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ARTHROPOD PREDATION LIMITS THE POPULATION DENSITY OF AN HERBIVOROUS LADY BEETLE, *HENOSEPILACHNA NIPONICA* (LEWIS)[1]

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INTRODUCTION

It has been widely accepted that populations of a given insect species have different demographic patterns from locality to locality. For herbivorous insects, some studies have revealed that population density varies in different types of habitat (e.g., DEMPSTER, 1971; WHITTAKER, 1971; GILBERT, 1980; RANDALL, 1982). Several authors have focused on the abundance and effectiveness of natural enemies associated with each type of habitat as a primary factor maintaining local populations at different densities (e.g., POLLARD, 1971; DEMPSTER and COAKER, 1974; SMITH, 1976; EICKWORT, 1977). Actually, a number of attempts of field release of natural enemies for biological control have been shown to reduce population densities of insect pests of various crops (DEBACH et al., 1971; DEBACH, 1974). Furthermore, field experiments excluding predators and/or parasites by the application of insecticides have resulted in sharp increases in population densities of herbivorous insects (DEMPSTER, 1969; MACPHEE and MACLELLAN, 1971; DEBACH, 1974; EHLER and VAN DEN BOSCH, 1974; MCCLURE, 1977).

The population density of a thistle-feeding lady beetle, *Henosepilachna niponica* (LEWIS) varies considerably from one habitat to the next. The local population living in a climax forest of Asiu, the northern part of Kyoto Prefecture, persisted at a relatively low density which rarely caused food depletion (NAKAMURA and OHGUSHI, 1979). Meanwhile, in Nyû-dani area which is only 20 km from Asiu, some thistle plants were completely defoliated by the lady beetle at the time of adult emergence in the years of high density (OHGUSHI and SAWADA, 1981). Furthermore, the population which was artificially introduced in Kyoto city from Asiu has reached a very high density so that most thistles have been seriously damaged by its feedings within a few years of the introduction (SAWADA, 1984).

Since 1976 we have been studying several local populations under different habitats including Nyû-dani area (study site A) to clarify the basic population processes and life history strategy of *H. niponica* (OHGUSHI, 1983; OHGUSHI and SAWADA, 1981, 1984, 1985).

[1] Recently, KATAKURA (1981) reclassified *Henosepilachna pustulosa* (KÔNO) into three distinct species and some unsettled populations. In this paper, the species name follows his classification.

Our previous paper reported the demographic attributes of local populations as shown by adult marking experiments. It suggested that the population density of new adults tended to decline from downstream to upstream areas in altitudinal order (OHGUSHI and SAWADA, 1981). In this paper, we examine what kind of factors cause such difference in new adult density. In particular, we focus on the action of natural enemies in each habitat.

MATERIALS AND METHODS

The lady beetle

H. niponica has usually one generation a year and exclusively feeds on leaves of a thistle, *Cirsium kagamontanum* (NAKAI) in the study area. After emergence from hibernation, in early May, reproductive females begin to lay eggs in clusters containing 20–40 eggs on the underside of thistle leaves. The larvae pass through four instars, then pupate on thistle plants. New adults begin to emerge in early July, feed on thistle leaves, and enter hibernation by early November (OHGUSHI and SAWADA, 1981, 1984).

Egg and adult counts

The census period extended from early May to early November during the years of 1976–1980. At intervals of 1 to 3 days, each thistle plant growing in the study plot was carefully examined and the numbers of eggs, fourth instar lavrae, pupae and pupal exuviae were counted. The size of all egg batches on leaves were recorded when they appeared and labelled to prevent double counting. Thereafter, they were checked at each census. The number of eggs hatched was evaluated by counting the empty egg shells which still remained on the leaves after hatching. Eggs cannibalized by adults and young larvae can be recognized by the basal parts of egg shells attached to the leaves. Arthropod predators were often observed feeding on eggs in the field; most of them were earwigs. Eggs killed by them can be easily distinguished by the characteristic traces of predation. Unhatched eggs that were blackened and shrivelled were occasionally observed after late June; this kind of egg death was probably due to high temperature in mid-summer. The total number entering the new adult stage was estimated by the JOLLY-SEBER method using the data of the mark-release-recapture censuses for adult populations. The detailed procedures for the adult marking experiments have been described in OHGUSHI and SAWADA (1981).

Predator exclusion experiments in the field

The field experiments were conducted in 1978 to evaluate the impact of arthropod predation on the immature stages in study site F.

Experiment **1.** On 31st May, ten thistle plants were selected randomly and each of them was covered by a nylon organdy cage which was large enough to allow further foliage growth. Two pairs of reproductive adults were introduced into each cage for oviposition. On following censuses, the numbers of eggs, fourth instar larvae, and pupae on the plants were carefully checked until the last emergence of adults. Survival rates of the immature stages in the cages were compared with those of the natural population exposed to various kind of predators.

Experiment 2. Three thistle plants, well separated from each other and with approximately the same height and the same numbe of leaf nodes were selected on 8th June. One of them was also covered by a nylon organdy cage as in Experiment 1. The other two plants were left to be exposed to all mortality sources. Forty newly-hatched larvae were placed on a leaf at the middle height of each thistle plant. The larval disappearance was recorded on both the predator-free and control plants until the last emergence of adults.

Study area

This study was conducted in six study sites (sites A–F) located in five different valleys along the River Ado and its branch. The population density was compared between site A (220 m in altitude) and site F (350 m in altitude) as examples in the downstream and upstream habitats, respectively. A map of the study area and more detailed description of study sites are given in Ohgushi and Sawada (1981).

Results and Discussion

Population densities of the egg and new adult stages were compared between the downstream site A and the upstream site F over the five years, 1976–1980 (Table 1). The average density of the new adult population at site A was significantly higher than that at site F although the average egg density was nearly identical in the two populations. Actually, some thistle plants at site A were considerably defoliated by the lady beetle at the time of adult emergence. In contrast, there were few thistles with serious damage at site F throughout the study period. Since egg densities were similar, the marked difference in new adult density between the two areas was chiefly due to differences in mortality of the immature stages.

The proportions of eggs killed by arthropod predators, by cannibalism, and by other causes at the two sites are showin in Fig. 1. Egg mortality of population A was lower

Table 1. Population densities (no. per 100 thistle shoots) on egg and new adult stages of downstream population A and upstream population F over the five years, 1976–1980.

Stage	Population	1976	1977	1978	1979	1980	Avarage over five years	t	P
Egg	A	3222.5	3397.3	3191.6	1691.6	3417.6	2984.1	0.13	NS
	F	3351.4	3011.8	2965.3	2939.9	2417.3	2937.1		
New adult	A	533.7	803.4	434.1	341.0	821.4	586.7	4.48	<0.008
	F	83.9	179.4	158.6	38.0	196.9	131.4		

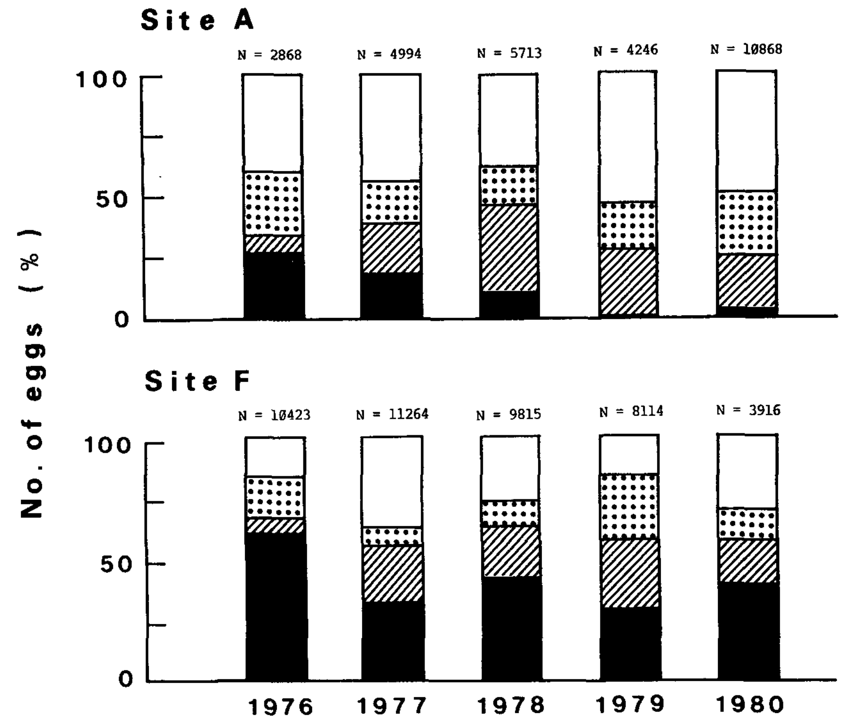

Fig. 1. Proportions of eggs hatched and killed by identified mortality factors over the five years, 1976–1980, at downstream site A and upstream site F. (■), eggs killed by arthropod predators; (▨), eggs cannibalized by adults or young larvae; (░), eggs blackened and/or shrivelled; (□), eggs hatched.

than that of population F. The overall mortality during the egg stage ranged from 46.2–61.2% (54.4%, on average) at site A and 62.5–83.2% (74.1%, on average) at site F. Of these discriminated mortality causes, arthropod predation was the most important factor responsible for larger egg losses at site F. Actually, 34.9–72.5% (54.3%, on average) of egg losses was due to predation at site F over the five years; but only 1.5–45.1% (20.1%, on average) at site A. The seasonal occurrence of cannibalism well synchronized with predation, and there was a compensatory relation between the egg mortalities caused by the two components (OHGUSHI, 1983). Thus, egg cannibalism was a more significant mortality factor in population A which was free from heavy predation. The importance of arthropod predation on egg mortality has also been supported by predator exclusion experiments (NAKAMURA and OHGUSHI, 1981).

Mortality in population F during the early larval period (1st–3rd instar), which ranged from 68.8–81.6% (78.0%, on average), was considerably higher and more constant than that in population A, which ranged from 26.5–57.0% (45.7%, on average) (OHGUSHI, 1983). As larvae grew, larval losses decreased considerably. Hence, the mortality during the late larval and pupal stages was insignificant compared to the early larval mortality. Two parasitic wasps, *Pediobius foveolatus* (CROWFORD) and *Watanabeia afissae* (WATANABE), sometimes killed fourth instar larvae; however, they had little effect on

Table 2. Comparison of survival rates on successive immature stages between the caged (predator-free) population in Experiment 1 and the natural population exposed to predation.

	Survival rate (%)		
	Egg	1st–3rd instar	4th instar-adult*
Caged population	47.4	66.1	44.1
Natural population	26.8	21.7	81.8
G	58.8	159.0	69.8
P	<0.001	<0.001	<0.001

* Adult numbers of the natural population were obtained from adult beetles marked in the field.

the overall larval mortality (OHGUSHI, 1983).

Survival rates of the immature stages obtained from the predator-free population in Experiment 1 and those from the natural population at site F are given in Table 2. During the study course, there was no evidence of intensive defoliation of thistle at this plot. The egg and early larval survival rates for the caged population were significantly higher than those of the natural population exposed to arthropod predators. In contrast, there was significantly higher survival rate from the fourth instar to adult emergence in the field. The higher mortality during the late larval period on the caged plants could be almost attributed to starvation due to severe defoliation of the thistle. The numbers

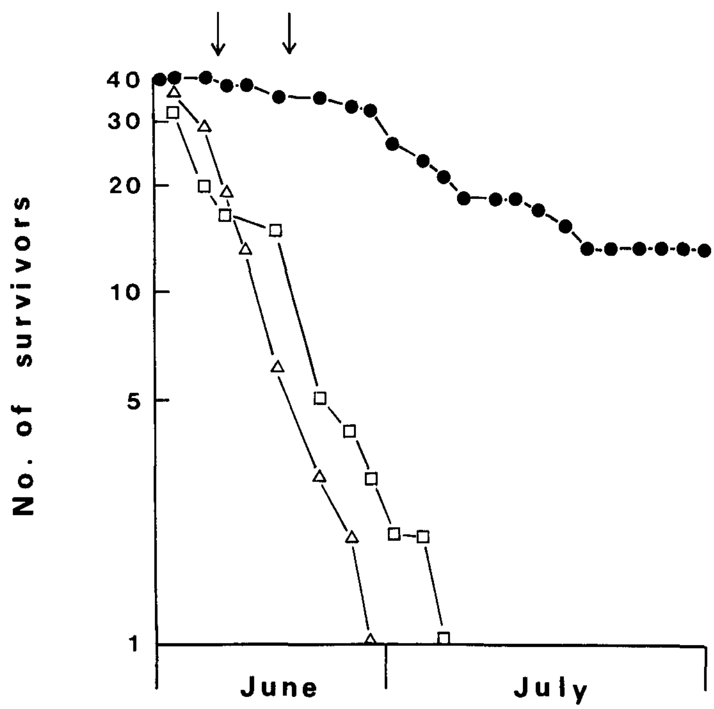

Fig. 2. Survivorship curves of the forty newly-hatched larvae inoculated on the caged and uncaged thistle plants in Experiment 2. (●), caged (predator-free) thistle; (△, □), uncaged thistle. Vertical arrows show occurrence of heavy rainfall.

of survivors on each thistle plant in Experiment 2 are plotted against time (Fig. 2). The result from this field experiment also suggested a marked effect of arthropod predation on larval disappearance. On 1st June, 65% of the introduced larvae remained on the thistle in the cage; but thereafter the number gradually decreased because of intensified intraspecific competition for food due to defoliation as in Experiment 1. The number of larvae on the two uncaged plants rapidly decreased soon after inoculation; only a small fraction (5% and 2.5% of the introduced larvae) remained on 1st July. In contrast to the marked effect of predation, no notable loss of larvae was observed on 13th and 20th June when heavy precipitation occurred (Fig. 2). Thus, heavy rainfall was unlikely to be a significant factor accounting for larval losses in natural populations. There remains a possibility that larval losses in the field could be due partly to larval dispersal. However, this is unlikely, because larval marking experiments wihch evaluated dispersal behaviour of larvae in the field revealed that larvae of the lady beetle rarely dispersed from thistle plants where they hatched even though the leaves were markedly damaged by them (OHGUSHI, 1983).

Finally, arthropod predators causing high mortality during the immature stages were identified. The following species were observed feeding on eggs and larvae of *H. niponica* in the field: larvae of the earwig, *Anechura harmandi* (BURR), larvae of the coccinellid beetle, *Harmonia axyridis* (PALLAS), ground beetles, *Dicranoncus femoralis* (CHAUDOIR), *Amara congrua* (MORAWITZ), predaceous stink bugs, *Picromerus lewisi* (SCOTT), *Adelphocoris triannulatus* (STÅL), *Piocoris varius* (UHLER), and spiders, *Theridion kompirense* (BÖS. et STR.), *Xysticus croceus* (FOX). Of these, the earwig was the most important and predominant predator in the study area. The population density of the earwig usually approached a peak on the host plant at the time of hatching of the lady beetle, i.e., from early June to mid-June. During this time, we frequently observed attacks of the earwig on eggs and young larvae of the lady beetle on thistles. The population density of the earwig was significantly higher at the upstream site F than at the downstream site A throughout the study (Table 3). These observations suggest that higher egg and larval mortalities were mainly caused by the earwig. The importance of the earwig as a mortality agent during the early immature stages has also been shown in other localities (NAKAMURA and OHGUSHI, 1981; SHIRAI, unpublished).

The higher level of predation in population F is more likely to be associated with higher diversity of background vegetation maintaining predator's fauna (OHGUSHI and SAWADA, 1981). All of the arthropod predators described above were polyphagous ones; they are maintained on alternative prey species whose abundance is greatly influenced

Table 3. Mean density of the earwig, *Anechura harmandi* (no. per 100 thistle shoots) observed on thistle plants in July at the two study sites over the five years, 1976–1980.

Site	1976	1977	1978	1979	1980	Average	*t*	*P*
A	1.9	2.2	3.7	0.5	1.6	2.0	4.90	<0.002
F	6.6	7.6	10.5	6.6	4.8	7.2		

by diversity of ground flora in each habitat. For instance, DEMPSTER and COAKER (1974) showed that arthropod predators on brassica crops grown in different background vegetation significantly influenced survival during the immature stages of the cabbage butterfly, *Pieris rapae*, which was important in determining pest status of this insect. Furthermore, EICKWORT (1977) tried to find possible limiting factors for populations of a relatively rare species of milkweed beetle, *Labidomera clivicollis*, by means of field experiments which excluded natural enemies using cages and sticky-trap barriers. She concluded that arthropod predation related to diversity of plants in the immediate environment was the most important factor accounting for its lower density as compared with the closely allied pest, Colorado potato beetle.

The results obtained here generally agree with the importance of effective predation in reducing population density. We conclude that arthropod predation during the immature stages is the main factor maintaining the different densities of new adults between the two local populations of the lady beetle. However, this does not mean that the predation is the only factor determining the relative population density in relation to food supply. The lady beetle has an effective regulatory mechanism which stabilizes egg density with respect to resource abundance (OHGUSHI and SAWADA, 1985). Thus, the egg density per unit food resource was almost equivalent in the two study sites (Table 1). Consequently, arthropod predation associated with each habitat has an important role in differentially limiting survival during the immature stages, resulting in the marked difference in population density of new adults of the lady beetle between the two habitats.

SUMMARY

1. The possible impact of arthropod predation on inter-population variation in adult density of a thistle-feeding lady beetle, *Henosepilachna niponica* (LEWIS) was evaluated by means of predator exclusion experiments conducted in the field.

2. The population density of newly-emerged adults at one habitat in the upstream area (site F) was significantly lower than at another in the downstream area (site A) although the egg density was nearly identical in the two habitats.

3. In the habitat with lower adult density, egg mortality was higher due to higher levels of predation. A predator exclusion experiment demonstrated that arthropod predation was the main factor causing high mortality during the immature stages, and physical factors such as heavy rains were unlikely to influence larval survivals.

4. Earwigs, ground beetles, predaceous stink bugs, and spiders were identified as the main predators in the study area. Of these, an earwig, *Anechura harmandi* (BURR) was more predominant than other predators and was significantly more abundant in the habitat with low adult densities.

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コブオオニジュウヤホシテントウの個体群密度を制限する要因としての捕食者の役割

大串隆之・沢田裕一

カガノアザミを食草とするコブオオニジュウヤホシテントウの地域個体群について滋賀県の安曇川流域で調査を行い，新成虫密度のレベルを決める捕食者の役割を調べた．下流域と上流域に位置する二つの調査地（AとF）の卵密度はほぼ同じであったが，新成虫密度は調査地Fの方が有意に低かった．ここでは卵期の捕食圧が大きく，このため死亡率はより高かった．捕食者除去の野外実験の結果から，卵および幼虫期の高い死亡率は主にハサミムシ，カメムシ，クモなどの捕食者によるもので，降雨などの物理的要因の影響は小さいようであった．特に，コブハサミムシが最も個体数の多い捕食者で，その個体群密度は調査地Fの方が有意に高かった．以上の結果から，両調査地間で見られた新成虫密度の有意な差は，未成熟期に作用する捕食圧の違いによるものと推測される．