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Distribution and Behaviour of Adult Ladybird, *Harmonia axyridis* PALLAS (Coleoptera, Coccinellidae), around Aphid Colonies[1]

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Abstract Field investigation was performed to clarify the mode of living in the predacious ladybird, *Harmonia axyridis* PALLAS, around aphid colonies. The number of beetles was positively correlated with the prey density. Their distribution pattern, however, was clumped even among trees infested equally by aphids. The marked sex-related differences in behaviour were found: the female was usually resting or feeding, while most males were walking restlessly. Behaviour of males was considered as that for mate-searching, and probably regulated the distribution pattern in this beetles as well as the prey density.

Introduction

Entomophagous coccinellid beetles are an important biological control agents against several insect pests, such as aphids and scale insects, and many field investigations have been performed (BANKS 1955; GAGNE & MARTIN, 1968; WRIGHT & LAING, 1980) in order to clarify their characteristics and usefulness as predators. The main emphasis of these previous studies has been the response to prey density or the efficiency of prey capture. Only one paper (HONĚK, 1985) has focused on individual behaviour of *Coccinella septempunctata* in the field.

We have intensively studied the adult biology of the aphidophagous coccinellid, *Harmonia axyridis* PALLAS, one of the most common species in Japan (OBATA, 1986 a, b), and made detailed field observations to examine the mode of living in this species around aphid colonies. Special attention was given to the behaviour of individuals, since few previous studies have considered this aspect of adult coccinellid biology. From such field observations a marked difference in the behaviour of males and females was revealed. Such a difference was not apparent under laboratory conditions. In this paper, we describe the characteristics of spatial distribution in *H. axyridis* and discuss how the observed sex-related

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differences in behaviour play a role in regulating the distribution of this beetle.

Methods

The study was performed along a road near Takaragaike in Kyoto City, Japan, where many tobera trees, *Pittosporum tobira*, which is resistant to air pollution, had been planted along the roadside. From May to June, when the tobera trees come into leaf, they are infested by two species of aphid, *Toxoptera odinae* and *Aphis citricola*, and are thereafter attacked by several species of aphidophagous ladybird, such as *H. axyridis*, *Coccinella septempunctata*, *Menochilus sexmaculatus*, *Propylea japonica* and *Scymnus posticalis*.

During this season, investigations were made on one hundred tobera trees which lined the north side of the road. The degree of aphid infestation was recorded as one of the following five groups: gr. 0: no infestation; gr. 1: each colony consists of a fundatrix (a stem mother) and a few young nymphs; gr. 2: each colony consists of 10–20 nymphs; gr. 3: each colony consists of 20–50 nymphs, and gr. 4: the colony extends from leaf to stem and the tree is sticky by honeydew. Secondly, the number of *H. axyridis* was counted for each tobera tree. The low maximum height of tobera (1.5 m) facilitated the easy surveying of the entire tree. The number of beetles was counted 4 times for each tree, during the afternoons (12:00–15:00) of the 15, 16, 17 and 23 May, 1985. On 17, 23, 27 and 30 May, the behaviour of each beetle at the time of encounter was recorded further. Behavioural observations were also made in the afternoons (12:00–15:00) of 17 and 23 May, and in the mornings (9:00–11:00) of 27 and 30 May.

Results

Table 1 shows the relationship between the grade of aphid infestation and the mean number (m) of *H. axyridis* for one hundred tobera trees for each day, together with m*, the mean crowding proposed by LLOYD (1967). The number of beetles was positively correlated with the grade of aphid infestation. As the grade of aphid infestation became higher, the number of beetles per tree (the value of m) increased significantly each day (χ^2-test, $P<0.01$). Although the increase in m* was not as closely related to the grade of aphid infestation as that of m, m* for the trees belonging to gr. 3 and gr. 4 was rather large (when m* was calculated, gr. 3 and gr. 4 were combined). To determine the distribution pattern of this beetle, the m*/m value was calculated for all trees and for trees belonging to each grade except gr. 0 (Fig. 1). $m^*/m=1$, >1 and <1, when the spatial distribution is random, clumpted and repulsive, respectively (IWAO, 1968). The value of m*/m calculated for all trees was high throughout the census period, which indicated that adults of *H. axyridis* were clumped in our study area. The m*/m value for trees belonging to gr. 1 fluctuated sharply, suggesting that beetles spent only a short time

Table 1. Mean number of *H. axyridis* per tree (m) and mean crowding (m*) for each grade of aphid infestation for each day. n: number of trees belonging to each grade. For grades 0–4, see Methods.

Date	Grade	0	1	2	3	4	Total trees	χ^2 value for m
15 May	m	0	0.340	0.684	2.000	2.667	0.650	45.38* (df=2)[b]
	m*	—	2.588	1.00	2.583[a]		1.966	
	n	(2)	(50)	(38)	(7)	(3)	(100)	
16 May	m	0	0.189	0.485	1.556	2.00	0.460	47.28* (df=2)[b]
	m*	—	0.00	1.001	3.40[a]		0.811	
	n	(2)	(53)	(33)	(9)	(3)	(100)	
17 May	m	0	0.151	0.471	1.50	0.50	0.380	16.61* (df=1)[c]
	m*	—	1.001	1.375	3.143[a]		1.959	
	n	(1)	(53)	(34)	(8)	(4)	(100)	
23 May	m	0	0.034	0.20	3.00	0.667	0.340	39.66* (df=1)[c]
	m*	—	0.00	0.333	8.308[a]		1.938	
	n	(1)	(58)	(30)	(8)	(3)	(100)	

[a] Grades 3 and 4 were combined when m* was calculated.

[b] Three groups (gr. 0–1, gr. 2 and gr. 3–4) were compared.

[c] Two groups (gr. 0–1 and gr. 2–4) were compared.

* $P<0.001$

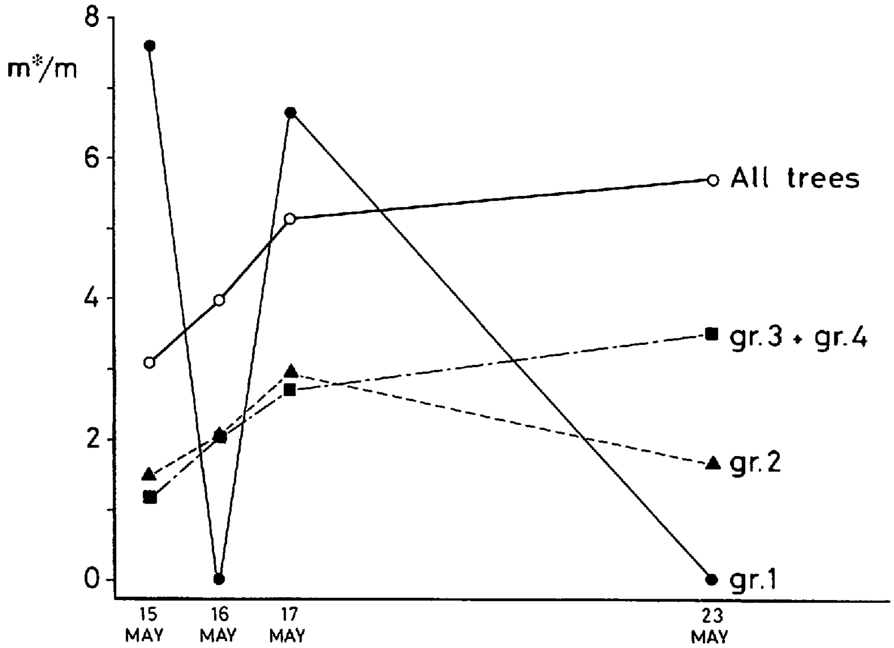

Fig. 1. Daily changes in the degree of contagion, m*/m, in distributions of *H. axyridis* for all trees, and for each grade.

Table 2. Number of trees carrying each type of *H. axyridis* group and the number of beetles in each group type.

Group type of beetles		Single	Unisexual	Bisexual	Total
Male	No. trees	18	2	37	57
	No. beetles (%)	18 (18.75)	4 (4.16)	74 (77.08)	96 (100.0)
Female	No. trees	53	15	37	105
	No. beetles (%)	53 (29.44)	31 (17.22)	96 (53.30)	180 (100.0)

χ^2-test for No. beetles: $\chi^2 = 16.922$ (df=2), $P < 0.001$

on a tree which harbored only a few aphids. In the case of gr. 2 and gr. 3-4, the change of m*/m was similar for first three days, *i.e.*, it increased, representing the shift of the distribution pattern from random to clumped. However, on 23 May, m*/m for gr. 2 decreased to an almost random distribution level, while m*/m of gr. 3-4 further increased to show high contagiousness.

Ninty six males and 180 females were found throughout the study period. All trees on which beetles were found, were divided into five categories: only one male (1) or female (2), only males (3) or females (4), or those where both sexes were found (5). Table 2 shows the number of trees belonging to each category, together with the number of beetles found. The distribution of males differed significantly from that of females ($\chi^2 = 16.922$, $P < 0.001$). Male *H. axyridis* seldom stayed alone or in male-only groups, but tended to stay together with females.

Fig. 2 represents the behaviour of beetles when located, for males and females separately. Each behaviour was recorded as one of resting, feeding, slow walking

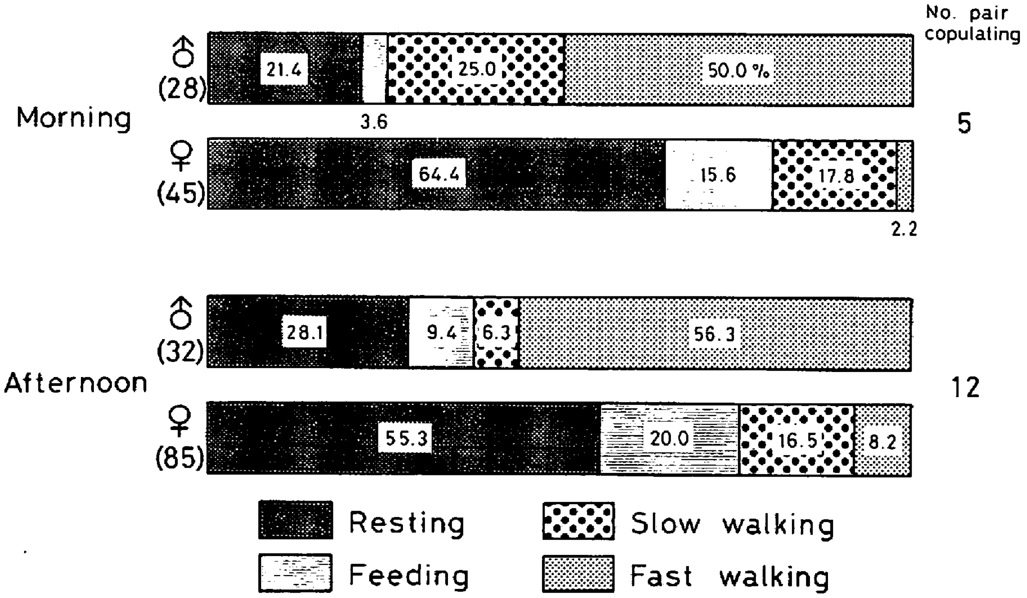

Fig. 2. Relative percentage time allocation of each behaviour of male and female *H. axyridis* at the time of observation.

or fast walking. For both sexes, no significant difference was detected between the morning and the afternoon behaviour patterns ($\chi^2=0.2369$, df=1, $P>0.5$ for males; $\chi^2=2.4944$, df=3, $P>0.3$ for females). It is notable that marked sex-related differences in behaviour were apparent, regardless of the time of day ($\chi^2=28.499$, df=2, $P<0.001$ for the morning; $\chi^2=31.969$, df=3, $P<0.001$ for the afternoon). Females were usually resting or feeding, while most males were walking around fast from one branch to another. Even if these males encountered an aphid colony, they did not attack it but passed by. However, when we experimentally presented a female resting on the leaf to such male, he dashed to her and attempted to copulate.

Discussion

The value of m*/m for all trees was higher than random level throughout the census period (Fig. 1), which indicated a contagious distribution of *H. axyridis* on one hundred tobera trees. The heterogeneity in aphid infestation was considered as the main factor contributing to such a distribution pattern, because the number of beetles per tree increased with the grade of aphid infestation (Table 1). For the trees with few aphids (gr. 1), m*/m fluctuated sharply day by day, suggesting that *H. axyridis* did not spend a long time on trees with few aphids. Probably beetles move from one tree to another, searching for sites where aphids are clumped. It was confirmed that *H. axyridis* tended to visit the tree infested by many aphids, this result agreeing with another study for the same species in an experimental field of wheat (KAWAI, unpublished data). OBATA (1986 b) analysed the prey-finding mechanism of *H. axyridis* under laboratory conditions and suggested that visual and olfactory cues helped in their prey searching, and that beetles may also be able to distinguish plants infested by many aphids using such cues in the field. Aphidophagous coccinellids are known to respond to prey density and to migrate to a better habitat when aphids decrease in number (BANKS, 1955; WRIGHT & LAING, 1980). SAKURATANI *et al.* (1984) described that the larvae of *H. axyridis* responded more to the aphid density per "block" of shoots (mass of several neighbouring shoots) than per individual shoot, and for adults the aphid density per whole tree might be more important in selecting the habitat than that per shoot.

The contagious distribution of *H. axyridis* in our study area, however, was not satisfactorily explained solely in terms of the heterogeneity in aphid infestation. Even among trees of the same grade of aphid infestation, the m*/m value was higher than random level in most cases (Fig. 1), indicating that beetles were clumped among trees which were equally infested by aphids.

BANKS (1954) described the distribution of adult *Adalia bipunctata* in the bean field, which was usually random, as sometimes being clumped among plants, and attributed such a temporary contagious distribution to mating pairs. The study of

YOSHIDA *et al.* (1952) on the phytophagous coccinellid, *Epilachna sparsa orientalis*, confirmed that their distribution in a field of egg plant, their host, was clumped, and considered that the distribution pattern was due to the aggregation of individuals for their reproduction and also to environmental heterogeneity. In the case of *Epilachna*, however, the former seems to be main factor, because the heterogeneity in the character of individual host plants is not so variable as to determine the distribution of beetles.

For *H. axyridis*, it is highly probable that factors other than aphid density, such as the attractiveness between males and females, also regulate the distribution pattern. As shown in Table 2, the group of *H. axyridis* on one tobera tree usually included both sexes, which resulted that male-only or female-only groups were rare. Furthermore, males seldom or never stayed alone on the tree, unlike females. This characteristic in the distribution indicates that there is some mechanism in this species which would attain the coexistence of both sexes on one tree. Probably it is the active approach of males to females, and not a mutual attraction.

So far only a few studies have shown any difference in behaviour between males and females, and actually, it is difficult to detect sex-related differences in the activity, feeding, and prey-searching behaviours, etc., under laboratory conditions. DIXON (1959) noted that both sexes of *A. decempunctata*, after enough feeding, were less active than usual and tended not to move. In our study area, however, the behaviour of male *H. axyridis* on tobera trees greatly differed from that of females (Fig. 2). Most females were resting or feeding on a leaf or the underside of it, while males were usually restlessly walking about from one branch to another. HONĚK (1985) reported that in *C. septempunctata* males were much more active than females in the field with abundant aphids, while no difference was detected under the low density of aphids. Our result agreeds with that of HONĚK (1985) because the tobera trees were infested by abundant aphids on the last half of May.

In order to attain sexual maturation newly emerged adults of *H. axyridis* need to feed on aphids. For mature adults, however, aphids seem to have a significance other than nutritional value. As confirmed in our study, mature females tended to stay in the vicinity of the place where they had caught and eaten prey. This behaviour leads to their ovipositing near an aphid colony, which is advantageous to the survival of larvae (BANKS, 1956; DIXON, 1959). For females, aphids are considered as the cue indicating the most favourable oviposition site, while males walk about on the aphid-infested tree mainly in order to search for females. A male motivated to copulate may eat little prey. Under laboratory conditions it was confirmed that aphid consumption by mature male coccinellids was less than half that of females (SMITH, 1965; KAWAI, unpublished data) and thus, for mature males, aphids seem more important as the key stimulus for mate searching behaviour than as a nutritional source.

The active approach of males to females, discussed above as influencing the characteristics of distribution, was also supported by the observation of behaviour. Perhaps the group of *H. axyridis* including both sexes on one tree is formed in a fashion whereby males walk about randomly and finally reach rather stationary females. It is unknown whether female *H. axyridis* attracted males with some sexual attractant, but no orientation from a long distance was observed in the male's approach to a female. The male's behaviour observed around an aphid colony, fast walking from one branch to another, might enhance the efficiency in mate findings.

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