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## Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics

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**Abstract** To clarify functional and numerical responses to temporal and spatial variations of resources (resource tracking), and the population characteristics of the ladybird beetle *Harmonia axyridis*, I analyzed the results of a 3-year field observation at 24 sites (seven plant species) on eight species of aphids. The seasonal changes in the number of beetles estimated by the Jolly–Seber method were significantly correlated with those of aphids in the total area. The estimated values of population parameters suggested frequent immigration and emigration of the *H. axyridis* population, although reproductive rates between spring and summer were rather stable all 3 years (1.87–3.49). The staying time and the daily number of adults and eggs at each site were influenced not only by a single factor but also by interactions among time and quantity and quality of the prey. The adult movement showed two patterns, which corresponded with the movement within and between the subpopulations when an assemblage of *H. axyridis* occurring on the plants of the same species or genus was regarded as a subpopulation. Adult movement intensely occurred within a subpopulation, although the beetles moving between subpopulations had a significantly greater chance to reach the habitat with a high aphid density. The habitats of *H. axyridis* could be categorized into a suitable habitat for survival and reproduction and a temporal refuge. The results obtained here suggest that *H. axyridis*, with high ability of prey searching and reproduction, maintains a stable population in heterogeneous and temporal habitats by its resource tracking mechanisms.

**Key words** Aphid · Polyphagous · Population Dynamics · Predator–prey interaction · Habitat

### Introduction

Many studies have been performed on the predator–prey interaction, which is one of the most important features in ecology (Solomon 1949, 1964; Holling 1961; Begon et al. 1986; Kuno 1987). From the aspect of population ecology, the role of predation as a regulatory or disturbing factor(s) of a prey population has been studied through theoretical and empirical researches (Kuno 1987). Life table analysis of field insect populations is closely related to the demands of pest management (Taylor 1984; Bellows et al. 1992).

In many animal populations, it is known that resources determine the level of a population (Begon et al. 1986). However, resource tracking, which is defined as functional and numerical responses to temporal and spatial variations of resources, is not fully clarified, especially in the field population of insect polyphagous predators. Furthermore, in previous population studies of insect polyphagous predators, the predator–prey interaction mainly has been analyzed from the aspect of the prey: the population dynamics of a predator, especially the view of the temporal and spatial variations of prey and population characteristics of predators in a natural population, have not been taken into consideration. Therefore, the population dynamics and processes should be investigated from the aspect of the predator, which is needed for a further clarification of the predator–prey interaction. Some predators, for example, birds, expand their food niche when the preferred prey type becomes scarce and shrink it when the prey becomes abundant (Korpimäki 1986). Moreover, breeding densities of predatory bird populations catch fluctuations of prey without a time lag (Korpimäki 1985; Korpimäki and Norrdahl 1991). Thus, vertebrate predators change their behavior and life history strategies in relation to the dynamics of the prey population. However, previous studies on polyphagous insect predators have not analyzed the temporal and spatial dynamics of the predator–prey interaction, especially in the field. It is important to clarify the resource tracking of insect predators: i.e., how insect predators utilize prey in tempo-

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rally and spatially changing habitats, because the population characteristics and life history of insect predators may be influenced by their resource tracking patterns.

Predaceous ladybird beetles are common insect predators and have received much attention, mainly from the aspect of biological control (Hagen 1962; Hagen and Van den Bosch 1968; Hodek 1967, 1973; Hodek and Honek 1996; Obrycki and Kring 1998). Moreover, many behavioral studies have been performed from the point of view of behavioral ecology (Banks 1954; Carter and Dixon 1982; Nakamuta 1982, 1983, 1984, 1985). In experimental field study of coccinellids, the cumulative effect of many individuals can produce strong population-level aggregation of the beetles in areas with a high aphid density, although the responses of individual beetles to aphid density is weak (Ives et al. 1993). However, no other study has revealed the population dynamics of a predaceous ladybird beetle in a field in relation to their resource tracking, mainly because of their higher ability of dispersal in adults and the difficulties of research on aphid abundance. Furthermore, no study has clarified the movement patterns in ladybird beetles and the consequences of the movement on a large scale. Apart from coccinellids, a few studies have clarified the population dynamics of polyphagous predators from the point of view of the predator's resource utilization in a large scale (Hori 1982), although the consequences of the movement are still unclear. To elucidate the population characteristics of polyphagous insect predators that utilize patchily distributed habitats, the factors affecting the population dynamics of the predator and their movement patterns should be unraveled in relation to the quantitative and qualitative resource variations in time and space.

In this field study, the resource tracking and population characteristics of the polyphagous ladybird beetle *Harmonia axyridis* Pallas have been analyzed to clarify what factors affect the population dynamics and reproduction of adult beetles, and how the beetles utilize a heterogeneous habitat in relation to their movement and reproduction patterns.

## Materials and methods

### The ladybird beetle

*Harmonia axyridis* is widely distributed in northeastern Asia (Sasaji 1971; Hodek 1973). The ladybird beetle has two or three generations per year (Okada et al. 1973; Osawa 1993). In the study area, the adults of the overwintering generation terminate hibernation in late March and mate and lay eggs in April and May. The adults of the first generation emerge, mate, and oviposit in mid-May to June. In midsummer, the beetles show an estival condition; the respiration rate decreases markedly, but the body weight increases and mating behavior and oviposition activity continue (Sakurai et al. 1992). The adults of the second generation reappear in autumn, and gradually the second- or the

third-generation individuals aggregate at hibernation sites in early November (Obata 1986). In this article, the overwintering generation is referred to as the spring generation and the first generation as the summer generation.

### Field observations

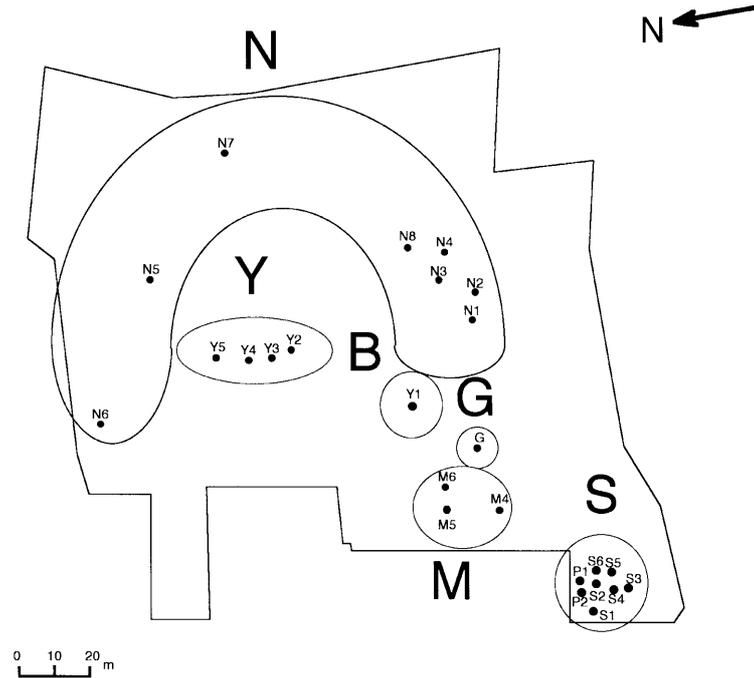
All observations were done at the Botanical Garden (~10000m<sup>2</sup> in area) of Kyoto University (35°02' N135°47' W), in central Japan. I chose 8 sites in 1985, 20 in 1987, and 24 in 1988 (two species in 1985, six in 1987, and seven in 1988) (Fig. 1). An assemblage of *H. axyridis* occurring on plants of the same species or genus was regarded as a subpopulation of *H. axyridis*, showing that *H. axyridis* feed on the same species of aphids in the same subpopulation. Six subpopulations were observed in the garden. Each site was composed of one plant, except a subpopulation G, which was composed of 36 grasses in 1987 and 56 in 1988.

At all sites, the number of aphids was censused once a week. For the site where the borderline of an aphid colony was clear, the number of colonies at the site was counted. Simultaneously, 50 colonies were randomly sampled from the site and the number of aphids in the colony was counted without the distinction of adult and nymph. Then, the number of aphids at each site was estimated by the equation  $NA = NC \times NAC$ , where  $NA$  is the number of aphids,  $NC$  the number of aphid colonies, and  $NAC$  the mean number of aphids per colony. The daily aphid density at each site was estimated by a linear regression between mean values of the nearest two observations. For the sites where the colony borderline was indistinct, all the aphids were counted. The aphid population phases were categorized as increasing, peak, and decreasing phases.

*Harmonia axyridis* adults were captured and individually marked by four dots with quick-drying paint and also by drilling four tiny holes with an insect pin to prevent the paint from falling off. Every day from early April to late July in 1985, 1987, and 1988, the marked individuals were released at the same site where they were caught after recording sex and the site code. For all the recaptured beetles, individual code, time, and site were also recorded. Individuals of a summer generation were distinguished from those of a spring generation on the basis of the pale and soft elytra of newly emerged adults (Brakefield 1984; Osawa and Nishida 1992).

The egg batches of *H. axyridis* found in all sites in 1987 and 1988 were individually marked with numbered red vinyl tape and the number of eggs per batch was recorded on a daily basis. Totally, 160 egg batches were recorded. The generation of eggs was followed by that of the adult, although not all the eggs can be distinguished into spring and summer generations. Then, the eggs (number of egg batches, 32) laid on the day when both spring and summer beetles were observed were eliminated from the following ANOVA analysis.

**Fig. 1.** Research plants in the Botanical Garden, Kyoto University, showing site code, subpopulation code, plant species, and aphid species



Site code	Sub-population code	Plant species	Aphid species
S1-S6	S	<i>Spiraea thunbergii</i>	<i>Apis spiraeicola</i>
P1-P2	S	<i>Spiraea blumei</i>	<i>Apis spiraeicola</i>
M4-M6	M	<i>Prunus persica</i>	<i>Hyalopterus pruni</i> , <i>Myzus varians</i>
G	G	<i>Typha angustifolia</i>	<i>Schizapis acori</i>
Y1	B	<i>Salix sieboldiana</i>	<i>Apis farinosa yanagicola</i> , <i>Tuberolachnus salignus</i>
Y2-Y5	Y	<i>Salix koriyanagi</i>	<i>Chaitophorus horii</i> , <i>Tuberolachnus salignus</i>
N1-N8	N	<i>Sambucus sieboldiana</i>	<i>Aulacorthum magnoliae</i>

### Analysis of data

The population parameters, the total number of marked adults, the total number of beetles, the total number recruited, daily survival rate, and the life span were estimated by the Jolly-Seber method in 1985, 1987, and 1988 (Jolly 1965; Seber 1973).

Stochastic adult movement patterns in 1985, 1987, and 1988 were analyzed by the method of Inoue (1978). This method uses the proportion of individuals staying at a distance  $R$ ,  $F(R)$ . If  $\log(1 - F)$  is plotted against the square of the distance traversed per unit time ( $R^2$ ), the relation can be fitted to a linear regression in both fundamental stochastic processes and movements of animals observed in the field and laboratory (Inoue 1978).

Factors affecting the daily number of beetles (number of observations, 971) and eggs (number of egg batches, 128) at each site, and the staying time at each site (number of observations, 1644), were analyzed by the ANOVA model after stepwise removal of nonsignificant terms (SAS Institute 1995), using the combined data in 1987 and 1988.

For the analysis of movement consequences in *H. axyridis*, only the continuous data (data that traced all the movements in the whole research area for at least 2 continuous days) were used ( $n = 88$ ). The movements were categorized into staying on the same site at the observation on the next day (=staying in a habitat), movement within a subpopulation, and movement between subpopulations. The movement consequences for the two movements were defined as the difference of aphid density between sites before and after the movement. In the case of staying in a habitat, the movement consequences were defined as the difference of aphid density between the observed day and the next day at the same site. The ANOVA model was used after the stepwise removal of nonsignificant terms, using the combined data including the aphid data when the movement occurred, in 1987 and 1988.

To analyze *H. axyridis* habitats, cluster analysis (hierarchical clustering; Ward's method) (SAS Institute 1995) was performed, using the data of the total number of adult beetles and eggs at each site in 1987 and 1988.

## Results

### Population dynamics of *H. axyridis* adult

The beetles visited the subpopulations at particular periods: S in April and May, and M and Y in May and June were favored by the beetles (Fig. 2). A total of 51 peaks of the density of the beetles and the aphids were observed in 1987 and 1988; it was significant that the beetles visited before and just at the time when aphid density peaked ( $\chi^2$ -test for number of peaks;  $\chi^2 = 4.02$ ,  $df = 1$ ,  $P = 0.05$ ) ( $n = 36$ ).

The daily number of *H. axyridis* adults was significantly different among the plants and the subpopulations (one-way ANOVA:  $F = 3.72$ ,  $df = 23$ ,  $P < 0.0001$ ;  $F = 7.17$ ,  $df = 5$ ,  $P < 0.0001$ , respectively). Year and generation significantly affected the daily number of *H. axyridis* adults (Table 1). Furthermore, among the other factors, aphid density and interaction between aphid density and aphid population phase significantly affected the daily number of *H. axyridis* adult, although the aphid population phase did not (Table 2). Thus, not only a single factor but also several internal and external factors and their interactions affected the daily number of beetles at each site.

Figure 3 shows the seasonal changes in the number of *H. axyridis* adults estimated by the Jolly–Seber method at the Botanical Garden. The number of aphids in the garden is also shown in 1987 and 1988. All the relationships between the number of beetles and aphids in the spring and summer generations in 1987 and 1988 were positive and significant (one-way ANOVA, 1987 spring, male:  $F = 28.39$ ,  $P < 0.0001$ ,  $R^2 = 0.36$ ; female:  $F = 47.17$ ,  $P < 0.0001$ ,  $R^2 = 0.48$ ; total:  $F = 41.09$ ,  $P < 0.0001$ ,  $R^2 = 0.45$ ; summer, male:  $F = 44.47$ ,  $P < 0.0001$ ,  $R^2 = 0.40$ ; female:  $F = 47.72$ ,  $P < 0.0001$ ,  $R^2 = 0.42$ ; total:  $F = 38.35$ ,  $P < 0.0001$ ,  $R^2 = 0.37$ ; 1988

**Table 1.** Two-way ANOVA of the daily adult number at each site versus year and generation

Source	<i>df</i>	<i>ss</i>	<i>F</i>	<i>P</i>
Year	1	22.83	7.56	0.0061
Generation	1	67.84	22.47	<0.0001

ANOVA model remaining after stepwise removal of nonsignificant terms (date, sex, year  $\times$  date, and generation  $\times$  sex) at the  $P < 0.05$  level

**Table 2.** Two-way ANOVA of the daily adult number at each site versus aphid density and aphid population phase

Source	<i>df</i>	<i>ss</i>	<i>F</i>	<i>P</i>
Aphid density	1	169.65	54.65	<0.0001
Aphid population phase <sup>a</sup>	1	5.41	1.74	0.1873
Aphid density $\times$ aphid phase	1	32.28	10.40	0.0013

ANOVA model remaining after stepwise removal of nonsignificant terms [the two categorized aphid phases (peak phase vs. increasing and decreasing phases combined), aphid density  $\times$  the aphid phase] at the  $P < 0.05$  level

<sup>a</sup>Aphid population phase in this analysis was categorized into increasing and decreasing phases by the stepwise procedure

spring, male:  $F = 34.77$ ,  $P < 0.0001$ ,  $R^2 = 0.38$ ; female:  $F = 38.57$ ,  $P < 0.0001$ ,  $R^2 = 0.40$ ; total:  $F = 60.28$ ,  $P < 0.0001$ ,  $R^2 = 0.51$ ; summer, male:  $F = 28.74$ ,  $P < 0.0001$ ,  $R^2 = 0.32$ ; female:  $F = 43.42$ ,  $P < 0.0001$ ,  $R^2 = 0.42$ ; total:  $F = 16.69$ ,  $P < 0.0001$ ,  $R^2 = 0.22$ ). These results reflect the fact that the adult beetles track the prey in the total habitat. Additionally, the generation gap of *H. axyridis* tended to coincide with the period when the aphid density was low. Thus, the seasonal changes in the number of beetles was greatly influenced and restricted by the seasonal changes in the number of aphids in the total habitat. Notably, there was also a strong positive and significant relationship between the number of males and the number of females (one-way ANOVA, 1987: spring,  $F = 30.21$ ,  $P < 0.0001$ ,  $R^2 = 0.37$ ; summer,  $F = 133.52$ ,  $P < 0.0001$ ,  $R^2 = 0.67$ ; 1988: spring,  $F = 20.34$ ,  $P < 0.0001$ ,  $R^2 = 0.26$ ; summer,  $F = 80.02$ ,  $P < 0.0001$ ,  $R^2 = 0.57$ ), being more intense in the summer generation.

### Population characteristics

Table 3 shows the population parameters of *H. axyridis* estimated by the Jolly–Seber method for each year, generation, and sex. The life span should be interpreted as the staying time at the Botanical Garden because the adult *H. axyridis* may have left the research area due to high movement ability. The mean life span (males and females combined) ranged from 5.38 to 7.56 days in spring and from 3.34 to 3.73 days in summer. Daily survival rates ranged from 0.81 to 0.87 in spring and 0.70 to 0.73 in summer, indicating that the beetles were imported and exported in this *H. axyridis* population. The reproductive rates between spring and summer generations (total number of recruitments in summer per total number of recruitments in spring) were 1.87 to 3.49, reflecting that the *H. axyridis* population was rather stable in spite of a large fluctuation in the daily number of the beetles at each site.

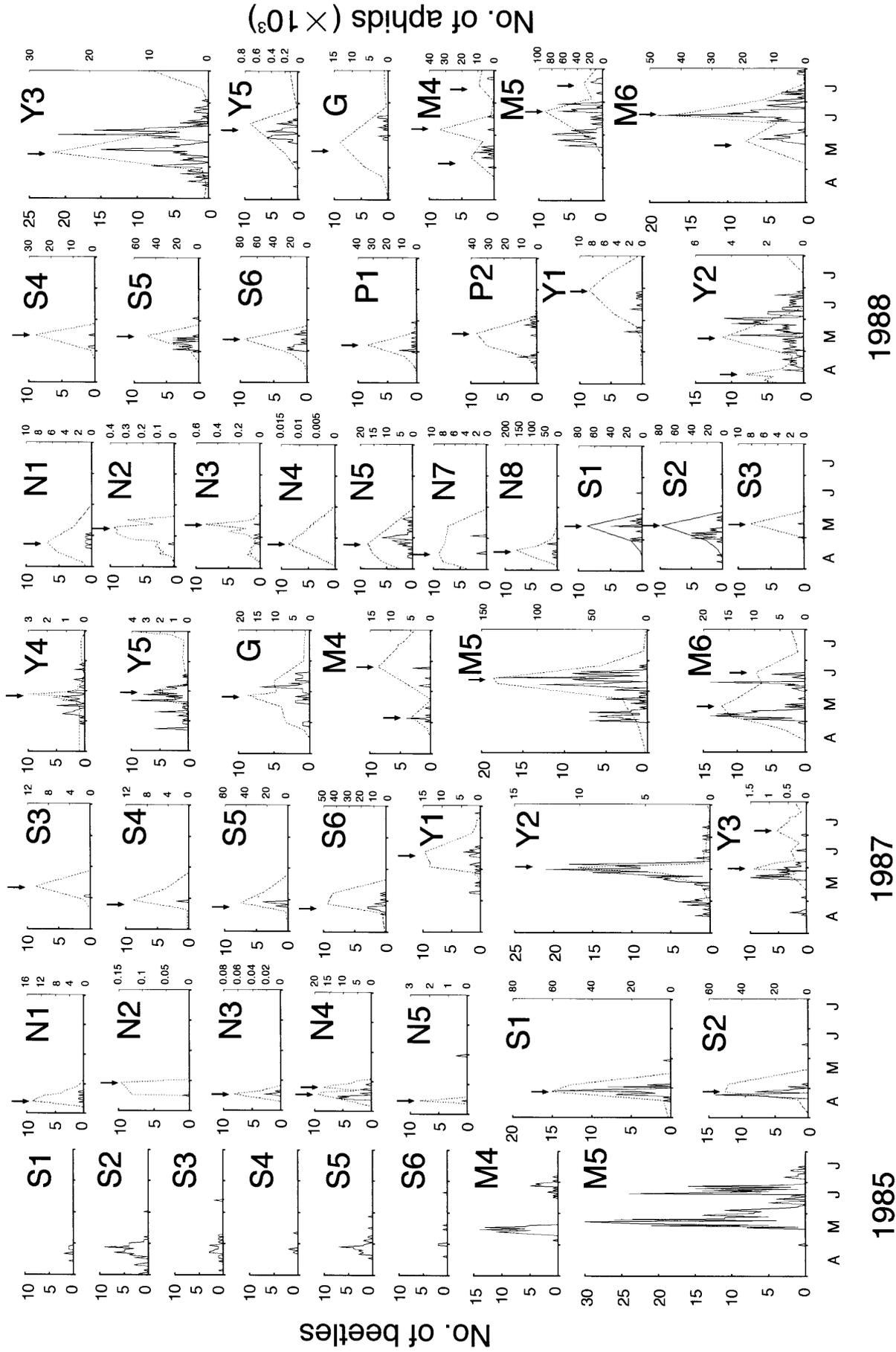
### Adult movement patterns

#### *Stochastic processes of adult movement and the movement patterns*

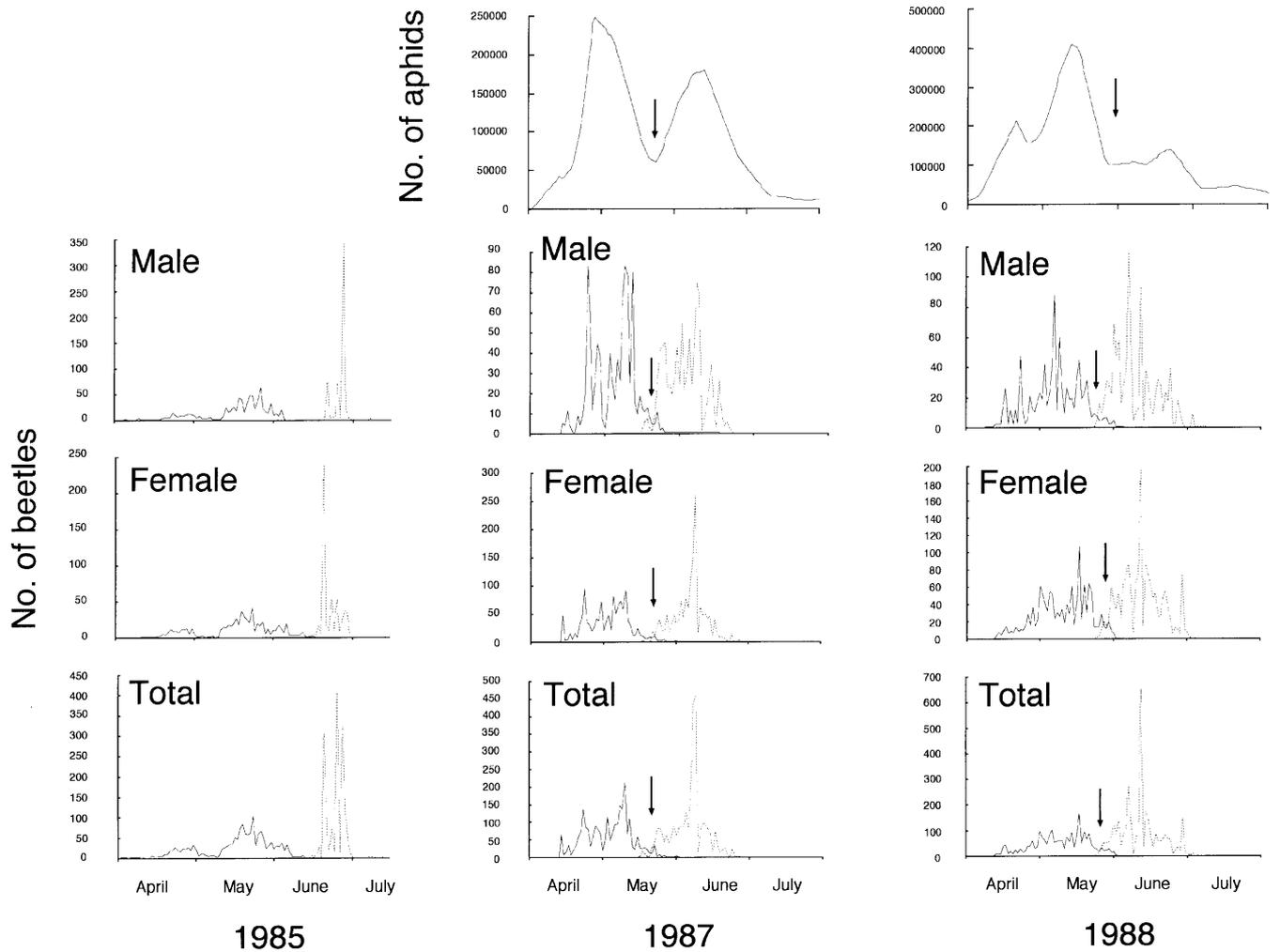
Figure 4 shows the adult movement patterns by the method of Inoue (1978). The movement patterns were categorized into the movement within and that beyond 9.71 m. The criteria of the long and short movements in females were larger than those in males. The long and short distance of the beetle's movement was the movement within and that between the subpopulations, respectively (see also Fig. 1). Many of the beetles mainly moved among the subpopulations in one direction, e.g., S to M and N to Y, while the reverse direction was also observed (Fig. 5).

#### *Adult movement and staying time*

The percentage of occurrence of adult movement within a subpopulation was significantly higher than that between



**Fig. 2.** Seasonal change in the number of *Harmonia axyridis* adults (solid lines) and aphids (dashed lines) at each site and seasonal changes in the number of aphids at each site in 1987 and 1988. Arrows indicate the time when the aphid density peaked. N6 and Y4 in 1988 were eliminated from the figure because no aphid or beetle was observed at N6, and Y4 was cut. Codes shown in Fig. 1

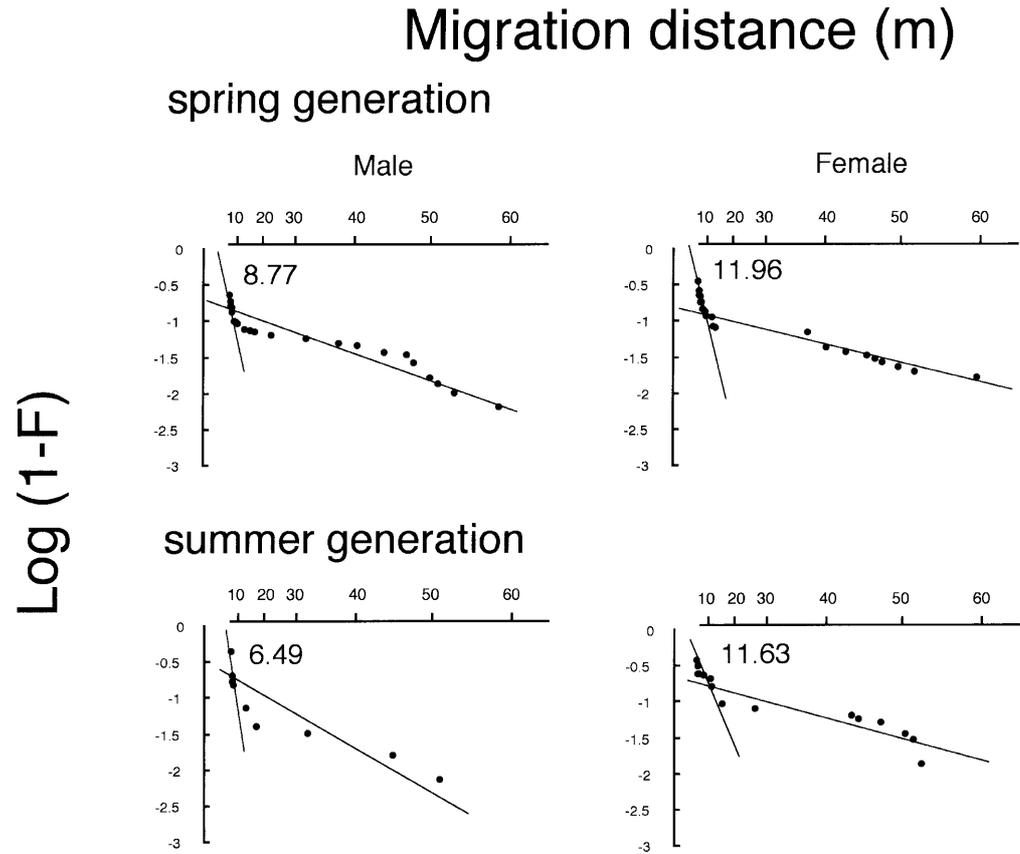


**Fig. 3.** Seasonal changes in the number of *H. axyridis* adult estimated by the Jolly–Seber method in the Botanical Garden. *Solid lines*, number of beetles in the spring generation; *dashed lines*, in the summer generation. Seasonal changes in the number of aphids in the Garden (total of average number of aphids at each site) in 1987 and 1988 are also shown. *Arrows* indicate a gap of seasonal change in the number of beetles and aphids

**Table 3.** The population parameters of *Harmonia axyridis* estimated by the Jolly–Seber method

Year	Generation	Sex	No. of beetles marked	No. of beetles estimated (mean $\pm$ SE)	No. of recruitments (total)	Daily survival (mean)	Life span (days) (mean)
1985	Spring	Male	88	207 $\pm$ 26	119	0.86	7.14
		Female	91	180 $\pm$ 40	108	0.86	6.93
		Total	187	355 $\pm$ 133	257	0.87	7.56
	Summer	Male	44	351 $\pm$ 89	361	0.72	3.53
		Female	51	258 $\pm$ 113	256	0.75	3.99
		Total	101	570 $\pm$ 832	612	0.70	3.34
1987	Spring	Male	105	284 $\pm$ 148	188	0.84	6.19
		Female	138	394 $\pm$ 122	247	0.78	4.49
		Total	244	707 $\pm$ 200	467	0.81	5.38
	Summer	Male	148	336 $\pm$ 89	257	0.70	3.36
		Female	170	504 $\pm$ 263	429	0.73	3.71
		Total	320	965 $\pm$ 555	874	0.72	3.59
1988	Spring	Male	68	278 $\pm$ 109	174	0.82	5.50
		Female	113	311 $\pm$ 103	191	0.83	5.77
		Total	182	506 $\pm$ 139	310	0.83	6.01
	Summer	Male	143	344 $\pm$ 128	267	0.75	4.04
		Female	185	650 $\pm$ 174	420	0.70	3.33
		Total	328	1332 $\pm$ 282	1081	0.73	3.73

**Fig. 4.** Relation between square migration distance ( $R^2$ ) and  $\log(1 - F)$  by the method of Inoue (1978). Numerals indicate the point of the two regression lines. The mean value is  $9.71 \pm 1.29\text{m}$  (mean  $\pm$  SE;  $n = 4$ )



**Table 4.** Four-way ANOVA of staying time at each site versus year, date, sex, and generation

Source	df	ss	F	P
Year	1	1.28	4.39	0.0364
Date	1	7.53	25.89	<0.0001
Sex	1	0.37	1.28	0.2588
Generation	1	3.80	12.99	0.0003
Sex $\times$ generation	1	1.30	4.48	0.0345

ANOVA model remaining after stepwise removal of a nonsignificant term (year  $\times$  date) at the  $P < 0.1$  level

subpopulations through the years ( $\chi^2$ -test for number of observations: 1985,  $\chi^2 = 8.82$ ,  $df = 1$ ,  $P = 0.003$ ; 1987,  $\chi^2 = 27.91$ ,  $df = 1$ ,  $P < 0.001$ ; 1988,  $\chi^2 = 12.51$ ,  $df = 1$ ,  $P = 0.004$ ) (Fig. 6). The staying time at each site was significantly different among sites and subpopulations (one-way ANOVA;  $F = 2.66$ ,  $df = 23$ ,  $P < 0.0001$ ,  $F = 6.07$ ,  $df = 5$ ,  $P < 0.0001$ , respectively). Year, date, generation, and interaction between sex and generation were significant factors that affected the staying time at each site, although sex was not significant (Table 4). Furthermore, among the other factors, aphid population phase significantly affected the staying time. Moreover, aphid density affected the staying time with marginal significance, although the interaction between aphid density and aphid population phase was not significant (Table 5).

**Table 5.** Two-way ANOVA of the staying time at each site versus aphid density and aphid population phase

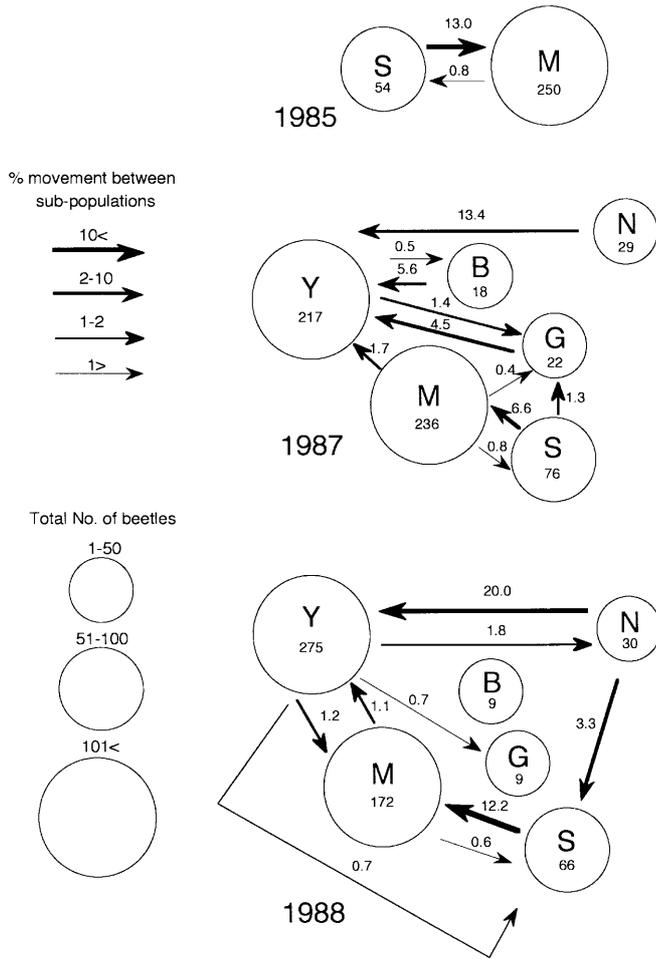
Source	df	ss	F	P
Aphid density	1	1.02	3.45	0.0636
Aphid population phase <sup>a</sup>	1	1.39	4.72	0.0299
Aphid density $\times$ aphid population phase <sup>a</sup>	1	0.744	2.52	0.1124

ANOVA model remaining after stepwise removal of nonsignificant terms (the two categorized aphid population phase (peak vs. decreasing phase) and aphid density  $\times$  the aphid population phase) at the  $P < 0.1$  level

<sup>a</sup>Aphid population phase in this analysis was categorized into increasing phase, and decreasing and peak phases combined, by the stepwise procedure

### Movement consequences

Figure 7 shows the movement consequences in *H. axyridis*. When the beetles stayed at the site, the aphid density in a habitat increased in 68.18% of the observations. Between subpopulations, the beetles reached a habitat with a better prey density in 75.00% of the observations. However, within a subpopulation, the beetles reached a habitat with a better prey density in only 43.64% of the observations (Fig. 7a). The ratio of the occurrence of increase and decrease in aphid density was significantly different among the three movement patterns ( $\chi^2$ -test for number of observations;

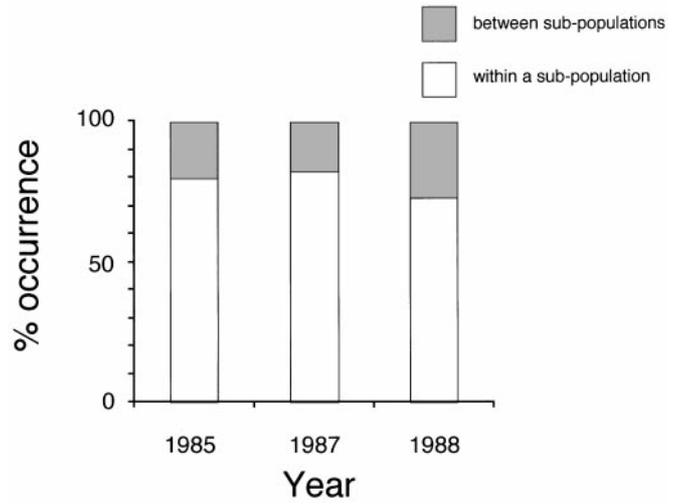


**Fig. 5.** Movement between subpopulations. Numerals in the circles, total number of beetles; arrows, direction of movement; numerals above the arrows, percentage of individuals moving per total number of beetles in a subpopulation

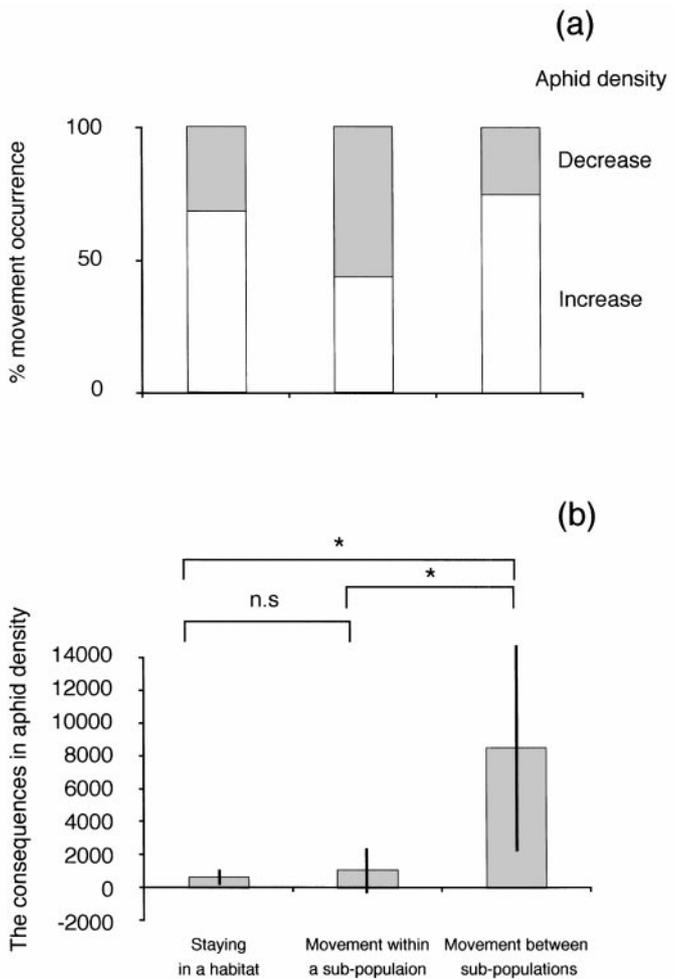
$\chi^2 = 6.29, df = 2, P = 0.0431$ ) (Fig. 7a). Notably, the density gain for staying in a habitat and the movement within a subpopulation was significantly smaller than that in the movement between subpopulations (Hsu's MCB test;  $P < 0.05$ ) (Fig. 7b). Among the factors that may affect the consequences of aphid density for the movements, movement patterns, aphid density, and interaction between movement patterns and aphid density showed a significant effect, although the effect of aphid population phase showed marginal significance (Table 6).

The oviposition patterns of *H. axyridis*

The seasonal change in the number of eggs on each plant is shown in Fig. 8. Totally, 36 peaks of the density of the beetle and the eggs were observed in 1987 and 1988. It was significant that the beetles preferentially oviposited before and just at the time when the aphid density peaked ( $\chi^2$ -test for number of peaks;  $\chi^2 = 9.00, P = 0.0027$ ) ( $n = 30$ ). The daily number of eggs at each site was significantly different among sites and subpopulations (one-way ANOVA:  $F =$



**Fig. 6.** The percentage of occurrence of the movement between subpopulations (dark bars) and that within a subpopulation (white bars)



**Fig. 7.** Consequences of aphid density for movements: the percentage of movement occurrence of increase (white bars) and decrease (dark bars) in aphid density (a), and the consequences of aphid density (b). The movements were categorized into staying in a habitat, movement within a subpopulation, and movement between subpopulations. Vertical lines, standard error; stars, significant, and n.s, nonsignificant difference in mean values at  $P = 0.05$  [from Hsu's MCB test (SAS Institute 1995)]

**Table 6.** Three-way ANOVA of the consequences of aphid density for the movements versus movement patterns, aphid density, and aphid population phase

Source	<i>df</i>	<i>ss</i>	<i>F</i>	<i>P</i>
Movement patterns <sup>a</sup>	1	2174790701	24.97	<0.0001
Aphid density <sup>b</sup>	1	3254037392	37.36	<0.0001
Aphid population phase <sup>c</sup>	1	315437321	3.62	0.0605
Movement patterns × aphid density	1	2513565595	28.86	<0.0001

ANOVA model remaining after stepwise removal of nonsignificant terms (movement patterns (staying vs. movement within a subpopulation), aphid population phase (peak vs. increasing phase), the movement patterns × the aphid population phase, aphid density × the aphid population phase (peak vs. increasing phase), aphid density × aphid population phase (increasing phase vs. decreasing and peak phases combined), aphid population phase (peak vs. increasing phase) × movement patterns (staying vs. movement within a subpopulation), aphid population phase (increasing phase vs. decreasing and peak phases combined) × movement patterns (staying vs. movement within a subpopulation), aphid population phase (peak vs. increasing phase) × movement patterns (movement between subpopulations vs. staying and movement within a subpopulation combined), aphid population phase (increasing phase vs. decreasing and peak phase combined) × movement patterns (movement between subpopulations vs. staying and movement within a subpopulation combined)) at the  $P < 0.1$  level

<sup>a</sup>Movement patterns were categorized into movement between subpopulations, and staying and movement within a subpopulation combined, by the stepwise procedure

<sup>b</sup>Aphid density at a site before the movement

<sup>c</sup>Aphid population phase in this analysis was categorized into increasing phase, and decreasing and peak phases combined, by the stepwise procedure

1.65,  $df = 20$ ,  $P = 0.0501$ ;  $F = 4.39$ ,  $df = 5$ ,  $P = 0.0009$ , respectively). Year and date significantly affected the daily number of eggs at each site (Table 7). Furthermore, among the other factors, aphid density and aphid population phase significantly affected the daily number of eggs (Table 8).

**Table 7.** Two-way ANOVA of the daily egg number at each site versus year and date

Source	<i>df</i>	<i>ss</i>	<i>F</i>	<i>P</i>
Year	1	23731.70	6.65	0.0111
Date	1	24202.91	6.78	0.0103

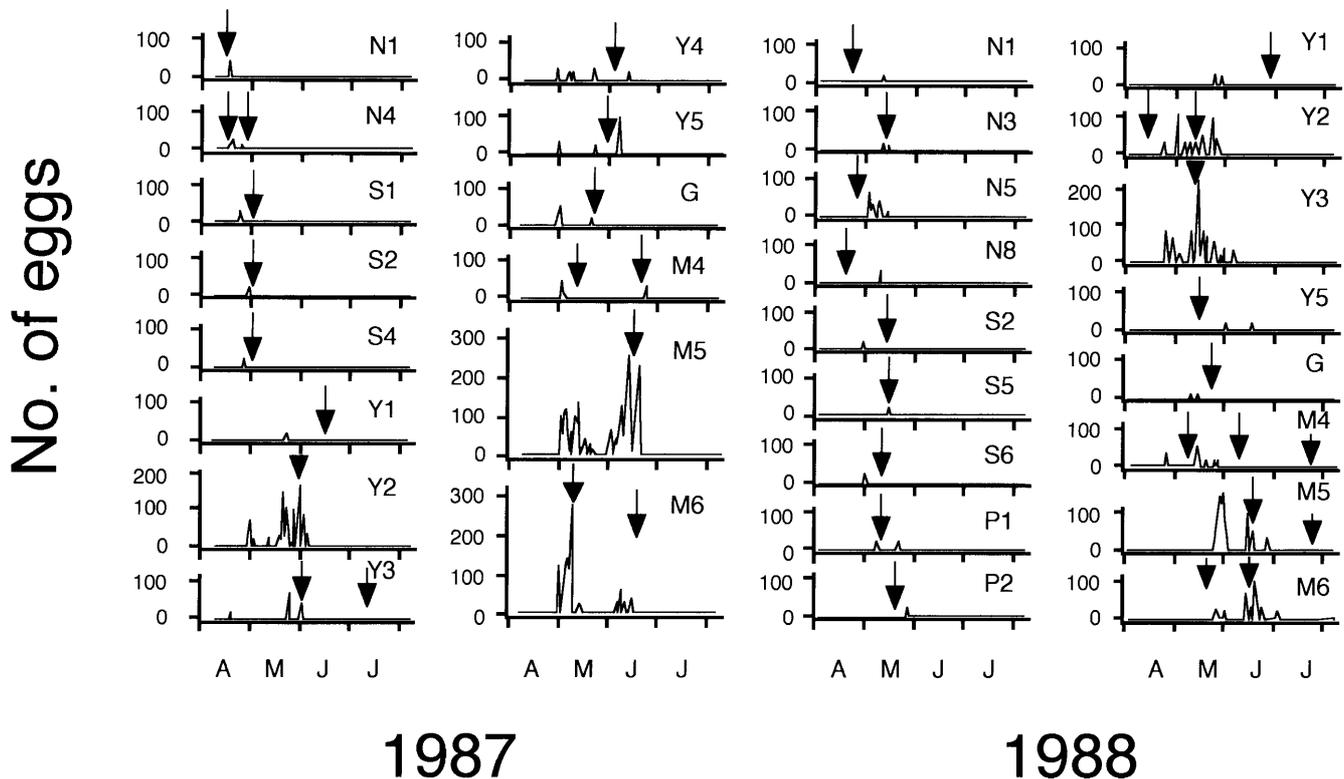
ANOVA model remaining after stepwise removal of a nonsignificant term (year × date) at the  $P < 0.05$  level

**Table 8.** Two-way ANOVA of the daily egg number at each site versus aphid density and aphid population phase

Source	<i>df</i>	<i>ss</i>	<i>F</i>	<i>P</i>
Aphid density	1	103438.18	33.68	<0.0001
Aphid population phase <sup>a</sup>	1	13990.21	4.55	0.0348

ANOVA model remaining after stepwise removal of nonsignificant terms (aphid population phase (peak phase vs. decreasing phase), aphid density × the aphid population phase (peak phase vs. decreasing phase), and aphid density × aphid population phase (decreasing phase, and increasing and peak phases combined)) at the  $P < 0.05$  level

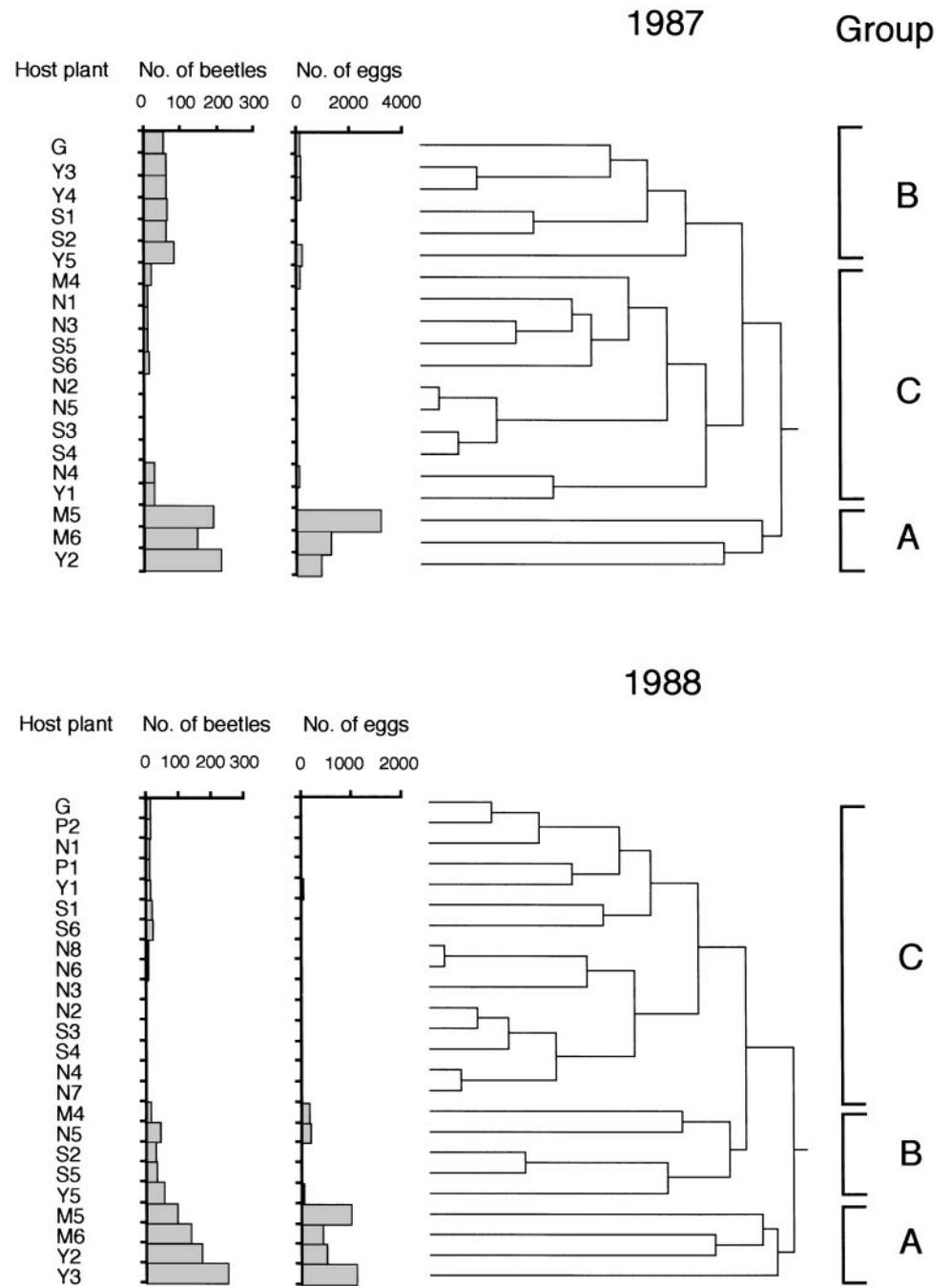
<sup>a</sup>Aphid population phase in this analysis was categorized into decreasing phase, and increasing and peak phases combined, by the stepwise procedure



**Fig. 8.** Seasonal changes in the number of eggs of *H. axyridis* at each site. Arrows indicate the time when the aphid density peaked

**Fig. 9.** Hierarchical clustering of *H. axyridis* habitats. The total number of beetles and eggs in *H. axyridis* at each site were used for this analysis. Group indicates the three early identified clusters in both years

### Hierarchical Clustering, Method=Ward



The variations of the habitat utilization in *H. axyridis*

Figure 9 shows the result of cluster analysis of the habitats. When the total number of beetles and that of eggs were used for the variables, the habitat can be categorized into a habitat for food and reproduction (group A), and a temporal refuge (groups B and C). Moreover, the refuge can be also categorized into a refuge mainly for food (group B) and that for food and reproduction (group C).

### Discussion

Resource tracking in time and space

In this study, the analysis of the seasonal changes in the numbers of beetles estimated by the Jolly-Seber method and those of aphids in the total area revealed that the seasonal changes of the beetle were correlated with those of

aphids, having females with a larger value than males. Moreover, the generation gap of the beetle tended to coincide with that of aphids. These results suggested that (i) the prey searching ability of *H. axyridis* adult was high in a large area, (ii) the life cycle of the beetle coincided with that of aphids, and (iii) *H. axyridis* females tracked the prey population better than males.

Hagen (1962) and Hagen and Van den Bosh (1968) emphasized that the coccinellid population can control the prey aphid population, which is contradictory to the view of Banks (1955) and Dixon (1971). The facts that (i) the difference of the peaked aphid density among the sites was rather small regardless of the large difference of beetle number among the sites and (ii) the population density of the beetles was low compared to that of aphids suggested that the number of beetles depends on the number of prey, rather than control of the aphid number. Therefore, seasonal variation in the number of *H. axyridis* may be caused by the seasonal change of prey aphids. Furthermore, this study also showed that there was a strong and positive relationship between the number of males and females. Mating was often observed at the same habitat during the period, suggesting that mating may be also involved in the *H. axyridis* concentration in a habitat.

This study revealed that the daily number of *H. axyridis* adults was significantly different among the sites. This result suggests that climate is also involved in the fluctuation of the daily number of beetles because the microclimate (e.g., temperature) influences the daily movement of coccinellids (Honek 1985). The fact that year and generation were significant factors affecting the daily number of beetles also supports this view.

This study showed that a subpopulation, aphid density, and an interaction between aphid density and aphid population phase were significant factors to influence the daily number of *H. axyridis*, indicating that the quantity and quality of prey also influence the daily number of beetles. Okamoto (1978) found in a laboratory observation that the quality of aphids is important for larval development and oviposition in *H. axyridis*: especially, *Aulacorthum magnoliae* was toxic for larva and ovary development. Considering the fact that there is a significant difference in the daily number of adults and eggs of *H. axyridis* among the sites and the subpopulations, being more intense in adult aggregation and oviposition at suitable habitats, *H. axyridis* adults can detect the quantity and quality of aphids in a field. This result reflects the present finding that the patterns of habitat utilization in *H. axyridis* were categorized into a habitat for food and reproduction and a temporal refuge, suggesting that *H. axyridis* effectively utilizes patchily distributed and heterogeneous habitats in relation to the habitat quality.

This study revealed that the reproductive rates for *H. axyridis* from spring to summer were rather stable. Osawa (1993) showed that the mortality of larva was a key factor for the population of *H. axyridis* and that the mortality at all stages, except for egg mortality caused by sibling cannibalism, tended to be density dependent. Furthermore, sibling and nonsibling cannibalism played an important role in population stability and persistence (Osawa 1993). There-

fore, the density-dependent mortality of larval stages and egg cannibalism made *H. axyridis* population rather persistent and stable under a fluctuating resource condition, whereas the adults aggregate and lay eggs in favorable habitats.

In *Coccinella septempunctata*, the prey searching pattern was categorized into long-distance migration and short-distance intensive searching (Nakamura 1985). Among these two searching patterns, short-distance searching has been studied in a laboratory condition in adults and larvae of many species of ladybird beetles from the point of view of behavioral ecology (Banks 1954; Kawai 1976; Nakamura 1982, 1983, 1984, 1985; Carter and Dixon 1982). However, no information had been obtained on long-distance searching patterns of adult beetles. This study clarified two categories of the beetle's long-distance movement, movement within and beyond about 10m in distance, which reflect the distribution of the site. Therefore, the movement patterns of *H. axyridis* adults are possibly determined by the distribution patterns of resources in a habitat. It is known that *C. septempunctata* larvae spend a longer time for searching edges of a leaf in the presence of aphid's honeydew, resulting in a greater exploitation of prey by the beetle than in the case of the absence of honeydew (Carter and Dixon 1984). This finding suggests that the honeydew of aphids is an important cue for the intensive searching of coccinellid larvae. The adult beetles tended to aggregate in a favorable habitat by frequent movements in a short distance in this study, indicating that the specific odor of honeydew, as well as the direct stimulus of contacting with a prey, may play an important role for the short-distance movement in coccinellid adults. However, the density gain for the movement within a subpopulation was smaller than that for the movement between subpopulations in this study. This result suggests that the specific odor of honeydew is not a reliable cue for a short-distance movement, which may be caused by a mixture of the odor from neighboring habitats.

This study showed that the gain in aphid density from movement between subpopulations was significantly larger than that from staying in a habitat and that from movement within a subpopulation. Furthermore, the direction of adult movement was mainly one way. These results suggest that the beetles can recognize the quality and quantity of prey before they reach the habitat in a long-distance movement, which may be the result of the specific odor of the prey. However, the long-distance movement may be more costly than staying in a habitat or movement within a subpopulation. Therefore, most movements were restricted within a subpopulation.

In coccinellids, visual and chemical cues are important to reach the habitat (Carter and Dixon 1982; Obata 1986). Therefore, the prey searching pattern of *H. axyridis* may be as follows. First, the beetle arrived near the habitat mainly by chemical cues. Second, by using chemical and visual cues and the direct stimulus of contacting a prey, the beetle continued short-distance movements near the habitat and landed on the habitat where the aphid density was the highest, in such a manner that staying time in a habitat with a high aphid density was longer than that in a habitat with low

aphid density. Ives et al. (1993) reported that the cumulative effect of many individuals can produce strong population-level aggregation of ladybird beetles in an area with a high aphid density. This study showed that aphid density, aphid population phase, and subpopulation also significantly affected the staying time, suggesting that both quantity and quality of aphids may affect the staying time, resulting in adult aggregation and oviposition concentration in *H. axyridis* in favorable habitats.

#### Timing of adult arrival and oviposition in females

This study indicated that the peak of beetle arrival and oviposition tended to occur before the peak of aphid density. If ladybird beetles are to complete their development, they should restrict oviposition to large aphid colonies that are in the early stages of population development (Hemptinne et al. 1992). Ovipositional behavior before aphid density peaks is adaptive for aphidphagous coccinellids to accomplish offspring development before the aphids are annihilated. Furthermore, the beetles may lay eggs at a small colony with early development because the aphid density of a large colony had already peaked and the large colony often has many alate, which are not suitable for their prey (Dixon 1959). Therefore, arrival and oviposition of the beetles in favorable habitats before an aphid colony peaks are adaptive because aphid density is high and many alate are not present in the colony. However, the concentration of adult arrival and oviposition caused a high mortality rate of *H. axyridis* larvae in favorable habitats (Osawa 1993).

Hemptinne et al. (1992) also suggested that the female of *Adalia bipunctata* assesses the potential of an aphid colony for their offspring by responding to the presence of conspecific larvae. In this study area, the aphid density for the whole plant was positively correlated with that for each colony (N. Osawa, unpublished data). Therefore, to increase reproductive success, female beetles could predict the quality of food in a whole plant by assessment of an aphid colony. The phenomenon of many conspecific larvae in an aphid colony showed that aphid density had already peaked. Therefore, in short-distance movement, the presence of conspecific larvae may be one of the criteria for the beetle to predict the habitat condition. Accumulation of this behavior may result in the arrival and oviposition near suitable aphid colonies before the aphid density peaks in short-distance movements.

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