

THE DYNAMICS OF NATURAL POPULATIONS OF A PHYTO-
PHAGOUS LADY BEETLE, *HENOSEPILOACHNA PUSTULOSA*
(KÔNO) UNDER DIFFERENT HABITAT CONDITIONS
I. COMPARISON OF ADULT POPULATION PARAMETERS AMONG
LOCAL POPULATIONS IN RELATION TO HABITAT STABILITY

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INTRODUCTION

The characteristics of a natural insect population are largely dependent on the components of habitat conditions fluctuating in time and space. Thus even within the same species, some important aspects of population dynamics, i.e., regulating mechanisms, factors determining population level, and factors causing fluctuations in numbers often differ considerably between different habitats; (e.g., DEMPSTER, 1971; WHITTAKER, 1971; BENSON, 1973; BALTENSWELER *et al.*, 1977). Consequently it is difficult to fully understand the population dynamics of a species without comparing its population dynamics among various habitats within its range (HUFFAKER and MESSENGER, 1964; CLARK *et al.*, 1967; RICHARDS and SOUTHWOOD, 1968).

Among phytophagous lady beetles of the genus *Henosepilachna*, intensive field population studies have been made on *H. vigintioctomaculata* (IWAQ, 1971) and *H. vigintioctopunctata* (NAKAMURA, 1976a, b). These species are serious pests of potato, eggplant and other solanaceous crops, and their habitats lie within the fields of these crops. In contrast, *H. pustulosa* is a non-pest species widely distributed over the relatively mountainous area of northern and central Japan. It feeds mainly on thistle plants which are usually distributed in patches along the mountain streams. In general, populations of *H. pustulosa* remain at such relatively low density levels that food depletion rarely occurs, and they are subdivided into small local populations which are relatively isolated from one another. We have already studied the dynamics of *H. pustulosa* in its most stable habitat; i.e., a cool temperate climax forest, for four years and showed that the population was kept fairly constant in size from year to year and was characterized by low reproductive and high winter survival rates (NAKAMURA and OHGUSHI, 1979). However, as will be shown in this study, the *H. pustulosa* population lives also near villages in more unstable habitats suffering from artificial disturbance. Furthermore, in this same species some local populations are known which live on hosts other than thistle, such as potato or blue cohosh (KATAKURA, 1976; KIMURA, 1978). Consequently, *H. pustulosa*, compared with the closely allied pest species, *H. vigintioctomaculata* and *H. vigintioctopunctata*, can live

in a wider range of habitat conditions. Therefore, to understand *H. pustulosa*'s population dynamics, we should simultaneously examine various local populations living in different habitats, and compare their characteristics in relation to the habitat conditions.

We carried out such a study on six local populations which feed on thistles in five different valleys located along the Ado river in central Japan. In this first paper of the series, we extract some demographic attributes and compare them among different local populations.

Study area

The study was carried out on six sites in Kutsuki village, which is located in the northwestern part of Shiga prefecture, central Japan. The village ranges in altitude from 200 m to 400 m, and is about 15 km east of the School Forest of Kyoto University at Asiu, where we had already studied the population dynamics of *H. pustulosa* from 1974 to 1977 (NAKAMURA and OHGUSHI, 1979). In and around the village, vegetation includes a plantation of *Cryptomeria japonica* and *Chamaecyparis obtusa*, while on the higher slopes and tops of mountains and in the upstream part of valleys, it is dominated by a broad-leaved forest that includes *Quercus mongolica*, *Aesculus turbinata*, *Pterocarya rhoifolia* and *Magnolia obovata*. Kutsuki is the transition zone between a temperate deciduous broad-leaved forest and an evergreen

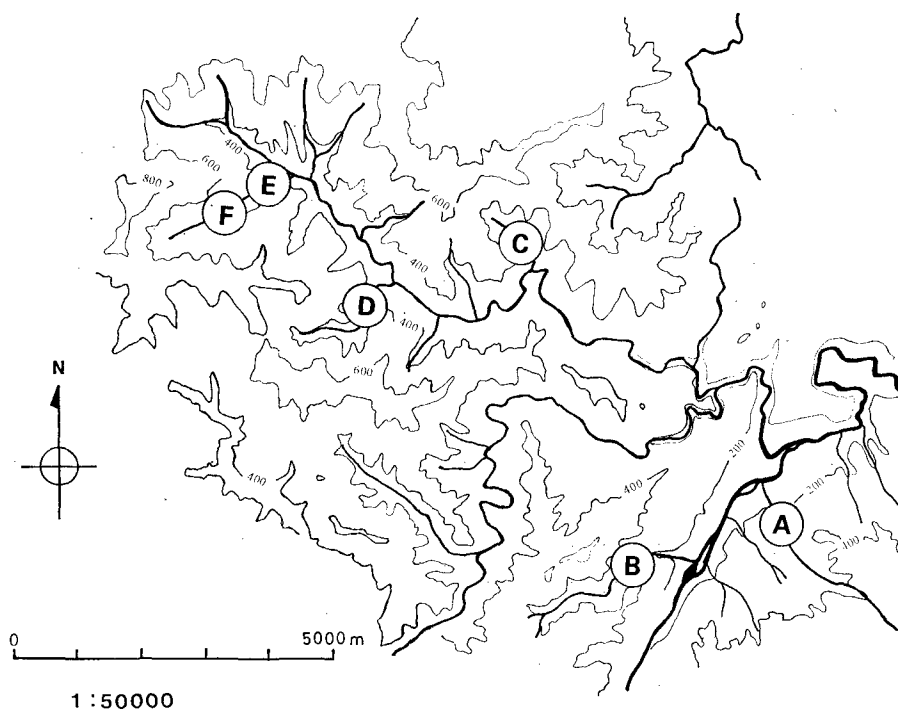


Fig. 1. Map of the study area. Each circle shows the location of each study site.

Table 1. Altitude, area, and characteristic vegetation at each study site.

Site	Altitude	Area	Characteristic vegetation	Remarks
A	220 m	60×30 m ²	<i>Polygonum filiforme</i> , <i>P. Thunbergii</i> , <i>Miscanthus sinensis</i> , <i>Rumex crispus</i> , <i>Geranium Thunbergii</i>	dam built in 1968
B	250 m	320×30 m ²	<i>Polygonum filiforme</i> , <i>Achyranthes japonica</i> , <i>Viola grypoceras</i> , <i>Leucosceptrum stellipilum</i> , <i>Deutzia crenata</i> , <i>Hydrangea paniculata</i>	forest road built in 1975
C	250 m	140×25 m ²	<i>Angelica pubescens</i> , <i>Plantago asiatica</i> , <i>Deutzia crenata</i> , <i>Rubus crataegifolius</i> , <i>Cercidiphyllum japonicum</i> , <i>Quercus mongolica</i>	dam built in 1967
D	280 m	90×20 m ²	<i>Carex</i> sp., <i>Stachyurus praecox</i> , <i>Actinidia polygama</i> , <i>Quercus mongolica</i> , <i>Pterocarya rhoifolia</i> , <i>Corylus heterophylla</i> var. <i>Thunbergii</i>	
E	350 m	30×30 m ²	<i>Polygonum cuspidatum</i> , <i>P. Thunbergii</i> , <i>Deutzia crenata</i> , <i>Quercus mongolica</i> , <i>Q. salicina</i> , <i>Carpinus Tschonoskii</i> , <i>Cephalotaxus Harringtonia</i> , <i>Menziesia ciliicalyx</i>	
F	350 m	90×15 m ²	<i>Impatiens Textori</i> , <i>Polygonum Thunbergii</i> , <i>Rubus palmatus</i> , <i>Quercus mongolica</i> , <i>Euonymus alatus</i> f. <i>striatus</i> , <i>Carpinus Tschonoskii</i> , <i>Pterocarya rhoifolia</i>	

broad-leaved forest. The six study sites are located in the five different valleys of the Ado river and its branch, the Ado river. The altitude, area, and characteristic vegetation of each site are given in Table 1. Detailed description of the study sites are as follows:

Nyudani Study Site (site A)

Site A is located in the valley farthest downstream. The site is located on an accumulation of sandy deposits caused by the construction of a dam which was built in 1968 to prevent erosion, and the ground surface of the rather flat and open area consists mainly of sandy deposits. As the deposits have not yet hardened, floods caused by heavy rain in June and September sometimes change the watercourse or wash away thistles beside it. Thus most of the ground flora that survives these inundations are annual or perennial herbs.

Ôhiko Study Site (site B)

Site B is located in a valley which is less than 10 meters wide. With steep slopes on the both sides, it is rather narrower and gloomier than the other sites studied, and is unfavourable for growth of thistles. In 1975, much soil was dumped into the stream when a forest road was built alongside it.

Yokotani Study Site (site C)

Site C has two distinct parts. A dam was built in 1967 to prevent erosion in the lowest part, so the lower half of the site consists of sandy deposits, and its vegetation is characterized by a plantation of *Cryptomeria japonica*. Thus it is rather

gloomy and, as at site A, the deposits have not yet hardened. In contrast, the upper half of the site is broader and more open than the lower half.

Kumadani Study Site (site D)

Site D is more mountainous than sites A, B and C. The stream at this point is about 5 meters wide, and there are some deciduous-leaved trees (e.g., *Quercus mongolica*, *Pterocarya rhoifolia*, *Castanea crenata* and *Lindera umbellata*) around the site.

Kijiyama Study Site (sites E and F)

Sites E and F are the highest and the most mountainous of the study sites. The riverside soil deposits are harder than at sites A and C so that, except in 1979, thistles have rarely been subjected to floods. Various deciduous trees can be found there. Unfortunately, in the early spring of 1977, some parts of site E were covered with soil during construction of a new forest road.

Host plant

In Kutsuki, adults and larvae of *H. pustulosa* feed exclusively on leaves of the thistle plant, *Cirsium kagamontanum*, which is a perennial herb. The new rosettes appear in mid-April and grow rapidly to become full-sized; i.e., 1.5-2.0 meters in height, by August. In mid-August the plant flowers, after which its lower leaves gradually wither. On all the study sites, *C. kagamontanum* is a dominant species among herbs growing along the riverside, usually growing in differently-sized discrete patches. There are slight differences in the growth form of these thistle plants from site to site (Table 2).

Census method

All the thistles at each study site could be examined within one day. From early May to early November, all the thistles were examined at one- to three-day intervals.

Table 2. Some characteristics of the population of host plant, *Cirsium Kagamontanum*, in late July.

Site	No. of plants examined	No. of shoots per plant	Height (cm)	No. of plants examined	No. of shoots per plant	Height (cm)
		Mean \pm S. E.	Mean \pm S. E.		Mean \pm S. E.	Mean \pm S. E.
1976			1977			
A	18	6.4 \pm 0.8	115.4 \pm 4.3	24	5.5 \pm 0.9	106.3 \pm 8.3
B	71	2.5 \pm 0.2	80.6 \pm 3.7	61	2.9 \pm 0.3	104.3 \pm 3.9
C	84	3.0 \pm 0.3	106.4 \pm 3.8	74	3.6 \pm 0.4	121.9 \pm 4.1
D	49	3.4 \pm 0.4	121.7 \pm 5.6	47	4.6 \pm 0.5	136.9 \pm 6.2
E	39	5.3 \pm 0.7	112.6 \pm 5.0	—	—	—
F	79	3.8 \pm 0.4	116.0 \pm 4.3	75	5.4 \pm 0.6	125.1 \pm 4.4
1978			1979			
A	24	7.8 \pm 1.3	95.9 \pm 5.9	33	8.7 \pm 1.2	99.1 \pm 5.3
F	76	4.9 \pm 0.6	109.6 \pm 4.3	74	4.2 \pm 0.5	88.0 \pm 4.0

All the adult beetles captured were marked during each census. Each adult was then given an individual mark with lacquer paint by using four marking points on the elytra and eight different colours coded to represent a number. The record of sex, body length and capture history in terms of place and time could thus be kept for individual beetles. Captured or recaptured adults were immediately released on the same host plant on which they were caught. The data thus obtained were analyzed by the method described by JOLLY (1965) and SEBER (1973). This study has continued since the spring of 1976, and the data used in this paper were those obtained in one year for site E (1976), two years for sites B, C and D (1976-77) and four years for sites A and F (1976-79).

RESULTS

1. *Life history*

H. pustulosa has one generation a year. The overwintered adults usually begin to emerge from hibernacula and go to the thistle plants from late April to mid-May (Figs. 2 and 3). Females begin to oviposit within a week after emergence and usually continue oviposition until early July, but occasionally continue until early August. Eggs are laid on the undersurface of the leaves of the host plants in masses of 10 to 40 eggs (20, on the average). New adults emerge from early July to late August. After emergence they continue to feed on the host plants, and by early November they may begin to hibernate in the soil of the thistle colonies.

Table 3. Total number of marked beetles and sex ratio, 1976-79.

Year	Site	Overwintered adult					Newly-emerged adult				
		Male	Female	Unkown	Total	% Female	Male	Female	Unkown	Total	% Female
1976	A	46	42	0	88	47.7	212	196	0	408	48.0
	B	18	51	0	69	73.9	63	143	0	206	69.4
	C	34	62	0	96	64.6	94	120	0	214	56.1
	D	52	132	0	184	71.7	106	231	2	339	68.1
	E	63	87	0	150	58.0	73	110	1	184	59.8
	F	62	153	0	215	71.2	80	128	2	210	61.0
1977	A	75	87	7	169	51.5	468	584	2	1054	55.4
	B	47	92	3	142	64.8	601	137	0	197	69.5
	C	49	76	3	128	59.4	299	324	1	624	51.9
	D	91	223	8	322	69.3	314	462	1	777	59.5
	F	96	215	9	320	67.2	257	337	2	596	56.5
1978	A	122	172	3	297	57.9	265	371	0	636	58.3
	F	238	398	7	643	61.9	202	265	0	467	56.7
1979	A	25	57	1	83	68.7	366	427	0	793	53.9
	F	222	375	3	600	62.5	35	56	0	91	61.5

2. Estimation of population size, \hat{N}_i

During the study period, the marking ratio (i.e., the proportion of marked individuals to the whole population) rapidly rose to more than 90% within two weeks after the first spring census. Sampling ratio (i.e., the proportion of individuals caught to the whole population estimated) was about 50%, and was relatively constant throughout the whole census period. Thus it is clear that the estimates of these population parameters were highly reliable and accurate. The seasonal trend of adult population at each site was estimated by the JOLLY-SEBER method (\hat{N}_i) and is shown in Fig. 2, which shows that each site had similar trends during each of the years examined. But comparison of the trends among local populations at the different sites indicates that some characteristics of the life history differed somewhat at each site.

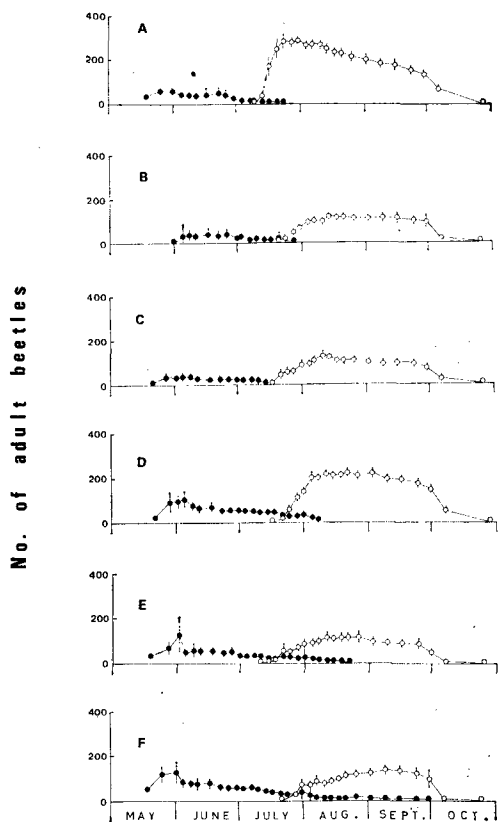


Fig. 2A. Seasonal fluctuations in the number of adult *H. pustulosa* populations in 1976 estimated by the JOLLY-SEBER method. Solid and open circles indicate the overwintered and newly-emerged adults, respectively. Vertical lines show the 95% confidence limits.

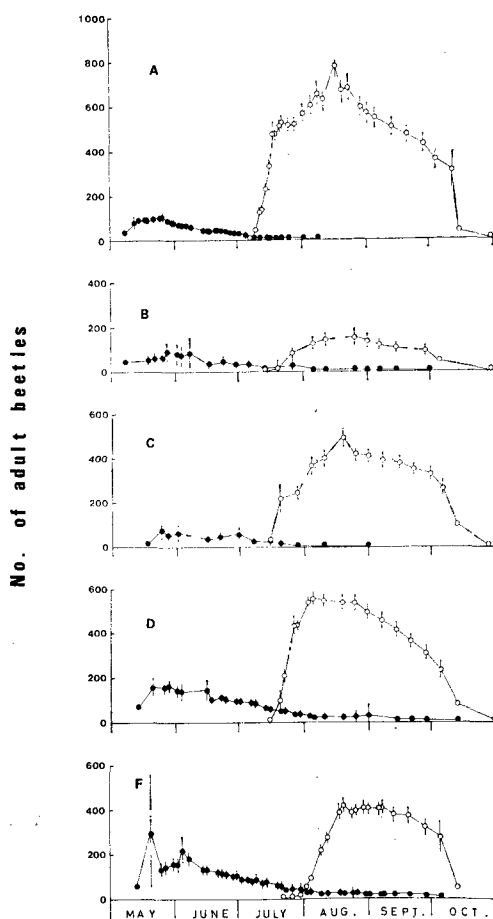


Fig. 2B. Seasonal fluctuations in the number of adult *H. pustulosa* populations in 1977. See Fig. 2A for more details.

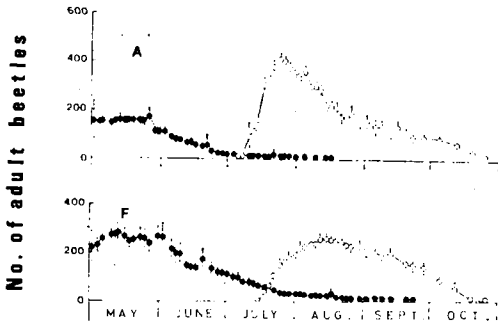


Fig. 2C. Seasonal fluctuations in the number of adult *H. pustulosa* populations in 1978. See Fig. 2A for more details.

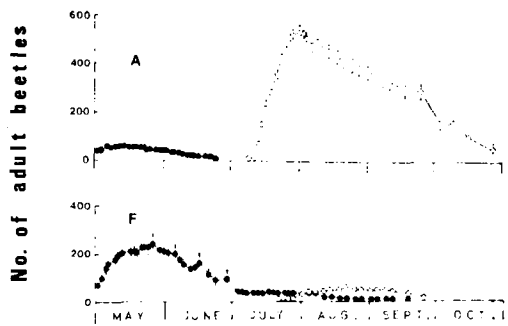


Fig. 2D. Seasonal fluctuations in the number of adult *H. pustulosa* populations in 1979. See Fig. 2A for more details.

Firstly, the longevity of overwintered adults was more prolonged at upstream than at downstream sites. For example, at site A, most of overwintered adults were dead by late July, whereas at site F, some still survived after mid-September. In fact, at site F there were a few adults that overwintered in two consecutive years, whereas no such individuals survived so long at site A (Table 5). Secondly, adults tended to emerge earlier and reached their peak in numbers more rapidly at downstream sites. For example, each year at site A new adults began to emerge in early July, so that 50% had emerged by 17 July–21 July in 1976-79. In contrast at site F, the adults

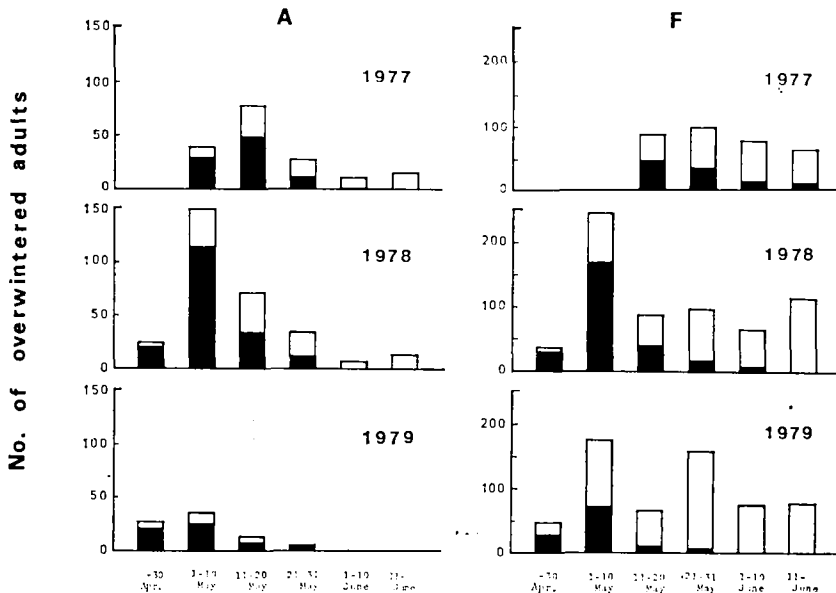


Fig. 3. The pattern of emergence and movement of overwintered adults from hibernacula to the host plants. Each column shows the number of adults captured first time in each period. Filled area shows the number of adults marked already in the previous year.

began to emerge late in July, so that in 1976-79 the time of 50% adult emergence was 1 August—14 August (Fig. 10). The pattern of emergence and movement of overwintered adults from hibernacula to the host plants at sites A and F is shown in Fig. 3. Most of the overwintered adults marked in the previous year were recaptured by late May, indicating that emergence from hibernacula had almost ended by then. Thus any overwintered adults which were captured for the first time after late May could be classified as new immigrants. (Dispersal activity of overwintered adults is higher during their oviposition period than at other times in their life history, so they frequently disperse from one patch to another during that period. The problem of adult dispersal will be discussed in another paper in relation to the stability of population.)

3. *Estimation of daily survival rate, $\hat{\phi}$*

Since emigration and death could not be distinguished, the term "survival" in this article means "residence" within that site. However, emigration of newly-emerged adults would be negligible, because their dispersal activity is very low. The survival rate per day was consistently very high throughout the census period in both overwintered (more than 0.92) and newly-emerged adults (more than 0.96). The daily survival rate among overwintered adults was lower than that for newly-emerged adults in every year of this study, but there was little difference among different sites or between sexes (Table 4).

4. *Total number of adult beetles entering the population, \hat{T}*

For the purpose of estimating the total number of adult beetles entering the population, \hat{B}_i (number of new beetles joining the population in the interval between the i and $i+1$ th census, and alive at time $i+1$) is not an appropriate parameter, since it leads to underestimates unless no mortality and/or emigration occur between the two census times. Accordingly, we adopted the corrected estimate \hat{T} derived by INOUE (unpublished). The value of \hat{T} thus obtained is shown in Table 4, and demonstrates that most of the newly-emerged adults entering the population could be marked.

5. *Sex ratio*

The sex ratio (% ♀ ♀) estimated from the analysis of capture-recapture data is shown in Table 4, whereas Table 3 gives the values obtained from direct counts of marked adults. The ratios for both overwintered and newly-emerged adults in sites A, C and E were slightly lower than those in the other sites every year. In most of the sites, the ratio in the following spring was slightly higher than that in the previous autumn, indicating that the mortality from the time of emergence until the following spring operates more severely on males than on females. The sex ratio in overwintered adults showed little change until mid-July. After that it fluctuated irregularly with the decrease in the number of adults.

Table 4. The estimates of mean survival rate per day ($\hat{\phi}_m$), and total recruit of the adult beetles (\hat{T}), together with sex ratio and reproductive rate (R) from \hat{T} .

Year	Site	Sex	Overwintered adult			Newly-emerged adult			R			
			$\hat{\phi}_m$	\hat{T}	% Female	$\hat{\phi}_m$	\hat{T}	% Female				
1976	A	Male	.952	51.9	104.7	50.4	.976	249.0	474.5	47.5	4.5	
		Female	.943	52.8			.978	225.5				
	B	Male	.920	26.7	107.0	75.0	.981	67.8	233.9	71.0	2.2	
		Female	.938	80.3			.984	166.1				
	C	Male	.945	35.4	114.7	69.1	.962	108.0	242.4	55.4	2.1	
		Female	.918	79.3			.973	134.4				
	D	Male	.946	58.7	238.5	75.4	.981	120.2	377.2	68.1	1.6	
		Female	.955	179.8			.980	257.0				
	E	Male	.944	89.9	205.8	56.3	.974	95.8	221.7	56.8	1.1	
		Female	.945	115.9			.975	125.9				
	F	Male	.953	67.4	269.3	75.0	.966	108.7	260.9	58.3	1.0	
		Female	.958	201.9			.978	152.2				
1977	A	Male	.943	89.4	183.0	51.1	.981	522.9	1180.8	55.7	6.5	
		Female	.944	93.6			.980	657.9				
	B	Male	.948	60.5	204.5	70.4	.983	70.9	241.4	70.6	1.2	
		Female	.951	144.0			.972	170.5				
	C	Male	.925	89.8	197.9	54.6	.985	337.0	704.7	52.2	3.6	
		Female	.928	108.1			.989	367.7				
	D	Male	.945	114.7	419.8	72.7	.978	345.9	849.5	59.3	2.0	
		Female	.962	305.1			.985	503.6				
	F	Male	.941	130.4	434.2	70.0	.982	275.1	670.7	59.0	1.5	
		Female	.959	303.8			.983	395.6				
	1978	A	Male	.944	152.1	362.1	58.0	.960	302.2	777.2	61.1	2.2
			Female	.944	210.0			.964	475.0			
F		Male	.964	298.3	811.5	63.2	.972	221.5	525.2	57.8	0.7	
		Female	.951	513.2			.971	303.7				
1979	A	Male	.963	30.8	92.5	66.7	.974	401.6	855.9	53.1	9.3	
		Female	.963	61.7			.982	454.3				
	F	Male	.952	278.3	789.3	64.7	.963	39.5	105.1	62.4	0.1	
		Female	.944	511.0			.976	65.6				

6. Reproductive rate, R

Reproductive rate (i.e., the ratio of the total recruitment (\hat{T}) of newly-emerged adults to that of overwintered adults) is also shown in Table 4 and Fig. 4. In Fig. 4 there is a definite tendency for higher reproductive rates at downstream sites in every year. For example, at site A, the value of R ranged from 2.2 (1978) to 9.3 (1979), whereas the values at site F ranged from 0.1 (1979) to 1.3 (1977). Other sites were intermediate between the two extremes at sites A and F. In 1979 at site F, R was very low, due to the large-scale flood from heavy late June rains which washed away many larvae on the host plants.

7. Adult survival rate from emergence to hibernation, S_A , and until the breeding season in the following spring, S_W

Since the interval from emergence to hibernation in newly-emerged adults is more

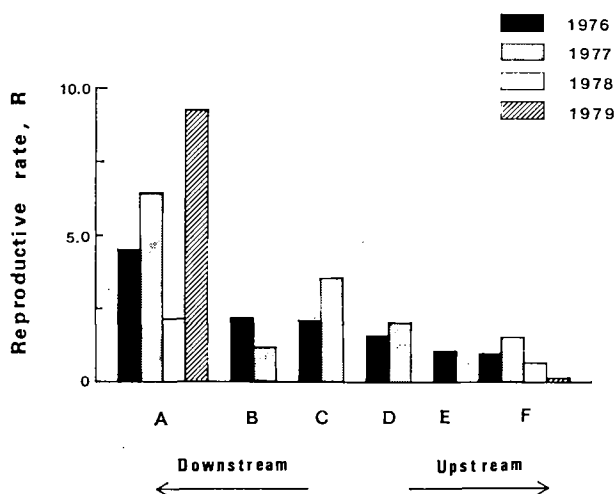


Fig. 4. Reproductive rate (R) at each site.

than 70 days, the mortality during this period must be considered separately from that during hibernation. In order to estimate adult survival rate from emergence to hibernation, the number of newly-emerged adults resident within the site and the proportion surviving in the following spring must be considered several times during the pre-hibernating period. The results of this sampling are shown in Fig. 5. The

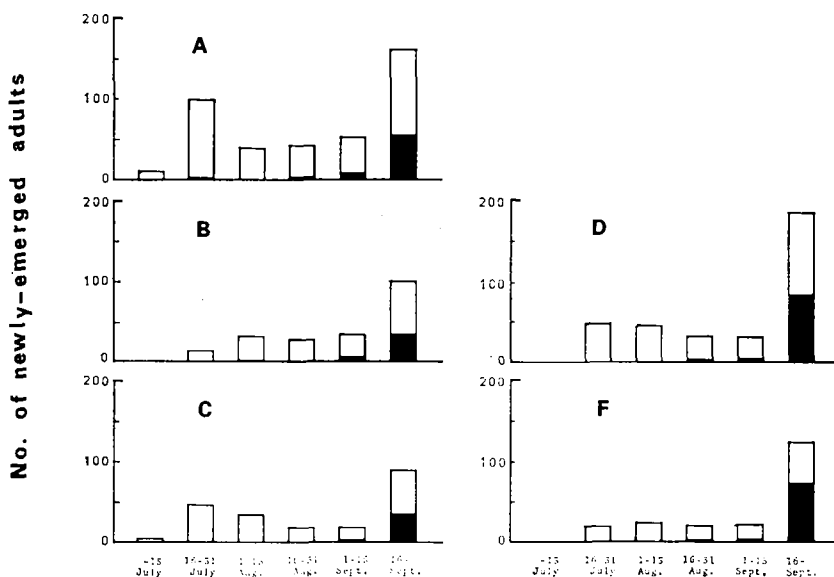


Fig. 5. The relationship between newly-emerged adults resident at several times during pre-hibernating period and survivors of them until the following spring. Each column shows the number of newly-emerged adults of which last capture in autumn falls on each period. Filled area shows the number of adults capture which were recaptured in the following spring.

information in Fig. 5 is based on several considerations. For example, in spring, occasional examinations of thistle plants along the stream allowed us to recapture most of the overwintered adults, even if they had emigrated outside the boundaries of the plot. Fig. 5 shows that virtually none of the newly-emerged adults whose last capture in autumn took place before mid-September survived to the following spring. In short, beetles must survive after mid-September if they are to contribute to the reproductive population in the following spring. Since most of the newly-emerged adults could be marked and since, as mentioned earlier, they rarely emigrate outside the plots in autumn, the survival rate of the local population from emergence to hibernation (S_A) and to the following spring (S_W) could be estimated reliably from the information obtained from the marked adults. The minimum estimate of S_A is the ratio of marked adults resident after mid-September to the whole population of newly-emerged adults. The comparable estimate of S_W is the ratio of marked adults recaptured in the following spring to the whole population of newly-emerged adults. Those estimates are shown in Fig. 6. There was a definite tendency for both S_A and S_W to be higher at upstream than at downstream sites. This tendency was clearer in

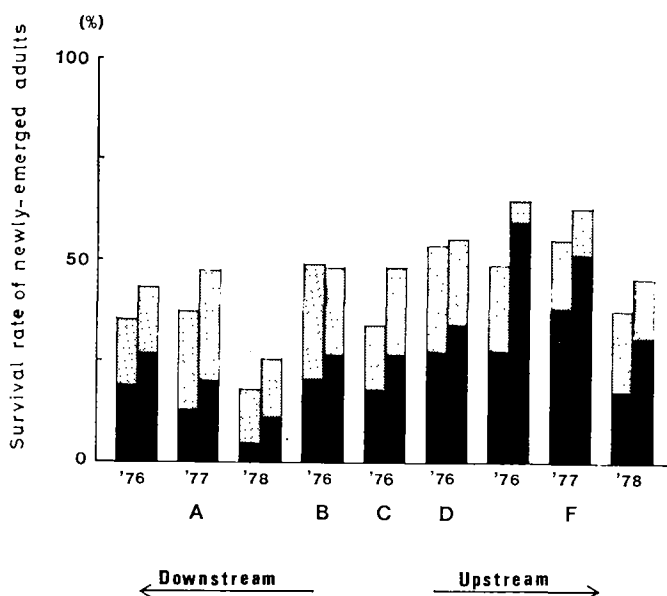


Fig. 6. Survival rate (%) of newly-emerged adults from the time of their emergence until hibernation (S_A : \square + \blacksquare), that during hibernation (S_H : \square) and that from the time of emergence until the following spring (S_W : \square).

S_A ; proportion of number of residents by 15 September to total number of adult emerged.

S_W ; proportion of number of recaptured in the following spring to total number of adult emerged. Left and right columns refer to male and female, respectively.

females, which play more important role on reproductive process in the following spring. There was also a tendency at each site for S_A and S_W to have lower for males than for females. As the mortality from emergence to hibernation is larger than that during hibernation in determining the fraction of newly-emerged adults contributing to the reproductive process in the next year, S_A has a rather more important role than the survival rate during hibernation (S_H). For example, for females, S_A and S_W at site A were 25.6-47.6% and 11.3-27.0% respectively, whereas the values at site F were 45.7-64.8% and 30.9-59.4% respectively. NAKAMURA and OHGUSHI (1979) reported that in Asiu there were a few adults which overwintered twice. The same phenomenon was observed in this study also, though the proportion of such individuals was very low (Table 5). There was a tendency for the proportion

Table 5. The number and proportion of marked beetles which overwintered twice.

Year	Site	No. marked in the 1st year	No. recaptured in the 3rd year	% overwintered twice
1975*-77	A	88	0	0.0
	B	69	0	0.0
	C	96	3	3.1
	D	184	4	2.2
	F	215	7	3.3
1976-78	A	408	0	0.0
	F	210	9	4.3
1977-79	A	1054	0	0.0
	F	596	6	1.0

* Newly-emerged adults of 1975 were marked only in the spring of 1976. (See text)

of adults which overwintered twice to be higher at upstream sites. For example, at site A, there were no such adults during the study period, while at site F, a certain fraction of adults (1.0-4.3%) were consistently found to have overwintered twice.

8. Stability of population size

We shall consider the stability of the population of overwintered adults in the reproductive season. Table 6 shows the population intensity of overwintered adults at sites A and F in four years, 1976-79. There was only a 2.5-fold variation at site F, whereas site A had a 6-fold variation. We shall now consider the trend of the reproductive segment of the population among different sites in relation to the population parameters mentioned above. The graphical method of key-factor analysis was used to detect the differences in the population parameters contributing to the population trend among different sites. The index of population trend (I) was expressed as follows:

$$I = A_{t+1}/A_t = R \times S_W = R \times S_A \times S_H$$

A_t : population intensity of overwintered adults of t th year;

Table 6. Population intensity of overwintered adults which recruited at sites A and F in 1976-79.

D_1 : Number per individual thistle plant;

D_2 : Number per 100 shoots of thistle plant.

Population intensity of overwintered adults				
	A		F	
Year	D_1 (per plant)	D_2 (per 100 shoots)	D_1 (per plant)	D_2 (per 100 shoots)
1976	6.0	94.1	3.4	99.0
1977	7.5	176.0	6.2	115.7
1978	15.7	213.0	10.3	211.1
1979	2.7	35.6	10.3	245.9

R : reproductive rate (i.e., the ratio of the total number of newly-emerged adults to that of overwintered adults);

S_A : survival rate during the period from emergence to hibernation;

S_H : survival rate during hibernation.

Taking logarithms,

$$\log I = \log R + \log S_A + \log S_H$$

The variations of these values among different sites are shown in Fig. 7. It can be seen that S_A is an important factor determining the variation in population trend among different sites, and the changes in $\log R$ are negatively correlated with those in $\log S_A$. Although the changes in $\log S_H$ are somewhat parallel with those in $\log S_A$, S_H seems to be less effective on the variation in population trend among different

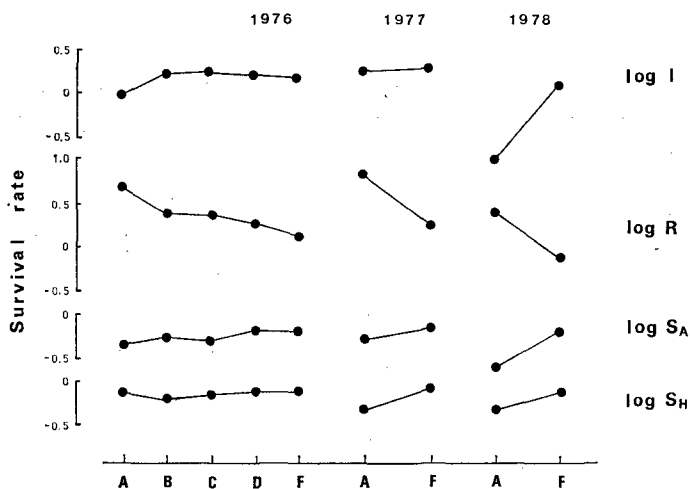


Fig. 7. Comparison of changes in population trend (I), reproductive rate (R), adult survival rate during pre-hibernating period (S_A) and that during hibernation (S_H) among different sites.

sites than S_A for S_H used in this article was underestimated and S_A was overestimated, since it was assumed that all new adults which were alive in mid-September could enter hibernation. This relationship will be discussed in detail in later section.

9. Stability of the host-plant population and habitat characteristics

As already mentioned, various adult population parameters and life-history characteristics have definite tendencies to change from downstream to upstream habitats. Annual changes of thistle plants in successive years are shown in Fig. 8, which compares the stability of this food plant at different sites. Both the rate of

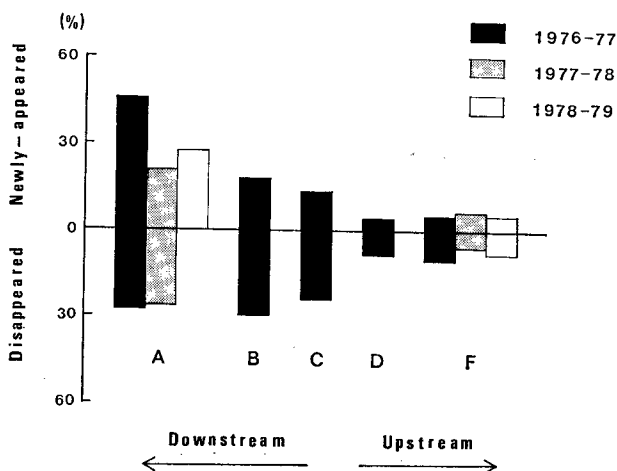


Fig. 8. Annual changes of the population of host plant, *C. kagamontanum*, in successive years.

Upper column; proportion of newly appeared plants in the year to total number of plants in that year.

Lower column; proportion of disappeared plants in the year to total number of plants in the previous year.

disappearance of old plants and the rate at which new plants appeared were higher at downstream than at upstream sites. Since site A is still in the early stage of succession and its sandy deposits have yet not become hard, floods caused by heavy rain have occasionally buried thistles under the sand or washed them away. Another assessment of the characteristics of habitat conditions compared the species composition of vegetation at each site. Species of all herbs and trees present within 10 meters from both river banks were recorded and classified in three categories; herbs, trees growing in the unstable habitat, and trees growing in the stable habitat; i.e., in the natural climax forest. Representative species for herbs were *Polygonum filiforme*, *P. Thunbergii*, *Miscanthus sinensis* and *Plantago asiatica*. Trees growing in the unstable habitat included *Deutzia crenata*, *Hydrangea paniculata*, *Mallotus japonicus* and *Rhus javanica*, and trees growing in the stable habitat included *Quercus mongolica*, *Q. salicina*, *Carpinus Tschonoskii* and *Corylus heterophylla* var. *Thunbergii*. The number of species in each category is shown in Fig. 9. The total number of plant

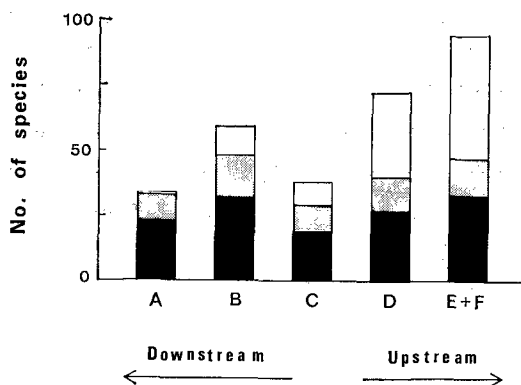


Fig. 9. Number of species of plants at each site.

■; shrubs, ▨; trees growing in the unstable habitat,
 □; trees growing in the stable habitat.

species present tended to increase upstream. This increase could not be explained by the size of each site (Table 1), and was mainly due to the presence of the trees growing in the stable habitat. For example, at site A, there were many herbs and few shrubs, *Polygonum Thunbergii*, *P. cuspidatum*, *Rumex crispus*, *Artemisia princeps* and *Alnus Sieboldiana*, etc., whereas at site F, there were many trees growing in the stable habitat, *Quercus mongolica*, *Q. salicina*, *Prunus Grayana*, *Cephalotaxus Harringtonia* and *Aucuba japonica*, etc. The analysis of the stability of the host-plant population and the characteristic vegetation clearly suggests that site A represents the most unstable habitat, whereas sites D and F represent more stable ones. Consequently we can conclude from the results of year-to-year variations of population intensity and habitat conditions at each site that the reproductive population of *H. pustulosa* is more stable in the stable habitat.

DISCUSSION

The significance of habitat stability as a favourable factor in the ecological strategies of animal populations has been recently emphasized (PIANKA, 1970; WHITTAKER *et al.*, 1973; SOUTHWOOD *et al.*, 1974; SOUTHWOOD, 1977). But there have been few studies which demonstrated the relationship between the stability of natural populations and that of their habitat. The results obtained in this study provide much information on the relationship between habitat conditions and the characteristics of local populations related to stability.

This study revealed that the characteristics of local populations and habitat conditions in upstream, as compared with downstream habitats, show some definite tendencies: (a) Firstly, as regards population parameters, reproductive rate (R) is lower, whereas adult survival rate from emergence to the breeding season in the following spring (S_w) is higher in the upstream habitats. (b) Secondly, as regards

life-history characteristics, longevity of overwintered adults is greater, adult emergence occurs later, and the newly-emerged adult population reaches its peak more gradually. (c) Lastly, as regards habitat conditions, these are smaller annual changes in the host plant population, and the species composition of the vegetation is more complex on the upstream sites. In addition, throughout the study period, the reproductive populations were more stable in size in the upstream habitats than in those downstream.

NAKAMURA and OHGUSHI (1979) reported the adult population parameters in Asiu, which was located about 10 km west of the site F in this study. The study area in Asiu is covered with a typical, cool-temperate natural climax forest. There the locations and numbers of the host plant (*C. kagamontanum*) remained fairly stable throughout the study period. In Asiu, R was 0.85-2.07 in three years, 1974-76, and S_w was more than 55%. Furthermore, the overwintered adults were fairly long-lived; e.g., some adults lived beyond mid-September, the earliest newly-emerged adults appeared in early August, and the population of new adults gradually peaked in early September. These results indicate that the population characteristics and habitat conditions in Asiu are similar to those in the upstream habitats in our present study.

In order to compare the stability of local populations among different habitats, we must consider more interrelations between the characteristics of the local population and the spatial and temporal changes in the conditions in its habitat. As mentioned earlier (Fig. 7), the pattern of changes in the population trend of overwintered adults among different sites is related to the interaction between R and S_w . Consequently, we should detect the factor(s) determining the population parameters, R and S_w .

1. Factors determining the value of R among different habitats

Key-factor analysis has shown that the key stage which contributed most to the variation of R among different sites was the egg and early larval (1st-3rd instar) period. The main mortality factor during this period proved to be arthropod predation (OHGUSHI and SAWADA, unpublished). The most important predator here was the earwig, *Anechura harmandi lewisi* (SAKAI), which is an active species present in large numbers at the time of hatching of the larvae of *H. pustulosa*. The mortality by arthropod predation during the egg and early larval period in upstream habitats was usually higher than that downstream. The relative number of species and abundance of the arthropod predators in different habitats should be dependent on the frequency of elimination by flood or the degree of vegetation coverage (DEMPSTER, 1971). The percentage mortalities during the egg and the early larval stages at site A in four years, 1976-79, were 46.2-61.2% and 24.4-57.9%, respectively, whereas those at site F were 68.4-83.2% and 78.3-80.6%, respectively.

As the population at site A was rarely subjected to heavy predatory pressure, it occasionally reached sufficiently high levels for intraspecific competition for food to occur. In fact, a few host plants were defoliated by the late larval stage in 1978. Furthermore, since sandy deposits have not yet hardened at site A, some host plants

were occasionally eliminated by the floods caused by heavy rains in June and September. The significant effects of flooding on the mortality processes of a population have also been reported for a chrysomelid beetle that lives on a river bank (WHITTAKER *et al.*, 1979). In 1979, the largest flood occurred at site F in late June and eliminated many larvae on host plants, so that R was greatly reduced. But such a large-scale flood seems to be different in nature from those small-scale ones which often occur in downstream habitats. In fact, there was no evidence of the influence of flooding on the population at site F except in 1979. In downstream habitats, the intraspecific competition for food at the late larval stage escaped from the heavy predatory pressure which always occurs upstream probably acts in conjunction with small-scale floods in June to affect the value of R .

2. Factors determining the value of S_w among different habitats

It was shown before (Figs. 6 and 7) that S_w is largely dependent on S_A , the survival rate of new adults during the pre-hibernating period. In every year, there were no significant differences among different habitats in the mean daily survival of newly-emerged adults or in the timing of their entry into hibernation (Table 4 and Fig. 2). But the time of adult emergence upstream was considerably later than in downstream habitats. It follows that the length of the period from emergence to hibernation must play an important role in determining the value of S_A ; i. e., a longer period from emergence to hibernation should reduce the overall survival rate of newly-emerged adults during the pre-hibernating period.

Fig. 10 shows the cumulative percentage curves for eggs laid and adults emerged, and the 50% points for both curves (E_{50} and A_{50}) for sites A and F in four years, 1976-79. Between site A and site F, there was a difference of about 10 days in the 50% points for the number of eggs laid and more than 20 days for the half-way points of adult emergence. Since there was no difference in the time that oviposition began on both sites, the difference in the oviposition curve was mainly due to the difference in longevity of overwintered adults. The increased difference in the curves for adult emergence was mainly attributable to the time-specific effect of arthropod predation.

Predation by arthropod predators is more or less time-specific each year; i. e., it operates mainly from mid-May to mid-June (OHGUSHI and SAWADA, unpublished). Thus, in upstream habitats where populations are usually subjected to heavy predatory pressure, the proportion of the larvae hatching in the latter half of the oviposition period becomes considerably higher than the proportion emerging from eggs laid in the first half. As a result, the time of adult emergence in upstream habitats is considerably delayed by the time-specific mortality attributable to arthropod predation.

On the other hand, the daily temperature at site F was always 1.0°C-1.5°C lower than that at site A. Although there was no significant difference in the developmental period of the egg stage between the sites, high temperature in summer is likely to

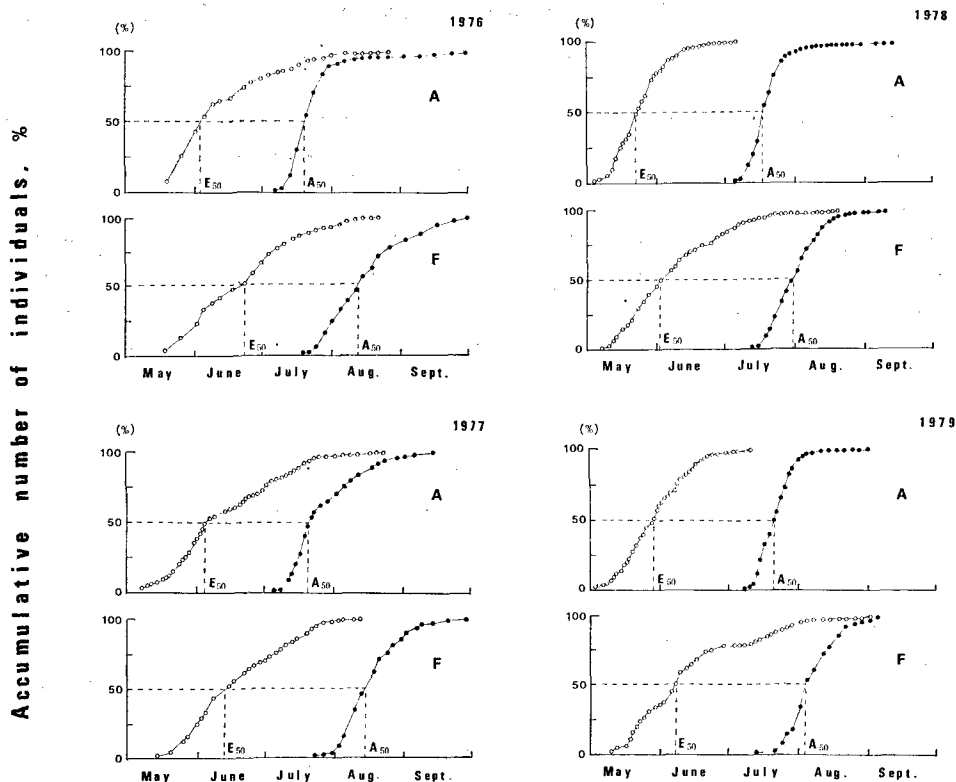


Fig. 10. Cumulative percentage curves of eggs laid ($-○-$) and adults emerged ($-●-$) at sites A and F, in 1976-79. E_{50} and A_{50} refer to the 50% points for both curves, respectively.

affect the survival of newly-emerged adults. In downstream habitats where the adult emergence usually starts in early July, newly-emerged adults must go through the hottest period in summer, and are subjected to intense radiation then because the valley is wider downstream. Such unfavourable weather, coupled with intraspecific competition for food when there is little pressure from predators, and floods caused by typhoons in September will impose modifying effects on the value of S_W . In addition, the accumulated stress of these unfavourable weather conditions and the intraspecific competition for food seem to be important factors responsible for the briefer life-spans of overwintered adults in downstream habitats.

The value of R in each habitat consequently is largely dependent on the magnitude of predatory pressure, which in turn is dependent on habitat conditions. In contrast, the value of S_W is largely dependent on the time of emergence, which in turn is determined by the longevity of overwintered adults and the time-specific operation of predation. Furthermore, in comparison with upstream habitats, modifying factors for R and S_W operate more strongly in downstream habitats. In downstream habitats, therefore, the value of R rises and that of S_W falls as compared with values upstream.

In addition, the variations in both parameters also appear to be larger than those in upstream habitats. As a result, the population in downstream habitats is likely to be more unstable than that in upstream habitats. Thus the interrelationship between seasonal changes in habitat conditions and the life-history characteristics which determine population parameters governs the stability of the local population in any habitat.

The results in this paper provide a general view of the population dynamics of *H. pustulosa*, with special reference to the interrelationships among habitat conditions, life-history characteristics, and population parameters. We shall construct life tables and analyze each process included in these relationships in more detail in subsequent papers.

SUMMARY

- (1) A field study was carried out on the population dynamics of a thistle-feeding lady beetle, *Henosepilachna pustulosa* (KÔNO), living in five different valleys in the northwestern part of Shiga prefecture, central Japan.
- (2) An intensive marking, release and recapture program was carried out on each population to estimate adult population parameters by the JOLLY-SEBER method.
- (3) Comparisons of population parameters and life-history characteristics in upstream habitats with those downstream showed definite trends. In upstream habitats, some overwintered adults could survive after September, and a few of them could overwinter twice. New adults started to emerge in late June and reached a peak more gradually than those in downstream habitats. The population had a low reproductive rate (0.1-1.3) and a high survival rate (30.9-59.4%) for its new adults during the period from their initial emergence to their reproductive season in the following spring. In contrast, in downstream habitats most of overwintered adults died by late July, and none could overwinter twice. New adults started to emerge in early July and reached their peak more rapidly. The population was characterized by a high reproductive rate (2.2-9.3) and a low survival rate (11.3-27.0%) for new adults, during the period from their initial emergence to their reproductive season in the following spring.
- (4) Habitat conditions also varied in accordance with these changes in population parameters and life-history characteristics among local populations. Vegetation was more complex and the size and location of the host-plant population varied less in upstream than in downstream habitats.
- (5) The most stable population in upstream habitats (site F) showed only 2.5 fold variation in population intensity of overwintered adults in four years, while the most unstable one in downstream habitats (site A) showed 6 fold variation.
- (6) Reproductive rate (R) among different habitats was largely dependent on the magnitude of predatory pressure, which in turn was closely dependent on habitat conditions. As compared with upstream habitats, modifying factors for the value of

R operated more strongly in downstream habitats.

(7) Survival rate of new adults from emergence to the reproductive season in the following spring (S_w) among different habitats was largely dependent on their time of emergence, which in turn was determined by the longevity of overwintered adults and the time-specific effects of predation. As compared with upstream habitats, modifying factors for the value of S_w also could operate more strongly in downstream habitats.

(8) As a result, populations in downstream habitats are likely to be more unstable than those in upstream habitats. The features of individual local populations of *H. pustulosa* are thus determined by the interrelationship between seasonally changing conditions in the habitat and the life-history characteristics.

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異なる環境条件下に生息するコブオオニジュウヤホシテントウ自然個体群の動態

I. 成虫個体群パラメーターの比較

大 串 隆 之・沢 田 裕 一

- (1) 滋賀県北部の朽木村にある安曇川水系の5カ所の谷で渓流沿いに分布す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の地域個体群を1976年から1979年まで調査した。
- (2) 個体識別法を用いて得られたデータを JOLLY-SEBER 法によって整理し、成虫個体群パラメーターを推定した。
- (3) 上流域と下流域について個体群パラメーターと生活史の特徴を比較したところ一定の傾向が認められた。上流域では越冬成虫の寿命は長く一部の個体は9月以降まで生存し、わずかではあるが2回越冬する個体も認められた。また新成虫は下流域に比べその羽化開始時期は遅れ(7月下旬)、個体数はゆっくりと上昇し9月上旬頃にピークに達する。更にこの個体群は低い増殖率(0.1~1.3)と羽化から翌春の繁殖時期までの高い生存率(30.9~59.4%)によって特徴づけられていた。一方下流域では、越冬成虫の寿命は短くほとんどの個体は7月下旬までに死亡し2回越冬個体は認められなかった。また新成虫の羽化開始時期は早く(7月上旬)、その後急激に個体数を増し7月下旬にはそのピークに達する。この個体群は高い増殖率(2.2~9.3)と羽化から翌春までの低い生存率(11.3~27.0%)によって特徴づけられていた。
- (4) 生息場所の条件も個体群パラメーターや生活史の特徴の変化と同様に地域個体群の間で異なっていた。上流域では下流域に比べ植生の種構成はより複雑であり、食草個体群の年間の変化はその大きさも、位置もはるかに小さかった。
- (5) 上流域の個体群では4年間の越冬成虫の population intensity の変動は2.5倍であったのに対し下流域の個体群では6倍であった。
- (6) 地域個体群間の増殖率の違いはその生息地の条件を反映した捕食圧の大きさに依存していた。また上流域に比べ下流域では増殖率の値に対する攪乱要因がより強く作用していた。
- (7) 地域個体群間の羽化から翌春の繁殖時期までの生存率の違いはその羽化時期に大きく依存していた。それはまた越冬成虫の寿命と time-specific に作用する捕食の効果に依存していた。上流域に比べ下流域では生存率に対する攪乱要因はより強く作用していた。
- (8) その結果下流域の個体群は上流域よりもより不安定になりやすいものと思われる。このようにコブオオニジュウヤホシテントウの各地域個体群の様相は季節的に変動する生息地の諸条件とその生活史の特徴の相互関係によって決定されているものと考えられる。