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What changed the demography of an introduced population of an herbivorous lady beetle?

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Summary

1. The population dynamics of an introduced population of *Epilachna niponica* (Lewis) (Coleoptera: Coccinellidae) was investigated for a 7-year period following its introduction to a site outside of its natural range. A population from Asiu Experimental Forest was introduced to Kyoto University Botanical Garden, 10 km south of its natural distribution.

2. Arthropod predation was much lower in the introduced than in the source population. As a result of the lower predation in the Botanical Garden, larvae reached densities five times higher than in the Asiu Forest and host plants were frequently defoliated. Food shortage caused larval deaths from starvation and increased dispersal.

3. The density of the introduced population was much more variable than that of the source population. The variation in population density in both the introduced and source populations is limited by density-dependent reduction in fecundity and female survival. However, variation in the introduced population's density was increased due to host plant defoliation that resulted in overcompensating density-dependent mortality. In years with high larval density plants were defoliated and this increased adult mortality during the prehibernation period. Besides, the density-dependent regulatory mechanisms that produce population stability were weaker in the introduced population than in the source population.

Key-words: Epilachna niponica, host plant defoliation, introduction experiment, natural enemies, population dynamics.

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Introduction

The importance of introduced species in altering community organization has attracted the attention of ecologists since Elton (1958) first emphasized their importance. The density, population stability and persistence of introduced species are often altered compared to the source populations (McClure 1986; Myers 1990). Colonizing species may be subjected to different habitat conditions and/or species interactions than their source populations (Diamond & Case 1986; Endler 1990; Settle & Wilson 1990; Schönrogge, Stone & Crawley 1996), which may alter their population dynamics. Population outbreaks of pest species have often occurred when species are introduced to new areas (Embree 1965; Hassell 1978, 1980; McClure 1980; Roland & Embree 1995). Since introduced species often become serious pests, it has often been necessary to introduce predators and parasitoids to reduce their population density (Huffaker 1971; Huffaker & Messenger 1976; Murdoch, Chesson & Chesson 1985). The success of some of these biological control programmes has demonstrated the importance of altered interactions with natural enemies in the population dynamics of introduced species (Roland 1994).

Despite the demonstrated importance of introduced species, surprisingly few studies have documented the population dynamics of herbivorous insect species immediately after introduction (e.g. Myers 1990). Therefore, we know little about how population dynamics of introduced insects are altered under these new environmental conditions. Climatic differences, natural enemies, potential competitors, host plant suitability, genetic variability, and intrinsic rates of

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increase may all influence the establishment and population dynamics of introduced species (Crawley 1987; Myers 1987). We need more information about the impact of these factors in order to understand why, after introduction, some insects go extinct, some are maintained at low density, and others erupt to outbreak densities. Long-term studies that compare the population dynamics of herbivorous insects in their native and new habitats are necessary to understand what factors are crucial in influencing the population dynamics of introduced species (McClure 1986). Artificial introduction experiments can be useful tools in understanding the important changes in the population dynamics of successfully colonizing species (Myers 1990).

Epilachna niponica (Lewis) is a univoltine herbivorous lady beetle that feeds exclusively on the leaves of thistle plants. Beetle populations persisted at relatively low densities with no evidence of defoliation of its host plant *Cirsium kagamontanum* (Nakai) in the Asiu Experimental Forest of Kyoto University (Nakamura & Ohgushi 1981). In May 1971, 15 males and 30 females of overwintering adults were collected from the Asiu population and were introduced into the Botanical Garden of Kyoto University, 30 km south of Asiu and 10 km south of the southern limits of its natural distribution. Such a female-biased sex ratio is typical in the source population. The introduced population successfully established and since 1974 thistle plants at the Botanical Garden have been heavily defoliated by beetles each year.

We began to study the Botanical Garden population in the spring of 1975. Compared with the source population, the introduced population had shifted its phenology 1 month earlier (Sawada & Ohgushi 1994) and it has a significantly higher population growth rate from reproductive adult to new adult stages (Ohgushi & Sawada 1995). The introduced population reproduces earlier at the cost of reduced longevity (Ohgushi & Sawada 1997).

This study examines the population dynamics of the introduced population and compares the results with those obtained in the source population (Nakamura & Ohgushi 1979, 1981). In particular we ask: (i) Have the population density and stability changed in the introduced population? (ii) What mechanisms are responsible for the changes in the demography of the introduced population?

Materials and methods

STUDY SITE

The Botanical Garden of Kyoto University is located in the north-eastern part of Kyoto City, 10 km south of the southern limit of the natural distribution of *E. niponica*. There was no evidence of the occurrence of *E. niponica* in the Botanical Garden before the introduction in 1971. Intensive mark–recapture experiments on adult beetles in eight local populations clearly demonstrated that the lady beetle has an extremely limited dispersal ability (Ohgushi 1983; Sawada 1984). Adults that travelled more than 100 m comprised less than 0·04% of the marked adults. There was a nearby natural population in Kurama, which is located 10 km north of the Botanical Garden. This population is geographically isolated from other populations farther to the north. A mark–recapture experiment for the Kurama population showed that there was no immigration to the Botanical Garden. The isolation of the Botanical Garden also indicates that it was unlikely to receive immigrants. It is located in urban area devoid of natural vegetation, and few thistle plants that could serve as a bridge for migrating lady beetles exist anywhere between Kurama and the Botanical Garden. All of these results strongly suggest that the introduced population has been completely isolated from any other *E. niponica* populations since introduction. Because it is located at a much lower elevation than the Asiu Experimental Forest, temperatures are 3–5 °C higher throughout the season in the Botanical Garden (Sawada & Ohgushi 1994).

LADY BEETLE

E. niponica overwinters in the adult stage and emerges 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 nearby their host plants.

In the Botanical Garden, overwintering adults emerged in early April, and most of them died by late June (Sawada & Ohgushi 1994). New adults began to emerge in 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. Defoliated host plants began to produce procumbent rosettes in autumn that the beetles eat during the prehibernation period. A detailed description of the life history is given in Sawada & Ohgushi (1994).

HOST PLANT

In the Botanical Garden, the introduced lady beetle feeds exclusively on leaves of a perennial thistle *Cirsium nipponicum* (Makino), which is patchily distributed as a dominant species among the understorey vegetation. *C. nipponicum* is a very common species that is widely distributed in central and southern parts of Japan. Our study plot of 50 × 30 m covered an area of high host density, including ≈ 520 individual thistle plants.

The thistle plant began shoot growth with leaf production in early April; growth increased steadily thereafter and plants reached a maximum height of 60–80 cm in late June (Sawada & Ohgushi 1994). The number of leaves increased until late May. However, heavy herbivory by the lady beetle proceeded throughout the rest of the season. In 1975, 1977, 1979 and 1981, more than 90% of leaves of most thistle plants were consumed by mid-June when the number of late instar larvae of *E. niponica* reached its peak. In spite of this heavy grazing, damaged plants sprouted rosette leaves several weeks after defoliation (Sawada & Ohgushi 1994).

POPULATION CENSUS

We conducted population censuses from 1975 to 1981. The adult population was monitored using mark–recapture techniques for individuals, to estimate the total number of adults, survival rate, sex ratio, and body size.

All the thistle plants in the study plot were individually examined every 3 days from early April to late June and every 10 days from early July to late October. Adult beetles were individually marked with differently coloured 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. Total numbers of overwintering (reproductive) and newly emerged adults in each year were calculated, using a stochastic model for mark–recapture experiments derived by Jolly (1965) and Seber (1973). The estimates were highly reliable because we obtained an extremely high marking ratio in the study period; more than 95% of adult beetles were successfully marked 1–2 weeks after the marking experiment commenced.

The numbers of eggs per batch, hatched larvae, and fourth instar larvae were recorded separately for each plant on each census date. 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. At the study sites, beetle eggs were subjected to two main sources of mortality: egg cannibalism by adults and newly hatched larvae, and arthropod predation. The total number reaching the age of the fourth instar was estimated using the method described by Southwood & Jepson (1962).

ESTIMATION OF SURVIVAL RATE

Based on the estimated numbers of eggs, newly hatched larvae, fourth instar larvae, and new adults, we calculated survival rates of eggs, early larvae (first to fourth instars), and late larvae (fourth instar to adult). Daily survival of reproductive adults was estimated by the Jolly–Seber stochastic model (Jolly 1965; Seber 1973). For new adults, survival from adult emergence to the reproductive season was obtained by dividing the total number of marked adults recaptured in the following spring by the number of marked adults which had emerged in the previous summer. For further analysis, overall adult survival was divided into two stage-specific survivals: survival during prehibernation and survival during hibernation. Ohgushi & Sawada (1995) found that most adult beetles that survived to the next year were recaptured after mid-September. Since new adults dispersed little in the prehibernation 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 rate during prehibernation as the number of adults at that point divided by the total number of adults emerged.

VARIABILITY OF POPULATION DENSITY

To compare the variability of population density among different life stages or seasons, we calculated the standard deviation of log-transformed densities, which is an appropriate index for temporal variability of population size or density (Pimm 1991; Gaston & McArdle 1994).

A FIELD EXPERIMENT TO ASSESS LARVAL DISPERSAL

We conducted an experiment to examine whether larvae were forced to disperse due to host defoliation. In 1975 and 1980, 129 and 166 fourth instar larvae were, respectively, marked and placed on highly damaged plants. Thereafter, we followed the fate of each individual larva, and classified them into three categories: larva pupating on the original plant, larva disappeared, and larva found on other plants.

Results

POPULATION SIZE IN RESPONSE TO RESOURCE ABUNDANCE

Thistle shoot density increased gradually throughout the study period, from 0·69 m^{-2} in 1975 to 1·18 m^{-2} in 1981 (Fig. 1). The beetle population was less stable than the host plant population. The reproductive adult population varied 7·4 fold and the new adult population 3·4 fold over the 7 years (Fig. 1).

The number of eggs and newly hatched larvae were significantly correlated with shoot numbers, while the numbers of other stages were not (Table 1). Host

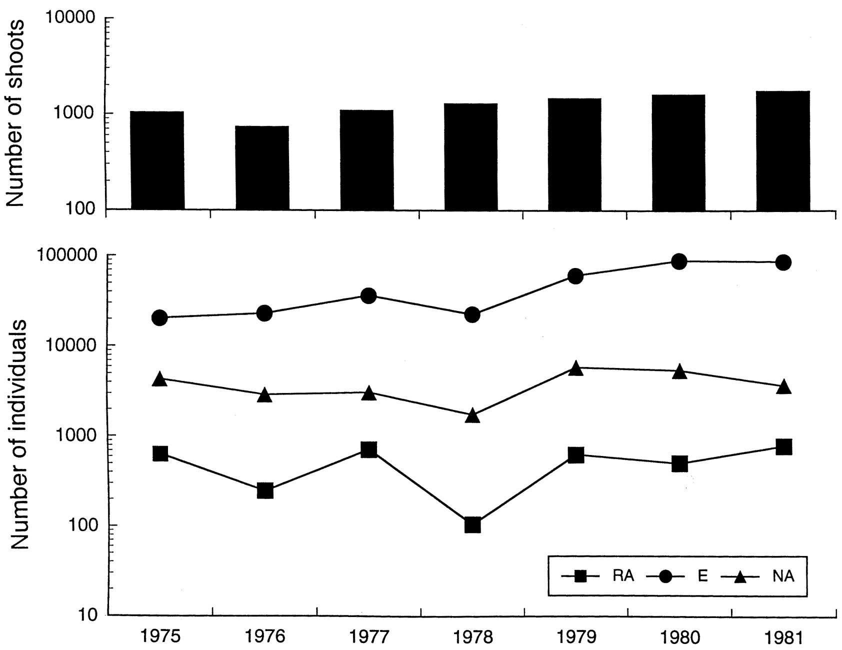

Fig. 1. Annual changes in the number of thistle shoots (top) and individuals in each life stage of *E. niponica* (bottom) for 1975–81: RA, reproductive adult; E, egg; NA, newly emerged adult.

Table 1. Regressions of population size of each life stage on number of thistle shoots for a 7-year study period

Life stage	*b*	r^2	*F*	*P*
Reproductive				
Adult	0·283	0·168	1·012	0·3607
Egg	73·310	0·765	16·286	0·0100
1st instar	32·420	0·717	10·146	0·0334
4th instar	1·396	0·042	0·219	0·6593
New adult	1·739	0·187	1·148	0·3329

abundance accounted for 77% and 72% of the variation in number of eggs and hatched larvae, respectively. This indicates that temporal resource tracking occurred during the egg and hatched larvae stages, but not during the later stages.

MECHANISMS OF POPULATION STABILIZATION

The variability in population density sharply declined from the reproductive to egg stage, and then remained constant until adult emergence (Fig. 2). It then increased in the reproductive stage in the following spring. This suggests that there were two processes involved in population stability. First, density-dependent processes led to a stabilization of population density during the reproductive season. Then the population was influenced by factors that led to population variability during the period from adult emergence until the following reproductive period.

Eggs laid per female in a reproductive lifetime were significantly reduced as population density increased ($y = -341{\cdot}3\,x + 279{\cdot}9$, $r^2 = 0{\cdot}826$, $n = 7$, $F = 23{\cdot}75$, $P = 0{\cdot}004$, Fig. 3). Fecundity decreased in a density-dependent manner until early May, but it was independent of adult density thereafter (15 April–5 May: $y = -206{\cdot}5\,x + 102{\cdot}9$, $r^2 = 0{\cdot}677$, $n = 6$, $F = 8{\cdot}38$, $P = 0{\cdot}044$; 6 May–25 May: $y = -454{\cdot}9\,x + 195{\cdot}6$, $r^2 = 0{\cdot}612$, $n = 6$, $F = 6{\cdot}30$, $P = 0{\cdot}058$; 26 May–15 June: $y = -375{\cdot}4x + 113{\cdot}6$, $r^2 = 0{\cdot}154$, $n = 6$, $F = 0{\cdot}73$, $P = 0{\cdot}441$). Female survival also decreased with increasing adult density early in the season, but the density-dependent female survival was no longer detected after late May (21 April–10 May: $y = -0{\cdot}51\,x + 1{\cdot}03$, $r^2 = 0{\cdot}754$, $n = 7$, $F = 15{\cdot}30$, $P = 0{\cdot}011$; 21 May–9 June: $y = 0{\cdot}11x + 0{\cdot}28$, $r^2 = 0{\cdot}073$, $n = 7$, $F = 0{\cdot}39$, $P = 0{\cdot}559$, Fig. 4). As a consequence of these strong density-dependent processes operating

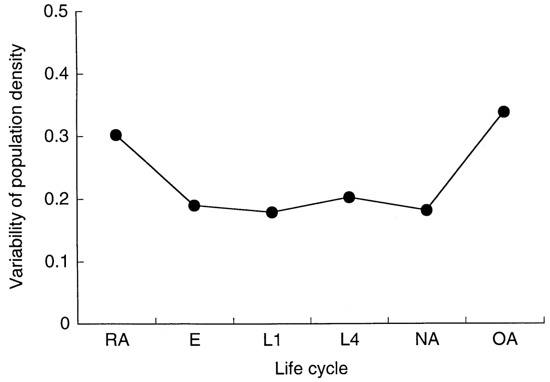

Fig. 2. Variability of population density expressed as SD log density for a 7-year period (1975–81): RA, reproductive adult; E, egg; L1, first instar larva; L4, fourth instar larva; NA, newly emerged adult; OA, overwintered adult.

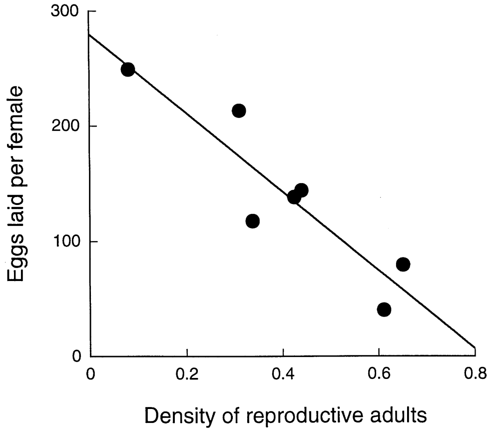

Fig. 3. The relationship between eggs laid per female in a reproductive lifetime and density of reproductive adults per shoot.

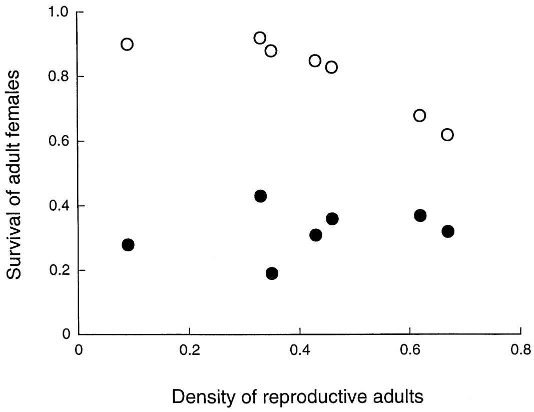

Fig. 4. The relationship between female survival per 20 days and density of reproductive adults per shoot for 1975–81. (○) early season (21 April to 10 May), and (●) late season (21 May to 9 June).

early in the reproductive season, the stability of egg density increased from mid-April to mid-May and then remained constant (Fig. 5).

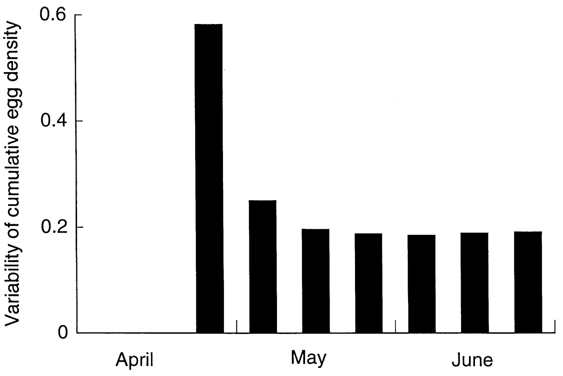

Fig. 5. Seasonal changes in variability of cumulative egg density. Variability was expressed as SD log density for a 7-year period (1975–81).

Egg, early larval, and late larval survivals were, respectively, 0·44 ± 0·02 (mean ± 1SE), 0·42 ± 0·08, and 0·63 ± 0·07 throughout the study period.

The main factors responsible for egg deaths were cannibalism and arthropod predation, which, respectively, killed 23·5 ± 2·44 and 25·6 ± 3·66% of eggs laid. Egg predators included larvae of the predacious lady beetle *Harmonia axyridis* (Pallas), larvae of the lacewing bug *Chrysopa nipponensis* (Okamoto), and adults of the cantharid beetle *Athemus vitellinus* (Kiesenwetter). Early instar larvae were also attacked by *H. axyridis*. However, the density of the predacious lady beetle remained relatively low over the study period (Fig. 6). There was no evidence of parasitism in the introduced population.

Low arthropod predation could not prevent larval density from reaching such high levels that intensive defoliation occurred every year. On average, 77·0 ± 5·63% (mean ± 1SE) of total leaf area were damaged by larval feeding in mid-June. Thus, larval death due to food shortage was the most important mortality agent in the Botanical Garden.

The dispersal experiment showed that larval dispersal was high in the Botanical Garden, 54% in 1975 and 44% in 1980 leaving their original host plants (Table 2). Most of the dispersing larvae disappeared, probably either due to predation while moving on the ground or due to failure to find another host plant. In both of these years plants suffered from high levels of defoliation (Sawada & Ohgushi 1994).

Adult survival during the prehibernation period had a substantial impact on the variation in lady beetle density in the reproductive season. The prehibernation survival rate varied considerably among years and accounted for 94% of the variation in overall adult survival (Fig. 7). The rate of population change of reproductive adults was strongly correlated with adult survival during the prehibernation period (Fig. 8). The variation in prehibernation survival explains 95% of the annual variation in the rate of population change, expressed as the log of the ratio of reproductive adult density in the following year to

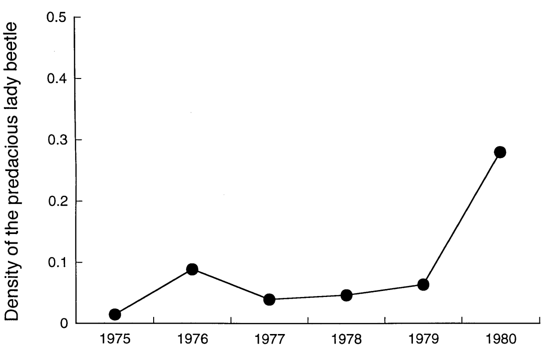

Fig. 6. Annual changes in density of the predacious lady beetle *Harmonia axyridis* per shoot for 1975–81.

Table 2. Fates of marked 4th instar larvae (%) in 1975 and 1980. The number of marked larvae in each category is given in parentheses

Year	Number of marked larvae	% pupating on original plant	% disappeared	% found on other plants
1975	129	55·8 (72)	38·8 (50)	5·4 (7)
1980	166	45·8 (76)	47·0 (78)	7·2 (12)

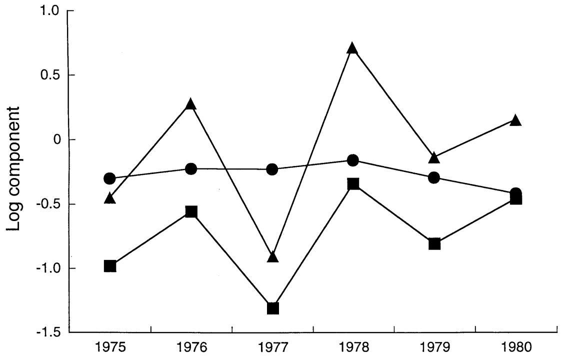

Fig. 7. Annual changes in overall adult survival to the reproductive season (■), adult survival during prehibernation (▲), and adult survival during hibernation (●) for 1975–80.

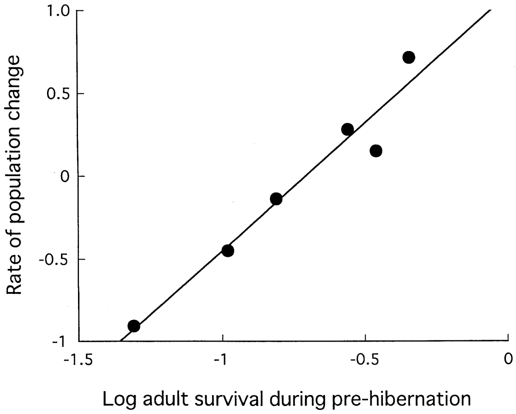

Fig. 8. The relationship between adult survival during prehibernation and the rate of population change. The rate of population change was calculated as the log of the ratio of reproductive adult density in the following year to density in the current year (see Royama 1981).

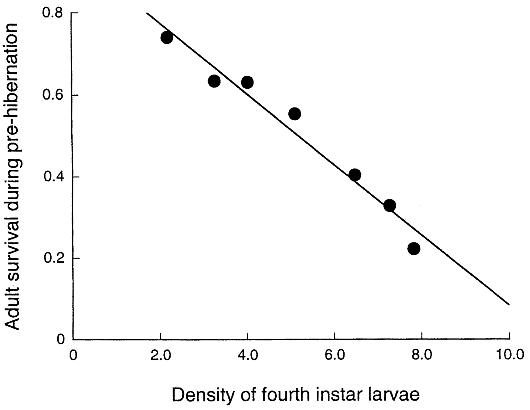

Fig. 9. The relationship between adult survival during prehibernation and density of fourth instar larvae per shoot.

density in the current year ($y = 1\cdot54x + 1\cdot09$, $r^2 = 0\cdot951$, $n = 6$, $F = 76\cdot84$, $P = 0\cdot0009$). On the other hand, adult survival during hibernation remained constant over the 7 years (Fig. 7).

There was a strong negative correlation between late larval density and adult survival during the prehibernation ($y = -0\cdot09x + 0\cdot95$, $r^2 = 0\cdot965$, $n = 7$, $F = 137\cdot91$, $P < 0\cdot0001$, Fig. 9). Since there is a strong positive correlation between larval density and defoliation levels ($y = 6\cdot49\ x + 43\cdot42$, $r^2 = 0\cdot859$, $n = 7$, $F = 30\cdot40$, $P = 0\cdot0027$), it is likely that high larval densities led to food shortages and lowered adult size. Since adult size is positively correlated with survival (Ohgushi 1996a), the ultimate effect of high larval densities reduced adult survival.

COMPARISONS OF THE INTRODUCED AND SOURCE POPULATIONS

To determine how the new environment altered the population dynamics of *E. niponica*, we compared the results of this study with data on the source population reported by Nakamura & Ohgushi (1979, 1981). The population density of the later life stages of introduced population was markedly higher than that of the source population (Table 3). Egg density and survival of immatures to adult emergence are the two major components determining the population density of new adults. Since egg density did not differ between the two populations, the significantly higher adult density of the introduced population was principally brought about by higher larval survival in the Botanical Garden. This is illustrated by the difference in survivorship curves of the two populations (Fig. 10). There were no differences in egg survival between the introduced and source populations ($0\cdot44 \pm 0\cdot02$ vs. $0\cdot40 \pm 0\cdot03$ [mean ± 1SE], Mann–Whitney *U*-test: $U = 12$, $P = 0\cdot44$). The introduced population had significantly higher larval survival from first instar to fourth instar than the source popu-

Table 3. Population density (number per shoot) and population variability (standard deviation of log densities) of the introduced and source populations

Population characteristics Life stage	Introduced population (1975–81)	Source population (1974–76)	Mann–Whitney *U*-test	
			U	*P*
Population density	(Mean ± 1SE)			
Reproductive adult	0·40 ± 0·07	0·66 ± 0·11	18·5	0·0682
Egg	35·22 ± 5·34	26·41 ± 1·02	15·0	0·3051
1st instar larva	14·27 ± 2·48	10·44 ± 0·77	12·0	0·4386
4th instar larva	5·17 ± 0·80	1·11 ± 0·18	21·0	0·0167
New adult	3·08 ± 0·40	1·01 ± 0·23	20·0	0·0304
Population variability	(SD log densities)			
Reproductive adult	0·302	0·121		
Egg	0·190	0·028		
1st instar larva	0·179	0·057		
4th instar larva	0·203	0·119		
New adult	0·182	0·169		

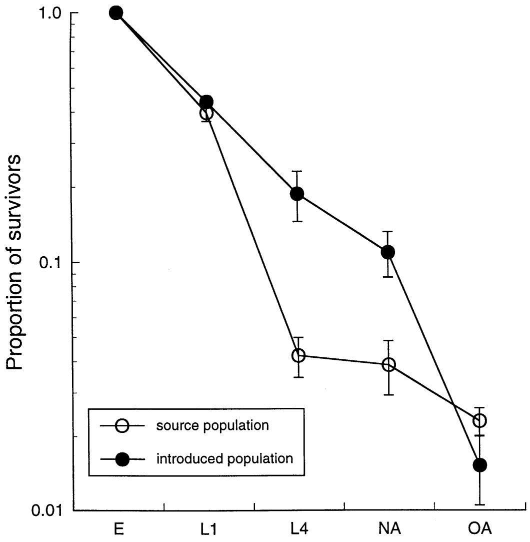

Fig. 10. Proportion of survivors of the introduced and source populations throughout the life cycle: E, egg; L1, first instar larva; L4, fourth instar larva; NA, newly emerged adult; OA, overwintered adult. Means and 1SE are represented in the introduced population for 1975–81 and the source population for 1974–76.

lation (0·42 ± 0·08 vs. 0·11 ± 0·03; $U = 18$, $P = 0·02$). Conversely, there was significantly lower survival from fourth instar to adult emergence in the introduced population (0·63 ± 0·07 vs. 0·90 ± 0·06; $U = 17$, $P = 0·04$). However, the higher survival of early larvae affected overall larval survival much more in the introduced population.

A comparison of population variability indicates that the introduced population was more variable than the source population throughout all life stages (Table 3), although the variability of the source population may be somewhat underestimated because of a shorter census period (see Lawton 1988). Although egg densities were stabilized by the density-dependent regulatory mechanism (see Fig. 2), egg density in the introduced population was 6·8 times more variable than the source population.

Discussion

DIFFERENCES IN THE POPULATION DYNAMICS

There were significant differences in the population dynamics of the source and introduced populations of *E. niponica*. In the introduced population, the density was stabilized during its reproductive period and destabilized during the adult period prior to reproduction. The source population, however, remained stable during the adult period prior to reproduction. The difference in population dynamics between the two populations is primarily due to the lack of predation in the Botanical Garden. In the absence of predation many thistles are defoliated and as a result many larvae starve or die in an attempt to disperse from defoliated hosts. The starved larvae that survive to the adult stage also suffer higher mortality.

MECHANISMS OF INCREASED POPULATION DENSITY

In spite of a lack of difference in egg density between the populations, the introduced population reached a significantly higher density in late larval and adult stages. Hence, the higher early larval survival increased adult density of the introduced population.

The increased early larval survival in the Botanical Garden was primarily due to the absence of arthropod predators and parasitoids. A cage experiment excluding predators in the source population demonstrated that arthropod predation was a key component of heavy larval mortality (Nakamura & Ohgushi 1981). The predaceous earwig *Anechura harmandi* (Burr) and the ground beetles *Platynus ehikoensis* (Habu) and *Platynus elainus* (Bates) were important predators in the source population but were absent in the Botanical Garden. Two parasitic wasps *Pediobius faveolatus* (Crowford) (Eulophidae) and *Watanabeia afissae* (Watanabe) (Eulophidae) found in the source population were also absent in the Botanical Garden. The only natural enemy in the Botanical Garden was the predacious lady beetle *Harmonia axyridis*. However, this lady beetle remained at low densities in the introduced population and was rare in the source population.

It is unclear why arthropod predators remained at such low density in the Botanical Garden. Two factors may contribute to this low predator density. First, few other prey are available on thistle plants in the Botanical Garden. During the study period the only other prey we observed were a negligible number of lepidopteran larvae and aphids. We saw no signs of herbivory by other phytophagous insects. This low prey density probably inhibited the maintenance of a large predator population. Secondly, the most abundant predator in the source population, the earwig *A. harmandi*, is absent. This is probably due to a lack of suitable habitat. The earwig strongly prefers open habitat such as is found along riversides, while the Botanical Garden has only understorey habitat.

The low levels of predation in the Botanical Garden also had an indirect effect on population dynamics mediated through the host plant. Reduced predation led to increased early larval survival which resulted in increased host plant defoliation. Host plant defoliation in turn caused increased larval mortality due to starvation and dispersal. Host plant defoliation has also been demonstrated to accelerate dispersal in the cinnabar moth *Tyria jacobaeae* (L.) (Dempster 1971; Myers & Campbell 1976), and ground predators lower the success of the dispersing larvae (Van der Meijden 1973). In addition, starvation led to smaller adults with low winter survival (Ohgushi & Sawada 1995; Ohgushi 1996a).

The absence of natural enemies has been documented to have an effect on population dynamics in a wide range of studies. Introduced species frequently reach such high densities that host plants are severely damaged (McClure 1980; Myers 1987; Crawley 1987). The importance of natural enemies in limiting herbivore population densities has been demonstrated in many biological control studies (Huffaker 1971; Huffaker & Messenger 1976; Murdoch, Chesson & Chesson 1985). For example, the introduction of parasitoids dramatically reduced winter moth densities, an introduced species in Nova Scotia that was a serious hardwood pest (Embree 1965, 1966; Hassell 1980; Roland & Embree 1995: but see Roland 1988). Studies where parasitoids were experimentally excluded (Faeth & Simberloff 1981; Stiling, Brodbeck & Strong 1982; McClure 1986) and where arthropod predators were removed (Edson 1985) have also shown that natural enemies maintain herbivores at low densities.

MECHANISMS OF INCREASED POPULATION VARIABILITY

The introduced population was the least stable among seven populations of *E. niponica* that we have studied (Nakamura & Ohgushi 1981; Ohgushi & Sawada 1985a; Ohgushi 1992, 1995). In every local population that we have studied, density-dependent population stabilization occurred during reproduction (Nakamura & Ohgushi 1981; Ohgushi 1992, 1995). The source population showed density-dependent reduction in fecundity and female survival (Nakamura & Ohgushi 1981). Ohgushi & Sawada (1985a) found that female movement while searching for the oviposition site, and egg resorption were the primary factors causing the density-dependent reduction in reproduction.

In the introduced population the density-dependent regulatory mechanisms that produce population stability were weaker than in the source population. Reproductive females in the source population moved on average five times as much as those in the introduced population (Nakamura & Ohgushi 1983; Sawada 1984). This implies that in the introduced population there was less of a density-dependent shift from egg production to movement. Density-dependent egg resorption may also not occur in the introduced population for two reasons. First, in the introduced population density-dependent fecundity occurred early in the season not late in the season when egg resorption occurs in response to increased host plant deterioration (Ohgushi & Sawada 1985a; Ohgushi 1996b). Secondly, the introduced population has an earlier reproductive effort and reduced longevity compared to the source population (Ohgushi & Sawada 1997). Since females in the introduced population have little possibility of surviving and ovipositing at a later time, resorption of eggs is disadvantageous.

Increased density in the introduced population may also have increased population variability. High larval densities led to severe intraspecific competition due to overexploitation of food resources. The rate of population change was primarily determined by adult survival until hibernation (Fig. 8), which decreased as larval density increased (Fig. 9). In the introduced population the larval survival rate and thus the level of defoliation was variable, which would result in variation in the adult survival rate until hibernation. Host plant defoliation frequently resulted in intraspecific competition for food resources which can accentuate fluctuations in population densities of herbivorous insects (Harcourt 1971; Dempster 1971, 1982; Southwood & Comins 1976). Dempster (1983) and Stiling (1988) reviewed life table data and found that resource overexploitation was the key factor contributing most to population variation in some insect herbivores. For example, the large population fluctuations of the cinnabar moth correspond to food availability which can be limited by overexploitation of host plants (Dempster 1971, 1982; Van der Meijden 1971; Myers & Campbell 1976).

An alternative hypothesis is that the differences in stability and density between the source (Asiu) and introduced (Botanical Garden) populations were due to year-to-year variation common to both sites. The census years at the two sites did not completely overlap and therefore temporal differences could explain some of the variance. We do not believe that this is an important factor for two reasons. First, we have extensively studied a population at Kutsuki, 10 km east of the Asiu population, during the same years we studied the Botanical Garden (Ohgushi & Sawada 1981). The Kutsuki population had the same demographic parameters of the Asiu population (Ohgushi & Sawada 1985a,b; Ohgushi 1986), and significantly differed from the Botanical Garden. Therefore, the contribution of common year-to-year variation among sites is probably minimal. Secondly, the high population densities and plant defoliation of the introduced population are unique. To our knowledge no natural populations of *E. niponica* have ever defoliated its host plant.

This study demonstrates that a comparison of introduced and source populations can provide valuable insights into the mechanisms that control herbivorous insect population dynamics.

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