Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle

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Abstract. 1. A univoltine herbivorous ladybird beetle *Epilachna niponica* (Coleoptera: Coccinellidae) shows a large variation in adult size within a population.

2. Large adults had higher survival from emergence to the reproductive season, and the size-dependent adult survival was most apparent during hibernation. On the other hand, adult survival during pre-hibernation contributed little to size-dependent overall survival.

3. Neither reproductive lifespan nor lifetime fecundity were a function of adult size, though large females produced larger size of egg batches.

4. Size of adult beetles was significantly reduced by leaf damage to plants on which they grew up on larval stage. Since leaf herbivory increases through the season, late emerged adults that were subjected to food deterioration during the larval period were smaller than early-emerged individuals.

Key words. Adult survival, *Epilachna niponica*, food deterioration, herbivorous insect, reproductive performance, size-dependent survival, size variation.

Introduction

The traditional view of insect population ecology has long assumed that individuals within a population are identical to each other in terms of survival and reproduction. Hence, individual phenotypic variations have been given little attention in insect populations. This is, however, a biologically unrealistic assumption, because in any population there are individuals of different ages, sizes, and degrees of fitness, which may, in turn, differ in their demography. The importance that such individual heterogeneity within a population may have on the dynamics of animal populations has not been emphasized until recently (Hassell & May, 1985; Smith & Sibly, 1985; Schoener, 1986; Lomnicki, 1988; Kingsolver, 1989; Ohgushi, 1992).

One of the obvious phenotypic variations within a population is the size variation among individuals (Begon, 1984). Size variation has received a great deal of attention in the context of life-history evolution, trade-offs have been demonstrated between body size and life-history parameters such as egg size, longevity, and growth rate (Peters, 1983; Roff, 1986, 1992; Stearns, 1992). Because of the conspicuous phenotypic plasticity in response to various environmental factors, the importance of size distribution on population dynamics has been recognized by plant population ecologists (see Sarukhán *et al.*, 1984, for a review).

Although the relationships between body size and population variability or abundance have been recently discussed in inter-species comparisons of insects (Gaston & Lawton, 1988a, b), our knowledge on how size variation among individuals affects survival and/or reproductive performance has remained very limited in insect populations (e.g. Palmer, 1985; Wall & Begon, 1986; Atkinson & Begon, 1987).

The ladybird beetle *Epilachna niponica* (Coleoptera: Coccinellidae) is a univoltine specialist herbivore that feeds on leaves of thistle plants. Overwintering adult females emerge from hibernation in early May, and begin to lay eggs in clusters of twenty–thirty eggs on the undersurface of thistle leaves. Larvae pass through four instars. New adults emerge from early July to late August, feeding on thistle leaves through the autumn. Then they enter hibernation by early November. My primary objectives in this study are to determine: (1) how mean body size of adult beetles varies within a population during the period from emergence to reproductive season in the following spring; (2) how body size affects adult survival and reproductive performance including reproductive life-span and lifetime fecundity; and (3) what causes within-population variation in adult size.

Methods

Study site and host plant. I studied populations of beetles at two sites, A and F, which are located in different valleys along the

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River Ado, in the northwestern part of Shiga Prefecture in central Japan. Site A was situated downstream at 220 m elevation. Site F, upstream at 350 m elevation, was approximately 10 km from site A. During the 5-year study period 1976–80 there was no evidence of exchange of adult beetles among these two populations. Because of the beetle's very limited dispersal ability, the local populations of the ladybird beetle were well separated from each other (Ohgushi, 1983). Detailed descriptions of sites A and F are given in Ohgushi & Sawada (1985).

In the study area, *E.niponica* feeds exclusively on leaves of the thistle *Cirsium kagamontanum*. The thistle occurs in discrete patches along the riverside. It grows rapidly, sprouting in late April, reaching its full size of about 1.5 m by late August, and flowers from early August to mid-September. Throughout the flowering season, old leaves become senescent.

Measurement of adult size. Adult beetles were individually marked with a system of four small dots of lacquer paint on their elytra. During the study period, I marked a total of 9476 adults at the two study sites. When first captured as a newly-emerged adult, I measured body size from the anterior edge of the head to the posterior edge of the elytra to the nearest 0.05 mm using vernier calipers. Newly-marked adults were released immediately on the thistle plant where they had been captured. Subsequent capture history (date and place) were recorded for individual beetles.

Estimation of adult survival. Adult survival from emergence to the reproductive season was estimated by dividing total marked adults that were recaptured in the following spring by total emerged adults in summer. In each summer, >92% of newly emerged adults were marked. Also, recapture rate on each census, the number of marked adults that were recaptured divided by the estimated number of adults by the Jolly-Seber model, was constantly >0.95 until hibernation in early November. Because of the exceptionally high marking and recapture rates, the estimated survivals were highly reliable. The overall survival to the reproductive season consists of two stage-specific survivals: survival during the pre-hibernating period and survival during hibernation. Since most adult beetles that survived to the following reproductive season were recaptured at least once after mid-September (Ohgushi, 1986) and new adults dispersed little in the prehibernating period (Ohgushi, 1983), most of the adult losses occurring before mid-September were probably due to death. Therefore, based on the assumption that all adults surviving at mid-September enter hibernation, I estimated the maximum survival until hibernation as the number of adults at that point divided by the total number of adults emerged. Also, adult survival during the hibernation was estimated as the proportion of adults overwintered to the next spring to adults alive on mid-September.

Laboratory experiment. In addition to the field observation, I conducted a laboratory experiment to examine relationships between adult body size and reproductive performance including lifetime fecundity, mean egg batch size, and reproductive lifespan. On 1 May 1987, I collected sixteen pairs of overwintered adults from site A and twenty-five from site F, which had just emerged from hibernation but not yet begun oviposition. 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 LD 16:8 in an environmental chamber. Ample amounts of fresh leaves were offered every 3 days throughout

the experiment. For each pair the number and size of egg batches were recorded daily until the death of the female.

Leaf damage of the plant that an adult beetle developed as a larva. To examine a relationship between leaf herbivory and adult size, I conducted visual estimation of leaf damage of individual plants by adults and larvae of the ladybird beetle on each census. Each plant was classified into one of five categories based on the proportion of the leaf area eaten. Since the mark–release–recapture experiments confirmed that a newly emerged adult is most likely to stay on the same plant that it developed upon as a larva. Also, >92% of newly emerged adults were successfully marked. Hence, a correlation between the leaf damage of each plant and size of new adults that emerged from the plant is highly reliable.

Statistical analysis. Adult survival was compared by body-size class in one-way ANOVA. I divided adult size into six size classes, and then tested for differences in adult survival among size classes. Significant differences were established with Scheffe's test. The percentage data were arcsin square-root transformed prior to analysis. Pearson correlation coefficient were calculated between body size and reproductive performance, including reproductive lifespan, lifetime fecundity, and egg batch size. In determining causes of adult size, body size of adults was compared by leaf damage of each plant and by timing of adult emergence in nonparametric one-way ANOVA (Kruskal-Wallis test).

Results

Size variation within a population

In the two study sites, body size of females was significantly larger than that of males at adult emergence in summer, before hibernation in autumn, and reproductive season in the following spring (Mann-Whitney U-test; $P < 0.0001$ for each year) (Fig. 1). A comparison of body size distributions at emergence and post-hibernation indicated that mean adult size after hibernation was larger than that at emergence in the previous summer. This suggests that large adults survived better to the reproductive season than small individuals.

Size and survival

The per cent survival from adult emergence to the reproductive season changed in a size-dependent manner, increasing significantly with body size of both sexes at the two sites (ANOVA; male: site A, df = 4, 19, $F = 23.03$, $P = 0.0001$; site F, df = 3, 16, $F = 4.36$, $P = 0.0200$; female: site A, df = 5, 22, $F = 14.93$, $P = 0.0001$; site F, df = 3, 15, $F = 6.00$, $P = 0.0068$) (Fig. 2). However, this size-dependent survival operated differently when overall survival was divided into two sub-survivals: survival during pre-hibernation and during hibernation. Although there was an increasing trend of survival during pre-hibernation with body size, the relationships were not significant, with the exception for female at site A (ANOVA; male: site A, df = 4, 19, $F = 2.11$, $P = 0.1188$; site F, df = 3, 16, $F = 0.15$, $P = 0.9286$; female: site A, df = 5, 22, $F = 4.44$, $P = 0.0060$; site F, df = 3, 15, $F = 2.62$, $P = 0.0892$)
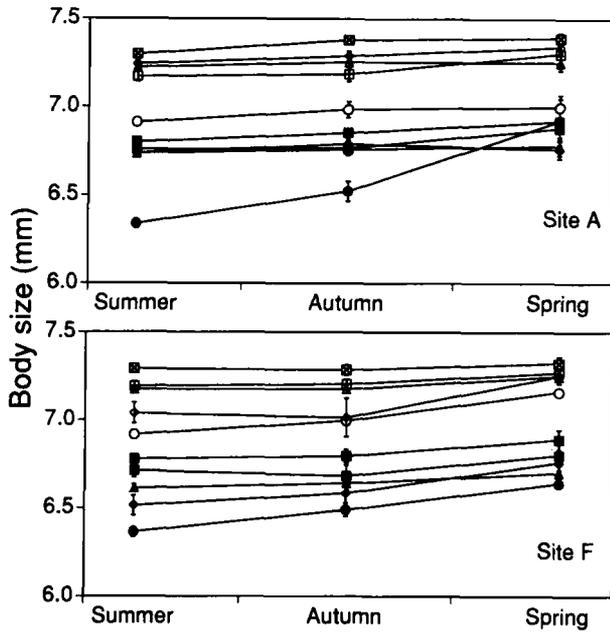
Fig. 1. Body size (mean ± 1 SE) of adult beetles at emergence (summer), those alive on 15 September (autumn), and those overwintered and survived up to the following spring (spring) at sites A and F. Male (■) and female (□) in 1976, male (▲) and female (△) in 1977, male (●) and female (○) in 1978, male (◆) and female (◇) in 1979, male (■) and female (☒) in 1980.

(Fig. 3). In contrast, there was a strong association between large adults and high winter survival during hibernation in both sexes at the two sites (ANOVA; male: site A, df = 4, 19, $F = 16.35, P = 0.0001$; site F, df = 3, 15, $F = 5.57, P = 0.0090$; female: site A, df = 5, 22, $F = 11.13$, $P = 0.0001$; site F, df = 3, 15, $F = 5.05$, $P = 0.0129$) (Fig. 4) Hence, high survival of large individuals during hibernation contributed substantially to the size-dependent overall survival from adult emergence to the reproductive season.

Size and reproductive performance

The laboratory experiment indicated that there were no significant relationships between body size and reproductive lifespan in both sexes at the two sites (Fig. 5). Likewise, lifetime fecundity was independent of body size of females (Fig. 6a). In contrast, lifetime fecundity was highly correlated with reproductive lifespan (site A: $r = 0.988$, $n = 16$, $P < 0.0001$; site F: $r = 0.531$, $n = 25$, $P = 0.0063$) (Fig. 6b), and the relationship was also significantly different between the sites (ANCOVA: $F = 6.845$, $P = 0.0128$). The longer reproductive life-span, the greater the lifetime fecundity. Note also that mean size of egg batches deposited over an individual's reproductive life had a marginally significant correlation with female body size (site A; $r = 0.484$, $n = 16$, $P = 0.0577$; site F; $r = 0.431$, $n = 25$, $P = 0.0312$) (Fig. 7). Mean size of egg batches consistently decreased over the female's reproductive life (Ohgushi, 1991). However, it is unlikely to affect the conclusion, because reproductive
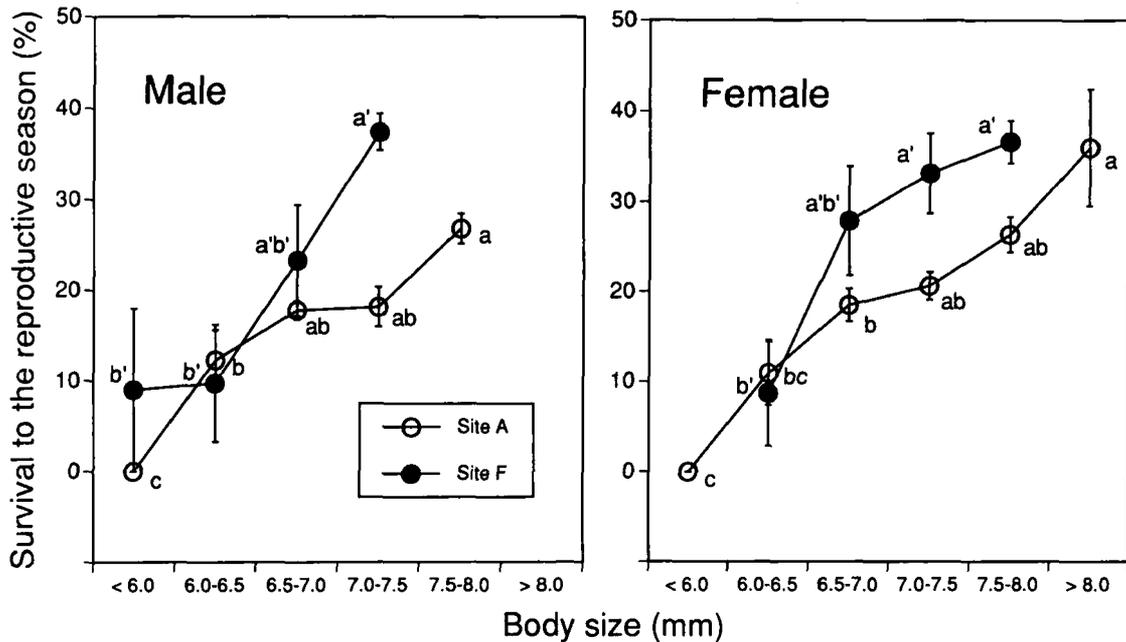

Fig. 2. Relationships between per cent adult survival to the reproductive season and body size classes in male and female at sites A (○) and F (●). Data were arcsin square-root transformed prior to analysis. Means and 1 SE for 1976–80 are represented. (ANOVA; male: site A, df = 4, 19, $F = 23.03$, $P = 0.0001$; site F, df = 3, 16, $F = 4.36$, $P = 0.0200$; female: site A, df = 5, 22, $F = 14.93$, $P = 0.0001$; site F, df = 3, 15, $F = 6.00$, $P = 0.0068$.) Means with different letters are significantly different (Scheffe's test: $P < 0.05$).
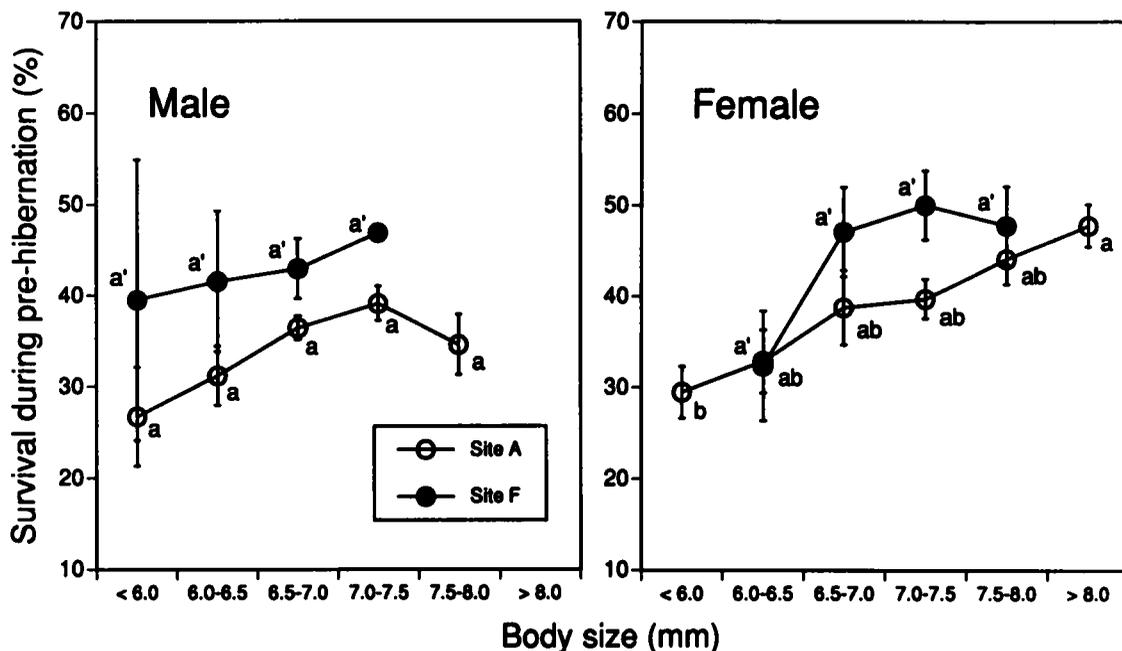
Fig. 3. Relationships between per cent adult survival during pre-hibernating period and body size classes in male and female at sites A (O) and F (●). Data were arcsin square-root transformed prior to analysis. Means and 1 SE for 1976–80 are represented. (ANOVA; male: site A, df = 4, 19, F = 2.11, P = 0.1188; site F, df = 3, 16, F = 0.15, P = 0.9286; female: site A, df = 5, 22, F = 4.44, P = 0.0060; site F, df = 3, 15, F = 2.62, P = 0.0892.) Means with different letters are significantly different (Scheffe's test: P < 0.05).
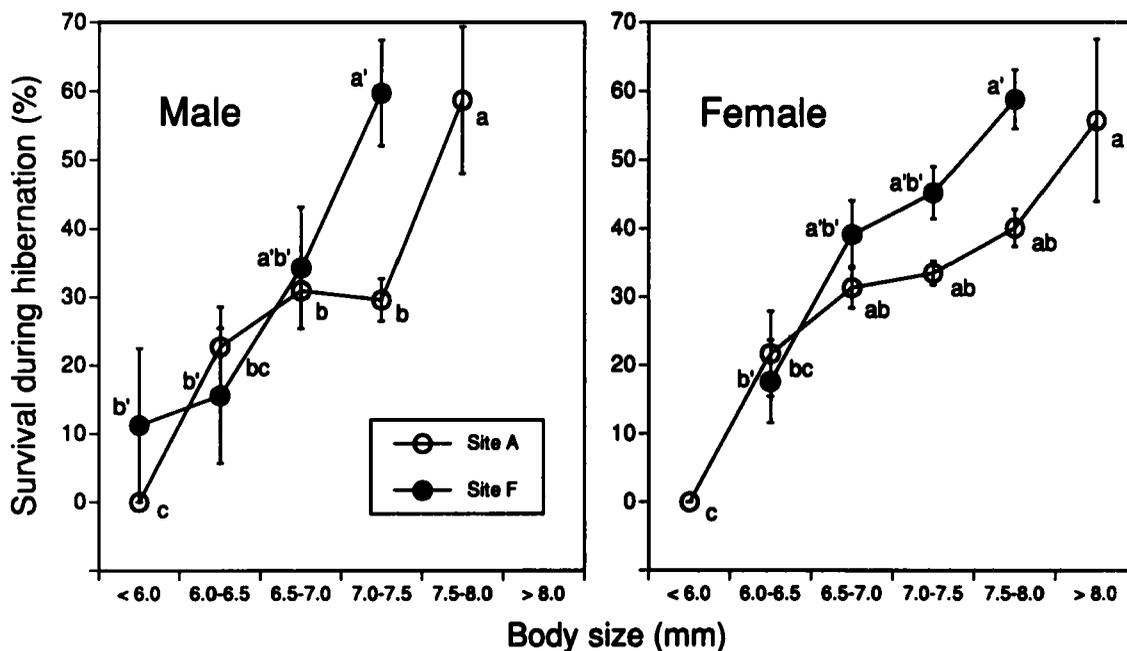

Fig. 4. Relationships between per cent adult survival during hibernation and body size classes in male and female at sites A (O) and F (●). Data were arcsin square-root transformed prior to analysis. Means and 1 SE for 1976–80 are represented. (ANOVA; male: site A, df = 4, 19, F = 16.35, P = 0.0001; site F, df = 3, 15, F = 5.57, P = 0.0090; female: site A, df = 5, 22, F = 11.13, P = 0.0001; site F, df = 3, 15, F = 5.05, P = 0.0129.) Means with different letters are significantly different (Scheffe's test: P < 0.05).
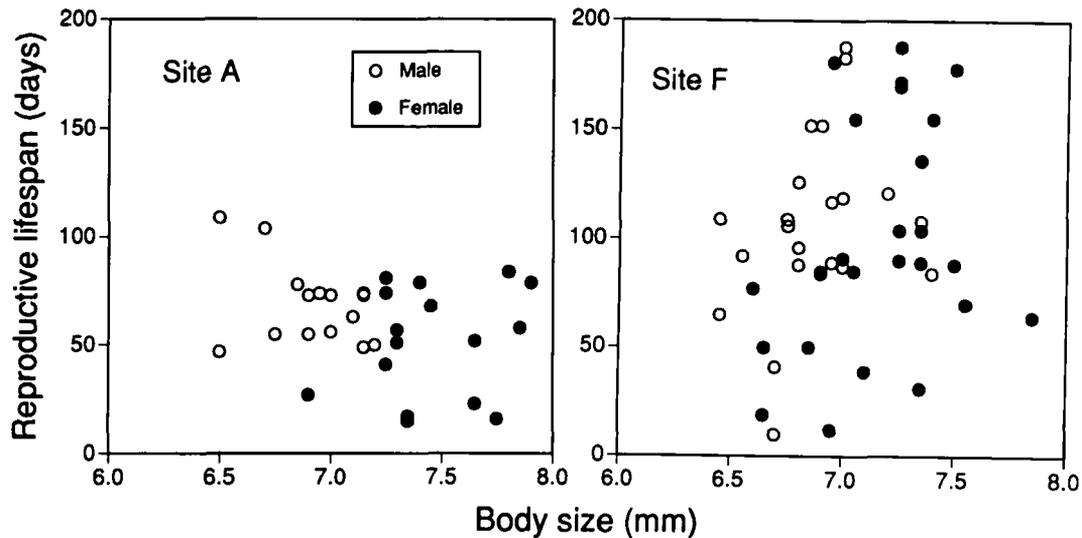
Fig. 5. Relationships between body size and reproductive lifespan in male (O) and female (●) at sites A and F. Site A (male: $y = -31.82x + 289.25$, $n = 16$, $r = 0.387$, $P = 0.1386$; female: $y = 17.74x - 81.05$, $n = 16$, $r = 0.192$, $P = 0.4724$). Site F (male: $y = 56.52x - 281.23$, $n = 25$, $r = 0.352$, $P = 0.0988$; female: $y = 53.03x - 308.93$, $n = 25$, $r = 0.265$, $P = 0.2979$).
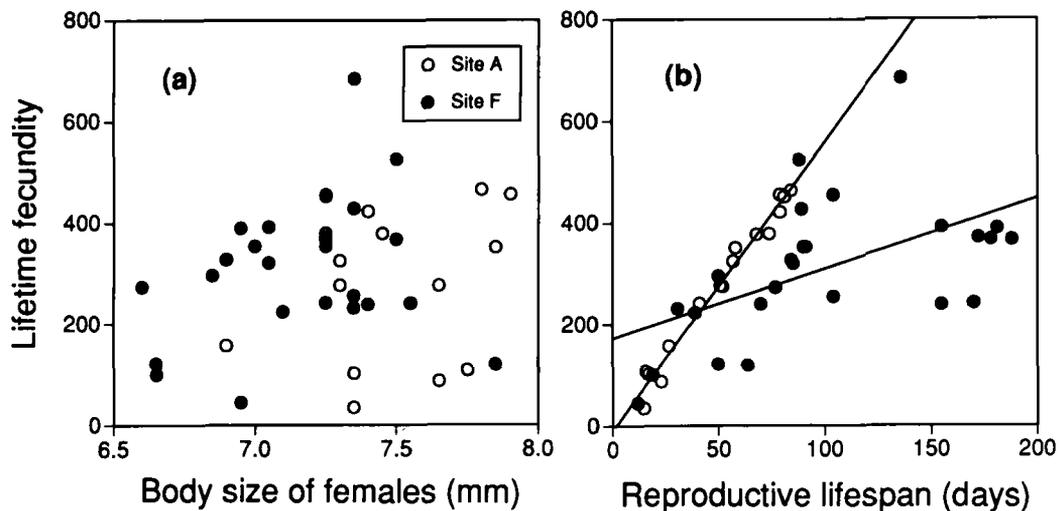

Fig. 6. Relationships (a) between female body size and lifetime fecundity and (b) between reproductive lifespan and lifetime fecundity at sites A (O) and F (●). Female body size (site A: $y = 114.81x - 574.17$, $n = 16$, $r = 0.217$, $P = 0.4177$; site F: $y = 115.09x - 515.62$, $n = 25$, $r = 0.251$, $P = 0.2249$). Reproductive lifespan (site A: $y = 5.68x - 9.48$, $n = 16$, $r = 0.988$, $P < 0.0001$; site F: $y = 1.38x + 172.19$, $n = 25$, $r = 0.531$, $P = 0.0063$).

lifespan of females was independent of body size, as shown above.

Causes of body size variation

Leaf damage to individual thistle plants greatly affected body size of adult beetles at emergence (Table 1). Adults that emerged from plants with heavier leaf damage were significantly smaller than those grown on plants with less leaf damage, with the exception of males at site F in 1976 (Kruskal-Wallis test: $P < 0.02$).

Since leaf damage of thistle plants by beetle feeding consistently increases with the season, late-emerged adults that were subjected to resource deterioration on larval stage tended to become smaller compared with early-emerged adults (Table 2).

Discussion

This study clearly demonstrated that large adults of *E.niponica* enjoyed higher survival from emergence to the reproductive season in the following spring. In particular, the size-dependent operation

Table 1. Mean body size (mm) (± 1 SE) of *E.noponica* beetles which grew up on thistle plants with different leaf damage.

| Site | Year | Sex | Leaf damage | | | | | Kruskal-Wallis test |
			0–20%	20–40%	40–60%	60–80%	80–100%	P
A	1976	Male	6.95 ± 0.04	6.67 ± 0.03	–	–	–	0.0001
		Female	7.36 ± 0.05	7.10 ± 0.03	–	–	–	0.0002
	1977	Male	6.84 ± 0.02	6.75 ± 0.03	6.66 ± 0.03	6.37 ± 0.10	–	0.0001
		Female	7.35 ± 0.03	7.23 ± 0.02	7.14 ± 0.03	6.77 ± 0.10	–	0.0001
	1978	Male	–	6.44 ± 0.04	6.29 ± 0.04	6.16 ± 0.05	–	0.0003
		Female	–	7.08 ± 0.03	6.82 ± 0.03	6.61 ± 0.05	–	0.0001
	1979	Male	6.94 ± 0.06	6.93 ± 0.03	6.81 ± 0.02	6.43 ± 0.06	6.14 ±0.06	0.0001
		Female	7.57 ± 0.03	7.45 ± 0.02	7.25 ± 0.02	6.95 ± 0.04	6.72 ±0.06	0.0001
	1980	Male	–	6.90 ± 0.02	6.82 ± 0.01	6.46 ± 0.03	–	0.0001
		Female	–	7.41 ± 0.02	7.32 ± 0.01	6.92 ± 0.03	–	0.0001
F	1976	Male	6.75 ± 0.04	6.57 ± 0.08	–	–	–	0.1919
		Female	7.23 ± 0.02	6.97 ± 0.05	–	–	–	0.0001
	1977	Male	6.67 ± 0.02	6.53 ± 0.02	–	–	–	0.0002
		Female	7.31 ± 0.01	6.95 ± 0.03	–	–	–	0.0001
	1978	Male	6.56 ± 0.06	6.37 ± 0.03	6.26 ± 0.04	–	–	0.0062
		Female	7.08 ± 0.04	6.97 ± 0.02	6.67 ± 0.04	–	–	0.0001
	1979	Male	6.67 ± 0.05	6.33 ± 0.08	–	–	–	0.0049
		Female	7.29 ± 0.08	6.87 ± 0.05	6.36 ± 0.10	–	–	0.0002
	1980	Male	6.87 ± 0.03	6.74 ± 0.03	6.60 ± 0.10	–	–	0.0139
		Female	7.42 ± 0.03	7.24 ± 0.02	7.11 ± 0.06	–	–	0.0001

Table 2. Mean body size (mm) (±1 SE) of *E.niponica* beetles that emerged at different times.

| Site | Year | Sex | Timing of adult emergence | | | | | | Kruskal-Wallis test |
			1–10 July	11–20 July	20–31 July	1–10 Aug.	11–20 Aug.	20–31 Aug.	P
A	1976	Male	6.99 ± 0.16	6.85 ± 0.03	6.67 ± 0.05	6.55 ± 0.17	6.37 ± 0.15	–	0.0057
		Female	7.37 ± 0.19	7.25 ± 0.03	7.07 ± 0.05	7.00 ± 0.29	7.01 ± 0.24	–	0.1159
	1977	Male	6.94 ± 0.05	6.80 ± 0.02	6.72 ± 0.04	6.70 ± 0.04	6.72 ± 0.04	–	0.0017
		Female	7.51 ± 0.07	7.31 ± 0.02	7.06 ± 0.05	7.29 ± 0.03	7.11 ± 0.04	6.92 ± 0.10	0.0001
	1978	Male	6.40 ± 0.04	6.37 ± 0.04	6.23 ± 0.04	6.22 ± 0.15	6.22 ± 0.28	6.17 ± 0.07	0.1183
		Female	7.04 ± 0.04	6.95 ± 0.03	6.75 ± 0.04	6.58 ± 0.13	–	–	0.0004
	1979	Male	6.83 ± 0.37	6.85 ± 0.03	6.61 ± 0.03	6.57 ± 0.08	6.62 ± 0.13	–	0.0001
		Female	7.37 ± 0.10	7.30 ± 0.02	7.19 ± 0.02	6.82 ± 0.11	–	–	0.0001
	1980	Male	7.28 ± 0.04	6.94 ± 0.02	6.80 ± 0.02	6.74 ± 0.06	6.47 ± 0.06	6.71 ± 0.08	0.0001
		Female	7.71 ± 0.07	7.39 ± 0.02	7.36 ± 0.01	7.24 ± 0.01	6.95 ± 0.07	–	0.0001
F	1976	Male	–	–	6.94 ± 0.06	6.71 ± 0.06	6.61 ± 0.07	6.75 ± 0.08	0.6238
		Female	–	–	7.28 ± 0.06	7.17 ± 0.07	6.16 ± 0.03	7.17 ± 0.07	0.0003
	1977	Male	–	–	–	6.72 ± 0.03	6.58 ± 0.03	6.51 ± 0.04	0.0008
		Female	–	–	7.38 ± 0.07	7.31 ± 0.03	7.11 ± 0.02	6.98 ± 0.05	0.0001
	1978	Male	–	6.50 ± 0.06	6.31 ± 0.04	6.37 ± 0.05	6.31 ± 0.06	5.96 ± 0.14	0.0093
		Female	–	7.02 ± 0.04	6.91 ± 0.03	6.92 ± 0.03	6.86 ± 0.06	6.52 ± 0.15	0.0001
	1979	Male	–	–	6.79 ± 0.02	6.44 ± 0.10	6.41 ± 0.10	6.48 ± 0.08	0.0067
		Female	–	–	7.09 ± 0.14	7.08 ± 0.08	6.97 ± 0.12	6.94 ± 0.14	0.0002
	1980	Male	–	–	6.92 ± 0.04	6.73 ± 0.05	6.69 ± 0.06	6.81 ± 0.09	0.0307
		Female	–	–	7.31 ± 0.04	7.37 ± 0.04	7.17 ± 0.10	7.17 ± 0.08	0.0001
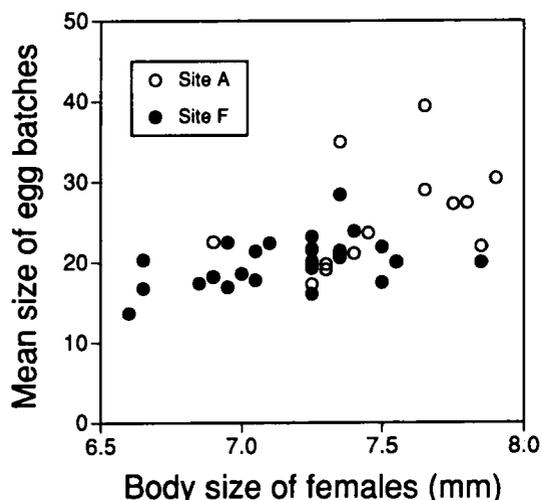
Fig. 7. Relationships between female body size and mean size of egg batches at sites A (O) and F (●). (Site A: $y = 10.82x - 56.04$, $n = 16$, $r = 0.484$, $P = 0.0577$; Site F: $y = 4.26x - 10.50$, $n = 25$, $r = 0.431$, $P = 0.0312$).

of mortality was large during the hibernation. In their study of an introduced population of *E.niponica*, Ohgushi & Sawada (1995) showed that mean body size of overwintered adults was higher than that of adults in the previous summer, suggesting size-dependent adult survival during a period from emergence to the reproductive season. Likewise, Landa (1992) reported that small-sized nymphs of two grasshopper species *Arphia sulphurea* and *Chortophaga viridifasciata* that hatched late in the season suffered higher overwintering mortality, compared to early-hatching individuals. Gilbert (1984) also found that larger pupae of the white butterfly *Pieris rapae* survived better than smaller ones during hibernation. However, adult size of the milkweed leaf beetle, *Labidomera clivicollis*, did not have consistent effects on winter survival of two sexes (Palmer, 1985); large females had significantly higher winter survival than small females, but the trend was reversed in males.

The underlying mechanism of the size-dependent mortality during hibernation of *E.niponica* remains to be determined. Although no intensive survey was conducted on mortality agents that would operate during hibernation, it is unlikely that predators attack overwintering adults in soils in a size-dependent manner. Rather, physiological causes related to the amount of metabolic reserves for overwintering successfully may generate the size-dependent mortality. This is because larger adults may reserve more lipid (fat body) or glycogen, which are important for survival during hibernation, than smaller individuals. In two Nymphalidae butterflies *Aglais urticae* and *Inachis io*, large adults associated with higher lipid content survived better during hibernation than smaller adults (Pullin, 1987; Pullin & Bale, 1989). In three species of Coccinellidae, *Coccinella septempunctata*, *Adalia bipunctata*, and *Propylea quatuordecimpunctata*, adult beetles consumed fat and glycogen for overwintering, resulting in a consistent decrease in their contents during hibernation (El-Hariri, 1966).

It has been generally thought that large females have higher fecundity than small ones within an insect species (Gilbert, 1984; Honek, 1993). There are a number of laboratory studies demonstrating that increased weight and/or size results in

increased fecundity within insect populations of; flies (Akey *et al.*, 1978), aphids (Dixon & Wratten, 1971), beetles (Price & Willson, 1976; Palmer, 1985), stinkbugs (Evans, 1982). However, some lepidopteran species show no correlation between fecundity and pupal weight or even adult weight (Karlsson & Wiklund, 1984; Boggs, 1986; see Leather, 1988, for references).

For *E.niponica*, adult size affected neither reproductive lifespan nor lifetime fecundity, although size of egg batches was positively correlated with female size. This implies that size variation is of secondary importance in determining important fitness components of the reproductive process in the ladybird beetle. Since oogenesis occurs after hibernation and thus oocytes in ovaries repeatedly mature during the reproductive lifetime of females, food supply of a reproductive female allocating egg production may determine lifetime fecundity. Interestingly, *E.niponica* females resorb their eggs in ovaries when exposed to increased leaf damage (Ohgushi & Sawada, 1985), which suggests that there is an important effect of resource condition on lifetime fecundity. The total amount of food acquired is dependent on the length of a female's reproductive life. It therefore follows that reproductive lifespan plays a substantial role in determining lifetime fecundity. In this context, Leather (1988) reviewed studies on factors responsible for variation in fecundity of lepidopteran species and emphasized that longevity and the factors influencing it would appear to be the most important single factor influencing fecundity.

What determines the size variation of adult beetles within a population? Size variation of *E.niponica* was mostly caused by leaf damage to thistle plants on which individual beetles matured (see Table 1). The underlying mechanism responsible for the negative correlation is likely to be the increased competition among larvae for deteriorating resources in quantity and quality with the season. Similarly, variation in adult size in natural populations has been attributed to deteriorating food availability for larvae in apple moths (Danthanarayana, 1976), stink bugs (Kiritani, 1964; Evans, 1982), and chrysomelid beetles (Palmer, 1984). Having reviewed laboratory experiments on effects of population density on adult size of insects in culture, Peters & Barbosa (1977) found negative relationships between adult size and larval density, suggesting the importance of intraspecific larval competition in producing adult size variation.

Since leaf damage is an increasing function of time, late-emerged adults that were exposed to deteriorated food resource during the larval period tended to be smaller than those emerged early (see Table 2). Similar associations between large adult size and early adult emergence in field populations have been seen in grasshoppers (Wall & Begon, 1987; Atkinson & Begon, 1988; Landa, 1992), chrysomelid beetles (Palmer, 1984), fruit flies (Atkinson, 1979) and ant-lions (Griffiths, 1985).

Finally, we turn to consider evolutionary and demographic consequences of size-dependent adult survival of *E.niponica*. Ohgushi & Sawada (1985) demonstrated exceptional temporal stability in these ladybird beetle populations, varying only 2.0- and 1.4-fold during a 5-year period at sites A and F, respectively. Furthermore, Ohgushi (1992, 1995) argued that coupled with egg resorption, oviposition behaviour in avoiding egg-laying on plants with higher egg densities is a mechanistic basis for the remarkable population stability. Because lifetime fitness of offspring

was negatively correlated with egg densities of individual plants, this oviposition behaviour is likely to be adaptive to improve a female's lifetime reproductive success (Ohgushi, 1995). The differences in winter mortality related to adult size may be responsible for density-dependent reduction in offspring fitness, because the scale of leaf herbivory is largely dependent on larval density. Hence, the size-dependent winter mortality may not only be a selective pressure favouring oviposition on plants with less herbivore load, but it may also indirectly increase population stability, by enhancing the oviposition site selection by reproductive females.

Acknowledgments

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