

# Insect Populations In theory and in practice.

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# Bottom-up population regulation of a herbivorous lady beetle: an evolutionary perspective

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## 16.1 INTRODUCTION

Population regulation is fundamental to most phenomena in ecology (Murdoch, 1994). Since the well-known debate on density-dependent population regulation in the late 1950s (Andrewartha and Birch, 1954; Nicholson, 1954; see Sinclair, 1989 for a historical review), a number of long-term studies on natural insect populations have been carried out to search for the factors that determine population persistence and fluctuations (e.g. Klomp, 1966; Baltensweiler *et al.*, 1977; Dempster, 1982; Southwood *et al.*, 1989). These studies have attempted to quantify the relative importance of density-dependent and density-independent processes. In particular, intensive studies on natural populations of insect herbivores have made a major contribution to our understanding of the causes of fluctuation and regulation of populations, population outbreaks, and host-parasitoid interactions (see papers in Southwood, 1968; Den Boer and Gradwell, 1971; Barbosa and Schultz, 1987; Cappuccino and Price, 1995). While stimulating conclusions and insights have been gained, the underlying mechanisms of insect herbivore population regulation are still poorly understood.

This chapter addresses bottom-up population regulation through resource availability for a lady beetle, *Epilachna niponica*, which is a specialist herbivore of thistle plants. I have chosen this topic because insect population ecologists have paid little attention to variability of host-plant

characteristics as factors that govern the population dynamics of herbivorous insects. In particular, I will illustrate how changes in the behaviour and physiology of adult females in response to host-plant conditions are important in generating population regulation through resource availability. In addition, I will discuss the importance of incorporating evolutionary perspectives into the understanding of the population regulation of herbivorous insects.

## 16.2 MECHANISTIC APPROACH TO POPULATION REGULATION

Empirical studies often consider population regulation to be indicated by a temporal constancy of population size (Connell and Sousa, 1983; Hanski, 1990). Regulation implies that a negative feedback mechanism acts upon a population as a result of density-dependent mortality, reproduction or dispersal. In this context, many insect ecologists have long searched for density-dependent processes as evidence for population regulation. However, the existence of density-dependent processes does not, in itself, ensure the existence of regulatory mechanisms. Demonstrating population regulation requires more than simply providing evidence that a population remains relatively constant through time, and that temporal or spatial density-dependent processes exist. As population regulation is defined as the tendency for the population to return towards an equilibrium density following perturbation, perturbation experiments provide the most crucial test for population regulation (Murdoch, 1970; Harrison and Cappuccino, 1995).

Although perturbation experiments may demonstrate population regulation, population manipulation will not necessarily reveal the underlying factors generating it. Thus, it is essential to continue to search for causal mechanisms of population regulation (Gaston and Lawton, 1987; Murdoch and Walde, 1989; Ohgushi, 1992). The traditional approach to this has been key-factor analysis (Varley and Gradwell, 1960), which rests largely on seeking correlations between population densities and factors that affect survival and reproduction. Correlation studies, however, have a weakness in that they do not prove causal mechanisms generating the observed population fluctuations (Royama 1977; Ohgushi, 1992). A more mechanistic approach to understanding population regulation requires greater attention to differences between individuals within the population, because important causes of population regulation may be overlooked when using mean numbers per generation (Hassell, 1986a). To incorporate differences between individuals into population ecology, we should recognize how individual attributes of behaviour and physiology affect demographic parameters through survivorship and reproduction (Hassell and May, 1985; Lomnicki, 1988; Sutherland, 1996). Having advocated such a mechanistic approach, Schoener (1986) argued that each

demographic parameter at the population level must be translated into behavioural and physiological parameters at the individual level.

### 16.3 BOTTOM-UP POPULATION REGULATION OF HERBIVOROUS INSECTS

Recent studies of insect populations have emphasized that a more exact understanding of the population dynamics of insect herbivores requires a thorough understanding of the dynamics of their food plants, i.e. bottom-up influences between the two trophic levels (Hawkins, 1992; Hunter *et al.*, 1992; Ohgushi, 1995; Harrison and Cappuccino, 1995). It is increasingly evident that a wide variety of plant characteristics greatly affect survivorship and reproduction of insect herbivores (Ohgushi, 1992). These characteristics are related to plant quality in terms of nitrogen, water and defensive chemicals (Scriber and Slansky, 1981; Haukioja and Neuvonen, 1987; Mattson and Scriber, 1987). In addition, large impacts of their host plants on the survivorship of herbivorous insects are caused by variations in spatial dispersion of their food plants (Root, 1973) and their phenology (Feeny, 1970; Connor *et al.*, 1994). Furthermore, recent discussions of multitrophic interactions have suggested that host-plant quality is of great importance to insect herbivores through both direct and indirect interactions (Price *et al.*, 1980; Faeth, 1987; Ohgushi, 1997).

Population ecologists have paid less attention to the possible effects of plant resources on the dynamics of insect herbivore populations than to the role of natural enemies as the principal agents for population regulation (Hairston *et al.*, 1960; Lawton and Strong, 1981; Hassell, 1985). However, Harrison and Cappuccino (1995) found that evidence for bottom-up regulation by resources appears to be much more common than evidence for top-down regulation by natural enemies. Evaluation of published life-table data on herbivorous insects has shown that host-plant characteristics are often important density-dependent agents for population regulation of insect herbivores, through intraspecific competition, reduced fecundity, and adult dispersal (Dempster, 1983; Stiling, 1988). Several authors have illustrated temporal and/or spatial resource tracking at the population level, thereby highlighting the importance of bottom-up influences of host plants on herbivore population dynamics (Mattson, 1980; Dempster and Pollard, 1981; Ohgushi and Sawada, 1985a, 1997a). Thus it is necessary to recognize the relative contributions of both top-down effects caused by natural enemies and bottom-up effects caused by host-plant dynamics on their survival and reproduction, to understand the population dynamics of herbivorous insects.

Insect tactics in resource use, in response to spatial and temporal variation of plants or plant parts, can play a significant role in determining survival and/or reproductive processes, so we need detailed knowledge

of how variability and heterogeneity of resources affect the survivorship and reproduction of individuals (Wiens, 1984). For example, the availability and quality of host plants greatly affects the fecundity of adult herbivorous insects by affecting larval nutrition and also by acting on the physiology and behaviour of the reproductive female (Leather, 1994). Since a wide variety of life-history tactics in resource use have evolved in insect-plant interactions, an individual-based mechanistic approach should provide a better insight into evolutionary perspectives of the population dynamics of herbivorous insects (Price, 1994).

#### 16.4 RESOURCE VARIABILITY AND LIFE-HISTORY TRAITS

Because of variations in the quality and quantity of plant food, insect life-history traits in resource use can play a dominant role in determining survivorship and/or reproduction of herbivorous insects (Hassell and May, 1985; Smith and Sibly, 1985; Leather, 1994). There is growing evidence that resource-use tactics of adult insects are critical in determining the population dynamics of many herbivorous insects (Price *et al.*, 1990; Ohgushi, 1995, see also Dempster, Chapter 4 in this volume). For example, a number of studies testing Root's (1973) 'resource concentration hypothesis' have suggested that the searching behaviour of adult insects for favourable resources is an important determinant of subsequent population densities in different vegetation structures (Kareiva, 1983; Stanton, 1983). In particular, oviposition behaviour has recently been hypothesized to generate the fundamental patterns of population dynamics in insect herbivores, by affecting offspring performance in terms of survivorship and reproduction (Preszler and Price, 1988; Craig *et al.*, 1989; Price *et al.*, 1990; Ohgushi, 1995).

For many herbivorous insects, the searching abilities of larvae are poor compared with those of adults. Adult oviposition behaviour is therefore of paramount importance in selecting suitable host plants or plant parts for their offspring (Renwick and Chew, 1994). Female herbivores whose offspring develop at the oviposition site are strongly favoured by natural selection to optimize their choice of oviposition site. Thus, the relationship between oviposition preference and growth, survival, and reproduction of offspring has been the crux of the evolution of insect-plant associations (Thompson, 1988). The preference-performance linkage has been recently explored in terms of the host-plant selection or site selection on a plant, revealing a positive correlation between oviposition preference and offspring performance (Rausher, 1980; Whitham, 1980; Craig *et al.*, 1989; Roininen and Tahvanainen, 1989). For example, ovipositing females of a willow-galling sawfly *Euura lasiolepis* have a strong oviposition preference for long shoots of young and vigorous willows, associated with a high larval survival (Craig *et al.*, 1989; see also Price *et al.*, Chapter 14 in this volume). Similarly, the aphid *Pemphigus betae* shows a

strong oviposition preference for young leaves of *Populus angustifolia* that will grow to be large, and more progeny of larger size are produced on these larger leaves (Whitham, 1980).

However, in some herbivorous insects there is a lack of correlation between preference and offspring performance, with females laying their eggs rapidly, irrespective of quality of oviposition site for their offspring. A poor preference–performance correlation may be brought about by oviposition onto introduced host plants, or by a relative shortage of suitable plants or plant parts (Thompson, 1988). There also may be ecological constraints, such as impacts of natural enemies which are independent of plant quality (Denno *et al.*, 1990), or life-history constraints such as a short time available for oviposition and a poor capacity for directed flight (Larsson and Ekbom, 1995), that may result in a weak preference–performance relationship. A weak correlation may also result from specific oviposition behaviours, so that a female lays her eggs away from the larval feeding site, and frequently long before foliage is available for larval feeding (Price, 1994). Oviposition behaviours of these kinds of insects therefore show poor correlation with larval survival (Karban and Courtney, 1987; Auerbach and Simberloff, 1989; Valladares and Lawton, 1991). It should be noted that evaluation of the relationship between oviposition preference and offspring performance is still useful in understanding the population dynamics in those species without apparent adult preference. If we can remove oviposition preference from our analyses, we can concentrate on resource-use tactics of the immature stage (Schultz, 1983), or on the effects of natural enemies and host-plant characteristics on the survival of immature insects (Auerbach and Simberloff, 1989; Denno *et al.*, 1990).

The traditional life-table approach has long ignored the important consequences of oviposition site selection by adult females on insect population dynamics (Price *et al.*, 1990). To understand the behavioural and physiological mechanisms that determine the selection of host plants or host-plant parts requires an evolutionary approach. Behavioural ecology investigates the evolutionary relationships between fitness and behaviour, and other variables including population density (Krebs and Davies, 1997). Therefore, the study of the behavioural ecology of herbivorous insects should reveal the underlying evolutionary mechanisms that potentially determine their population dynamics (Smith and Sibly, 1985; Ohgushi, 1992; Sutherland, 1996). This approach, which focuses on how life-history tactics and resource availability can result in population regulation, bridges the two disciplines of behavioural ecology and population ecology.

#### 16.5 POPULATION REGULATION OF A HERBIVOROUS LADY BEETLE

*Epilachna niponica* is a univoltine species and a specialist herbivore of this-  
tle plants. Over a period of 10 years, this species has been censused in

several areas in central Japan (Nakamura and Ohgushi, 1981; Ohgushi and Sawada, 1981, 1995; Ohgushi, 1992, 1995). Here I will discuss the behavioural and physiological mechanisms of bottom-up population regulation in *E. niponica*, and its evolutionary implications. The results are from two populations (A and F) in Kutsuki, in the northern part of Shiga prefecture, central Japan, together with those from a population in the Botanical Garden introduced from Asiu (Fig. 16.1). 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*.

The study sites A and F are located in different valleys along the River Ado. Site A (60×30 m) is situated at 220 m elevation on an accumulation of sandy deposits resulting from a dam construction in 1968. The surface of the rather flat and open area consists mainly of unhardened, sandy deposits. Floods caused by heavy rainfall often submerge and wash away the ground flora along the watercourse, and most of the surviving vegetation is composed of annual and perennial herbs. Site F (90×15 m) is situated at 350 m elevation, about 10 km upstream from site A. The more hardened soil deposits at this site mean that most grasses and shrubs successfully escape serious flood damage, except during large-scale floods. Vegetation in and around the site includes various deciduous trees such as *Quercus mongolica* and *Quercus salicina*.

In the study area, the lady beetle feeds exclusively on leaves of its host plant, *Cirsium kagamontanum*, which is a perennial herb, patchily distributed along the riverside. It grows rapidly from sprouting in late April to late June, becoming full-sized at 1.5–1.8 m in height by late August, and then flowers over 2 months from mid-August. Old leaves begin to wither after summer. Although the number of thistle leaves gradually increases until late August, leaf quality (in terms of amino acid and water content) consistently declines during the growing season (Ohgushi, 1986).

Over-wintering adult females emerge from hibernacula in the soil in early May and begin to lay eggs in clusters on the under surfaces of thistle leaves. Larvae pass through four instars. New adults emerge from early July to early September, feeding on thistle leaves through the autumn. They enter hibernation in the soil by early November. Seasonal changes in numbers of adults and immature stages are given by Ohgushi and Sawada (1981).

Each population was censused from early May to early November in each year between 1976 and 1980. All thistle plants growing in the study sites were carefully examined; the numbers of eggs, fourth-instar larvae, pupae, pupal exuviae and adult beetles were recorded separately for each plant. Each adult beetle was individually marked with four small dots of lacquer paint on its elytra. Newly marked adults were released immediately on the thistle plant where they had been captured. Sex, body size and subsequent capture history (date and place) were recorded for individual

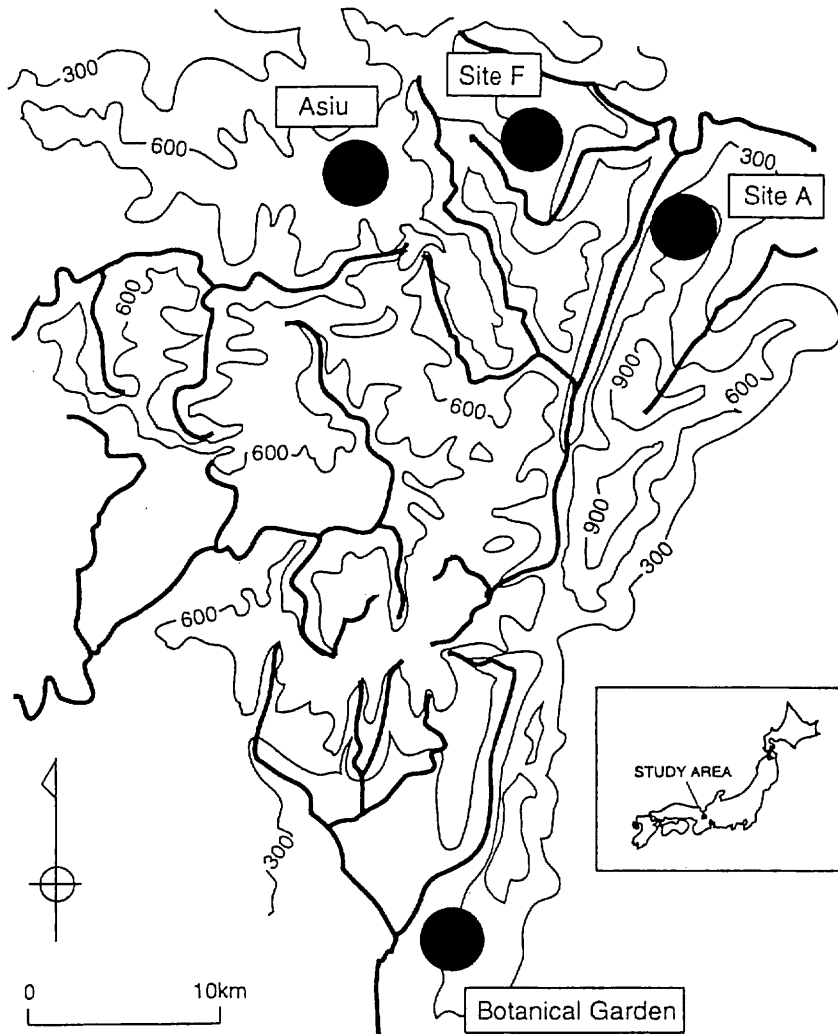


Fig. 16.1 Location of study sites A and F in Kutsuki, and an introduced population in the Botanical Garden, which came from Asiu in 1971. Thin lines show altitude in metres above sea level; thick lines show rivers.

beetles. The survival rate and numbers of adult beetles were estimated by the Jolly-Seber stochastic model based on the mark and recapture data (Jolly, 1965; Seber, 1973). In each spring, >98% of over-wintered adults that emerged from hibernation were marked 1 week after the census commenced. Also, >92% of newly emerged adults were successfully marked. Recapture rate on each census date (the number of marked adults that



were recaptured divided by the estimated number of adults) was >85% throughout the census period. Because of the exceptionally high marking and recapture ratios, the estimated survival rates were highly reliable. The same capture–recapture experiments were carried out on the Asiu population between 1974 and 1976 and the Botanical Garden population between 1975 and 1981. Based on these data, detailed life tables were then constructed for every census year (Nakamura and Ohgushi, 1981; Ohgushi, 1986; T. Ohgushi and H. Sawada, unpublished data).

### 16.5.1 Demonstration of population regulation

#### (a) High level of stability in population density

Egg density of the two populations at sites A and F remained remarkably stable over a 5-year study period (Fig. 16.2). To examine their stability, the standard deviation of log-transformed egg densities during the study period, which is an appropriate index for temporal variability of a population (Gaston and McArdle, 1994), was calculated. The variability indices of sites A and F respectively, were 0.135 and 0.051, indicating the highest level of population stability that has been reported for an insect species (Hanski, 1990). The other five populations studied, including Asiu and the Botanical Garden populations, also showed exceptionally high stability, ranging from 0.0002–0.190.

Note that the average egg density per thistle shoot at site A ( $29.8 \pm 3.34$  [mean  $\pm$  s.e.]) was almost identical to that at site F ( $29.4 \pm 1.49$ ) over the 5-

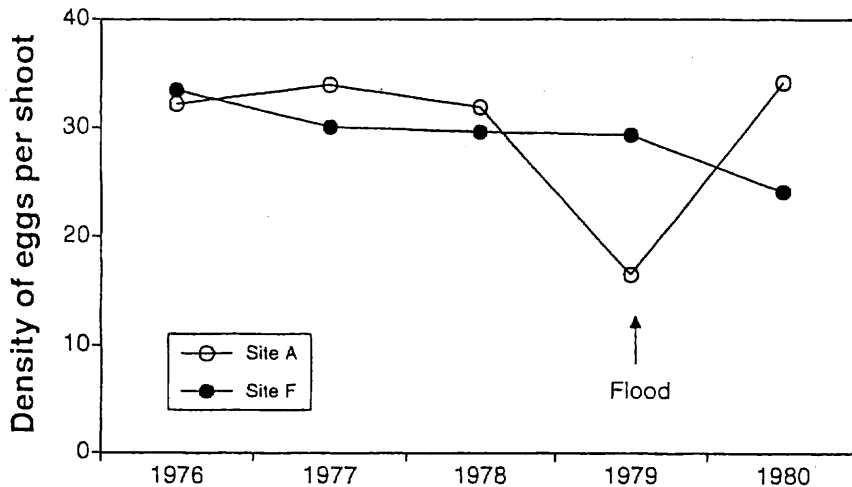


Fig. 16.2 Temporal changes in egg density per shoot at sites A and F. A large flood in late June 1979 considerably reduced reproductive adults at site A. Modified from Ohgushi (1995).

year study period, suggesting that the two different populations are maintained at a certain level in relation to resource availability. This 'equilibrium' density was, however, far below the level where defoliation of host plants occurs. Low leaf herbivory continued through late June when old larvae reached a peak density, averaging 30% of the total leaf area at site A and less than 20% at site F.

*(b) Population regulation in relation to resource availability*

Population regulation is defined as the return of a population to an equilibrium density, following departure from the density, as a result of density-dependent processes. To determine whether a population is regulated, we need to look at two points: (i) the tendency of the population to return towards the equilibrium density when disturbed from it, and (ii) the existence of a density-dependent process or processes that cause the population to return to equilibrium.

(i) A return toward an equilibrium density: a large-scale flood in June 1979 washed away all of the reproductive females at site A, and considerably reduced egg density. Despite this large population reduction, the egg population quickly returned to the previous density in the next year (Fig. 16.2). This implies that the beetle population has an effective regulatory mechanism to return it to the previous level of density following disturbance.

(ii) Density-dependent reproductive processes: to determine the life stage at which a population is stabilized, the year-to-year variability of densities was compared among different life stages over a 5-year study period. The variability index declined sharply from reproductive adult to egg stage at both sites. This indicates that the populations were highly stabilized during the reproductive process. In contrast, a destabilization of density occurred during the survival process from egg to adult stage. In other words, population stabilization was completed in the reproductive process, and no other regulatory agents operated in the survival from egg to reproductive age in the following spring.

The reproductive process involved two density-dependent relationships. Firstly, lifetime fecundity was negatively correlated with adult density (Fig. 16.3a). Secondly, female survival sharply decreased with adult density (Fig. 16.3b). On the other hand, there were no density-dependent survival processes during the period from egg to over-wintered adult in the following year.

The population meets the definition of a regulated population because it shows density-dependent processes during the reproductive season and because it returns to its previous density following perturbation. Density-dependent population regulation in the reproduction of *E. niponica* has been demonstrated in seven independent populations: the

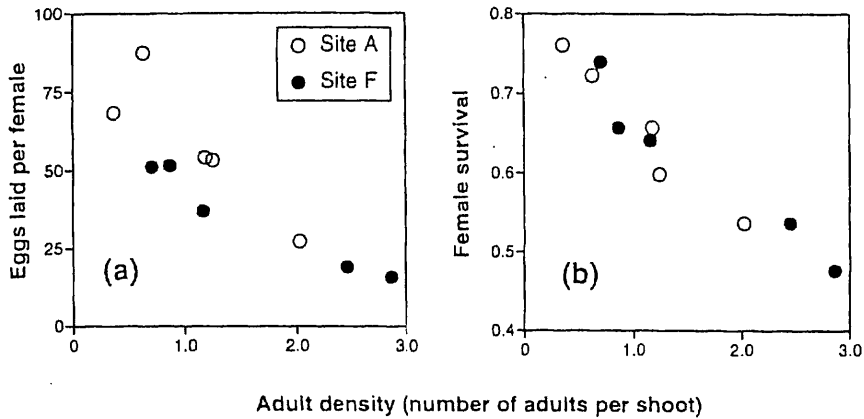


Fig. 16.3 Density dependence in reproductive processes. (a) Relationship between lifetime fecundity and adult density (site A:  $r=-0.90$ ,  $F=12.49$ ,  $P=0.038$ ; site F:  $r=-0.98$ ,  $F=61.00$ ,  $P=0.004$ ). (b) Relationship between female survival per 10 days and adult density (site A:  $r=-0.98$ ,  $F=59.27$ ,  $P=0.005$ ; site F:  $r=-0.97$ ,  $F=46.65$ ,  $P=0.006$ ).

two populations described here, and five other populations (Nakamura and Ohgushi, 1981; Ohgushi and Sawada, 1997a, 1998; T. Ohgushi, unpublished data).

### 16.5.2 Bottom-up population regulation

#### (a) The influence of resource limitation on population size

Next, let us consider how resource availability affects the lady beetle's population size (Fig. 16.4). Resource abundance changed independently at the nearby sites, which were separated by 10 km. Shoot numbers of thistles at site A consistently increased over the study period; while at site F they remained fairly constant from 1976–79, and then dropped in 1980 as a result of two large floods in the previous autumn. Shoot numbers showed 3.6- and 2.3-fold variations throughout the study period at sites A and F, respectively. Despite these two very different patterns of change in host abundance, the egg populations closely tracked the variation in resource availability through time. Indeed, the annual variation in egg population was mostly determined by the variation in resource abundance. Host abundance explains 66 and 98% of variation in population size at sites A and F, respectively. Population regulation was completed during the oviposition process when resource limitation determined egg density. This conclusively demonstrates bottom-up regulation of the lady beetle population.

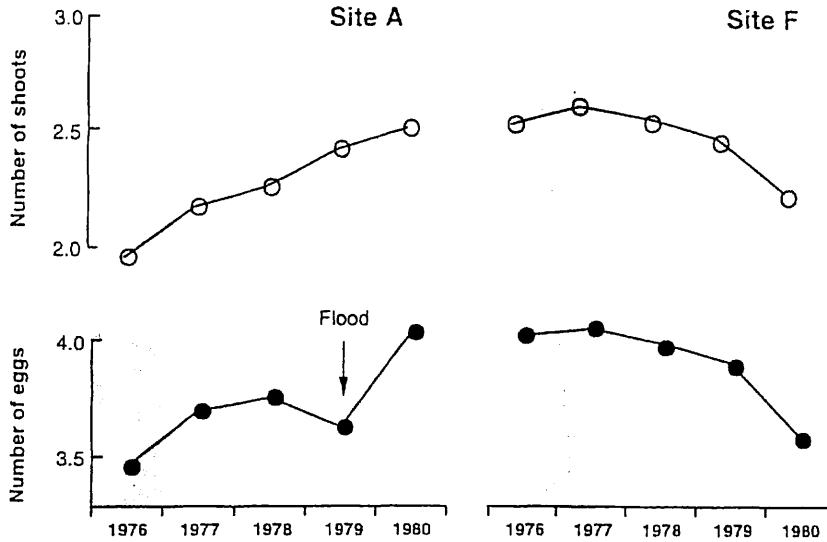


Fig. 16.4 Temporal changes in host-plant abundance (number of shoots) and egg population at sites A and F. Data were log transformed. Note that a large flood in 1979 considerably reduced the egg population at site A. From Ohgushi (1992) by courtesy of Academic Press.

(b) Top-down influences of natural enemies on population regulation

Since the role of natural enemies as regulatory agents of herbivorous insect populations has long been emphasized, I will summarize how top-down influences contribute to regulation of the lady beetle populations. Eggs and larvae were frequently subjected to heavy arthropod predation, mainly by nymphs of an earwig, *Anechura harmandi*. A cage experiment illustrated that arthropod predation was a main cause of mortality during the larval period (Ohgushi and Sawada, 1985b). The higher predation on immature stages at site F resulted in a significantly lower density of new adults, compared with that at site A where there was less predation (Fig. 16.5).

In contrast to their importance in determining new adult density, natural enemies are unlikely to function as a regulatory agent for three reasons. Firstly, arthropod predation operates in neither a spatially nor a temporally density-dependent manner (Ohgushi, 1988). Secondly, despite the significant difference in adult densities at emergence due to differential predation, egg densities in the next generation of the two populations were almost identical (Fig. 16.2). In other words, the large difference in adult density between the two populations caused by natural enemies was mostly compensated for by the regulatory process in the reproductive season. Thirdly, in contrast to egg and larval stages, natural

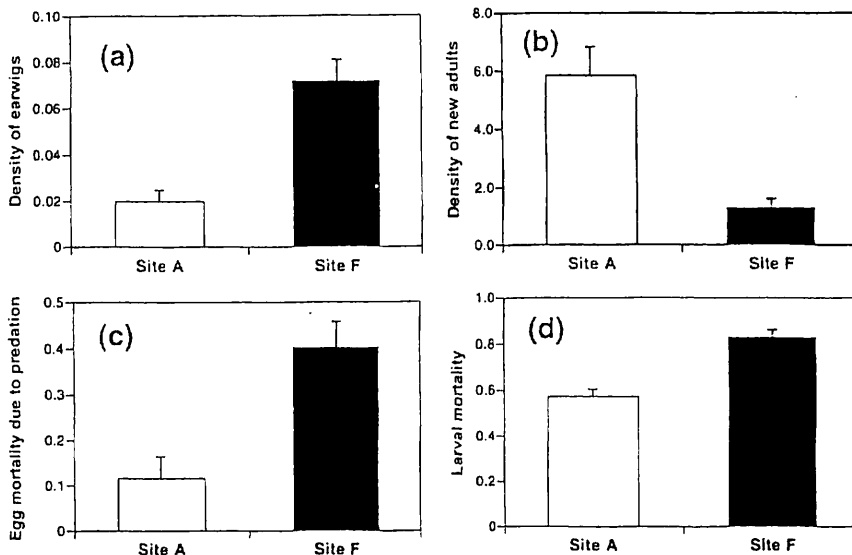


Fig. 16.5 Top-down effects of natural enemies. (a) Density of earwigs (number of earwigs per shoot). (b) Density of new adults of the lady beetle (number of newly emerged adults per shoot). (c) Egg mortality due to arthropod predation. (d) Larval mortality. Each column represents mean and s.e. in 1976–80. There are significant differences in density or mortality between the two sites (Mann–Whitney  $U$  test:  $U=25$ ,  $P<0.01$  for each case).

enemies had little effect on adult survival during the reproductive period, when population regulation occurred.

### 16.5.3 Mechanisms of population regulation

Next, let us search for the underlying mechanisms of population regulation. Density-dependent reduction in fecundity and female survival suggest that oviposition tactics play an important role. The density and spatial distribution of eggs among plants by herbivorous insects is determined by the strategy employed by females in searching for and choosing oviposition sites. The evolution of this oviposition strategy is determined by the life-history constraints of the herbivore. In *E. niponica* the trade-off between energy allocation to movement and reproduction, combined with an avoidance of high densities of conspecific eggs, regulates population density and spatial distribution.

#### (a) Behavioural mechanism: female movement for oviposition

The strategy used by a female in searching for an oviposition site determines the spatial distribution of eggs. Females avoid ovipositing on

plants with high egg densities. Therefore as egg densities increase, female movement increases and egg distribution becomes more uniform. Several pieces of evidence support this hypothesis. Firstly, female mobility, expressed as the variance of distances travelled per day, increased with adult density (site A:  $r=0.80$ ,  $F=5.38$ ,  $P=0.103$ ; site F:  $r=0.96$ ,  $F=34.98$ ,  $P=0.01$ ). Secondly, the seasonal change in the movement pattern of ovipositing females was correlated with changing egg density. Female movement increased from early May to mid-June as egg densities increased, but thereafter it consistently decreased (Fig. 16.6a). In early June, female movement was positively correlated with cumulative egg density (site A:  $r=0.90$ ,  $F=13.26$ ,  $P=0.036$ ; site F:  $r=0.98$ ,  $F=65.16$ ,  $P=0.004$ ). This enhanced movement was synchronized with an increasingly uniform distribution of eggs among plants (Fig. 16.6b).

As energy allocation is shifted from reproduction to movement, with increasing egg density, female survival and/or fecundity decreases in a

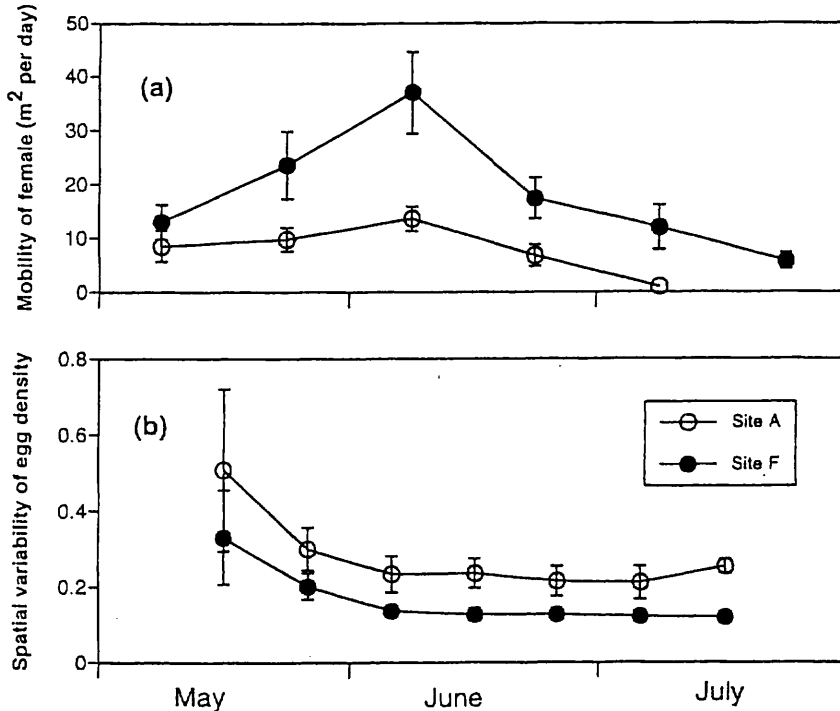


Fig. 16.6 Female mobility and spatial stabilization of egg density. (a) Seasonal changes in mobility of ovipositing females. Each point represents mean and s.e. in 1976–80. Mobility is expressed by the variance of distances travelled per day. From Ohgushi (1992). (b) Seasonal changes in spatial variability of cumulative egg density in terms of individual plants. Each point represents mean and s.e. in 1976–80. Spatial variability is expressed by the standard deviation of the log-transformed egg densities of individual plants. Modified from Ohgushi (1995).

density-dependent manner. Ohgushi and Sawada (1985a) demonstrated that increased female movement results in a reduction in oviposition rate through decreased fecundity and/or increased female loss. This is the result of the trade-off between egg production and female survival (Ohgushi, 1996a).

*(b) Physiological mechanism: egg resorption*

Egg resorption by females is a physiological mechanism that contributes to the density-dependent reduction in oviposition rate. Field-cage experiments showed that as host plants deteriorate in quality, females resorb eggs in the ovaries (Ohgushi and Sawada, 1985a), and this finding was confirmed by sampling females in the field. This process is reversible, so that when host plant quality improves the ovaries again become productive. Ohgushi and Sawada (1985a) found that egg resorption increased after mid-June as leaf damage increased, and the proportion of females that resorb eggs increases in years with high egg densities because of the high levels of early-season leaf damage in those years. Thus egg resorption directly contributes to the density-dependent changes in oviposition rate.

#### 16.5.4 Evolutionary background of population regulation

We would expect that natural selection would have produced an oviposition strategy that would maximize lifetime fitness. To test this hypothesis, offspring lifetime fitness was calculated to evaluate the contribution of oviposition traits to the lifetime reproductive success of a female. Lifetime fitness of offspring is expressed as the total number of eggs produced in the following generation due to the expected reproductive contribution of one egg at the moment of birth.

*(a) Oviposition site selection*

In the previous section, I established that female avoidance of plants with high egg densities substantially influences egg distribution. The adaptive nature of this behaviour is demonstrated by the decline of lifetime fitness of offspring as egg density on a plant increases (Fig. 16.7). Fitness decreased sharply when egg density rose beyond the lowest levels. The egg density where fitness declined sharply corresponds well with the equilibrium densities of the two populations.

The decrease in fitness with increasing egg density is caused by both larval and adult mortality up to reproductive age. It is likely that the decrease in fitness is determined by changes in the plant caused by increasing lady beetle densities, as leaf damage results in decreased leaf quality in terms of amino-acid concentration and water content

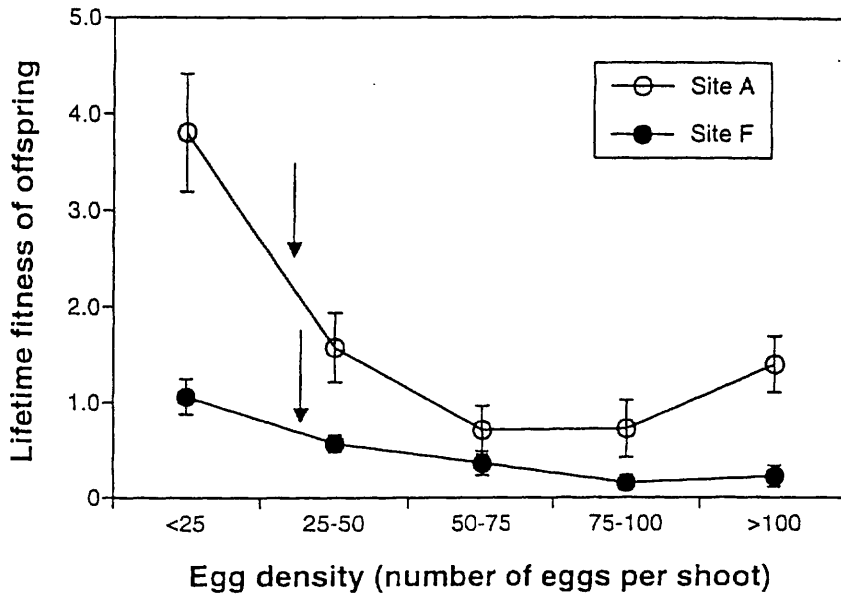


Fig. 16.7 Lifetime fitness of offspring which were born on plants with different egg densities. Each point represents mean and s.e. in 1976–80. Vertical arrows show the average egg densities at sites A and F. The lifetime fitness of offspring grown on the  $i$ th plant ( $F_i$ ) is defined as follows:  $F_i = E_i \times L_i \times A_i \times R_i$ , where  $E_i$  = egg survival to hatching,  $L_i$  = larval survival from egg hatching to adult emergence,  $A_i$  = survival of adult females from emergence to the reproductive season in the following year, and  $R_i$  = lifetime fecundity of females estimated by reproductive lifespan. From Ohgushi (1995) by courtesy of Academic Press.

(Ohgushi, 1986). As a consequence, as leaf damage increases with increasing larval density, we see density-dependent mortality on a spatial scale. Also, thistles with high egg densities produced small-sized adults, which suffered higher mortality before reproductive age (Ohgushi, 1987, 1996b). In contrast, arthropod predation does not operate in a density-dependent manner (Ohgushi, 1988), and thus cannot be responsible for the observed spatially related patterns of mortality.

#### (b) Oviposition time selection

Egg resorption causes females to stop laying eggs and so it will not lead to increased lifetime fitness unless they are able to resume ovipositing later. Future oviposition may be classified into two categories. The first category is within-season oviposition, which is the resumption of oviposition in the same season; the second is inter-season oviposition, which is



oviposition by a female that survives long enough to oviposit in the next reproductive season.

Females resorb eggs when host plants are highly exploited, or when the plants are destroyed or damaged by other forces. A large flood at site F in June 1979 washed away some thistle plants and buried others with soil. Following this disturbance females resorbed eggs and ceased oviposition for a 2-week period (Fig. 16.8a). When the damaged plants recovered and reflushed new leaves in mid-July, females resumed oviposition. Females thus avoided reproduction when food was unavailable to larvae, and resumed oviposition when offspring fitness was no longer reduced by food shortage.

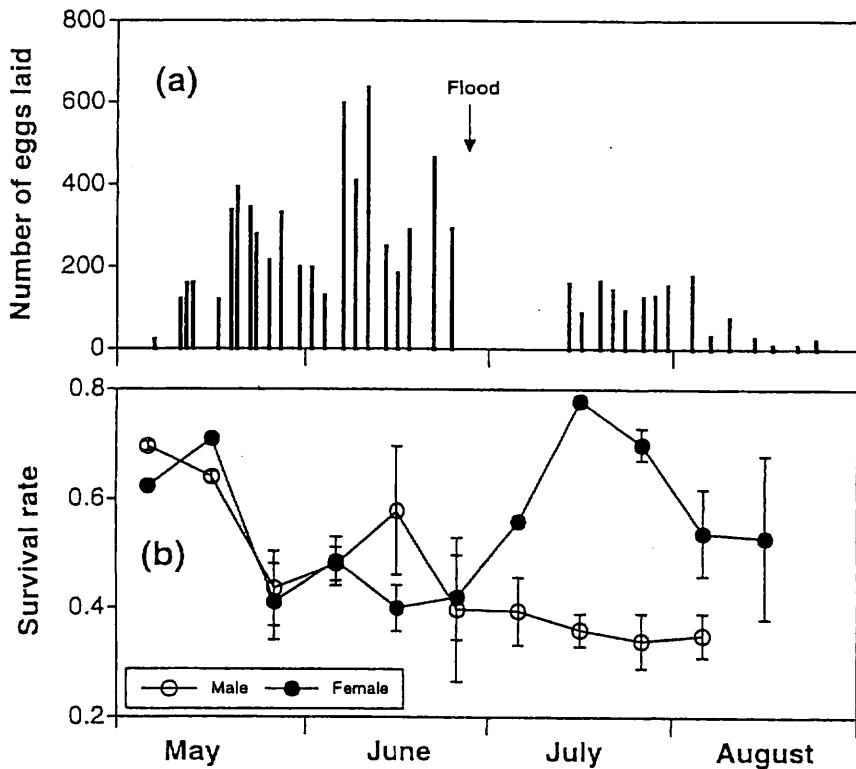


Fig. 16.8 Egg resorption caused by a large flood at site F and survival of reproductive adults. (a) Number of eggs laid on each census date. (b) Seasonal changes in survival rate of reproductive adults per 10 days. Each point represents estimated survival rates and 95% confidence limits, which were calculated by the Jolly-Seber stochastic model based on the mark-recapture data. From Ohgushi (1996a) by courtesy of Springer-Verlag.

Egg resorption can also be adaptive if it increases female survival so that reproduction is possible in a second season. There are two lines of evidence that a trade-off exists between egg production and female survival (Ohgushi, 1996a). Firstly, periods of low oviposition due to egg resorption were correlated with periods of higher female survival, but not higher male survival. Secondly, the severe flooding at site F in 1979 and the resulting egg resorption was correlated with changes in female survival (Fig. 16.8b). When females stopped laying eggs, their survival increased immediately up to mid-July. Then, after oviposition resumed, it began to decline. Again, male survival was unaffected. This indicates that reduced investment in reproduction through egg resorption increases investment in survival.

Females which resorbed eggs and then over-wintered oviposited in the following season. At site A, where egg resorption was low, most of the females died by mid-July and none survived until the next reproductive season. In contrast, at site F, where females resorbed eggs, 56 reproductive females were alive until mid-August, and nearly 40% survived until the next spring (Ohgushi, 1996a). Most of these females were observed ovipositing in the second year, thus demonstrating that long-lived females gain fitness by ovipositing in a second reproductive season.

Egg resorption is an adaptive response that increases lifetime fitness. No adults emerged from the cohort that was initiated in August (Fig. 16.9). This indicates that females will have higher reproductive success if they stop ovipositing late in the reproductive season and invest energy in surviving to the next spring, when an egg cohort has a higher probability of producing survivors.

The results of these studies indicate that there is a strong link between oviposition preference and offspring performance on both spatial and temporal scales.

#### 16.5.5 Evolutionary implications of reproductive schedule

Since population regulation is largely due to the timing of reproduction, next I will examine the relationship between the reproductive schedule and lifetime fitness. There were different patterns of lifetime fitness among cohorts that emerged at different times at the two sites (Fig. 16.9). At site A, early cohorts enjoyed consistently higher lifetime fitness than later ones. In contrast, later cohorts at site F had higher lifetime fitness, except for the last cohorts in August. If the schedule of oviposition is a heritable trait, we would hypothesize that natural selection would favour early reproduction in population A, and delayed and/or prolonged reproduction in population F.

A laboratory experiment where environmental variation had been eliminated showed that populations A and F had different reproductive

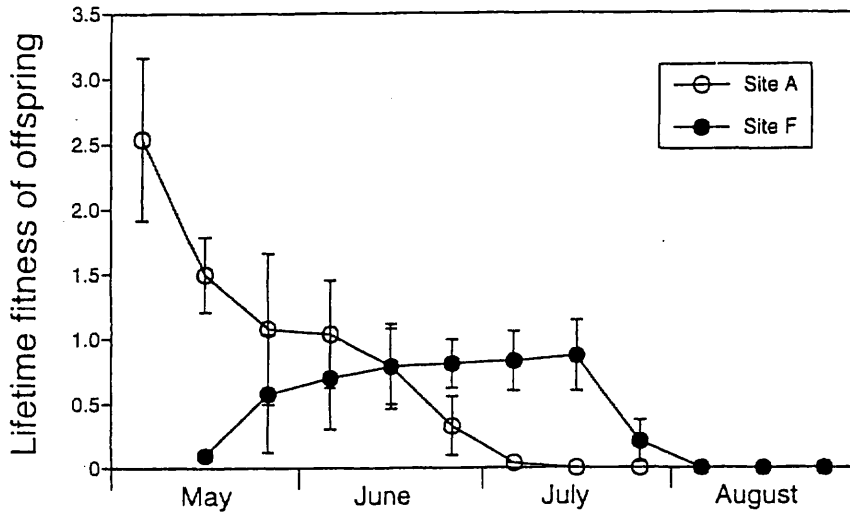


Fig. 16.9 Lifetime fitness of offspring which were born at different times in the reproductive season. Each point represents mean and s.e. for each cohort in 1976–80. The lifetime fitness of the  $i$ th cohort ( $F_i$ ) is defined as follows:  $F_i = E_i \times L_i \times A_i \times R_i$ , where  $E_i$  = egg survival to hatching,  $L_i$  = larval survival from egg hatching to adult emergence,  $A_i$  = survival of adult females from emergence to the reproductive season in the following year, and  $R_i$  = lifetime fecundity of females living to average age of the  $i$ th cohort. Data from Ohgushi (1991).

schedules. When females from both populations were reared under constant laboratory conditions, the survivorship curves of females differed significantly (Fig. 16.10). Females from site A had a significantly shorter reproductive lifespan (Mann–Whitney  $U$  test:  $U=332$ ,  $P=0.002$ ). As a result, the distribution of oviposition differed between sites (Fig. 16.11). At site A, the oviposition rate declined slightly during the first 60 days and then declined sharply during the last 15 days. At site F, the oviposition rate peaked during the first 20 days and then declined until a second peak of oviposition near the end of the reproductive period at day 180. The maintenance of different reproductive schedules under identical environmental conditions indicates that oviposition timing is a heritable trait.

#### 16.5.6 Natural selection alters population regulation

Since oviposition traits are heritable and influence population regulation, we expected that natural selection which alters egg-laying behaviour would indirectly influence population regulation. An introduction experiment strongly supported this hypothesis (Ohgushi and Sawada, 1997a, b, 1998). In May 1971, 15 males and 30 females from the Asiu

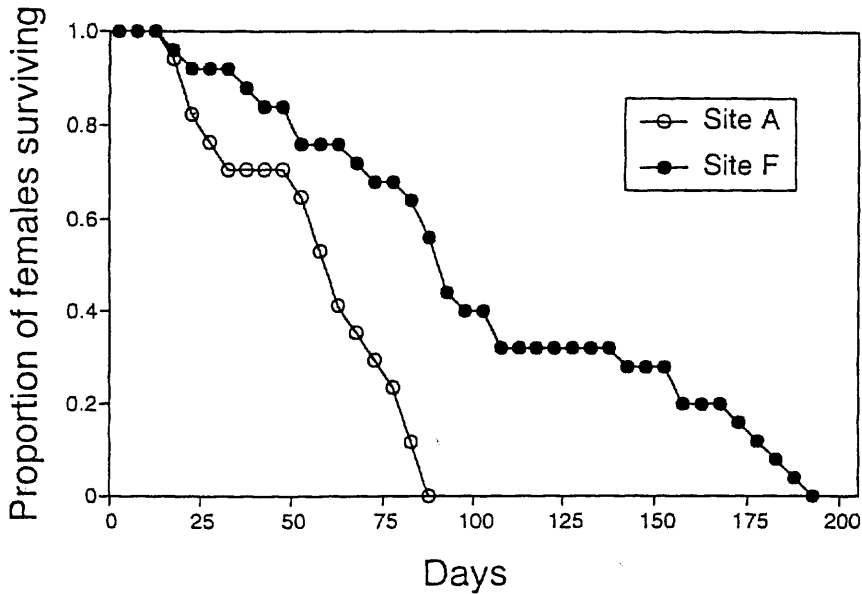


Fig. 16.10 Survivorship curves of adult females collected from sites A and F (Logrank test:  $\chi^2=16.022$ , d.f.=1,  $P<0.0001$ ). Adult beetles were kept under constant conditions of 20 °C and LD 16:8 in an environmental chamber. Data from Ohgushi (1991).

Experimental Forest were released in the Kyoto University Botanical Garden (see Fig. 16.1). This is 30 km south of Asiu and 10 km beyond the southern limits of the lady beetle's natural range. There was no evidence of the occurrence of *E. niponica* in the Botanical Garden before introduction. The lady beetle has an extremely limited dispersal ability; mean distance travelled throughout its lifetime is less than 10 m for both sexes (T Ohgushi, unpublished data), suggesting that 10 km is a sufficient distance for population isolation. Hence, it is most likely that the introduced population has been genetically isolated from any other *E. niponica* populations since the introduction. The introduced population was successfully established, and because of low arthropod predation the thistles were heavily defoliated. The introduced population had a significantly higher density at adult emergence than the source population that is maintained at a relatively low density (Nakamura and Ohgushi, 1981).

Because Botanical Garden larvae in late cohorts suffered from a severe food shortage resulting in high mortality, we predicted that selection would favour early reproduction in this population, leading to a higher oviposition rate and shorter reproductive lifespan. A laboratory experiment strongly supported this prediction. Firstly, females from the intro-

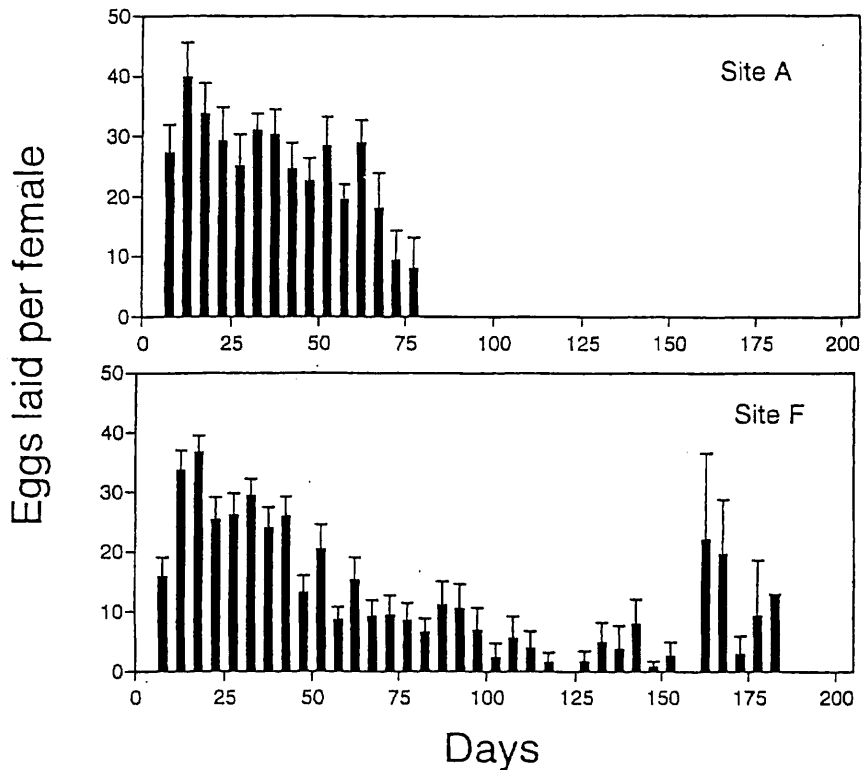


Fig. 16.11 Temporal changes in the number of eggs laid per female in consecutive 5-day intervals for females collected from sites A and F (Kolmogorov–Smirnov test:  $\chi^2=14.69$ , d.f.=2,  $P=0.001$ ). Each point represents mean and s.e. Adult beetles were kept under constant conditions of 20° C and LD 16:8 in an environmental chamber. Data from Ohgushi (1991).

duced population had a higher oviposition rate early in their reproductive period in the laboratory (Fig. 16.12). Secondly, the lifespan of reproductive females from the introduced population was significantly shorter than that of the source population (Ohgushi and Sawada, 1997b; see also Fig. 16.13a), suggesting that reduced longevity had selected for earlier reproduction, as we expected.

Female mobility was also decreased in the introduced population (Mann–Whitney  $U$  test:  $U=19.5$ ,  $P=0.039$ ) (see Fig. 16.13b). We did not measure egg resorption in the introduced population, but we believe that it does not occur for two reasons (Ohgushi and Sawada, 1997a). Firstly, females resorb eggs in response to leaf damage that occurs late in the season. However, in the introduced population the density-dependent reduction in fecundity occurred early in the season. Moreover, a cage

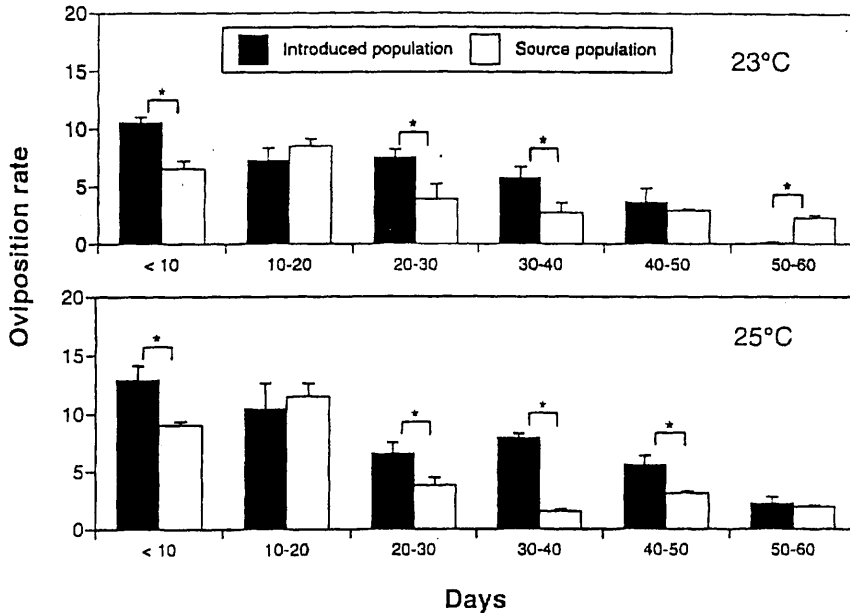


Fig. 16.12 Oviposition rate (eggs laid per female per 2 days) throughout the experimental period. Each point represents mean and s.e. Asterisks show significant differences between the introduced and source populations (Scheffe's test:  $P < 0.05$ ). Modified from Ohgushi and Sawada (1997b).

experiment showed that oviposition was greatly reduced even at low levels of leaf damage. Secondly, egg resorption would be disadvantageous in the introduced population. Females in this population had a shorter lifespan and thus would have little chance of using the energy saved by resorption in future oviposition. Indeed, we found no females that survived to the second reproductive season.

We predicted that reduced female movement and the probable lack of egg resorption would prevent efficient population regulation in the introduced population. In support of this prediction, we found that the introduced population had 6.8 times higher temporal variability in egg density than the source population (Fig. 16.13c), suggesting a lack of an efficient mechanism of population regulation in the introduced population. As a result, the introduced population had the lowest temporal stability in egg density among the seven populations that we studied (Nakamura and Ohgushi, 1981; Ohgushi and Sawada, 1981, 1997a; Ohgushi, 1992). However, the introduced population was stabilized by density-dependent reduction in fecundity and female survival. No other regulatory agents operated, as was the case for the source population, and for site A and F populations. This indicates that the population density of the introduced

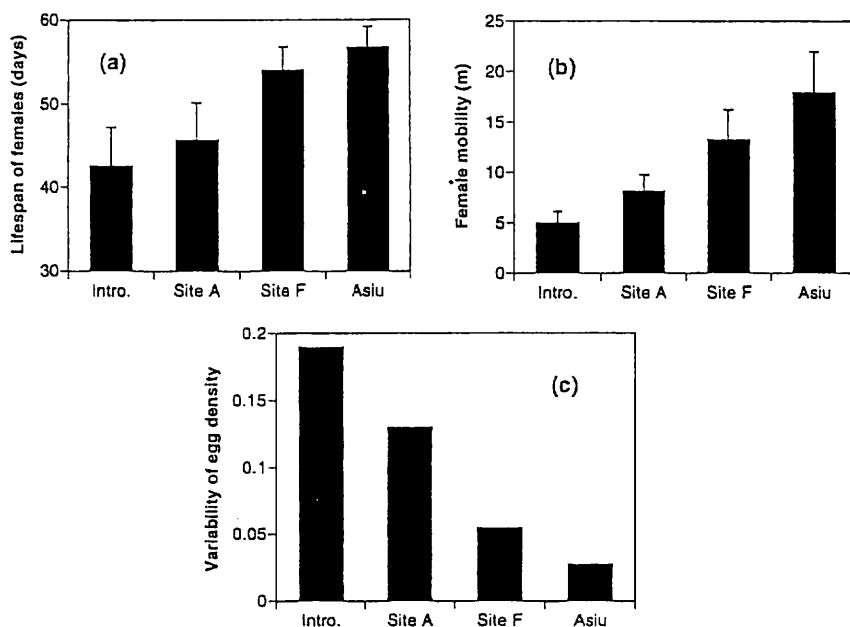


Fig. 16.13 Relationship between reproductive traits and temporal variability in four populations of the lady beetle. (a) Reproductive lifespan of females; (b) female mobility; (c) temporal variability of egg density. Intro. = Botanical Garden population introduced from Asiu. Means and s.e. are presented in (a) and (b). Female mobility was measured by mean distance moved per week by individual females. Reproductive lifespan was measured under constant conditions of 20 °C and LD 16:8 in an environmental chamber

population was also regulated through reproduction, even though survival was greatly modified by a lack of effective predation. This demonstrates again that top-down effects by natural enemies are unlikely to influence population regulation of the lady beetle populations.

Clearly, oviposition traits are the mechanism of population regulation of this lady beetle. We found strong correlations between oviposition traits responsible for population regulation (i.e. female movement and reproductive lifespan) and the temporal variability of four populations (Fig. 16.13). Thus we conclude that the oviposition traits that respond to resource availability regulate the population of the lady beetle *E. niponica*.

## 16.6 CONCLUSIONS

In this chapter, I have shown how the behavioural and physiological responses to resource availability are important in population regulation.

Our results also suggest that natural selection has altered oviposition traits that regulate population density.

Population studies have long ignored the important consequences of behavioural and physiological characteristics of adult insects in population regulation. However, recent studies have highlighted the role of oviposition tactics of females as regulatory processes generating stability in herbivorous insect populations (Preszler and Price, 1988; Craig *et al.*, 1989; Price *et al.*, 1990; Ohgushi, 1995). Recent analyses of density-dependent factors have also concluded that many insect populations are regulated in the adult stage by such factors as adult dispersal and reduced fecundity (Dempster, 1983; Stiling, 1988; Denno and Peterson, 1995). Individual-based population models have shown that life-history, physiology and behaviour have significant consequences for population dynamics (Murdoch and Nisbet, 1996; Uchmanski and Grimm, 1996). These models provide a framework for bringing together evolutionary and ecological studies to further our understanding of population regulation.

In the past, studies of insect population dynamics have focused exclusively on direct effects of biological agents such as killing power, and this has given us an inadequate understanding of population regulation. In the lady beetle, the lifetime fitness of offspring on different plants or cohorts is largely determined by the specific patterns of seasonal changes in predation and host-plant quality (Ohgushi, 1991). Thus, both these biological processes may operate as selective forces on the evolution of oviposition behaviours, including between-plant movement and egg resorption. This demonstrates that we should pay much more attention to natural enemies and host-plant quality as selective forces, through their influence on resource-use tactics of herbivorous insects, when seeking to understand population dynamics. This approach will undoubtedly provide new insights, giving an evolutionary perspective to insect population dynamics.

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