

STUDIES ON THE POPULATION DYNAMICS OF A THISTLE-
FEEDING LADY BEETLE, *HENOSEPILOCHNA PUSTULOSA*
(KÔNO) IN A COOL TEMPERATE CLIMAX FOREST
III. THE SPATIAL DYNAMICS AND THE
ANALYSIS OF DISPERSAL BEHAVIOUR

Koji NAKAMURA* and Takayuki OHGUSHI**

* Ecological Laboratory, Faculty of Science, Kanazawa University, Kanazawa 920, Japan

** Entomological Laboratory, College of Agriculture, Kyoto University, Kyoto 606, Japan

INTRODUCTION

Since the 1950s, our knowledge of dynamics of natural populations has been much advanced through the development of the life table approach (MORRIS and MILLER, 1954; VARLEY and GRADWELL, 1960; RICHARDS and WALOFF 1961, etc.). However, since construction of a life table is so laborious, the study plot is usually so small that the dispersal range of the animal under study is far greater than the limits of the plot. As a result, the losses due to dispersal, or migration out of the study area, are rarely separated from those due to mortality. Thus, workers have not been able to use life tables to evaluate the significance of dispersal in the dynamics of populations. In a considerable number of the species hitherto studied, the key-factor in the population fluctuation has proved to lie in the adult stage, suggesting that dispersal may be important in the population dynamics of these species (WATT, 1963; KUNO, 1968; KIRITANI et al., 1970; NAKAMURA and OHGUSHI, 1981).

Recently IWAO (1971), reappraising ELTON's (1949) earlier comments on population interspersion, emphasized the importance of knowing how the splitting up of a population into partly isolated units affects the natural control of an animal population in a wider area. He also stressed the point that, in any study of animal population dynamics, temporal changes in number should be analysed in relation to the changes in the spatial structure of the population under study. The importance of subdivision of population into minor units and dispersal of individuals between them in stabilizing population density have also been claimed by many authors (ANDREWARTHA and BIRCH, 1954; THOMPSON, 1956; EHRLICH and BIRCH, 1967; DEN BOER, 1968; BIRCH, 1971).

Although there have been several attempts to trace movement patterns of insects by marking-recapture censuses (FISHER and FORD, 1947; MACLEOD and DONNELLY, 1963; EHRLICH, 1965; EHRLICH and GILBERT, 1973; GILBERT and SINGER, 1973), no detailed study on spatio-temporal dynamics of insects populations has been done under field conditions, except for a few trials (MORISHITA, 1950; PAJUNEN and JANSSON,

1969; PAJUNEN, 1971; IWAO, 1971). In field studies, therefore, we should ideally construct life tables on the one hand and assess the animal's movements in detail on the other, and then relate the two to the changes in number in larger and smaller habitat units.

From this point of view, a phytophagous lady beetle, *Henosepilachna pustulosa* (KONO) (henceforth abbreviated to *H ϕ*) is a suitable animal for studying the population dynamics in space and time; firstly because the spatial distribution of thistle plants (the food of *H ϕ*) in its habitat shows different levels of discrete patchiness, and secondly, because adult mobility is relatively restricted, so that marking-recapture procedures are easily applicable.

In the preceding papers, we estimated the adult population parameters and presented life tables, indicating the stabilization of *H ϕ* population below the carrying capacity of food plant was caused by the density-dependent inter-patch dispersal of overwintered beetles (NAKAMURA and OHGUSHI, 1979, 1981). The present paper deals with the spatial dynamics of *H ϕ* populations, i.e. the changes in adult numbers in the different patches of food plant and adult movements between them. This article includes the analyses of patterns of adult movement, such as the distance moved per day and the angle turned between the successive locations.

H. pustulosa has one generation a year. Only a few days after the snow melts in early May, adults begin to emerge from overwintered sites and appear in the thistle patches. Oviposition extends from late May to mid July. After four larval instars, the new adults emerge from late August to early September. These newly emerged adults disappear from the host plants by early October.

STUDY SITE AND METHODS

The study was carried out from 1974 to 1977 in the School Forest of Kyoto University at Asiu, 100 km north of Kyoto City. The Kamitani study area is rather flat, at an altitude of about 700 m and is covered with cool temperate climax forest of *Fagus crenata* and *Quercus mongolica*, etc (Fig. 1 in NAKAMURA and OHGUSHI, 1979). The food plant of *H ϕ* population, *Cirsium kagamontanum*, a perennial thistle, was one of the most dominant herb species on the stream sides in the study area. *C. kagamontanum* grows in discrete clusters of different sizes on the small clearings and sand deposits along the stream. Such aggregations of thistles growing together are referred to as "patches" in this article. The patches themselves were not uniformly distributed in the Kamitani area, so that the study site could be split up into several "subareas", each of which contained a cluster of thistle patches (Fig. 1). The Mondori subarea, selected for the main study site, contained 11 small discrete patches. An enlarged map of the Mondori subarea, showing the location and the size of the thistle patches, was presented in NAKAMURA and OHGUSHI (1981, Fig. 1). Each of the subareas I~V was composed of several small patches. While in subarea VI, the

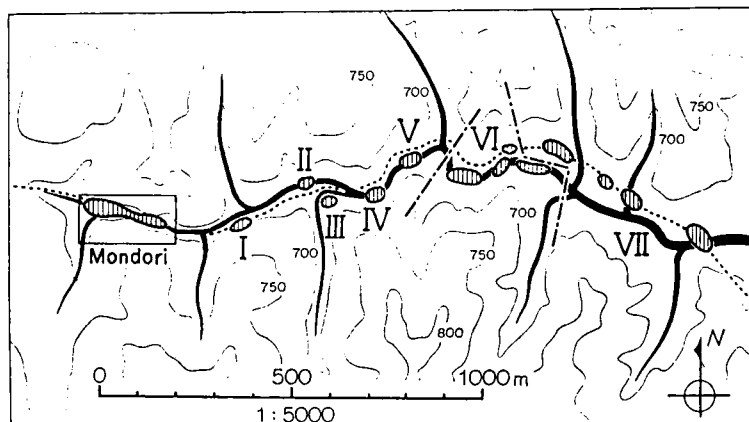


Fig. 1. Sketch map of the Kamitani study area, the School Forest of Kyoto University located at Asiu, showing the location of the thistles, *Cirsium kagamontanum* (shaded areas). The rectangle shows the Mondori subarea which was studied more intensively. The Roman numerals refer to the names of the subareas.

thistles grew on a series of large sand deposits along the stream sides, so the large thistle patches, each of which contained more than 100 thistle stocks, stretched continuously in a row. Subarea VII was in the grassland, where the thistles were scattered along a trail and so their patchiness was less distinguishable. Although some of the thistle patches which we identified had blurred and arbitrary boundaries (especially for subareas VI and VII), the spatial distribution of the thistles as a whole showed a clear range of different levels of patchiness. There was only a slight change in the location and size of the thistle patches during the study period, 1974-1977.

The routine census

The Mondori subarea was selected for the main study site and all the thistles were checked on each census. Sampling quadrats of 2×2 m² were set up in other subarea except in subareas I and III. Seventeen and thirty quadrats were placed at intervals of about 10 metres in subareas VI and VII, respectively. Besides sampling quadrats, some additional thistles were examined in the subareas II, IV, V and VI. On each census all the beetles found were marked individually with lacquer by using four points on their elytra. The beetles tended to stay sluggishly on the host plants, so that we could catch them easily. The beetles captured or recaptured were immediately released on the same plant on which they were caught. The beetles did not show any "marking effect", such as escape reaction, or other abnormal behaviour when they were released. The routine censuses were carried out from mid-May to early October every third or fourth day in 1974, and once a week in 1975 and 1976.

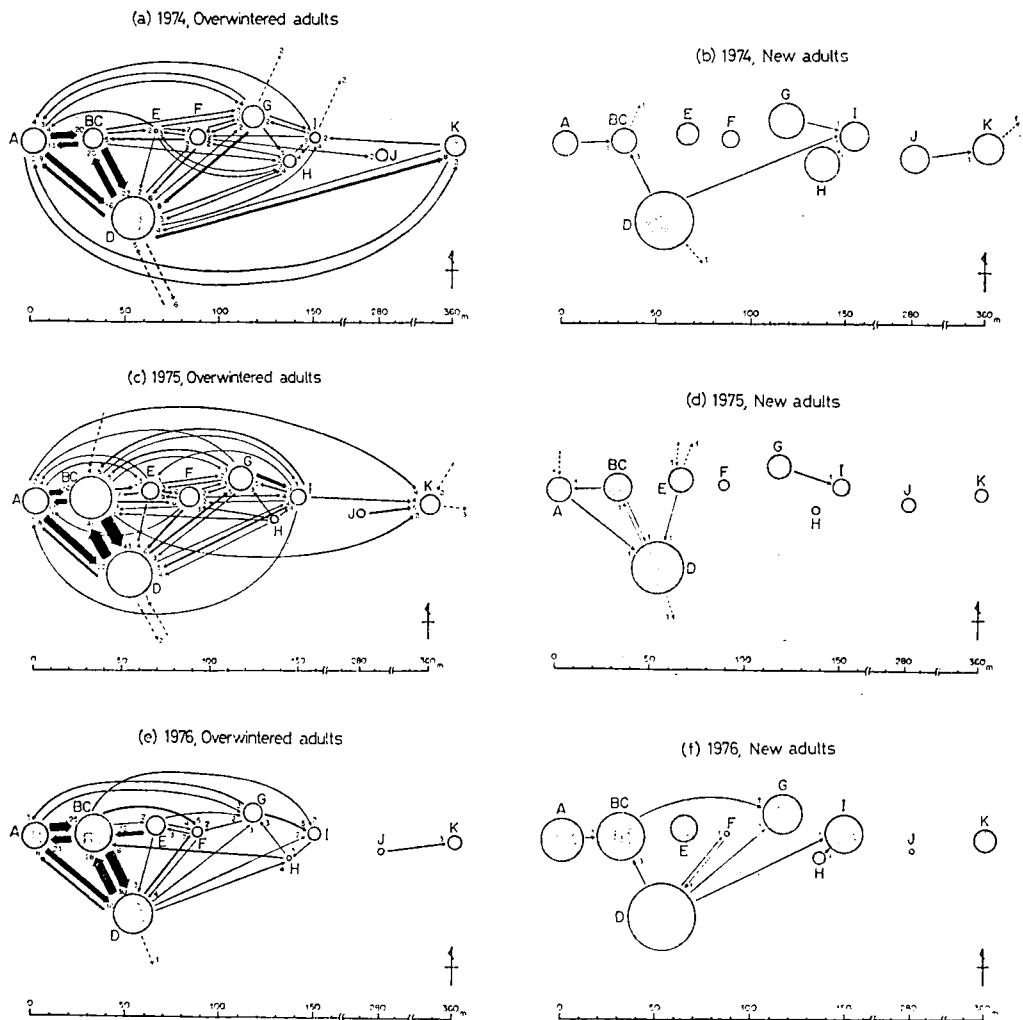


Fig. 2. Schematic representation of changes in adult numbers in different thistle patches in the Mondori subarea, and the interconnection by movements between them. The centre of each circle indicates the location of a patch, and the area of circle is proportional to its population size. An arrow indicates the direction of movement of marked individuals and thickness of line is roughly proportional to the number of emigrants. The figure beside the arrow indicates the number of marked individuals that moved between the patches. A dashed arrow indicates the movement between the Mondori and other subareas. To avoid being too complicated the arrows which indicate the movement of one individual are omitted in the figures (a), (c) and (e).

The exhaustive search

The thistles which were not covered on the routine censuses (i.e. the thistles growing sparsely between subareas and those between sampling quadrats) were examined to follow the movement of marked individuals and to count the numbers of unmarked individuals. These exhaustive searches covered the whole Kamitani study

area at 7-10 day intervals each year.

RESULTS

1. Movements of adults among thistle patches in the Mondori subarea

The changes in adult numbers in the different patches, and the degree of interchange of beetles among them, for the period from spring of 1974 to autumn of 1976, are shown in Fig. 2. The movement paths of the marked beetles were obtained by connecting the two consecutive points where they were caught or recaptured. In Fig. 2, the area of each circle is proportional to the size of *Hp* population. This is

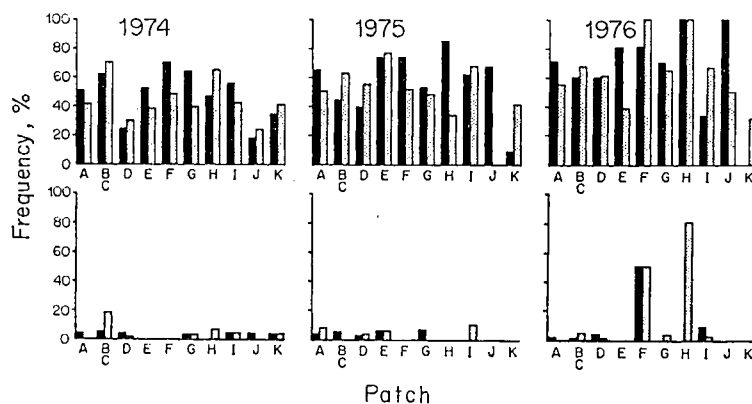


Fig. 3. The proportion of "emigrants" (closed) and "immigrants" (dotted) to the total number of residents in each patch in the Mondori subarea. Upper: overwintered adults. Lower: new adults.

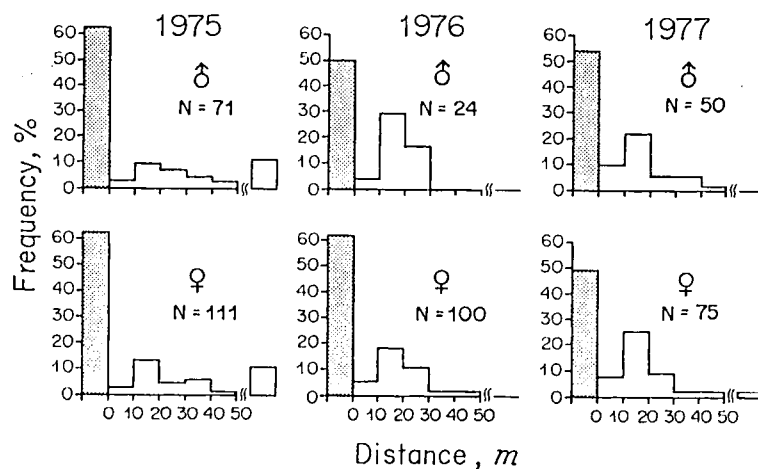


Fig. 4. Frequency distribution of the distances between the patch where a marked beetle was last found in the autumn and the patch where it was recaptured first in the following spring. Hatched columns indicate the frequency of a beetle's reappearance in the very same patch. N: number of marked beetles recaptured the following spring.

estimated from the average number of beetles per census on or near the days when they were at the maximum (A_0 or A_E in Fig. 5, NAKAMURA and OHGUSHI, 1981). The arrows which indicate the movement of only one individual are omitted in Figs. 2a, c and e to reduce the complexity. The figures show that thistle patches in the Mondori subarea were closely connected with each other through the movement of the overwintered adults. In fact, even patch K was connected with other patches; some of which were at distances of more than 100 m. From these data we can obtain an approximate rate of immigration and emmigration in terms of the total number of the residents in each patch, as shown in Fig. 3. These figures show that more than fifty percent of the overwintered beetles which were found on each patch, i. e.

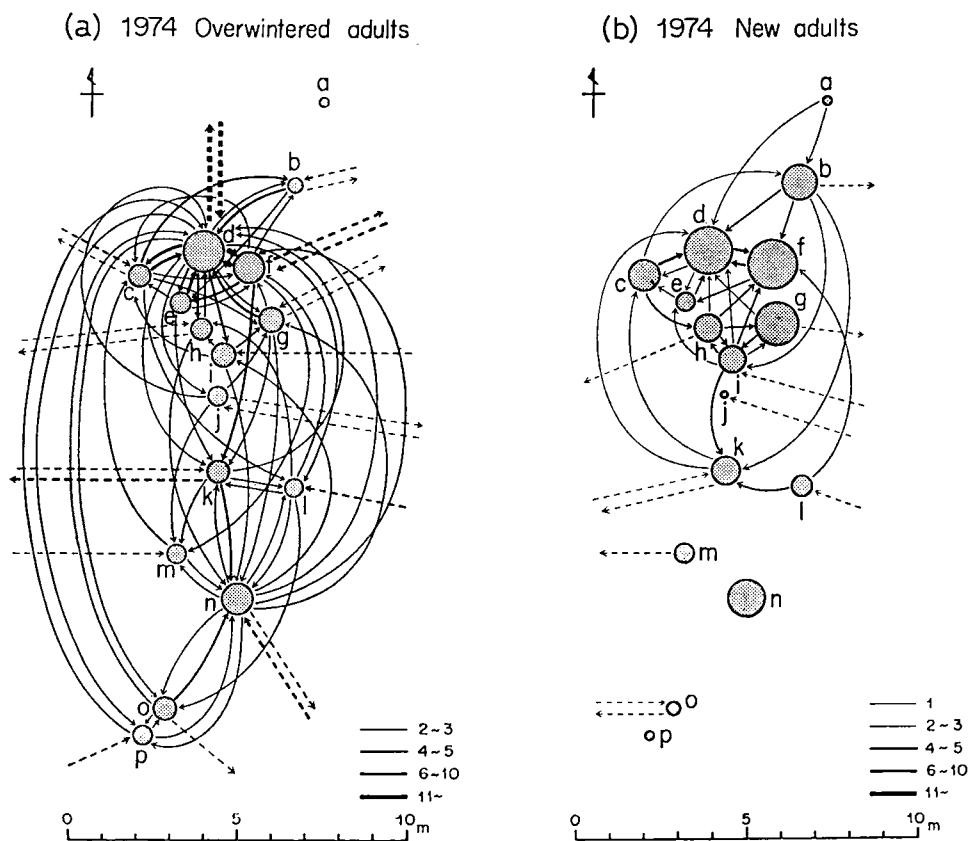


Fig. 5. Schematic representation of changes in adult numbers on the individual thistles within a single patch, and movement of adult beetles between them, taking patch D as an example. The centre of each circle indicates the location of the thistle. A dashed arrow indicates the movement between patch D and outside of it. To reduce complexity, the arrows which indicate the movement of one individual are omitted in the figure (a). Small letters refer to the individual thistle plants. See also explanation of Fig. 2.

the residents of a patch, were immigrants from the other patches (i.e. emigrants to the other patches). However, most newly emerged adults tended to remain feeding in the original patch where they emerged until they entered hibernation (Figs. 2 and 3). In the following spring, most of the marked beetles were recaptured first in the same patches where they were last found in the autumn (Fig. 4). Figure 4 shows that in the spring of 1975, about 10 percent of individuals were found at more than 50 m away from their last position in the preceding autumn; the movement being mainly during the post-hibernating period. This can be inferred by the fact that the winter of 1975 was so mild that the thistles had already sprouted leaves and were 20-30 cm in height when we started the census in mid May; while in other years the snow had just melted, and the thistles were small rosettes at this time, as in 1974 and 1976. The beetles apparently hibernated in the litter or soil under the thistle patches.

2. Movement of adults within a patch

Overwintered adults freely changed their locations to and fro among the thistle plants within a patch (movements of adults within patch D are given as an example in Fig. 5). New adults also frequently shifted their location within a patch, although they rarely migrated to other patches (Figs. 2 and 3). The thistles on each patch grew closely in contact with one another, so that beetles could move between plants by walking through leaves as well as by flight.

3. Movement of adults among subareas

The movement of adult beetles between subareas is schematically shown in Fig.

6. The area of each circle in Fig. 6 is proportional to the size of *Hp* population in

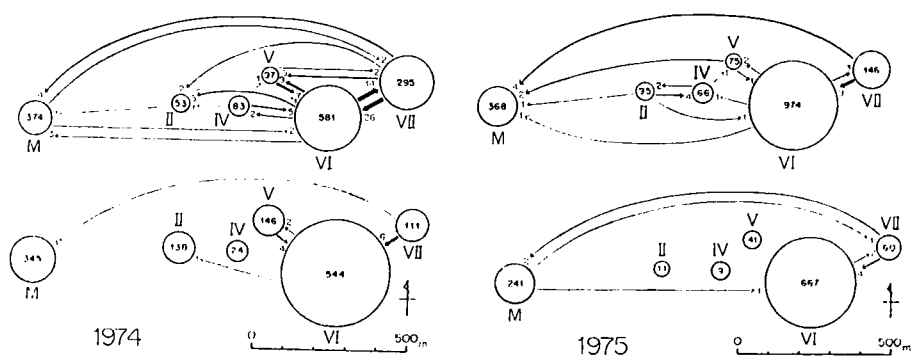


Fig. 6. Schematic representation of changes in adult numbers in the subareas and the movements of adult beetles between them. The centre of each circle indicates the location of the subarea. The numbers in the circles refer to the total number of beetles marked on each subarea. M refers to the Mondori subarea. See the explanation of Fig. 2. Top: overwintered adults. Bottom: new adults.

each subarea, which is given by sum of the average number of beetles in the sampling quadrats and outside of the sampling quadrats, on or near the days when the number of the beetles was at a maximum. Subareas I and III, where no sampling quadrat was placed, were omitted in Fig. 6 due to insufficient data. Figure 7 shows

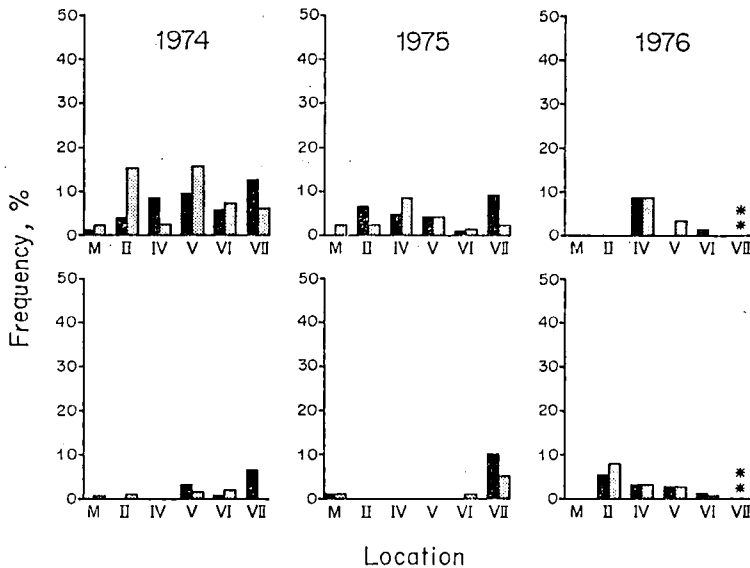


Fig. 7. The proportion of "emigrants" (closed) and "immigrants" (dotted) to the total number of residents in each subarea. Roman numerals on the abscissa indicate the subareas. Top: overwintered adults. Bottom: new adults. *: subarea VII was not examined in 1976.

that the proportion of emigrants and immigrants to the total residents in each subarea. Figures 6 and 7 show that the *Hp* population on the Mondori area was nearly self-contained, although thistle patches at Mondori were closely interconnected through the movements of overwintered adults (Figs. 2 and 3). Similarly, Figs. 6 and 7 indicate that the total *Hp* population at Kamitani was divided into several subpopulations which were nearly confined to particular clusters of patches.

4. Analysis of dispersal patterns of adult *Hp* population

The location of a beetle when it was caught or recovered, is referred to as a "fix" in this article. Figure 8 shows the schematic representation of the movement path of a beetle. P_i is the fix at i th recapture. l_i is the distance between the two consecutive fixes. α_i and β_i are the relative and absolute angles turned during three successive fixes, respectively.

(1) *Distribution of l_i .* In the Mondori subarea, the distance from a thistle patch to its nearest neighbour was more than 10 m, except for the distances between patches B and C and between patches H and I, which were only 3.5 and 5.5 m, respectively.

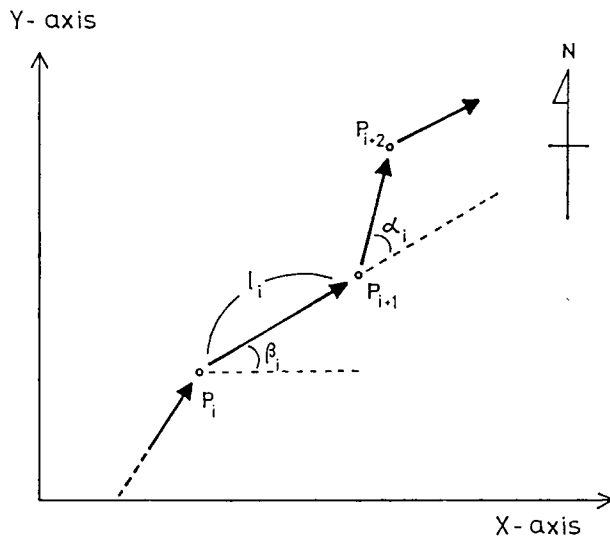


Fig. 8. Schematic representation of movement paths of a marked beetle during consecutive recaptures. P_i =the fix at i th recapture. l_i , α_i and β_i =the distance moved, the relative and absolute angles turned during successive fixes (i to $i+1$), respectively.

Therefore l_i which is more than 10 m indicates an inter-patch movement. Figure 9 shows the distribution of l_i , indicating that overwintered adults were relatively sedentary, i.e. the probability that they tended to stay on the very same thistle plant, or within the same thistle patch, during two consecutive recaptures is more than 60%. The frequency decreases monotonously with increasing length of l_i and has a long right-hand tail. New adults were far more sedentary than the overwintered adults, for more than 90% of instances they remained within the same thistle patch. If an individual is captured after a long interval of time, the value of l_i naturally would become larger than the values at shorter intervals, so values of l_i based on more than 7 days intervals are excluded from Fig. 9. The distribution of distance moved per day is conveniently calculated by l_i/I , where I is the length of time between i and $i+1$ th recaptures (NAKAMURA, 1980). The results show that most overwintered adults did not move more than 2 m per day and new adults tended to stay on the same thistle plant and rarely moved more than 0.5 m per day. SOUTHWOOD (1962) classified animal movement into two types: trivial and migratory. He claimed that the species that is a denizen of temporary habitats shows a high power of dispersal or migratory movements. The *Hp* population studied in Asiu, lived in a stable climax forest, and did not show any migratory tendency, although the overwintered adults frequently moved among patches (trivial movements). l_{sum} , the sum total of the distances moved during the residence time (L) can be obtained by adding up l_i for each beetle which was captured at least twice (Fig. 10). The distribution of L was shown in Table 2 and Fig. 7 in the previous article (NAKAMURA and OHGUSHI,

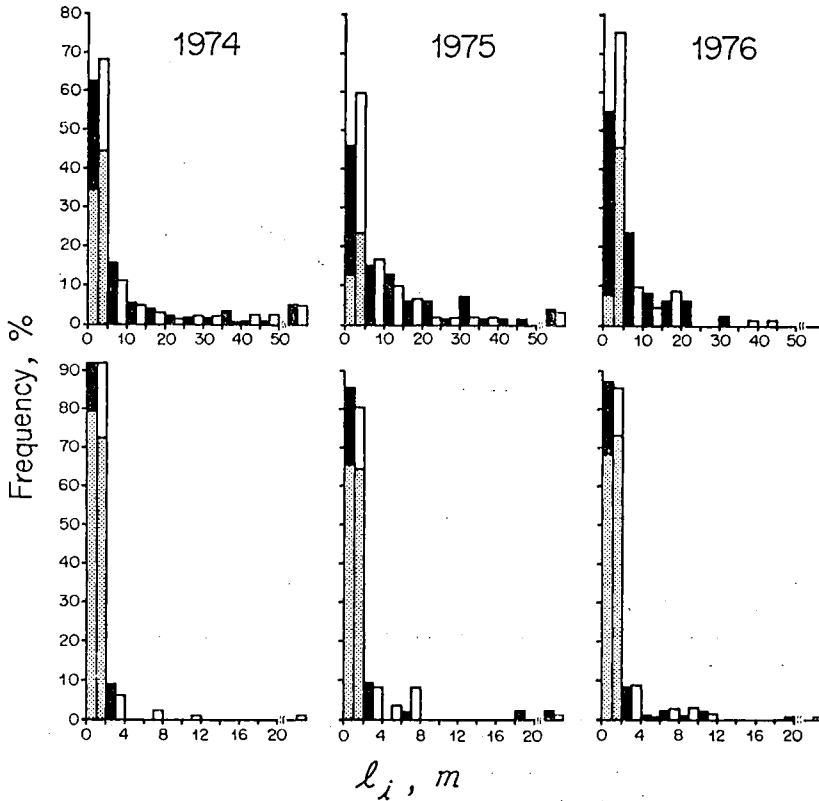


Fig. 9. Frequency distribution of the distances moved during two successive fixes (l_i) of overwintered (top) and new adults (bottom). The filled and the open columns refer to male and female, respectively. Dotted areas refer to the individuals which stayed in the very same thistle plant during two successive recaptures.

1979). The graphs in Fig. 10 are drawn from the data processed collectively, regardless of the residence time. When l_{sum} is examined separately with respect to the length of residence time of a beetle, it is positively correlated with the length of the residence time. For instance, when the overwintered beetles in 1974 whose residence time was less than 10 days and more than 31 days were separately examined, the proportion of the beetles which moved more than 100 metres was only 3% in the former and 54% in the latter. In contrast, 33% of the former and 14% of the latter did not move more than 10 metres during their residence time. The maximum values of l_{sum} attained by overwintered adults in 1974 were 3000 m (female) and 1800 m (male), respectively. The number of individuals whose l_{sum} exceeded 1000 m were 3 ♂♂ + 7 ♀♀ in 1974 and 4 ♂♂ + 2 ♀♀ in 1975. However, the maximum values of l_{sum} in 1976 were only 900 m (male) and 240 m (female). The dispersal tendency of overwintered adults in 1976 was smaller than that in 1974 or 1975 as seen in Figs. 9 and 10, which will be discussed later (see Table 1).

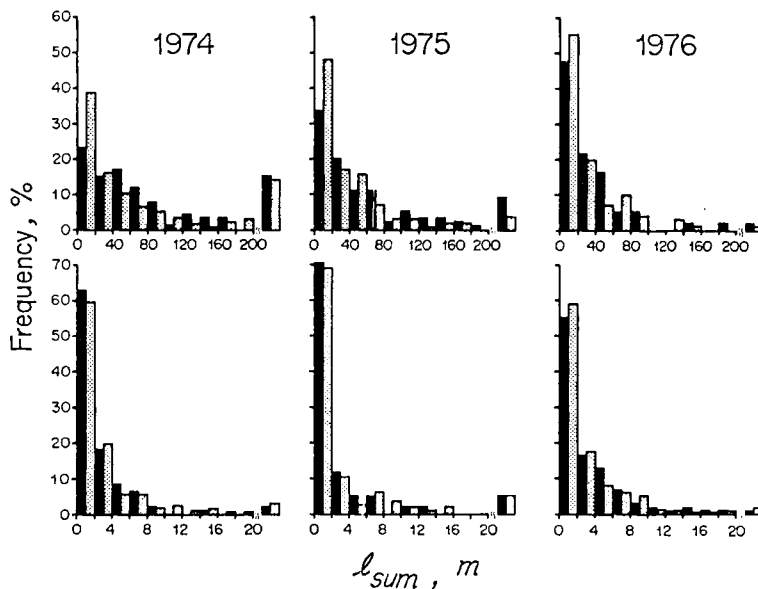


Fig. 10. Frequency distribution of the sum total of the distances moved during the residence time (L). The closed and the dotted columns refer to male and female, respectively. Top: overwintered adults. Bottom: new adults.

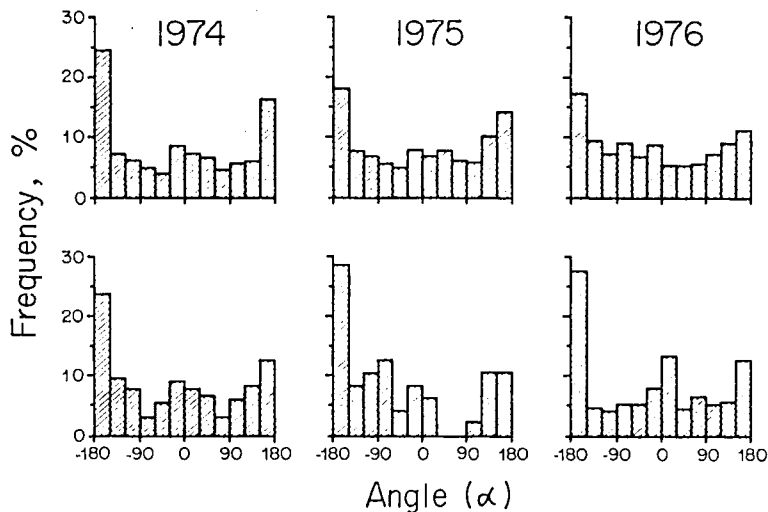


Fig. 11. Frequency distributions of relative angles (α_i) turned between three successive fixes for overwintered (top) and new adults (bottom), respectively.

(2) *Distribution of angles.* Figure 11 shows the frequency distribution of relative angles turned during three successive fixes (α_i). The graphs appear to be bimodal, with peaks at about ± 180 and 0 degrees, although the peaks of the latter are less conspicuous than the former. A relative angle (α_i) of 0° is the direction "straight ahead", while angles of $\pm 180^\circ$ are "directly behind". The distributions of

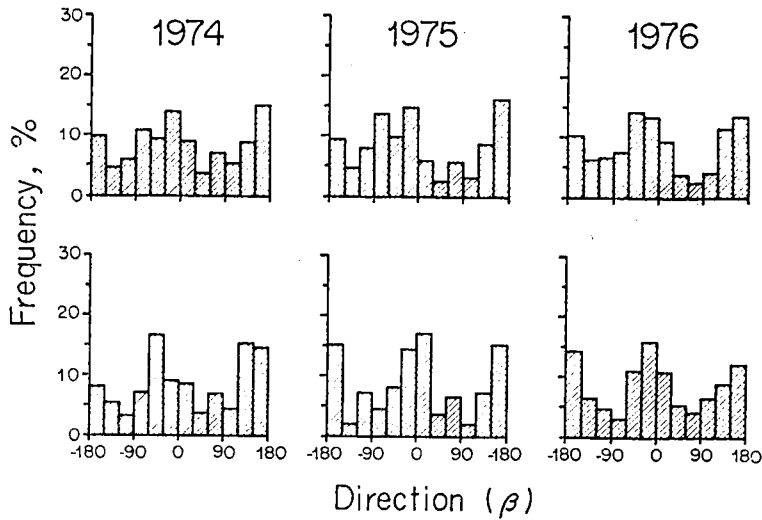


Fig. 12. Frequency distributions of direction of movement paths (β_i) of overwintered (top) and new adults (bottom), respectively.

compass direction of movement paths of beetles (β_i) are shown in Fig. 12, which are also bimodal with the peaks at -45° (SE) and 135° (NW). This shows that beetles tended to move mainly along the stream, but equally up- and downstream.

(3) *Analysis of movement patterns by INOUE's regression method.* INOUE's (1978) regression method is most useful for analyzing our data of beetle's movement, because the method is applicable not only to the populations whose movements are random (i.e. the frequency distribution of α_i is uniform) but also to those whose movements are not random (i.e. the frequency distribution of α_i is not uniform, as shown in Fig. 11). The method is based upon the regression of $F(D)$ to D , where the proportion of individuals staying within a certain distance D during a unit interval of time is called $F(D)$. Figure 13 shows that this regression method is fitted well to the data on the frequency distribution of l_i (Fig. 9). The movement pattern of overwintered beetles is considered as a compound process of two different random walks defined by INOUE (1978). In Fig. 13, ϕ shows the probability that the small-scale random walk takes place, ρ_l and ρ_s are the "coefficients of activity" for large- and small-scale random walk, and D_0 is the distance over which large-scale movements prevail over the small movements. Figure 13 shows, for example, that about 95% of male beetles ($\phi=0.95$) moved distances similar to the small-scale random walk ($D_0=30.1$ m, i.e. the distance travelled in the small-scale random walk was within 30 m); and only 5% of them dispersed according to a large-scale random walk. In practice, the small-scale and large-scale movements would refer to the movement of beetles within a patch or between neighbouring patches, and those between patches in distance or between subareas, respectively. The coefficient of activity for the large-scale movements (ρ_l) is about sixty times greater than the small-scale one (ρ_s).

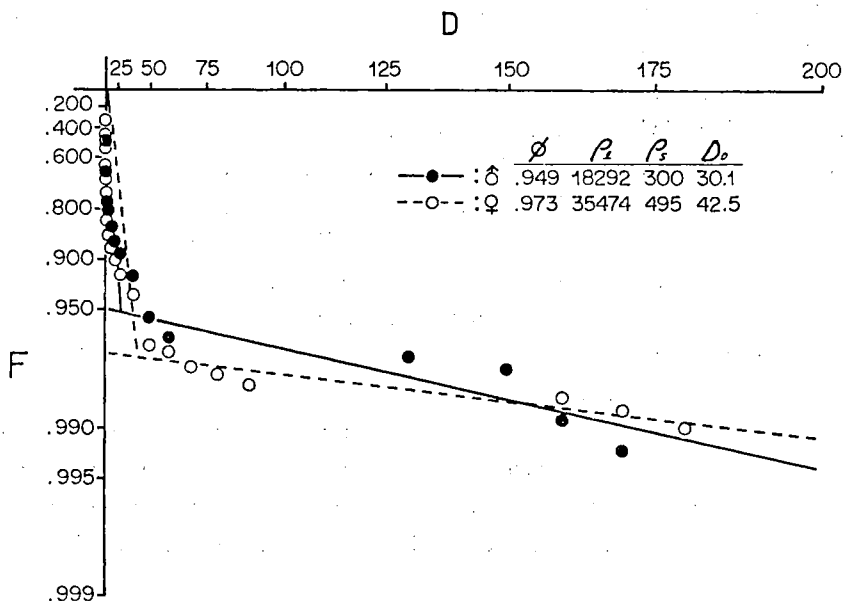


Fig. 13. The relation of F to D of the dispersal of the overwintered beetles of *H. pustulosa* in 1974. Ordinate: $\ln(1-F)$. Abscissa: D^2 . (●) and (○) show the male and female, respectively. (Data from Fig. 9, for details see the text).

There are some difficult points in applying INOUE's method to our data, i.e. first, the habitats were patchily distributed along the river (the method assumes that an animal moves in two-dimensional space); secondly, the census time-intervals were not uniform; and thirdly, the recovery or oversight of an individual at long distance seriously affects the general trend. These points are common to many field data as well as ours. In spite of these points, the conclusions derived from Fig. 13 are generally consistent with the data in Figs. 9 to 12. The values for ρ_1 , ρ_s and D_0 in Fig. 13 suggest that the females might be more active in their dispersal than the males, but the difference seems to be insignificant and due to sampling errors, because the frequency distributions (Figs. 9 to 12) indicate no significant difference between the sexes.

DISCUSSION

As JOHNSON (1969) rightly pointed out, "the part is not a model for the whole" and we cannot understand the mechanism of natural control of a population if we neglect the movements of individuals between habitats and the spatial structure of the population. Many workers have reported that in field populations density-dependent dispersal, which occurred at extremely high densities (CLARK, 1962, 1964; DEMPSTER, 1968; WATMOUGH, 1968) or even relatively low density levels (DIXON, 1969, 1970; KUNO and HOKYO, 1976) would be important in controlling population densities. However, they usually conducted the population studies in the areas which were so

small relative to dispersal power of the insect species concerned that they failed to relate the changes in numbers within their study plots to those in wider areas. While in the present study, the mobility of adult *Hp* was relatively restricted, the Kamitani study area which included several subareas containing a cluster of thistle patches was sufficiently large to understand how the *Hp* population split up into minor units, and how adult movements between them affected the regulation of population density.

The previous articles clarified that the size of *Hp* population remained remarkably constant and never reached a level where food depletion occurred. Results of key-factor analysis strongly suggested that the stabilization of population size was attained through density-dependent regulatory processes operating in inter-patch dispersal and oviposition of overwintered adults (NAKAMURA and OHGUSHI, 1979, 1981). The following processes were involved: 1) The exodus and interchange of overwintered beetles among patches occurred density-dependently, which led to reduced variation in density among patches. 2) Density-dependent regulation of fecundity on each patch was mainly attributed to density-induced adult dispersal rather than to direct effects of overcrowding.

Although we could not make detailed observations on take-off, flight and oviposition of adults, we obtained some circumstantial evidence, suggesting that decreased fecundity would be caused by increased adult dispersal activity. Firstly, Table 1 summa-

Table 1. Seasonal changes in the dispersal activity of overwintered adults of *H. pustulosa*. *n*, number of incidence; *l*, the distance moved during two successive fixes (in metres); *speed*, the distance moved per day (in metres).

Period	1974			1975			1976		
	<i>n</i>	<i>l</i>	<i>speed</i>	<i>n</i>	<i>l</i>	<i>speed</i>	<i>n</i>	<i>l</i>	<i>speed</i>
Middle-late May	59	44.8	4.1	243	46.5	3.0	231	15.1	0.8
Early-middle June	475	33.2	3.0	227	18.8	1.8	108	13.1	0.6
Middle June-Middle July	333	27.4	2.2	162	17.8	1.0			
Middle July-	276	10.1	1.7	114	6.1	0.1	159	3.8	0.2
The whole term	1143	26.5	2.5	746	25.7	1.8	498	11.1	0.6

rizes the seasonal changes in dispersal activity of overwintered adults and shows that the peak of the activity was observed during the period from middle to late May, coinciding with the peak of egg-laying activity, and thereafter the activity gradually declined. The overwintered adults emerged on the thistle patches almost simultaneously, once the snow had melted. At that time, the thistles were in the small rosette stage, so that the amount of mutual contact between individuals was very high, resulting in a higher level of dispersal activity than that found in later period when the thistles were larger. Secondly, Table 1 also shows that the dispersal activity in 1976 was only about a third of that recorded in 1974 and 1975. The longevity of overwintered adults was much longer in 1976 (50<days) than those in 1974 (30 days)

and 1975 (40 days), and the total overwintered beetles in the Mondori area was by far the smallest in 1976. Also, the fecundity in 1976 was higher (89.5 per female) than in 1974 (51.6) and 1975 (51.2) as shown in NAKAMURA and OHGUSHI (1979, 1981). These facts strongly suggest that the increased fecundity in 1976 was due to the decrease in dispersal activity of the beetles as well as the longer longevity. However, if the beetles are more vulnerable and/or consume more energy during dispersal, which is usually the case, the longevity of beetles itself would be affected by population density through density-dependent dispersal.

The dispersal behaviour of *Hp* populations was also studied near Sapporo, Hokkaido by HINOMIZU (1976) and KIMURA (1978), though their studies were restricted within small areas. The results obtained by them are generally consistent with those from the Asiu population, except that some of the new adults in the populations near Sapporo were compelled to move, owing to the withering of thistles in August. However, the dispersal behaviour of the two closely related species, *H. vigintioctomaculata* (*Hvm*) and *H. vigintioctopunctata* (*Hvp*), which are the harmful pests of potato and egg plant showed somewhat different characteristics in their dispersal. For both *Hvm* (IWAO et al., 1963; IWAO 1971) and *Hvp* (IWAO and MACHIDA, 1963; NAKAMURA, 1976), overwintered adults were more sedentary than those of *Hp*, but the newly emerged adults were by far mobile than *Hp*. IWAO (1971) showed that the intermingling of subpopulations of *Hvm* occurred mainly through the movements of new adults during the pre-hibernating period. Probably, the overwintered beetles of the two pest species, once settled in the suitable field, began to lay eggs without further dispersal. The dispersal of newly emerged adults of *Hvm* and *Hvp* was frequently induced by food shortage, due to overcrowding or harvesting of food plants.

IWAO (1971) studied the dynamics of *Hvm* populations in patchily distributed habitats by mark and recapture method. He claimed that the stabilization of numbers of *Hvm* populations was brought about by density-dependent processes, such as adult mortality in dispersal and larval competition for food, and that the spreading of risk by splitting up of the population (DEN BOER, 1968; REDDINGIUS and DEN BOER, 1970) was not sufficient to keep his population within a restricted range of fluctuation in number, if no density-dependent mechanism is included. The results from our study support IWAO's view, and also demonstrates the importance of density-dependent processes acting in adult dispersal in the stabilization of *Hp* populations.

SUMMARY

From 1974 to 1977, a field study was carried out on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KONO), in Kyoto Prefecture, Japan. The food plant, *Cirsium kagamontanum* grows in discrete clusters of different size. Such an aggregation of thistles is referred to as a "patch" in this article. The

patches themselves tended to be clustered in the Kamitani study area, so that the Kamitani study area could be split up into several "subareas", each of which contained a cluster of patches. The Mondori subarea which contained 11 thistle patches was studied more intensively. We executed an intensive marking, release and recapture program to investigate the dispersal behaviour of adult beetles. The implications of adult movements in a patchily distributed habitat were studied in relation to the population dynamics, in particular to the process of stabilizing population size. The adults were relatively sedentary; i.e., overwintered beetles generally moved less than 2 m per day, and new adults were at first inclined to stay on the same thistle, rarely moving more than 0.5 m per day. The movement patterns of overwintered beetles consisted of frequent, short-distance diffusions, and could be considered as a compound process of two different random walks, as defined by INOUE (1978). As a result, the population in the Mondori subarea was relatively isolated from those in other subareas. But its own thistle patches were connected with each other by these short-distance movements of the overwintered adults. New adults were extremely sedentary, remaining in the same patch where they had emerged until the following spring. The total *H. pustulosa* population at Kamitani was divided into several subpopulations which were nearly confined to particular clusters of patches. The dispersal activity of overwintered beetles seemed closely associated with ovipositing activity, and was seriously affected by adult density, resulting in the stabilization of population size below a level where food depletion occurred.

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REFERENCES

- ANDREWARTHA, H. G. and L. C. BIRCH (1954) *The distribution and abundance of animals*. Univ. of Chicago Press, Chicago.
- BIRCH, L. C. (1971) The role of environmental heterogeneity and genetical heterogeneity in determining distribution and abundance. *Proc. Adv. Study Inst. Dynamics Numbers Popul.* (Oosterbeek, 1970) pp. 109-128.
- BOER, P. J. DEN (1968) Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18: 165-194.
- CLARK, L. R. (1962) The general biology of *Cardiaspina albicollis* (Psyllidae) and its abundance in relation to weather and parasitism. *Aust. J. Zool.* 10: 537-586.

- CLARK, L. R. (1964) The population dynamics of *Cardiaspina albitextura* (Psyllidae). *Aust. J. Zool.* 12: 362-380.
- DEMPSTER, J. P. (1968) Intra-specific competition and dispersal: as exemplified by psyllid and its anthocorid predator. *Symp. R. Ent. Soc.*, Lond. 4: 8-17.
- DIXON, A. F. G. (1969) Population dynamics of the sycamore aphid *Drepanosiphum platanoides* (Sch.) (Hemiptera: Aphididae): migratory and trivial flight activity. *J. Anim. Ecol.* 38: 585-606.
- DIXON, A. F. G. (1970) Quantity and availability of food for a sycamore aphid population. In A. Watson (ed.) *Animal populations in relation to their food resources*, pp. 271-287.
- EHRlich, P. R. (1965) The population biology of the butterfly, *Euphydryas editha*. II. The structure of the Jasper Ridge colony. *Evolution* 19: 327-336.
- EHRlich, P. R. and L. C. BIRCH (1967) The 'balance of nature' and 'population control'. *Am. Nat.* 101: 97-107.
- EHRlich, P. R. and L. E. GILBERT (1973) Population structure and dynamics of tropical butterfly *Heliconius ethilla*. *Biotropica* 5: 69-82.
- ELTON, C. (1949) Population interspersal: an essay on animal community patterns. *J. Ecol.* 37: 1-23.
- FISHER, R. A. and E. B. FORD (1947) The spread of a gene in natural conditions in a colony of the moth *Panaxia dominura* L. *Heredity* 1: 143-174.
- GILBERT, L. E. and M. C. SINGER (1973) Dispersal and gene flow in a butterfly species. *Am. Nat.* 107: 58-72.
- HINOMIZU, H. (1976) Phenology and dispersal of *Henosepilachna pustulosa* (KÔNO) at thistle stands near a potato field in Sapporo. *J. Fac. Sci. Hokkaido Univ., Ser. VI, Zool.* 20: 329-342.
- INOUE, T. (1978) A new regression method for analyzing animal movement patterns. *Res. Popul. Ecol.* 20: 141-163.
- 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. 129-147.
- IWAO, S. and A. 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., K. MIZUTA, H. NAKAMURA, T. ODA and Y. SATO (1963) Studies on a natural population of the large 28-spotted lady beetle, *Epilachna vigintioctomaculata* MORSCHULSKY. I. Preliminary analysis of the overwintered adult population by means of the marking-and-recapture method. *Jap. J. Ecol.* 13: 109-117.
- JOHNSON, C. G. (1969) *Dispersal of insects by flight*. Methuen, London.
- KIMURA, T. (1978) 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 University*.
- KIRITANI, K., N. HOKYO, T. SASABA and F. NAKASUJI (1970) Studies on population dynamics of the green rice leafhopper, *Nephotettix cincticeps* UHLER: regulatory mechanism of the population density. *Res. popul. Ecol.* 12: 137-153.
- **KUNO, E. (1968) Studies on the population dynamics of rice leafhoppers in a paddy field. *Bull. Kyushu Agr. Exp. St.* 14: 131-246.

- **KUNO, E. and N. HOKYO (1976) Population regulation and dispersal of adults in the green rice leafhopper, *Nephotettix cincticeps* UHLER (Hemiptera: Deltocephalidae). *Physiol. Ecol.* 17: 117-123.
- MACLEOD, J. and J. DONNELLY (1963) Dispersal and interspersal of blowfly populations. *J. Anim. Ecol.* 32: 1-32.
- *MORISHITA, M. (1950) Dispersal and population density of a water-strider, *Gerris lacustris* L. *Contr. Physiol. Ecol. Kyoto Univ.* No. 65.
- MORRIS, R.F. and C.A. MILLER (1954) The development of life tables for the spruce bud worm. *Can. J. Zool.* 32: 283-301.
- **NAKAMURA, K. (1976) 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.
- NAKAMURA, K. (1980) Spatio-temporal dynamics of a natural population of the phytophagous lady beetle, *Henosepilachna pustulosa* KÔNO, in relation to habitat structure. *Ph.D. Thesis, College of Agriculture, Kyoto University.*
- 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.
- PAJUNEN, V.I. (1971) Adaptation of *Arctocoris carinata* (SAHLB.) and *Callocoris producta* (REUT.) populations to a rock pool environment. *Proc. Adv. Study Inst. Dynamics Numbers Popul.* (Oosterbeek, 1970) pp.148-158.
- PAJUNEN, V.I. and A. JANSSON (1969) Dispersal of the rock pool corixids *Arctocoris carinata* (SAHLB.) and *Callocoris producta* (REUT.) (Hemiptera, Corixidae). *Ann. Zool. Fenn.* 6: 391-427.
- REDDINGIUS, J. and P.J. DEN BOER (1970) Simulation experiments illustrating stabilization of animal numbers by spreading of risk. *Oecologia* 5: 240-284.
- RICHARDS, O.W. and N. WALOFF (1961) A study of a natural population of *Phytodecta olivacea* (FORSTER) (Coleoptera, Chrysomelidae). *Philos. Trans. R. Soc. London Ser. B. Biol. Sci.* 244: 205-257.
- SOUTHWOOD, T.R.E. (1962) Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.* 37: 171-214.
- THOMPSON, W.R. (1956) The fundamental theory of natural and biological control. *Ann. Rev. Entomol.* 1: 379-402.
- VARLEY, G.C. and G.R. GRADWELL (1960) Key factors in population studies. *J. Anim. Ecol.* 29: 399-401.
- WATMOUGH, R.H. (1968) Population studies on two species of Psyllidae (Homoptera: Sternorhyncha) on broom (*Sarothamnus scoparius* (L.) Wimmer). *J. Anim. Ecol.* 37: 283-314.
- WATT, K.E.F. (1963) Mathematical population models for five agricultural crop pests. *Mem. Ent. Soc. Canada.* No. 32 pp.83-91.

- 1) Single asterisked: papers written in Japanese.
- 2) Double asterisked: ditto with English summary.

ブナ原生林地帯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 Ⅲ. 成虫の分散行動と個体群の空間動態

中村 浩二・大串 隆之

京都市の北方 100 km にある京大芦生演習林でコブオオニジュウヤホシテントウの個体群動態を 1974 年から 1977 年まで調査した。食草のカガノアザミは溪流にそって点々と群落（パッチ）をつくってはえていた。これらのアザミ群落は調査地域内に均一に分布しているのではなく、谷の出口や范らん原などのような開けた場所にいくつかずつかたまって分布していた。このパッチのまとまり具合によって調査地を 7 つのサブエリアに分割した。最も詳しい調査をしたモンドリ谷には 11 のパッチが存在した。成虫にはラッカーで個体識別マークをつけ、放逐一再捕をくりかえして、分散行動を詳しく追跡した。越冬成虫は雪どけ直後から出現し、頻りに近接したパッチ間の分散をくりかえすが、サブエリア間に交流をもたらすような長距離移動はまれであった（1 日あたりの平均移動距離は 2m 以下にすぎなかった）。新成虫は極端に定着的で 8 月中旬以降に羽化してから 9 月下旬に越冬に入るまで羽化したパッチ内にとどまって摂食を続けた。越冬は同じパッチの地表部あるいはそのごく近くで行われるらしく、越冬直後の成虫は再び同じパッチに出現することが多かった。成虫の長距離分散力が小さいために本種個体群は食草パッチの局在性に対応したいくつかのサブ個体群にわかれていた。それらはモンドリ谷でみられたように、サブエリアに含まれるパッチの間ではよく交流しまとまっている反面、他のサブエリア内の個体群とは相対的に独立していた。

INOUE (1978) の回帰分析法を適用したところ、越冬成虫の分散行動は 1 回に 30 m 以下しか移動しない小さきみなランダムウォーク（動きの 95% を占める）とより大きなランダムウォーク（5% を占める）の複合したプロセスとして解釈できる可能性があった。越冬成虫の分散活動力の季節変化や年次差の検討を通して、越冬成虫の密度に依存したパッチ間分散と産卵数の調節の関連について論じ、本種個体群の調節要因としての分散行動の重要性を指摘した。さらに本種と近縁の害虫種（オオニジュウヤホシテントウやニジュウヤホシテントウ）の産卵期の分散行動の差についても論じた。