Res. Popul. Ecol. (1983) Suppl. 3, 46—60.

COMPARATIVE STUDIES ON POPULATION DYNAMICS OF CLOSELY RELATED PHYTOPHAGOUS LADY BEETLES IN JAPAN

Koji NAKAMURA

Ecological Laboratory, Faculty of Science, Kanazawa University
1-1 Marunouchi, Kanazawa 920, Japan

INTRODUCTION

Detailed studies of differences in demographic characteristics between closely related species or between populations within the same species are most profitable for understanding of population dynamics and evolution of life history traits (STEARNS, 1976, 1977; TINKLE and BALLINGER, 1972; EHRLICH et al., 1975). The phytophagous 28-spotted lady beetles including *Henosepilachna vigintioctopunctata* and the so-called *H. vigintioctomaculata* complex (hereafter abbreviated as Hv-complex) are very promising as materials for studying speciation and comparative demography. The Hv-complex has thus attracted much attention to the process of speciation because of its remarkable variations in both external morphology and biology (e.g. KATAKURA, 1977, 1981). Empirical study of population dynamics on these phytophagous beetles has lagged behind taxonomic investigations, but now information gathered over a decade is available and a preliminary comparison of ecological and evolutionary strategies of the beetles can be made. The purpose of this paper is to summarize recent knowledge on the taxonomy and biology of the *Henosepilachna* beetles in Japan. The paper also aims to throw light on the diversity in demographic characteristics of these phytophagous lady beetles.

TAXONOMY AND BIOLOGY OF *Henosepilachna* BEETLES IN JAPAN

Since many reviews are available for this interesting group of beetles (EHARA, 1952; KOYAMA, 1962; SASAJI, 1971; KATAKURA, 1977, 1981), I do not intend to repeat the details but only to summarize the recent knowledge of the beetles.

H. vigintioctomaculata complex: *H. vigintioctomaculata* (hereafter abbreviated as Hvm) is a serious pest of potato in the northern part of Japan, southern part of Soviet Far East, north China and Korean Peninsula (Fig. 1-a). In 1937, KÔNO described a new species *Epilachna pustulosa* from central Hokkaido. The new species was evidently closely related to Hvm. But, it had two distinct characters not found in Hvm: first, the hind margin of elytron was extremely expanded laterally with a distinct tubercle on the base of the expansion, and secondly, *E. pustulosa* fed on the wild thistles (*Cirsium* spp., Compositae), whereas Hvm fed on solanaceous crops.

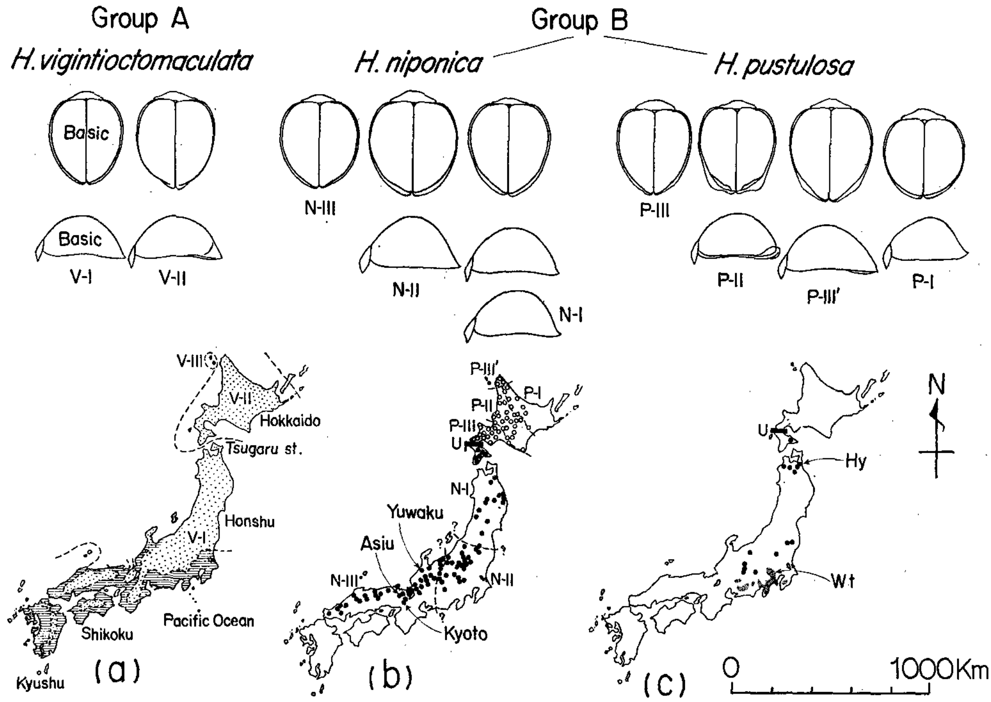

Fig. 1. Variation in the elytral shape and geographic distribution of *Henosepilachna vigintioctomaculata*-complex and *H. vigintioctopunctata* in main islands of Japan. (a): *H. vigintioctomaculata* (group A, dotted area) and *H. vigintioctopunctata* (hatched area). (b): the members of group B, *H. pustulosa* (open circle) and *H. niponica* (solid circle). Broken lines show the approximate position of boundaries of forms of these species. (c): *H. yasutomii* (Hy, solid circle) and unsettled population, Wt (hatched area). Abbreviation refers to the form. u: unoccupied zone by the thistle feeders. (These figures were redrawn from KATAKURA (1981) by his courtesy)

WATANABE and SAKAGAMI (1948) were first to open an argument about the so-called Hv-complex, reporting that the thistle-feeding beetles collected from different localities of Hokkaido were quite variable in their elytra shape and the food habit. Subsequent studies have revealed that the thistle-feeders occurred sympatrically with Hvm in Honshu and Hokkaido, the two main islands of Japan, and the Hv-complex consisted of more than ten local forms of closely allied lady beetles (Fig. 1). It has been also revealed that KÔNO's nominate form of *pustulosa* is one of these local forms: it is equivalent to form P-II in KATAKURA's (1981) system (Fig. 1-b). The external morphology of the thistle-feeders, such as elytra shape, coloration of legs and shape of elytra maculation was quite variable from locality to locality, but not so variable in Hvm (Fig. 1).

The diversity in the food plants of the Hv-complex is considerable: Hvm and the thistle-feeders mainly depend on cultivated potato and wild thistles respectively, although fourteen species (all thistles combined as *Circium* spp.) belonging to six families have been documented as host plants of the Hv-complex under natural conditions. The thistle feeders often invade potato fields cultivated near thistle stands. The beetles collected from the thistles can feed on potato, blue cohosh (*Caulophyllum robustum*, Berberidaceae) and some solanaceous plants under laboratory conditions. The thistle-feeders collected from different localities show different acceptability to these plants. Moreover, IWAO (1959) and IWAO and MACHIDA (1991) detected a considerable individual variation in potato acceptability of the thistle-feeders even within a population. In contrast to the thistle-feeders, Hvm did not accept the thistles either under natural or laboratory conditions.

Among the forms of the Hv-complex, the cohosh-feeder and so-called Western Tokyo form (Wt) are most puzzling. FUKUDA (1970) firstly reported a new form which fed on blue cohosh. Some subsequent studies (e.g. YASUTOMI and FUKUDA, 1974; KATAKURA, 1976a) revealed that this form occurred sporadically from southernmost part of Hokkaido to central Honshu (Fig. 1-c). The morphology of the cohosh-feeders are very close to the thistle-feeders, but the former do not feed on thistles, although they grow with potato under laboratory condition (KATAKURA, 1981).

Wt is also a pest of potato and is distributed in the Pacific coastal areas of Honshu (Fig. 1-c). Morphologically Wt is similar to the thistle-feeder, or more to the cohosh-feeder when the elytral shape is taken into account (KATAKURA, 1981). In laboratory, Wt prefers blue cohosh and grows normally with it, but it less prefers thistles or can not accept it as food plant (WATANABE and SUZUKI, 1965; YASUTOMI, 1976; HINOMIZU, 1976).

Although many studies have revealed the considerable variations of Hv-complex, "the taxonomy of Hv-complex has been quite confused because of the lack of sufficient information and accurate documentation on the relations among various forms", as KATAKURA (1981) rightly pointed out. Recently, KATAKURA (1981) published a comprehensive work on the classification and evolution of this group. I believe that his work is well compiled based on sufficient morpho-biological data and the system adopted by him is most appropriate for classifying the Hv-complex, and therefore, I follow his system in the present paper.

KATAKURA (1981) divided the Hv-complex into two groups, A and B, by many subtle morphological differences. Group A involves only one species *H. vigintiocto-maculata* (MOTSCHULSKY) which consists of three local forms, V-I, II, and III. The difference between A and B is far little compared to the differences among most of other species of epilachnine beetles. Mainly based on the biological evidence and geographic distribution pattern, group B was further subdivided into three subgroups which were tentatively treated as three distinct species, *H. pustulosa* (KÔNO), henceforth abbreviated as Hp, *H. niponica* (LEWIS, Hn), and *H. yasutomii* (KATAKURA, Hy), each of which consists of 4, 3, and 1 forms, respectively. Hy corresponds to the cohosh feeders. KATAKURA (1981) also mentioned that Wt and some populations are no doubt closer to group B but their taxonomical position still remains unsettled.

Henosepilachna vigintioctopunctata FABRICIUS (henceforth abbreviated as Hvp): This species, called as 28-spotted lady beetle, is also notorious for the serious pest of solanaceous crops such as potato and egg plant in the south-western part of Japan. Since TAKAHASHI (1932) many authors have reported the allopatric distribution of Hvp and Hvm; namely the northern limit of Hvp is replaced by Hvm with relatively narrow transitional zone (IWAO, 1954; YASUE, 1963; SIMBO, 1978, Fig. 1-a). The boundary between the distributions of the two species has often been discussed in relation to the thermal condition, e.g. 14°C isotherm of the annual temperature (TAKAHASHI, 1932). Hvp has been subjected to study as material for analyzing spatial distribution pattern and movement (YOSHIDA et al., 1952; IWAO and MACHIDA, 1963; IWAO et al., 1963). We rarely find the variations in body shape and elytra maculation among local populations of the Hvp. According to DIEKE (1947), Hvp has many closely related species in tropical Asia.

MATERIALS AND METHODS

Hereafter I will show the results of field studies on population dynamics of three species of *Henosepilachna* beetles executed by myself since 1970. All these studies were conducted by similar methods. Census was carried out at regular intervals, i.e. 2-3 (Hvp), 3-7 (Hvm and Hn at Asiu) and 7-10 days (Hn at Yuwaku), covering the whole period from appearance of overwintered adults through disappearance of new adults to hibernation. The routine census consisted of two procedures, i.e. marking, release and recapture of adults (both overwintered and newly emerged adults), and counting eggs, larvae, and pupae for construction of life tables. The adult population parameters such as mean daily survival rate and total number of resident were estimated by using the JOLLY (1965)-SEBER (1973) method. Fig. 1 shows the location of populations and external morphology of the beetles studied and Table 1 summarizes the main features of the study sites.

H. vigintioctopunctata (Hvp): From 1970 to 1972, the study was carried out in the northern suburbs of Kyoto city (Fig. 1-b). The study site was a strip of cultivated field (10×100 m) surrounded by secondary forest. Food plants such as potato, egg plant, and tomato were cultivated in the study area. In Kyoto Hvp had two generations a year: overwintered adults appeared in early May and mass emergence of new adults occurred in early-middle July from potato. After potatoes were harvested new adults moved to egg plant and tomato, and 2nd generation emerged in August. Hvp repeatedly had caused a serious damage to potato and egg plant in this site. The details of the study were given in NAKAMURA (1976a, b).

H. vigintioctomaculata (Hvm): The study was conducted in Yuwaku, 15 km southeast of Kanazawa in 1981. A small potato field (20×20 m) was selected for the study site. The field was delimited with a bush and isolated from another field at least several hundred meters. Hvm had one generation a year. It seriously defoliated the potato in the study site. Hvm in this area belonged to Form V-1 (Fig. 1-a). KATAKURA (1981) defined V-1 as basic elytral shape for Hv-complex, which appeared in diverse members of the Hv-complex and regarded as the generalized state from which other specialized states have evolved.

H. niponica at Asiu: From 1974 to 1977, the study was conducted in the School Forest of Kyoto University at Asiu, one hundred kilometers north of Kyoto city (Fig. 1-b). The study area embracing the source of the Yura river is covered with cool temperate climax forest of *Fagus crenata*. In Asiu, adults and larvae of Hn fed on the leaves of the thistle, *Cirsium kagamontanum*, a perennial herb. This thistle grew in discrete clusters of different sizes along a stream. The thistle patches showed a high degree of stability both in location and size throughout the four-year study period. Hn had one generation a year in Asiu, and apparently belonged to Form N-III (KATAKURA, 1981), whose elytra shape was similar to the basic form (Fig. 1, V-1). The Asiu population remained at a relatively constant, low density level when compared with the pest species, Hvp and Hvm. The details were presented in NAKAMURA and OHGUSHI (1979, 1981, 1983).

H. niponica at Yuwaku: Since the spring of 1981, I have investigated the Hn populations in Yunokawa Valley, Yuwaku. Two study plots, 80×20 m and 115×15 m, were established along the valley which was less than 20 m wide. Both sides of the valley were of steep slopes covered with the trees, *Alnus fauriei*, *Juglans ailanthifolia*, *Cryptomeria japonica*, etc. Hn at Yuwaku fed on the wild thistle *Cirsium matsumurae* which grew on the stream side. This thistle species did not form so discrete patch as *C. kagamontanum* in Asiu.

The habitat condition in Yunokawa Valley was evidently less stable than in Asiu because of, first, frequent snowslides caused by heavy snowfall coupled with the steep slope of the valley, and second, artificial disturbance such as the construction of forest roads and dams to prevent erosion and afforestation. The snowslide and these artificial disturbances were responsible for the irregular and rapid change of vegetation in the valley. Elytra shape of Hn in Yuwaku was quite different from that of Asiu; the former was characterized by the features such as elytra expanded at hind edge, profile sharply curved and apex projected postward. According to KATAKURA's map (Fig. 1), the Yuwaku population was located in N-III's range, but as stated above Hn at Yuwaku resembled N-II, which was not strange because, as KATAKURA (1981) mentioned, the geographic variation of elytral shape of Hn was not yet exactly known. Moreover, the body size of the Yuwaku population was significantly greater than that of the Asiu population (Table 1).

Table 1. Comparison of demographic attributes among *Henosepilachna* lady beetles.

Characteristics \ Species	*H. vigintioctopunctata* (Hvp)	*H. vigintioctomaculata* (Hvm, V-I)	*H. niponica* at Asiu (Hn, N-III)	*H. niponica* at Yuwaku (Hn, N-II)
Study period	1970-72	1981	1974-77	1981-
Location (elevation, meters)	Kyoto (100)	Yuwaku (200)	Asiu (700)	Yuwaku (200)
Mean annual temperature (°C)	14.8	13.1	11.3	13.1
Habitat	Crop field	Crop field	Cool temperate climax forest	Warm temperate secondary forest
Host plant	Cultivated potato	Cultivated potato	Wild thistle, *Cirsium kagamontanum*	Wild thistle *Cirsium matsumurae*
No. of generations per year	2	1	1	1
Total body length of overwintered female (mm)	6.3 ± 0.3*	7.3 ± 0.1	7.6 ± 0.1	7.9 ± 0.1
Average number of eggs per mass	38.9 ± 1.3*	34.9 ± 1.4	17.2 ± 0.5	26.4 ± 0.8
Average egg volume (mm^3)	0.153 ± 0.06*	0.277 ± 0.010	0.397 ± 0.013	0.437 ± 0.020
Fecundity per female in field	500(600-1000?)**	311 (?)	50-90(200-400?)	50-60 (?)
Reproductive effort index, *RE* (see text)	0.31	0.22	0.045-0.081	0.044-0.053
Longevity of overwintered female (days)	15-23	23	26-53	11-16
Length of immature stages (days)	26	29	54	41
Mortality rate during immature stages (%)	89 (27)***	81 (31)	94-97 (55-64)	81-84 (41-49)
Reproductive rate, *R*	20-60	22	1-3	5-7
Successful overwintering rate (%)	1.6-3.8	?	>50	?
Density level	very high	very high	below the food limit but not rare	higher than Asiu

* 95% confidence limits
** potential
*** egg mortality

RESULTS

Table 1 summarizes the main demographic features in *Henosepilachna* beetles studied.

Body length: Average body length of overwintered females was significantly different among the four populations.

Number of eggs per batch: The size of egg mass also differed significantly among the four populations. Hvp with the smallest body size had the largest egg mass among the four populations. In addition, there was significant difference in egg mass size between Yuwaku and Asiu populations.

Adult fecundity and reproductive effort index: No direct measurement of fecundity was possible in the field, but it was obtained indirectly as follows:

$$\text{mean fecundity} = \frac{\text{total number of eggs laid in the study site}}{\text{total number of overwintered resident females in the study site } (N_G)}$$

Since eggs were counted through the search for all of the host plants in the study area and N_G was estimated by using intensive marking procedures and applying the JOLLY-SEBER formula, the estimated values were reasonable in accuracy.

In order to compare the allocation of energy for reproduction among the species, I calculated a reproductive effort index (RE) as follows:

$$RE = \frac{(\text{mean fecundity}) \times (\text{mean egg volume})}{(\text{body length of the female})^3}$$

The mean fecundity per female of the two pest species was much higher, 500 (Hvp) and 311 (Hvm), than that of each of the two Hn populations (50-90). The RE values of the pest species were also much higher, 0.31 (Hvp) and 0.22 (Hvm) than the two Hn populations (0.044-0.081), indicating that the pest species allocated much more energy for reproduction than the Hn populations. Potential fecundity so far revealed by the field cage experiment or rearing in the laboratory are available for Hvp (>600, NAKAMURA, 1976a, b), Hvm (700, IWAO, 1971), and Hn at Asiu (200-400?, NAKAMURA, 1981), but no data is available for Hn at Yuwaku.

Longevity of adults: The longevity of adult beetles is derived from $L = \frac{1}{1-\phi_m}$ where ϕ_m is the mean value of JOLLY's daily survival estimate. Overwintered adults of Hn at Asiu showed longest longevity (26-53 days), whereas Hn at Yuwaku showed shortest value (11-16 days).

Sex ratio: Females outnumbered males in overwintered beetles in all the four populations (the proportions of females to the whole population were around 60%). With regard to newly emerged adults, the ratio was not the same between the pest species (Hvm and Hvp) and the two Hn populations: the former showed 1:1 ratio, but around 60% in the latter. This showed that the males of the pest species suffered a higher mortality than the females during winter but that no such differential mortality occurred in the Hn populations. Reasonable explanations for this difference in sex ratio between the pest species and Hn populations have not been detected.

Survivorship curves and mortality for immature stages: Fig. 2 shows the com-

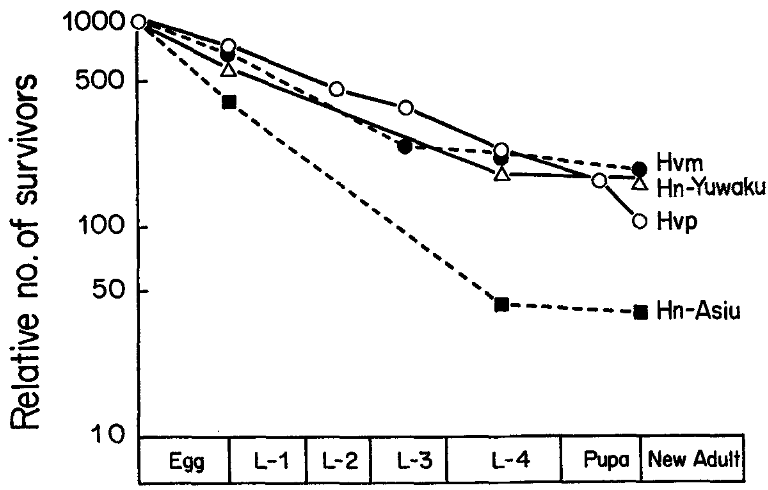

Fig. 2. Comparison of survivorship curves among the *Henosepilachna* beetles. Abbreviation: Hvm=*H. vigintioctomaculata*, Hvp=*H. vigintioctopunctata*, and Hn=*H. niponica*.

parison of survivorship curves among the species studied. Firstly, Hvm and Hvp were characterized by low egg mortality (only 27% in Hvp and 31% in Hvm), followed by low larval mortality (86 and 73%, respectively). These species had neither parasitoids nor predators which caused a serious mortality during their immature stages and the populations reached high levels, resulting in the heavy defoliation, followed by mortality due to starvation. In contrast, the Hn population in Asiu suffered serious egg (>50%) and larval mortality (84-94%) from arthropod predators such as an earwig *Anechura harmandi harmandi*, a staphilinid *Paederus poweri* and some ground beetles. The Hn population in Yuwaku exhibited different features from the Asiu population: the egg mortality was not so high (41-49%) as in Asiu and a larval mortality was least (67-69%) among the species studied. The Yuwaku population did not seem to have effective predators, and therefore its population reached a higher density level than the Asiu population and some of the thistles were defoliated.

Reproductive rate (R), density level and fluctuation of population size: In this paper reproductive rate (R) is defined as the number of newly-emerged females produced per overwintered female for convenience. R values of the pest species were very high (20-60 for Hvp and 22 for Hvm) and they frequently reached high density levels where severe starvation occurred. This was mainly due to a higher fecundity and lower mortality during immature stages. In my small study areas, Hvp and Hvm did not have any effective regulation mechanism by which their populations were maintained under the food ceiling. My study sites for these pest species were too small to draw a general conclusion on the fluctuation of the population size in a larger habitat (see Discussion).

In contrast to the pest species, the Asiu population of Hn showed very low R value ranging from 1 to 3, due to a lower fecundity and higher predation pressure during egg and larval periods. The Asiu population maintained a fairly constant population size below the food limit. Results of key-factor analysis indicated that the stabilization of population size was attained through density-dependent regulatory processes operating in inter-patch dispersal and oviposition by overwintered adults (NAKAMURA and OHGUSHI, 1981).

The Yuwaku population was characterized by a higher R value ranged from 5 to 7, than that of the Asiu population and its fecundity was as small as that of Asiu (Table 1). Thus, the higher R value in Yuwaku resulted from the higher survival rate during egg and larval periods.

DISCUSSION

Table 1 indicates that the pest species Hvp and Hvm showed quite different demographic traits from the thistle-feeding populations. The fact that Hvp and Hvm whose fecundity, reproductive efforts, and reproductive ratios were much higher than the thistle-feeding populations implied that they were more r-strategic when compared to the thistle-feeders (see PIANKA, 1970; SOUTHWOOD, 1977). Moreover, Hvp were thought to be more r-strategic than Hvm, because as compared with Hvm, it was smaller in body size but higher in reproductive efforts, fecundity, and reproductive rate. These r-strategic traits found in Hvm and Hvp were advantageous for pest species living in unstable and discontinuous habitats.

The thistle beetle population in Asiu living in a permanent and stable habitat, however, showed a low reproductive rate with low fecundity and longest adult life, maintaining fairly constant population size below (or just below, see NAKAMURA and OHGUSHI, 1981) the food limit. These suggested that Hn at Asiu was most K-strategic among the four populations studied.

However, it should be mentioned that some important aspects of population dynamics such as regulating mechanism, density level, and factors responsible for mortality often differ considerably in different habitats even within the same species (OHGUSHI and SAWADA, 1981). OHGUSHI and SAWADA (1981) reported that the Hn population at Nyudani which located only 15 km east of Asiu frequently defoliated the food plants and underwent a violent fluctuation in population size. They claimed that the habitat conditions at Nyudani was so unstable that arthropod predators attacking Hn could not be well established. According to their observation in the field, there was no difference in body size, elytra shape, and average size of egg mass between the Asiu and Nyudani populations. I suppose that the two populations are identical or quite similar in genetic composition.

But, the Hn population at Yuwaku revealed traits which were different from those of Asiu population, although data was available only for 1981. Hn in Yuwaku had a larger body size and larger average egg mass size than the Asiu population. The longevity of overwintered females in Yuwaku was much shorter than that in Asiu, but no difference was found in fecundity and the value of reproductive effort between the two populations. In my succeeding studies, these distinct traits found in the Yuwaku population would be considered in relation to the unstable habitat conditions.

Another Hn population belonging to N-II was studied by SHIRAI at Ohshika, Nagano Prefecture, Central Part of Honshu from 1978 to 1980. Elytra shape of the Ohshika population was in profile much sharply curved than that of N-II in other locality (SHIRAI, pers. commun.). The Ohshika population, feeding on another thistle *Cirsium nipponicum* was characterized by low potential fecundity (152 eggs per female, with an average egg mass size ranging from 23 to 26) and high mortality due to arthropod predation during immature stages. The population did not reach a high density level at which depletion of the food plant occurred. This was mainly brought about by the density dependent dispersal of overwintered adults and reduced fecundity (SHIRAI, 1981). As a whole, demographic traits of the Ohshika population were similar to those of the Asiu population.

P-III (*H. pustulosa*) population around Sapporo was exposed to different habitat condition. The main host of P-III, *Cirsium kamtschaticuum*, in this area withered in August, and blue cohosh, another important host plant was also usually over-exploited by the larvae and new adults. As a consequence, newly emerged adults and late instar larvae suffered food shortage in late summer and fall (KATAKURA, 1976 b; KIMURA, 1979).

Among the various forms of the Hv-complex, the two puzzling forms, the cohosh feeder (Hy) and the potato-feeder (Wt) are most interesting from the point of population dynamics as well as taxonomy. Hy populations were distributed sporadically from location to location, and in Central Honshu each population often consisted of amazingly small numbers of individuals ranged from 200 to 400. These tiny population, in most cases, seriously defoliated the blue cohosh in summer (IWAO, pers. commun.). Many researchers have repeated a question "how such a tiny population can exist at a high population density from generation to generation ?". Unfortunately, demographic data for these interesting forms are completely lacking.

Since various forms of Hv-complex are distributed in a variety of environments in which habitat stability, predation pressure, and meteorological condition vary, comparative demographic studies in different field conditions must be most crucial for understanding the evolution of life history traits and the mechanisms of population regulation. However, the comparative method sometimes can only present the field evidence showing only the correlations between environmental factors and demographic trends. Evidence collected from the field often remains inconclusive (STEARNS, 1976, 1977). In order to overcome this problem, we should carry out laboratory rearing and field experiment. Firstly, we need reliable information on demographic traits of Hv-complex from various localities under controlled laboratory conditions. So far we have no reliable data even on oviposition and mortality schedules or potential fecundity for any form of the Hv-complex. As KUBOKI (1978) pointed out, gel electrophoretic techniques should be applied to analyze variations of isozymes among local populations. Secondly, we need artificial manipulation in respect to habitat stability and carrying capacity of the food plant in the field, because these are most difficult to measure quantitatively under natural conditions. Thirdly, we should pay more attention to the spatial structure of populations and dispersal behaviour of the beetles. IWAO (1971) revealed that Hvm often depleted the food plant within a single subpopulation, indicating that Hvm would be attributed to an r-strategist whose population size would be expected to fluctuate violently. His study, however, showed that a large population consisted of several subpopulations tended to be stabilized through dispersal of adult beetles among patches (IWAO, 1971). Thus, we should assess the dispersal ability of the species in relation to habitat structure.

As regard to the second point, SAWADA and OHGUSHI (pers. commun.) have studied an artificially introduced population in Kyoto city. In 1971, fourty-five adults were transferred from Asiu to a new habitat which was located at 20 km south of the southern fringe of the species' distribution range. SAWADA (pers. commun.) stated that in spite of the unfavorable hot climate, the population was well established within a few years after introduction and thereafter it reached a level where serious food depletion occurred. This was thought to be due to a low predation pressure in the new habitat. Although this situation should select for K-strategic traits in the population, SAWADA (pers. commun.) found an increased fecundity in the newly introduced population, though no changes occurred in body size of the beetles and egg mass size.

Theoretical predictions on insect life history evolution based on the r- and K-selection or bet-hedging theory seem to be imcomplete and ambiguous for full understanding the morpho-ecological diversity existing among local populations of the Hv-complex (WILBUR et al., 1974; STEARNS, 1976; 1977; TALLAMY and DENNO, 1981). In order to develop more comprehensive view, comparative studies on population dynamics of the Hv-complex should be extended over a wider scale both in time and space.

SUMMARY

The phytophagous lady beetles which belong to the so-called *Henosepilachna vigintioctomaculata* complex are characterized by the considerable morpho-biological variations. The first part of this paper summarized recent knowledge on the taxonomy

and biology of this interesting but troublesome group, in which I mainly followed the system proposed by KATAKURA (1981).

Main part of this paper covered the comparative field studies on population dynamics of the Hv-complex and *H. vigintiocto-punctata* (Hvp) in Japan. The populations studied are: *H. vigintioctomaculata* (Hvm) at Yuwaku, *H. niponica* (Hn) at Asiu, Hn at Yuwaku, and Hvp in Kyoto. Hvp and Hvm are notorius as pests of potato, whereas the two Hn populations fed on wild thistles. All the populations were studied by the same methods which consisted of the two procedures: firstly marking-recapture of adult beetles for estimating population parameters, and secondly construction of life tables for analyzing the reproduction and mortality processes. Several demographic traits, e. g. body size of adults, fecundity per female, reproductive effort index, reproductive rate per generation, adult longevity, population density were estimated for each population. Comparison of these traits among the populations studied clearly showed that the two pest species, Hvp and Hvm, had higher fecundity and reproductive rates than did the two thistle feeders. Hvp and Hvm frequently reached density levels where severe starvation occurred. On the contrary, Hn in Asiu living in a permanent and stable habitat showed a low reproductive rate per generation with low fecundity, maintaining fairly constant population size below (or just below) the food limit. The body size of the Yuwaku population was significantly larger than that of Asiu and the elytra shape of the former was evidently distinct from the latter. Although the longevity of the beetles in Yuwaku was much shorter than that of Asiu, the former attained a larger reproductive rate than the latter. According to the *r*-*K* continuum defined by SOUTHWOOD (1977), Hvp and Hn in Asiu are likely to correspond to *r*- and *K*-strategic species, respectively.

ACKNOWLEDGEMENTS: I am most grateful to the late Prof. S. IWAO (Kyoto Univ.) for his valuable advices throughout the course of this study. I wish to express my sincere thanks to Dr. A. TAKAFUJI (Okayama Univ.) for critical reading of the first draft of the manuscript and to my coworkers, Messrs. T. OHGUSHI and H. SAWADA (Kyoto Univ.) for their helpful discussions. Cordial thanks are also due to Dr. H. KATAKURA (Hokkaido Univ.) who kindly allowed me to cite his figures, to Messrs. Y. SHIRAI (Shinshu Univ.) and T. KIMURA (Hokkaido Univ.) who kindly permitted me to cite their unpublished data. I am indebted to Mr. M. KAWAMOTO (Kanazawa Univ.) for drawing figures. This study was supported in part by Grant-in-Aid No. 56740267 and No. 57740350 from the Ministry of Education, Science, and Culture.

REFERENCES

DIEKE, G.H. (1947) Ladybeetles of the genus *Epilachna* (sens. Lat.) in Asia, Europe and Australia. *Smithonian Misc. Coll.* **106**: 1-183.

EHARA, S. (1952) Several problems concerning the genus *Epilachna* of Japan. *Shin-Kontyû* **8**: 2-9. (In Japanese)

EHRLICH, P.R., R.R. WHITE, M.C. SINGER, S.W. MCKECHNIE, and L.E. GILBERT (1975) Checkerspot butterflies: A historical perspectives. *Science* 188: 221-228.

FUKUDA, A. (1970) An unrecorded form of *Epilachna vigintioctomaculata* complex feeding on *Caulophyllum robustum* MAXIM. *Kontyû* 38: 348-352. (In Japanese with English summary)

HINOMIZU, H. (1976) Influence of food plants in larval stage on the host preference of adult lady beetles, *Henosepilachna vigintioctomaculata* complex (Coleopetera, Coccinellidae). *Kontyû* 44: 93-101.

IWAO, S. (1954) On the distribution of *Epilachna sparsa orientalis* DIEKE and *E. vigintioctomaculata* MOTSCHULSKY at the boundary of their geographical distributions. (I). *Ôyo-Kontyû* 9: 135-141. (In Japanese with English summary)

IWAO, S. (1959) Some experiments on the host-plant preference in a phytophagous lady-beetle, *Epilachna pustulosa* KÔNO, with special reference to its individual variation. *The Insect Ecology* 8: 10-21. (In Japanese with English summary)

IWAO, S. (1971) Dynamics of numbers of a phytophagous lady-beetle, *Epilachna vigintioctomaculata*, living in patchily distributed habitats. *Proc. Adv. Study Inst. Dynamics Numbers Popul.* (*Oosterbeek, 1970*) pp. 124-147.

IWAO, S. and M. MACHIDA (1961) Further experiments on the host-plant preference in a phytophagous lady-beetle, *Epilachna pustulosa* KÔNO. *The Insect Ecology* 9: 9-16. (In Japanese with English summary)

IWAO, S. and M. MACHIDA (1963) A marking- and recapture analysis of the adult population of a phytophagous lady-beetle, *Epilachna sparsa orientalis*. *Res. Popul. Ecol.* 5: 107-116.

IWAO, S., H. MIZUTA, H. NAKAMURA, T. ODA and Y. SATO (1963) Studies on a natural population of the large 28-spotted lady beetle, *Epilachna vigintioctomaculata* MOTSCHULSKY. I. Preliminary analysis of the overwintered adult population by means of the marking- and recapture method. *Jap. J. Ecol.* 13: 109-117.

JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration—stochastic model. *Biometrika* 52: 225-247.

KATAKURA, H. (1976 a) Notes on a form of *Henosepilachna vigintioctomaculata* complex feeding upon *Caulophyllum robstum* in Ohnuma Park, southern Hokkaido. *Kontyû* 44: 526-529. (In Japanese with English summary)

KATAKURA, H. (1976 b) Phenology of two sympatric phytophagous ladybirds of *Henosepilachna vigintioctomaculata* complex in and near Sapporo, nothern Japan (Coleoptera: Coccinellidae). *Jour. Fac. Sci., Hokkaido Univ., Ser. VI, Zool.* 20: 313-328.

KATAKURA, H. (1977) A review of the *Henosepilachna vigintioctomaculata* complex, phytophagous lady beetles. *The Insectarium* 14: 80-87. (In Japanese)

KATAKURA, H. (1981) Classification and evolution of the phytophagous ladybirds belonging to *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). *Jour. Fac. Sci., Hokkaido Univ., Ser. VI, Zool.* 22: 301-378.

KIMURA, T. (1979) Studies on the population dynamics of the phytophagous lady bird beetle *Henosepilachna pustulosa* (KÔNO) on two species of host plants. *Master's thesis, Faculty of Agriculture, Hokkaido Univ.*

KÔNO, H. (1937) Eine neue *Epilachna*-Art. *Ins. Matsumurana* 11: 99.

KOYAMA, N. (1962) *Epilachna* lady beetles in Nagano Prefecture. *Ent. Soc. Shinshu, Ueda.* (In Japanese)

KUBOKI, M. (1978) Studies on the phylogenic relationship in *Henosepilachna vigintioctomaculata* complex based on variation of isozymes. (Coleoptera: Coccinellidae). *Appl. Ent. Zool.* 13:

250-259.

NAKAMURA, K. (1976 a) Studies on the population dynamics of the 28-spotted lady beetle, *Henosepilachna vigintioctopunctata* F. I. Analysis of life table and mortality process in the field population. *Jap. J. Ecol.* **26**: 49-59. (In Japanese with English summary)

NAKAMURA, K. (1976 b) Ditto. II. Analysis of regulatory system under semi-natural and laboratory conditions. *Jap. J. Ecol.* **26**: 125-134. (In Japanese with English summary)

NAKAMURA, K. and T. OHGUSHI (1979) Studies on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO) in a cool temperate climax forest. I. The estimation of adult population parameters by the marking, release and recapture method. *Res. Popul. Ecol.* **20**: 297-314.

NAKAMURA, K. and T. OHGUSHI (1981) Ditto. II. Life tables, key-factor analysis, and detection of regulatory mechanisms. Res. Popul. *Ecol.* **23**: 210-231.

NAKAMURA, K. and T. OHGUSHI (1983) Ditto. III. The spatial dynamics and analysis of dispersal behaviour. *Res. Popul. Ecol.* (In press)

OHGUSHI, T. and H. SAWADA (1981) The dynamics of natural populations of a phytophagous lady beetles, *Henosepilachna pustulosa* (KÔNO), under different habitat conditions. I. Comparison of adult population parameters among local populations in relation to habitat stability. *Res. Popul. Ecol.* **23**: 94-115.

PIANKA, E. R. (1970) On *r*- and *K*-selection. *Amer. Natur.* **104**: 592-597.

SASAJI, H. (1971) *Fauna Japonica, Coccinellidae (Insecta: Coleoptera)*. Keigaku Publ. Co., Tokyo.

SEBER, G. A. F. (1973) *The estimation of animal abundance and related parameters.* Griffin, London.

SHIRAI, Y. (1981) Studies on population ecology of the thistle-feeding lady-beetle, *Henosepilachna pustulosa. Master's thesis, Faculty of Agriculture, Shinshu Univ.* (In Japanese)

SIMBO, T. (1978) Application for thermal limiting factors to the Japanese distributions of *Epilachna sparsa orientalis* and *E. vigintioctomaculata. Sci. Rep. Shiga Pref. Junior Coll.*, No. **15**: 80-82. (In Japanese)

SOUTHWOOD, T. R. E. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.* **46**: 337-365.

STEARNS, S. C. (1976) Life history tactics: A review of the ideas. *Q. Rev. Biol.* **51**: 3-47.

STEARNS, S. C. (1977) The evolution of life history traits: A critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8**: 145-171.

TAKAHASHI, S. (1932) Studies on *Epilachna* lady beetles in Japan. *Jour. Tokyo Nôgyô Daigaku* **3**: 1-113.

TALLAMY, D. W. and R. F. DENNO (1981) Alternative life history patterns in risky environments: An example from lacebugs. In: *Insect life history patterns.* R. F. DENNO and H. DINGLE (eds.) pp. 129-147.

TINKLE, D. W. and R. E. BALLINGER (1972) *Sceloporus undulatus*: A study of the intraspecific comparative demography of a lizard. *Ecology* **53**: 570-584.

WATANABE, C. and S. SAKAGAMI (1948) Contributions to the knowledge of *Epilachna pustulosa* KÔNO (Coleoptera: Coccinellidae). *Matsumushi* **2**: 96-106. (In Japanese with English summary)

WATANABE, C. and S. SUZUKI (1965) A consideration of the food preference of the *Epilachna vigintioctomaculata* complex, with special reference to the so-called "Tokyo west suburbs form". *Kontyû* **33**: 191-198. (In Japanese with English summary)

WILBUR, H. M., D. W. TINKLE and J. P. COLLINS (1974) Environmental certainty, trophic level, and resource availability in life history evolution. *Amer. Natur.* **108**: 805-817.

YASUE, Y. (1963) Studies on the geographical distribution of the 28-spotted lady beetles, *Epilachna sparsa orientalis* DIEKE and *Epilachna vigintioctomaculata* MOTSCHULSKY. *Nôgyô Kenkyû* **50**: 1-36. (In Japanese)

YASUTOMI, K. (1976) Notes on geographical distribution and host preference in the Tokyo West-suburb form of *Epilachna vigintioctomaculata* complex. *Kontyû* 44: 111-114. (In Japanese with English summary)

YASUTOMI, K. and A. FUKUDA (1974) Notes on Towada form of the *Epilachna vigintioctomaculata complex* (Coleoptera, Coccinellidae) from Togakushi, Nagano Prefecture. *Kontyû* 42: 204-205. (In Japanese with English summary)

YOSHIDA, T., S. UTIDA, T. KONO and S. WATANABE (1952) On the distribution pattern of the spotted lady-beetle, *Epilachna sparsa orientalis.* Patterns of the spatial distribution of insect 3. *Res. Popul. Ecol.* 1: 83-93. (In Japanese with English summary)

近縁な植食性テントウムシ数種の比較個体群動態

中 村 浩 二

いわゆるオオ28ホシテントウ群（*Henosepilachn vigintioctomaculata* complex，以下 Hv 群とする）は形態と生態（食性など）の両面にわたって非常に変異にとんだグループとして多くの注目を集めてきた。本報ではまずこれまで膨大に蓄積されてきた本群に関する知見と問題点を整理した。これに際しては KATAKURA (1981) の記述を参考にし，そのシステムに従った。次に筆者が1970年以来続けている本群および同属の28ホシテントウ（*H. vigintioctopunctata*）の個体群動態の野外調査の結果を比較考察した。ジャガイモの害虫である28ホシテントウ（Hvp，調査地は京都）およびオオ28ホシテントウ（Hvm，金沢市湯涌）と，アザミを食草としているコブオオニジュウヤホシテントウ（*H. niponica*, Hn）の2個体群（京都府芦生と湯涌），以上の4つの個体群に (1)生命表の作製，(2)成虫をマーキングして生存率や個体数の推定をする，という共通した方法を適用した。4つの個体群のメスの体長，総産卵数，卵塊サイズ，繁殖投資量，寿命，増殖率（1メスあたり次世代メス羽化数），個体群密度などを比較検討した。害虫であり小型な Hvp が最も *r* 的，ブナ原生林の安定したハビタートにすむ芦生の Hn が最も *K* 的であることがわかった。湯涌の Hn は芦生の Hn より大型で鞘翅のカーブなど形態も異なるほか，成虫の寿命が非常に短かいにもかかわらず産卵数は芦生とかわらず卵一幼虫期の死亡率が低いため増殖率はかえって芦生よりずっと高いことがわかった。筆者以外の研究者によってもたらされた野外個体群の調査結果も総合すると，生息環境の安定性や捕食による死亡の大きさのちがいが個体群動態の特性を支配しているといえる。また *r-K* 学説や bet-hedging などの学説だけで各地の Hv 群の多様な実態を解釈できるとは思えない。今後この Hv 群を対象とした個体群動態研究のありかたについても論じた。