LIFETIME FITNESS AND EVOLUTION OF REPRODUCTIVE PATTERN IN THE HERBIVOROUS LADY BEETLE[1]

Takayuki Ohgushi[2]
Laboratory of Entomology, Faculty of Agriculture, Kyoto University, Kyoto 606 Japan

Abstract. The adaptive significance of the timing of oviposition in the thistle-feeding lady beetle *Epilachna niponica* was investigated at two localities (site A and site F) in the northwestern part of Shiga Prefecture, central Japan. I followed cohorts produced over a season and measured four components of lifetime fitness: egg survival, larval survival, female adult survival from emergence to the reproductive season in the following year, and lifetime fecundity. These data are based on mark-recapture data for >9000 adult beetles and detailed life tables over 5 yr.

Large variation in lifetime fitness was evident among cohorts within a population, but the two local populations showed a clear difference in patterns of cohort fitness. At site A, cohorts produced early in a season had higher lifetime fitness than later cohorts, whereas at site F, later cohorts (except for the last one) tended to have higher lifetime fitness. The major causes of these between-site differences were seasonal variation in intensity of egg and larval mortalities due to arthropod predation and host plant deterioration.

Field observations revealed a significant difference in oviposition phenology between the two sites: early reproduction at site A and delayed reproduction at site F. The relatively longer reproductive life-span of females was responsible for the prolonged reproduction at site F. Results of a laboratory experiment that eliminated environmental variables agreed with the field observations, and suggested a genetic basis for the oviposition schedules. Correlation of reproductive pattern at each site with higher lifetime fitness of offspring suggests selection on the timing of oviposition to improve the lifetime reproductive success of females.

Key words: Epilachna niponica; herbivorous insect; host plant deterioration; life history evolution; lifetime fitness; oviposition schedule; plant–insect interaction; predation; reproductive life-span; seasonal variation.

INTRODUCTION

A central theme in the evolutionary ecology of herbivorous insects concerns the nature of adaptations of a wide variety of life history traits that affect host plant use (Denno and Dingle 1981, Kareiva 1983, Rausher 1983, Futuyma and Peterson 1985). Since variation in life history traits and differences in the fitness of phenotypes associated with these traits are necessary for the process of natural selection to occur (Endler 1986), direct measures of how fitness varies among individuals with different life histories should contribute toward an understanding of the evolution of host use. Correlations between traits and fitness components are important factors in the evolutionary maintenance of host-use patterns, which may vary among individuals within a population.

Several recent studies of host plant selection have considered the relationship between oviposition preference and relative offspring performance on different plants (Rausher 1980, Via 1986, Ng 1988, Singer et al. 1988, see Thompson 1988 for a review), while other

examples concerning habitat selection of gall-making insects within host plants have shown relationships between the position of galls and the fitness of offspring for aphids (Whitham 1980, 1986) and wasps (Sitch et al. 1988).

However, none of these studies measured the fitness of individual herbivorous insects throughout their lifetimes. If fitness is estimated only over a small fraction of an individual's life-span, then lifetime fitness is likely to be under- or overestimated (Endler 1986). Furthermore, partial fitness fails to reveal important costs and benefits of different phenotypes affecting several components of fitness and any ecological constraints operating on different stages in the life history. Accordingly, analyses of the adaptive nature of life history traits should be based on the evaluation of lifetime fitness in the field. Such estimates require (a) construction of life tables that cover the complete demography of individuals with differing life histories throughout their lifetimes, (b) mark-recapture studies to follow the fate of individuals, and (c) replication within and among years to assess the intensity and variability of possible selective forces in temporally changing environments. This approach has proven successful in field studies focusing on lifetime reproductive success and variation in life history traits in natural populations of a wide

variety of animals (Clutton-Brock et al. 1982, Grant 1986, Koenig and Mumme 1987, Clutton-Brock 1988, Grant and Grant 1989).

I studied the population biology of the herbivorous lady beetle, *Epilachna niponica* Lewis, a specialist herbivore of a thistle, *Cirsium kagamontanum* Kitamura, in several localities in central Japan (Ohgushi and Sawada 1981, 1984, 1985a, b, Ohgushi 1983, 1986, 1987, 1988). The abundance of local populations of this lady beetle closely tracks annual changes in host plant abundance (Ohgushi and Sawada 1985a). This temporal resource tracking depends strongly on oviposition behavior, with the causal mechanism that maintains the population equilibrium being based on oviposition behavior. Females avoid laying eggs on plants that already have many eggs; moreover, females resorb developed eggs in the ovary in response to host plant deterioration. Each of these responses generates a density-dependent reduction in oviposition rate (Ohgushi and Sawada 1985a). An accurate interpretation of the population biology of *E. niponica* requires not only knowledge of demographic features at the population level, but also an understanding of the adaptive nature of oviposition behavior at the individual level.

This study addresses the question of whether an ovipositing female lady beetle has greater lifetime reproductive success when her offspring have higher lifetime fitness in a seasonally changing environment, with special attention paid to the timing of oviposition. For this purpose, lifetime fitness of offspring in two local populations was estimated for nine cohorts annually over a 5-yr period, using detailed life tables and data from individually marked beetles. I investigated (1) the extent of differences in lifetime fitness among cohorts within a population, (2) sources of variation in cohort lifetime fitness within a population, (3) the extent to which cohort lifetime fitness varied between populations, and (4) whether oviposition schedule and offspring lifetime fitness were correlated in each population.

MATERIALS AND METHODS

Study sites and organisms

The study was performed over a 5-yr period (1976–1980) at two sites located in different valleys along the River Ado, in the northwestern part of Shiga Prefecture in central Japan (Fig. 1). Site A (60 × 30 m) was situated at 220 m elevation on an accumulation of sandy deposits caused by dam construction in 1968. The surface of the rather flat and open area consisted mainly of unhardened sandy deposits. Floods caused by heavy rainfall have often submerged and washed away the ground flora along the watercourse and most of the surviving ground flora were annual and perennial herbs, such as *Polygonum thunbergii* Sieb. et Zucc., *P. cuspidatum* Sieb. et Zucc., and *Rumex crispus* L. Site F (90 × 15 m) was situated at 350 m elevation, ≈10 km upstream of site A. The more hardened soil deposits

at this site mean that most grasses and shrubs present can successfully escape from serious flood-induced damage, except for large-scale floods. Vegetation in and around the site included various deciduous broad-leaved trees, such as *Quercus mongolica* Fisch. ex Turcz. and *Q. salicina* Blume and coniferous species such as *Cephalotaxus harringtonia* Koch. Since dispersal of the beetle *Epilachna niponica* is very limited (Ohgushi 1983), these two local populations of this species are highly isolated from each other. Mark-recapture experiments for 9476 adult beetles revealed the average distance traveled by individual beetles throughout their lifetime to be ≈15 m, with a maximum distance of 120 m (Ohgushi 1983). In addition to these two populations, I studied four intermediate populations located between the two sites. During the 5-yr study period, there was no evidence of exchange of individuals among any of these local populations.

In the study area *E. niponica* feeds exclusively on leaves of a thistle, *Cirsium kagamontanum*. There is one generation a year. Overwintering adult females begin to lay eggs in clusters on the undersurfaces of thistle leaves in early May. Larvae pass through four instars. New adults emerge from early July to early September. Adult beetles enter hibernation in the soil by early November (Ohgushi 1983).

From sprouting in late April to late June, the thistle plants grow rapidly, reaching full size (i.e., 1.5–1.8 m in height) by late August. The thistles flower over 2 mo, beginning in mid-August. Old leaves wither after August (Ohgushi 1986). The host plant abundance varied from 0.05 shoots/m² (in 1976) to 0.18 shoots/m² (in 1980) at site A, and from 0.12 shoots/m² (in 1980) to 0.18 shoots/m² (in 1978) at site F for 1976–1980. Annual changes in population size of the thistle plant at the two study sites are given in Ohgushi and Sawada (1985a).

Definition of lifetime fitness

Natural selection can operate at any stage of the life cycle, and the fitness of an individual is the outcome of all processes in terms of survival and reproduction (Endler 1986, Grant and Grant 1989). Therefore, in analyzing natural selection in natural populations, lifetime fitness or lifetime reproductive success has been partitioned into its component parts (see Clutton-Brock 1988 for examples in a wide variety of animals). This paper defines lifetime fitness as the expected total number of eggs produced in the following generation in terms of the expected reproductive contribution of one egg at the moment of birth (oviposition). Here I focus on lifetime fitness of offspring produced at different times within one reproductive season, such that the lifetime fitness of the *i*-th cohort (F_i) is expressed as

$$F_i = E_i \times L_i \times A_i \times R_i, \tag{1}$$

where E_i = probability of egg survival to hatching, L_i = probability of larval survival from egg hatching to adult emergence, A_i = probability of survival of adult
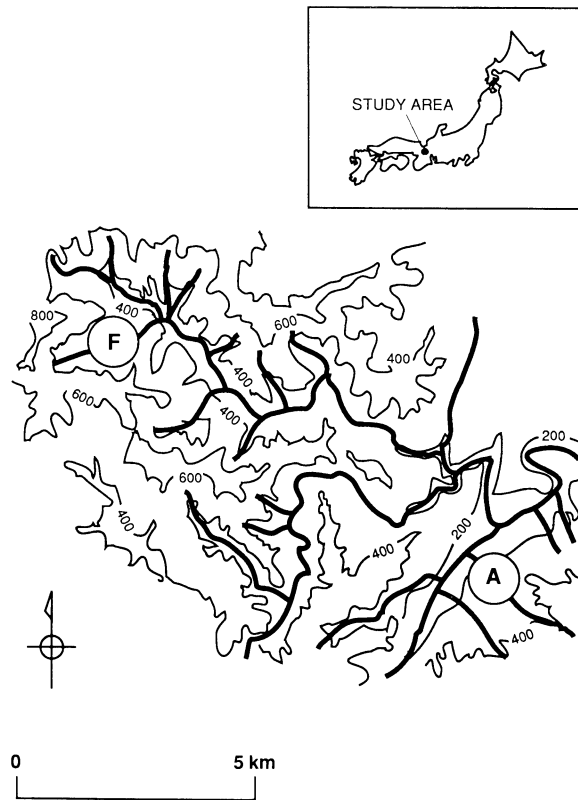
FIG. 1. Location of sites A and F in the northwestern part of Shiga Prefecture in central Japan. The thin lines show altitude in metres above sea level, the thick lines show rivers. The inset shows the location of the study area.

females from emergence to the reproductive season in the following year, and R_i = lifetime fecundity of females living to average age of ith cohort. For calculations of mean and variance of the lifetime fitness, it is convenient to express Eq. 1 using logarithms.

$$f_i = e_i + l_i + a_i + r_i. \qquad (2)$$

The variance is derived from the following equation (Feller 1957):

$$\begin{aligned}\text{Var}(f_i) = {} & \text{Var}(e_i) + \text{Var}(l_i) + \text{Var}(a_i) + \text{Var}(r_i) \\ & + 2[\text{Cov}(e_i, l_i) + \text{Cov}(e_i, a_i) + \text{Cov}(e_i, r_i) \\ & + \text{Cov}(l_i, a_i) + \text{Cov}(l_i, r_i) + \text{Cov}(a_i, r_i)],\end{aligned}$$
$$(3)$$

where $f_i = \log(F_i)$, $e_i = \log(E_i)$, $l_i = \log(L_i)$, $a_i = \log(A_i)$, $r_i = \log(R_i)$.

Population censuses

Each population was censused at 1–3 d intervals from early May to early November in each year, 1976–1980. 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. Adult beetles were individually marked with four small dots of lacquer

paint on their 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 beetles. I marked a total of 5969 beetles at site A and 3507 beetles at site F.

Estimation of egg survival

When found on a thistle leaf, the number of eggs in an egg batch was counted. To facilitate following the fate of individual eggs on subsequent censuses, each egg batch was marked by attaching a small numbered tag to the leaf. The number of eggs hatched was obtained by counting the empty egg shells that remained on the leaves after hatching. At the study sites, beetle eggs were subjected to three main sources of mortality: arthropod predation, egg cannibalism by adults and newly hatched larvae, and miscellaneous causes (Ohgushi 1986). Following egg predation by arthropods, a characteristic black spot remained on the leaf surface at the position where the egg was formerly attached. Cannibalized eggs were recognizable by the characteristic basal remains of egg shells. Hence, cannibalized eggs were easily distinguished from arthropod-predated eggs. However, as it was occasionally difficult to distinguish cannibalism by adults from cannibalism by larvae, both categories are included here under egg cannibalism. Egg death from miscellaneous causes, which was characterized by a blackened and shriveled egg shell, occurred principally in summer. Using these criteria I was able to obtain the exact number of egg deaths due to each source of mortality.

Estimation of larval survival

Since I did not follow the fate of individual larvae, I used the numbers of newly hatched larvae and newly emerged adults to estimate larval survival up to emergence as adults for each cohort. Mean egg and larval life-spans in the field were 11.4 ± 0.3 d (mean ± 1 SE, $n = 1884$) and 49.5 ± 1.2 d ($n = 80$), respectively. There were no significant differences in developmental periods of egg and larval stages between the two sites or among different years at each site. Hence, for simplicity of calculation, I used 10 and 50 d, as standardized egg and larval periods, respectively. I then calculated larval survival as the ratio of the number of newly emerged adults to that of newly hatched larvae for each cohort. Table 1 shows standardized dates of egg laying, egg hatching, and adult emergence for each cohort. The seasonal changes in numbers of eggs, larvae, and new adults are given in Ohgushi and Sawada (1981, 1984).

Estimation of adult survival

Female survival from adult emergence to the reproductive season in the following spring was estimated as the ratio of the number of newly emerged adult females to that of marked adult females of each cohort

TABLE 1. Standardized histories for nine cohorts of *Epilachna niponica* (dates of three significant life history events).

Cohort number	Egg laying	Egg hatching	Adult emergence
1	1–10 May	10–20 May	1–10 July
2	10–20 May	20–31 May	10–20 July
3	20–31 May	1–10 June	20–31 July
4	1–10 June	10–20 June	1–10 August
5	10–20 June	20–30 June	10–20 August
6	20–30 June	1–10 July	20–31 August
7	1–10 July	10–20 July	1–10 September
8	10–20 July	20–31 July	10–20 September
9	20–31 July	1–10 August	20–30 September

that were recaptured in the following spring. Over 98% of newly emerged adult beetles were marked in every year (Ohgushi 1983).

Estimation of lifetime fecundity

Lifetime fecundity of females for each cohort was determined from field estimates of the fecundity schedule and reproductive life-span in each year. Fecundity (number of eggs per female) during consecutive 5-d intervals was calculated as the ratio of the total eggs laid to the average number of female adults in each interval. Number of adult females was estimated from capture-recapture data using a stochastic model (Jolly 1965, Seber 1973). Reproductive life-span of individual females was estimated from the field capture-recapture data for adult beetles. I calculated reproductive life-span of each female as the duration of the period from 1 May to the final recapture date of that individual, although a slight underestimation was unavoidable.

The lifetime fecundity for each cohort in a given year was then calculated by the estimated fecundity and the average duration of reproductive life-span of adult females of each cohort, i.e., the lifetime fecundity was the number of eggs laid by a female living to the average age for each cohort. Since it was impossible to distinguish fecundity schedules among different cohorts in the field, I used the same fecundity schedule for every cohort in the following reproductive season each year. A laboratory experiment showed that fecundity schedules were mostly determined by the reproductive life-span of adult females, which did not differ significantly among cohorts in the field (T. Ohgushi, *personal observation*). Hence, in the calculation of lifetime fecundity, the assumption that every cohort had the same fecundity schedule in a given year is unlikely to bias lifetime fecundity significantly.

Laboratory experiment to detect oviposition schedule

The reproductive life-span and fecundity schedules of adult females from the field were compared under constant laboratory conditions. On 1 May 1987, 17 and 25 pairs of overwintered adults, which had just emerged from hibernation but not yet begun oviposition, were collected from sites A and F, respectively. Each pair was placed in a separate plastic cup (13 cm

in diameter and 6 cm in depth) with a plastic lid and was kept under constant conditions of 20°C and L:D 16:8 in an environmental chamber. Ample amounts of fresh thistle leaves were offered every 3 d throughout the experiment. For each pair the numbers and sizes of egg batches were recorded daily until the death of the female.
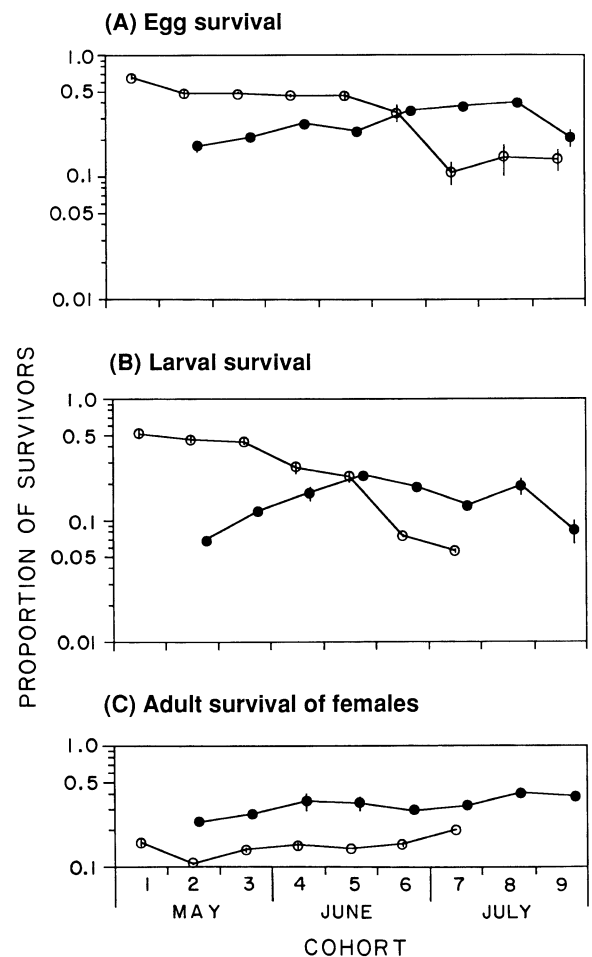

FIG. 2. Egg survival, larval survival, and adult female survival for each cohort at site A (O) and site F (●). Each point represents mean ± 1 SD^2 (n = 5 yr for 1976–1980). (A) Egg survival to hatching; (B) larval survival from egg hatching to adult emergence; (C) adult survival of females from emergence to the reproductive season in the following year.
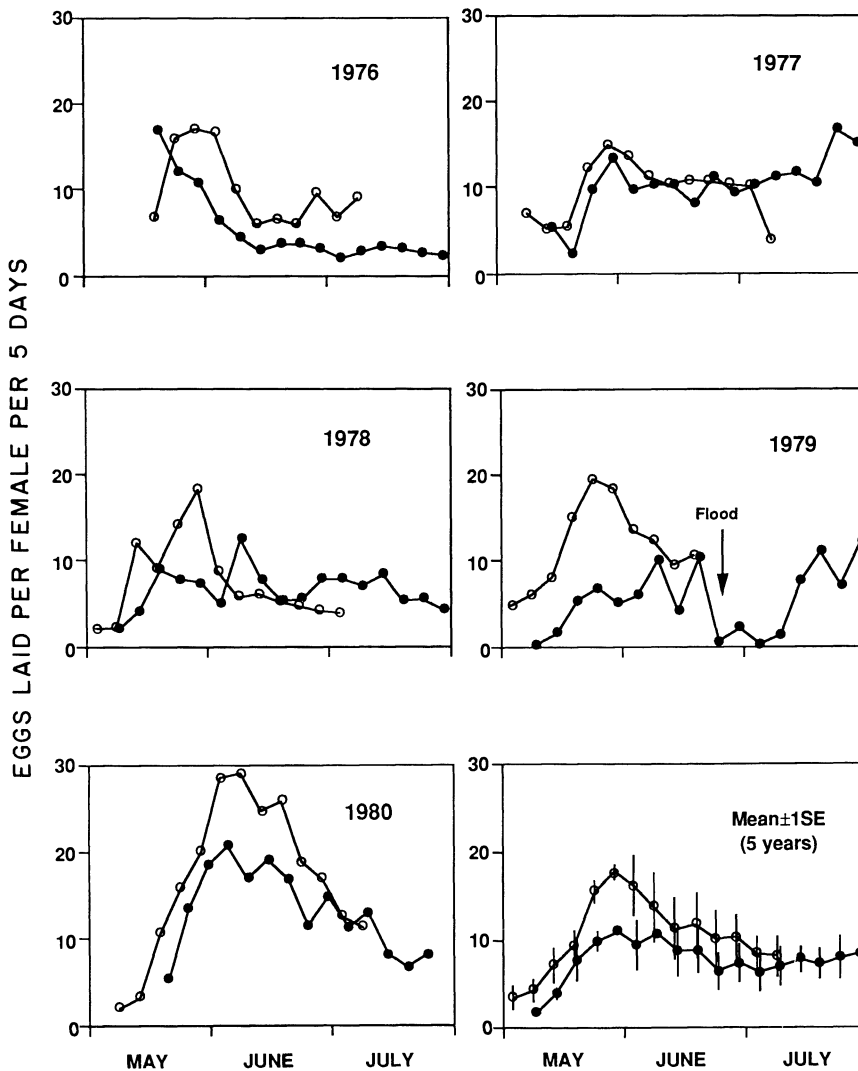
FIG. 3.   Seasonal changes in number of eggs laid per female in consecutive 5-d intervals in each year from 1976 to 1980 together with mean ($\pm$ 1 SE, $n = 5$ yr for 1976–1980) at site A (O) and site F (●). Vertical arrow shows the occurrence of a flood in 1979.

RESULTS

Variation in cohort lifetime fitness

Egg survival.—Egg survival (Fig. 2A) varied significantly among cohorts within a population (Kruskal-Wallis test; Site A: $H = 24.18$, $P < .01$; Site F: $H = 15.97$, $P < .05$), and different patterns of changes in egg survival were also evident among cohorts between the populations. At site A, egg survival decreased during the season, whereas at site F, later cohorts (except for the last one) had higher egg survival.

Larval survival.—Larval survival closely resembled egg survival throughout the reproductive season (Fig. 2B). There were significant differences among cohorts at site A (Kruskal-Wallis test: $H = 16.39$, $P < .02$) but not at site F ($H = 9.05$, NS). At site A, larval survival declined consistently throughout the season. At site F,

however, larval survival gradually increased to a peak with Cohort 5, then decreased.

Adult survival.—Survival of adult females from emergence to the reproductive season in the following spring was higher at site F than at site A for all cohorts (Fig. 2C). Adult survival tended to increase during the season at both sites, the there were no significant differences among cohorts within either population (Kruskal-Wallis test; Site A: $H = 8.78$, NS; Site F: $H = 2.91$, NS).

Fecundity schedule.—Fecundities at site A were higher than at site F in most years, especially in the early reproductive season (Fig. 3). Oviposition rate at site A increased from early May to reach a peak in late May, then declined consistently during the rest of the reproductive season. In contrast, at site F, the oviposition period was prolonged with a lower peak compared to
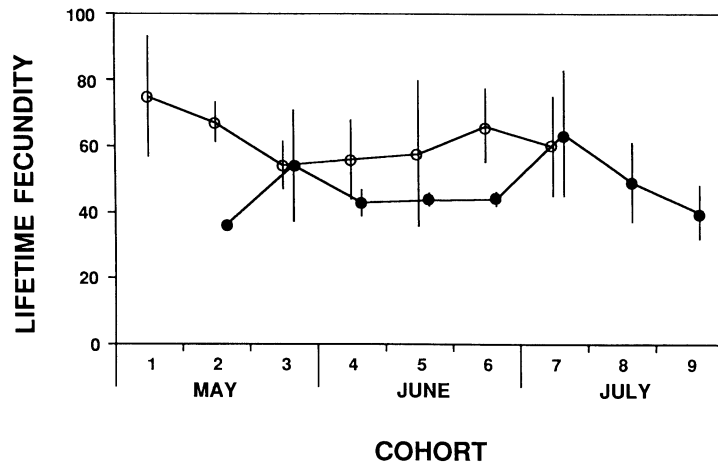
FIG. 4. Lifetime fecundity for each cohort at site A (O) and site F (●). Each point represents mean ± 1 SE ($n = 5$ yr for 1976–1980). Lifetime fecundities were calculated from field estimates of fecundity schedules (see Fig. 3) and average reproductive life-span of adult females for each cohort in each year.

site A. The exceptionally low fecundity for 15 consecutive days at site F in late June 1979 was likely due to the resorption of eggs in the ovaries of ovipositing females in response to severe host plant damage by a severe flood.

Lifetime fecundity.—Using the average duration of reproductive life-spans of adult females for each cohort and the fecundity schedules obtained above, I calculated means and variances of lifetime fecundity during the period 1976–1980 (Fig. 4). Adult females at site A had greater lifetime fecundity than those at site F for every cohort except Cohorts 3 and 7. Lifetime fecundity did not differ significantly among cohorts within a population (Kruskal-Wallis test; Site A: $H = 2.56$, NS; Site F: $H = 1.93$, NS).

Cohort lifetime fitness.—I calculated means and variances of cohort lifetime fitness at sites A and F by Eq. 2 and Eq. 3 (Fig. 5). The pattern of lifetime fitness differed between the two sites. At site A, early cohorts

had higher lifetime fitness than later ones. On the other hand, later cohorts at site F had higher lifetime fitness except for the last cohort (Cohort 9). Comparisons of all possible pairs of cohort lifetime fitnesses indicated that several pairs differed significantly (Table 2). At site A, early cohorts had a significantly higher lifetime fitness than late cohorts. On the other hand, Cohort 2 differed from all the others except for Cohort 9, and the last cohort had a significantly lower lifetime fitness than the middle cohorts (Cohorts 6 and 7).

Sources of among-cohort variation in lifetime fitness

Lifetime fitness varied widely from one cohort to another within a population at each site, and the pattern of changes differed between the two populations. The next problem is to determine which fitness components contributed most to the among-cohort variation in lifetime fitness at the two sites.

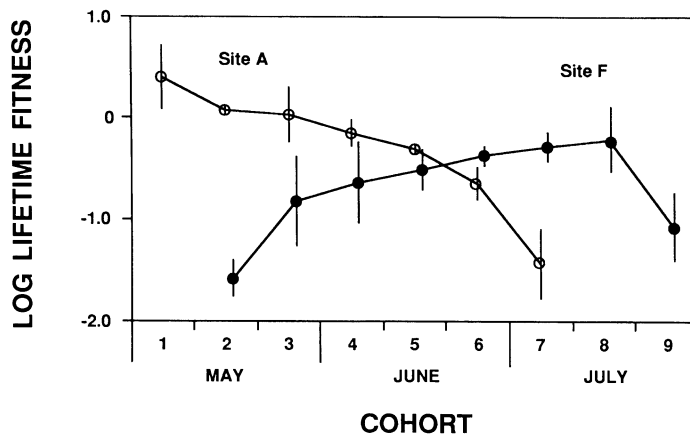Following Arnold and Wade (1984*a, b*), I used the

FIG. 5. Lifetime fitness for each cohort at site A (O) and site F (●). Each point represents mean ± 1 SD^2 ($n = 5$ yr for 1976–1980). Data are expressed as log-transformed fitness. Mean and SD^2 were calculated by Eqs. 2 and 3, respectively.

TABLE 2. Comparison of lifetime fitness of pairs of different cohorts of *Epilachna niponica*.

Site	Cohort	1	2	3	4	5	6	7	8
A	2	NS							
	3	NS	NS						
	4	NS	NS	NS					
	5	*	*	NS	NS				
	6	*	*	*	*	NS			
	7	*	*	*	*	*	NS		
F	3		*						
	4		*	NS					
	5		*	NS	NS				
	6		*	NS	NS	NS			
	7		*	NS	NS	NS	NS		
	8		*	NS	NS	NS	NS	NS	
	9	NS	NS	NS	NS	*	*	NS	

* = $P < .05$ for the Mann-Whitney U test; NS = not significant.

variance in fitness components divided by the square of the mean (standardized variance) as an estimate of the variability of fitness (Table 3). The overall variance in lifetime fitness was then partitioned according to its four components: egg survival, larval survival, survival of adult females to the reproductive age, and lifetime fecundity, using the method devised by Brown (see Brown 1988 for details) (Table 4). At site A, egg and larval survival accounted for 23.7 and 44.0% of the overall variance of lifetime fitness among cohorts, respectively, but only 5.3 and 2.0% of the overall variance were due to adult survival and lifetime fecundity, respectively. Similarly, at site F, egg and larval survival accounted for 29.2 and 40.5% of the overall variance of lifetime fitness, respectively, whereas only 4.8 and 4.5% of the overall variance were attributable to adult survival and lifetime fecundity, respectively. Thus, most of the variance in lifetime fitness among cohorts lay in egg and adult survival, implying that mortality factors operating during the egg and larval stages were the

principal determinants of the variations in cohort lifetime fitness.

Egg mortality. — The major cause of egg mortality varied considerably among seasons (Fig. 6). Predation gradually increased from early May to reach a peak in mid-June, and then declined throughout the rest of the season. Nymphs of an earwig, *Anechura harmandi* Burr, were the most numerous arthropod predators of eggs at the sites, and they were most abundant in early June (see Fig. 7), when maximum egg predation occurred. The higher egg predation at site F was associated with the higher densities of earwigs at that site (see Fig. 7). The miscellaneous causes of egg death were of little importance in the early reproductive season, but became the dominant mortality source in July at both sites, although peak mortality was delayed at site F. The earlier peak of this mortality at the downstream site A may have been associated with the slightly higher ambient temperatures at that site. Egg hatching declines drastically at high temperature ($>27°C$) in the

TABLE 3. Mean and variance of the components of lifetime fitness of *Epilachna niponica*.

Component*	Site A†			Site F†		
	Mean	Variance	Standardized variance‡	Mean	Variance	Standardized variance‡
E	0.402	0.035	0.217	0.260	0.010	0.148
L	0.273	0.030	0.403	0.121	0.003	0.205
A	0.144	0.001	0.048	0.287	0.002	0.024
R	58.729	62.116	0.018	44.388	45.067	0.023
EL	0.133	0.012	0.678	0.034	0.001	0.376
EA	0.054	0.001	0.343	0.077	0.001	0.169
LA	0.036	0.001	0.312	0.035	0.000	0.229
ER	24.005	165.621	0.287	11.973	35.192	0.245
LR	16.539	139.239	0.509	5.470	6.908	0.231
AR	8.416	3.470	0.049	12.787	8.928	0.055
ELA	0.017	0.000	0.725	0.010	0.000	0.458
ELR	8.190	58.397	0.871	1.575	1.047	0.422
EAR	3.219	2.844	0.274	3.533	4.174	0.334
LAR	2.163	2.012	0.430	1.572	0.639	0.259
ELAR	1.059	1.026	0.915	0.464	0.109	0.506

* E = egg survival; L = larval survival; A = survival of adult females to the reproductive season in the following year; R = lifetime fecundity.

† Site A: $n = 7$ cohorts; Site F: $n = 8$ cohorts.
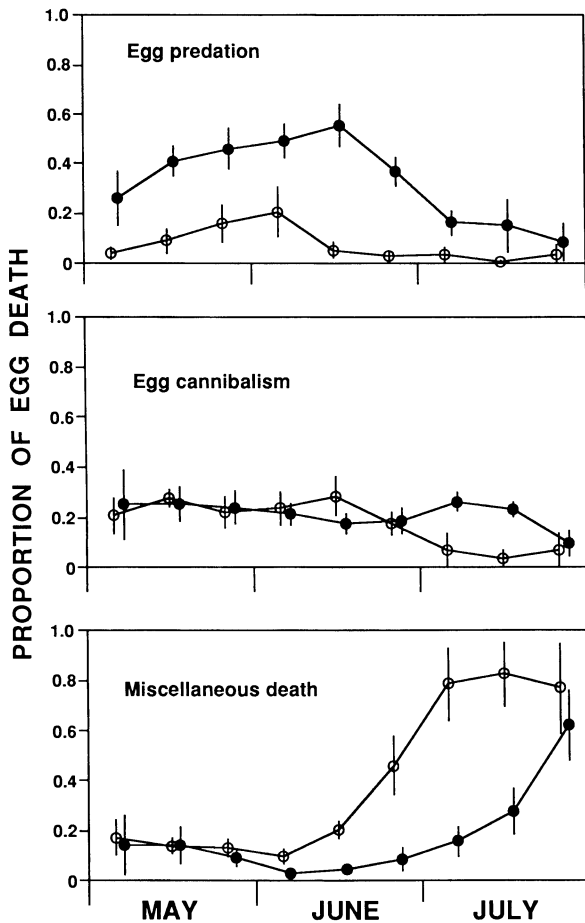
‡ Variance divided by (mean)².

FIG. 6. Seasonal changes in egg mortality from three different sources during 1976–1980, at site A (O) and site F (●). Each point represents mean ± 1 SE (n = 5 yr for 1976–1980). Newly oviposited eggs take 1–2 wk to hatch.

laboratory (T. Ohgushi, *personal observation*). Egg cannibalism was relatively constant throughout the reproductive season. Cannibalism by adult beetles was dominant early in the season, while most cases of egg cannibalism later in the season were attributable to newly hatched larvae feeding on unhatched eggs in their own egg batches.

Larval mortality.—Arthropod predation, especially by earwig nymphs, was the principal cause of larval mortality, particularly in young larvae (Ohgushi and Sawada 1985b, Ohgushi 1986). Earwig nymphs were found only from late May to late June (Fig. 7), which suggests that larvae hatching after June were mostly free from earwig predation. Larvae at site A suffered relatively less from predation compared to those at site F.

Food shortage caused by defoliation of host plants due to feeding by beetles was another possible cause of larval mortality, especially after late June. Larval mortality was an increasing function of leaf damage of thistle plants, even when host plant injury remained

TABLE 4. Percentage contribution of the fitness components to overall variation in lifetime fitness (ELAR).

Site	Com-ponent*	E	L	A	R
A	E	23.67			
	L	6.48	44.00		
	A	8.54	−15.20	5.27	
	R	5.77	9.67	−1.88	1.97
	3+	11.71			
F	E	29.22			
	L	4.64	40.47		
	A	−0.70	0.01	4.80	
	R	14.75	0.61	1.47	4.52
	3+	0.22			

* E = egg survival; L = larval survival; A = survival of adult females to the reproductive season in the following year; R = lifetime fecundity. 3+ = three-way and higher order interactions.

at low levels (Ohgushi 1983). Visual estimates of percentage leaf damage of thistle plants are shown in Table 5. The leaf damage by beetle feeding was greater at site A than at site F in every year. The lower degree of leaf herbivory seen at site F probably reflected the lower larval density there resulting from higher predation pressure. The density of fourth-instar larvae at site F (1.6 ± 0.3 individuals per thistle shoot; mean ± 1 SE, n = 5 yr) was significantly lower than that at site A (7.5 ± 1.4 larvae per shoot) during the study period (Mann-Whitney U test: U = 25, P < .01). Apart from the quantitative aspect of leaf damage, host plant quality, assessed by amino acid and leaf water content, declined during the growing season (Ohgushi 1986). Therefore, the food stress in terms of quantity and quality was likely to reduce larval survival of later cohorts at both sites.

Reproductive pattern in the field

If oviposition phenology is heritable, the between-population differences in cohort lifetime fitness imply that early reproduction should be favored in population A, whereas delayed or prolonged reproduction should be favored in population F (see Fig. 5).

Oviposition patterns of the lady beetle in the field were consistent with this prediction. The duration of oviposition at site A was significantly shorter than at site F (Kolmogorov-Smirnov test: P < .001 for every

TABLE 5. Visual estimates of percentage of leaf damage on thistle plants due to beetle feeding in early July during 1976–1980.

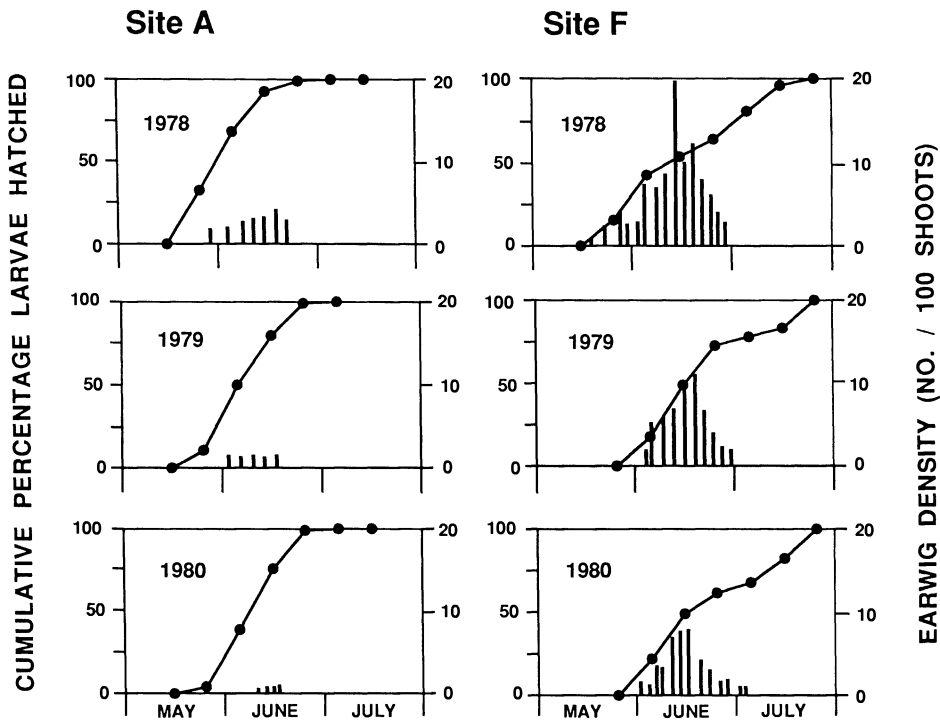|	Leaf damage (%)			
	Site A		Site F	
Year	No. plants	Mean ± 1 SE	No. plants	Mean ± 1 SE
1976	14	28.6 ± 3.6	76	16.9 ± 3.0
1977	23	32.6 ± 5.1	69	22.5 ± 2.8
1978	23	47.4 ± 4.7	67	21.9 ± 2.2
1979	27	47.5 ± 4.5	66	16.1 ± 1.7
1980	35	54.6 ± 2.7	53	15.5 ± 1.8

Site A   Site F

FIG. 7. Seasonal changes in density of an earwig egg predator (vertical bars), and cumulative percentages of numbers of newly hatched larvae (O), for 1978–1980 at sites A and F.

year) (Fig. 8). At site A females usually began oviposition in early May and continued until mid-July, whereas at the upstream site F, females continued to lay eggs up to late August. Female longevity in the reproductive season at site F was significantly longer than at site A (ANOVA: $F = 33.94$, $P < .001$; Table 6) and the prolonged oviposition at site F is more likely explained in terms of this difference.

Reproductive pattern in laboratory

The two survivorship curves of reproductive females from sites A and F differed markedly (Fig. 9). Female longevity at site A was significantly shorter than that at site F (Mann-Whitney U test: $Z = 3.063$, $P < .001$). No adults from site A survived >90 d, but 60% of females from site F were still alive after 90 d (maximum life-span was 188 d after the beginning of the experiment). This result was consistent with the field observation that adult females at site F had a significantly longer reproductive life-span than those at site A.

The fecundity schedules of collected females reared under the same conditions are shown in Fig. 10. There was a significant difference in the distribution of egg laying of females from sites A and F (Kolmogorov-Smirnov test: $D = 0.564$, $P < .01$). The oviposition rate of females from sites A declined slightly for 60 d, then decreased sharply in the remaining 15 d. The oviposition by females from site F began to decline after 20 d, but they continued to oviposit until ≈ 180 d; the oviposition rate gradually decreased over their reproductive lives. Furthermore, during the first 60 d, the oviposition rate at site A was higher than that at site F, which was consistent with field observations (see Fig. 3). This laboratory experiment confirmed that early reproduction at site A and delayed and prolonged reproduction at site F occurred even when environmental differences were eliminated. It is likely that the oviposition schedule of this lady beetle is determined genetically.

DISCUSSION

Variation in cohort lifetime fitness

The present study clearly demonstrates the temporal variation and its principal cause in cohort lifetime fitness of E. niponica. First, lifetime fitness varied markedly from one cohort to another within a population. Second, there were different patterns of cohort lifetime

TABLE 6. Reproductive life-span (in days) of female Epilachna niponica beetles.

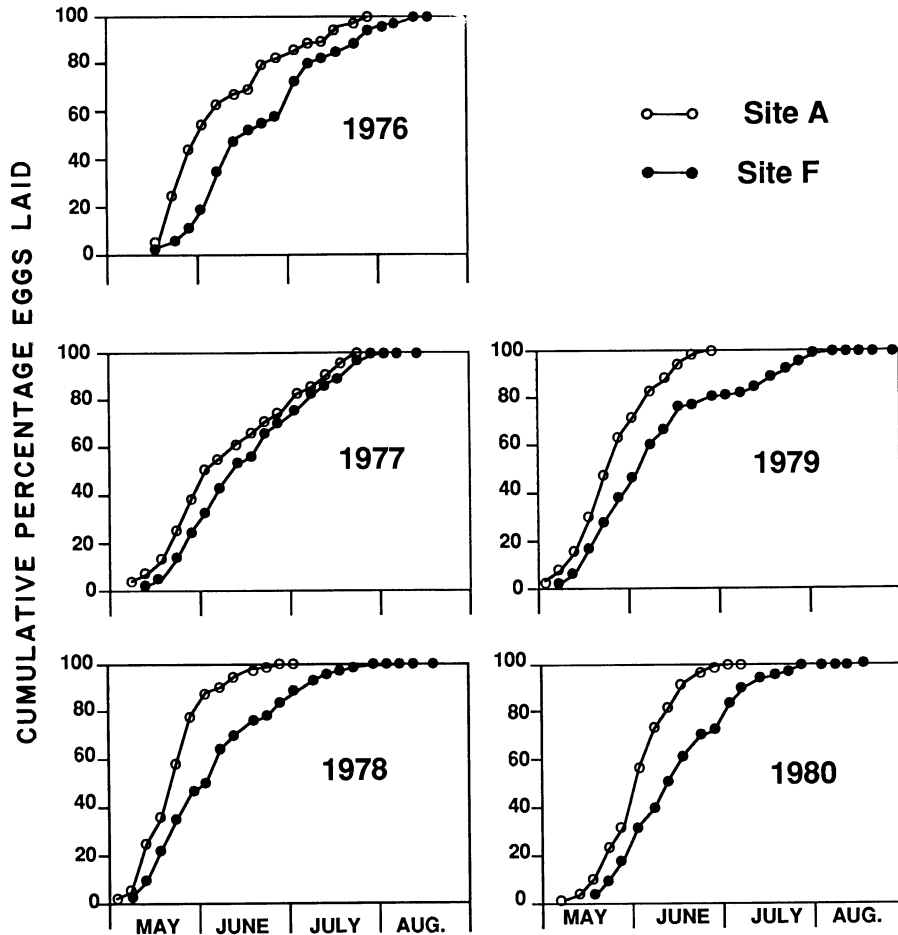| Year | Site A | | Site F | |
	n	Mean ± 1 SE	n	Mean ± 1 SE
1976	42	45.7 ± 3.3	152	54.0 ± 2.7
1977	86	42.8 ± 3.1	215	54.0 ± 2.3
1978	163	29.9 ± 1.5	376	40.5 ± 1.5
1979	57	33.0 ± 2.3	364	38.5 ± 1.4
1980	114	38.1 ± 1.4	52	60.7 ± 5.0

FIG. 8. Cumulative percentages of number of eggs laid in each year from 1976 to 1980 at site A (O) and site F (●).

fitness between the two populations. Third, the major fitness components responsible for these different patterns at the two sites were specific seasonal changes in mortalities from the egg to adult emergence.

The main factor responsible for both among-cohort and between-population variation in lifetime fitness was the intensity of time-specific arthropod predation, which acted early in the reproductive season. In comparison with that at site A, which had little predation pressure, the heavy arthropod predation at site F resulted in greatly reduced egg and larval survival in early cohorts up to mid-June (see Figs. 6 and 7). Recent detailed population studies on other herbivorous insects have revealed the effects of such seasonal variability ("temporal window") of arthropod predators or parasitoids on the population dynamics of the prey or host (e.g., Münster-Swendsen 1980, Myers 1981, Clancy and Price 1986, Jones et al. 1987). Besides arthropod predation, there were two seasonally specific factors affecting egg and larval survival in later cohorts: heat stress at the egg stage and host deterioration at the larval stage. Egg deaths due to heat stress became im-
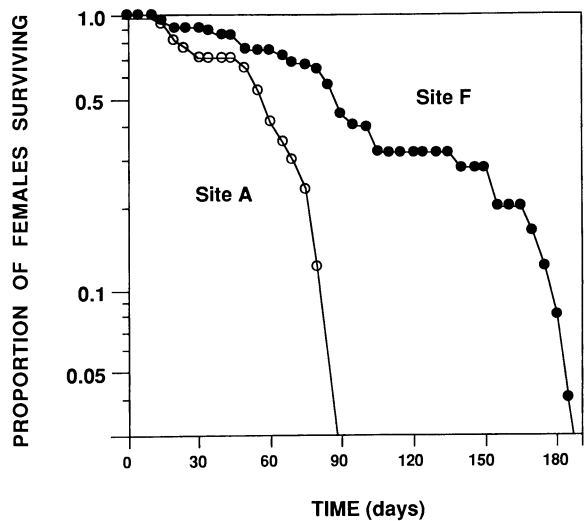

FIG. 9. Survivorship curves of adult females collected from site A (O) and site F (●) on 1 May 1987. Adult beetles were kept under constant conditions of 20°C and L:D 16:8 in an environmental chamber, and supplied with fresh thistle leaves.
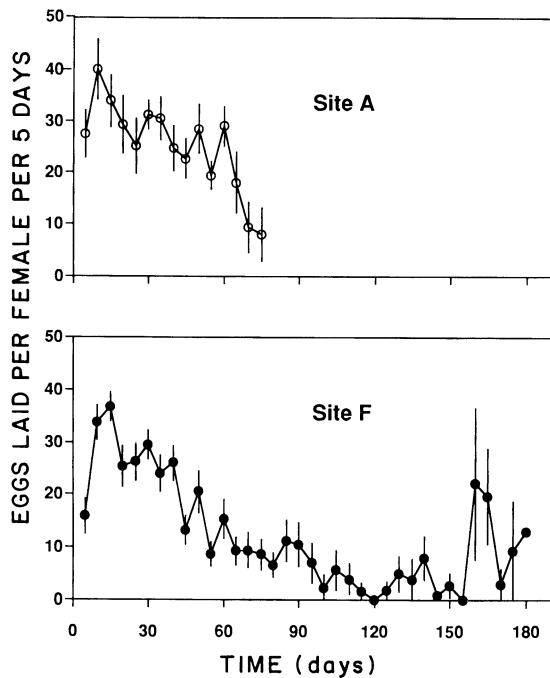
FIG. 10. Temporal changes in the number of eggs laid per female in consecutive 5-d intervals for females collected from site A (O) and site F (●) on 1 May 1987. Adult beetles were kept under constant conditions of 20°C and L:D 16:8 and supplied with fresh thistle leaves every 3 d in an environmental chamber. Each point represents mean ± 1 SE (n = number of females surviving at each interval). Day 0 was 1 May 1987.

portant in summer (see Fig. 6); this was more apparent at the downstream site A, probably due to the higher ambient temperatures there (Ohgushi and Sawada 1984). Leaf quality of thistle plants measured by water and amino acid contents consistently declined with the growing season, and beetle feeding accelerated qualitative deterioration of thistle leaves (Ohgushi 1986). Reduced water and amino acid contents in leaves of host plants cause reductions in larval performance in many herbivorous insects (see Scriber and Slansky 1981 for a review). Also, larval survival of the lady beetle decreased with leaf damage on thistle plants where the larvae developed (T. Ohgushi, *personal observation*). Although possible effects of host deterioration on larval performance were not evaluated quantitatively, the evidence that site A, associated with higher leaf damage, showed significantly lower larval survival in later cohorts than did site F (see Fig. 2), suggests detrimental effects of reduced leaf quality and quantity. Hence, it is more likely that the gradual deterioration in the quality and quantity of host condition reduces larval survival in later cohorts. Consequently, the combined effects of these factors, which operate on egg and larval stages in a different manner between the two populations, determine the respective patterns of cohort lifetime fitness in each population.

Correlation of reproductive pattern with offspring lifetime fitness

Since natural selection favors individuals with higher fitness, the different life history strategies for timing of reproduction in the two local populations of the lady beetle can be explained by selection for early reproduction in population A and delayed reproduction in population F (see Fig. 5). Field observations on oviposition pattern during the study period were consistent with this evolutionary prediction: a marked predominance of early oviposition at site A and delayed oviposition at site F. These oviposition patterns were mainly due to differences in the reproductive life-span of females. An experimental study that eliminated environmental factors during the reproductive season strongly supported the field data showing different oviposition schedules. This implies that there is some genetic base for female longevity. The lady beetle has limited dispersal power and individuals move a maximum of only 120 m during their lifetime (Ohgushi 1983), which suggests little or no gene flow between the two study populations. Recent laboratory experiments on artificial selection on reproduction of *Drosophila* have shown that female longevity is genetically determined and can be modified by selection (Rose and Charlesworth 1981, Luckinbill et al. 1984), and heritable aspects of phenology have also been suggested in other herbivorous insects (e.g., Morris and Fulton 1970, Holliday 1985, Clancy and Price 1986). One could argue, however, that environmental influences operating on immature or prereproductive adult stages may have a marked effect on reproductive attributes of females in the following year. One possible effect could derive from host deterioration depending on larval density, which produces smaller adults (Ohgushi 1987). However, the body size of adult females showed no correlation with lifetime fecundity or reproductive life-span (T. Ohgushi, *personal observation*). Hence, it is unlikely that environmental influences determining body size generate the between-population difference in oviposition schedules.

The adaptive nature of the oviposition schedules in this lady beetle has also been suggested in an introduced population of *E. niponica*. Sawada (1984) studied a population of this species that had been artificially introduced into the botanical garden of Kyoto University in 1971. Since 1974 the introduced population has reached such a high density that thistle plants are extensively defoliated by early summer due to beetle feeding. Thus later cohorts of larvae have been subjected to severe food shortage in this new habitat. In the original habitat, heavy predation pressure early in the reproductive season held the population in check and prevented such food depletion (Nakamura and Ohgushi 1981). The difference in temporal patterns of lifetime fitness between the introduced and the original populations is thus similar to the respective differences

in patterns at sites A and F of this study. Ten years after the introduction, Sawada (1984) compared oviposition schedules of the original and the introduced populations under controlled rearing conditions, and found that females in the introduced population had a shorter reproductive life-span and a higher oviposition rate than the original population. This modification of oviposition schedule toward early reproduction in the introduced population supports a genetic basis for the oviposition schedule of the lady beetle.

CONCLUSIONS

An integrated picture of three-trophic-level interactions is of crucial importance for understanding population biology in herbivorous insects (Price et al. 1980). The present study emphasizes that seasonal variability of natural enemies and host plants are both important selective forces for life history patterns of herbivorous insects (Denno and Dingle 1981, Denno and McClure 1983). It should also be noted that life table statistics for different categories of individuals throughout their lifetimes, and a marking technique for individuals, both of which were used in this study, provide powerful tools for estimating lifetime fitness and clarifying differences in lifetime fitness among phenotypic classes within a population. This approach also highlights the demographic consequences of temporal and spatial heterogeneity in mortality and fecundity within a generation (Hassell and May 1985, Hassell 1986) and those of individual differences within a population (Łomnicki 1988), features that have long been ignored in traditional population ecology (Hassell and May 1985, Smith and Sibly 1985).

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