickly in the postmale substage. After the first males emerged, foraging activity for liquid food was higher than that for flesh.

Foraging activity for pulp was also low in the pre-emergence stage and increased gradually after the first workers emerged; it reached a maximum 20 days before the emergence of the first male and then slowly decreased.

Behavior of foundresses and workers.

Foundresses were engaged in all foraging tasks after the first larvae hatched in each nest. The mean proportion of time spent by a foundress for outside work to the total time of observation was 28.5%.

Fig. 5 shows the relation between the age of workers and the mean proportion of time spent by a worker for outside work to the total time of observation. The mean proportion was 25% in young workers (0 to 4 days after emergence), 61–72% in middle-age workers (5 to 14 days after emergence) and 4–29% in old workers (more than 15 days after emergence). There was a significant difference in the mean proportions between foundresses and middle-age workers ($p < 0.01$, MANN-WHITNEY 'U' test).

Fig. 6 presents the relation between age of workers and the percentage allocation of trips to each task. Young workers were more frequently engaged in collecting pulp and water than in collecting flesh and liquid food. In contrast, middle-age workers collected flesh and liquid food more often than pulp and water.

Fig. 4. Foraging activities for liquid food (solid line with solid circle) and pulp (dashed line with open circle) of *P. chinensis antennalis* in relation to its colony development. Activities are shown in terms of the mean number of foraging trips for liquid food and pulp per colony per hour. See legend of Fig. 2 for colony stage. Curves of both kinds of foraging are drawn by the same method as in the case of the hunting activity (Fig. 2).

Fig. 5. Ontogenetic change in proportion of time spent by the workers of *P. chinensis antennalis* for outside work to total time of observation.

Fig. 6. Ontogenetic change in collecting activity of the workers of *P. chinensis antennalis*. Activity is shown in terms of the percentage allocation of trips to each task.

Table 2. TIME SPENT BY FOUNDRESSES AND WORKERS OF *P. chinensis antennalis* IN COLLECTING DIFFERENT KINDS OF LOADS

	Time (minutes)		
	Flesh	Liquid	No load
Foundress	4.4±1.36 ^a (18 ^b)	3.6±0.49 (18)	2.9±0.03 (153)
Worker	19.9±3.27 (177) ^c	33.4±1.26 (99) ^c	19.2±4.74 (134) ^c

^a Mean ±2 S.E.

^b Number of trips observed.

^c Significantly different between foundresses and workers at 1 per cent level.

Table 2 shows time spent by foundresses and workers on one trip during which they collected three different types of loads. No significant difference in the time spent on a particular type of load was noted within either group, however, there was a significant difference in the comparative time the foundresses and workers spent on the same type of load. ($p < 0.01$, MANN-WHITNEY 'U' test).

Mean number of flesh pellets brought by foundresses and workers per hour of outside work was 1.72 and 1.16, respectively. There was no significant difference in these figures ($p > 0.05$, MANN-WHITNEY 'U' test). Mean percentage of the number of successful trips for flesh foraging to the number of flesh collecting trips plus that of trips without load was 7.2% for foundresses and 28.5% for workers. There was a significant difference in the mean percentage between foundresses and workers ($p < 0.01$, χ^2 -test).

Number of larvae in relation to colony development.

The 3rd to 5th instar larvae live on meat. Fig. 7 shows a change in the mean number of larvae per colony as it developed. The number of larvae increased in the larval substage but decreased in the pupal substage, increasing again after the first workers emerged. It reached a maximum just before the emergence of the first male and reduced rapidly in the postmale substage. There was a positive correlation ($r = 0.69$, $p < 0.01$) between the number of 3rd to 5th instar larvae and the number of flesh pellets brought to a colony per hour.

Frequency of cannibalism in relation to colony development

Fig. 8 presents changes in the mean number of eggs and larvae cannibalized by adults per colony per day as the colony developed. No cannibalism on the eggs was detected in the egg substage. In larval and pupal substages, cannibalism on the eggs and larvae by foundresses was rarely observed. The frequency of the cannibalism during the first 30 days of pre-male substage was as low as that in pre-emergence stage. The frequency increased rapidly in the second half of the latter substage and reached

Fig. 7. Number of 3rd to 5th instar larvae of *P. chinensis antennalis* in relation to its colony development. See legend of Fig. 2 for colony stage.

Fig. 8. Frequencies of cannibalism on eggs and larvae by adults of *P. chinensis antennalis* in relation to its colony development. See legend of Fig. 2 for colony stage.

Fig. 9. Number of males and new queens of *P. chinensis antennalis* in relation to its colony development. See legend of Fig. 2 for colony stage.

a maximum in postmale substage.

Number of reproductives in relation to colony development

Males and new queens quickly increased in number in postmale substage (Fig. 9). In this substage there was a negative correlation ($r = -0.92$, $p < 0.05$) between the number of these reproductives and the number of flesh pellets brought to a colony per hour.

DISCUSSION

Investigating the hunting activity of *P. c. antennalis*, MORIMOTO (1960a) reported

that the number of flesh pellets brought to a colony is lower in pre-emergence stage than in pre-male substage; the present study also showed that the hunting activity is low in pre-emergence stage. MORIMOTO (1960b) stated that this low hunting activity is due partly to the solitariness of foundresses and partly to the few larvae in the nest in this stage. Another reason, however, is that time spent by foundresses for one foraging trip is shorter than by workers (Table 2). Since nests of *P. c. antennalis* are usually initiated by a single foundress, all tasks in the nest are made by only one foundress in pre-emergence stage. By reducing her foraging time, the foundress might reduce the risk of attack on the colony by such predators as ants when she is absent. The behavior of the foundress is thus considered to be adaptive. Assessing the area, efficiency and time of the foraging of this species, SUZUKI (1978) and KASUYA (1980) stated similar opinions. SUZUKI (1978) further pointed out that hunting efficiency of foundresses is lower than that of workers. In the present study, there was no difference in the number of flesh pellets brought to a colony per hour of outside work between foundresses and workers, but the proportion of time spent for outside work to the total time of observation was lower in foundresses than in middle-age workers. Thus, a larger number of flesh pellets were brought to a colony by middle-age workers than by foundresses. The percentage of successful trips for flesh to the number of foraging trips observed was smaller in foundresses than in workers. This finding agrees with SUZUKI's (1978) data. In short, the low number of flesh pellets brought by foundresses in pre-emergence stage is due partly to their low hunting efficiency as compared with that of workers.

A few days after the emergence of the workers, they assumed the colony tasks instead of the foundresses. In the first half of pre-male substage, however, they did not increase in number because of their short life under field conditions. Thus, there was no rapid increase in hunting activity during the month following the emergence of the first workers. As the number of workers increased, the colonies were able to quickly raise their hunting activity.

In *Polistes*, age polyethism is not as clear as in the honey bee (YOSHIKAWA, 1963). The present study, however, shows that both young and old workers have a tendency to participate in domestic work and collect pulp and water, and that middle-age workers mainly engage in foraging for food. As a result of this age polyethism among workers, middle-age workers could work devotedly at foraging, and thus their hunting efficiency was higher than that of the foundresses. The rapid increase of hunting activity in the second half of pre-male substage is due partly to this high hunting efficiency of the workers.

In spite of the presence of numerous workers, hunting activity rapidly decreased in postmale substage, indicating that the change in hunting activity cannot be fully explained in terms of the number of workers. There was a rapid decrease in the number of larvae in postmale substage because of cannibalism by adults. A decline of the hunting activity in this substage is caused by the decrease in the number of larvae. On the other hand, the abundance of males and new queens increased in postmale substage. These adults are not engaged in any colony task and may solely consume liquid food taken by workers. After the emergence of males and new queens the hunting activity rapidly decreased, probably because workers spent more labor in collecting liquid food than in hunting. In fact, there was a negative correlation between the abundance of these reproductives and the degree of hunting activity during

this period. A similar finding was reported by RABB (1960) on *P. fuscatus*. There seems no doubt that the hunting activity in postmale substage is affected by a qualitative change in colony demands.

The causes and function of cannibalism on larvae by adults in postmale substage are little understood. One possible explanation of its purpose is that it makes workers concentrate their labor on taking care of the reproductives. Since the emergence of workers ceased in postmale substage while the death of workers continued to occur, their numbers were steadily decreasing. Thus, there is little probability that larvae are reared by the workers; these larvae would be in vain in the colony from a reproductive point of view. It seems reasonable to suppose that workers spent their time and energy not in rearing the larvae but in taking care of the reproductives in postmale substage.

In conclusion, the hunting activity of *P. c. antennalis* is influenced by the number of workers in a colony and their hunting efficiency. On the other hand, colony demands, which are reflected by the number of 3rd to 5th instar larvae, also have an effect on the hunting activity. A qualitative change in colony demands after the emergence of the first males is responsible for a rapid decrease of the hunting activity in the latter part of colony development. Such a change in hunting activity may be a characteristic of predatory social wasps in the temperate regions.

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