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COMRARATIVE POPULATION STUDIES OF THREE *PIERIS* BUTTERFLIES, *P. RAPAE*, *P. MELETE* AND *P. NAPI*, LIVING IN THE SAME AREA
II. UTILIZATION OF PATCHY HABITATS BY ADULTS THROUGH MIGRATORY AND NON-MIGRATORY MOVEMENTS

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INTRODUCTION

The closely related species of butterflies belonging to the genus *Pieris*, *P. rapae*, *P. melete* and *P. napi*, have some differences in their preferences for oviposition plants (HIURA, 1968; TAKAHASHI, 1975; OHSAKI, 1979), adult nectar plants (OHSAKI, 1979), roosting-sites (OHSAKI, 1979) and favourable light conditions (HIURA, 1968; TAKAHASHI, 1975; OHSAKI, 1979), and habitat segregation among them has been observed in their areas of coexistence (HIURA, 1968; TAKAHASHI, 1975; OHSAKI, 1979).

The stability and continuity of habitat for the three species are much different from one another in the same area. The habitat of *P. rapae* is temporary, localized and unstable. That of *P. metete* is more permanent, widespread and stable than that of *P. rapae*. *P. napi* seems to live in the intermediate, i. e., permanent, localized and stable, one (OHSAKI, 1979).

The spatial continuity or discontinuity of habitat for a given species can be clarified only through careful observations of movement of the butterflies, especially of reproductive females.

In this paper, we describe the characteristics of movements of the three *Pieris* spp. in relation to utilization of habitat resources on the basis of the results of mark-recapture experiments conducted in the field.

STUDY AREA AND CENSUS METHOD

The study area, about 3×1.5 km, was situated in a farm village in mountains, Inabu, Aichi Prefecture. Twenty-eight subsites in which most of the adults of *Pieris* can be observed are patchily distributed in the area as described in detail in OHSAKI (1979).

Marking and recapture censuses for the adults of three *Pieris* species were carried out on almost every fine day in August, 1975, and during the period from April 18

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to November 3 in 1976. It took 2 days to patrol the whole area in a census. Adults found were captured by butterfly net. The butterflies newly captured were numbered individually with red or black coloured felt pen on the undersurface of both hindwings. Every butterfly captured was released immediately at the capture site after recording the species, sex, individual number, adult age and locality. When butterflies were captured outside the subsites, the locality was recorded as if they were at the middle point between the nearest two subites.

Approximate age of adult was estimated on the basis of physical condition of their wings, i. e., it was classified into four categories as follows: age-class 0, no visible damage and lustrous scales; age-class 1, fine tears and less lustrous scales; age-class 2, notched tears and frayed scales ; age-class 3, extensive tears and frayed scales (Fig. 1).

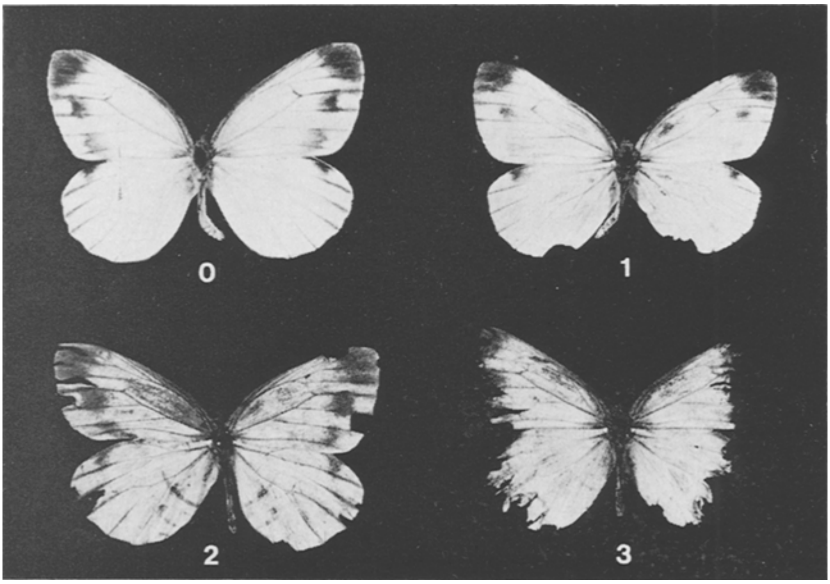

Fig. 1. Representative specemins males of adult *P. melete* showing wing-wear: 0, age-class 0; 1, age-class 1; 2, age-class 2; 3, age-class 3.

Daily egg numbers laid per female of *P. melete* and *P. napi* were observed in the field cages (1.8×1.8×2.0 m) in June in 1976 and 1978, respectively. A female of *P. melete* or *P. napi* immediately after mating was introduced in each cage in which *Cardamine appendiculata* or *Arabis hirsuta* and *Aster fastigiatus* were planted as oviposition plants and nectar plants, respectively.

For the spatial distribution patterns of habitats, areas occupied by the oviposition plants and the adult nectar plants, and the number of butterflies in each subsite were researched in June 1977.

RESULT

(1) *Adult age-class*

Mean adult age in days of individuals belonging to each age-class was estimated by the physical conditions of the wings of the recaptured butterflies which belonged to age-calss 0 at the first capture (Table 1). There were no remarkable differences in mean age of each age-class among species, sexes and generations. So, this index will be useful for the estimation of the age of the butterflies.

Table 1. Mean adult age in days of successive age-classes of three *Pieris* species in 1976.

Adult age-class		0	1	2	3
P. rapae	♂	2.2	5.6	8.8	10.4
	♀	—	4.7	11.5	14.5
P. melete (except August)	♂	2.2	4.5	11.7	19.1
	♀	2.0	5.3	10.0	29.0
P. melete (August)	♂	1.8	4.4	10.1	—
	♀	1.5	4.4	10.0	—
P. napi	♂	2.0	4.8	—	—
	♀	1.5	4.7	—	—

Mean adult age of each age-class could be roughly estimated as follows: 0, within 3 days after emergence; 1, about 5 days; 2, about 11 days; 3, 2 weeks or more.

(2) *Seasonal fluctuation in the number of adults*

Seasonal fluctuations in the numbers of adults captured of three *Pieris* species are shown in Fig. 2.

P. rapae: The adults began to emerge in mid April, and the number of adults increased gradually and reached a peak in mid June. They decreased gradually thereafter. This downward trend continued till autumn. The cause of this decrease might be due to the decrease in the amount of larval food plants, i. e., cultivated cruciferous plants, in summer. The number of females was always less than that of males. The predominancy in the number of recaptured males was common among three *Pieris* species, and this was due to a difference in sampling ratio between sexes as described later. The number of generations was supposed to be about six on the basis of the number of peaks of incidence curves and the number of adults of age-class 0 in Fig. 2.

P. melete: The adults of the overwintering generation emerged during a relatively short period in late April. The adults of the first and second generations emerged in mid June and August, respectively.

P. napi: The adults of the overwintering, first and second generations emerged in

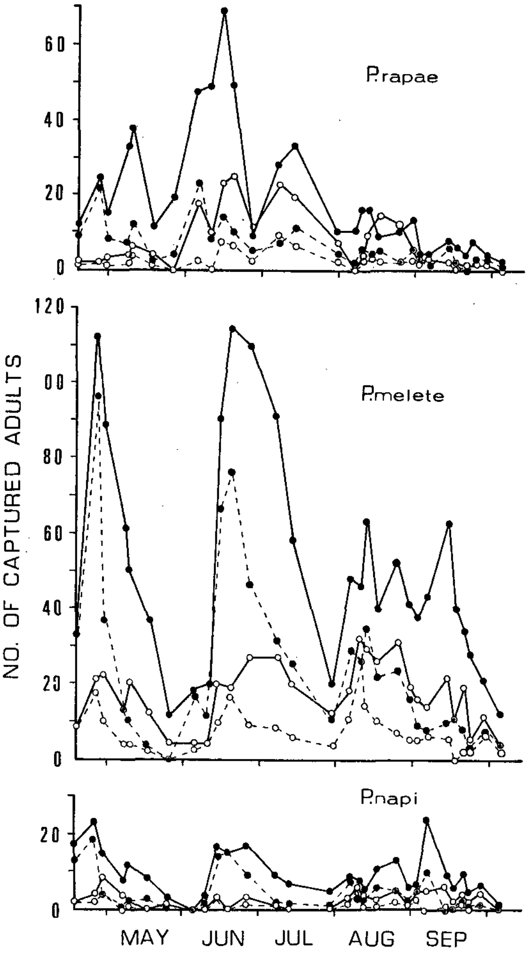

Fig. 2. Seasonal fluctuations in the number of captured adults of three *Pieris* species in 1976. Broken line indicates the number of individuals belonging to age-class 0. ● Males; ○ Females.

late April, mid June and in and after August, respectively.

As compared with *P. rapae*, both *P. melete* and *P. napi* had relatively high peaks in the number of adults of the overwintering generation, and the number of annual generations, three, was less than that of *P. rapae*.

The number of adults on each census date was estimated by applying JOLLY's stochastic model (JOLLY, 1965) to the mark-and-recapture data, but estimated values of N_i had large variances because the number captured and recaptured were not large. The average sampling ratio, however, can be estimated by using the data when relatively many individuals were captured. Further, sampling ratio was estimated by another method as follows: For the marked butterflies that were belonging to age-class 0 at their first capture, the recapturing rates ($\frac{m_i}{M_0}$) were plotted in logarithm against

Table 2. Sampling rates of three *Pieris* butterflies estimated by two methods, Jolly's stochastic model and *Y*-intercept of the regression line of recapture duration decay plot, in 1976.

	P. rapae		*P. mletee*				*P. napi*
			(except August)		(August)		
	♂	♀	♂	♀	♂	♀	♂
Jolly	0.70-0.78	—	0.13-0.15	—	0.28	0.37	—
Y-intercept	0.69	0.35	0.16	0.07	0.26	0.37	0.09
r^2	0.95	0.78	0.88	0.75	0.88	0.92	0.76

the recapture dates. The relation fitted well to the linear regression. Then, the *Y*-intercept of the regression line can be regarded as the sampling ratio. The estimates by two different methods are very similar (Table 2). Sampling ratio of females was much lower than males, and this is the main reason of the smaller number of females in Fig. 2.

The actual numbers of both sexes in the whole study area were supposed to be approximately equal, because sex-ratio of male to female adults was about 1 : 1 when larvae collected in the census area were reared under laboratory conditions.

The numbers of males at the highest peak of *P. rapae*, *P. melete* and *P. napi* were estimated as about 100, 700 and 250, respectively, by using the sampling ratio given in Table 2. Estimates for females were approximately equal to those for males.

(3) *Dispersal distance and recapture duration decay curve*

Dispersal ability of the three *Pieris* species is described by dispersal distances and recapture duration decay curves. The dispersal distances of marked butterflies from the releasing point on various days elapsed after release were estimated for adults of different age-classes at their first capture. When an individual was recaptured in the releasing subsite or moved less than 50 m, the dispersal distance was treated as zero. Similarly, the dispersal distance of individual moved between 50 and 149 m as 100 m. Those moved between 150 and 249 m as 200 m. The recapture duration decay curve shows the change in the recapture rate of marked butterflies with time after first release.

1. *Pieris rapae*

The recapture duration decay curves of *P. rapae* were shown separately for three categories of the subsites in relation to the different combination of the oviposition plants and the nectar plants as follows: both plants were present; only the oviposition plants or the nectar plants were present.

The dispersal distance and recapture duration decay curve of *P. rapae* are shown in Fig. 3 and Fig. 4, respectively. Fig. 3 shows that males of *P. rapae* in every age-class scarcely dispersed from the releasing subsite. Fig. 4 shows that recapture rates of males in age-class 0 and age-class 1 on 1.5th day after the first capture were 52.6% and 42.3%, respectively, in the subsite where the oviposition plants and

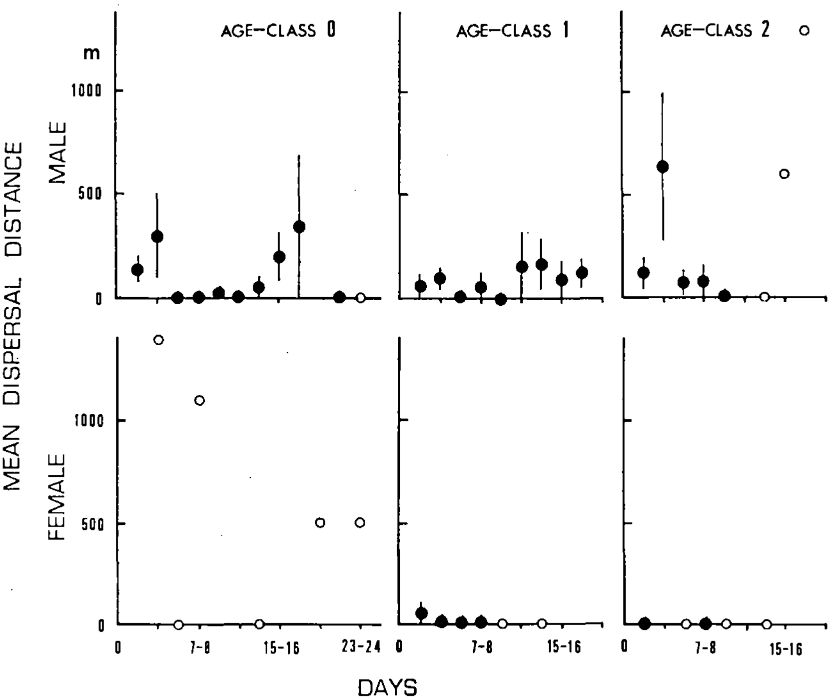

Fig. 3. The mean dispersal distances of *P.rapae* from the releasing point on various days after the first capture (1976). Open circles show the datum from only one individual, and solid circles show the data from 2 to 16 individuals. The vertical bar shows the standard error.

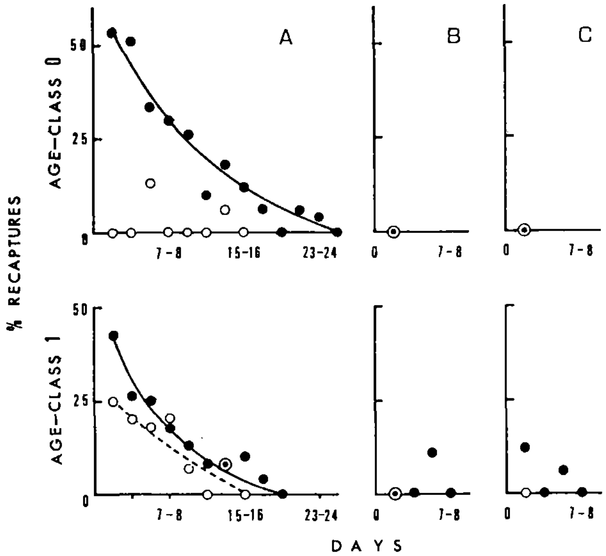

Fig. 4. Recapture duration decay curves for *P.rapae* in each of the subsites belonging to the following categories: A, subsites with oviposition plants and adult nectar plants ; B, subsites with oviposition plants ; C, subsites with nectar plants only (1976). -●- Males; -○- Females.

the nectar plants were growing together. These values and the data on the dispersal distances suggested a strong tendency of residence of males at least in the suitable subsite. On the other hand, females in age-class 0 at first catch were scarcely recaptured, though total 63 females in age-class 0 were marked and released; all the females recaptured were at subsites located 500 m to 1,400 m from the subsites of their first catch. Moreover recapture rate of females of age-class 0 on 1.5th day after the first catch was 0%. However, females older than age-class 1 scarcely dispersed. The recapture rate of age-class 1 on 1.5th day after the first catch was 25.0%, and this fact suggested that the resident tendency of old females was not weaker than that of males in every age-class. In the incomplete subsites where only oviposition plants or nectar plants was growing, males and females in every age-class dispersed quickly, even if they had immigrated into such subsites.

As described above, in the subsites where both oviposition and nectar plants were growing abundantly, males of all age-classes and females older than age-class 1 show a strong tendency of residence. These mean that their trivial movements were limited within areas which were clearly enclosed by geographical boundaries, for example, low ridges, low hills, rivers, afforested lands or paddy fields. In a subsite where the oviposition and nectar plants were patchily distributed, adults of *P. rapae* flew about actively throughout the subsite. In a subsite where the oviposition plants grew in a small cultivated field, and nectar plants grew only in a neighbouring place, *P. rapae* devoted themselves to travelling between these small areas. The fewer the nectar plants were, the shorter the resident times of adults were.

2. *Pieris melete*

Considerable differences in the dispersal pattern of *P. melete* were observed among generations, i.e., the adults of second generation in autumn were less active than those of the overwintering and first generations. The dispersal distance and the recapture duration decay curve are, therefore, shown separately for these two generation groups in Fig. 5-8.

Overwintering and 1st generations: Fig. 5 shows that the males of *P. melete* moved more actively than those of *P. rapae* and dispersed gradually over a considerable distance.

The mean dispersal distances of males of *P. melete* which were recaptured on the released day at different subsites from releasing ones were 367±33 m, 238±32 m, 233±67 m and 150±50 m in adults of age-class 0, 1, 2 and 3, respectively. These data show the young butterflies were more active in their flight activity than the old ones. Though *P. melete* males have so much flight activity, *P. melete* population seemed to be divided into two or three sub-populations among which interchange of individuals is relatively rare even within the study area of 4.5 km^2. Fig. 6 shows the recapture duration decay curves. Recapture rates of males of age-classes 0 and 1 on 1.5th days after releasing were 13.3% and 18.3%, respectively. And both recapture duration

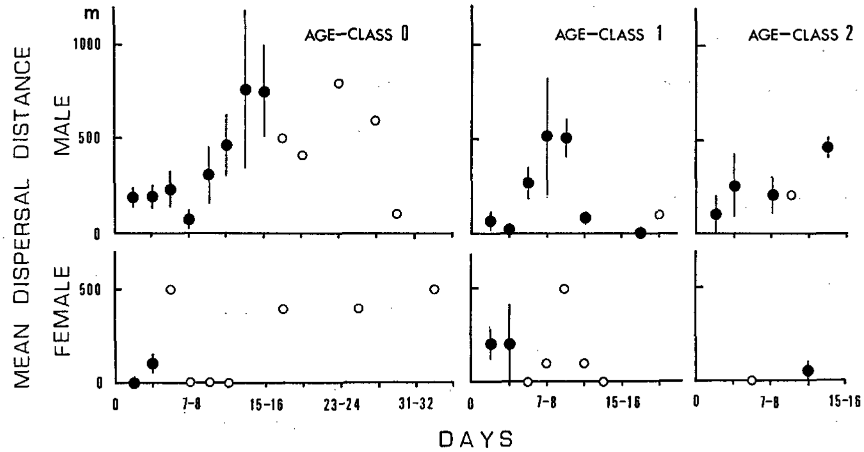

Fig. 5. The mean dispersal distances of *P. melete* from the releasing point on various days after the first capture (1976). Data for August were not included (see text for this reason). Open circles show the datum from one individual only, and soil circles show the data from 2 to 20 individuals. The vertical bar shows the standard error.

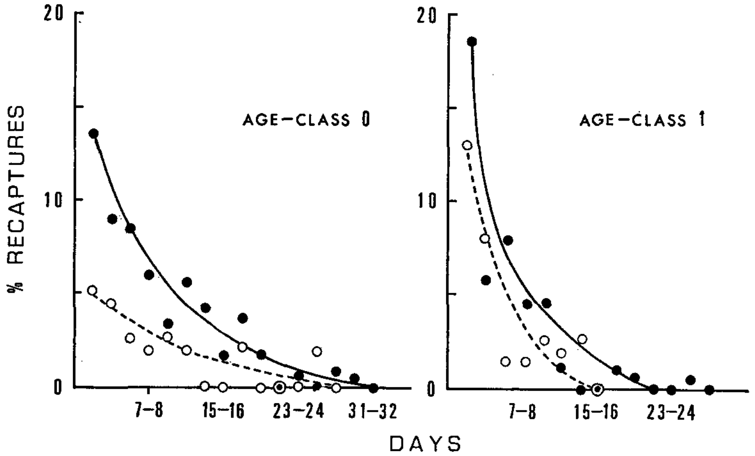

Fig. 6. Recapture duration decay curves for *P. melete* (1976). Data for August were excluded. -●- Males; -○- Females.

decay curves slowly decreased.

Females of *P. melete* were not easily recaptured irrespective of age. Fig. 5 shows, however, that about 5% of females of age-class 0 at their first capture were recaptured at 400 m or 500 m far from the releasing subsites, and the recapture duration decay curve slowly decreased. These may suggest that the flight activity of young females of *P. melete* was lower than young females of *P. rapae*. On the other hand, females of *P. melete* older than age-class 0 were rather active in comparison with females of *P. rapae* of corresponding age-classes. The recapture rate of age-class 1 was 12.8%, and the recapture duration decay curve also slowly decreased.

The dispersal distances and resident times of females of *P. melete* suggested by the recapture duration decay curves had a similar tendency to those of males; both males and females were considered to be resident within a certain area, but this area is wider than that of males of *P. rapae*. In an isolated small subsite by a forest or mountains, some individuals were repeatedly recaptured over two weeks when nectar plants were abundant together with the oviposition plants.

Second generation in August: The dispersal distance and recapture duration decay curve of adults of *P. melete* of this generation as shown in Fig. 7 and 8 are considerably

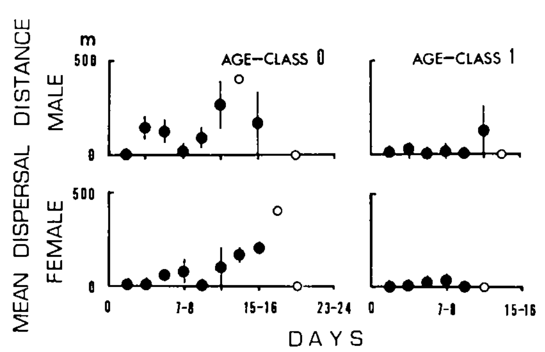

Fig. 7. The mean dispersal distances of *P. melete* in August from the releasing point on various days after the first capture (1976). Open circles show the datum from one individual, and solid circles show the data from 2 to 49 individuals. The vertical bar shows the standard error.

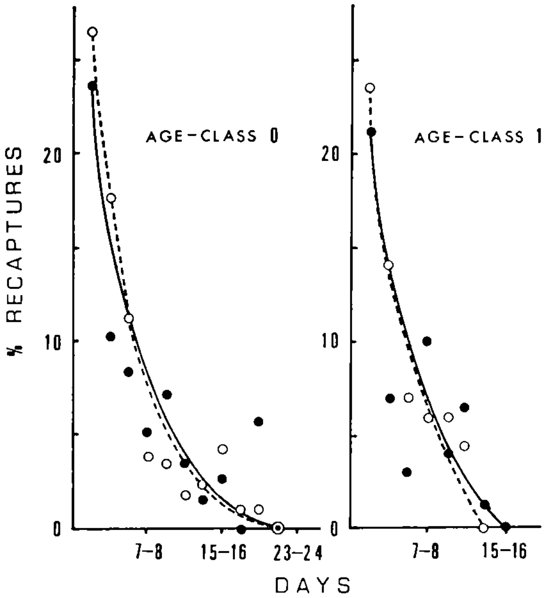

Fig. 8. Recapture duration decay curves for *P. melete* in August (1976).

different from those of other generations. Fig. 7 shows that both males and females in this season were less active than those in other seasons. This tendency was common in all age-classes. The sex ratio of captured *P. melete* in the subsites where adult nectar plants were abundant became almost 1 : 1. Recapture rates of males and females of age-class 0 after 1.5th day were 23.4% and 26.2%, respectively. These values were higher than those in other seasons, suggesting that adults of both sexes in this season were much more resident than those in other seasons. Fig. 9 presents the seasonal fluctuation in the number of adults in a subsite where there were no oviposition plants throughout flight seasons. This figure shows that males of the first generation and both sexes of the second generation in August were abundant in this subsite, because much nectar plants grew in this subsite from June to late August. Adults, however, disappeared from the subsite as soon as the flowering season in this subsite ended in late August. In early September, when cultivated cruciferous plants sprouted in the field near this subsite, females began to lay eggs actively on these plants.

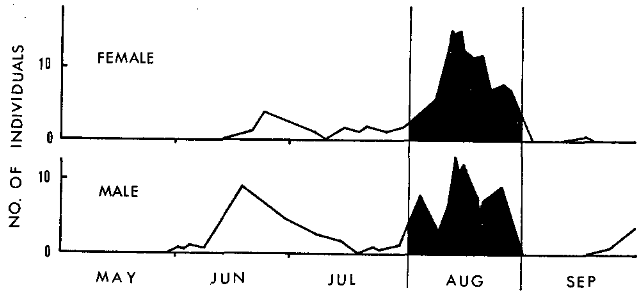

Fig. 9. The seasonal fluctuation in the number of *P. melete* in a subsite where there were no oviposition plants throughout all flight seasons.

Fig. 10 shows the seasonal fluctuation in the number of adults and of eggs on *Cardamine appendiculata* in a subsite where *C. appendiculata* grew densely and a roosting-site also existed. In addition, cruciferous crops were always cultivated except in August and nectar plants were distributed abundantly from June to early August in this subsite. The presence of males in this subsite was almost limited to the first generation. The duration coincided with the period of flowering of nectar plants. While females were captured throughout the flight seasons there, the number was small. The number of eggs was remarkably large in mid-May and from early July to early August when adults of the overwintering and the first generations appeared, respectively. Number of eggs decreased in middle August, but adults of the second generation began to lay more eggs on the sprouts of cruciferous crops rather than *C. appendiculata* in early September.

As mentioned above, oviposition plants might not be necessary for females of *P. melete* to stay in a habitat in August, and even if oviposition plants were growing

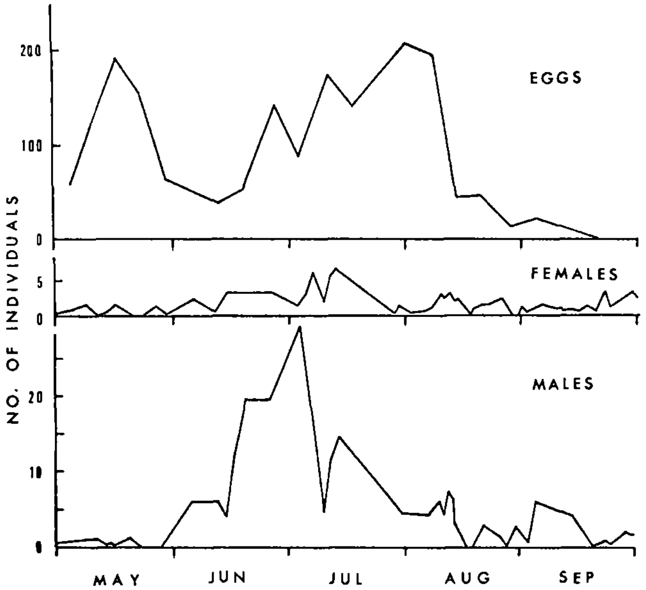

Fig. 10. The seasonal fluctuations in the numbers of eggs and adults of *P. melete* at a subsite where *Cardamine appendiculata* occurred.

there, eggs were scarcely laid on those plants.

Fig. 11 shows the distribution of butterflies marked in a subsite where nectar plants were flowering in the first half of August in 1975, but the flowers decreased in the latter half of August. When nectar plants were flowering, as many as fourteen of 35 marked individuals of *P. melete* were recaptured in the same subsite after four days. In the latter half of August when flowers had faded almost all of marked

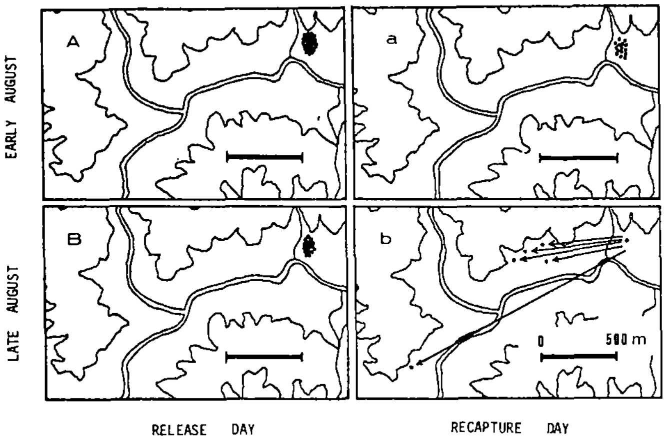

Fig. 11. Changes in the distribution of *P. melete* in a subsite during two two-day periods (1975). Upper, nectar plants were flowering (Early August); Lower, flowers had faded (Late August); A and B, release day; a and b, recapture day. Circles indicate individual butterflies.

butterflies except for only one were recaptured after four days in the other subsites where nectar plants were still flowering. Ovaries of females which were caught and dissected in the middle of August were mostly immature.

3. *Pieris napi*

The dispersal distance and recapture duration decay curve of *P. napi* are shown in Fig. 12 and 13, respectively. Fig. 12 shows that, irrespective of age-classes, dispersal distances of both sexes were generally short. Recapture rates of males of age-class 0 and of age-class 1 on 1.5th day were 5.8% and 6.8%, respectively (Fig. 13). Recapture duration decay curves gradually decreased. Since very few females were captured, it was impossible to analyze the recapture duration decay curves for females. Fig. 13 (Total 1975) shows the recapture duration decay curves

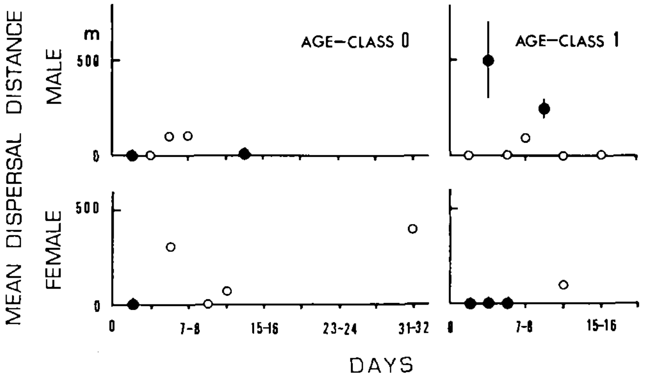

Fig. 12. The mean dispersal distances of *P. napi* from the releasing point on various days after the first capture (1976). Open circles show the datum from only one individual, and solid circles show the data from 2 to 4 individuals. The vertical bar shows the standard error.

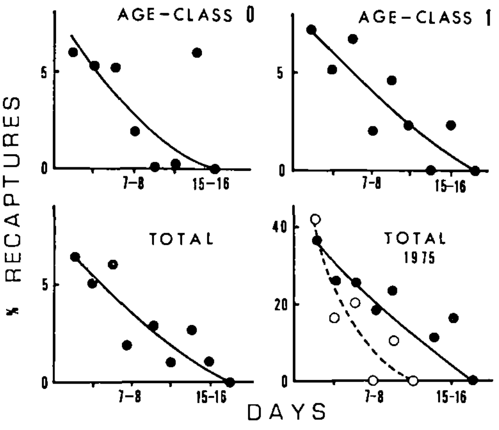

Fig. 13. Recapture duration decay curves for *P. napi* in 1976 and 1975 (Total 1975). -●- Males; -○- Females.

in August, 1975. These data were obtained from some subsites where males were relatively abundant. In this year, adults were not divided into age-classes. The recapture duration decay curves for both sexes were similar. Considering the recapture duration decay curves in 1975 together with the data in 1976, *P. napi* seemed to be resident. Recapture rates of males and females in 1975 on 1.5th day were 39.5% and 43.0%, respectively. These were much higher than those in 1976. Such differences between the two years might be due to difference in sampling efficiency, because the time spent for the census of a subsite varied, for example, from about 90 minutes in 1975 to 20 minutes in 1976.

Recapture data for *P. napi* were not enough to discuss the dispersal pattern, because the population density was very low in 1976. Detailed studies for *P. napi* remain in the future, but the data mentioned above suggest that *P. napi* is not similar in flight behaviour to *P. rapae* but rather resembled to *P. melete.*

(4) *Oviposition pattern*

Oviposition patterns of *P. rapae* and *P. melete* were different from each other. Fig. 14 shows the fluctuations in number of eggs which were laid on the cruciferous crops in small cultivated fields in the fringe of the forest by females of *P. rapae* and *P. melete.* Eggs of *P. rapae* increased rapidly within a short period in both early June and mid September. At the same time, the number of eggs of *P. melete* changed slightly. This difference might be partly due to the difference in the synchronism of emergence of adults of *P. rapae* and *P. melete* in a habitat and partly due to the difference in dispersal radius of adults. But this may also be fundamentally due to the difference in the innate nature of egg production of both species.

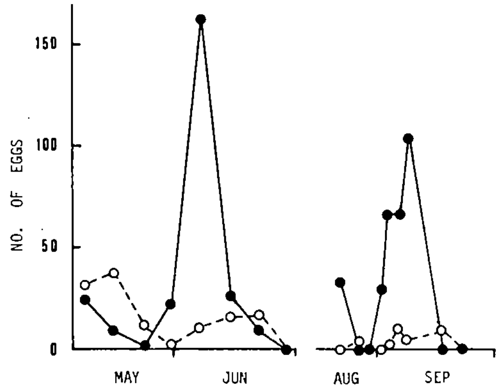

Fig. 14. The seasonal fluctuations in the numbers of eggs of *P. rapae* and *P. melete* in the small cultivated fields (4×2m) in 1976. *B. oleracea* was grown after a harvest of *R. sativus.* -●- *P. rapae*; -○- *P. melete.*

Daily egg number laid per female of *P. melete* and *P. napi* were observed in the field cages. The results are shown in Fig. 15 together with oviposition pattern of

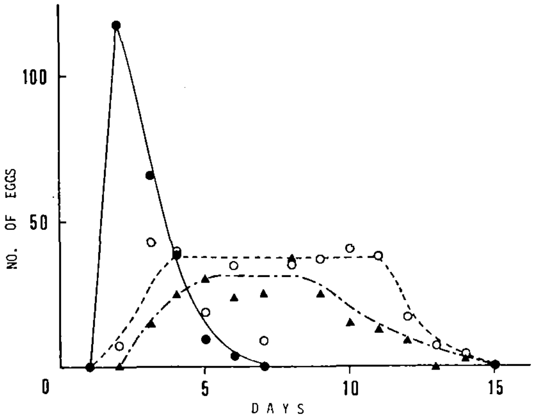

Fig. 15. Daily egg numbers laid per female in the field cages. -●- *P. rapae* (adapted from TAKATA and ISIDA, 1957); --○-- *P. melete* (1976); --▲-- *P. napi* (1978).

P. rapae reported by TAKATA and ISHIDA (1957). Females of *P. rapae* laid explosively more than one hundred eggs on the second or third day after emergence, and then the number of eggs laid rapidly decreased. Females of *P. melete* also began to lay eggs on the second or third day after emergence and continued to lay some constant numbers of eggs for about 10 days. The oviposition pattern of *P. napi* was similar to that of *P. melete*.

As mentioned above, the patterns of daily egg laying were much different between *P. rapae* and *P. melete*. Besides, the dispersal radius of mature females were also different between them. The sexually matured females of *P. rapae* become resident in a habitat and lay eggs abundantly within a short period there. Females of *P. melete* show a tendency to lay eggs in a wider area than *P. rapae*. These differences may be reasonable for the observed patterns of egg deposition in a habitat.

(5) *Spatial distribution pattern of habitats*

Spatial distribution patterns of habitats for the three *Pieris* species are shown in Fig. 16 and Fig. 17. Main nectar plants visited by some species of three *Pieris* species in middle June, 1977, are shown in Table 3. Main oviposition plants were

Table 3. Main nectar plants visited by *Pieris* spp. in middle and late June, 1977.

Nectar plant	*P. rapae*	*P. melete*	*P. napi*
Compositae *Erigeron annuus*	35.9%	15.4	9.1
Leguminosae *Trifolium repens*	24.6	3.4	
Compositae *Cirsium japonicum*	16.9	20.1	45.5
Saxifragaceae *Deutzia crenata*		36.9	36.4
Betulaceae *Castanea crenata*		10.7	

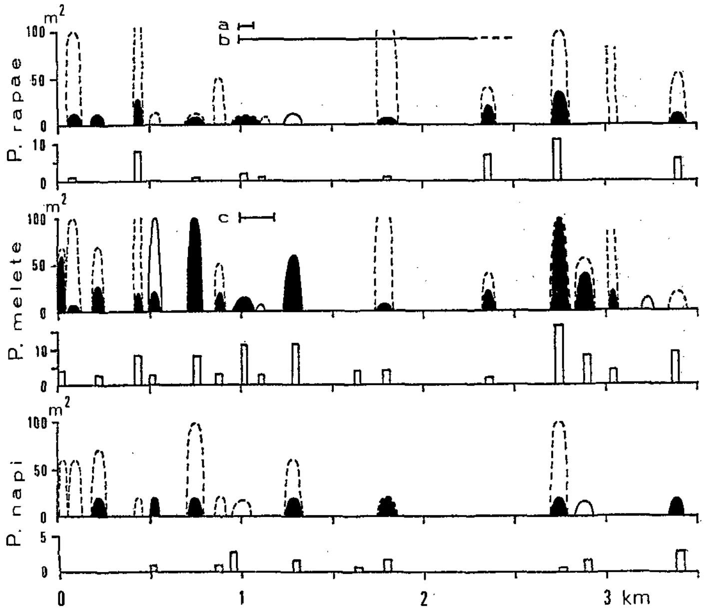

Fig. 16. The spatial distribution patterns of subsites for each *Pieris* species in middle and late June, 1977. The distances from the northernmost subsite to each subsite in which either oviposition plants or nectar plants, or both grew are plotted in the abscissa and abundances in acreage of oviposition plants (solid line) and/or nectar plants (dotted line) in each subsite are roughly represented by the height of the bell shape. The height of oviposition plants for *P. napi* does not show the abundance, but shows the existence of these plants. The width of the base of bell shape indicates the size of the subsite and solid part in the bell shape indicates the acreage with both plants coexisting. Bars show the number of males captured per day during this period in each subsite. The length of arrow indicates the mean dispersal distance per day of butterflies. (a, females older than age-class 0 and males of *P. rapae*; b, age-class 0 females of *P. rapae*; c, *P. melete*).

Brassica oleracea var. *capitata* and *Raphanus sativus* var. *hortensis* for *P. rapae* and *P. melete*, *Cardamine appendiculata* for *P. melete* and *Arabis hirsuta* for *P. napi*. Total abundance in acreage of oviposition plants (solid line) and/or nectar plants (dotted line) in each subsite are roughly represented by the height of the bell shape in Fig. 16. Solid part in the bell shape indicates the acreage of both plants coexisting. The number of butterflies of each subsite tended to be large when the solid parts of its were large. Each of them was regarded as a patch of habitat. If the distance between adjoining patches (subsites) shown in Fig. 16 was shorter than trivial flight distance of females per day, these patches were considered to be a single habitat. According to this consideration, Fig. 16 is reduced to Fig. 17. In Fig. 17, vertices of adjoining solid bell shapes (patch of habitats) within the trivial flight distances of females in Fig. 16 are joined by a line. The height in Fig. 17 shows the relative abundance of habitat resources for each *Pieris* species. It can be seen in this figure

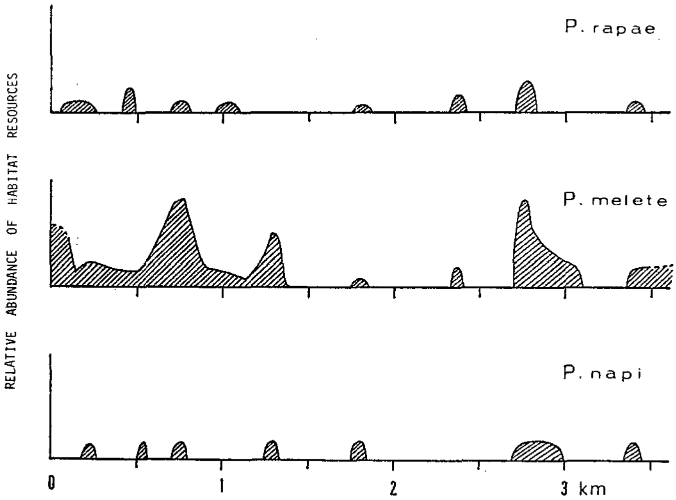

Fig. 17. The spatial distribution patterns of habitats for each *Pieris* species in middle and late June, 1977. This figure is redrawn from Fig. 16. The details are described in the text. The height shows the relative abundance of habitat resources for each *Pieris* species.

that habitats are continuously distributed for age-class 0 females of *P. rapae*, but for males and females older than age-class 0 those are isolated from each other. In the latter, butterflies could utilize only one patch. For *P. melete*, the distance between adjoining patches appears to be shorter than trivial flight distances, and so habitats are distributed continuously for them. Each patch may form discontinuous habitat for *P. napi*.

DISCUSSION

Newly emerged females (age-class 0) of *P. rapae* tended to move for some km away from a native subsite where they emerged even if the subsite was very suitable for adult life, while females of this species older than age-class 0 became resident. Mean adult age of individuals belonging to age-class 0 was estimated to be less than 3 days after emergence, and the pre-ovipositional period of females was around two days in field cages (TAKATA and ISHIDA, 1957). Consequently it seems likely that sexually immature, mated females just after teneral stage emigrate immediately and invade other suitable areas. JOHNSON (1969) pointed out that migration or adaptive dispersal was often performed by pre-reproductive females having immature ovaries. The migration of young females of *P. rapae* fits his theory. Thereafter, they become strongly resident and begin to lay eggs explosively within such suitable areas. SHAPIRO (1970) pointed out that the migration of *P. protodice* was caused by sexual interactions in a densely crowded habitat. From the facts mentioned above, the migration of females of *P. rapae* may possibly be caused by sexual interactions in dense populations, but their migration would occur anyway due to the innate nature of the post-teneral flight.

On the other hand, males of *P. rapae* were strongly resident within suitable native habitats judged by high rate of recapture, and hence males tended to accumulate in such habitats, which led to predominance of males in the adult populations. Since females can mate already in the teneral stage, the high density of males would certainly increase the percentage of fertilized females before dispersing.

WATANABE (1958) and OSADA and ITÔ (1974) studied dispersal of *P. rapae* by using the mark-recapture method, though not so intensive. WATANABE estimated that males were resident and females were more dispersive. This is in essential agreement with the conclusion of the present paper.

Males of *P. melete* of any age-class dispersed gradually from the releasing points, and their mean dispersal distances were estimated to be about 1 km from places of emergence for 2 weeks.

Females of *P. melete* do not migrate so extensively as females of *P. rapae* in age-class 0, but they tended to disperse gradually like the males. Consequently, they are considered to lay about 30 eggs per day for about 10 days in a relatively wide area. But their dispersal range is limited to such an extent that in the study area of about 3×1.5 km, the population of *P. melete* was divided into three sub-populations by slightly elevated ridges and the forests.

Adults of *P. melete* of the second generation in August were strongly resident within small sites where both nectar and roosting-sites were available.

The mode of life of *P. napi* is not understood definitely at present. Males of *P. napi* appeared to be strongly resident within suitable habitats. Females were more dispersive than males. The dispersal distance of females of *P. napi* was shorter than that of females of *P. rapae* in age-class 0, and the radius of trivial movement was narrower than that of *P. melete.*

SOUTHWOOD (1962) pointed out that migratory behaviour has evolved particularly in the species which utilize temporary habitats. Main oviposition plants for *P. rapae* are cultivated plants (OHSAKI, 1979), so its habitats periodically become adverse for breeding or often disappear during harvests, and *P. rapae* can utilize a habitat for only one or two generations. Consequently, displacement of *P. rapae* among habitats is indispensable to maintain the populations, so the remarkable migratory movement in the pre-reproductive stage of females is undoubtedly adaptive for this species. The reproductive females of *P. rapae* become strongly resident within the subsites where they have invaded, and lay eggs abundantly for few days. In this way they increase reproductive efficiency.

In *P. melete,* oviposition plants are wild cruciferous plants which are perenial, and the niche breadth of *P. melete* is wide. Thus, it can be said that they live in permanent habitats. Consequently, it would not be necessary for *P. melete* to do migratory movements for displacement among habitats. But distances between resources of *P. melete* were longer than those of *P. rapae* (OHSAKI, 1979), and hence the range of trivial movement of *P. melete* is wider than that of *P. rapae*. As niche breadth of *P. melete* was wide, the resources available for *P. melete* could be found anywhere, and shaded regions like forests, which constitute a strong barrier for trivial movements of *P. rapae*, do not disturb movements of *P. melete*. Consequently, *P. melete* would gradually disperse from emergence sites.

The habitats of *P. napi* were permanent, but the niche breadth was narrow due to its restriction to use narrow ranges of host species, so the habitat would be more localized than that of *P. melete*. Consequently, *P. napi* would be relatively sedentary.

Utilization of the habitats by adults of *P. rapae* and *P. melete* is schematically shown in Fig. 18.

DINGLE and ARORA (1973) compared three species of African cottonstainer bugs by a tethered flight technique, and pointed out that the higher the flight ability was,

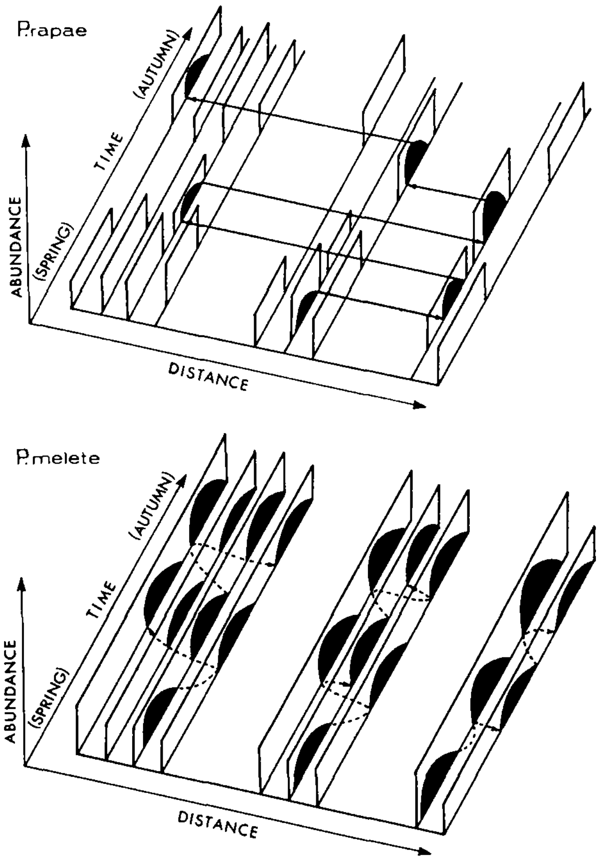

Fig. 18. Schematic representation of the utilization of habitats by the adults of *P. rapae* and *P. melete*. Squares indicates the habitats (subsites). Solid parts indicate the periods of larval development in successive generations. Arrows indicate migratory movements (solid line) and non-migratory movements (dotted line) of adult females.

the higher the reproductive potential was also.

Pieris could be described in terms of r-K strategy (MACARTHUR and WILSON, 1967 ; GADGIL and BOSSERT, 1970). SOUTHWOOD *et al.* (1975) suggested that r-K selection spectra could be found in all taxa, for example, birds and Lepidoptera, associated with stability of habitat, number of generations, fecundity and so forth.

The estimated number of generations of *P. rapae*, six generations, was twice as many as those of the other two species. But there were few differences in the developmental period from egg to adult under a constant temperature among the three species (OHSAKI, unpublished data): *P. rapae* preferred the oviposition plants growing in sunny situations, while *P. melete* and *P. napi* preferred those in shaded situation (OHSAKI, 1979), so warmer air temperature in the habitat of larvae of *P. rapae* brings about rapid development of larvae. Furthermore, almost all of eggs are laid for a few days after the pre-ovipositional period. These habits of *P. rapae* may heighten the intrinsic rate of increase under natural conditions.

P. melete is probably more of a K-strategist than *P. rapae*, because this species continued to lay some constant numbers of eggs every day, and eggs of *P. melete* were scarcely laid on those plants in autumn when there were few available oviposition plants. Actually, seasonal fluctuation in the number of captured adults of *P. melete* was more damped than in *P. rapae.*

P. napi may be more similar to *P. melete* than *P. rapae.*

The larvae of *P. rapae* are attacked heavily by a parasitoid, *Apanteles glomeratus*. *P. rapae* may escape to some degree from attack by this parasitoid as a result of migration of pre-reproductive females.

Interestingly, *P. melete* was not attacked by *A. glomeratus*. SATO (1976) indicated that the eggs of *A. glomeratus* deposited in *P. melete* were killed by the physiological defence reaction of the host, i. e., encapsulation by host hemocytes. It is interesting to consider this fact in connection with the resident habit of *P. melete*. PIANKA (1970) pointed out that K-strategist live in stable habitats, but on the other hand, they have been surrounded by many natural enemies and competitors, and they have survived within such environments. *P. melete* lays eggs over the whole area of relatively permanent habitats, and its mode of oviposition may lessen the fatal destruction of larval populations by local mortality factors like predations, and may avoid the danger of starvation caused by overcrowding. Though SATO (1976) pointed out that *P. napi* could be attacked by *A. glomeratus* under laboratory conditions, the details of parasitization under the natural conditions are not known.

SUMMARY

Utilization of patchy habitats by adult populations of three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi* was studied throughout the flight season in an area of their coexistence, about 3×1.5 km, in a farm village in the mountains in Inabu,

Aichi Prefecture. Field study was by the mark-recapture method. Results were analyzed by dispersal distances and recapture duration decay curves for adults of different age-classes estimated on the basis of physical condition of their wings, together with supplementary information of daliy egg-laying rate of females, obtained in field cages.

Sexually immature, mated femals of *P. rapae* after teneral stage showed a migratory flight. On the other hand, reproductive females and all males of *P. rapae* were strongly resident within suitable habitats, and reproductive females begun to lay eggs abundantly at sunny places of newly suitable areas within a short period. *P. melete* seemed to disperse gradually from emerged stites and females of this species continued to lay some constant numbers of eggs for more than ten days over a wider area. *P. napi* appeared more like *P. melete* than *P. rapae*.

The habitats of the three species can be characterized as follows: *P. rapae*, temporary, continued for pre-reproductive females but localized for reproductive females and all males, and unstable; *P. melete*, permanent, widespread, and stable; *P. napi*, permanent, localized, and stable.

The numbers of generations of *P. rapae*, *P. melete* and *P. napi* were estimated to be about six, three and three, respectively. Seasonal fluctuations in the number of adults were influenced by the stability of their habitats, i. e., the population size fluctuated sharply in *P. rapae*, but it was much more stable in *P. melete* and *P. napi*. In view of these results, it can be said that *P. rapae* fits the general characteristics of a r-strategist, whereas *P. melete* and *P. napi* are more K-strategic than *P. rapae*.

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混生地におけるモンシロチョウ属3種個体群の比較生態学的研究

II. 移動分散からみた成虫の生息場所の利用の仕方

大崎直太

モンシロチョウ属の3種，モンシロチョウ（モンシロ），スジグロシロチョウ（スジグロ），エゾスジグロシロチョウ（エゾ）の成虫期の生息場所の利用の仕方を調べる為に，3種の混生している奥三河の山間部(約3×1.5 km）で調査を行なった。調査は標識再捕法を用い，成虫の羽の痛み具合から推定した成虫のおおまかな日齢別の移動距離と再捕率の経時的変化，及び網室で調べた日当り産卵数の変化を基に結果を比較検討した。

空間的にも時間的にも不連続で不安定な生息場所を利用すると思われるモンシロでは，メスは羽化後に旺盛な移動を行ない，その後定住的となった。産卵は初期に集中的に行なわれることから，交尾後の前繁殖期に移動を行ない，新たな繁殖地に短期間に集中的な産卵を行なうものと考えられた。オスは定住的であった。従って，生息場所の空間的分布は，繁殖メスやオスにとっては不連続に分布しているが，前繁殖期のメスにとっては移動範囲内に連続的に分布していた。空間的にも時間的にも連続的で安定した生息場所を利用するスジグロは，分散的な日常移動を繰り返しながら，メスは毎日均等な数の卵を広い地域に産んでゆき，空間的には不連続だが時間的には連続的で安定した生息地を利用するエゾは，スジグロに近い生活様式を持つと考えられた。

調査地での年間世代数は，モンシロは約6世代，スジグロとエゾは3世代と推定され，季節的な個体数の変動は生息地の安定度を反映して，モンシロでは激しく，スジグロとエゾはより安定していた。モンシロは，いわゆるr戦略の方向に進んだ種であり，スジグロとエゾはよりK戦略的な生活様式を持つことが推定された。