Population Stability in Relation to Resource Availability in an Introduced Population of an Herbivorous Lady Beetle

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Abstract. Mechanisms responsible for population stability in relation to resource availability were studied in an introduced herbivorous lady beetle, *Epilachna niponica*. The introduced population was relatively constant over a seven-year study period. Egg density was related to the variation in host-plant abundance in different years, and was highly stabilized during the period from reproductive adult to egg stage. Two density-dependent processes were identified in the reproductive season: (1) density-dependent reduction in fecundity and (2) density-dependent increase in female mortality and/or emigration, all of which operated early in the season. As a result, temporal variability in cumulative egg density was greatly reduced by mid-May, by which time approximately 40% of total eggs were laid. A field cage experiment demonstrated that egg-laying of individual females was largely limited by resource availability even at low levels of leaf herbivory. Since movement activity of ovipositing females increased in a density-dependent manner, inter-plant movement is more likely to cause density-dependent reduction in fecundity and female loss, due to enhanced energy expenditure. The introduced population was less stable than the source population, probably because of decreased inter-plant movement of females and the unlikelihood of egg resorption, both of which contribute significantly to the temporal stability of *E. niponica* population densities.

Key words: *Epilachna niponica*, density-dependence, inter-plant movement, introduced population, oviposition limitation, population stability.

Introduction

Animal populations show a wide range of population fluctuations through time. Thus, a search for patterns and mechanisms of population stability has been a central issue in population ecology (Schoener 1985; Pimm 1991). Interspecific comparisons of population stability have attracted the attention of ecologists interested in community stability and food webs (Wolda 1978; Connell and Sousa 1983; Schoener 1985; Redfearn and Pimm 1988; Pimm 1991; Cappuccino 1992; Gaston and McArdle 1994).

An understanding of the mechanisms that stabilize populations in response to resource availability provides many insights in understanding the dynamic behavior of populations in a changing environment. If populations are regulated by resource availability, they would be ex-

pected to closely track the temporal dynamics of resources (Wiens 1984). For insect herbivores, however, previous studies have rarely monitored temporal variability of host-plants over the long-term. This is a reflection of the notion that herbivores are not resource-limited, and that herbivore populations are usually held to levels well below the carrying capacity set by host-plant abundance (Hairston et al. 1960; Lawton and Strong 1981). Thus, we know little about how insect populations manage to temporally track resource availability (Dempster and Pollard 1981).

Epilachna niponica is a univoltine herbivorous lady beetle that feeds exclusively on the leaves of thistle plants. Natural populations of the lady beetle exhibit a close synchronization between their population size and host-plant abundance, resulting in exceptionally high levels of population stability with respect to resource availability among insect herbivores (Ohgushi 1992, 1995). For example, populations A and F in Kutsuki showed 2.0 and 1.4-fold variations in egg density over a five year period (Ohgushi and Sawada 1985). Frequent inter-plant movement in

search of suitable oviposition sites early in the season, coupled with egg resorption in response to deterioration of resource availability late in the season, are behavioral and physiological mechanisms for the density-dependent reduction in reproductive rate, thereby stabilizing egg density among generations (Ohgushi and Sawada 1985).

Nakamura and Ohgushi (1979, 1981) studied a natural population of *E. niponica* in the Asiu Experimental Forest of Kyoto University, and showed that population size remained relatively constant at low population densities through time. In May 1971, 15 males and 30 females from overwintered adults collected from the Asiu population 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 range. The introduced population successfully established and, in 1974, thistle plants were observed to be heavily defoliated by the lady beetle. Investigations on the introduced population began in the spring of 1975, four years after its introduction (Sawada and Ohgushi 1994; Ohgushi and Sawada 1995, 1997).

Thus, our focus is on whether the *E. niponica* population is still stabilized by resource availability after its introduction, and if so, we ask what mechanisms are responsible for population stability.

Materials and methods

Study site

The Botanical Garden of Kyoto University is located in the northeastern part of Kyoto City, 10 km south of the southern limit of the natural distribution of *E. niponica* in Kyoto. The lady beetle has an extremely limited dispersal ability (Nakamura and Ohgushi 1983; Ohgushi and Sawada 1985), and there was no evidence of the occurrence of *E. niponica* in the Botanical Garden before the introduction in 1971. Because of a much lower elevation than in the Asiu Experimental Forest, temperatures are 3–5°C higher throughout the season in the Botanical Garden than Asiu (Sawada and Ohgushi 1994).

Lady beetle

Epilachna 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 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 had died by late June (Sawada and 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. A detailed description of the life history is given in Sawada and Ohgushi (1994).

Host plant

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

The thistle plants 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 and 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 spite of the heavy grazing, most of the damaged plants sprouted rosette leaves several weeks after defoliation.

Estimation of population size and survival rate

We conducted population censuses from 1975 to 1981. During this period, the adult population was monitored using mark-recapture techniques for individuals, to estimate the total number and survival rate of adults.

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-colored lacquer paint by dotting four points on the elytra. Capture date, place, and body size were recorded before release onto 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 overwintered (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). 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. Thus, the estimates were highly reliable.

The numbers of eggs, hatched larvae, and fourth instar larvae were recorded separately for each plant on each census date. When 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 middle of the fourth instar period was estimated using the method described by Southwood and Jepson (1962).

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 instar), and late larvae (fourth instar to adult). Daily survival rate of reproductive adults was also estimated by the Jolly-Seber stochastic model mentioned above. For new adults, survival from adult emergence 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. Since we could not discriminate between emigration and mortality, we included both terms as loss.

We also estimated movement activity of marked adults, using the mark and recapture data. Movement activity was expressed by the mean squared displacement of marked adults per 10 days (see Kareiva 1982).

A cage experiment to examine oviposition behavior

To examine how individual females respond to resource availability in terms of reproductive output, we conducted a cage experiment in 1979 and 1980. Twelve thistle plants were randomly selected, and each plant was covered by a
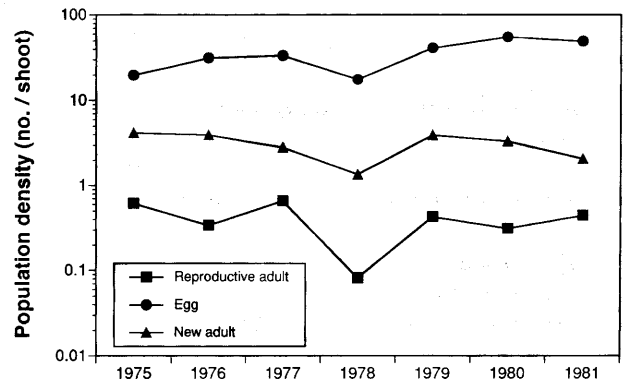

Fig. 1. Annual changes in the population densities (individuals per shoot) of reproductive adults, eggs, and newly-emerged adults for 1975–1981.

nylon organdy cage with wooden frames (1 m long, 1 m wide, and 1.5 m high). One pair of reproductive adults was introduced into each cage. Eggs laid were checked every 4–5 days throughout the experimental period (60 days). All eggs deposited were removed to prevent larval feeding on thistle leaves. Leaf areas of individual leaves were measured every 20 days for each caged plant. In addition, daily activity of each category of behavior (feeding, resting on leaves or cage surface, laying eggs, moving, and mating) was monitored for individuals on 9 and 10 May 1980.
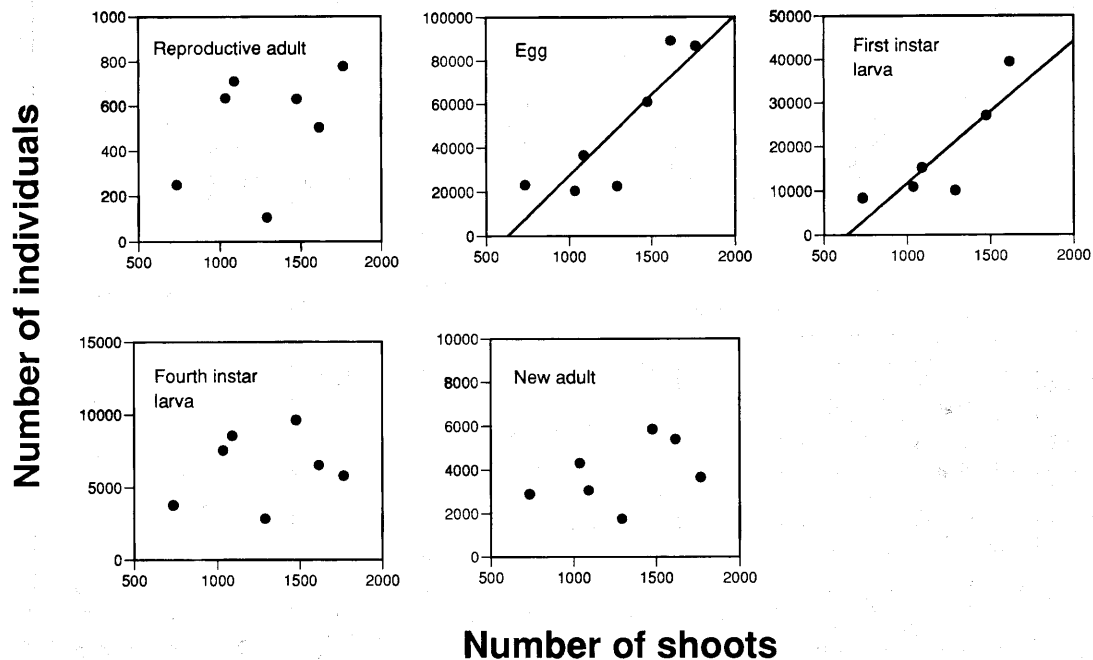

Number of shoots

Fig. 2. Relationships between the number of thistle shoots and population size at different life stages.

Results

Population stability in terms of host plant abundance

Annual changes in population densities per thistle shoot are shown for reproductive adults, eggs, and new adults (Fig. 1). When compared to other herbivorous insects that have been studied (see reviews by Hassell et al. 1976; Connell and Sousa 1983; Wolda 1978; Redfearn and Pimm 1988), the density of reproductive adults, which was the most variable among the stages of life cycle, was very stable through time (7.4-fold variation for seven years). Even more stability in population density can be seen at the egg stage, which had only a 3.2-fold variation.

Host plant abundance varied from 733 to 1765 shoots through the study period. The notable stability of population densities suggests that there is a temporal resource tracking at the population level. To examine how the population copes with changes in resource availability, the population size of each life stage was regressed on the number of thistle shoots (Fig. 2). Although there was no significant relationship between thistle number and the number of reproductive adults, the populations of eggs and newly-hatched larvae were significantly correlated with shoot number (egg: $b=73.31$, $r^2=0.765$, $n=7$, $F=16.29$, $P=0.010$; newly-hatched larva: $b=32.42$, $r^2=$
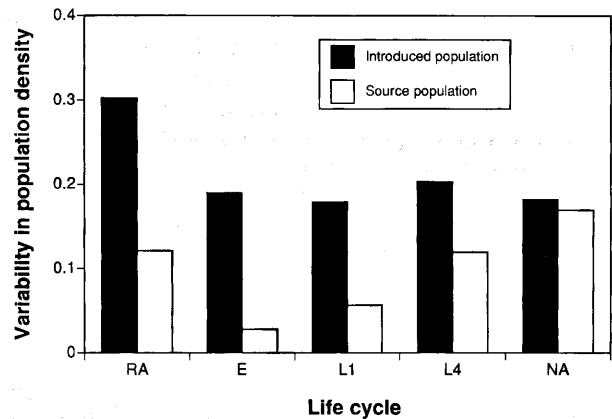

Fig. 3. Variability in population density of the introduced and source populations at different life stages. Variability was expressed as the standard deviation of the logarithms of the densities for 1975–1981 in the introduced population and for 1974–1976 in the source population (Nakamura and Ohgushi 1981). RA, reproductive adult; E, egg; L1, first instar larva; L4, fourth instar larva; NA, newly-emerged adult.

0.717, $n=6$, $F=10.15$, $P=0.033$). However, later stages no longer exhibited significant correlations between population size and resource abundance. This implies that the temporal resource tracking at the population level occurred early in the beetle's life.

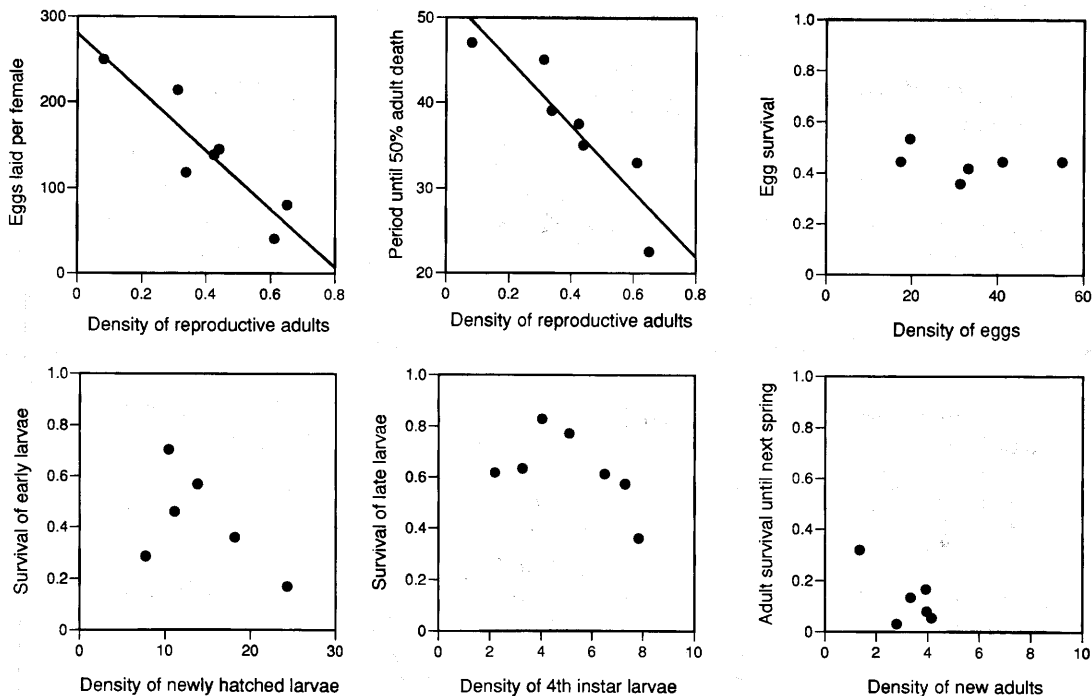This is well illustrated when variability of population

Fig. 4. Temporal density-dependence of reproductive and survival components.

density was compared among different life stages, expressed by standard deviation of the log_{10} of population density (see Gaston and McArdle 1994) (Fig. 3). Population density was stabilized at the egg stage, and no further population stabilization occurred thereafter. This is also true for the source population. Although the variability of the introduced population was low, the source population was consistently destabilized throughout the rest of the life cycle. Also, the introduced population was evidently less stable than the source population at every life stage.

Factors responsible for population stability

Let us examine the factors that contribute substantially to the temporal stability of egg density. There are two possibilities: (1) density-dependent reduction in fecundity, and (2) density-dependent increase in female loss. The number of eggs laid per female was negatively correlated with adult density ($b= -341.3$, $r^2=0.826$, $n=7$, $F=23.75$, $P=0.004$) (Fig. 4). Likewise, the period from adult emergence in spring (15 April) to the date of 50% loss of reproductive females decreased significantly in a density-dependent manner ($b= -38.5$, $r^2=0.829$, $n=7$, $F=24.16$, $P=0.004$). On the other hand, density-dependent survival rates were no longer detected at the larval and new adult stages.

How does stabilization in egg density proceed?

The next question is when the two density-dependent factors operate in the reproductive season. The response of fecundity and female survival to variation in adult density was compared in different periods of the reproductive season (Table 1). Density-dependence of the two factors changed in the different periods. Both fecundity and female survival significantly decreased with adult density until early May; but they were not a function of density thereafter.

Through these density-dependent processes operating early in the season, year-to-year variation in cumulative
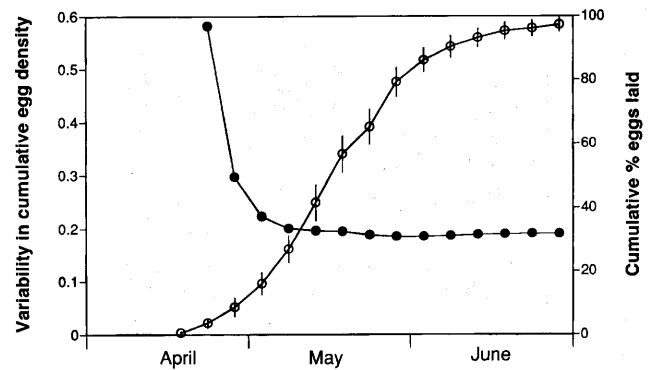

Fig. 5. Seasonal changes in variability in cumulative egg density (●) and cumulative percent of eggs laid (mean ± 1SE) (○). Variability was expressed as the standard deviation of the logarithms of the densities for 1975–1981.

egg density was sharply reduced from late April to mid-May (Fig. 5). This indicates that population stabilization was completed by mid-May, by which time approximately 40% of the total number of eggs were laid.

Oviposition limitation by resource availability

The cage experiment clearly indicates that fecundity was strongly limited by resource abundance ($b=2.34$, $r^2= 0.792$, $n=12$, $F=38.10$, $P<0.0001$) (Fig. 6). Note that leaf herbivory remained insignificant throughout the experimental period, because larval feeding was prevented by removing all eggs in each cage. This implies that density-dependent reduction in fecundity occurred even when leaf damage was maintained at a relatively low level. Also, this supports the observation that reduction in fecundity in response to increased adult density was detected early in the reproductive season (Table 1), when leaf damage was still insignificant.

Daily activity in behavior of reproductive adults is summarized in Fig. 7. They spent most of time in feeding and resting on leaves early in the morning. Thereafter,

Table 1. Regressions of eggs laid per female and female survival on density of reproductive adults at different periods of the reproductive season. Survival data were arcsin square-root transformed prior to analysis.

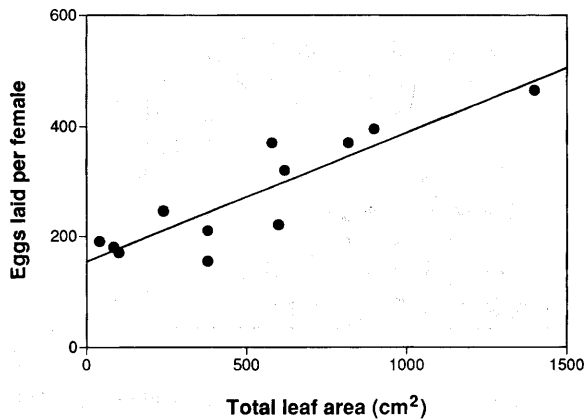| Component	Period	n	b	r^2	F	P
Eggs laid per female						
	15 April–5 May	6	−206.5	0.677	8.38	0.044
	6 May–25 May	6	−454.9	0.612	6.30	0.058
	26 May–15 June	6	−375.4	0.154	0.73	0.441
Female survival						
	15 April–5 May	7	−0.460	0.707	12.06	0.017
	6 May–25 May	7	−1.126	0.435	3.84	0.107
	26 May–15 June	7	0.376	0.039	0.20	0.673

Fig. 6. Relationship between resource availability (total leaf area of thistle plant) and number of eggs laid by individual females for 50 days in the cage experiment.

Fig. 7. Daily activities of different behavioral categories of 24 caged adults on 9 and 10 May 1980.

movement within the plant and dispersal increased. In particular, from 12 : 00 to 16 : 00, half of the caged adults showed a tendency for active movement and dispersal, with many being found on surfaces of the cage. This suggests that reproductive adults tend to move among plants in the daytime, even if there remains an ample amount of food and/or oviposition sites.

Density-dependent movement for oviposition

The cage experiment suggests that reproductive adults have a tendency for inter-plant movement. Movement activity of ovipositing females increased with adult density in April and May, but not in June (April: $b=15.33$, $r^2=0.901$, $n=6$, $F=36.25$, $P=0.0038$; May: $b=19.07$, $r^2=0.684$, $n=7$, $F=10.83$, $P=0.0217$; June: $b=9.87$, $r^2=0.126$, $n=6$, $F=0.72$, $P=0.433$) (Fig. 8). It should be
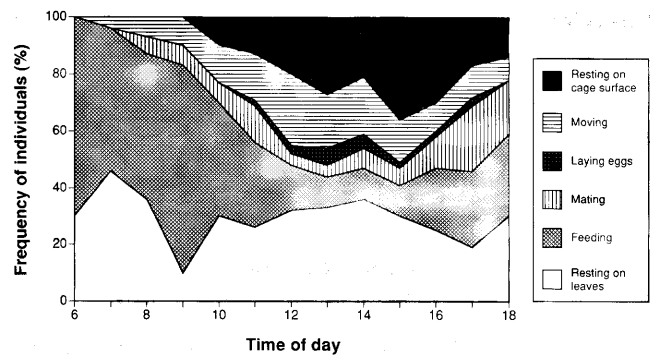
noted that the increased movement activity of females corresponded well with a period when temporal stabilization in egg density occurred (see Fig. 5).

Discussion

Population stability in relation to resource availability

This study demonstrated that the density of the introduced population of *E. niponica* was markedly stabilized during the reproductive season, resulting in only 3.2-fold variation in egg density over a seven-year study period. Also, we detected temporal resource tracking at the population level, through density-dependent reproductive processes.

Since previous studies of insect herbivore populations have rarely monitored the temporal variability of host-plant abundance, we know little about how insect populations manage to temporally track resource availability.
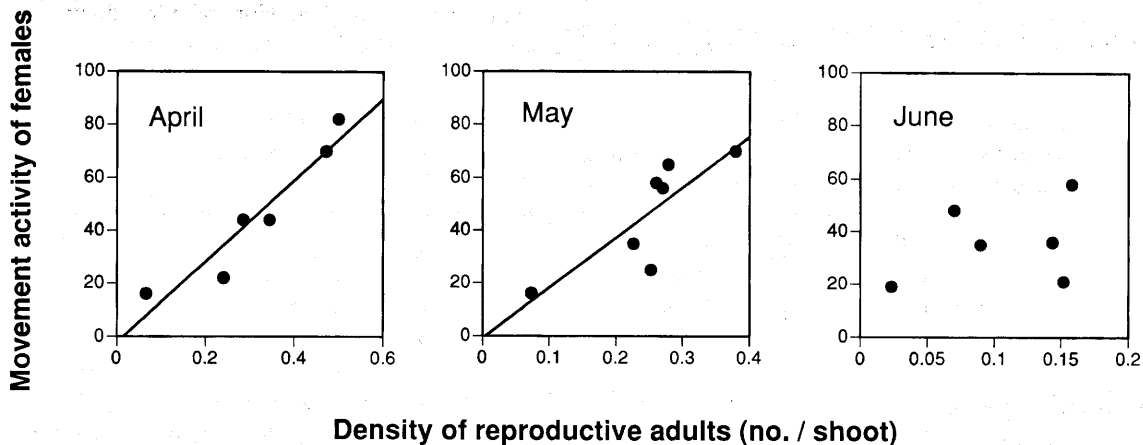

Fig. 8. Relationships between adult density and movement activity of reproductive females. Movement activity was expressed as the mean squared displacement of marked adults per 10 days (see Kareiva 1982).

However, a few studies have convincingly illustrated a close synchronization between host-plant abundances and population size. These studies include those of the red pine cone beetle *Conophthorus resinosae* (Mattson 1980), the cinnabar moth *Tyria jacobaeae* (Dempster and Pollard 1981) and the herbivorous lady beetle *E. niponica* in Kutsuki, 10 km east of Asiu (Ohgushi 1992), all of which emphasized the important role of host-plant availability as a powerful agent limiting the population size of insect herbivores.

Recently, several authors (Hunter et al. 1992; Price 1992; Ohgushi 1992; Harrison and Cappuccino 1995) have argued that bottom-up regulation by host-plant characteristics is of primary importance in controlling herbivorous insect population dynamics. This argument contrasts with traditional view that top-down regulation by natural enemies controls herbivorous insect population dynamics (Hairston et al. 1960; Lawton and Strong 1981). The view of bottom-up regulation suggests that plants may set the carrying capacity for insect herbivores that populations are kept in a stable state over generations (Price 1992).

Mechanisms for population stability

The introduced population was highly stabilized in the reproductive season; no further population stabilization occurred in immature and new adult stages, as was the case with the source population (see Fig. 3). Similarly, two local populations of the lady beetle in Kutsuki were highly stabilized in terms of resource abundance at egg stage; then, population destabilization proceeded throughout the rest of its life cycle (Ohgushi 1992, 1995). Hence, population stabilization determined by resource availability during reproductive season is a notable feature in the population dynamics of *E. niponica*.

Seasonal changes in density-dependent regulation

We detected two density-dependent processes: density-dependent reduction in fecundity and density-dependent increase in female loss. However, their responses to adult density differed at different periods of the reproductive season. For both the processes, density-dependence was found only early in the reproductive season, and did not operate during the rest of the season. The seasonal changes in the density-dependent processes resulted in population stabilization early in the reproductive season (see Fig. 5).

Oviposition limitation through inter-plant movement

The cage experiment convincingly showed that numbers of eggs laid by individual females were largely limited by resource availability even at low levels of leaf damage. This strong link between fecundity and resource availability corresponds with the observation that density-dependent reduction in fecundity was observed early in the season, when leaf damage still remained insignificant. In the context of the fecundity control, inter-plant movement of females seeking suitable oviposition sites is likely to cause density-dependent reduction in fecundity, as the cage experiment suggested (see Fig. 7). In addition, the increased inter-plant movement of reproductive females in response to population density may result in increased female loss by enhanced energy expenditure in a year of high adult densities.

Nakamura and Ohgushi (1981, 1983) suggested that density-related reduction in fecundity induced by female dispersal contributed to a high level of population stability in the source population. Ohgushi and Sawada (1985) studied details of behavioral and physiological mechanisms of population stability of *E. niponica* in Kutsuki, and showed that frequent inter-plant movement early in the season contributes greatly to population stability, through the density-dependent reduction in oviposition rate.

The above stabilizing mechanism of the lady beetle population density substantially contrasts with that of the cinnabar moth, which showed a close synchronization of variation in population size and its host plant abundance, as mentioned earlier (Dempster and Pollard 1981). The temporal resource tracking of the cinnabar moth population was brought about by frequent host-plant depletion, resulting in larval starvation and reduced female size with low fecundity (Dempster 1971, 1982). In other words, severe intraspecific competition resulting from resource depletion is a necessary condition for stability of the moth population. In contrast, for the lady beetle, density-dependent reduction in fecundity and female survival responsible for population stabilization occurred early in the reproductive season, when host-plants are rarely depleted.

Traditional population studies of insect herbivores have focused mainly on mortality factors during immature stages as key agents responsible for population dynamics (see reviews by Varley et al. 1973; Dempster 1975; Podoler and Rogers 1975). However, Dempster (1983) and Stiling (1988) reviewed the use of key factors and density-dependent factors in population dynamics studies. They concluded that more emphasis was needed on the study of density-dependent reduction in fecundity and dispersal of adult insects which can have large impacts on herbivorous insect populations. This implies that behavioral and physiological traits of adult insects may play an important role in governing insect population dynamics. For example, Romstöck-Völkl (1990) demonstrated that density-dependent adult dispersal and oviposition behavior were
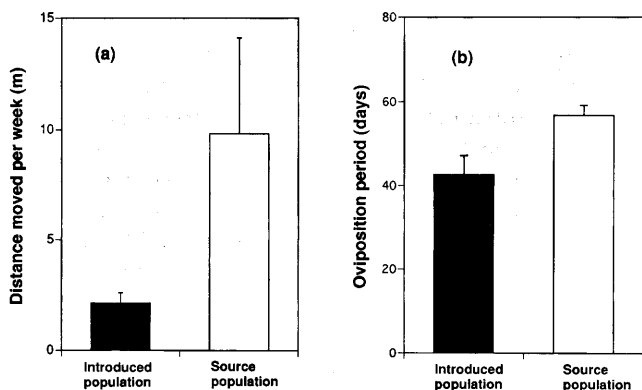
Fig. 9. A comparison of (a) distance moved in a week by reproductive females and (b) reproductive lifespan of females between the introduced population and the source population. Reproductive lifespan was measured in females that were reared in a controlled-environmental chamber at 20°C under a 16L : 8D photoperiod.

implicated in the regulation of *Tephritis conurs*. Also, Preszler and Price (1988) found that oviposition responses of adult females to host-plant quality were the critical factors regulating the densities of a shoot-galling sawfly, *Euura lasiolepis*.

Changes in oviposition behavior decreased population stability

Although the introduced population was very stable through time compared to other insect herbivores (Hassell et al. 1976; Wolda 1978; Connell and Sousa 1983; Redfearn and Pimm 1988), it was the least stable among seven lady beetle populations that our research group has studied (Nakamura and Ohgushi 1981; Ohgushi and Sawada 1981, 1985; Ohgushi unpublished data). In the much more stable Kutsuki populations, frequent inter-plant movement of females seeking suitable oviposition sites early in the season, coupled with egg resorption in response to deteriorating resource availability late in the season, caused density-dependent stabilization in egg densities throughout the reproductive season (Ohgushi 1992, 1995). Since mechanisms of the population stability in *E. niponica* involve the above oviposition tactics, we can expect that an alternation of the oviposition tactics may substantially change population stability.

The oviposition tactics relevant to population stabilization may have been altered after introduction. In the field, movement activity of reproductive females was significantly lower in the introduced than in the source population (Mann-Whitney U-test: $U=19.5$, $P=0.039$) (Fig. 9). Note that even decreased inter-plant movement could still operate as an effective regulatory agent in the introduced population (see Fig. 6). Although we did not

examine whether reproductive females resorbed eggs in the introduced population, it is unlikely that ovipositing females frequently resorbed eggs. First, since females resorb eggs in ovaries in response to increased leaf herbivory (Ohgushi and Sawada 1985), we should expect that the cessation of oviposition by egg resorption and thus reduced fecundity in response to density would occur late in the season with heavy leaf damage. However, density-dependent reduction in fecundity was found early in the season, but not late in the season (Table 1). In addition, the cage experiment showed that egg-laying was greatly reduced even when leaf damage was kept at low levels (see Fig. 6). Second, the introduced population has moved toward earlier reproduction and reduced longevity (Ohgushi and Sawada 1997). When compared under the same rearing conditions in the laboratory 10 years after introduction, the introduced population had a significantly shorter reproductive lifespan than the source population (Mann-Whitney U-test: $U=18.5$, $P=0.0124$) (Fig. 9). This implies that egg resorption is a disadvantageous tactic in the introduced population, because a short-lived female that resorbs eggs has little chance of future oviposition (Ohgushi 1996). Thus, the decreased inter-plant movement and unlikelihood of egg resorption could result in a less stable state in the introduced population, compared to the source population. In conclusion, this introduction experiment has provided many insights into how the alternation of behavior influences population stability in herbivorous insects.

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