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Temporal Decrease in Clutch Size of the Herbivorous Lady Beetle *Epilachna niponica** (Coleoptera, Coccinellidae)

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Abstract Temporal changes in clutch size of *Epilachna niponica* were monitored over a 5-year period in two local populations at study sites A and F in northwestern part of Shiga Prefecture. The average clutch size at site A was significantly larger than that at site F. A seasonal decrease in clutch size was detected in both of the populations. In particular, at site F clutch size late in the season was approximately half of that early in the season. However, the clutch size did not significantly differ between the two populations when compared for each half-monthly period. A temporal decrease also occurred in the laboratory. The laboratory experiment revealed the age-dependent reduction in clutch size for individual females. The significant inter-population difference in clutch size was accounted for by the differential length of oviposition period in the two populations: population F with a longer oviposition period had a higher proportion of smaller clutches deposited late in the season, compared with population A which had a shorter oviposition period. Average number of ovarioles of individual females did not significantly differ between the two populations, and coincided closely with the clutch size at the beginning of the season.

Key words: Clutch size; *Epilachna niponica*; herbivorous lady beetle; ovariole; reproductive load.

Introduction

Clutch size in insects has often received much attention relevant to life history evolution (DINGLE, 1981; TALLAMY & DENNO, 1981). In particular, recent theoretical and empirical studies have focused on the optimal size of an egg batch for improving offspring performance under the condition of limited food resources (PARKER & COURTNEY, 1984; PARKER & BEGON, 1986; BEGON & PARKER, 1986; GODFRAY, 1986; PILSON & RAUSHER, 1988; DAMMAN, 1991).

Epilachna niponica (LEWIS) is an herbivorous lady beetle, which feeds on the leaves of thistle plants. Overwintering females lay their eggs in clusters on undersurfaces of thistle leaves. Studies on natural populations of *H. niponica* reported inter-population variations in the average number of eggs per clutch, ranging from 17 to 26 (NAKAMURA 1983; SHIRAI, 1987). On the other hand, how clutch size varies within a population has been little documented. Since the oviposition

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period of the lady beetle extends three months from early May, clutch size may temporally change in response to external and/or internal factors. In order to clarify what determines the number of eggs per batch throughout the reproductive season, we need to conduct not only field observations but also laboratory experiments to separate the effects of these factors which may affect clutch size.

This paper will show temporal decreases in clutch size of two local populations, and then suggest physiological senescence of ovipositing females as a principal cause of the decreasing clutch size over a time period.

Study Sites

The study was performed over a 5-year period (1976–80) 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. Site F (90 × 15 m) was situated at 350 m elevation, about 10 km upstream of site A. A full description of the study sites is shown in OHGUSHI & SAWADA (1985).

Materials and Methods

The lady beetle

In the study area, *E. niponica* feeds exclusively on the leaves of a thistle, *Cirsium kagamontanum*. The insect has one generation a year. Overwintering adult females begin to lay their eggs in clusters on the undersurfaces of thistle leaves in early May. Oviposition period ends in early July at site A but continues up to early August at site F. Larvae pass through four instars. New adults emerge from early July to early September. Adult beetles enter hibernation by early November.

Field observation

I censused each population at 1 to 3 day intervals from early May to early November in each year, 1976–80. All thistle plants growing in the study sites were carefully examined. The number of eggs in an egg batch was recorded when found on a thistle leaf.

Laboratory experiment

A laboratory experiment was conducted to eliminate effects of environmental factors on clutch size. Seventeen and twenty-five pairs of reprodutive adults 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 16L8D in an environmental chamber. Ample amounts of fresh thistle leaves were offered every three days throughout the experiment. For each pair the number of eggs of egg batches was recorded daily until the death of the female.

Also, I dissected reproductive females to examine number of ovarioles in each ovary.

Results

Average clutch size

The average clutch size at site A was significantly larger than that at site F in every year except for 1976 (Table 1). Also, the clutch size changed annually at each site. In the laboratory experiment, females from site A deposited significantly larger egg batches than those from site F. The average size of an egg batch was larger than that in the field over the study period.

Temporal changes in clutch size in the field

The clutch size apparently decreased with the season at the two study sites in every year (Fig. 1). As a result, the number of eggs per egg batch deposited late in the reproductive season was approximately half of that early in the season at site F. It should be noted, however, that there was no significant difference between the two populations when compared for each half-monthly period.

Temporal changes in clutch size in the laboratory

The average clutch size in the laboratory also exhibited a decreasing tendency over the experimental period (Fig. 2). This trend was more apparent in population A. Although a significant difference was detected between the two populations (Table 1), clutch size did not significantly differ when compared for each half-monthly period. For individual females, clutch size tended to decrease with age,

Table 1. Clutch size of *E. niponica* at sites A and F in the field for 1976-80 and that in the laboratory.

Site	Year	*N*	Mean	95% confidence limits
A	1976	150	19.12	18.03-20.21
	1977	256	19.23	18.31-20.16
	1978	256	22.29	21.31-23.28
	1979	237	17.90	16.98-18.81
	1980	486	22.35	21.61-23.09
	Lab.	205	22.98	21.46-24.49
F	1976	173	19.52	18.35-20.69
	1977	646	17.36	16.83-17.89
	1978	533	18.41	17.79-19.03
	1979	497	16.23	15.65-16.80
	1980	206	18.98	17.95-20.01
	Lab.	389	19.83	19.02-20.64

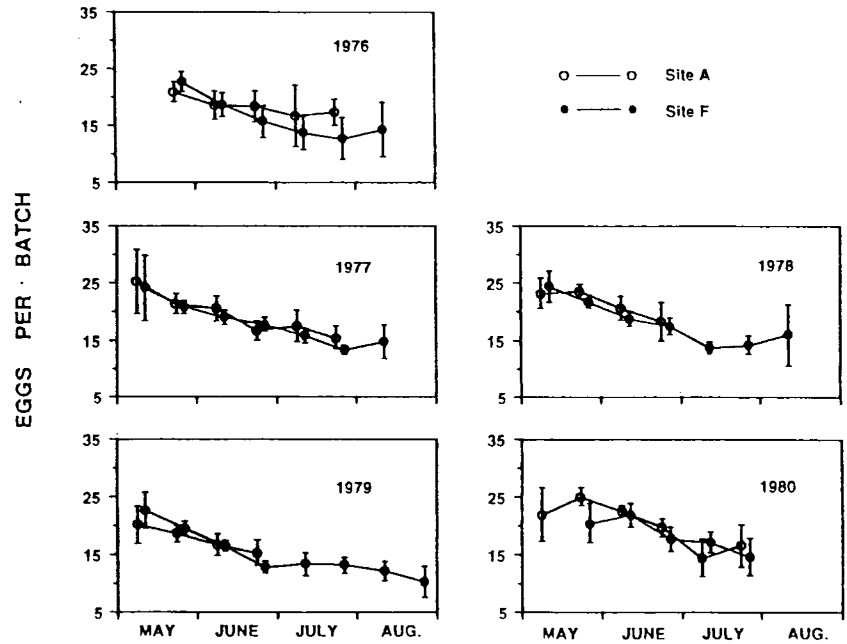

Fig. 1. Temporal changes in the average clutch size for half-monthly periods at site A (○) and site F (•) throughout the reproductive seasons for 1976–80. Vertical bars show 95% confidence limits.

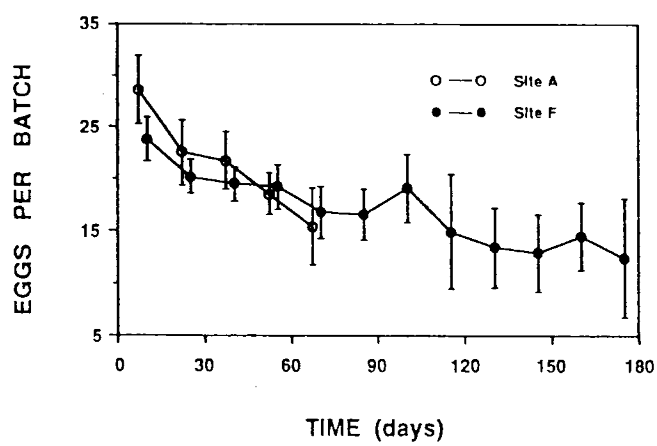

Fig. 2. Temporal changes in the average clutch size of females from site A (○) and site F (•) in the laboratory experiment. Vertical bars show 95% confidence limits.

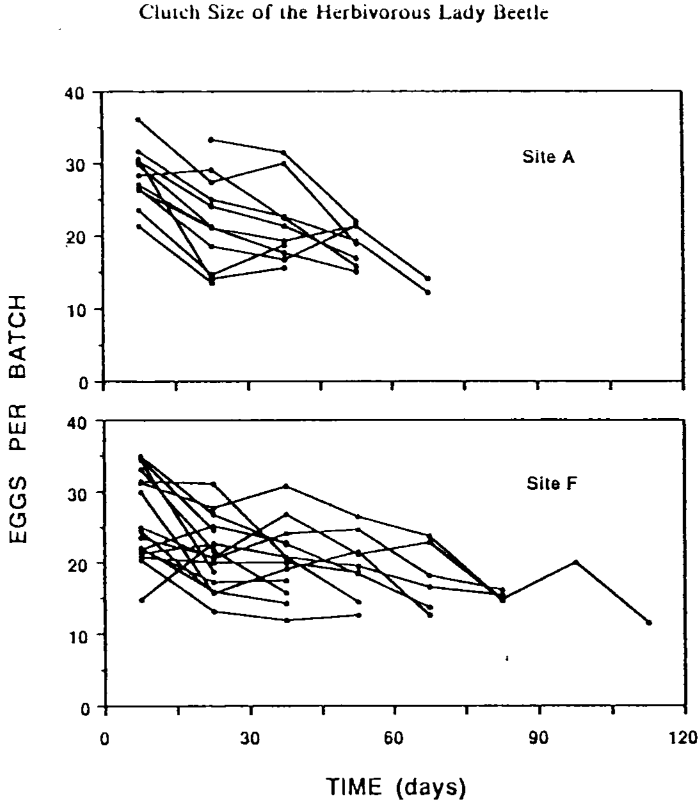

Fig. 3. Temporal changes in the average clutch size for each 15-day interval for individual females during their reproductive lifespans in the laboratory experiment. Females that laid less than 15 egg batches were omitted.

measured as days since the beginning of the experiment, throughout their reproductive lifetimes (Fig. 3). Actually, all females, which laid more than 15 egg batches, showed negative correlations between clutch size and their reproductive age. Of these, six out of nine cases of population A and nine out of sixteen cases of population F were statistically significant (SPEARMAN's rank correlation: $P<0.05$). On the other hand, clutch size was not significantly correlated with female size in the two populations.

The number of ovarioles per ovary did not significantly differ between the two

Table 2. Number of ovarioles per ovary of reproductive females.*

Site	N	Mean±S.E.	Range
A	17	26.47±0.44	24–30
F	19	26.63±0.85	21–36

* Reproductive females were collected on 15 May 1981.

populations (Table 2). Note that the ovariole number coincided closely with the average clutch size at the beginning of the oviposition period both in the field and in the laboratory.

Discussion

Temporal decreases in clutch size

This study clearly demonstrates that the clutch size of *E. niponica* consistently decreases over the oviposition period. As a consequence, the mean number of eggs per clutch deposited late in the season was approximately half of that early in the season at site F (Fig. 1). This seasonal decline resulted in a differential clutch size of the two populations (Table 1). In spite of no inter=population difference for each half-monthly period, the average clutch size of population F was significantly smaller than that of population A. This difference can be accounted for by the differential length of oviposition period. Since females at site F lay their eggs much longer than those at site A (OHGUSHI & SAWADA, 1984), smaller egg batches late in the season present a greater proportion of the total batches at site F. Thus, it should be noted that an estimation of clutch size as a population property of the lady beetle may give erroneous results when all data in the reproductive season are pooled.

Causes of temporally decreasing clutch size

The temporal decline in the clutch size of *E. niponica* also occurred under laboratory conditions, in which ample amounts of fresh leaves were provided during the experimental period. It was, thus, unlikely that environmental factors such as increasing temperature or decreasing food quantity throughout the season principally caused the decreasing clutch size, although effects of leaf quality that may change seasonally remain unclear.

Similar temporal decreases in the clutch size of herbivorous insects under laboratory conditions have been reported in the spruce budworm (OUTRAM, 1971; HARVEY, 1977), the cinnabar moth (RICHARDS & MYERS, 1980), and the checkerspot butterfly (MURPHY *et al.*, 1983). Most studies agreed that maternal effects, especially reproductive age, play a key role in the decreasing tendency over the oviposition period. This explanation is likely to be applicable to the case of *E. niponica*. The laboratory experiment clearly indicates that the clutch size for individual females decreases in an age-dependent manner. On the other hand, clutch size was rather independent of size of adult females.

In the *Epilachna* lady beetle, the clutch size is physiologically constrained by the number of ovarioles (KURIHARA, 1967, 1975). Ovarioles of *E. vigintiocto-maculata* are divided into two categories by their position in an ovary: outer and inner ovarioles (KURIHARA, 1975). Half of them are classified as the outer and the other half the inner. Among basal matured oocytes in ovarioles assigned to one category, one half of the oocytes develop synchronously, and go down to the egg calyx. Subsequently, the other half repeat this process and move to the egg calyx. Eggs from one category of ovarioles in both ovaries are temporally stored together in the egg calyx, then they are oviposited as an egg batch. Clutch size is, thus, generally equivalent to the number of ovarioles per ovary. This is supported by the evidence that the clutch size of *E. niponica* at the beginning of the oviposition period coincided closely with the ovariole number per ovary (Table 2).

The age-dependent decrease in clutch size suggests a relatively heavy physiological senescence by reproductive load for ovipositing females late in the season. It is likely that the physiological senescence of ovipositing females delays egg maturation or resorbs developed oocytes (OHGUSHI & SAWADA, 1985), and that oocytes in each ovariole develop asynchronously. In addition to smaller clutch size, intervals of consecutive egg-layings of individual females tend to be longer late in the oviposition period; consequently, oviposition rate, measured as number of eggs deposited per day, declines with female's reproductive age (OHGUSHI, unpublished).

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