

POPULATION EQUILIBRIUM WITH RESPECT TO
AVAILABLE FOOD RESOURCE AND ITS BEHAVIOURAL
BASIS IN AN HERBIVOROUS LADY BEETLE,
HENOSEPILOACHNA NIPONICA

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SUMMARY

(1) Population studies of a thistle-feeding lady beetle, *Henosepilachna niponica* (Lewis), were conducted from 1976 to 1980 at two different study sites to examine whether the local populations exist in a dynamic equilibrium state with respect to available food resources. Adult populations were estimated using the Jolly-Seber method based on mark-release–recapture data. Direct counts were applied to eggs and larvae on every thistle plant.

(2) Food resource abundance measured as the number of thistle shoots changed from year to year rather independently in the two sites, but the egg populations surprisingly tracked the year-to-year changes in available food supply throughout the study period in each habitat.

(3) The average egg density relative to food resource abundance over 5 years was almost identical between the two local populations.

(4) After detectable external perturbations, mainly large-scale floods and arthropod predation, the egg populations quickly returned to the previous level of density.

(5) It is concluded that the local populations of the lady beetle actually persist in a dynamic equilibrium, maintaining a constant density with respect to the amount of available food resource.

(6) The egg populations approached, asymptotically, a plateau of a certain level of density per unit resource throughout the reproductive season in every year.

(7) The possible regulatory process responsible for the population saturation involves the reduction in oviposition rate responding to cumulative egg load in the later season and, to a lesser extent, density-dependent losses of reproductive females probably due to dispersal in the early season.

(8) The resorption of developing eggs in the ovary and frequent inter-plant movements of females for oviposition are causal behavioural bases producing a dynamic equilibrium state in the lady beetle and thistle system in every year.

INTRODUCTION

The balance of nature has been frequently assumed in natural history since antiquity (Egerton 1973). However, there have been many attempts to challenge this concept for some decades. The most exciting of these can be found in the well-known debate on density-dependent population regulation. Utida (1967) reviewed the contrasting

hypotheses to explain population persistence and emphasized the need to study the equilibrium status of populations in the real world to resolve the argument.

The notion of population equilibrium is also the major premise of current theories of life history evolution based on the ideas of *r*- and *K*-selection of MacArthur & Wilson (1967). They identified the density of species with respect to restricted resources as a major selective force capable of explaining many life history differences within and between species. Therefore, one cannot infer selective forces leading to particular life history strategies until ideas of population equilibrium are tested in nature (Caswell 1982; Boyce 1984). In developing our understanding of life history evolution, one must first summarize a complex interaction between a population and its resources and determine whether the population actually exists in a dynamic equilibrium state.

Since 1976 we have made a comparative study on several local populations of a thistle-feeding lady beetle, *Henosepilachna niponica* (Lewis), living under different habitat conditions to clarify the basic population processes and life history strategy (Ohgushi & Sawada 1981, 1984, 1985; Ohgushi 1983). Nakamura & Ohgushi (1979, 1981) gave evidence of marked population stability in *H. niponica* in a cool temperate climax forest and suggested the importance of inter-patch dispersal as a regulatory agent.

In this paper, we first describe the temporal changes in both the size of population of *H. niponica* and the abundance of its host plant over 5 years at the two different localities, and then show that the local populations of the lady beetle persist in a dynamic equilibrium state with respect to the abundance of food resource. Last, we identify causal mechanisms responsible for population equilibrium.

STUDY AREA

This study was conducted at six sites (A–F) located in several valleys of the River Aso and its branch, the River Aso, which flow through the northwestern part of Shiga Prefecture, central Japan. Here, we will show the results of the 5-year investigations obtained from site A and site F which are representative of the downstream and upstream habitats, respectively. The characteristics of the two study plots are summarized as follows.

Site A (*Nyû-dani*)

This site (60 × 30 m) was situated in the valley farthest downstream of the study plots, i.e., 220 m in altitude. It was on an accumulation of sandy deposits caused by the construction of a dam which was built in 1968 to prevent erosion; the ground surface of the rather flat and open area consisted mainly of unhardened sandy deposits. Accordingly, floods caused by heavy rainfall have often submerged and washed away the ground flora along the watercourse. Thus, most of the ground flora that survived these inundations were annual and perennial herbs, such as *Polygonum thunbergii* (Sieb. et Zucc.), *P. cuspidatum* (Sieb. et Zucc.), and *Rumex crispus* (L.).

Site F (*Kijiyama*)

This plot (90 × 15 m) was the highest and the most mountainous of all the study sites, i.e., 350 m in altitude. It was located some 10 km upstream from site A, and covered riverbanks of a mountain stream, about 5–6 m wide. Because of more hardened soil deposits, most grasses and shrubs growing here can successfully escape from serious damage by usual floods except for large-scale ones. In and around the site, vegetation

included various deciduous broad-leaved trees such as *Quercus mongolica* (Fisch. ex Turcz.), *Q. salicina* (Blume), and coniferous species such as *Cephalotaxus harringtonia* (Koch.). Further descriptions of other sites and the map of each plot are given in Ohgushi & Sawada (1981).

MATERIALS AND METHODS

The lady beetle

Henosepilachna niponica has usually one generation a year. It feeds exclusively on leaves of a thistle, *Cirsium kagamontanum* (Nakai) in this study area, and spends its entire life on the host plant. Overwintering adults emerge from hibernation around the beginning of May; within 1–2 weeks after emergence, adult females begin to lay eggs in clusters containing from fifteen to forty eggs on the underside of thistle leaves. The oviposition period sometimes extends up to 3 months, i.e. until mid-August. The larvae pass through four instars, and then, pupate on thistle plants. New adults begin to emerge in early July, feeding on thistle leaves, and enter hibernation by early November.

The estimation of population size

The census was performed at intervals of 1–3 days throughout the season from early May to early November during the course of the study (1976–80). On each census date, all the thistle plants growing within the study site were carefully checked and recorded with regard to the numbers of eggs, fourth instar larvae, pupae, pupal exuviae and adult beetles found on each plant. Procedures of population estimation for successive life stages are as follows.

Egg and larval stages

The size of all egg batches on leaves were recorded when they were found and labelled to prevent double counting. Thereafter, we checked the number of eggs that hatched on every census. The total recruitment to the egg stage was thus obtained by accumulating these data. Since the larvae in earlier instars are too small to be counted exactly, only fourth instar larvae were counted directly. The total number of fourth instar larvae reaching the medial age of this instar was estimated using the graphical method described by Southwood & Jepson (1962).

Adult stage

Adult populations were studied by intensive mark-release-recapture censuses over the study period. We marked, individually, 5969 beetles at site A and 3507 beetles at site F during 1976–80. Accordingly, the total recruitment entering the reproductive and new adult stages were estimated using the Jolly-Seber stochastic model based on capture-recapture data (Jolly 1965; Seber 1973). Fortunately, highly accurate estimates of adult numbers could be obtained with this method (Ohgushi & Sawada 1981). Also, we evaluated overwintering adults just after hibernation in the beginning of May at the study sites. As newly-emerged adults exhibited very little tendency to disperse during the pre-hibernating period (Ohgushi 1983), survival from adult emergence to the following spring immediately after hibernation can be accurately estimated based on the number of marked adults that were recaptured in the next spring. We could then reasonably estimate the number of overwintering adults using the total recruitment of new adults in conjunction with the estimated adult survival until the following spring. Further descriptions of other

related adult population parameters such as daily survival estimated by the Jolly-Seber method are already given in Ohgushi & Sawada (1981).

The estimation of oviposition rate

The oviposition rate, i.e., the number of eggs laid by an individual female, in a 5-day period was measured throughout the reproductive season in the field. It was calculated from the total number of eggs deposited divided by the mean number of reproductive females during each 5-day period. The half-monthly oviposition rate was thus obtained by accumulating these estimates. The adult numbers on each census date estimated by the Jolly-Seber method had a high level of reliability (Ohgushi & Sawada 1981). The intensive censuses for egg populations covered all thistle plants growing in the study plots. Furthermore, we could check most of the eggs disappearing due to predation and cannibalism by counting the characteristic traces of the basal area of egg shells that remain on thistle leaves. Therefore, the oviposition rate obtained in the present study provides a reliable estimate for the actual eggs oviposited by an individual female.

The estimation of adult mobility

Adult mobility was evaluated by the mark-release-recapture experiments for adult beetles. All the adult beetles found on every census date were marked individually with lacquer paint on four marking points on the elytra. Sex, body size, and capture history at each time and place were recorded for individual beetles, and newly-marked beetles were immediately released on the thistle plants where they were captured. On following censuses, the date, capture position, and the reference number of each marked adult were recorded by sight without recapturing. Movement paths traversed by each adult were followed by successive recaptures throughout its life-span. Linear distances between consecutive pairs of recaptures of individuals were measured. By using these data, we calculated the variance of distances covered per day, which is a good indicator of the amount of movement (Inoue 1978; Okubo 1980).

Field experiments evaluating oviposition behaviour

Experiment 1

This experiment was conducted to examine responses of egg-laying schedules according to the relative leaf damage of host plants. In mid-May 1979, eight thistle plants with approximately the same height and the same number of leaf nodes were selected, and each plant was covered with a nylon organdy cage with a metal frame which was large enough to allow further foliage growth; one pair of reproductive adults was introduced into each cage for oviposition. Thereafter, the number of eggs laid was checked almost every day until the death of the female. Three cages were designed as follows. In the first two cages, each female was transferred to another cage containing a new thistle without leaf damage, 2–3 weeks after the female ended egg-laying. In the third cage, two old larvae of the earwig, *Anechura harmandi* (Burr), a predominant egg predator in this study area, were initially released to remove all eggs deposited during the experimental course. The remaining five cages were kept for control. In addition, we sometimes carried out a visual estimation of leaf damage of the caged thistles due to adult and larval feedings.

Experiment 2

Reproductive females in the genus of *Henosepilachna* readily resorb oocytes and the ovary eventually degenerates when they are kept under starved conditions in the

laboratory (Kurihara 1975, 1981, personal communication). This experiment was thus designed to evaluate possible impacts of the deterioration of the host plant on ovarian status in ovipositing females. On 22 May 1981, six thistle plants were selected and each plant was covered with a nylon organdy cage like that described in Experiment 1. Different numbers of reproductive adults were then introduced into corresponding cages (see Table 2). On 26 June, 35 days after the experiment started, we took out all adult females which survived in each cage and dissected their ovaries immediately; the ovarian status was classified into four categories (normal maturation and three stages of resorption) according to Kurihara (1975, 1981). Additionally, we collected reproductive females from the two study sites on five dates over the reproductive season in 1981 and checked ovarian status of the individuals to evaluate the seasonal changes in ovarian development in the field.

RESULTS

Annual changes in population size

The annual fluctuations in the numbers entering the egg stage over the period of study, 1976–80, at the two sites are shown in Table 1. It can be seen that the observed population size fluctuated somewhat differently between the two localities. Thus, the population size at the downstream site A exhibited a tendency for progressive increase during this study, whereas the population at upstream site F was relatively constant in size, although some decline was observed after 1979.

TABLE 1. Annual changes in population size on the egg stage at the two study sites

Site	1976	1977	1978	1979	1980
A	2868	4994	5713	4246	10 868
F	10 423	11 264	9815	8114	3916

Annual changes in food resource abundance

We now examine the temporal changes in available food resource. The host plant, *C. kagamontanum*, is a perennial and dominant species in the flora surviving along the riverside, usually growing in different-sized discrete patches. In the study area, new plants appear in mid-April and then show rapid foliage growth until late June. Thereafter, they gradually grow to become full-sized, i.e. 1.5–1.8 m in height, by August. From early August the lower leaves become mature and gradually wither. Seasonal changes in quantity and quality of thistle leaves as available food and their effects on demographic consequences of local populations will be analysed elsewhere. Annual changes in the number of thistle shoots over the 6 years, 1976–81, at the study site A and site F are shown in Fig. 1. The total number of thistle shoots present at downstream site A increased 4.2-fold from the beginning of this study up to 1981. On the other hand, the number of thistle shoots at upstream site F fluctuated in a quite different manner: it remained rather constant except in 1980. Evidently, a marked reduction observed in 1980 was attributable to the heavy autumn floods in the previous year. However, the host population successfully recovered from the serious damage of this catastrophe and immediately returned to the previous level of abundance in the spring of 1981. As a result, the thistle shoots showed remarkably limited fluctuation over 6 years, i.e., only 2.3-fold variation (1.4-fold variation if the 1980 data are omitted). Since downstream site A is located on an accumulation of unhardened sandy deposits, the river discharge has often covered the deposits. Thus, the

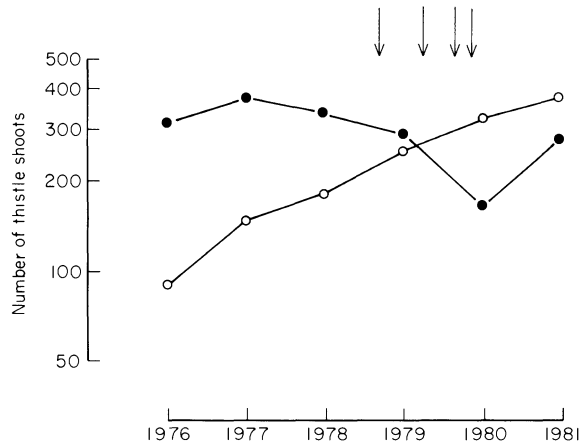
Population equilibrium in an herbivorous insect

FIG. 1. Annual changes in the number of thistle shoots for 1976-81 at Site A (○) and site F (●). Vertical arrows show the occurrence of heavy floods.

ground flora, including thistles beside the watercourse, has been frequently washed away and/or buried with soil. In contrast, the flora on the deposits has still remained in the early stage of succession and new thistle plants have continuously colonized unoccupied sites every year. This is followed by a continuous increase in thistle shoots at the less exploited site. In fact, the autumn floods in 1979 also caused marked thistle losses here, but new colonizers compensated and indeed surpassed the former densities in the following spring. Meanwhile, upstream site F is made of firmly hardened riverbanks, so the ground flora has been rarely subjected to serious damage by occasional floods except for such larger ones as occurred in 1979. Hence, the thistles growing at the upstream site tend to remain fairly constant in number and location for several years. Furthermore, the rapid recovery of the thistle population from the unusual flood damage implies high resistance of the host population to such catastrophic perturbations so as to provide a relatively stable food supply at the upstream habitat.

Population density and its stability relative to available food resources

We now analyse the numerical relationship between the lady beetle population and its food supply. In order to evaluate how the *H. niponica* population can respond numerically to temporal changes in the abundance of food resource, the total numbers entering each life stage were plotted against those of thistle shoots remaining in each year (Fig. 2). No significant correlation was observed between the abundances of the insect at the reproductive adult stage and the host, but its egg population was closely related with total number of thistle shoots in both of the study sites (site A: $r = 0.81$, $0.05 < P < 0.1$; site F: $r = 0.99$, $P < 0.01$). The lower correlation detected at site A is evidently accounted for by the unexpected reduction in the number of eggs laid in 1979 owing to a heavy flood that occurred in late June. This environmental catastrophe washed away most adult beetles surviving in the plot and as a result no further oviposition followed. At upstream site F, however, such serious losses of reproductive adults were not detected. On the other hand, such a close relationship between the insect and its host could no longer be observed in the latter stages. In fact, the number of fourth instar larvae and that of newly-emerged adults did not respond to annual changes in thistle shoots as closely as did the number of eggs, because of the disturbance due to external factors affecting survival after the egg stage.

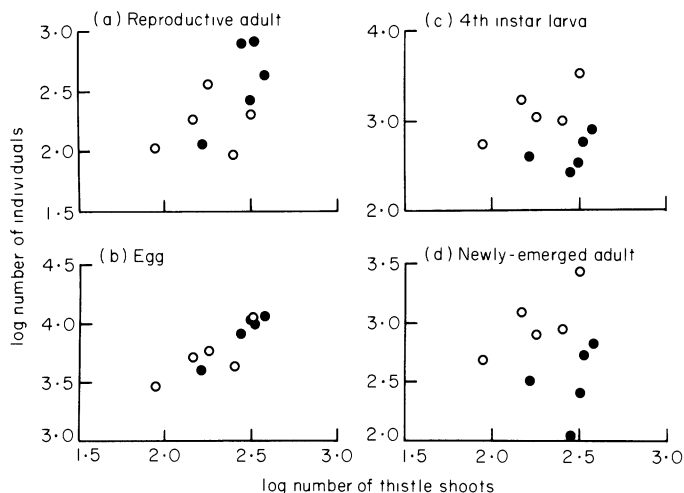


FIG. 2. Relationships between population size and thistle abundance for 1976–80 at site A (○) and site F (●) (a) Reproductive adult (A: $y = 0.22x + 1.73$, $r = 0.20$, N.S.; F: $y = 1.84x - 1.92$, $r = 0.73$, N.S.); (b) egg (A: $y = 0.80x + 1.91$, $r = 0.81$, $0.05 < P < 0.1$; F: $y = 1.31x + 0.72$, $r = 0.99$, $P < 0.01$); (c) fourth instar larva (A: $y = 1.03x + 0.77$, $r = 0.76$, N.S.; F: $y = 0.63x + 1.11$, $r = 0.47$; N.S.); (d) newly-emerged adult (A: $y = 1.02x + 0.71$, $r = 0.79$, N.S.; F: $y = 0.69x + 0.80$, $r = 0.31$, N.S.).

This implies that the lady beetle population can track temporal changes in food resource abundance by regulatory mechanisms that operate mainly during the reproductive season.

Having apparently detected such close synchronization between the lady beetle and the thistle abundance, we next examine average population density expressed in terms of the number per unit food resource, i.e., number per 100 shoots, throughout the study at sites A and F (Fig. 3). By comparing observed annual trends of the population density between the two sites, some definite points can be noticed with regard to population equilibrium.

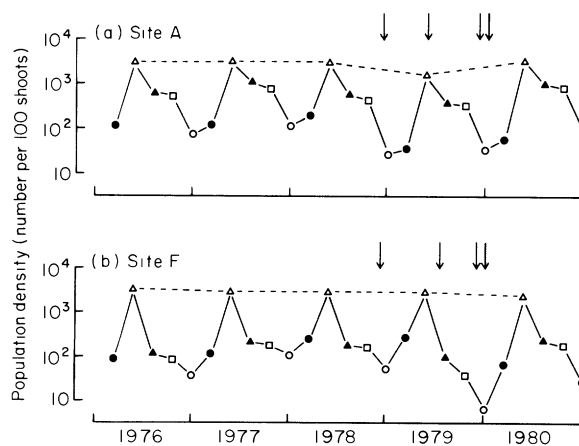


FIG. 3. Annual changes in population density relative to food resource abundance (number per 100 thistle shoots) for 1976–80 at (a) the downstream site A and (b) the upstream site F. (○) overwintering adults just after hibernation; (●), reproductive adults; (△), eggs; (▲), fourth instar larvae; (□), newly-emerged adults. Vertical arrows show the occurrence of heavy floods. Dashed line (---) shows the annual trend egg density.

Firstly, the average egg density over 5 years was almost identical between the two local populations, being 2984 eggs (ranging from 1692 to 3418) at site A and 2937 eggs (ranging from 2417 to 3351) at site F. Secondly, the egg population relative to the available food resource fluctuated within extremely narrow limits because of tight food resource tracking. Thus, the egg density over 5 years at site A and site F represented only 2.0-fold and 1.4-fold variations, respectively. Lastly, the lady beetle population in either site exhibited remarkable resistance to external disturbances. In 1979, for example, the egg density at site A and the new adult density at site F were considerably reduced by the heavy floods that occurred in late June and late September, respectively. Nevertheless, in both the cases, the two populations quickly returned to their previous level of egg density in the next generation following such unpredictable perturbations. Furthermore, notwithstanding that the population level of adults was differently depressed and disturbed by arthropod predation particularly during the immature stages in every year (Ohgushi & Sawada 1985), the egg density was maintained remarkably constant over 5 years at both of the study plots.

Population saturation in the reproductive season

Having considered the numerical relationship between the lady beetle and its host plant, we now turn to the problem of how the egg populations are regulated with respect to resource abundance.

Seasonal changes in cumulative egg densities at the two study sites are shown in Fig. 4. It is clear that both of the egg populations approached, asymptotically, a plateau of a nearly equivalent density per unit food resource (about 3000 eggs per 100 shoots) and that annual variations of the egg density declined progressively during the season. In particular, the rate of population growth was highly depressed in June; as a result, there appeared population saturation throughout the later reproductive season. Thus, regulatory mechanisms seem to maintain the egg population at a certain level of density at the end of the reproductive season in every year.

The growth rate of the egg population largely depends on two reproductive attributes: oviposition rate and number of reproductive females. Let us examine possible

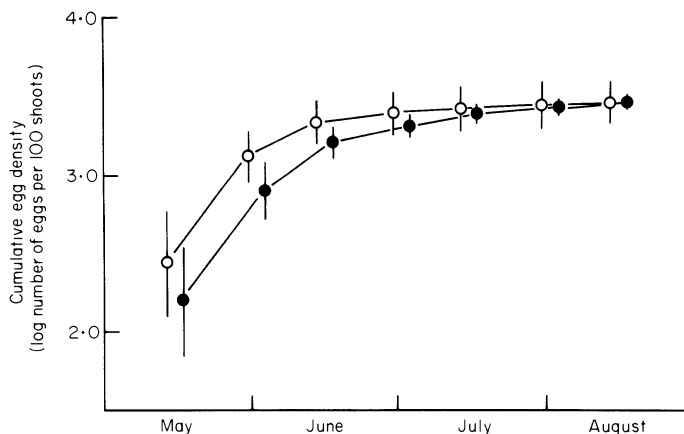


FIG. 4. Seasonal changes in cumulative egg density (means \pm S.D.) at site A (O) and site F (●).

contributions of the two agents on the limitation of the further upward population growth observed in the later reproductive season. The half-monthly oviposition rates were plotted against the cumulative egg densities (Fig. 5). The oviposition rate in May fluctuated little among different years in spite of considerable variations in the cumulative egg density. On the other hand, after June, significantly negative correlation existed between the two components at both of the study sites. Meanwhile, the survival rate of adult females in May exhibited a declining tendency in a density-dependent manner at the two plots, although the relationships were not statistically significant (Fig. 6). However, such a trend was not observed after June. Actually, year-to-year variations in female density decreased from May to June at site F. The density-dependent female losses would involve

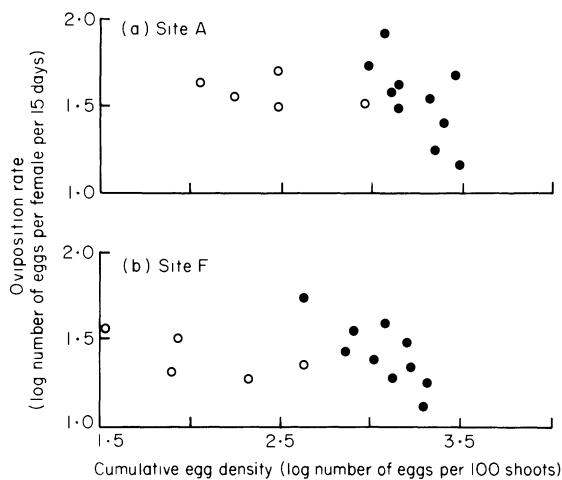


FIG. 5. Relationships between half-monthly oviposition rate and cumulative egg density in May (○) and June (●). (a) Site A (May: $y = -0.12x + 1.86$, $r = -0.45$, N.S.; June: $y = -0.83x + 4.19$, $r = -0.66$, $P < 0.05$); (b) site F (May: $y = -0.20x + 1.82$, $r = -0.70$, N.S.; June: $y = -0.68x + 3.50$, $r = 0.80$, $P < 0.01$).

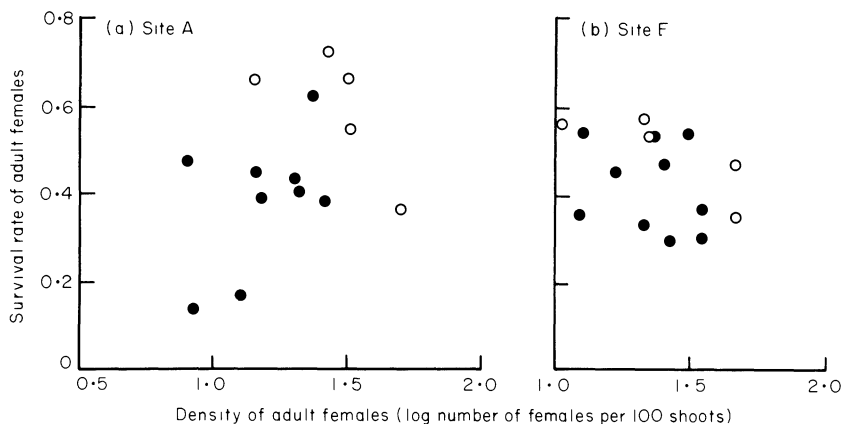


FIG. 6. Relationships between half-monthly survival rate in adult females and female density in May (○) and June (●). (a) Site A (May: $y = -0.49x + 1.31$, $r = -0.69$, N.S.; June: $y = 0.40x - 0.08$, $r = 0.49$, N.S.); (b) site F (May: $y = -0.27x + 0.88$, $r = -0.81$, N.S.; June: $y = -0.15x + 0.62$, $r = -0.25$, N.S.).

density-dependent adult mortality and/or dispersal. Predominant density-dependent adult mortality agents were unlikely to operate during the reproductive season; but the female's mobility was significantly related to adult density at site F (Ohgushi 1983). Also, movement activity of reproductive females are more intensified from late May to early June as will be shown later (see Fig. 8). Thus, the enhanced dispersal tendency of adult females in high density years probably accelerates adult disappearance due to emigration out of the plot in the early reproductive period when adult population numbers reach a peak.

Thus, the control of oviposition rate in response to the egg density in the later reproductive season and density-dependent female losses in the early season are chiefly responsible for the limitation of the further upward growth of the egg population with respect to abundance of food resource provided in each year.

Oviposition behaviour responsible for population equilibrium

Having described the responses of reproductive attributes to possible regulatory processes, let us now analyse the oviposition behaviour in the field experiments. The oviposition schedules of each cage in Experiment 1 are shown in Fig. 7. In every cage except for the one with egg predators, the females refrained from laying eggs around mid-June when the foliage injury due to adult and larval feeding became particularly clear (cages a–g). It is notable, however, that the damage to thistle leaves stayed far below the level that provides no area available for oviposition. Interestingly, such females resumed oviposition again in a short time when they were released into another cage with an undamaged thistle (cages f–g). However, in the cage with egg predators, the

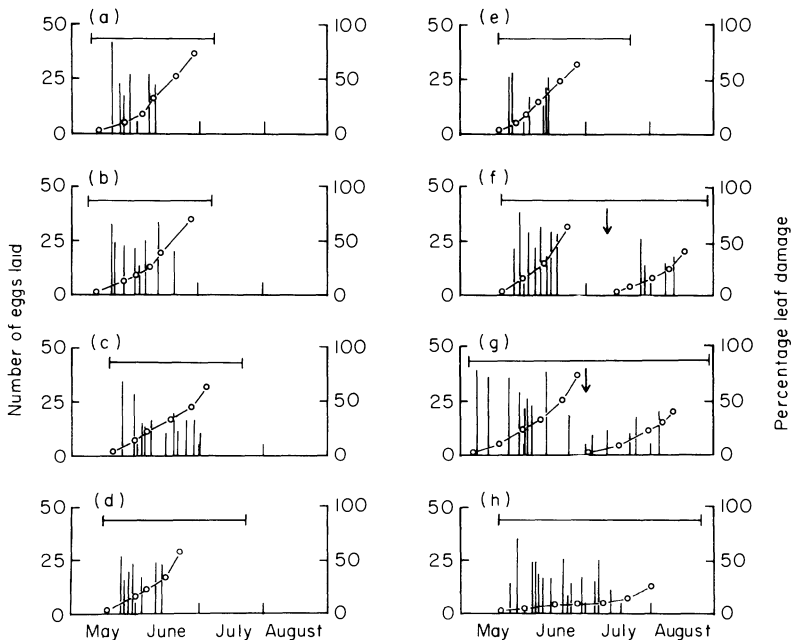


FIG. 7. Oviposition schedules of each cage in Experiment 1. The number of eggs deposited (vertical bars) and the percentage of leaf damage (O) are shown. The horizontal lines show the female's life-span. (a)–(e), control; (f)–(g), the female was transferred to another cage with a new thistle at the date indicated by the vertical arrow; (h), cage with egg predators.

TABLE 2. Ovarian status of adult females in Experiment 2

Cage	Thistle plant		Number of adults introduced		Ovarian status*			
	height (cm)	number leaves	introduced		normal maturation	Resorption of oocyte		
			male	female		early stage	middle stage	late stage
a	80	7	1	1	1			
b	60	6	1	1	1			
c	110	9	1	1	1			
d	65	5	1	2		1	1	
e	80	9	4	5			1	3
f	45	8	4	7			1	5

* Adult females died before the final date of the experiment were omitted.

foliage damage remained at a comparatively low level throughout the course of the experiment because of no larval appearance resulting from heavy egg predation. In this cage oviposition occurred continually until late July (cage h).

The results from Experiment 2 are given in Table 2. The resorption of oocytes evidently occurred in reproductive females in high density cages (cages d–f) at the end of the experiment when most leaves were highly exploited. In contrast, every female had a normally developed ovary for egg production in one-pair cages; a number of leaves remained undamaged in these low density cages. Our results suggest some notable points of oviposition behaviour of the lady beetle with regard to regulatory processes. Firstly, ovipositing females readily resorb developing oocytes in the ovary, following no further egg-laying. Secondly, deteriorating food resources during the season are the most likely cause driving the resorption of oocytes. Lastly, the process of resorption is reversible: when the host plant becomes favourable, the resorption immediately ceases and the ovary again becomes productive. This physiological mechanism can well explain the control of oviposition rate in response to egg load, which in turn is related to the degree of deterioration in the thistle leaves.

There remains the possibility that the resorption of developing eggs revealed in the field experiment may not occur in the natural populations, being at a low density compared to the experimental conditions. Table 3 shows seasonal changes in ovarian status of reproductive females sampled from the field populations, confirming that females evidently

TABLE 3. Seasonal changes in ovarian status at the two populations in 1981

Date	Site	Number of adults examined	Ovarian status				ovary without developed eggs
			normal maturation	early stage	middle stage	late stage	
27 April	A	14	14				
	F	11	11				
12 May	A	8	8				
	F	10	10				
24 May	A	9	9				
	F	11	11				
19 June	A	5			3		2
	F	6		3	2		1
9 July	A	2				1	1
	F	8	5	1			2

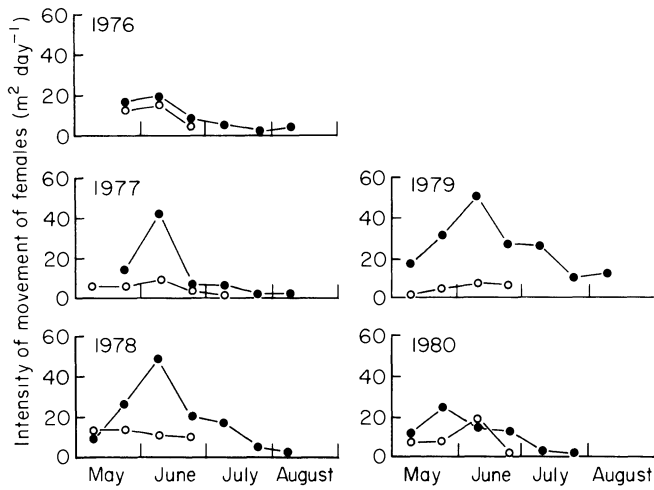


FIG. 8. Seasonal changes in the variance of distances traversed per day, an indicator of movement intensity, of reproductive females for 1976–80 at site A (O) and site F (●).

resorbed oocytes in the later season in the field. The ovaries of overwintering females matured in early May; whereas, the proportion of individuals with resorbed oocytes rapidly increased after late June. Besides resorption, some females without normally developed eggs in the ovary were detected in the later season. The evidence of ovarian degeneration in the later reproductive season has been known in other localities (Katakura 1976; Katakura, Hoshikawa & Kimura 1978).

Seasonal changes in movement activity, as expressed by the variance of distances traversed per day, of ovipositing females at the two study sites are shown in Fig. 8. The mobility of females increased gradually from the beginning of the season, reaching a peak around early June. Thereafter, the movement activity consistently declined to the low level again as the season advanced. The scale of adult dispersal tendency at site F was more

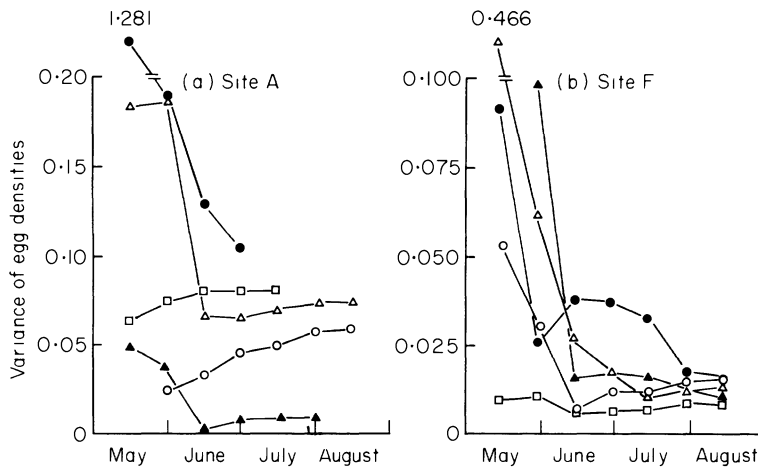


FIG. 9. Seasonal changes in the variance of cumulative egg densities among five different thistle groups based on plant size at (a) site A and (b) site F. (O), 1976; (Δ), 1977; (□), 1978; (●), 1979; (▲), 1980. Only data in 1977 at site A are on the scale of 1/10.

than twice or three times that at site A. Actually, the variance ranged from 20 to 50 m² day⁻¹ in its peak at site F, compared to that being less than 20 m² day⁻¹ at site A.

Seasonal changes in the variance of cumulative egg densities (transformed log scale) among different thistle groups according to plant size are shown in Fig. 9. The variance clearly dropped rapidly from late May to mid-June when the movement activity of ovipositing females became highest at both of the study sites. This implies that the egg density among different thistle patches scattered widely over the habitat are fairly well stabilized during the early reproductive season when ovipositing females actively move from one thistle patch to another. The resultant spatial stabilization of egg density was thus particularly pronounced at site F with higher female activity.

DISCUSSION

Previous arguments on the equilibrium and/or stability of natural animal populations have often been confused and the ambiguity in these terms is one of the main difficulties in testing hypotheses about population equilibrium (Murdoch 1970; Holling 1973; Connell & Sousa 1983). In this study we define a dynamic equilibrium, on empirical grounds, as a constant ratio through time of population size to amount of available food resource. If populations persist in a dynamic equilibrium state in this way, the following phenomena can be predicted: (i) synchrony in fluctuation between population size and its resource abundance, i.e. population regulation with respect to available units of resource (Nicholson 1933, 1954); (ii) similarity in equilibrium level between different populations (unless marked differences exist in major population processes and genetic composition of individuals); and (iii) tendency to return immediately towards the equilibrium level following external disturbances (Holling 1973; May 1973).

The numerical relationship observed between the lady beetle and the host plant abundance throughout this study has satisfied all of these possible criteria since the population actually persists in a dynamic equilibrium. Firstly, the egg populations of the lady beetle fluctuated in fairly close accordance with the annual changes in thistle abundance over 5 years at both of the study sites (see Fig. 2). Secondly, the average egg density per unit food resource at downstream site A remained almost equivalent to that at upstream site F (see Figs 3 and 4). Finally, in spite of considerable reduction in larval and new adult population levels caused by external disturbances, including heavy floods and arthropod predation, the egg population of the following generation has quickly returned to its previous level of density relative to food supply (see Fig. 3). Consequently, it is concluded that the natural populations of the lady beetle actually exist in a dynamic equilibrium with respect to the available food resource.

Our analysis of the population regulatory process demonstrated that egg populations approach asymptotically a certain level of density with respect to food supply in every year. This limited population growth depended on the reduction in oviposition rate in relation to cumulative egg load in the later reproductive season and, to a lesser extent, on density-dependent losses of reproductive females in the early season. As a result, egg populations eventually become saturated in terms of available resources within one reproductive season, being independent of events in previous generations unless catastrophic perturbations occurred. Egg populations can thus track closely temporal changes in resource abundance without a time lag. This intrinsic regulatory process allows us to predict general features of long-term population fluctuations of the lady beetle by evaluating the variability of host plant abundance. Populations will fluctuate greatly in unstable habitats expressed by large temporal changes in host populations, and fluctuate

much less in stable habitats. This prediction is strongly supported by the evidence that the population size at the downstream habitat characterized by large temporal changes in host abundance fluctuated more than that at the upstream habitat with less resource variability (see Table 1). Nevertheless, the stability of both of the populations is undoubtedly much higher compared to many other natural insect populations so far studied (see Hassell, Lawton & May 1976; Wolda 1978).

The population saturation of the lady beetle in terms of available food resource is undoubtedly a product of the innate regulatory process based on the oviposition behaviour responding to seasonal changes in the condition of the resource. The characteristic egg-laying behaviour is summarized as follows. At the start of the reproductive season, adult females tend to stay and lay eggs on the thistle patch where they first emerged from hibernation. After a short while, they begin to exhibit frequent movements among thistle plants for oviposition on less exploited patches. As the season advances, they become less mobile and often resorb developing eggs when there is considerable deterioration in the resource. The spatial stabilization of egg density resulting from inter-plant movements of ovipositing females, and the female's control of oviposition combine to keep the population at an equilibrium density in the later season. Thus, the fewer thistle patches receiving no eggs, the more saturated patches there are with a certain density at which females begin to resorb oocytes in the ovary. By switching these characteristic egg-laying tactics in response to seasonal changes in resource, a constant population level is maintained, and an efficient utilization occurs of available resources changing in time and space.

Hairston, Smith & Slobodkin (1960) proposed some general rules for factors limiting terrestrial populations in each trophic level, and emphasized that herbivorous are seldom resource-limited since cases of obvious depletion of green plants are exceptions to the general picture in the field. Also, most recent studies on competition and coexistence between members of a guild of herbivorous insects have assumed non-equilibrium populations which are less affected by resource dynamics (e.g. Shapiro 1974; Rathcke 1976; Strong 1981; Risch & Carroll 1982; see Lawton & Strong 1981 for a review). But in none of these studies were the actual dynamics of resource availability directly measured over the long-term. As shown in Experiment 1, females refrained from laying eggs even when half of the available leaves remained undamaged. For this reason, the equilibrium population evidently exists at an 'endemic level' such that absolute food depletion is unlikely to occur. This is, therefore, a counterexample to the cases mentioned above. That is, the evidence to demonstrate that population density is sufficiently low and much food supply remains unused does not always imply that the food resource is insignificant in determining general features of population dynamics. This view has also been supported by the evidence that several populations of herbivorous insects are maintained at such 'endemic levels' by innate regulatory mechanisms (e.g. Klomp 1966; Kuno & Hokyo 1970; Dixon & McKay 1970).

Current arguments on insect-plant interrelationship have emphasized the causes of spatial and temporal variation in host plants and the impact of variable resources on population dynamics and life history evolution of herbivorous insects (Southwood 1973; Root 1973; Feeny 1976; McNeill & Southwood 1978; Gilbert 1979; Denno & Dingle 1981; Kareiva 1982; Denno & McClure 1983; Crawley 1983; Root & Kareiva 1984). One of the largest obstacles to understanding the general picture of population dynamics and life history strategies of phytophagous insects arises from a conspicuous lack of available data concerning spatio-temporal dynamics of the resources (Gilbert 1979). Therefore, it is necessary in further refining ecological theories about herbivorous insects, to conduct long-term population studies that include careful monitoring of abundance and

availability of essential resources, and then, to provide reliable evidence to demonstrate whether the real state of the dynamic equilibrium being maintained between populations and their restricted resources exists in the field.

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