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An Introduction Experiment of an Herbivorous Lady Beetle: Characteristics of the Adult Population

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Abstract. In May 1971, 45 adults of an herbivorous lady beetle *Epilachna niponica* (Coleoptera: Coccinellidae) from Asiu Experimental Forest were introduced into a botanical garden of Kyoto University, where is 10 km south of the southern limits of its distribution with being 3–5°C warmer than the original site. The introduced population of the lady beetle was thus investigated from 1975 to 1981. Mark-release-recapture experiments were applied to individual adult beetles, to estimate population size and daily survival rate. Overwintering adults emerged from hibernation around early April, reaching peak numbers in late April to early May, then gradually declined to late June. No adults remained at the end of June. Adult survival was maintained at a high level to early May, and declined consistently until late in the reproductive season. New adults began to emerge in late June and quickly reached a peak in early July; thereafter they decreased in number and had entered hibernation by late October. In spite of seasonally deteriorating food resources and heat stress in summer, new adults showed moderately high survival during the inimical period. New adults which emerged later in the season tended to be smaller in body size than those that emerged early. The proportion of females in the new adult population gradually increased throughout the pre-hibernating period, suggesting that male-biased mortality occurred during this period. When compared to the source population, the introduced population had a higher rate of population growth. Coupled with the improved population growth, heavy leaf damage during the larval period suggested that intensive intraspecific competition was most likely to occur among larvae in the introduced population.

Key words: adult survival, *Epilachna niponica*, herbivorous insect, introduced population, lady beetle, mark-recapture method, population dynamics, population growth, seasonal changes.

Introduction

Colonization, defined as the establishment of a population in an area not previously occupied by the species, is a necessity for species living in temporally and spatially fluctuating environments (Southwood 1977; Dingle 1984; Hanski 1987). Successful colonization has been considered to be critical to population dynamics in terms of persistence of animal populations (Elton 1958; Den Boer 1981) and, more recently, metapopulation dynamics under highly fragmented habitats (Hanski and Gilpin 1991). Colonization is also a vital component of the introduction of biological agents for pest control (Huffaker 1971; Huffaker and Messenger 1976) or weed control (Crawley 1987; Myers 1987).

After successful colonization, colonizing populations could experience different habitat conditions and species interactions, which in turn alter population dynamics of the colonizing species (e.g., Embree 1965; Hassell 1978, 1980; Murdoch et al. 1985). For example, population outbreaks of pest species have often occurred when they are introduced to new habitats (Elton 1954; Myers 1987). The direct observation of colonization into new habitats is extremely difficult. However artificial introduction experiments which follow subsequent population dynamics of the introduced species are useful manipulations for understanding the process of successful colonization (Myers 1990).

We conducted such an introduction experiment for an herbivorous lady beetle *Epilachna niponica* (Coleoptera:

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Coccinellidae). The main objectives of this study were: (1) to clarify demographic features and life history patterns of the introduced population, then (2) to compare these population parameters with those of the source population, to understand how the introduced lady beetle changed in its properties at both the individual and population levels.

In May 1971, 15 male and 30 female overwintering adults, which were collected from Asiu Experimental Forest at 700 m elevation, were introduced into a botanical garden of Kyoto University at 70 m elevation in the northwestern part of Kyoto City. Such a female-biased sex ratio was typical of the overwintering adults in the Asiu population (Nakamura and Ohgushi 1979). We initiated a study of the introduced population in the spring of 1975, four years after the introduction.

Epilachna niponica is a univoltine herbivorous lady beetle, which feeds exclusively on leaves of thistle plants. Having studied a natural population of *E. niponica* in a cool-temperate natural forest at Asiu Experimental Forest of Kyoto University, Nakamura and Ohgushi (1979, 1981) showed that the lady beetle population persisted at a low density that never caused defoliation of host plants. In addition to the low density, the Asiu population showed a low rate of population increase from overwintering adult to newly emerged adult. After the introduction, the lady beetle population successfully established, and reached a high population density in 1974, when many thistle plants throughout the botanical garden were highly defoliated by the lady beetle.

Here, we report seasonal changes in adult population attributes of *E. niponica* in the botanical garden, based on a seven-year study (1975–1981) using mark-recapture experiments for the adult beetles.

Study Sites and Methods

Study site

The botanical garden of Kyoto University in the northeastern part of Kyoto City is 16,000 m^2 in area. It is about 10km south of the southern limits of the distribution of *E. niponica*. Because the botanical garden is located at a much lower elevation than Asiu Experimental Forest, temperatures are 3–5°C higher throughout the season in the botanical garden than in Asiu Experimental Forest (Fig. 1). The lady beetle has extremely limited dispersal abilities (Nakamura and Ohgushi, 1983; Ohgushi and Sawada, 1985), and there was no evidence of *E. niponica* in the botanical garden before the introduction in 1971. The study plot of 50 × 30 m covered an area of high host density, including approximately 520 thistle plants. The host density in the botanical garden was 3.8 times that in

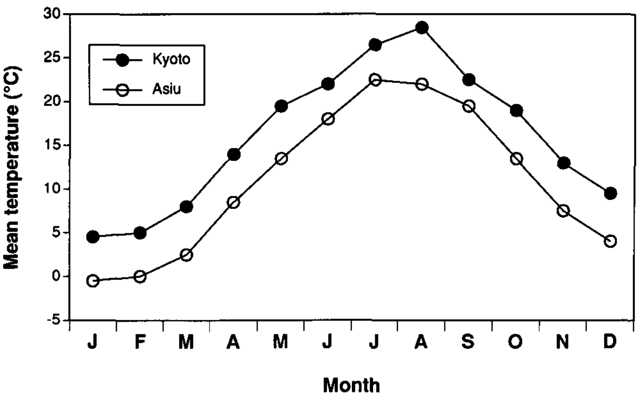

Fig. 1. Mean temperatures in the botanical garden of Kyoto University (●) and Asiu Experimental Forest (○). Mean temperatures were calculated based on meteorological data of a 56-year period from 1925 to 1980 in the botanical garden and those of a 30-year period from 1929 to 1958 in Asiu Experimental Forest.

Asiu Experimental Forest. The host plant, *Cirsium nipponicum*, is a perennial thistle and patchily distributed as a dominant species among the understory vegetation of the botanical garden. Various plant species mainly in Oleaceae and Rosaceae were planted at the study plot. In the botanical garden, there were a few thistle plants 100 m west of the study plot, but we did not observe any overwintering adults throughout the study period. Also, no host plants were found in an adjacent area outside the botanical garden. Thus, immigration and emigration of adult beetles were most unlikely to occur.

Crisium nipponicum begins its vegetative growth in early April, one month earlier than *C. kagamontanum*, the host plant of the source population in Asiu. To evaluate host plant characteristics, we measured height, diameter, and number of shoots of each thistle plant twice a month during the growing season in 1975, 1978, 1980, and 1981. Plant height was used as an index of size of thistle plants. Besides, the percentage of feeding damage to full grown leaves of thistle plants by the lady beetle was evaluated by visual estimation for each plant. Since both adults and larvae of *E. niponica* left characteristic feeding traces on the leaves, we could easily discriminate leaf damage by the lady beetle from that by other herbivorous insects. In fact, only few caterpillars were observed feeding on thistle leaves in the botanical garden, but they contributed little to overall herbivory throughout the season.

Lady beetle

Epilachana niponica overwinters in the adult stage, and emerges from hibernation in early spring. Female adults oviposit eggs in clusters on the undersurface of thistle

Table 1. Numbers of adult beetles estimated by the Jolly-Seber method, together with rate of population growth.

Year	Overwintering adults	Newly emerged* adults	Rate of population growth
1975	679	4304	6.3
1976	261	2883	11.0
1977	635	3050	4.8
1978	103	1730	16.8
1979	630	5894	9.4
1980	507	5391	10.6
1981	776	5192	6.7

* Newly emerged adults in 1975, 1977, and 1981 were numbers of marked adults, thereby somewhat providing underestimation of the rate of population growth.

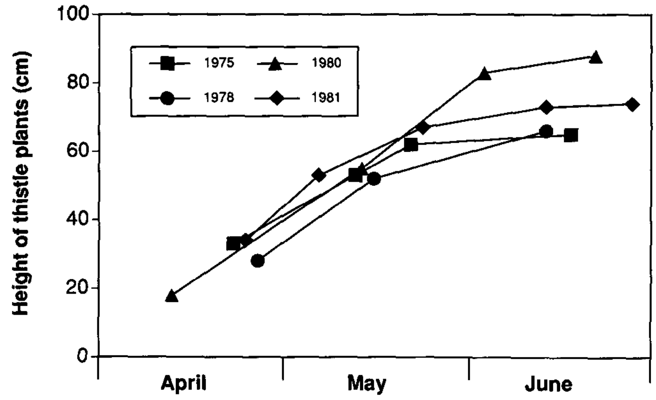

Fig. 2. Seasonal changes in the mean height (cm) of thistle plants.

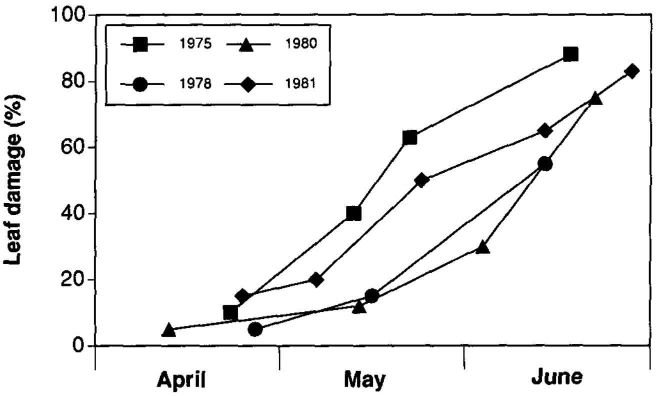

Fig. 3. Seasonal changes in the mean leaf damage (%) of thistle plants.

leaves. Larvae pass through four instars and pupate on the plant. New adults also feed on thistle leaves and by late autumn enter hibernation in leaf litter or soil nearby host plants.

In the native site of Asiu Experimental Forest, *E. niponica* feeds exclusively on leaves of a thistle, *C. kagamontanum*. The thistle is a perennial herb, growing patchily along a riverside. Overwintering adults emerge from hibernation in early May, reaching a peak in early June. Then, they decrease gradually in number until late September. A few long-lived adults survive to the following spring. New adults begin to emerge in late July and reach a peak in early September. Most of the new adults disappear by middle October in entering hibernation in the litter or soil nearby the thistle plants on which they emerged. A detailed description of the study site of the source population is given in Nakamura and Ohgushi (1979, 1981).

Adult population census

We conducted population censuses from 1975 to 1981. During this study period, adult population was monitored, using mark-recapture experiments for individuals, to estimate parameters of the adult population, including population size, survival rate, sex ratio, and body size. When adult beetles emerged, body size from the anterior edge of the head to the posterior edge of the elytra was measured to the nearest 0.05 mm using vernier calipers.

From early April to late October, all thistle plants in the study plot were individually examined every 3 days for overwintering (reproductive) adults and every 10 days for newly emerged adults. Adult beetles found were individually marked with differently-colored lacquer paint by dotting four points on the elytra. Capture date, place, and body size were recorded before release on the plant where they were captured. On subsequent censuses, marked adults were checked by sight without recapturing. For new adults in 1975, 1977, and 1981, we applied with a group-marking technique. A total of 18,276 adult beetles were individually marked in this study.

Estimation of population parameters

Using a stochastic model for a mark-recapture experiment derived by Jolly (1965) and Seber (1973), we calculated the numbers of adult beetles recruited in each year, and the number and survival rate of adult beetles on each census date, except for new adults in 1975, 1977, and 1981. We obtained extremely high marking ratio in the study period; >95% of adult beetles was successfully marked in 1–2 weeks after the marking experiment commenced for both overwintering and newly emerged adult populations. Since patterns of seasonal changes in adult population parameters differed little among years, we show here results in 1978, 1979, and 1980 to avoid redundancies.

Results

Numbers of adult beetles recruited

Table 1 summarizes estimated annual numbers of overwintering and new adults during the study period from 1975 to 1981. To illustrate population increase of the introduced population, we calculated rate of population growth, i.e., the number of new adults produced by an overwintering adult. Throughout a seven-year study period, rate of population growth varied from 4.8 to 16.8.

Seasonal growth of host plant and damage by the lady beetle

The thistle plant began shoot growth with leaf production in early April, increasing steadily in size to the maximum height of 60–80cm in late June (Fig. 2). Thistle leaves available to the lady beetle increased until late May, thereafter declined considerably because of heavy herbivory by overwintering adults and larvae (Fig. 3). The beetle herbivory was particularly apparent in 1975 and 1981, when most plants were completely defoliated by late June. This implies that severe intraspecific competition for food occurred among beetle larvae in the years of high larval density, and many larvae were more likely to die of starvation. In spite of the heavy herbivory, the highly damaged plants compensatingly sprouted rosette leaves several weeks after defoliation, and most of new adults depended on the sprouted leaves until hibernation when thistle defoliation by larval feeding occurred.

Seasonal changes in adult population parameters

Sampling effort

Sampling ratio, i.e., the observed number of adults divided by the estimated number of adults by the Jolly-Seber method, of overwintering adults remained >0.6 until late May, but gradually declined during June and July (Fig. 4). On the other hand, the sampling ratio of new adults was maintained at a high level (>0.5) throughout the pre-hibernating period except during the period from early August to early September. The low sampling ratio in mid summer is probably due to aestivation of new

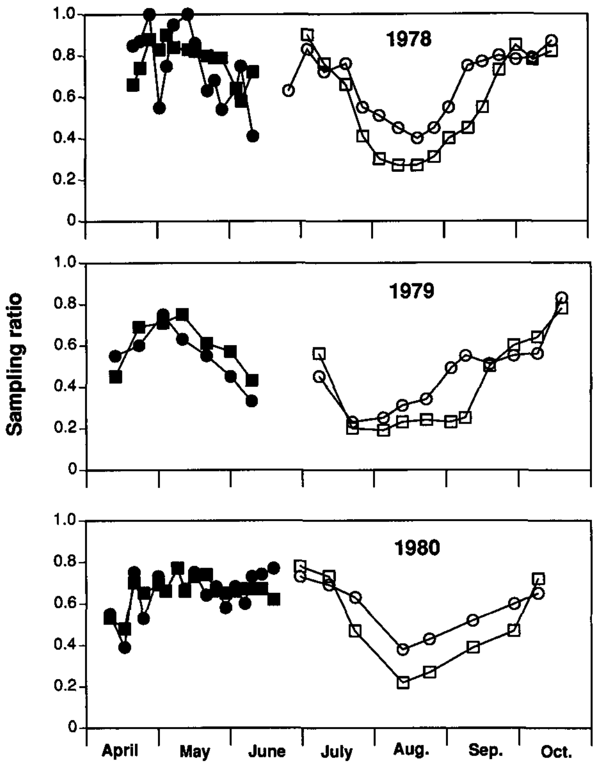

Fig. 4. Seasonal changes in sampling ratio, i.e., the number of adult beetles captured at each census data divided by the number of adults estimated by the Jolly-Seber method. Closed and open symbols represent overwintering and new adults, respectively. Circles and squares show males and females, respectively.

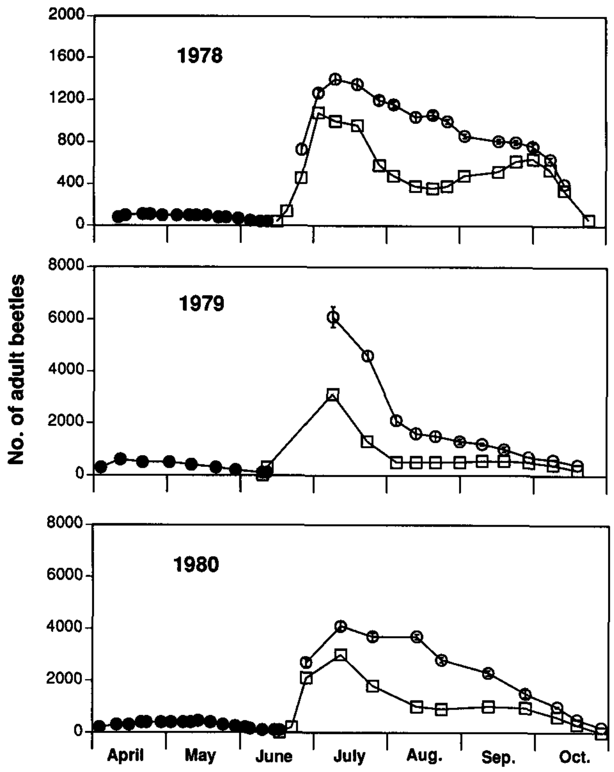

Fig. 5. Seasonal changes in the number of adult beetles. Vertical bars show standard error. (●), overwintering adults estimated by the Jolly-Seber method; (○), new adults estimated by the Jolly-Seber method; (□), new adults captured.

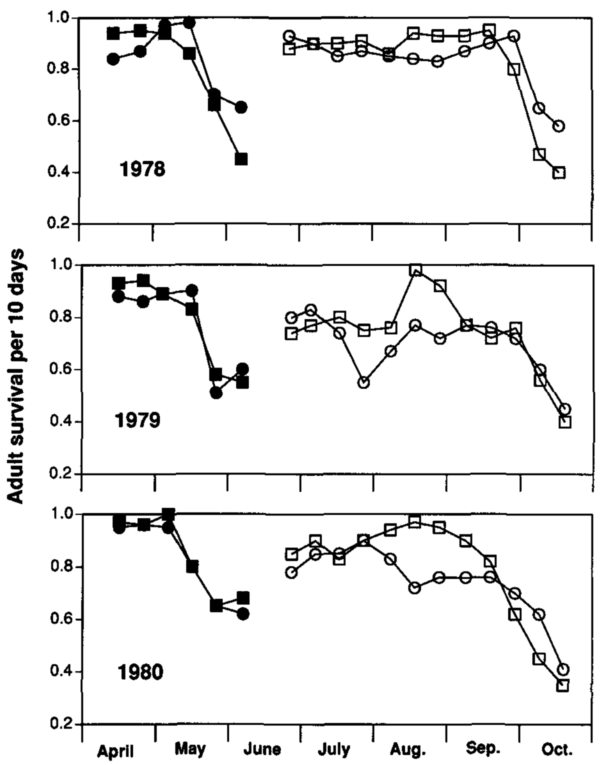

Fig. 6. Seasonal changes in adult survival per 10 days. Closed and open symbols represent overwintering and new adults, respectively. Circles and squares show males and females, respectively.

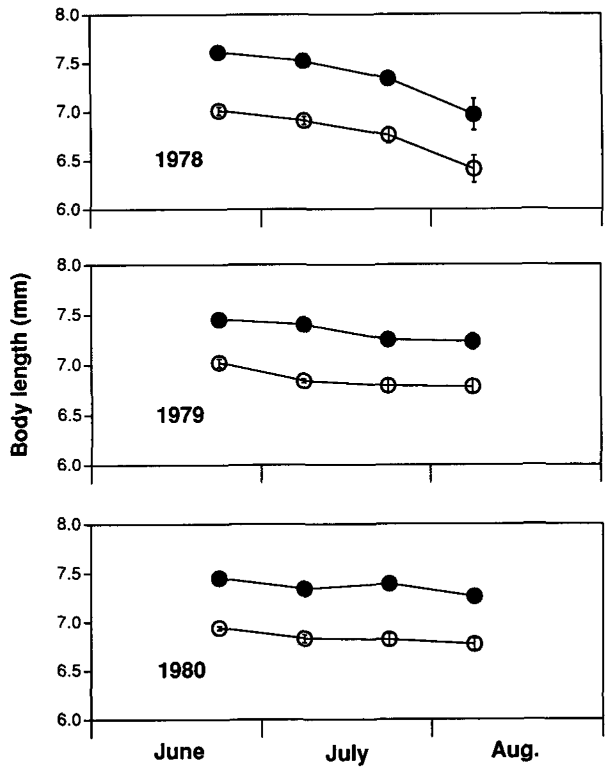

Fig. 7. Seasonal changes in the body size of new adults at emergence in males (●) and females (○). Mean and 95% confidence limits are represented.

adults. The high levels of marking and sampling effort thus guaranteed that adult population parameters calculated from the Jolly-Seber stochastic model were highly reliable.

Numbers

Overwintering adults emerged from hibernacula around early April, increasing in number gradually in April (Fig. 5). Thereafter, they decreased steadily from late May, and no adults survived by late June. New adults began to emerge from late June and increased rapidly in number, reaching a peak in early July. Then, the number of new adults decreased steadily and they entered hibernation from middle to late October. The observed numbers of new adults temporarily declined from late July to late August, compared to the estimated numbers. As mentioned above, this is probably attributable to disappearance by entering aestivation in mid summer; many adults stopped feeding and stayed inactive within withered leaves or under litter nearby host plants in August. However, when defoliated host plants began to produce rosettes, the beetles from aestivation resumed feeding on the rosette leaves.

Survival rate

Overwintering adults had high survival rate (>0.8 per 10 days) until early May, then adult survival apparently declined for the remainder of the season (Fig. 6). There were no clear differences in adult survival between the sexes. The declining survival rate late in the reproductive season may be the result of the physiological senescence of old age.

In spite of heat stress in mid summer and frequent host depletion, new adults still maintained high survival rates during the pre-hibernating period. This was particularly true for females during August. An apparent declining pattern of new adult survival in October resulted from initiation of hibernation when adults left plants and found hibernation sites in litter or soil.

Body size

The body length of new adults that emerged early in the season was significantly greater than that of new adults that emerged later for both sexes (Fig. 7). Since larvae were more likely to experience depletion of thistle plants by late June, we suggest that severe intraspecific competition for food resulted in the temporal decrease in body size at adult emergence.

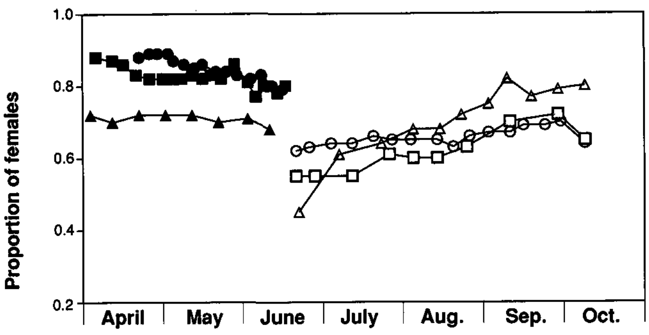

Fig. 8. Seasonal changes in the proportion of female adults in the lady beetle populations. Closed and open symbols represent overwintering and new adults, respectively. Circles, triangles, and squares show 1978, 1979, and 1980, respectively.

Sex ratio

The proportion of females in the overwintering population was high, being >0.7 throughout the reproductive season (Fig. 8). The proportion of females was particularly high just after hibernation in 1978 and 1980. On the other hand, the sex ratio in the new adult population was around 0.5–0.6 at adult emergence, but increased slightly over the pre-hibernating period. The sex ratio was significantly higher in late September than in late June (*G*-test, $P<0.002$ for every year except 1978). This implies that male-biased mortality operated during the period from adult emergence until hibernation. Likewise, there was a significantly higher proportion of females just after hibernation in the following year than in late September (before hibernation) (*G*-test, $P<0.002$ for every year), suggesting that winter mortality acted more strongly on males than on females.

Discussion

The mark-recapture experiments of adults in this study describe general features of seasonal changes in adult population parameters of the introduced lady beetle. Nakamura and Ohgushi (1979, 1981) studied adult demographies of the source population at Asiu, using the same marking technique, during 1974–76. The results obtained here are thus comparable with those of the source population.

Seasonal changes in adult population parameters

Phenology of the lady beetle in the botanical garden was more likely to be influenced by the warmer weather compared with Asiu (see Fig. 1). We can point out apparent changes in phenological attributes of the introduced population. Overwintering adults of the introduced population began to emerge from hibernation in early April, which was one month earlier than the source population. No adults survived until July. In contrast, in the source population, overwintering adults often remained in early October, and some of them survived to the following spring after hibernation. New adults also emerged one month earlier than those in the source population. In addition to the earlier emergence, new adults rapidly reached peak numbers in early July compared with early September in the source population. In contrast to the differential timing of adult emergence, there was no clear difference in the timing of hibernation between the two populations.

Survival of overwintering adults of the introduced population declined after mid-May. In the source population, however, adult survival varied little throughout the reproductive season. Although we did not conduct a quantitative survey on adult mortality, adult beetles were rarely subjected to predation in the introduced population. Hence, more intensive heat stress and seasonally deteriorating host plant conditions in the botanical garden were probably responsible for the reduced adult survival late in the reproductive season. The average reproductive life-span (mean ± SE days) of overwintering adults in the introduced population (male: 28.46 ± 3.8; female: 25.67 ± 3.2) was actually shorter than that in the source population (male: 44.33 ± 5.9; female: 38.9 ± 7.8).

New adults in the introduced population often entered aestivation during mid summer, but there was no evidence of aestivation in the source population. High daily survival of new adults (>0.97) during the pre-hibernating period in the introduced population, comparable to 0.96 in the source population, may thus result from aestivation in mid summer when new adults were subjected to resource deterioration and heat stress. Aestivation of new adults was also reported in a closely related lady beetle *E. vigintioctomaculata*, which feeds on potatoes and solanaceous crops, in the northern part of Kyoto City (Iwao et al. 1971).

It should be noted that survival of new adults was higher in females than males particularly in August and September. This was supported also by the fact that the proportion of females consistently increased over the pre-hibernating period (see Fig. 8). Ohgushi (1986) also reported such male-biased mortality during the pre-hibernating period of *E. niponica* in Kutsuki, 10km east of Asiu.

Population growth and variability

The rate of population growth of the introduced population was remarkably high, varying from 4.8 to 16.8, when compared with other populations so far studied (Nakamura and Ohgushi 1979; Ohgushi and Sawada 1981;

Shirai 1987). For example, in the source population it ranged from 0.9–3.3 in a three-year study period. Since density of overwintering adults did not differ significantly between the introduced and source populations (Ohgushi and Sawada unpublished), the large difference in rate of population growth is probably due to differential predation pressure on the immature stage. Nakamura and Ohgushi (1981) suggested that strong predation pressure by arthropods including an earwig, *Anechura harmandi*, and ground beetles such as *Platynus ehikoensis* and *P. elainus* operated during immature stages in the source population. On the other hand, escape from heavy predation on the egg and larval stages probably enhanced the increase of the introduced population. As a result, thistle plants in the botanical garden were highly defoliated in years of high beetle densities, leading to severe intraspecific competition that was not observed in the Asiu population.

In addition to the greater population growth, the introduced population was highly variable among generations compared to the source population. Population size of overwintering and new adults of the introduced population varied 7.5- and 3.4-fold during a period of 1975–81, compared to 1.9- and 1.6-fold in the source population during a period of 1974–1976.

Apparently, the introduced population was characterized by a greater population growth and higher population variability compared to the source population. Hence, further analysis will be necessary to specify possible causes of the changes in the population properties, to substantially understand mechanisms responsible for population persistence of colonizing species.

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