

STUDIES ON THE POPULATION DYNAMICS OF A THISTLE-
FEEDING LADY BEETLE, *HENOSEPILOACHNA PUSTULOSA*
(KÔNO) IN A COOL TEMPERATE CLIMAX FOREST
I. THE ESTIMATION OF ADULT POPULATION PARAMETERS
BY THE MARKING, RELEASE AND RECAPTURE METHOD

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INTRODUCTION

Major developments in population ecology have been coming from the applied fields, therefore most field studies of insect populations are inevitably concerned with pests living generally in habitats greatly modified by man. Most insect species are, however, not pests, relatively rare and seemingly more stable in their population levels. Consequently, we should investigate the population dynamics of such non-pest species, especially those living in complex natural communities (CLARK *et al.*, 1967; WILSON, 1968; SOUTHWOOD, 1975).

The purpose of this study is to provide basic information concerning population structure and dynamics of the thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO), and to compare its demographic attributes with two allied species, *H. vigintioctomaculata* and *H. vigintioctopunctata* (Henceforce, abbreviated these as *Hp*, *Hvm* and *Hvp*, respectively). *Hvm* and *Hvp* are notorious pests of potato, egg-plant and other *Solanaceous* crops in nothern and central parts (*Hvm*) and the warmer part (*Hvp*) of Japan, respectively. *Hp* is closely related and nearly sympatric to *Hvm*, but it feeds mainly on thistles growing in the more mountaneous areas. In these habitats, *Hp* populations are subdivided into small local populations which are patchily distributed and more or less isolated from one another.

It seems that *Hp* populations remain fairly constant in their size rather than undergo violent fluctuations and they seldom reach a level where intraspecific competition for food occurs. By the remarkable differences in elytral structure and food plants under natural conditions, several local forms have been recognized in *Hp* (KATAKURA, 1974 a, b). Thus *Hp* is one of the most interesting materials for evolutionary biology as well as for population dynamics. Although some information have been gathered on the population dynamics of *Hvm* (IWA0, 1971) and *Hvp* (NAKAMURA, 1976 a, b), basic quantitative data on *Hp* are almost lacking.

A field study was carried out in a temperate climax forest in the School Forest

of Kyoto University at Asiu, northern Kyoto Prefecture.

This first paper of the series presents some demographic parameters of adult beetles such as population size, sex ratio, survival rate, longevity, reproductive rate, etc. These parameters are estimated by the marking, release and recapture method.

STUDY AREA

The Kamitani study area, embracing the source of the Yura river, is rather flat and at an altitude about 700 meters, and covered with cool temperate natural climax forest with *Fagus crenata* and *Quercus mongolica*, etc (Fig.1). In Asiu, adults and

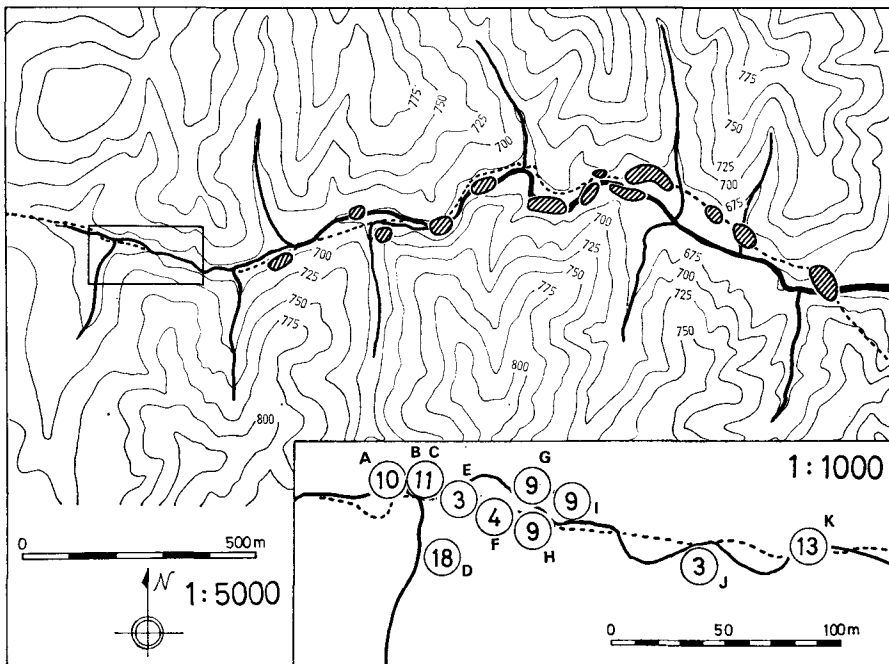


Fig. 1. Sketch map of the Kamitani study area, the School Forest of Kyoto University located at Asiu, showing the location of the thistles, *Cirsium kagamontanum* (shaded areas). In the rectangle, enlarged map of the Mondori sub-area, studied most intensively, showing the location of thistle patches (circles) and the number of thistle plants in a patch (numericals in the circle).

larvae of *Hp* feed exclusively on the leaves of a thistle, *Cirsium kagamontanum*. *C. kagamontanum* is a perennial herb. It grows in discrete patches of different size which occupy the stream side (Fig.1). There was only a slight change in the location and size of these thistle patches throughout the study period, 1974-77. *C. kagamontanum* is one of the most abundant and dominant herb species on the stream side. This paper deals mainly with a subpopulation of *Hp* in the Mondori area, the upper end of the Kamitani.

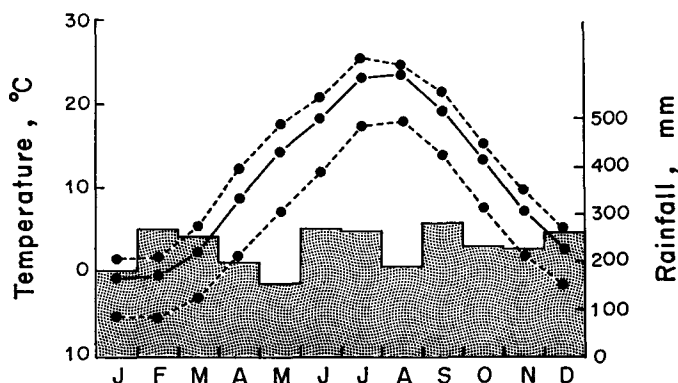


Fig. 2. Meteorological data observed at Chojidani Station, east end of the study area, for 30 years, 1928-58. Solid and broken line show the mean, maximum and minimum monthly temperature, respectively. Histogram shows the mean monthly precipitation.

Meteorological data at Chojidani Station, east end of the study area is available for thirty years (1928-58) (Fig. 2). The study area has a mean annual temperature of 11.3°C and an annual mean precipitation of 2787.6 mm . The mean monthly temperatures are ranging from -5.2° (January) to 24.1°C (August). Precipitation is concentrated in both summer and winter. From December to April, the study area is buried under 2-3 meters depth of snow. In the study period, weather conditions were not much different from the average, except that about one third of the thistle colonies were affected by a flood occurred in the late August in 1975.

CENSUS METHODS

The Mondori area was amenable to study because, for the first, the adult beetles are relatively poor in their dispersal power, so that the population in the Mondori area was virtually self-contained (NAKAMURA and OHGUSHI, in preparation), and secondly, in that area there were not so many thistles, i.e., 11 thistle patches or 89 thistle plants, therefore all of them could be censused within one or two days. From mid May to early October, all the thistles were examined every third or fourth day in 1974, and once a week in 1975 and 1976. In 1977, censuses were carried out only three times in both spring and early autumn, respectively.

On each census all the adult beetles discovered were marked with lacquer paint. The adult beetles tend to stay sluggishly on the host plants, and so could be caught easily. By using four marking points on elytra, individual beetle could be kept record of sex and capture history in terms of place and time; the adults captured or recaptured were immediately released on the same plant on which they were caught, and on release "marking effect" such as escape reaction or other abnormal dispersal behavior could not be seen. The data thus obtained were analysed by the method described by JOLLY (1965) and SEBER (1973) using Fortran programming.

RESULTS

1. *Life history*

H. pustulosa has one generation a year. Only a few days after the snow melting, usually in early May, post-hibernating adults begin to emerge from hibernacula to the thistles, when they are in small rosette form. Thereafter thistles grow rapidly and often reach to the height of 2 meters or more in August. The oviposition is begun within a week after the beginning of emergence and continued to mid June. Eggs are laid on the undersurface of the host plants in clusters containing an average of 17 eggs. The fully fed fourth instar larvae pupate on the lower side of the thistles. The new adults emerge from late August to early September. After about two weeks of feeding they hibernate beneath the thistle colonies and up to 50-60% may survive the winter. Most of the post-hibernating adults die in the current year, but at least a few percent of them (see Table 4) hibernate for the second time and reproduce in the following season. The beetles which emerge as post-hibernating adults are thus a mixed population, consisting of the autumn adults of the previous year and that of two years ago.

2. *Estimates of population size, \hat{N}_t*

A full accounts of capture and recapture data from 1974 to 1976 are presented in the Appendix. In most cases, the parameters estimated were not significantly different

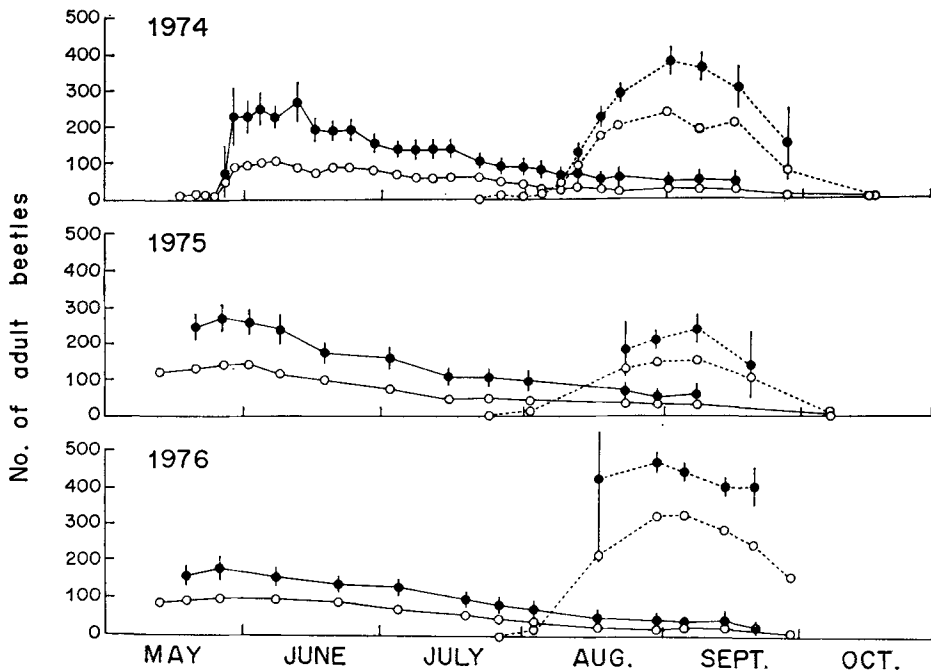


Fig. 3. Seasonal fluctuations in the number of adult *H. pustulosa* population. The number of beetles observed ($\text{—}\bullet\text{—}$, $\cdots\circ\cdots$) and estimated by JOLLY-SEBER method ($\text{—}\bullet\text{—}$, $\cdots\bullet\cdots$). Solid and dotted lines show the overwintered and new adults, respectively. Vertical lines show the 95% confidence limits.

between two sexes, so the sexes processed collectively through the JOLLY-SEBER analysis. The number of adult beetles estimated by JOLLY-SEBER method (\hat{N}_i) are plotted together with that of observed (n_i) in Fig.3. The number of adult beetles in both post- and pre-hibernating periods are seen as similar seasonal trends in three years, 1974-76 (Fig.3). At the onset of this study, in early May 1974, only a small portion of thistle patches in the area were examined and from late May onwards all the colonies became to be censused.

Sampling ratio, which is the ratio of n_i to \hat{N}_i , is nearby 50% and fairly constant throughout the study period (Fig.4).

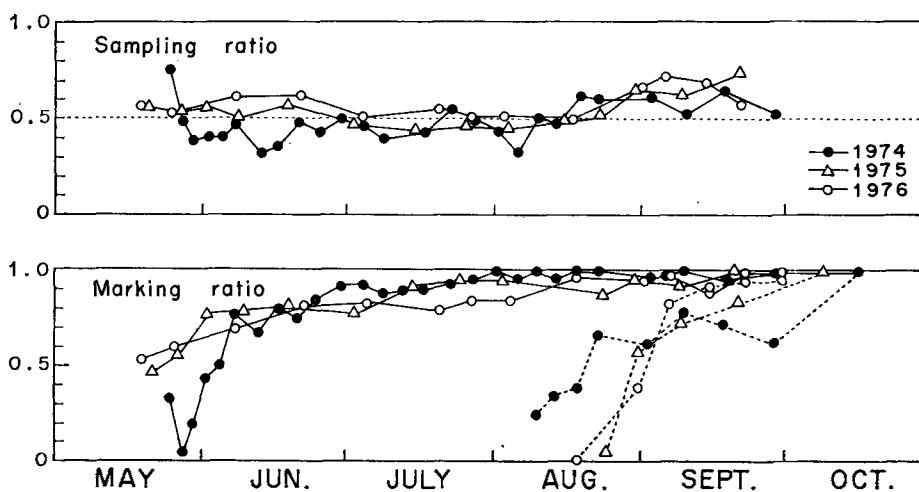


Fig. 4. Seasonal fluctuations in the sampling and marking ratios of adult *H. pustulosa* populations estimated by JOLLY-SEBER method.

Marking ratio, which is the proportion of marked individuals to the whole population, rapidly rised as the census progressed and approached to 100 percent. In late May in 1974, the ratio showed a sudden drop as a result of the extention of study area mentioned above (Fig.4). As it is clear from the sampling and marking ratios mentioned above, the population parameters could be estimated with a high accuracy.

3. Sex ratio

In marked beetles, the ratio of females to the whole population was 63.1-67.0% for overwintered adults and 67.2-68.9% for new adults, respectively in the years 1974-77 (Table 1). Seasonal fluctuations in the sex ratio in overwintered adults showed little change until late July, but henceforce the adults decreased in numbers, so the ratios fluctuated accidentally (Fig.5). There was little difference in the sex ratio between new adults in autumn and oberwintered adults in the next spring.

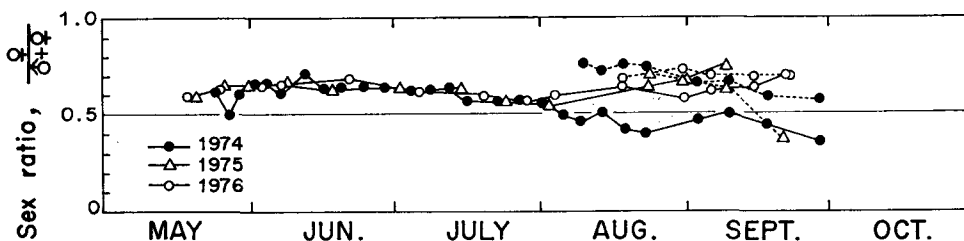


Fig. 5. Seasonal fluctuations in the sex ratios (% female) of adult *H. pustulosa* populations. Solid and broken lines refer to overwintered and new adults, respectively.

Table 1. Total sum of marked beetles and sex ratio, 1974-77.

| Year | Overwintered adult | | | | | New adult | | | | |
|------|--------------------|--------|---------|-------|----------|-----------|--------|---------|-------|----------|
| | Male | Female | Unknown | Total | % Female | Male | Female | Unknown | Total | % Female |
| 1974 | 114 | 231 | 32 | 377 | 66.96 | 117 | 259 | 15 | 391 | 68.88 |
| 1975 | 125 | 214 | 29 | 368 | 63.13 | 79 | 162 | 0 | 241 | 67.22 |
| 1976 | 72 | 134 | 0 | 206 | 65.05 | 160 | 339 | 0 | 499 | 67.94 |
| 1977 | 63 | 125 | 0 | 188 | 66.50 | — | — | — | — | — |

4. Daily rate of survival, $\hat{\phi}_i$

Since emigration and death could not be distinguished here as the causes of loss, the term "survival" used in this paper, strictly speaking, means "residence" in the Mondori area. But adult beetles in the Mondori area rarely emigrated to other areas, there would be little discrepancy between "survival" and "residence". Therefore we will refer to residence as survival, for which we will use JOLLY's symbol $\hat{\phi}_i$. The survival rate were converted per day* and presented in Fig.6 and Table 2. The survival rate is constantly very high (more than 0.95 per day or 0.75-0.85 per week) throughout the seasons in both overwintered and newly emerged adults. In most cases variances are very small and there are no differences between sexes.

5. Longevity or residence times, L

Two method have been used to measure the adult longevity which, in this paper, is synonymous with the length of time spent on the thistle patches within the Mondori area. For convenience, the length of time resident from emergence to hibernation (or death before entering the hibernation) is used as the longevity of new adults. For the first, the estimation of minimum length of survival (residence) was made by the distribution of the time intervals between the first capture and last

* If $\hat{\phi}_i$ is the survival rate between i th sample and $i+1$ th sample, by assuming the constant rate of mortality, $\hat{\phi}_i$ is given by $\hat{\phi}_i = \hat{\phi}_i^{\frac{1}{n}}$ and we have $V(\hat{\phi}_i) = \left[\frac{1}{n} \hat{\phi}_i^{\left(\frac{1}{n}-1\right)} \right]^2 \times V(\hat{\phi}_i)$ where $\hat{\phi}_i$ is the survival rate per day and n is the length of interval (in days) between i th and $i+1$ th sample. (The above equation for variance is derived by Dr. E. KUNO.)

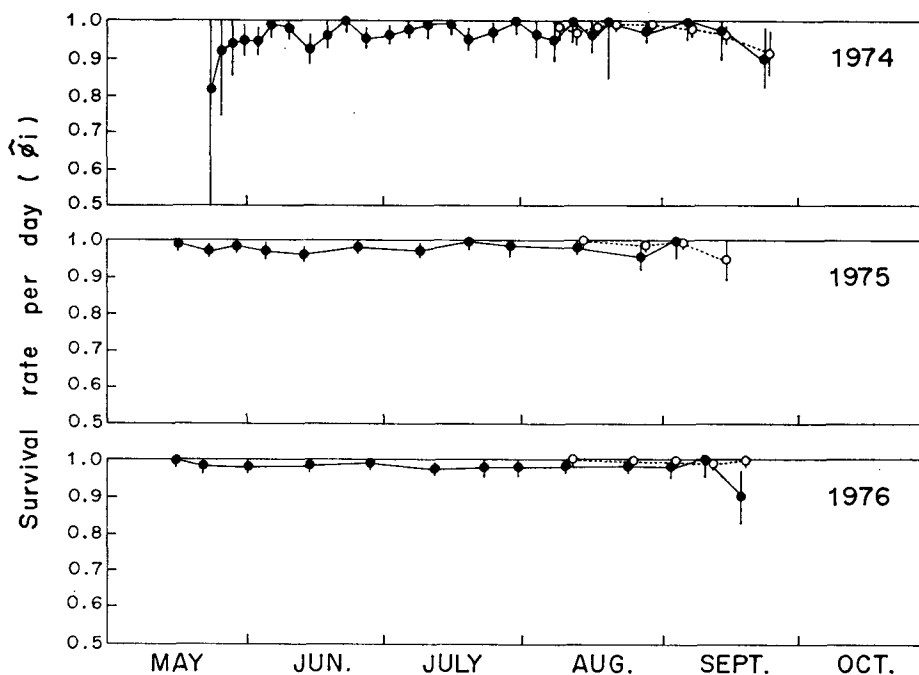


Fig. 6. Seasonal fluctuations in the daily survival rate ($\hat{\phi}_i$), estimated by JOLLY-SEBER method, of adult *H. pustulosa* populations. Vertical lines show the 95% confidence limits.

Table 2. The estimates of mean survival rate per day (ϕ_m), mean length of residence time (L), and total sum of the adult beetles per season (N_G), together with the winter survival (S_w) and reproductive rate (R) from N_G .

| Generation | | Overwintered adult | | | | New adult | | | S_w | R |
|------------|--------|-----------------------------|--------------------------------|-------|-------------|----------------|--------------------------------|-----------|-----------------------------|-----------------------------|
| Year | Sex | ϕ_m | $L = \frac{1}{1 - \phi_m} N_G$ | N_G | $(N_G^*)^a$ | ϕ_m | $L = \frac{1}{1 - \phi_m} N_G$ | (N_G^*) | | |
| 1974 | Male | .972 (.820) ^d | 35.7 | 145 | 476 (523) | .963 (.768) | 27.0 | 188 | — | 1.18 (1.18) ^c |
| | Female | .961 (.757) | 25.6 | 331 | | .961 (.757) | 25.6 | 372 | | |
| 1975 | Male | .976 (.844) | 41.7 | 159 | 459 (461) | .950 (.735) | 20.0 | 182 | 0.82 (0.75) ^b | 0.87 (0.85) |
| | Female | .974 (.832) | 38.5 | 300 | | .957 (.698) | 23.3 | 216 | | |
| 1976 | Male | .982 (.881) | 55.6 | 95 | 264 (274) | .962 (.762) | 26.3 | 261 | 0.66 (0.70) | 3.28 (2.07) |
| | Female | .981 (.874) | 52.6 | 169 | | .960 (.751) | 25.0 | 604 | | |

^{a)} N_G^* : N_G , estimated by the second method. ^{b), c)}: Estimates based on N_G .

^{d)} The estimates of mean survival rate per week.

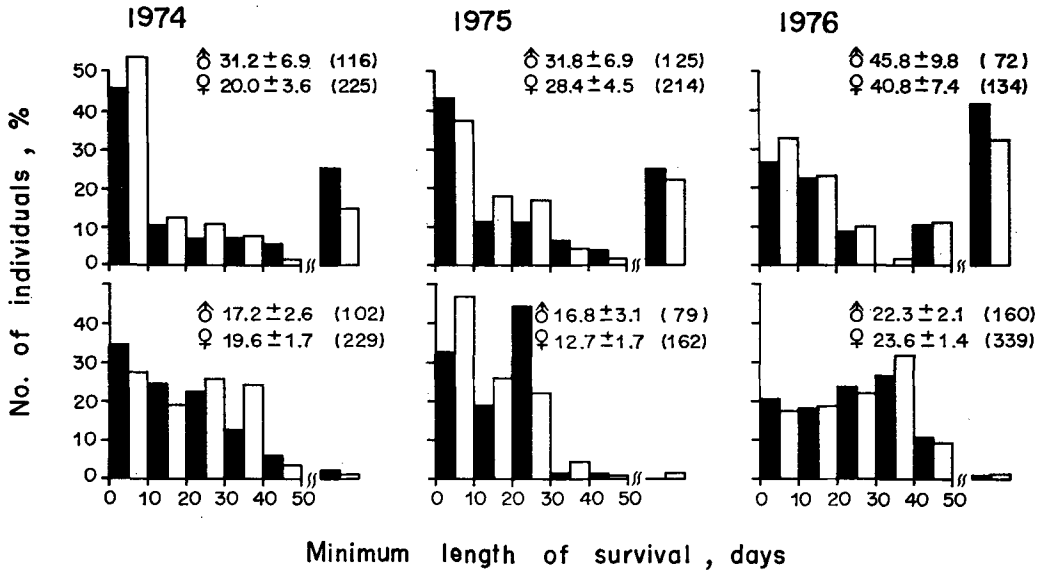


Fig. 7. Frequency distribution of the minimum survival lengths of overwintered (top) and new adults (bottom). Filled and open columns refer to male and female, respectively. Numericals show the mean ± 95% confidence limits, and (no. of individuals examined).

recapture. The results are shown in Fig. 7. In the overwintered adults, the minimum length of survival was ranging from 30 to 45 days (male) and from 20 to 40 days (female), respectively. Male seems to have longer longevity than female, though there is no significant difference between sexes. In new adults, it was ranging from 17-22 days (male) and 13-24 days (female) before entering hibernation, respectively.

The second estimates can be obtained: $L = \frac{1}{1 - \phi_m}$, where ϕ_m is the mean of JOLLY's survival estimate (per day), and L is the mean length of survival in days. The results, shown in Table 2, are 5-10 days longer than minimum estimates obtained above.

6. Total number of adult beetles resident per season, N_G

As mentioned above, we carried out intensive marking, release and recapture program throughout the seasons during which time a considerably high percentage of individuals were marked. Thus the total sum of adult beetles marked in each generation, summarized in Table 1, can be regarded as the minimum estimates of N_G . N_G can be estimated, for the first, by $\frac{S}{L}$ where S is the area enclosed by seasonal prevalence curve of adult beetles (\hat{N}_i) and time axis (Fig. 3), and L is the mean longevity of adult beetles (Table 2).

The other method used in estimating N_G is as follows: if new adults joined the population at a constant rate (b_i) during the interval between the i th and $i+1$ th day, the number of adults which joined the population and survived to $i+1$ th day is $\frac{1 - e^{-r_i}}{r_i} b_i$ and $\hat{N}_{i+1} = \hat{N}_i \hat{\phi}_i + \frac{1 - e^{-r_i}}{r_i} b_i$, therefore $N_G = \sum b_i = \sum_{i=1}^{l-1} \left(\frac{\hat{\phi}_i \log \hat{\phi}_i}{1 - \hat{\phi}_i} \hat{N}_i - \right.$

$\frac{\log \hat{\phi}_i}{1 - \hat{\phi}_i} N_{i+1}$), where $e^{-r_i} = \hat{\phi}_i$. The figures based on these two methods agree fairly well with each other and show 1.2-1.3 and 1.1-1.7 times larger than the minimum estimates for overwintered and new adults, respectively. (The equations mentioned above are derived by Mr. Tamiji INOUE, in personal communication).

7. Survival rate between autumn and the following spring: S_w

Method 1: Since the marked adults that were marked and released in autumn were recaptured in considerable numbers in the next spring, the minimum estimates of S_w can be obtained by the ratios between the marked adults released in autumn and those of recaptured in the following spring, which are 0.52 (1974-75), 0.51 (1975-76), and 0.37 (1976-77), respectively (Table 3). Fortunately, during the autumn-spring period the detachment of marks seemed to be negligible and dilution

Table 3. The use of the fraction of marked beetles, which were recaptured in the following spring, to estimate the winter survival rate.

| Year | 1974-75 | | | 1975-76 | | | 1976-77 | | |
|--|---------|--------|-------|---------|--------|-------|---------|--------|-------|
| | Male | Female | Total | Male | Female | Total | Male | Female | Total |
| No. marked in autumn | 122 | 269 | 391 | 79 | 162 | 241 | 160 | 339 | 499 |
| No. recaptured in the following spring | 73 | 132 | 205 | 40 | 83 | 123 | 61 | 123 | 184 |
| % survival during hibernation | 59.8 | 49.1 | 52.4 | 50.6 | 51.2 | 51.0 | 38.1 | 36.3 | 36.9 |

* In 1977, Overwintered adults were censused only three times. (See text)

of marked beetles due to emigration rarely happened. Accordingly, the figures obtained above are considered as fairly good approximations of S_w (though they are more or less underestimated). In 1977 overwintered adults were censused only three times, and therefore the efforts to recapture marked beetles might be smaller than the preceding years. Thus the winter survival during 1976-77 period could be considerably underestimated.

It is confirmed by virtue of individual marking method that a small portion of beetles emerging in the autumn of year 1 can overwinter twice and they reproduce in the spring of year 3 as well as in year 2. Number of these adults recaptured are summarized in Table 4. New adults emerged in the autumn of 1974 and 1975 were marked not only before hibernation but also in the following spring to minimize the number of no-marked individuals. As this study was started in the spring of 1974, the beetles emerged in the autumn of 1973 could be marked only in the spring of 1974, and therefore survival rate from 1973 to 1975 might be much underestimated. The low number of marked beetles which overwintered twice is not only due to mortality but also due to detachment and indistinctness of marks until the spring of year 3.

Table 4. The number and the ratio of marked beetles which overwintered twice.

| Year | 1973*-75 | | | 1974-76 | | | 1975-77 | | |
|--|----------|--------|-------|---------|--------|-------|---------|--------|-------|
| | Male | Female | Total | Male | Female | Total | Male | Female | Total |
| No. marked in the year 1 | 125 | 252 | 377 | 235 | 330 | 565 | 127 | 179 | 306 |
| No. recaptured in the spring of year 3 | 0 | 2 | 2 | 2 | 6 | 8 | 2 | 3 | 5 |
| % survival | 0 | 0.8 | 0.5 | 0.9 | 1.8 | 1.4 | 1.6 | 1.7 | 1.6 |

* New adults of 1973 were marked only in the spring of 1974. (See text)

Method 2: As has been mentioned earlier, total number of adult beetles resident per season (N_G) are summarized in Table 2. Winter survival are inferred from the difference between the estimated N_G of pre-hibernating adults and that of post-hibernating adults.

The estimates of S_W obtained in this way, given in the last column of Table 2, are 82% (75%) in 1974-75 and 66% (70%) in 1975-76, respectively (Figure in the parentheses are calculated from the value of N_G^*).

Method 3: Average number of adult beetles per census over three or four sampling occasions when they were being at a maximum are summarized in Table 5.

Table 5. Average number of adult beetles per census on or near the days when they were at a maximum, together with the estimates of winter survival (S_W) and reproductive rate (R). N : total sum in the Mondori area, d : mean number per individual thistle plant.

| Year | Average no. of adult beetles per census | | | | Winter survival (S_W) | Reproductive rate (R) |
|------|---|----------|-----------|-----------|---------------------------|---------------------------|
| | Overwintered adult | | New adult | | | |
| | N_{ow} | d_{ow} | N_{new} | d_{new} | | |
| 1974 | 104.3 | 1.2 | 231.3 | 2.6 | 62.8 | 2.22 |
| 1975 | 145.3 | 1.6 | 150.7 | 1.7 | | 1.04 |
| 1976 | 99.7 | 1.1 | 323.0 | 3.6 | 42.7 | 3.24 |
| 1977 | 138.0 | 1.6 | 204.7 | 2.3 | | 1.48 |

These figures provide us with a comparison of relative abundance of adult beetles in spring and autumn generations in 1974-77. We thus obtained the estimates of S_W , 62.8% (1974-75), 66.2% (1975-76) and 42.7% (1976-77), which compare favorably with the other estimates.

Estimates of S_W based on three different methods, although agreements are not very good, tend to support one another and we can conclude with assurance that S_W is 50-60% or more.

8. Reproductive rate, R , and stability of population size

In this paper, reproductive rate, R , is defined conveniently as the number of

newly emerged females produced per overwintered female. The method of estimating the total number of adult beetles per generation (N_G) is described above, from which R is easily estimated as shown in the Table 2. Since the sex ratio of *Hp* is not significantly different between overwintered and new adults, R can also be derived from the ratio of N_{new} to N_{ow} as shown in the Table 5. It can be seen that reproductive rate of *Hp* population is considerably small, ranging from 0.87 (1975) to 3.28 (1976) or from 1.04 to 3.24, based on the data of Tables 2 and 5, respectively. It is doubtless that the smallest value of R in 1975 was due to a heavy rain in the late August when about one third of thistle colonies were flooded. We now consider the variation in the number of adult beetles present at the peak of the breeding seasons (overwintered) and emerging seasons (new adult) in 1974-77. From the data in Table 5, it can be seen that there were only 1.46- and 2.14-fold variations in overwintered and new adult generations, respectively. Using N_G (or N_G^*), Table 2 also provide the variation in the total number of adult beetles emerged per season each year. From these data, there were 1.80-(or 1.91) and 2.17-(1.58) fold variations in overwintered and new adult, respectively in 1974-76.

DISCUSSION

To our knowledge, this study of *H. pustulosa* is the first long-term investigation on the population dynamics of an insect that lives in a natural climax forest of cool temperate zone.

The distinctive characteristics of demographic attributes of *Hp* were revealed as follows: for the first, over four years of this study the population size of *Hp* remained fairly constant at a relatively low level and it never reached to such a high density where intraspecific competition for food occurred. Secondly, although the reproductive rate, R , is relatively small (only a three-fold increase, at maximum), the winter survival rate (S_w) is sufficiently high (more than 50%) to counterbalance the small R . By comparing the data of this species with two closely related species, *H. vigintioctomaculata* (*Hvm*) and *H. vigintioctopunctata* (*Hvp*), which are the serious pests of potato and other *Solanaceous* crops, we can clarify the population characteristics of *Hp* and draw a more general conclusion. Fortunately, the population dynamics of *Hvp* was investigated in a similar detail as *Hp* (NAKAMURA, 1976 a, b). Although the density of overwintered adult of *Hvp* was only less than 0.5 adults per potato plant at its peak, in the late larval stages *Hvp* populations frequently reached a high level where severe food shortage occurred. Then as a result of food shortage, newly emerged adults were forced to disperse in a density-dependent manner. NAKAMURA (1976 a, and in preparation) reported that the rate of population increase per generation of this species was much greater and fluctuated much violently than *Hp*, i. e., R varied from 61.6 to 17.7 in two successive years. On the contrary, the winter survival was much lower than *Hp*, which varied from 3.8 to 1.6%. For

this species such a large R combined with strong power of dispersal is seemed to be a proper reproductive strategy as a pest. Such a difference in R between the two species is mainly attributable to the differences in fecundity and in the intensity of predation to which the eggs and larvae are exposed (in preparation).

The mean fecundities of Hp and Hvp tested by field cage experiments are 74 (maximum, 258) and 588, respectively, though the figure estimated for Hp is based on small number of adults reared. The number of eggs actually laid per female in the field is about 50 in Hp and nearly 500 in Hvp . On the other hand, the longevity of overwintered adults of Hp is 10-20 days longer than Hvp .

In Hp populations, egg mortality was up to 60% and total mortality from egg to adult emergence was 98-99%, where the mortality mainly due to arthropod predation. While, Hvp populations, seemingly free from arthropod predation, egg mortality was only 27% and total mortality was 90%, where larval mortality was mainly due to starvation. It is concluded that low fecundity and intensive arthropod predation have resulted in low reproductive rate of Hp population.

IWAO (1971) reported that the other potato feeding pest, Hvm has the demographic characteristics similar to Hvp , i.e., this species frequently reaches the population density where severe food shortage occurs in the late larval stages. IWAO (1971) also reported that the average fecundity of laboratory reared females was 700 and in the potato field Hvm increased about 14-fold per generation and S_w was equal to 14%. As outlined above, there are clear-cut differences in the population dynamics between Hp and the two allied potato lady beetles.

The colonies of the thistle, *C. kagamontanum*, as the habitat of Hp , showed a high degree of stability throughout the study period. In fact, changes could be found neither in the location nor in the size of thistle patches from 1974 to 1977. The thistle colonies, damaged by the flood in August of 1975, almost recovered in the spring of 1976, since flood leveled and carried away some of the areal shoots but plant bodies under ground had remained intact. *C. kagamontanum* grows in colonies on the small openings and sand deposits along the streams. Although such pockets on which thistle colonies grow will change in the location and size gradually as the stream changes its water course, the total biomass of thistle colonies in the study area may remain fairly constant as a whole. Consequently, in Kamitani area, surrounded with the vegetation of cool temperate climax forest, habitat stability is very high. Hp lives in a fairly constant environment, shows low reproductive rate per generation, maintains fairly constant population size, and has long adult longevity, and hence it can be said that Hp is more K -strategic than the two pest species (especially than Hvp) (PIANKA, 1970; SOUTHWOOD *et al.*, 1974).

In the subsequent reports, we shall describe the life tables and discuss the key factors and density relationships in the population dynamics of Hp . We are now investigating several local populations of Hp which distribute over a wide instability-

stability habitat spectrum. A comparison of population characteristics between local populations will give more general conclusions on the evolution and ecology of *H. pustulosa* in the future.

SUMMARY

1. A field study was carried out on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO) living in a cool temperate climax forest in northern Kyoto Prefecture, central Japan.
2. Intensive marking, release and recapture program was carried out to estimate the adult population parameters by using JOLLY-SEBER method.
3. Sampling ratio was around 50%. Marking ratio rapidly rised as the census progressed and approached to 100%.
4. Sex ratio (% ♀) was 63–69% in both overwintered and new adults.
5. Daily survival rate was as high as 0.95 or more and constant throughout the season. Adult longevity in the spring was longer than 40 days.
6. Reproductive rate i.e., the ratio of the number of newly emerged adults in a given generation to that of overwintered adults in the preceding generation, is very small, ranging 1–3, whereas winter survival is higher than 50%, consequently the size of populations in the study area remain in a remarkably constant size and it never reached a level where intraspecific competition occurred.
7. The population characteristics of *H. pustulosa* are compared with those of the two closely related species, *H. vigintioctopunctata* and *H. vigintioctomaculata*, which are the pests of *Solanaceous* crops. *Hp* is more *K*-strategic than the two pest species.

ACKNOWLEDGEMENT: We are most grateful to Dr. S. IWAO of Kyoto University for his constant advices throughout the present study and critical reading of the manuscript. We are indebted to Drs. S. UTIDA, E. KUNO, T. TSUTSUMI and K. OGINO and Mr. T. INOUE for their encouragement and helpful discussions. Thanks are also due to the staff members of the School Forest of Kyoto University at Asiu for giving us many facilities to the work in Asiu, to Mr. K. TAKAGI and Mr. Y. SAWADA for their assistance in the field work, and Mr. M. KAWAMOTO for drawing many figures in this paper. Computations were performed by the computer, FACOM-M190 at Data Processing Center, Kyoto University.

REFERENCES

- CLARK, L. R., P. W. GEIER, R. D. HUGHES and R. F. MORRIS (1967) *The ecology of insect populations in theory and practice*. Methuen, London.
- 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)* 129–147.
- JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration —stochastic model. *Biometrika* 52; 225–247.
- KATAKURA, H. (1974a) Variation analysis of elytral maculation in *Henosepilachna vigintiocto-*

- maculata* complex (Coleoptera, Coccinellidae). *Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* 19: 445-455.
- KATAKURA, H. (1974b) Morphology and distribution of the forms of *Henosepilachna vigintioctomaculata* complex in Hokkaido. *Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool.* 19: 657-680.
- NAKAMURA, K. (1976a) Studies on the population dynamics of the 28-spotted lady beetle, *Henosepilachna vigintioctopunctata* F. I. Analysis of life tables and mortality process in the field population. *Jap. J. Ecol.* 26: 49-59. (in Japanese)
- NAKAMURA, K. (1976b) Ditto. II. Analysis of regulatory system under semi-natural and laboratory conditions. *Jap. J. Ecol.* 26: 125-134. (in Japanese)
- SEBER, G. A. F. (1973) *The estimation of animal abundance and related parameters*. Griffin, London.
- SOUTHWOOD, T. R. E., R. M. MAY, M. P. HASSELL and G. R. CONWAY (1974) Ecological strategies and population parameters. *Amer. Natur.* 108: 791-804.
- SOUTHWOOD, T. R. E. (1975) The dynamics of insect populations. *Insects, Science and Society* (Ed. by D. PIMENTEL). pp. 151-199. Academic Press, New York.
- WILSON, F. (1968) Insect abundance: prospect. *Symp. Roy. Entomol. Soc. Lond.* 4: 143-158.

APPENDIX

Mark-recapture tables for application of JOLLY's method and the estimates of adult population parameters of *Henosepilachna pustulosa*, 1974-76. n_i is the number captured in the i th sample. m_i is the number of marked beetles in the i th sample. s_i is the number released from the i th sample after marking. See JOLLY (1965) for other symbols and further explanation.

1974 Overwintered adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| i | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\phi}_i \pm \sqrt{V(\hat{\phi}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 23 May | 3 | — | 3 | | 0.0 | | 0.667 ± 0.272 | |
| 25 | 6 | 2 | 6 | 0.33 | 2.0 | 4.7 ± 1.6 | 0.784 ± 0.238 | 74.7 ± 36.9 |
| 28 | 49 | 2 | 49 | 0.04 | 4.7 | 78.4 ± 36.0 | 0.885 ± 0.087 | 156.9 ± 54.1 |
| 30 | 88 | 17 | 88 | 0.19 | 45.8 | 226.2 ± 42.8 | 0.857 ± 0.066 | 30.1 ± 40.3 |
| 2 June | 93 | 41 | 93 | 0.44 | 100.1 | 224.0 ± 24.5 | 0.835 ± 0.057 | 64.5 ± 26.2 |
| 5 | 102 | 51 | 102 | 0.50 | 127.0 | 251.6 ± 23.3 | 0.975 ± 0.059 | -22.1 ± 20.8 |
| 8 | 107 | 83 | 107 | 0.78 | 173.5 | 223.1 ± 16.0 | 0.918 ± 0.082 | 65.6 ± 19.3 |
| 13 | 87 | 58 | 87 | 0.67 | 181.2 | 270.3 ± 27.5 | 0.719 ± 0.067 | -6.1 ± 15.7 |
| 17 | 70 | 56 | 70 | 0.80 | 151.1 | 188.2 ± 16.2 | 0.859 ± 0.058 | 26.7 ± 11.4 |
| 21 | 92 | 69 | 92 | 0.75 | 141.7 | 188.3 ± 14.1 | 1.000 ± 0.063 | 5.8 ± 10.6 |
| 25 | 85 | 72 | 85 | 0.85 | 165.1 | 194.4 ± 15.7 | 0.794 ± 0.061 | -1.6 ± 6.6 |
| 30 | 79 | 73 | 79 | 0.92 | 141.4 | 152.9 ± 12.0 | 0.836 ± 0.056 | 5.9 ± 4.7 |
| 5 July | 63 | 58 | 63 | 0.92 | 123.2 | 133.6 ± 11.0 | 0.939 ± 0.058 | 12.1 ± 6.5 |
| 9 | 55 | 48 | 55 | 0.87 | 120.3 | 137.5 ± 12.1 | 0.983 ± 0.069 | 4.2 ± 7.2 |
| 13 | 58 | 52 | 58 | 0.90 | 125.1 | 139.3 ± 12.7 | 0.949 ± 0.084 | 5.6 ± 6.3 |
| 17 | 61 | 55 | 61 | 0.90 | 124.4 | 137.7 ± 13.6 | 0.735 ± 0.069 | 1.6 ± 4.2 |
| 23 | 58 | 54 | 58 | 0.93 | 95.8 | 102.8 ± 9.7 | 0.880 ± 0.063 | 1.4 ± 3.1 |
| 28 | 45 | 43 | 45 | 0.96 | 87.8 | 91.8 ± 9.3 | 0.993 ± 0.085 | -2.0 ± 2.1 |
| 2 Aug. | 40 | 40 | 40 | 1.00 | 89.2 | 89.2 ± 10.3 | 0.867 ± 0.109 | 3.1 ± 2.7 |
| 6 | 25 | 24 | 25 | 0.96 | 77.3 | 80.4 ± 11.1 | 0.807 ± 0.094 | -1.7 ± 2.3 |
| 10 | 30 | 30 | 30 | 1.00 | 63.2 | 63.2 ± 7.6 | 1.000 ± 0.102 | 2.7 ± 2.3 |
| 14 | 25 | 24 | 25 | 0.96 | 66.9 | 69.6 ± 9.9 | 0.822 ± 0.099 | -1.4 ± 1.9 |
| 19 | 24 | 24 | 24 | 1.00 | 55.8 | 55.8 ± 7.5 | 1.000 ± 0.165 | 0.0 ± 0.0 |
| 23 | 18 | 18 | 18 | 1.00 | 63.3 | 63.3 ± 11.4 | 0.732 ± 0.124 | 1.6 ± 1.0 |
| 3 Sept. | 30 | 29 | 30 | 0.97 | 46.4 | 47.9 ± 6.9 | 1.000 ± 0.165 | -0.6 ± 1.1 |
| 10 | 24 | 24 | 24 | 1.00 | 50.9 | 50.9 ± 10.0 | 0.825 ± 0.271 | 2.0 ± 1.7 |
| 18 | 21 | 20 | 21 | 0.95 | 42.0 | 44.0 ± 14.0 | 0.364 ± 0.194 | -0.4 ± 0.8 |
| 29 | 9 | 9 | 9 | 1.00 | 15.7 | 15.7 ± 7.5 | | |
| 17 Oct. | 4 | 4 | 4 | 1.00 | | | | |

1974 New adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| <i>i</i> | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\phi}_i \pm \sqrt{V(\hat{\phi}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 6 Aug. | 16 | — | 16 | | 0.0 | | 0.960 ± 0.065 | |
| 10 | 51 | 13 | 51 | 0.25 | 15.4 | 57.1 ± 5.1 | 0.879 ± 0.055 | 82.7 ± 13.2 |
| 14 | 84 | 29 | 84 | 0.35 | 46.9 | 132.9 ± 13.2 | 0.908 ± 0.035 | 113.9 ± 15.7 |
| 19 | 179 | 70 | 179 | 0.39 | 92.5 | 234.5 ± 11.9 | 0.995 ± 0.024 | 63.2 ± 13.3 |
| 23 | 209 | 141 | 209 | 0.67 | 200.5 | 296.5 ± 11.1 | 0.883 ± 0.036 | 126.0 ± 14.4 |
| 3 Sept. | 246 | 150 | 246 | 0.61 | 237.0 | 387.7 ± 17.8 | 0.876 ± 0.047 | 27.8 ± 14.4 |
| 10 | 198 | 157 | 159 | 0.79 | 291.7 | 367.4 ± 20.8 | 0.761 ± 0.072 | 59.4 ± 11.3 |
| 18 | 219 | 158 | 159 | 0.72 | 223.6 | 309.4 ± 27.0 | 0.404 ± 0.157 | 42.3 ± 18.2 |
| 29 | 81 | 51 | 52 | 0.63 | 90.8 | 143.1 ± 54.5 | | |
| 17 Oct. | 6 | 6 | 6 | 1.00 | | | | |

1975 Overwintered adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| <i>i</i> | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\phi}_i \pm \sqrt{V(\hat{\phi}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 13 May | 126 | — | 126 | | 0.0 | | 0.922 ± 0.048 | 70.6 ± 19.6 |
| 21 | 134 | 63 | 134 | 0.47 | 116.2 | 245.1 ± 19.2 | 0.827 ± 0.048 | 8.6 ± 15.5 |
| 27 | 142 | 80 | 142 | 0.56 | 154.8 | 273.3 ± 18.8 | 0.916 ± 0.054 | 32.9 ± 11.3 |
| 2 June | 145 | 111 | 145 | 0.77 | 198.6 | 258.9 ± 16.5 | 0.803 ± 0.067 | 13.5 ± 8.6 |
| 9 | 115 | 89 | 115 | 0.77 | 186.9 | 240.9 ± 20.1 | 0.658 ± 0.062 | 22.9 ± 8.7 |
| 19 | 96 | 78 | 96 | 0.81 | 140.0 | 171.9 ± 14.6 | 0.790 ± 0.077 | -3.1 ± 6.6 |
| 3 July | 74 | 58 | 74 | 0.78 | 124.9 | 158.7 ± 16.3 | 0.688 ± 0.071 | -0.8 ± 4.4 |
| 16 | 45 | 41 | 45 | 0.91 | 97.0 | 106.2 ± 11.2 | 0.981 ± 0.095 | 2.5 ± 3.3 |
| 25 | 47 | 45 | 47 | 0.96 | 99.0 | 103.3 ± 12.0 | 0.892 ± 0.124 | 6.8 ± 3.9 |
| 3 Aug. | 41 | 39 | 41 | 0.95 | 90.1 | 94.6 ± 13.6 | 0.662 ± 0.108 | -1.6 ± 2.9 |
| 24 | 32 | 28 | 32 | 0.88 | 61.0 | 69.4 ± 10.4 | 0.732 ± 0.100 | 2.9 ± 2.3 |
| 31 | 29 | 28 | 29 | 0.97 | 47.6 | 49.2 ± 7.3 | 1.000 ± 0.226 | |
| 9 Sept. | 31 | 29 | 31 | 0.94 | 54.6 | 58.2 ± 13.4 | | |
| 21 | 17 | 17 | 17 | 1.00 | | | | |

1975 New adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| <i>i</i> | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\phi}_i \pm \sqrt{V(\hat{\phi}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 3 Aug. | 10 | — | 10 | | 0.0 | | 0.957 ± 0.106 | |
| 24 | 130 | 6 | 130 | 0.05 | 9.6 | 179.2 ± 39.9 | 0.905 ± 0.039 | 47.3 ± 38.1 |
| 31 | 148 | 85 | 148 | 0.57 | 120.9 | 209.5 ± 11.4 | 0.960 ± 0.069 | 38.9 ± 11.0 |
| 9 | 154 | 113 | 154 | 0.73 | 176.5 | 240.0 ± 18.3 | 0.518 ± 0.189 | 9.6 ± 6.5 |
| 21 Sept. | 100 | 84 | 85 | 0.84 | 112.7 | 133.9 ± 48.4 | | |
| 9 Oct. | 3 | 3 | 3 | 1.00 | | | | |

1976 Overwintered adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| <i>i</i> | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\theta}_i \pm \sqrt{V(\hat{\theta}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 13 May | 88 | — | 87 | | 0.0 | | 1.000 ± 0.048 | |
| 19 | 93 | 50 | 90 | 0.54 | 88.8 | 163.7 ± 13.0 | 0.879 ± 0.064 | 42.5 ± 14.1 |
| 26 | 98 | 60 | 98 | 0.61 | 113.2 | 183.7 ± 15.0 | 0.747 ± 0.056 | 21.9 ± 10.4 |
| 8 June | 99 | 70 | 97 | 0.71 | 113.0 | 159.1 ± 11.3 | 0.819 ± 0.054 | 9.5 ± 6.9 |
| 22 | 87 | 72 | 79 | 0.83 | 114.7 | 138.2 ± 10.2 | 0.910 ± 0.078 | 13.2 ± 6.3 |
| 5 July | 68 | 57 | 59 | 0.84 | 110.7 | 131.7 ± 12.9 | 0.703 ± 0.076 | 12.4 ± 5.9 |
| 20 | 55 | 44 | 46 | 0.80 | 79.3 | 98.6 ± 10.2 | 0.873 ± 0.085 | 3.9 ± 5.3 |
| 27 | 43 | 37 | 37 | 0.86 | 70.9 | 82.1 ± 9.7 | 0.860 ± 0.103 | 5.4 ± 4.7 |
| 4 Aug. | 35 | 30 | 30 | 0.86 | 61.0 | 70.8 ± 9.7 | 0.803 ± 0.109 | -3.9 ± 3.0 |
| 18 | 24 | 24 | 24 | 1.00 | 49.0 | 49.0 ± 7.5 | 0.810 ± 0.101 | 1.7 ± 1.1 |
| 31 | 24 | 23 | 24 | 0.96 | 39.7 | 41.3 ± 6.3 | 0.875 ± 0.083 | -0.6 ± 1.0 |
| 6 Sept. | 28 | 28 | 28 | 1.00 | 35.6 | 35.6 ± 5.7 | 1.000 ± 0.236 | 4.1 ± 2.5 |
| 15 | 21 | 19 | 21 | 0.90 | 41.0 | 45.1 ± 11.3 | 0.456 ± 0.135 | -1.0 ± 1.3 |
| 22 | 14 | 14 | 14 | 1.00 | 19.6 | 19.6 ± 5.1 | | |
| 30 | 10 | 10 | 10 | 1.00 | | | | |

1976 New adults

| Sampling date | Number captured | | Number released | Proportion marked | Total marked | Population size | Survival rate | Number joining |
|---------------|-----------------|--------|-----------------|-------------------|--------------|-------------------------------------|---|-------------------------------------|
| | Total | Marked | | | | | | |
| <i>i</i> | n_i | m_i | s_i | $\hat{\alpha}_i$ | \hat{M}_i | $\hat{N}_i \pm \sqrt{V(\hat{N}_i)}$ | $\hat{\theta}_i \pm \sqrt{V(\hat{\theta}_i)}$ | $\hat{B}_i \pm \sqrt{V(\hat{B}_i)}$ |
| 4 Aug. | 15 | — | 15 | | 0.0 | | 1.000 ± 0.076 | |
| 18 | 226 | 7 | 226 | 0.03 | 15.3 | 433.5 ± 116.4 | 0.868 ± 0.025 | 105.0 ± 103.9 |
| 31 | 335 | 141 | 334 | 0.42 | 203.4 | 481.3 ± 19.3 | 0.955 ± 0.018 | -7.1 ± 17.6 |
| 6 Sept. | 333 | 279 | 333 | 0.84 | 378.7 | 451.8 ± 11.4 | 0.896 ± 0.025 | 8.1 ± 6.2 |
| 15 | 294 | 276 | 294 | 0.94 | 387.6 | 412.8 ± 12.6 | 0.996 ± 0.054 | 7.9 ± 4.7 |
| 22 | 250 | 241 | 241 | 0.96 | 404.0 | 419.1 ± 28.4 | | |
| 30 | 164 | 158 | 158 | 0.96 | | | | |

ブナ原生林に生息するコブオオニジュウヤホシテントウの個体群動態

I. 標識再捕法による成虫個体群パラメーターの推定

中村 浩二・大串 隆之

京都府北部にある京都大学芦生演習林のブナ原生林内の 溪流ぞいにはえる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を1974年から1977年まで調査した。

個体識別法によりえられたデータを JOLLY-SEBER 法で整理した。成虫の発見率は約50%、標識虫率は100%近くに達し、精度の高い推定値をえた。本種は年1化性であり、性比(%♀)は越冬成虫、新成虫とも63-69%であった。越冬成虫、新成虫とも日あたり生存率は安定して高く0.95以上であった。増殖率(越冬雌あたりの新羽化雌数)は1~3と低かったが、新成虫の越冬率は50%以上であった。調査期間を通じて本種はアザミの量に比して低い密度レベルで生息し、餌不足のおこるような密度には達しなかった。越冬成虫の総出現数、新成虫の総羽化数の年次変動は1.5~2倍で、安定した個体群サイズであった。本種の個体群動態は、ナス科作物の害虫である近縁2種(ニジュウヤホシテントウとオオニジュウヤホシテントウ)に比して、*K*-戦略的な特徴を有していることがわかった。