TEMPORAL AND SPATIAL RELATIONSHIPS BETWEEN AN HERBIVOROUS LADY BEETLE *EPILACHNA NIPONICA* AND ITS PREDATOR, THE EARWIG *ANECHURA HARMANDI*

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INTRODUCTION

Natural enemies have long been recognized to play a key role in determining the population level and/or population stability of many herbivorous insects (VARLEY et al., 1973; LAWTON and McNEILL, 1979; STRONG et al., 1984). In contrast to the well-studied interactions between insect parasitoids and prey species in this context (see for reviews HASSELL and WAAGE, 1984; STILING, 1987), fewer field studies have focused on temporal and spatial relationships between predators and specific prey populations (e.g., MATSURA, 1976; TAKAFUJI, 1980; EVANS, 1982). This is mainly due to the practical difficulty of the accurate evaluation of predation in the field. Namely, the prey are often completely consumed and even when not, partially eaten prey are difficult to find. Thus, population studies of herbivorous insects have traditionally put a loss imposed by predation into "unknown" category of mortality causes in a life table (e.g., KLOMP, 1966; KIRITANI et al., 1970; DEMPSTER, 1971; WALOFF and THOMPSON, 1980).

Epilachna (=Henosepilachna) niponica (LEWIS) is a univoltine thistle-feeding lady beetle. OHGUSHI and SAWADA (1985a) showed that arthropod predation acting on chiefly egg and early larval stages is a main factor responsible for differences in new adult density between local populations of the lady beetle. Since egg predation left the characteristic black spot which was a mark of egg shell attached to the surface of leaves, I could obtain an exact number of eggs which were preyed upon by counting these spots. Among arthropod predators detected, an earwig, *Anechura harmandi* (BURR), was the predominant and most active predator. I frequently observed attacks of the earwigs, most of which were fourth instar nymphs, on egg batches of the lady beetle. In this paper I analyze both temporal and spatial relationships between the earwig and the beetle eggs.

STUDY AREA

This study was conducted at Kijiyama (study site F), which is one of the six

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study sites situated in different valleys along the River Ado in central Japan (OHGUSHI and SAWADA, 1981). This site was the highest (350 m in altitude) and most mountainous of all the study plots. Further descriptions of the study site are given in OHGUSHI and SAWADA (1985b).

MATERIALS and METHODS

In this study area, *E. niponica* feeds exclusively on leaves of a thistle, *Cirsium kagamontanum* (NAKAI). Overwintered adult females start to lay eggs in clusters on the undersurface of thistle leaves in early May; the oviposition period extends up to three months (to mid-August). Larvae pass through four instars, and new adults emerge from mid-July to early September and enter hibernation by early November. Seasonal occurrences of adult and immature beetles are given in OHGUSHI and SAWADA (1981, 1984).

Censuses were performed at intervals of 1–3 days throughout the season from early May to early November, in the years 1976-80. I carefully checked all thistle plants growing in this study site. The size of all egg batches was recorded, and batches were labelled for further censuses. The number of eggs that hatched from labelled egg batches was evaluated by counting the empty egg shells that still remained on the leaves after hatching. Egg predation was distinguished from egg losses due to another mortality cause, egg cannibalism by adults and young larvae of the lady beetle, which left characteristic remains of egg shells on the leaves.

The number of earwig nymphs found on thistle plants was counted several times in 1976-77; a more intensive search for earwigs on each thistle plant was made on every census date in 1978-80. Thus, I principally present the data of 1978-80 for detailed analysis.

RESULTS

1. Annual changes in egg predation

First it is useful to summarize the annual changes in egg predation. Egg density, the proportion of eggs preyed upon, and earwig density over the five years, 1976-80,

Table 1. Annual variation in egg density, egg predation, and earwig density for 1976-80.

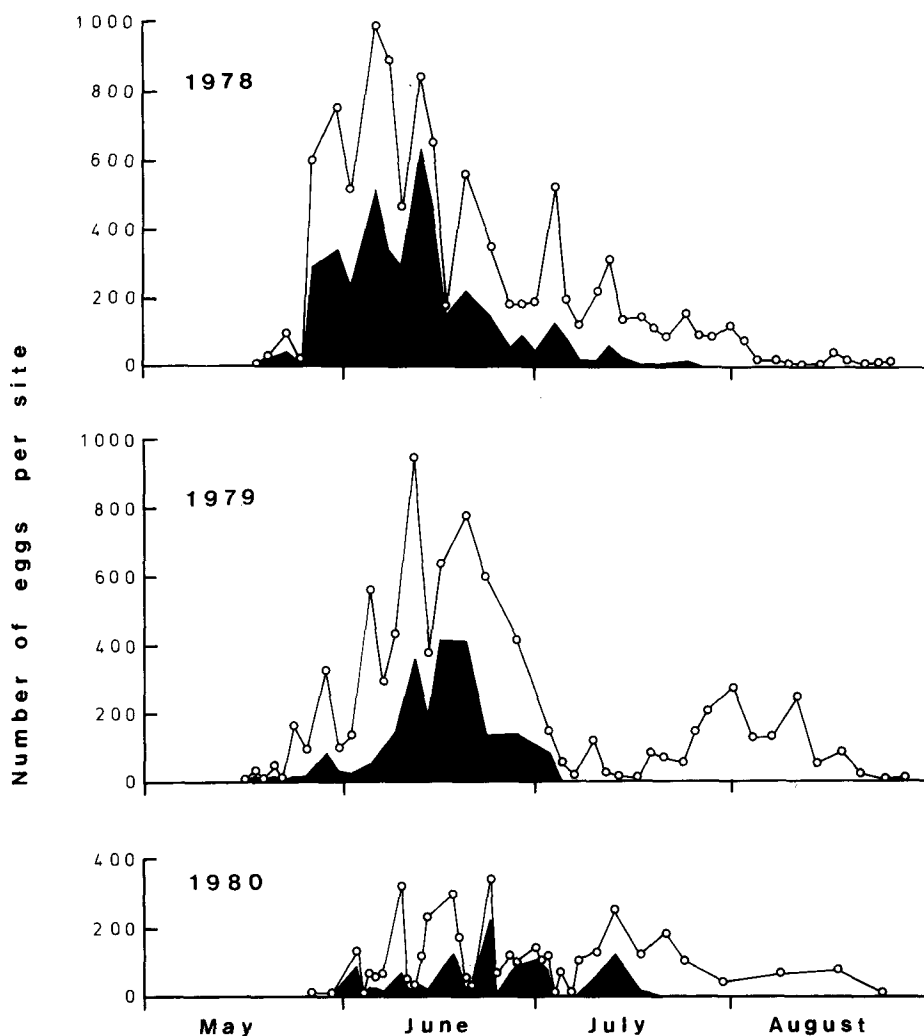|	1976	1977	1978	1979	1980
Egg density (number per shoot)	33.5	30.1	29.7	29.4	24.2
Egg mortality due to predation (%)	60.3	31.8	41.8	29.1	38.4
Earwig density in mid-June (number per shoot)	6.6	7.6	10.5	6.6	4.8

Fig. 1. Numbers of eggs per site (both hatched and dead) on each census date for 1978–80.
Filled area shows the egg loss due to predation.

are shown in Table 1. In spite of little variation in egg densities throughout the five generations, the egg mortality due to predation varied considerably, from 29.1% (1979) to 60.3% (1976) of the total eggs deposited. However, there was no density-dependent operation of egg predation (arcsine-square-root transformed proportion) ($r=0.52$, N.S.). Furthermore, earwig density did not show a significant correlation with egg density ($r=0.40$, N.S.) or egg predation (arcsine-square-root transformed proportion) ($r=0.01$, N.S.) over the five years. The reduction in both egg and earwig densities observed in 1980 compared to those in the previous year was apparently due to habitat disturbance by a large autumn flood occurred in 1979 (OHGUSHI and SAWADA, 1985b), which removed nearly half of the thistle plants growing in this study area.

2. Seasonal changes in egg predation

Now, let us examine temporal and spatial relationships in more detail using the data obtained in 1978-80. Seasonal variations in egg losses due to predation for 1978-80 are shown in Fig. 1. We can see a clear seasonal pattern of egg predation for these three years. Egg predation was evidently restricted in a period from late May to early July. The proportion of egg mortality from predation during this period was conspicuously high. On the other hand, egg predation was of little importance late in the season, so that eggs laid after mid-July were almost free from predation. The differential egg predation associated with the timing of oviposition was particularly clear in 1979, when a number of eggs were laid in the late season. Because they had no possibility of being exposed to predation, the eggs laid after mid-July were omitted from further analyses.

3. Seasonal occurrence in earwig abundance

Seasonal occurrences in nymphs of A. harmandi which visited the thistle plants are shown in Fig. 2. The earwig nymphs built up rapidly in early June, reaching a peak at mid-June. Thereafter, they dropped to a small fraction of these peak numbers by the beginning of July. It should be also noted that this seasonal change in predator numbers was closely synchronized with that of egg predation revealed in Fig. 1. Furthermore, we can see the considerable variation of earwig abundance from one year to another. For instance, the peak number in 1978 was almost six times that in 1980, probably because of the habitat disturbance by the large flood mentioned earlier.

4. Spatial density dependence of egg predation

Then we turn to the problem of whether predatory earwigs respond to spatial variation in local egg density. Spatial density dependence was examined by regressing the arcsine square root transformed proportionate egg predation against egg density. This was done on two spatial scales (see HEADS and LAWTON, 1981): individual thistle plants and clumps of plants (several plants growing nearby and clearly separated from other clumps). The analysis showed there was no indication that egg predation was density dependent at either scale (Fig. 3).

The earwig numbers were plotted against local egg densities at two spatial scales: by thistle plant and thistle patch for 1978-80 (Fig. 4). The earwig density was not an increasing function of local egg density of the lady beetle at either spatial level, suggesting that earwigs do not aggregate to thistle plants or patches associated with high density of prey eggs.

5. Spatial distribution of the earwig and the beetle eggs

In order to determine spatial association between the earwigs and the beetle eggs over the study site, I calculated IWAO's (1977) index of spatial overlap (γ), which was theoretically derived from LLOYD's (1967) mean crowding and also identical to
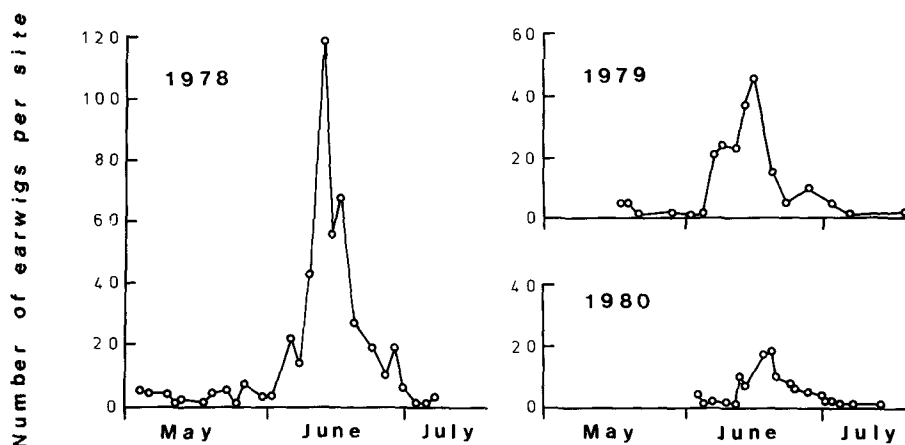
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Fig. 2. Seasonal occurrence of earwigs, *Anechura harmandi*, on thistle plants per site for 1978–80.
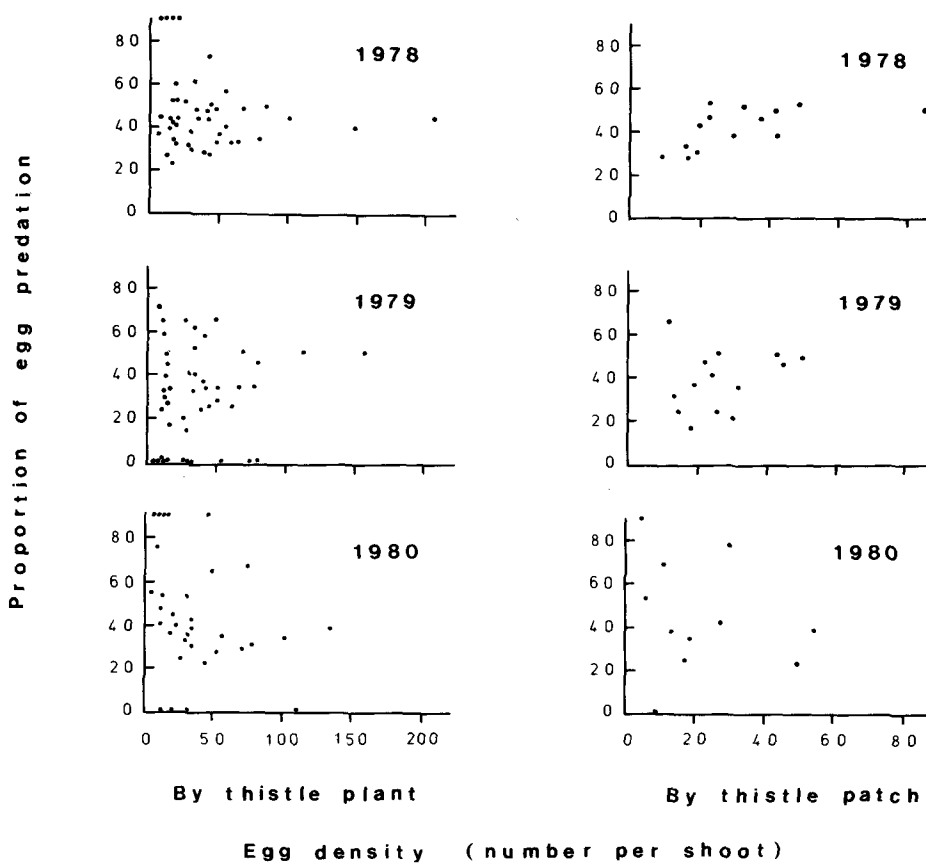

Fig. 3. Relationship between egg predation (arcsine-square-root transformed proportion) and local egg density (number per shoot). By thistle plant with eggs (1978: $N=51$, $r=0.05$, NS; 1979: $N=52$, $r=0.27$, NS; 1980: $N=34$, $r=-0.33$, NS). By thistle patch (1978: $N=14$, $r=0.37$, NS; 1979: $N=14$, $r=0.25$, NS; 1980: $N=12$, $r=-0.26$, NS).
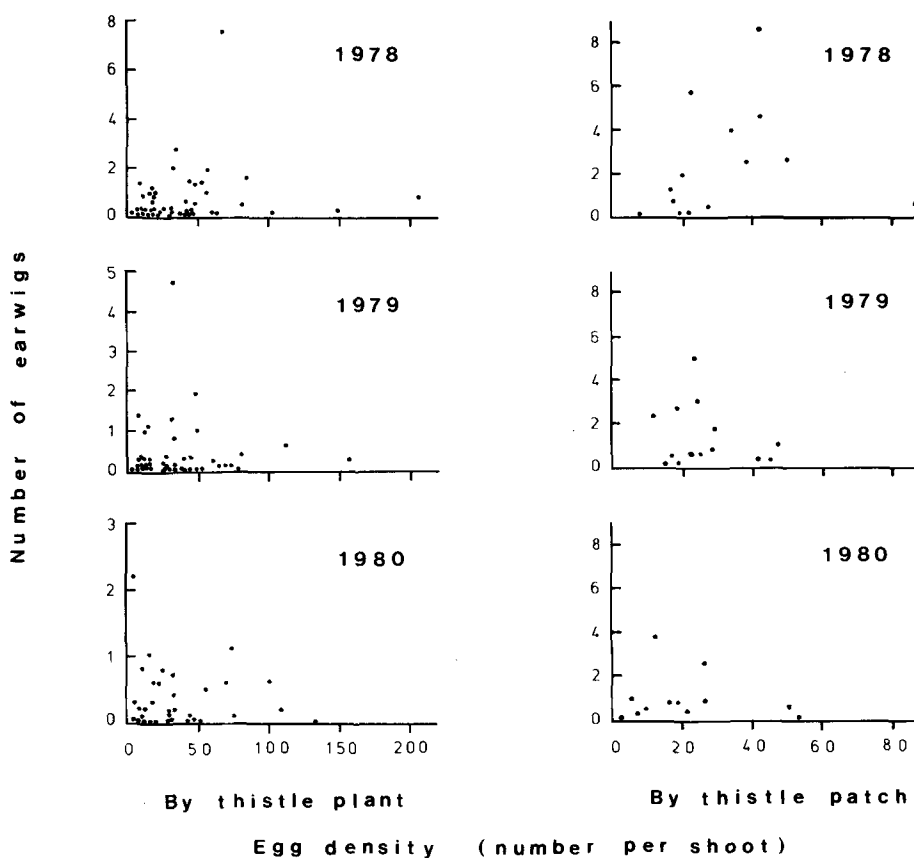
Fig. 4. Relationship between the number of earwigs found on thistle plants per day and local egg density (number per shoot). By thistle plant with eggs (1978: $N=51$, $r=0.15$, NS; 1979: $N=52$, $r=0.03$, NS; 1980: $N=34$, $r=-0.06$, NS). By thistle patch (1978: $N=14$, $r=0.12$, NS; 1979: $N=14$, $r=-0.14$, NS; 1980: $N=12$, $r=-0.11$, NS).

PIANKA's (1973) measure of niche overlap. The value of γ varies from 0 (when the distributions of the two species do not overlap) to 1.0 (when the distributions are completely overlapping).

Seasonal changes in spatial association between the two species for 1978–80 are shown in Fig. 5. All the values obtained were below 0.5 throughout the season, and did not show a definite seasonal change. This again implies that the earwigs are distributed rather independently of local abundance of the beetle eggs over the study site.

6. Factors influencing local earwig density

The findings obtained above suggest that the earwigs are not closely related to eggs of the lady beetle distributed patchily over the study area, so that egg predation did not operate in a density dependent manner. Then, the problem addressed next is
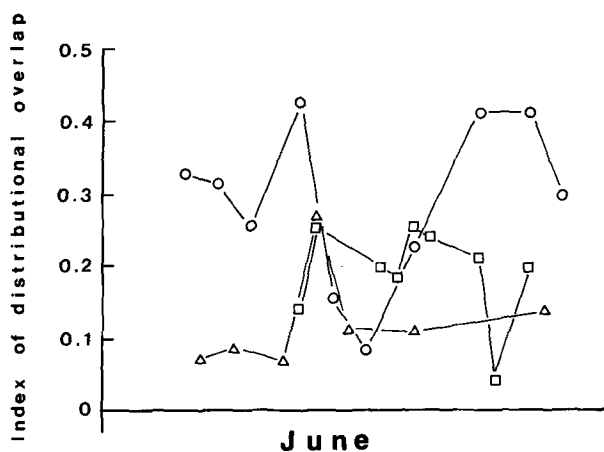
Fig. 5. Seasonal changes in the index of distributional overlap (γ) between egg batches and earwigs on each thistle plant. (O), 1978; ($\triangle$), 1979; ($\square$), 1980. The value of γ varies from 0 (when the distributions do not overlap at all) to 1.0 (when the distributions overlap completely) (Iwao, 1977).
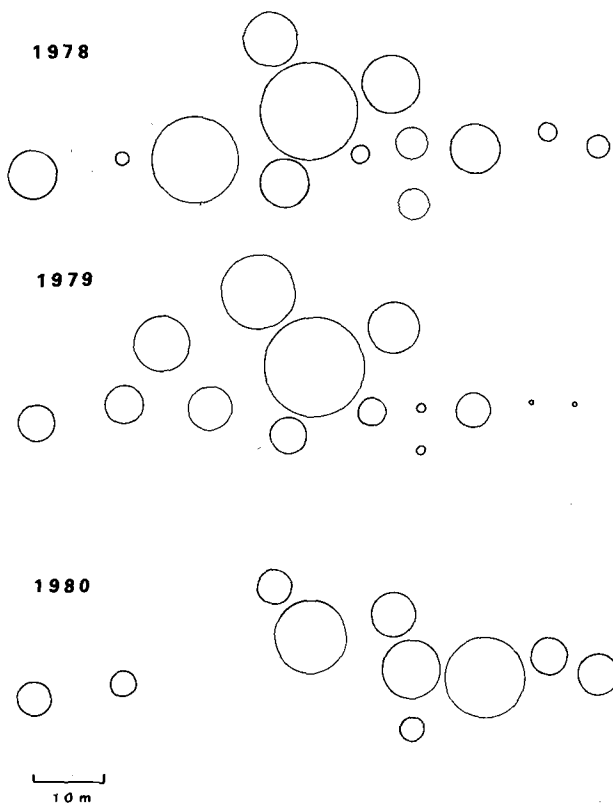

Fig. 6. Illustrations of spatial dispersion of earwigs for 1978–80. The size of each circle located at the position of each thistle patch indicates the relative density of the earwig.

Table 2. Correlations in earwig density (number per shoot) on each thistle patch between pairs of years.

	F	P	r^2
1978 vs. 1979	83.9	0.0001	0.903
1978 vs. 1980	24.2	0.0008	0.729
1979 vs. 1980	20.0	0.0016	0.690

which factors determined local earwig density.

The spatial distributions of earwigs on each thistle patch for 1978–80 are illustrated in Fig. 6. High earwig densities were consistently associated with particular localities over the three year period. This is confirmed by the correlation analysis of the earwig density on each thistle patch between different years (Table 2). We can see a significantly positive correlation between the earwig density of one year and that of another. Some differences in the spatial dispersion and abundance of the earwig in 1980 compared to other two years were undoubtedly due to the habitat perturbation by the large flood in the previous autumn.

<center>DISCUSSION</center>

In this study, I focused on the earwig, *A. harmandi*, as the egg predator of the lady beetle, *E. niponica*. In fact, two other species (larvae of a coccinellid beetle, *Harmonia axyridis* (PALLAS), and a cantharid beetle, *Athemus suturellus* (MOTSCHULSKY)) were seen attacking the beetle eggs in the field, and an additional three species (a ground beetle, *Amara congrua* (MORAWITZ), and two cantharid beetles, *Cantharis lewisi* (PIC), and *Themus episcopalis* (KIESENWETTER)) were identified as possible egg predators in laboratory experiments (OHGUSHI, 1986). However, compared to the earwig all of these were negligible in numbers as thistle plant visitors in the study area. In addition, a careful census for egg predators at several nights in June 1978 revealed no other possible predators. Hence, it is likely that nymphs of the earwig were responsible for most of the egg deaths due to predation. This is strongly supported by the close synchronization between the occurrences of earwigs and egg predation (see Figs. 1 and 2). The importance of earwigs as an egg predator of the lady beetle has also been reported in other populations (NAKAMURA and OHGUSHI, 1981; KIMURA and KATAKURA, 1986; SHIRAI, 1987).

A laboratory experiment showed that an individual earwig nymph consumed on average 27 eggs of *E. niponica* per day (OHGUSHI, unpublished). However, the present study revealed that the egg predation did not act in a density dependent manner at least over the five years. This implies that the heavy predatory pressure on the egg stage apparently suppresses the population density of the lady beetle but contributes little to the remarkable stability of egg population over years (Table 1).

Recent studies have emphasized individual differences, which have long been ignored by traditional studies of insect population dynamics, as a crucial factor in determining population dynamics generally (ŁOMNICKI, 1978, 1980; HASSELL and MAY, 1985; May, 1986). In this context, the results presented here clearly showed temporal heterogeneity of egg predation. The heavy predation observed was mostly restricted to a period from late May to early July. This time-restricted operation of predation, in turn, results in a large variation in egg mortality within a population. Egg cohorts after mid-July are certainly no longer vulnerable to earwigs. Such temporal heterogeneity in egg mortality, producing cohort differences in fitness, could play an important role in determining the differential reproductive schedules between the two study sites (OHGUSHI, unpublished).

There has been an increasing interest of spatial density-dependent mortality imposed by aggregating natural enemies, which has a profound effect of population dynamics of host species (HASSELL and MAY, 1974; HASSELL, 1978; HEADS and LAWTON, 1981; but see REEVE and MURDOCH 1985; MORRISON and STRONG, 1980). The present study demonstrated that both the proportion of egg predation and earwig density were independent of local egg density on at least two spatial scales. This is presumably due to a lack of aggregation of the earwig to good patches with high egg densities of the lady beetle. An explanation for this should be sought in the habits of the earwig. First, the earwig is a polyphagous predator, in which food preference is largely dependent on the relative abundance of possible food items. In general, earwigs feed on not only harbivorous insects, such as aphids (SUNDERLAND, 1975; SUNDERLAND and VICKERMAN, 1980), eggs and larvae of the broom beetle (DEMPSTER, 1960) and of the broom moth (AGWU 1974), but also plant materials including pollen, flower petals and young leaves (SUNDERLAND, 1975). In this study area, egg and young larvae of the lady beetle are evidently an abundant food for the earwig on thistle plants. However, the relative importance of the beetle eggs as food items for old nymphs of the earwig still remains unclear.

Second, newly-hatched nymphs of *A. harmandi* are under maternal care in the nest, which is usually situated under gravel on sandy deposits as riverbanks. After dispersing from their nests in late May, the earwig nymphs become principally arboreal foragers, climbing on herbs and shrubs which grow along riverbanks (KONO, *personal communication*). Their foraging area seems to be more or less restricted to the area adjacent to their nest sites. This is supported by the fact that the earwig nymphs tend to concentrate on particular localities associated with sandy deposits suitable for their nests (see Fig. 6). Such favourable nest sites are, however, unlikely to persist for long periods, because of habitat disturbance by large floods such as occurred in autumn 1979, which resulted in a lower correlation between local earwig density in 1979 and that in 1980.

At the population level, the earwig is undoubtedly responsible for a large egg loss and, thus, is an important agent in suppressing the population level of the lady beetle.

On the other hand, at an individual level, it does not respond tightly to the beetle eggs distributed patchily over the habitat, probably because of its polyphagy and site-dependent foraging.

SUMMARY

The relationships between egg predation of an herbivorous lady beetle *Epilachna niponica* (LEWIS) and its predator, the earwig *Anechura harmandi* (BURR), were examined in both time and space. In spite of little annual changes in egg densities, egg mortality due to predation varied considerably. There was no clear relationship between the earwig density and the proportionate predation over the five years. The seasonal occurrence of earwig nymphs on thistle plants, however, was closely synchronized with that of egg predation. Predator attacks on the beetle occurred in a time-restricted manner. Thus, later cohorts mostly escape from heavy predatory pressure. No spatially density-depenent egg predation was detected at the level of either thistle plants or thistle patches. Furthermore, there was no indication of aggregative behaviour of the earwig in response to local egg density. The earwig density was more likely to be associated with particular localities with sandy deposits available for its nest site.

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ヤマトアザミテントウとその卵捕食者であるコブハサミムシの時間的・空間的関係

大 串 隆 之

滋賀県北西部の安曇川流域で, アザミを食草とするヤマトアザミテントウ（コブオオニジュウヤホシテントウ）の個体群調査を1976年から5年間にわたって行い, 卵捕食者として最も重要なコブハサミムシとの関係について調べた.

調査期間を通して卵密度はほぼ一定であったが, 捕食率は大きな年次変化（30％―60％）を示した. しかし, 捕食率には密度依存性は認められなかった. 卵捕食率の季節変化は, アザミ上で見つかるハサミムシの個体数とよく同調しており, 捕食された卵はハサミムシが出現する特定の時期（5月下旬から7月上旬）に限られていた. このため, 捕食にさらされるのは繁殖期の前半に生まれた卵だけで, 遅く生まれた卵は捕食から逃れていた.

捕食率と卵密度との関係を株単位およびパッチ単位で調べたところ, 両者の間には密度依存性は検出されなかった. また, ハサミムシも卵密度の高い株やパッチに集中するような傾向は見られなかった. 調査地内部でみると, 毎年特定の場所でハサミムシの個体数が多く, そこは彼らの営巣場所に好適な小石混じりの砂地であった.