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Demographic Attributes of an Introduced Herbivorous Lady Beetle

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Abstract. Demographic attributes of the adults of an introduced herbivorous lady beetle *Epilachna niponica* (Coleoptera: Coccinellidae) were investigated from 1975 to 1981 in the Botanical Garden of Kyoto University. Population growth rate varied from 4.8 to 16.8 throughout the study period. Fecundity and mortality in the late larval period contributed most to annual changes in the population growth rate. Population growth rate was negatively correlated with the density of overwintering adults. Adult survival from emergence to the reproductive season, which varied from 0.03 to 0.36 throughout the study, was almost completely determined by survival during the pre-hibernation period. Adult survival to the reproductive season changed in a size- and sex-dependent manner. Larger adults survived better than smaller individuals; male-biased mortality occurred from adult emergence to the reproductive age. Severe intraspecific competition among late instar larvae due to host plant defoliation produced a higher proportion of small-sized adults, resulting in lower adult survival to hibernation. The introduced population had a higher population growth rate and a lower adult survival to the reproductive season than the source population.

Key words: Adult survival, body size, *Epilachna niponica*, herbivorous insect, intraspecific competition, introduced population, population growth rate, source population.

Introduction

It has been emphasized that the introduction of species into new areas can modify demography in terms of the stability and persistence of introduced populations (Myers 1990; Hails and Crawley 1991; Harrison 1991). After successful colonization, colonizing species may be subjected to different habitat conditions and/or species interactions than their source populations (Diamond and Case 1986; Endler 1990), which in turn alters their subsequent population dynamics. In this context, it is well documented that population outbreaks of pest species have often occurred when species are introduced to new areas (e.g., Embree 1965; Hassell 1978, 1980; McClure 1980; Murdoch et al. 1985).

Artificial introduction experiments are useful manipulations for understanding the ability for successful colonization by insect populations (Myers 1990). For insect herbivores, the frequent trials of introduced insects for biological control of weeds have suggested many factors that may limit the establishment of introduced herbivorous insect species (Crawley 1987; Myers 1987). Climatic differences, natural enemies, potential competitors, host plant suitability, genetic variability, and intrinsic rate of increase are involved. These factors are also important in determining population persistence after successful colonization. Nevertheless, few studies have followed the subsequent dynamics of insect populations after the introduction (e.g., Embree 1965; McEvoy et al. 1991), or provided census data of the source population comparable to that of the introduced population (e.g., McClure 1986; Myers 1990). Hence, we know little about whether the population dynamics of introduced insects change substantially in response to different habitat conditions in the new areas, or why some introduced insects erupt into outbreak densities whereas others maintain low densities or go extinct following colonization. Long-term studies that compare the population dynamics of herbivorous insects in their native habitat with introduced populations are required to highlight whether demographic features change after introduction and, if so, what causes the demographic changes in the introduced species.

Epilachna niponica is a univoltine herbivorous lady bee-

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tle, which feeds exclusively on the leaves of thistle plants. Nakamura and Ohgushi (1979, 1981) studied a natural population of *E. niponica* in Asiu Experimental Forest of Kyoto University in the three-year period 1974-76, and showed that the beetle population persisted at relatively low densities. There was no evidence that host plants were highly depleted. In May 1971, 15 males and 30 females of overwintering adults collected from Asiu Experimental Forest at 700 m elevation were introduced into the Botanical Garden of Kyoto University at 70 m elevation, 40 km south from Asiu. The introduced population had successfully established, and thereafter it reached high densities, often severely defoliating many thistle plants over the Botanical Garden. In addition to increased density, the introduced population showed a phenological shift with the emergence of both overwintered and new adults, being one month earlier than the source population (Sawada and Ohgushi 1994). These facts strongly suggest a change in population dynamics of the introduced population in the new habitat, responding to different habitat conditions such as weather and/or species interactions with host plants and natural enemies.

We started to investigate the introduced population in the spring of 1975, four years after introduction. Sawada and Ohgushi (1994) illustrated seasonal changes in adult occurrence and population parameters, specifically population size, daily survival, body size, and sex ratio of the artificially introduced population. This paper focuses on year-to-year changes in adult demographic attributes in the introduced population. In particular, we examined (1) how population growth rate and adult survival to the reproductive season changed from one year to another, because the two properties play an important role in determining population dynamics, and (2) what caused the pattern of annual changes in these demographic parameters.

Materials and Methods

Study site

The Botanical Garden of Kyoto University is 16,000 m^2 in area and is in the northeastern part of Kyoto City, which is about 10 km south of the southern limit of the natural distribution of *E. niponica,* (Fig. 1). Since the lady beetle has extremely limited dispersal (Nakamura and Ohgushi 1983; Ohgushi and Sawada 1985a), there was no evidence of the occurrence of *E. niponica* in the Botanical Garden before the introduction in 1971. 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 (Sawada and Ohgushi 1994).

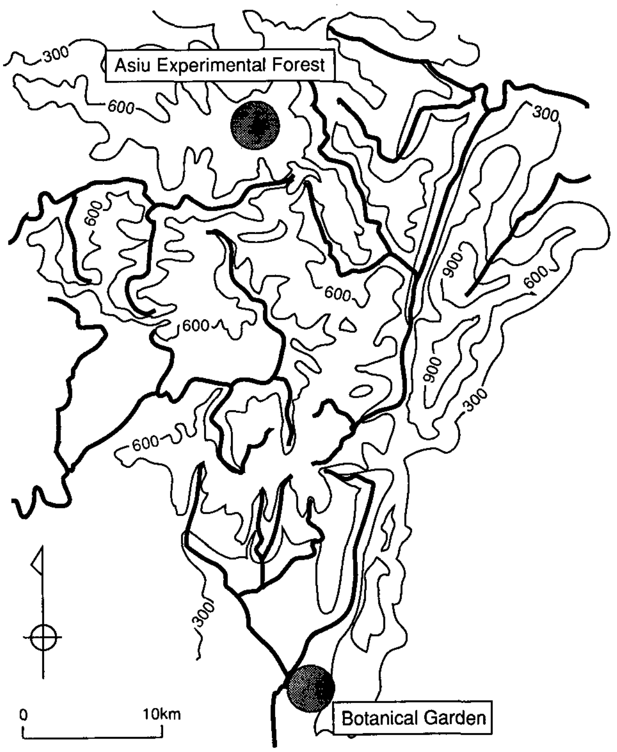

Fig. 1. Location of the Botanical Garden of Kyoto University and Asiu Experimental Forest. The thin lines show altitude in meters above sea level, the thick lines show rivers. Overwintering adults were introduced from Asiu to the Botanical Garden in May 1971.

Lady beetle

E. niponica overwinters in the adult stage, and emerges from hibernation in early spring. Females lay eggs in clusters on the undersurface of thistle 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 close to their host plants.

In the Botanical Garden, overwintering adults emerged in early April and disappeared by early July. New adults began to emerge from late June and increased rapidly in number, reaching a peak in early July, and then decreased steadily to the end of October as individuals entered hibernation. The observed number of new adults temporarily declined from late July to late August, which is probably attributable to aestivation; some adults stopped feeding and remained inactive within senescent rolled-leaves or under litter near the host plants. However, when defoliated host plants began to produce procumbent rosettes in autumn, these beetles resumed feeding during the pre-hibernating period.

Host plant

In the Botanical Garden, the introduced lady beetle feeds exclusively on leaves of a perennial thistle, *Cirsium nipponicum,* which is patchily distributed as a dominant species among the understory vegetation. The study plot of 50×30 m covered an area of high host density, including approximately 520 thistle plants.

The thistle plant began shoot growth with leaf production in early April; thereafter it increased steadily in size to the maximum height of 60–80 cm in late June. The number of leaves increased until late May, then declined considerably throughout the rest of the season because of heavy herbivory by the lady beetle (Sawada and Ohgushi 1994). The leaf herbivory was particularly apparent in 1975, 1977, 1979, and 1981, when more than 90% of leaves of most thistle plants were consumed by the lady beetle in mid-June which was when the number of old larvae reached its peak. In spite of the heavy grazing, damaged plants sprouted rosette leaves several weeks after defoliation.

Population census

We conducted population censuses from 1975 to 1981. In this period, the adult population was monitored using mark-recapture experiments for individuals, to estimate the total number of adults, survival rate, sex ratio, and body size.

From early April to late October, all the thistle plants in the study plot were individually examined every 3 days for overwintering adults and every 10 days for newly emerged adults. Adult beetles 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 to the plant on which they were captured. On subsequent censuses, marked adults were checked by sight without recapturing. In 1975, 1977, and 1981, only a group-marking technique was applied to new adults. A total of 18,276 adult beetles were marked in this study. Based on the data obtained, total numbers of overwintering and newly emerged adult beetles in each year were calculated, using a stochastic model for a mark-recapture experiment derived by Jolly (1965) and Seber (1973). To evaluate adult size at emergence, body length 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.

The numbers of eggs, fourth-instar larvae, pupae, and pupal exuviae were recorded separately for each plant on each census date. When they were found on a thistle leaf, the number of eggs in an egg batch was counted. To facilitate following the fate of individual eggs, each egg batch was marked by attaching a small numbered tag to the leaf. The number of eggs hatched was obtained by counting the empty egg shells that remained on the leaves after hatching. The total number reaching the medium age of the fourth-instar larval stage was estimated using the method described by Southwood and Jepson (1962).

Population growth rate and adult survival

We calculated the population growth rate, i.e., number of newly emerged adults produced by an overwintering adult, as an index of population growth. Population growth rate (R) is thus expressed as

$$\begin{aligned} R &= NA/OA \\ &= OA_f/OA \times E/OA_f \times L_1/E \times L_4/L_1 \times NA/L_4 \\ &= P_f \times F \times S_E \times S_{L1} \times S_{L2}. \end{aligned}$$

Using logarithms, population growth rate can also be expressed as

$$\log R = \log P_f + \log F + \log S_E + \log S_{L1} + \log S_{L2},$$

where OA = number of overwintering adults, NA = number of new adults, OA_f = number of overwintering females, E = number of eggs, L_1 = number of larvae hatched, L_4 = number of fourth-instar larvae, P_f = proportion of females of overwintering population, F = number of eggs oviposited by a female, S_E = egg survival, S_{L1} = larval survival from hatching to fourth-instar larva, S_{L2} = survival from fourth-instar larva to adult emergence.

Adult survival to the reproductive season was obtained by the total number of marked adults recaptured in the following spring divided by that of marked adults which had emerged in the previous summer. For further analysis, the overall survival was divided into two stage-specific survivals: survival until hibernation and survival during hibernation.

Results

Population growth rate

Population growth rate changed more or less cyclically over the study period, varying from 4.8 to 16.8 (Fig. 2). To determine what causes the pattern of changes, we divided population growth rate into five components: proportion of females in overwintering adult population (P_f), number of eggs oviposited by a female (F), egg survival (S_E), larval survival from hatching to fourth-instar larva (S_{L1}), and survival from fourth-instar larva to adult emergence (S_{L2}). We calculated the regression coefficient (*b*) of each component on population growth rate to determine which component(s) contributed most to the pattern of changes in population growth rate (Podoler and Rogers 1975). Annual changes in these components are compared in Fig. 3. Of these components, eggs produced by a

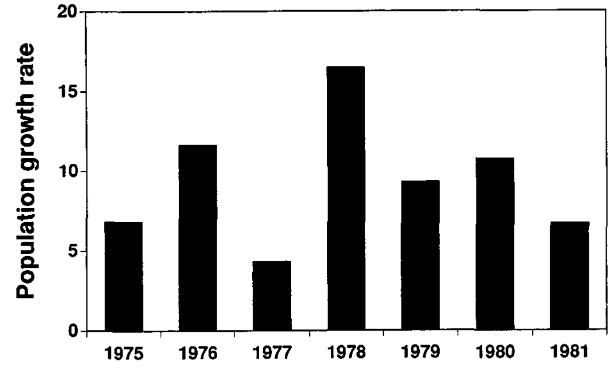

Fig. 2. Population growth rate, the number of new adults divided by that of overwintering adults, throughout the study period (1975—1981).

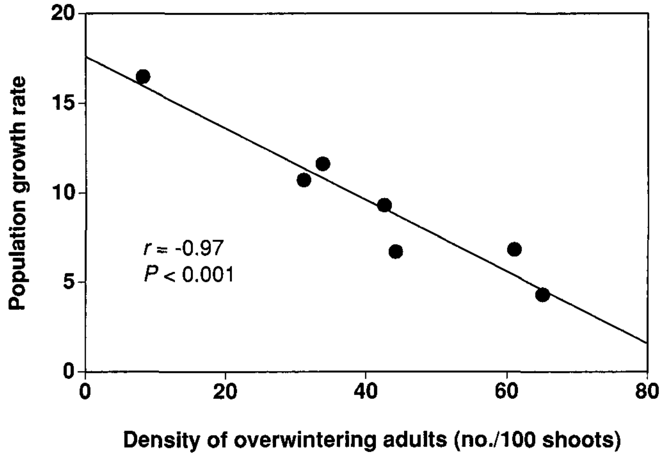

Fig. 4. Relationship between population growth rate and density of overwintering adults (number of adults per 100 shoots) ($r=-0.97$, $P<0.001$).

female (F) contributed most to the changes in population growth rate throughout the study period ($b=1.06$). Also, survival of late instars (S_{L2}) tended to change in a similar pattern to the population growth rate ($b=0.49$). On the other hand, larval survival from hatching to fourth-instar larva (S_{L1}) changed rather in counterbalance with the population growth rate ($b=-0.69$). It should be noted also that some components showed consistent changes over the study period. Early larval survival (S_{L1}) decreased consistently (Spearman's rank correlation; $r_S=-0.89$, $P<0.05$) but fecundity (F) increased ($r_S=0.77$, $P=0.085$).

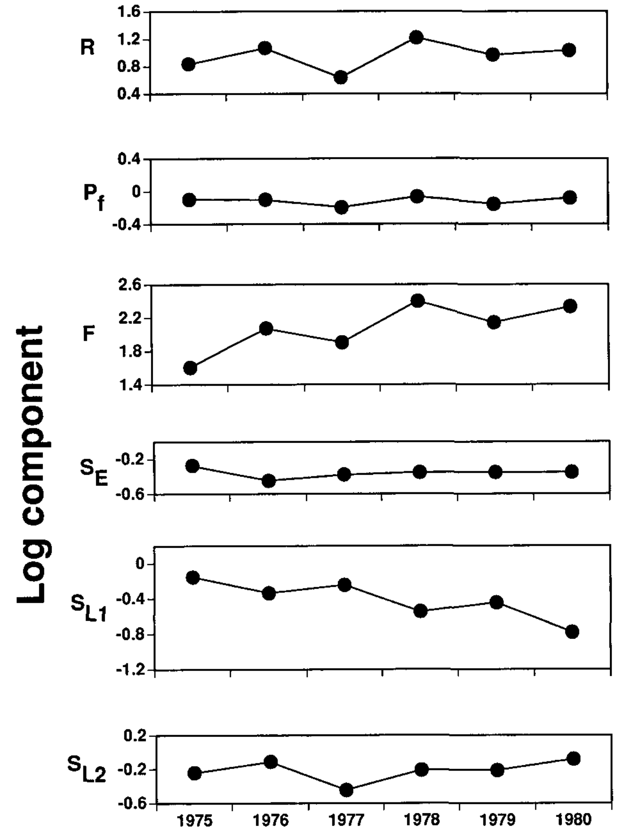

Fig. 3. Annual changes in the components of population growth rate (R). P_f, proportion of females among overwintering adults; F, number of eggs oviposited by a female; S_E, egg survival; S_{L1}, larval survival from hatching to fourth-instar larva; S_{L2}, survival from fourth-instar larva to adult emergence.

Also notable was the population growth rate which showed a highly negative correlation with the density of overwintering adults ($r=-0.97$, $P<0.001$; Fig. 4), implying that density dependent agent(s) acted on reproduction and/or survival until adult emergence.

Adult survival

Adult survival to the reproductive age in the following spring also fluctuated considerably over the study period, varying from 0.03 to 0.36 (Fig. 5). We examined what generated the pattern of changes in adult survival to the reproductive season. This consisted of two stage-specific survivals: survival during the pre-hibernating period and survival during hibernation. When the seasonal changes in the number of new adults which disappeared in each 10-day period were compared with the proportion of survivors to the following reproductive season, we found that most adult beetles that survived to the next year were recaptured after mid-September (Fig. 6). Since new adults dispersed little in the pre-hibernating period, and no host plants grew in the area adjacent to the Botanical Garden, most of the adult losses occurring before mid-September were probably due to death. Therefore, based on the assumption that all adults surviving at mid-September enter hibernation, we estimated the maximum survival until hibernation as the number of adults at that point divided by the total number of adults emerged.

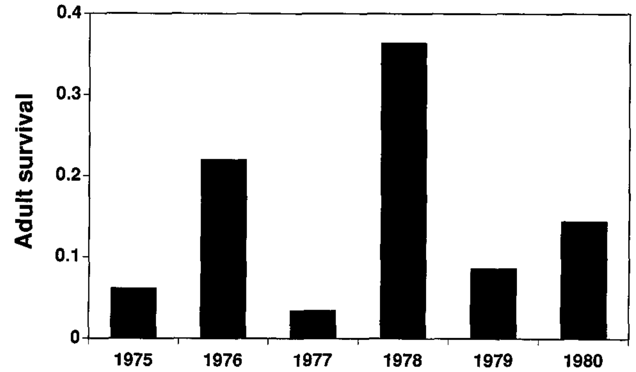

Fig. 5. Adult survival to the reproductive season in the following spring throughout the study period.

Annual changes in the overall survival to the reproductive season and its subdivided survivals are shown in Fig. 7. Survival during the pre-hibernating period coincided well with overall survival, indicating that annual variation in overall survival was mostly explained by survival until hibernation. In contrast, survival during hibernation remained at a constant high level throughout the study period, thereby contributing little to annual variation in overall survival.

Body size and a proportion of females

Body size of overwintering adults in 1980 for males and in 1978, 1979, 1980, and 1981 for females was significantly larger than that of new adults at emergence in the previous year (Mann-Whitney U-test; $P<0.05$; Fig. 8). This implies that mortality from emergence to the reproductive season operated in a size-dependent manner. There was a significantly positive correlation between adult size and survival until hibernation (male: $r=0.77$, $P<0.05$; female: $r=0.92$, $P<0.01$). It should be noted that a reduction in adult size was particularly apparent in 1977 and 1979 when severe host defoliation occurred. Actually, the body size of new adults of both sexes significantly decreased with increasing density of fourth-instar larvae (male: $r=-0.76$, $P<0.05$; female: $r=-0.88$, $P<0.01$). Thus it is more likely that in years of high larval densities severe intraspecific competition during the larval stage results in a higher proportion of small-sized adults. This is also supported by the fact that adults that emerged later, and experienced food deterioration due to thistle defoliation during the larval stage, were significantly smaller than those that emerged early (Sawada and Ohgushi 1994).

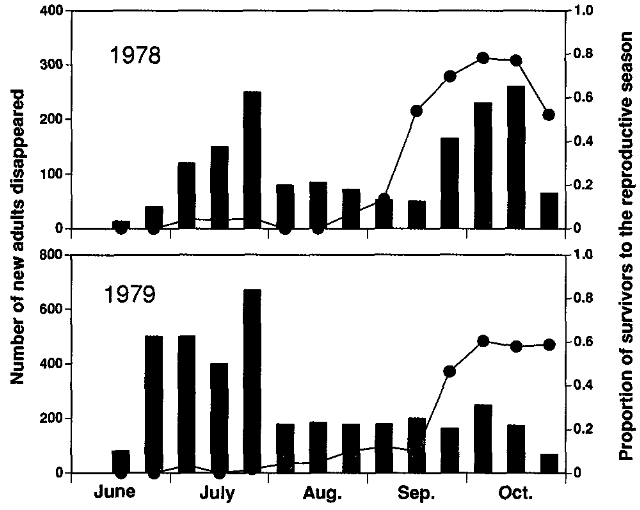

Fig. 6. Numbers of new adults disappearing (solid columns) in each 10-day period during pre-hibernation and the proportion surviving to the reproductive age in the following spring (closed circles).

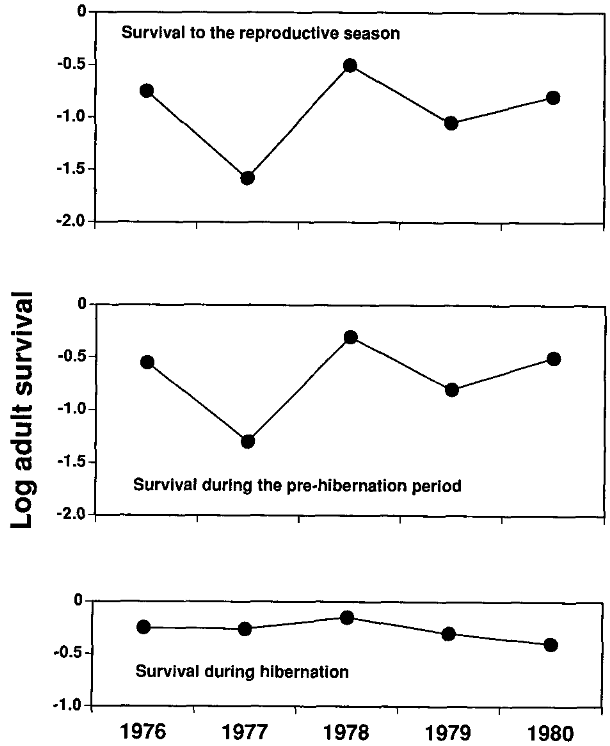

Fig. 7. Annual changes in adult survival to the reproductive season and its components: survival during the pre-hibernating period and survival during hibernation. See text on the division of overall survival into these survival components.

The proportion of females in the overwintering adult population in the Botanical Garden was significantly higher than that of the new adult population at emergence in the previous year (G-test; $P<0.001$ for every year except 1977 [$0.05<P<0.1$]; Fig. 9). This implies that adult mortality until the reproductive season operated differently in the two sexes.

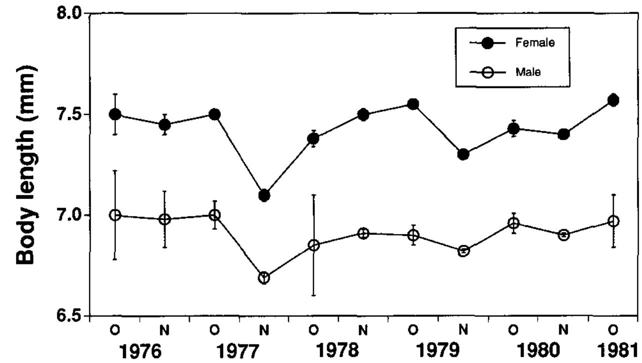

Fig. 8. Annual changes in body length of overwintering adults and new adults. Means and 95% confidence limits are presented.

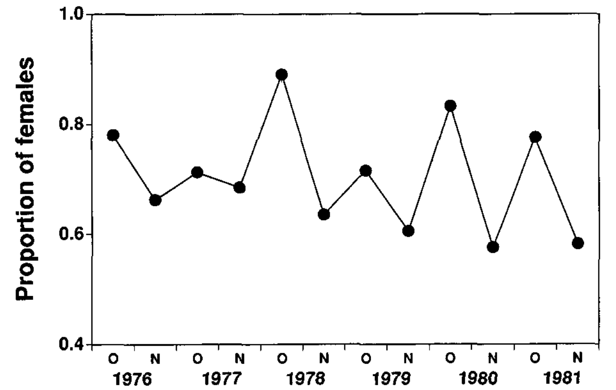

Fig. 9. Annual changes in the proportion of females in overwintering adults (O) and new adults (N).

Overall, the adult mortality during the period from emergence to the reproductive season had a significant role in altering the population structure in terms of body size and sex ratio in the reproductive season after hibernation.

Discussion

Adult demographic attributes of introduced and source populations

Nakamura and Ohgushi (1979, 1981) studied the source population in the native site of Asiu Experimental Forest in the three-year period 1974–76, and found that the beetle population persisted at relatively low densities, without host plant depletion. Although the source population was investigated for a short period of time, the present study has highlighted the differences in adult demographic attributes of the introduced and source populations.

Table 1 compares population growth rate and its components of the introduced and source populations. The growth rate of the introduced population was significantly higher than that of the source population, which was chiefly due to the improved survival of young larvae. Nakamura and Ohgushi (1981) suggested that arthropod predation by an earwig, *Anechura harmandi*, and by ground beetles including *Platynus ehikoensis* and *P. elainus* caused heavy mortality of early instars in the source population. Having monitored arthropod predation on the lady beetle in Kutsuki, 10 km east of Asiu Experimental Forest, Ohgushi and Sawada (1985b) found that predation on eggs and young larvae by the earwig, *A. harmandi*, contributed significantly to variability in the overall survival of immature stages of *E. niponica* among local populations, and thus played an important role in suppressing the population density of new adults. On the other hand, in the Botanical Garden, only larvae and adults of a predacious lady beetle, *Harmonia axyridis*, were observed feeding on the eggs, larvae and pupae of *E. niponica*. Although two parasitic wasps, *Pediobius foveolatus* (Eulophidae) and *Watanabeia afissae* (Proctotrupidae), killed larvae in the source population, no parasitism was observed in the Botanical Garden popula-

Table 1. Components of population growth rate and adult survival to the reproductive season in the introduced and source populations.

Component	Introduced population (1975–1980)	Source population (1974–1976)	Mann-Whitney *U*-test	
	(Mean ± 1SE)		*U*	*P*
R	9.86±1.71	1.77±0.76	18	0.02
P_f	0.77±0.03	0.66±0.02	15	0.12
F	139.9 ±32.4	64.1±12.7	14	0.20
S_E	0.44±0.02	0.40±0.03	12	0.44
S_{L1}	0.42±0.08	0.11±0.03	18	0.02
S_{L2}	0.63±0.07	0.90±0.06	17	0.04
S_{ad}	0.15±0.05	0.75±0.03	12	0.05

R, population growth rate; P_f, proportion of females of overwintering adults; F, number of eggs oviposited by a female; S_E, egg survival; S_{L1}, larval survival from hatching to fourth-instar larva; S_{L2}, survival from fourth-instar larva to adult emergence; S_{ad}, adult survival to the reproductive season.

tion. In contrast to the reduced mortality of early larvae from arthropod predation, old larvae of the introduced population were often subjected to severe food shortage because of heavy herbivory by the beetle. Considerable defoliation of thistle plants frequently occurred in late June throughout the Botanical Garden. In particular, host defoliation was apparent in 1977, 1979, and 1981 associated with high densities of larvae. As already mentioned, intraspecific competition for reduced food resources among late-instar larvae was more likely to produce small adults with poor survival to the reproductive season. Since reduced predation allowed high larval density followed by increased intraspecific competition, there was a link between arthropod predation and intraspecific competition. This implication was supported by the fact that survival of late-instars in the Botanical Garden was counterbalanced by survival of young larvae (see Fig. 3).

It has been demonstrated frequently in studies of biological control that introduced insect herbivores reach such high densities that host plants are severely damaged (Myers 1987; Crawley 1987). Successful biological control programs have emphasized that this rapid population growth of pest herbivores is brought about by a lack of natural enemies that effectively suppress densities of pest populations in endemic levels (Huffaker 1971; Huffaker and Messenger 1976; Murdoch et al. 1985; McClure 1986). For example, two introduced parasitoids dramatically reduced winter moth populations, which had been introduced in Nova Scotia. The moth had become a serious pest in hardwood forests, and after parasitoid introduction the moth populations were maintained at low densities (Embree 1965, 1966; but see Roland 1988).

The introduced population had a significantly lower adult survival to the reproductive season than the source population (see Table 1). Among the components of the overall survival, survival until hibernation was the most important factor determining the overall survival in the introduced population (see Fig. 7). Although Nakamura and Ohgushi (1979) did not divide the overall survival of the source population into these components, the difference in the level of the overall survival between the two populations was most likely attributable to that of survival until hibernation. This was because survival until hibernation of the introduced population remained much lower than that of the source population, even if we assume that all adult loss of the source population would have occurred in the period until hibernation (Mann-Whitney U-test; $U=10$, $P=0.052$).

Because the introduced population experienced unfavorable habitat conditions due to high temperature and host plant depletion in mid summer, it is surprising that daily survival of new adults in the introduced population was rather higher than that of the source population (Sawada and Ohgushi 1994). Aestivation of new adults observed in the Botanical Garden, which enables escape from the heat stress and food shortage in August, may result in the higher daily survival. Ohgushi and Sawada (1984) showed that adult survival until hibernation of *E. niponica* is not only affected by mean survival per day but also by the duration of residence until hibernation. New adults of the introduced population emerged one month earlier than the source population, but there was no difference in the timing of hibernation (Sawada and Ohgushi 1994). This indicates that there was a longer period of pre-hibernation in the introduced population than in the source population (Mann-Whitney U-test; $U=9$, $P<0.05$ for both male and female), thereby resulting in lower adult survival from emergence to hibernation, despite the higher daily survival during this period.

Ohgushi (1986) found that survival of *E. niponica* adults to the reproductive season differed by body size and sex in populations in Kutsuki. Similarly, in the introduced population, larger adults enjoyed higher survival to the reproductive age. Since adult size was negatively associated with population densities of fourth-instar larvae, it is suggested that heavy herbivory of thistle plants generated small-sized adults with poor survival. Also, adult mortality operated more intensively on males than females. However, this male-biased mortality was not detected in the source population (G-test; NS for each year).

Causes of changes in the demographic attributes of the introduced population

Myers (1987) and Crawley (1987) suggested several factors that have the potential to limit the establishment of introduced insect herbivores; these are climatic differences, natural enemies, potential competitors, host plant suitability, genetic variability, and intrinsic rate of increase. Once introduced populations have established, these factors will continue to influence significantly the subsequent patterns of dynamics of the introduced populations.

The reduced predation in the Botanical Garden allowed higher larval density, thereby contributing to a higher population growth rate. Severe food shortage due to high larval density produced a higher proportion of small-sized adults associated with lower adult survival to reproductive age. It should be noted also that increased fecundity made a major contribution to improved population growth rate in the latter phase of the study period, compensating for the lowered survival of early instars because of increased predation by *H. axyridis* (see Fig. 3).

Climatic differences affect indirectly introduced populations through changing the phenology of introduced herbivores (McClure 1986; Myers 1987). Warmer weather in the Botanical Garden, approximately 3-5°C higher in monthly mean temperature than Asiu, leads to early adult emergence (Sawada and Ohgushi 1994). The introduced population had a sharp peak of adult emergence in early July, compared with a gradual emergence from early to late August in the source population (Nakamura and Ohgushi 1979). Because there was no large difference in the timing of entering hibernation between the introduced and source populations, the longer period from emergence to hibernation was brought about by the earlier adult emergence of the introduced population. As mentioned above, earlier adult emergence was responsible for reduced survival until hibernation due to the longer residence of new adults. Overall, both lower arthropod predation and warmer weather in the Botanical Garden are most likely to alter the demographic attributes in terms of population growth and adult survivorship of the introduced population, when compared with the source population.

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