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A reproductive tradeoff in an herbivorous lady beetle: egg resorption and female survival

Abstract A reproductive tradeoff between current egg production and subsequent survival in a lady beetle, *Epilachna niponica*, a specialist herbivore on a thistle, *Cirsium kagamontanum*, was investigated at the two study sites, A and F. Survival of reproductive females decreased consistently from early May until mid-June, but apparently increased thereafter. In contrast, males showed a consistent decrease in survival throughout the reproductive season, without any sign of recovery. Dissection of ovaries of sampled females revealed that egg resorption increased late in the reproductive season, coincident with increased female survival. Reproductive females stopped oviposition immediately after a large flood in 1979 at site F. Two weeks after the habitat perturbation, females resumed oviposition in response to a flush of new leaves on damaged plants. Female survival sharply increased during the non-oviposition period, and declined when egg-laying resumed. Approximately 40% of long-lived reproductive females at site F survived up to the following reproductive season in the next year. Also, some of these long-lived females were observed ovipositing in the following reproductive season. The long-lived reproductive females which had previously invested in reproduction survived equally well as newly emerged females which had not reproduced in summer. These results suggest that there is a reproductive tradeoff between current egg production and subsequent survival. Egg resorption may be an adaptive ovipositional response to habitat perturbation such as flooding, which considerably reduces offspring fitness due to absolute shortage of food. Also, increased female survival accompanied by egg resorption enhances the likelihood of the future oviposition in the second reproductive season, thereby increasing a female's lifetime reproductive success.

Key words Adult survival · Cost of reproduction · Egg resorption · *Epilachna niponica* · Lifetime reproductive success

Introduction

The cost of reproduction and hence tradeoffs between reproductive effort and maintenance or growth have been a central issue in theories of life-history evolution (Calow 1979; Bell and Koufopanou 1986; Partridge 1989; Stearns 1989; Roff 1992). Since resources within an individual are competitively allocated among growth, maintenance, and reproduction, if resources are limited, an increase in the allocation to one function necessarily results in a decrease to other functions. Thus, different life-history patterns can evolve as a consequence of reproductive tradeoffs (Partridge and Harvey 1985).

There is much evidence of reproductive tradeoffs in phenotypic and genotype manipulation experiments in the laboratory (Bell and Koufopanou 1986; Partridge 1989; Stearns 1989; Roff 1992). However, laboratory experiments may underestimate costs of reproduction because they exclude many important factors occurring under field conditions. Also, little attention has been paid to understanding the ecological significance of reproductive tradeoffs in variable environments (Partridge and Harvey 1985; Boggs 1992). Hence, an adequate test of the importance of reproductive tradeoffs requires experiments under field conditions (Partridge and Harvey 1985). On the other hand, relevant field evidence that suggests that there are costs of reproduction is largely dependent on phenotypic correlation between reproductive effort and survival or growth. However, correlation studies have a weakness

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in that they do not prove causality (Reznick 1985; Bell and Koufopanou 1986; Roff 1992), and even when costs of reproduction are observed to exist, these studies tell us little about the mechanisms generating negative effects of reproduction on other functions that potentially compete for resources (Reznick 1985, 1992; Roff 1992; Bell and Koufopanou 1986). Thus, we need to know the physiological and/or ecological mechanisms underlying these reproductive tradeoffs. To do this, one must evaluate costs of reproduction: for example, by directly preventing an organism from expending its resource investment in reproduction and monitoring subsequent adult survival.

In this context, a useful system in which the underlying physiological mechanisms responsible for tradeoffs between reproduction and survival can be studied is egg resorption in insects. Egg resorption is a specific reproductive trait in which oocytes degenerate instead of being laid as eggs, characterized by the cessation of yolk deposition. Egg resorption is widespread across various taxa of insects (Bell and Bohm 1975). Among ecological, behavioral, and physiological factors, resource stress (starvation) is a major cause of egg resorption (Bell and Bohm 1975). For example, when females are resource stressed, oocyte resorption occurs in herbivorous lady beetles (Kurihara 1975) and butterflies (Dunlap-Pianka et al. 1977; Boggs and Ross 1993). Egg resorption means the cessation of current investment in reproduction and thus reallocation of resources to other functions of maintenance, by alternating energy expenditure on reproduction and survival. Hence, if physiological costs of reproduction exist, reproductive tradeoffs may be detected by monitoring subsequent survival of adult insects following egg resorption.

I studied two local populations of a univoltine herbivorous lady beetle, *Epilachna niponica*, which feeds exclusively on leaves of a thistle, *Cirsium kagamontanum*, in the northwestern part of Shiga Prefecture, central Japan (Ohgushi and Sawada 1981). In field experiments using caged thistle plants, Ohgushi and Sawada (1985) demonstrated that reproductive females resorbed eggs in response to increased leaf damage to host plants, this occurring at 50% consumption of a total leaf area, and that the process of resorption was reversible. Resorption ceased immediately and the ovaries again became productive when fresh thistle leaves were provided. If the physiological costs of egg production reduce resource investment in maintenance, subsequent female survival might be expected to improve following egg resorption. The underlying model here is a contrast between resource allocation patterns of individual females before and after egg resorption. Before egg resorption, resource intake is invested in both reproduction and survival, but only survival after egg resorption. The question is whether survival after egg resorption is greater than survival before egg resorption. However, higher survival after

egg resorption does not necessarily indicate a reproductive tradeoff if the intake of food before egg resorption is less than after egg resorption, because increased survival after egg resorption may be a reflection of this increased intake. This is probably not the case in *E. niponica*. Its intake of resources after resorption of its eggs is more likely to be smaller than that before egg resorption, because resource availability consistently declines over with the season, due to deteriorating leaf quality and quantity of thistle plants (Ohgushi 1986). The main focus of this study is on the tradeoff between egg resorption and subsequent survival of adult females of *E. niponica*, and on the possible adaptive and ecological consequences of egg resorption.

Material and methods

Study site and organisms

The study was performed over a 5-year period (1976–1980) at two sites located in different valleys along the River Ado, in the northwestern part of Shiga Prefecture in central Japan. 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. Most of the surviving ground flora was composed of annual and perennial herbs, such as *Polygonum thunbergii*, *P. cuspidatum* and *Rumex crispus*. Site F (90 × 15 m) was situated at 350 m elevation, about 10 km upstream of site A. The more hardened soil deposits at this site meant that most grasses and shrubs present can successfully escape from serious flood-induced damage, except during large-scale flooding. Vegetation in and around the site included various deciduous broad-leaved trees, such as *Quercus mongolica* and *Q. salicina* and coniferous species such as *Cephalotaxus harringtonia*.

In the study area, both adults and larvae of *E. niponica* feed exclusively on leaves of a thistle, *Cirsium kagamontanum*. It has a single generation a year. Overwintering adult females begin to lay eggs in clusters on the undersurface of thistle leaves in early May. Oviposition often continues to early August. 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 and Sawada 1981). 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; they flower over 2 months, beginning in mid-August. Old leaves wither after August (Ohgushi 1986). Annual changes in population size of the thistle plant are given in Ohgushi and Sawada (1985).

Population census

I censused each population at 1 to 3 day intervals from early May to early November in each year from 1976 to 1980. All thistle plants growing in the study sites were carefully examined at each census; the numbers of eggs, fourth-instar larvae, pupae, pupal exuviae and adult beetles being recorded separately for each plant. The number of eggs in each egg batch was counted. To trace the fate of individual eggs on subsequent censuses, each egg batch was marked by attaching a small numbered tag to the leaf.

Estimation of adult survival

In each year, I conducted mark-recapture experiments for adult beetles to estimate adult survival rates. Adult beetles were individ-

ually marked with four small dots of lacquer paint on their elytra. Newly-marked adults were released immediately onto the thistle plant on which they had been captured. Sex and subsequent capture history (date and place) were recorded for individual beetles. A total of 5969 and 3507 beetles were marked at sites A and F, respectively. The survival rate of adult beetles for each 10-day period and 95% confidence limits were estimated by the Jolly-Seber stochastic model based on the mark and recapture data (Jolly 1965; Seber 1973). In each spring, over 98% of overwintered adults that emerged from hibernation were marked 1 week after the census commenced. Also, recapture rate on each census date (the number of marked adults that were recaptured divided by the estimated number of adults) was more than 0.85 throughout the reproductive season. Because of the exceptionally high marking and recapture ratios, the estimated survival rates were highly reliable. However, to avoid under- or over-estimation due to small sample size, survival rates estimated based on fewer than 10 individuals were excluded from the analysis. In general, *E. niponica* has little dispersal power; the averaged distance that it moved was less than 10 m over an individual's reproductive life (Ohgushi 1983). Although reproductive females often moved from one plant to another in early June, the inter-plant movement decreased with the season (Ohgushi and Sawada 1985). Thus, it is likely that emigrants from the study sites had little effect on the estimates of survival rate, especially late in the reproductive season.

Detection of egg resorption

To determine when egg resorption occurred throughout the reproductive season, I collected females five times during the reproductive season at both sites in 1978. Their ovaries were dissected to determine whether they had resorbed oocytes in ovarioles, employing the method described in Kurihara (1975).

Results

Seasonal changes in egg resorption and adult survival

Mean survival rates of reproductive adults for 1976–1980 exhibited specific changes in terms of sex and season (Fig. 1). Female survival rates consistently decreased until late June at site A (Kendall's rank correlation: $n = 6, \tau = -0.733, P = 0.0388$) and to mid-June at site F ($n = 5, \tau = -0.800, P = 0.0500$). However, subsequent survival rates increased during the remainder of the summer at both sites (site A: $n = 4, \tau = 1.000, P = 0.0415$; site F: $n = 7, \tau = 0.619, P = 0.0509$). In contrast, a decreasing tendency of male survival rates was observed late in the reproductive season (site A: $n = 4, \tau = -1.000, P = 0.0415$; site F: $n = 7, \tau = -0.714, P = 0.0243$). This different pattern of changes in adult survival between the two sexes before and after mid-June indicates that there was a similar probability of survivorship both in males and females early in the reproductive season but sex-dependent survival appeared as the season advanced.

Seasonal changes in ovarian status showed a similar pattern at the two sites (Fig. 2). Reproductive females had ovaries with developed eggs in ovarioles until late May. On the other hand, egg resorption was detected after mid-June. Also, several females had ovaries with no developed oocytes late in the season. There was no difference between female and male sur-
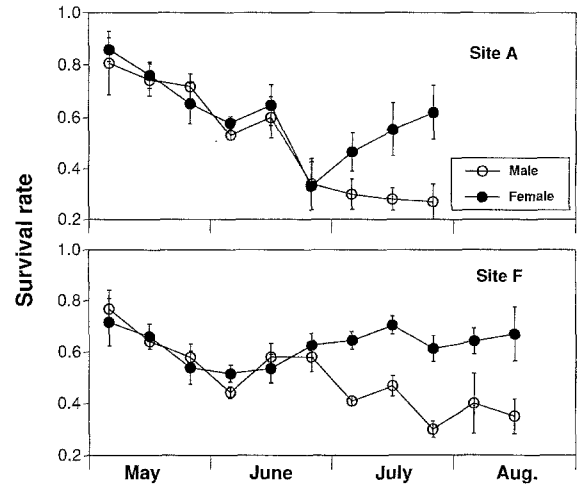

Fig. 1 Seasonal changes in survival rates of reproductive adults per 10 days at sites A and F. Mean survival rates and 1 SE for the 5 years from 1976 to 1980 are presented. Adult survival for each 10-day period was calculated by the Jolly-Seber stochastic model based on the mark-recapture data
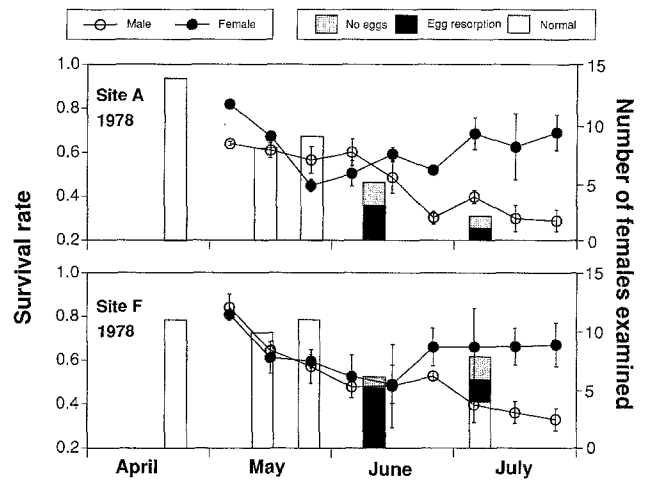

Fig. 2 Seasonal changes in ovarian status of reproductive females (*columns*) and survival rates of reproductive adults per 10 days (*circles*) at sites A and F in 1978. Ovarian status was classified into three categories: normally matured ovary with developed eggs, egg resorption, and ovary without developed eggs. Estimated survival rates and 95% confidence limits are presented. Mean survival rates and 95% confidence limits for each 10-day period were calculated by the Jolly-Seber stochastic model based on the mark-recapture data

vivals until mid-June, both decreasing with the season. Thereafter, female survival rates increased (site A: $n = 5, \tau = 0.600, P = 0.1416$; site F: $n = 5, \tau = 1.000, P = 0.0143$), but there was no sign of increase in male survival rates (site A: $n = 5, \tau = -0.800, P = 0.0500$; site F: $n = 5, \tau = -0.800, P = 0.0500$). As a result, females had significantly higher survival rates than males after late June at both sites (Mann-Whitney U-test; Site A: $U = 16, P = 0.0209$; site F: $U = 16, P = 0.0209$). Note that the apparent recovery of female survival exactly coincided with an increase in egg resorption and ovaries without eggs late in the repro-
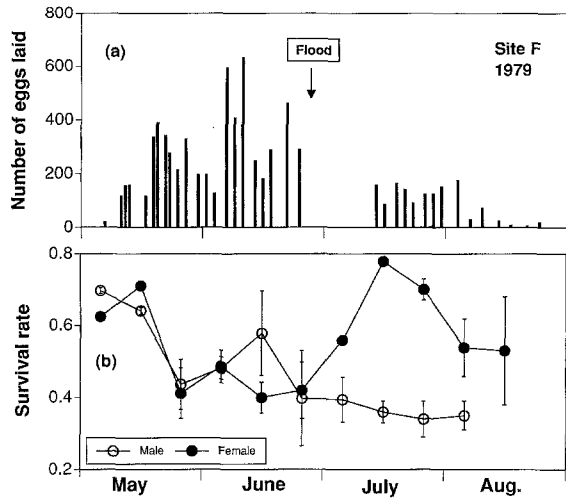
Fig. 3 a Number of eggs laid on each census date at site F in 1979. Note that females stopped laying eggs for a 2-week period following a large-scale flood (indicated by a *vertical arrow*). **b** Seasonal changes in survival rates of reproductive adults per 10 days at site F in 1979. Estimated survival rates and 95% confidence limits are presented. Mean survival rates and 95% confidence limits for each 10-day period were calculated by the Jolly-Seber stochastic model based on the mark-recapture data

ductive season. This suggests that there was a reproductive tradeoff between current egg production and subsequent survival of females.

Egg resorption following habitat perturbation by a flood

In late June 1979, there was a large-scale flood at site F. As a result, some thistle plants were washed away and others were buried under soil. Following this habitat disturbance, even though females continuously remained on thistle plants that had escaped from the flood-induced damage within the study site, they stopped laying eggs for 2 weeks (Fig. 3a). When the damaged thistle plants recovered and reflushed new leaves in mid-July, the females resumed oviposition. Reproductive females reared in the laboratory with ample amounts of fresh leaves usually deposit an egg batch every other day. Moreover, Ohgushi and Sawada (1985) experimentally demonstrated that when adequate food was available, egg resorption immediately ceased and the ovaries again became productive. Thus, it is more likely that most of the females resorbed their eggs following flooding.

Interestingly, female survival changed in exact accordance with occurrences of oviposition after the flooding. When females stopped laying eggs, their survival rates appeared to increase immediately up to mid-July ($n = 4$, $\tau = 1.000$, $P = 0.0415$) (Fig. 3b). Then, female survival rates declined again after oviposition was resumed in mid-July ($n = 4$, $\tau = -1.000$, $P = 0.0415$). However, this apparent response of survival did not occur in males; male survival rates still decreased continuously over the season, independent of egg-laying ($n = 5$, $\tau = -0.800$, $P = 0.0500$). Thus, survival rate of females was significantly higher than that of males after the flooding disturbance (Mann-Whitney U-test; $U = 20$, $P = 0.0143$). This strongly supports the implication that the resources saved by not producing eggs were used to improve the subsequent survival of females.

Survival to the second reproductive season

Nakamura and Ohgushi (1979) found that some of the long-lived reproductive adults in *E. niponica* overwintered and survived until the next spring. Let us consider, then, the possibility of surviving to the next reproductive season in adults that were alive at the end of the reproductive season, i.e., mid-August (Table 1). At site A, only a few adults remained in mid-August and none of them survived to the next reproductive season. This is not surprising because most of the adult beetles died by mid-July at this study site (Ohgushi and Sawada 1981). On the other hand, at site F, over the course of this study a total of 56 reproductive females were alive at mid-August, and nearly 40% of those females survived up to the next spring. The fact that only 7.1% of reproductive females survived to the spring in 1980 was due to heavy floods in the previous autumn, which caused unusually high adult mortality (Ohgushi 1986; see also Fig. 4). Hence, half of the long-lived females survived up to the second reproductive season, when the 1979 data were omitted. In addition, females had a significantly higher survival rate to the next spring than males over the 5-year period at site F (G-test with the Williams' correction, $G_{adj} = 7.07$, $df = 1$, $P < 0.01$).

There were no significant differences in survival rates to the following spring between the long-lived reproductive females and those that emerged in summer and immediately went into reproductive diapause ($G_{adj} < 2.23$, $df = 1$, NS in each year) (Fig. 4),

Table 1 Percentage survival to the next reproductive season of adults alive at the end of reproductive season (15 August). The number of reproductive adults is given in parentheses

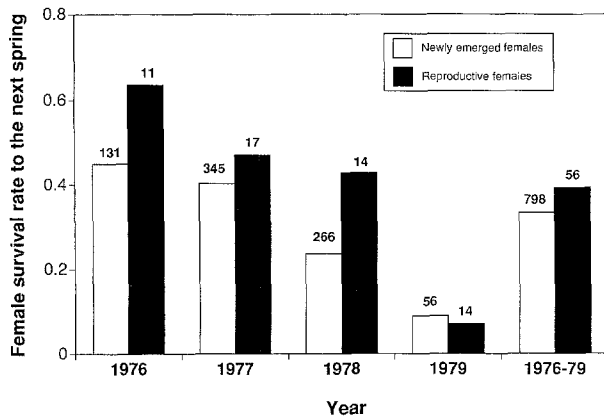| Site | Sex | Percentage survival rate to the next reproductive season | | | | |
		1976	1977	1978	1979	Total
A	Male	0 (2)	0 (1)	0 (5)	0 (0)	0 (8)
	Female	0 (0)	0 (2)	0 (0)	0 (0)	0 (2)
F	Male	20.0 (5)	33.3 (3)	0 (7)	0 (6)	9.5 (21)
	Female	63.6 (11)	47.1 (17)	42.9 (14)	7.1 (14)	39.3 (56)

Fig. 4 Survival rates of adult females to the following reproductive season. *Open* and *filled columns* show newly emerged and reproductive females, respectively. *Numbers* on each column show the number of newly emerged females in summer or the number of reproductive females alive on 15 August

indicating that females which had already invested in reproduction survived equally as well as newly emerged females which had not reproduced in summer.

Discussion

A reproductive tradeoff

There are two lines of evidence that suggest a tradeoff between egg production and female survival in *E. niponica*. First, independently within both sites, periods of low oviposition due to egg resorption are correlated with periods of higher female survival, but not higher male survival. Second, the severe flooding disturbance at site F produced a further magnification of the effect: the loss of host plants, and the reduction in oviposition that followed, were correlated with higher levels of female survival. Again, male survival was unaffected. Although this conclusion largely depends on the correlation between egg resorption and subsequent female survival within the reproductive season, the "natural experiment" by flooding strongly suggested the physiological mechanism of the tradeoff imposed by egg resorption. Egg resorption in the lady beetle is likely to cause higher investment in survival at the expense of reproduction under resource deterioration. In other words, the energy saved by not producing and ovipositing eggs may be used in subsequent survival.

Note that females resorbed eggs even when more than half of the total leaf area was intact (Ohgushi and Sawada 1985). Thus, it is unlikely that the cessation of egg-laying late in the season was simply because the eggs remaining in the ovaries were provisioned more slowly when food was scarce. Actually, in each year leaf damage remained around 40% at site A and 20% at site F in late June when egg resorption was detected in the field (Ohgushi 1992).

It could be argued that increased female survival could be brought about, not by egg resorption, but by external factors affecting adult survival. This is unlikely, because this hypothesis cannot explain why increasing survival was not observed in males, unless the factor(s) operate in a sex-dependent manner. Also, there was no evidence of the operation of external factors (except for floods) that principally determined adult survival, especially late in summer. A second hypothesis would be that increased dispersal of females may have resulted in decreased survival late in the reproductive season because of enhanced emigration from the study sites. However, this hypothesis is also unlikely, because female dispersal showed an opposite trend, decreasing with the season (Ohgushi and Sawada 1985). In particular, movements of adult females rarely occurred late in the season when the relation between egg resorption and increased female survival was observed. A third hypothesis is that feeble individuals may have been selected out, thereby leaving only more robust ones that could survive to the end of the season. However, this hypothesis cannot explain (1) why female survival changed synchronously with the cessation and resumption of egg-laying after the flooding (see Fig. 3), and (2) why male survival decreased consistently throughout the reproductive season (see Figs. 1, 2, and 3b).

Likewise, tradeoffs between egg resorption and survival have been suggested in butterflies *Heliconius charitonius* (Dunlap-Pianka et al. 1977) and *Speyeria mormonia* (Boggs and Ross 1993). Oocytes in ovaries of *S. mormonia* were resorbed and resources were reallocated away from reproduction when they were starved in the laboratory. As a result, female lifespan of the butterfly was prolongated at the expense of reproduction. The negative effect of reproduction on survival is often exacerbated when resources are scarce (Kaitala 1991; Boggs and Ross 1993). This is also true in the lady beetle; egg resorption occurred when food intake was apparently suppressed due to competition induced by increased leaf herbivory late in the season or thistle plants were badly damaged from flooding. Having experimentally prevented rosehip fruit flies *Rhagoletis basiola* from laying eggs in the laboratory, Roitberg (1989) also demonstrated a reproductive tradeoff between oviposition and survival in the fly. Ovipositing flies suffered significantly higher mortality rates than oviposition-deprived ones. Flies deprived of oviposition lived much longer (43.9 days, on average) than those that were permitted to oviposit (27.1 days, on average).

What is the mechanism responsible for the decreased survival imposed by costs of reproduction in *E. niponica*? In general, costs of reproduction originate from ecological and physiological constraints (Calow 1979; Tallamy and Denno 1982; Partridge 1989; Roff 1992). The former occurs when reproduction increases the level of exposure to external mortality agents, such as disease and predation. Physiological costs occur when

energy allocated to egg production decreases energy allocated to other functions, such as growth or maintenance. Although the crab spider *Xysticus croceus* was observed attacking adult lady beetles at both sites, an intensive survey of adult mortality agents indicated that spider predation was not a major cause of mortality. Also, there were no parasitoids to kill adult beetles. Therefore, the physiological costs of reproduction must be considered in generating the observed pattern of female survival. In this context, the cumulative load of reproduction may incur physiological costs that reduce survival throughout a female's reproductive life. Even in the laboratory with ample amounts of fresh thistle leaves, survival of reproductive females also decreased with aging (T. Ohgushi, unpublished work). Thus, the cumulative load of reproduction that accelerates physiological senescence is more likely to generate the seasonal decrease in female survival rates until the occurrence of egg resorption late in the season.

Adaptive significance of egg resorption

Traditional studies have focused mainly on the tradeoffs between reproductive effort and maintenance, with little attention to ecological or evolutionary implications involved in those tradeoffs (see Roff 1992 for discussion). Hence, the emphasis of the present study is not only on the demonstration of the reproductive tradeoff, but also on the adaptive significance of the increased survival of reproductive females that resorbed eggs. Since a female's lifetime reproductive success is positively correlated with reproductive output, the fitness principle precludes selection for egg resorption unless the resorbed females are able to oviposit at a future time, thereby allowing more offspring to reach reproductive maturity. Future reproduction of females with egg resorption should be considered as within- and between-season oviposition. The former means a resumption of oviposition later in the same reproductive season. This is more likely to occur because egg resorption in the lady beetle is a reversible process (Ohgushi and Sawada 1985). The latter concerns oviposition in the next reproductive season.

The fact that reproductive females stopped ovipositing immediately after flooding and resumed oviposition in response to a reflush of thistle leaves strongly suggests that the resorbed females are capable of laying eggs later in the season if food resources become favorable. The flood caused considerable damage to thistle plants, leaving few thistle leaves available to newly hatched larvae. It is more likely that females refrained from reproduction during the period unfavorable to larval survival due to food shortage, and became reproductive again when offspring fitness was no longer reduced by the habitat perturbation. Thus, egg resorption may be an adaptive trait in response to habitat disturbances such as flooding during the rela-

tively long reproductive season, thereby increasing a female's lifetime reproductive success.

It is surprising that in spite of physiological senescence with aging, the survival rate of reproductive females was not significantly lower than that of newly emerged females. In this context, egg resorption may substantially contribute to the improvement of female survival to the next reproductive season. Also, some of the previously reproductive females that survived to the next spring were observed ovipositing in 1977, 1978, and 1979. Thus, long-lived reproductive females have a high probability of oviposition in the second reproductive season. The next question is the ultimate cause of occurrence of egg resorption late in the reproductive season. There is a correlation between timing of egg resorption and decreased offspring fitness. Lifetime fitness of offspring was highly suppressed after mid-July at site F (Ohgushi 1992). In particular, no adults emerged in the late cohorts, which were born in August. Thus, females will have higher reproductive success if egg-laying is terminated by egg resorption late in the season in view of the poor lifetime fitness of offspring, and postpone oviposition until the second reproductive season when offspring have higher fitness, by the improved winter survival.

It should be noted also that relative importance of egg resorption for reproductive success may vary between the two populations. Reproductive lifespan of females was shorter at site A than at site F. As a result, there were no reproductive females surviving to the next reproductive season at site A in the study period. Hence, 2nd-year reproduction may contribute little to lifetime reproductive success of females at site A. It is unlikely, however, that environmental factors such as higher temperature at site A resulted in the shortened female longevity. Under identical rearing conditions, the difference in reproductive lifespan of females between the two populations was still found, suggesting a genetic basis for the between-population difference (Ohgushi 1991).

Demographic consequences of egg resorption

Egg resorption may contribute substantially to a remarkable population stability of *E. niponica*. The lady beetle populations exhibited only 2.0- and 1.4-fold variations (expressed as the ratio of maximum to minimum densities) in egg stage over the 5-year period at site A and site F, respectively, both of which are an exceptional levels of stability for herbivorous insect populations (see Hassell et al. 1976; Wolda 1978; Connell and Sousa 1983 for references). This remarkable population stability was mainly generated by strong density-dependent oviposition control by females (Ohgushi and Sawada 1985; Ohgushi 1995). Since females resorb eggs in response to host plant deterioration, which is largely dependent on larval density, egg resorption is more likely to occur in a

density-dependent manner, resulting in a density-dependent reduction in eggs laid per female. The density-dependent oviposition control, in turn, leads to the temporal population stability. This implication is also supported by the fact that density-dependent reduction in oviposition rate occurred late in the season (Ohgushi and Sawada 1985), when egg resorption was observed in the field. Egg resorption as an regulatory agent for population density was also suggested in gall-making sawflies on willows (Preszler and Price 1988; Craig et al. 1990).

The density-dependent physiological response to resource deterioration may play an important role in determining population dynamics in herbivorous insects through oviposition process. This suggests a strong connection between properties at individual and population levels (Schoener 1986; Lomnicki 1988; Price et al. 1990; Ohgushi 1992, 1995), which traditional population studies have long ignored. Therefore, understanding the exact ecological consequences of adaptive life history traits, which may govern insect population dynamics, requires the incorporation of life history traits into the dynamics of populations, mediated through reproductive and survival processes.

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