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COMPARATIVE POPULATION STUDIES OF THREE *PIERIS* BUTTERFLIES, *P. RAPAE, P. MELETE* AND *P. NAPI,* LIVING IN THE SAME AREA III. DIFFERENCE IN THE ANNUAL GENERATION NUMBERS IN RELATION TO HABITAT SELECTION BY ADULTS.

Naota Ohsaki

Entomological laboratory, College of agriculture, Kyoto
university, Sakyo, Kyoto 606, Japan

Introduction

In general, animals which utilize temporary habitats may be higher in their ability for increase than those in permanent habitats (MacArthur, 1960; Cody, 1966; Pianka, 1970; Southwood et al., 1974).

As a criterion of ability for increase of animals, the intrinsic rate of natural increase, r_m, is widely used. The r_m is approximately given by $r_c = \ln R_0/T$ (r_c= capacity for increase; R_0=net reproductive rate; T=generation time) (Andrewarth and Birch, 1954; Laughlin, 1965). The value of r_c is more seriously affected by generation time rather than fertility, because fertility affects r_c as natural logarithm, but generation time affects as antilogarithm. There are, however, only a few studies of reproductive strategy which discuss the effect of the generation time on the rate of increase (e.g., Lewontin, 1965; Heron, 1972; Southwood, 1977).

The multivoltine butterflies, *P. rapae, P. melete* and *P. napi* living in Japan are much different in the number of annual generations from each other, though they are closely related species belonging to the genus *Pieris*. Their numbers of annual generations are estimated as 6-7, 2-4 and 2-4, respectively, in areas where they coexist (Fukuda et al., 1972). The stability and continuity of the habitats for the three species are different from one another in the same areas. The habitat of *P. rapae* is temporary, localized and unstable, because it depends mainly on annual cruciferous crops which are periodically planted and harvested. On the other hand, *P. melete* and *P. napi* lay eggs on the perennial native plants in shaded situations, so their habitats are more permanent and stable (Ohsaki, 1979).

What factors are responsible for the difference in the number of annual generations among the three species under natural conditions? In this paper, we analyze the cause of differences in the number of generations in the field. Furthermore, we discuss the significance of the different number of generations in relation to their reproductive strategies and compare the modes of life of the three *Pieris* butterflies.

STUDY AREA AND CENSUS METHOD

The study area was located in a farm village in the mountains, Inabu, Aichi Prefecture. It is situated at lat. 35°N. and long. 137°E., and about 500 m above sea level as described in detail in OHSAKI (1979).

Marking and recapture censuses for adult of three *Pieris* species were carried out on almost every fine day through all flight seasons in 1976 and 1977. Newly emerged adults were estimated on the basis of physical condition of their wings. The details are described in OHSAKI (1979).

Maximum-minimum thermometers were situated in the stocks of larval food plants of three *Pieris* species for recording the air temperature of each larval microhabitat in 1978. The larval food plants chosen were *Raphanus sativus* var. *hortensis* BAKER and *Brassica oleracea* var. *capitata* L. in the cultivated fields for *P. rapae*, *Cardamine appendiculata* FR. et SAR. along a gentle stream in dales for *P. melete*, and *Arabis hirsuta* (L.) SCOP. in the narrow fringe area of the forested lands on the hillsides for *P. napi*. The thermometers were placed only in those stocks of the larval food plants where many eggs and larvae of each species were observed.

Light intensity directly on the egg sites of oviposition plants just after egg-laying was measured by an illuminometer on fine days (120000 *lx*) in 1979.

Forewing lengths of butterflies were measured as an index of their body size in 1978. Additional data on forewing length of *P. rapae* were taken in 1980.

Eggs laid by females captured near Kyoto University were reared individually at constant temperatures of 15°C, 20°C, 25°C and 30°C with 16 hr day length in 200 m*l* plastic cups in 1979. The larvae of *P. rapae*, *P. melete* and *P. napi* were given fresh leaves of *B. oleracea*, *C. appendiculata* and *Arabis flagellosa* MIQ., respectively.

RESULTS

Seasonal fluctuation in the number of adults

Fig. 1 shows the seasonal fluctuation in the number of captured adults of three *Pieris* species. The adults of *P. rapae* began to emerge in mid April, and their number increased gradually towards a peak in June or July, and then decreased gradually. The generations overlapped considerably, and breaks in the flight season are not clear. The number of generations was estimated as about six on the basis of the number of peaks of incidence curves and the number of newly emerged adults (OHSAKI, 1980).

The breaks in flight periods of *P. melete* and *P. napi* were clear, and the estimated number of generations was three for both species. Population sizes of their successive generations were more stable than those of *P. rapae*.

Influence of temperature of development

To compare the developmental duration from egg to adult emergence among the

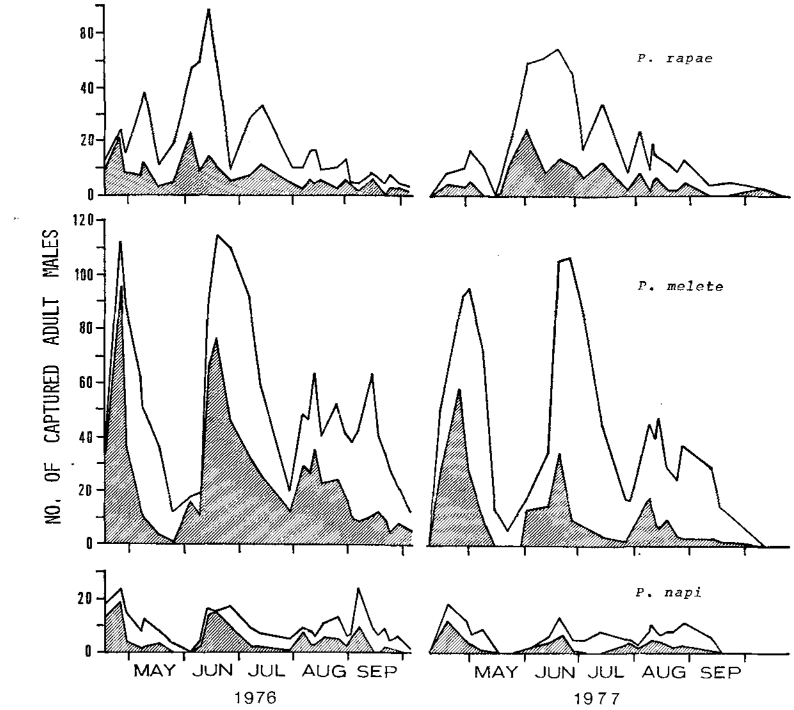

Fig. 1. Seasonal fluctuations in the number of captured adult males of three *Pieris* species. The shadowed portion indicates the number of young adults that were estimated to be within three days after emergence.

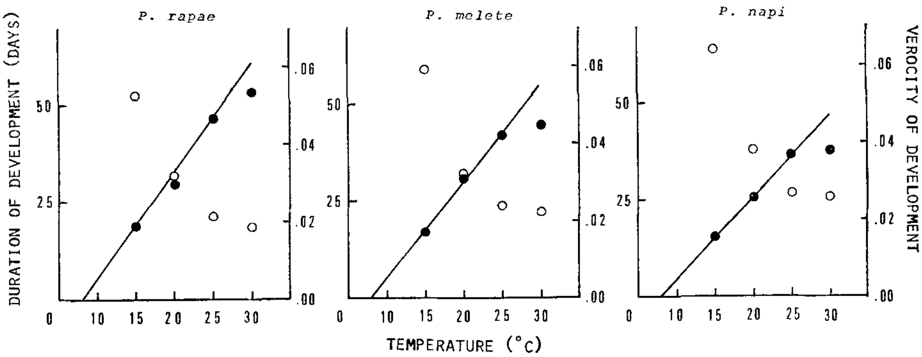

Fig. 2. Relation of temperature (T) to the developmental duration from egg to adult emergence (D, hollow circle) or the velocity of development ($V=1/D$, solid circle). Regression lines are calculated from three levels of temperatures, excluding 30°C.

three *Pieris* species, individuals of the three species were reared singly from eggs under the following conditions: 15°C, 20°C, 25°C and 30°C with 16 hr day length. Fig. 2 shows the relationship between temperature (T) and the duration (D) or velocity ($V=1/D$) of development from egg to adult emergence. High temperature (30°C) seemed to be unfavourable for development of all three species, especially *P.*

melete and *P. napi*. Therefore, the threshold temperature for development (t) and the effective temperature accumulation (K) of each developmental stage were calculated from three levels of temperatures, excluding 30°C. The results are shown in Table 1. The total effective temperature accumulation of females of *P. rapae* was 92.7% of that females of *P. melete* and 80.8% of that of *P. napi*.

These differences in the total effective temperature accumulation, however, do not provide a reasonable interpretation of observed differences in the number of annual generations among three *Pieris* species.

Mean reproductive age of adult females and net reproductive rate

Generation time (T) and net reproductive rate (R_0) are given approximately by

Table 1. The lower threshold temperature (t) and thermal constant (K) for the development of immature stage of three *Pieris* species, based on the linear regression of velocity of development on temperature.

Developmental stage	Regression equation	r	t	K	Heat unit above 8°C
	Female of *P. rapae*				
Egg	$V=0.0190T-0.1389$	0.997	7.3	52.6	49.8
Larva	$V=0.0051T-0.0416$	0.994	8.2	196.1	198.7
Pupa	$V=0.0088T-0.0771$	0.997	8.8	113.6	121.3
Egg to emergence				362.3	369.8
	Male of *P. rapae*				
Egg	$V=0.0190T-0.1389$	0.997	7.3	52.6	49.8
Larva	$V=0.0049T-0.0399$	0.988	8.1	204.1	206.5
Pupa	$V=0.0082T-0.0708$	0.995	8.6	122.0	128.8
Egg to emergence				378.7	385.1
	Female of *P. melete*				
Egg	$V=0.0153T-0.1303$	0.997	8.5	67.4	68.3
Larva	$V=0.0053T-0.0437$	0.998	8.2	188.7	192.6
Pupa	$V=0.0072T-0.0570$	0.993	7.9	138.9	137.9
Egg to emergence				395.0	398.8
	Male of *P. melete*				
Egg	$V=0.0152T-0.1285$	0.997	8.5	65.8	68.4
Larva	$V=0.0050T-0.0379$	0.990	7.6	200.0	193.2
Pupa	$V=0.0075T-0.0631$	0.993	8.4	133.3	138.1
Egg to emergence				399.1	399.7
	Female of *P. napi*				
Egg	$V=0.0153T-0.1299$	0.997	8.5	65.4	68.1
Larva	$V=0.0037T-0.0270$	0.998	7.3	270.3	255.3
Pupa	$V=0.0074T-0.0585$	0.998	7.9	135.1	134.1
Egg to emergence				470.8	457.5
	Male of *P. napi*				
Egg	$V=0.0152T-0.1274$	0.997	8.4	65.8	68.0
Larva	$V=0.0038T-0.0275$	0.998	7.2	263.2	247.4
Pupa	$V=0.0079T-0.0609$	0.995	7.7	126.6	123.6
Egg to emergence				454.5	439.0

the following formulae. $T=\Sigma x l_x m_x/\Sigma l_x m_x$ and $R_0=\Sigma v_x/2=\Sigma l_x m_x/2$. In this paper, l_x means survivorship of adult females. Therefore, the mean reproductive age of adult females from emergence (*Ta*) is given by the former formula. R_0 is the mean number of female eggs produced by one female in her lifetime.

Solid lines in Fig. 3 show the m_x curves of *P. rapae* in laboratory cages (SUZUKI, 1978), and of *P. melete* and *P. napi* in field cages (OHSAKI, 1980). In the field, YAMAMOTO and OHTANI (1979) estimated very similar m_x curves for *P. rapae* and *P. napi*. When R_0 and *Ta* are calculated in the cages, *P. rapae*, *P. melete* and *P. napi* were 378, 174 and 114, respectively. Their *Ta* were 5.4, 7.3 and 7.2 days, respectively (Table 2).

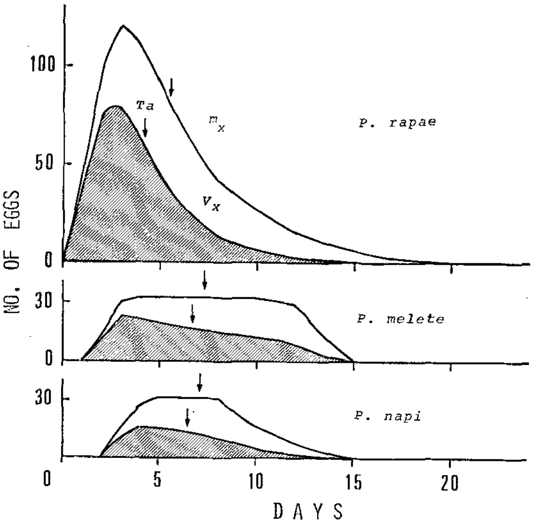

Fig. 3. Continuous m_x and v_x schedules. Arrows indicate the mean reproductive age of females (*Ta*). l_x curves are adopted from those of males of respective species, but for that of *P. napi*, that of *P. melete* is substituted. The details are described in Fig. 4 and the text.

Table 2. Fertility, net reproductive rate (R_0) and mean reproductive age of adult females (*Ta*) in cage and field.

		P. rapae	*P. melete*	*P. napi*
Cage				
	Fertility	757	348	228
	R_0	378	174	114
	Ta	5.4	7.3	7.2
Field				
	Fertility	386	169	114
	R_0	193	85	57
	Ta	4.2	6.6	6.5

R_0 is the mean number of female eggs produced by one female in her life time, because we assume that the females do not die during the period from egg to adult emergence.

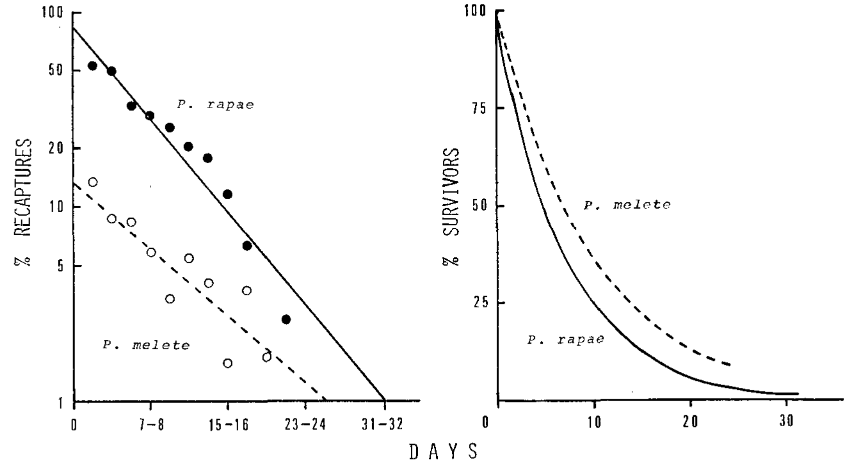

Fig. 4. Regression lines of recapture duration decay plots of males of *P. rapae* and *P. melete* (fresh individuals that were supposed to be less than three days in age at their first captures), and their l_x curves. The details are described in the text.

Figure 4 shows the regression lines of recapture duration decay plots of males of *P. rapae* and *P. melete* of fresh individuals at their first capture, probably within three days after emergence (Ohsaki, 1980). When the values of the y-intercepts of these regression lines are adjusted to 100, these lines can be regarded as changes of residence rates within the census areas. It was impossible to estimate the l_x curve of females of *P. rapae,* because sexually immature, mated females of *P. rapae* after the teneral period showed a migratory flight (Ohsaki, 1980). On the other hand, males of *P. rapae* were strongly resident within suitable native habitats (Ohsaki, 1980), and the l_x curves for both sexes in the cages were very similar to each other (Ohsaki, 1979). In this paper, therefore, we substituted the l_x curve of males for that of females of *P. rapae,* though the migration of pre-reproductive females possibly produces higher mortality for them. The l_x curve is also shown in Fig. 4, from which the mean life span of adults is calculated to be 6.8 days.

In Fig. 4, the changing curves of residence rates of males of *P. melete* are also shown by using the recapture data of newly emerged individuals at first recapture. From this curve, the mean life span of adults is calculated as 9.5 days. This curve was regarded as the l_x curve of females of *P. melete.* But in *P. napi,* the changing curve of residence rates cannot be drawn from its recapture data. For convenience's sake, here, the l_x curve of *P. melete* was substituted for that of *P. napi,* because the mode of life of *P. napi* seems to be very similar to that of *P. melete* in comparison with that of *P. rapae* (Table 3).

Thus, m_x and l_x of three species were calculated and v_x, Ta and R_0 of each species were estimated. V_x curves are shown in Fig. 3. *Ta* and R_0 are given in Table 2.

Ta and R_0 of each generation are undoubtedly affected by the prevailing temperature and other environmental conditions, but in this paper, such an influence of temperature, etc. is ignored. *Ta* of *P. rapae* is 2 days shorter than *Ta* of *P. melete* and *P. napi*. Their total generation times (T) at 18°C for example are 41.2 days (*P. rapae*), 46.7 days (*P. melete*) and 50.3 days (*P. napi*). This means that *P. rapae* reduced its generation time by 4.5% from 92.7% which is the difference in the total effective temperature accumulation to 89.2% of that of *P. melete*. It is due to the early maturation and the decrease of the turnover age of m_x curve of *P. rapae*. This reduction of *Ta*, however, does not also provide a reasonable interpretation of the observed difference in the number of annual generations among three *Pieris* species.

Air temperature in larval habitat

Figure 5 shows the daily mean air temperatures, (max.+min.)/2, of larval habitats through all flight seasons. The curves are approximately fitted to the quadratic equation obtained by a least squares method. When we put t=1st April

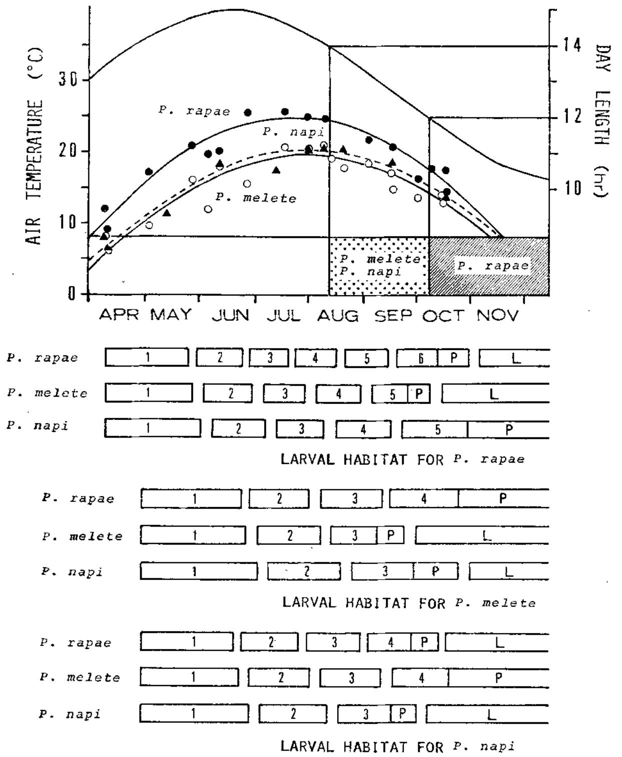

Fig. 5. Daily changes of mean air temperatures of larval habitats and day length through all flight seasons, and the seasonal life cycle illustrated on the basis of air temperature of larval micro-habitats. The threshold temperatures for development of all three species are about at 8°C. The critical day length is adopted from YATA et al. (1979). —●—, mean air temperature of larval habitat of *P. rapae*; —○—, *P. melete*; ---▲---, *P. napi*; ▨, range of critical day length of *P. rapae*; ░, *P. melete* and *P. napi*; P, pupa; L, larva.

and $c=0°C$ as the origin, we get

$c=7.74148+0.29189t-0.0012536t^2$ (for *P. rapae*),

$c=3.03846+0.26593t-0.0010852t^2$ (for *P. melete*),

$c=4.16566+0.25626t-0.0010221t^2$ (for *P. napi*).

Daily mean temperature of *P. rapae* habitat was about 5°C higher than those of *P. melete* and *P. napi* habitats through all flight seasons. Temperature in *P. napi* habitat seems to be slightly higher than that in *P. melete* habitat. The differences among the air temperatures of larval habitats may mainly depend on the differences in light preference of ovipositing female butterflies (Ohsaki, 1979). Figure 6 shows the light conditions preferred for oviposition by *Pieris* butterflies as measured by an illuminometer on fine days (120000 *lx*).

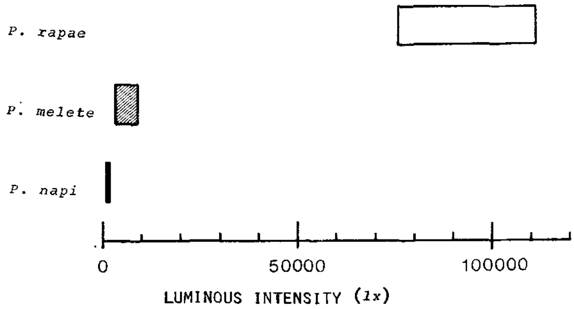

Fig. 6. The light conditions preferred for oviposition by *Pieris* butterflies. Range shows $\bar{x}\pm$S. D. (The direct ray of the sun was 120000 l_x). *P. rapae* (*B. oleracea*); *P. melete* (*C. appendiculata*); *P. napi* (*A. flagellosa*).

Thus, when the larval habitat of *P. rapae* reaches 23.7°C, those of *P. melete* and *P. napi* would be 18.0°C and 19.0°C, respectively. The total generation times of three species are calculated as 27.3, 46.7 and 48.1 days, respectively.

The seasonal life cycle

On the basis of the effective temperature acccumulation (*K*) and the mean reproductive age of adult females (*Ta*), the seasonal life cycle of *P. rapae, P. melete* and *P. napi* living in respective larval habitats can be predicted. All those species hibernate as pupae in diapause. In calculation, butterflies which first appeared in spring were regarded as laying eggs on April 10th in *P. rapae*, and May 1st in *P. melete* and *P. napi*. Results are shown in Fig. 5.

The numbers of generations of *P. rapae, P. melete* and *P. napi*, when all of them are assumed to live in larval habitat for *P. rapae*, are calculated to be 6, 5 and 5 in a year, respectively. On the other hand, generation numbers of these species would be 4, 3 and 3 when living in the habitat for *P. melete* and 4, 4 and 3 when living in the habitat for *P. napi*, respectively.

Actually, the number of generations of *P. rapae* living in its native habitat, six generations, is twice as many as those of the other two species living in their native habitats. These numbers of generations coincide well with the number of generations inferred from the seasonal fluctuations (Fig. 1). Thus, the difference in air temperature between larval habitats for the respective species seems to be the key factor causing a marked difference in the number of generations between *P. rapae* and the other two.

Air temperature in the larval habitat inferred from the forewing length of butterflies

It is well known that body size of multivoltine insects varies seasonally, probably because air temperature, photoperiod, quality of food and other environmental conditions change seasonally in the habitat. Consequently, it may be possible to infer the approximate conditions of larval habitat of a given insect population by measuring the body size of insects captured in the field.

Figure 7 shows the forewing length of male butterflies of every generation measured in the field. The insects having the longest forewings were the first generation ones in June in every species. On the other hand, the individuals having the shortest forewing were belonging to 3rd or 4th generation in August in *P. rapae*, and the overwintering generation in April or May in *P. melete* and *P. napi*. Throughout the season, forewing length was longest in *P. melete*, medium in *P. rapae* and shortest in *P. napi*.

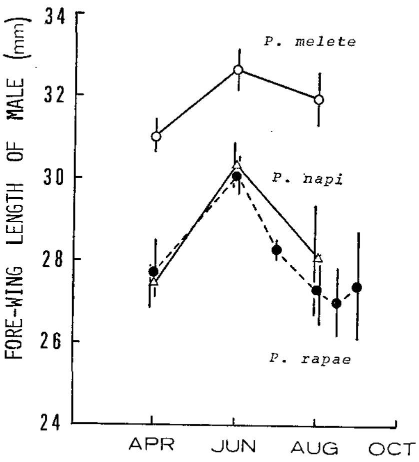

Fig. 7. The forewing lengths of male butterflies of every generation measured in the field. Circles and triangles indicate means, vertical bars 95% C. L. ---●---, *P. rapae*; —○—, *P. melete*; —△—, *P. napi*.

Figure 8 shows the relationship between the temperature and the length of forewing. In all three species, the length of forewing decreased with the rise of the temperature. At any temperature, forewing of *P. melete* was the longest, but, contrary to the result in the field, the wing of *P. napi* was longer than that of *P.*

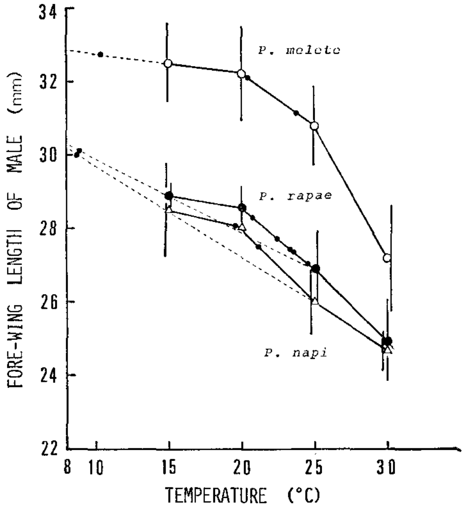

Fig. 8. The relationship between temperature and the length of forewing of male butterflies. La ge circles and triangles indicate means, vertical bars 95% C. L.. Small solid circles indicate the mean forewing lengths of every generation measured in the field. —●—, *P. rapae*; —○—, *P. melete*; —△—, *P. napi*.

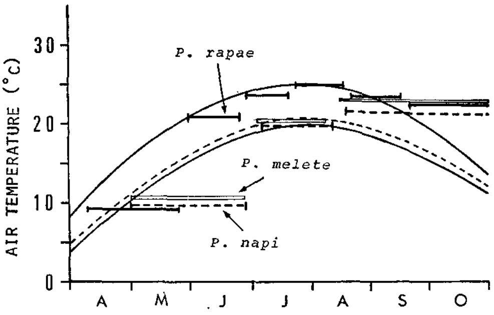

Fig. 9. Changes of air tempereture in larval habitats estimated from the forewing length of male butterflies captured in the field. Length of lateral bars indicates the duration from egg to emergence. The curves show the seasonal changes of daily mean air temperatures in the typical larval habitats shown in Fig. 5. |——|, *P. rapae*; ▭, *P. melete*; |- - -|, *P. napi*.

rapae.

Using the relationship as shown in Fig. 8, the air temperature at which the butterflies might grow in their larval period could be inferred from the size of the field-collected specimens. This is shown in Fig. 9. The curves show the seasonal change of daily mean air temperatures in the typical larval habitats for the three species. The approximate temperatures inferred from forewing length as indicated by bars coincide well in the air temperatures measured by the thermometers except for the overwintering generation. Also, it is obvious that the larvae of *P. rapae* live in the warmer habitat than those of the other two species.

DISCUSSION

In the study area, the number of annual generations is estimated to be about six for *P. rapae*, and three for *P. melete* and *P. napi*, respectively. Such a difference between *P. rapae* and the other two is mainly due to the difference of the air temperature in the larval habitats characteristic of the respective species. That is, *P. rapae* prefers the oviposition plants growing in sunny situations at the open land, while *P. melete* and *P. napi* prefer those in shaded situations in forest edge. Consequently, daily mean temperatures of the larval habitats of *P. rapae* are about 5°C higher than those of *P. melete* and *P. napi* through all flight seasons. Larvae of *P. rapae* develop faster than those of the other two in relation to this difference in temperature.

The numbers of generations of *P. rapae*, *P. melete* and *P. napi* would be 6, 5 and 5, respectively, if they are grown in *P. rapae* habitat, or 4, 3 and 3 if grown in *P. melete* habitat. The difference of the number of generations among species in the same habitat is, of course, due to the difference in the physiologic generation time, which is a total of the developmental duration from egg to adult emergence on native larval food plants in the field and the mean reproductive age of adult females estimated from v_x. The physiologic generation time of *P. rapae* is shorter than those of *P. melete* and *P. napi*, but the difference is only one generation a year when they are grown under identical habitat conditions as mentioned above. The difference in preference for light conditions in ovipositing females brings about a greater difference of the numbers of generations among them. The warmer microclimate in the larval habitat characteristic of *P. rapae* results in 6 annual generations in this species, which is twice as many as those of *P. melete* and *P. napi* grown in their native larval habitats.

Thus, the difference of the numbers of generations among three *Pieris* species is mainly due to the differences of air temperature in the micro-habitats preferred by female adults.

The differences of the air temperature of larval micro-habitats among three *Pieris* species are also likely to be reflected in differences of the photoperiodic responses inducing their pupal diapause. The seasonal change of day length, including 30 minutes of twilight in Nagoya (35°N, same latitude as study area) is shown in Fig. 5. According to YATA et al. (1979), the critical day length of *P. rapae* ranges from 10 hr to 12 hr, whilst those of *P. melete* and *P. napi* range from 12 hr to 14 hr (individuals in North Kyūshū, 33°N). The threshold temperature for development is about 8°C in all of the three species (Table 1). When the season enters the critical day length for inducing diapause, the air temperature in their larval micro-habitats was similarly about 18°C, though the actual dates are very different between *P. rapae* and the other two species. Then the growing period for *P. rapae* lengthened about 2 months more than those for *P. melete* and *P. napi*. Consequently, if the critical day length of *P. rapae* was as long as those for *P. melete* and *P. napi*, *P. rapae* will enter diapause in pupa of 5th generation leaving out one generation whose larvae would be able to pupate successfully. Conversely, if the critical day lengths of *P. melete* and *P. napi* are as short as that of *P. rapae*, almost all larvae of *P. melete* and *P. napi* would enter the 4th generation, which would perish due to cold before pupating.

That is, the difference in photoperiodic reaction among three *Pieris* species may be regarded as representing their adaptations to the air temperature of larval microhabitats. However, high temperature seems to be more unfavorable for *P. melete* and *P. napi* than *P. rapae*, and so *P. melete* and *P. napi* may not widen their distributions toward the south in comparison with *P. rapae*.

Figure 10 is constructed by using the formula $r_c = \ln R_0 / T$ to show the relationship between the mean generation time of female (T) and net reproductive rate (R_0) in terms of the possible gain in the capacity for increase (r_c). In this paper, we assume that the females do not die during the period from egg to adult emergence, so R_0 means the half of the average fertility per one female.

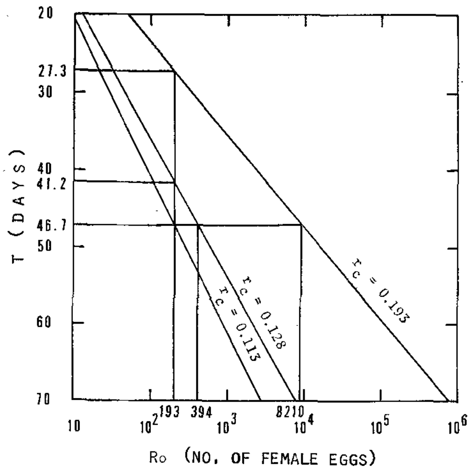

Fig. 10. The relationship between the mean generation time of female (T) and net reproductive rate (R_0) in terms of the possible gain in capacity for increase (r_c), when the air temperature in larval habitat of *P. melete* is 18°C and the corresponding temperature in *P. rapae* habitat is 23.7°C. Under this condition, T of *P. rapae* and *P. melete* are 27.3 and 46.7 days, respectively. If *P. rapae* lays eggs in the larval habitat of *P. melete*, T of *P. rapae* is 41.2 days. Mean number of female eggs produced by one *P. rapae* female in her life time is 193. For details, see the text.

Now we consider the effect of shortening the total generation time. For example, when the air temperature in larval habitat of *P. melete* is 18°C, the corresponding temperature in *P. rapae* habitat will be 23.7°C. Then, R_0 of *P. rapae* is calculated as 193, or the total number of eggs per female is 386. If *P. rapae* lays eggs in the larval habitat of *P. melete* and its mean generation time is equal to that of *P. melete* (i. e. $T=46.7$ days), r_c would be 0.113. But in reality, T of *P. rapae* is slightly shorter than that of *P. melete*, i. e., 41.2 days under the above-mentioned condition, and hence r_c will be 0.128. To increase r_c from 0.113 to 0.128 without any change in T, the number of eggs per *P. rapae* female should increase from 386 to 788 ($R_0=394$). Actually, *P. rapae* lays eggs on cruciferous plants in sunny situations, the mean generation time is further reduced to 27.3 days, and r_c becomes 0.193. If *P. rapae* has the same generation time as *P. melete*, it is necessary to increase the number of eggs laid by a female from 386 to 16420 ($R_0=8210$) to attain the increment of r_c from 0.113 to 0.193. Such a 42.54 times increase of the number of eggs is evidently impossible. *P. rapae* attains the corresponding increase of r_c by reducing the generation time up to 41.5%, of which 11.8% is due to developmental physiology (shortened 7.3% by the acceleration of development from egg to adult emergence and 4.5% by the mean reproductive age of adult female due to early maturation and the decrease of the turnover age of m_x curve) and the remaining 29.7% is due to selection of sunny oviposition sites.

This reduction of the generation time of *P. rapae* increases the finite rate of increase about 8.7×10^7 and 2.7×10^8 times as high as those of *P. melete* and *P. napi*, respectively in a year. Under this condition, r_c of *P. melete* and *P. napi* are calculated as 0.095 and 0.084, respectively.

Table 3 shows the comparison of life modes of three *Pieris* species. It exhibits a striking contrast in the differences between those of *P. rapae* and those of the other two species. These differences are very similar to the correlates of r- and K-selection dichotomy shown by PIANKA (1970) and SOUTHWOOD (1977). That is, *P. rapae* seems to be r-selected and *P. melete* and *P. napi* seem to be more K-selected.

In 1976 and 1977, STEARNS posed some questions about r- and K-selection. The main points of his discussion are as follows: 1) r and K cannot be reduced to units of common currency, because r is a population parameter, whilst K which is an artifact of logistic thinking is not a population parameter, but a composite of a population, its resources, and their interaction; 2) The stochastic models predict the association of the same traits for different reasons. In considering the case where environment fluctuates and population is near equilibrium, MURPHY (1968) showed the traits similar to those of K-selection by fluctuation of adult mortality, whilst SCHAFFER (1974) predicted the traits similar to those of r-selection by fluctuation of juvenile mortality.

The first is certainly true if one uses the same narrow idea of K-selection as introduced by MACARTHUR (1962). The second case may apply in natural populations. For example, WAY et al. (1980) discuss that the Sphaeriid clam, *Musculium partumeium*, is probably an example of this case. However, when we consider the pattern of variation in space and time of relevant environmental variables, and the

Table 3. The comparison of life modes of three *Pieris* species.

	P. rapae	*P. melete*	*P. napi*
Food plants[a]	temporary, mainly cultivated crops	perennial	perennial
Pattern of habitat distribution[a]	temporary, localized	permanent, continuous	permanent, medium
Satbility of roosting-site for bad weather[a]	heavily disturbed (grasses in open land)	scarcely disturbed (shrubs under tall trees)	scarcely disturbed (shrubs under tall trees)
Parasitization by *Apanteles glomeratus*[b]	heavy	little (killed by encapsulation of host hemocytes)	?
Distribution of virgin females (Places of adult emergence)[c]	localized	widespread	widespread
Movement pattern of males[c]	strongly resident (accumulating in the emergence places)	gradually dispersed (searching for widespread virgin females)	gradually dispersed (searching for widespread virgin females)
Movement pattern of females[c]	resident after migration at pre-reproductive stage (colonizing new suitable habitats from old temporary habitats and escaping from parasitoids)	gradually dispersed (escaping from overcrowding and finding new habitats)	gradually dispersed (escaping from overcrowding and finding new habitats)
Oviposition pattern[c]	localized	widespread	widespread
Fertility	757 in cage 386 in field	348 in cage 169 in field	228 in cage 115 in field*
Egg size[d]	0.4×0.8 mm	0.5×1.2 mm	0.5×1.0 mm
(Egg volume)	0.075 mm^3	0.177 mm^3	0.147 mm^3
The total effective temperature accumulation (above 8°C) of females from egg to adult emergence	370 day degrees	399 day degrees	458 day degrees
Mean life span of adults (males)	6.8 days	9.5 days	?
Mean reproductive age of adult females	4.2 days	6.6 days	6.5 days*
Air temperature in larval micro-habitat (An example)	higher (23.7°C)	lower (18.0°C)	lower (19.0°C)
Number of annual generations	6	3	3
Finite rate of natural increase in a year	5.2×10^{13}	6.0×10^{5}	1.9×10^{5}*
Seasonal fluctuation pattern in the number of adults	variable	stable	stable

[a] from Ohsaki (1979); [b] from Sato (1976); [c] from Ohsaki (1980);
[d] from Shirōzu and Hara (1960); * assuming that l_x of *P. napi* is equal to l_x of *P. melete*.

remarkable life-history characteristics of *Pieris* butterflies, *r*- and *K*-selection in a broader sense as shown by PIANKA and SOUTHWOOD distinguishes conveniently the life modes of *Pieris* butterflies.

It seems intuitively obvious, as the energy expended on each individual egg increases, the survivorship of the individual egg increases. If the species living in the unpredictable habitat lays eggs which are large in size but few in numbers, the increase of the survivorship of individual eggs by their large size will not able to cope with the decrease of the survivorship by adverse conditions of the habitat, and the population will easily become extinct. But, when it lays eggs which are small in size but many in numbers, the number of survivors will increase, though the survival rate will decrease. On the other hand, when the species lives in the predictable habitat, it is very suitable that its eggs are large in size but few in number, because large size may increase the survivorship of individual eggs, but enormous fertility would cause the exhaustion of the food supply.

The habitat of *P. rapae* is temporary, localized and unstable, whilst those of *P. melete* and *P. napi* are permanent, continuous and stable (OHSAKI, 1979; 1980). So, *P. rapae* will live in the unpredictable habitat, and *P. melete* and *P. napi* will live in the relatively predictable habitats. Then, *P. rapae* may need the high reproductive potentiality. Its egg size is only half of those of *P. melete* and *P. napi* (Table 3). The pre-reproductive females migrate (OHSAKI, 1980) and a few females must build up the population in new colonies. At that time, the increase in fertility is very advantageous. Indeed the fecundity of *P. rapae* is higher than those of *P. melete* and *P. napi*, though the fecundity will have a physiologic limit. The reduction of the generation time of 41.5% including the reduction of that by habitat selection behaviour is equivalent to increase of fertility of 4254%. Therefore, *P. rapae* may highten its reproductive potentiality by reducing its generation time via both physiologic and behavioural means. Consequently, outbreaks may occur in suitable environments, and common ruin may occur by overcrowding. But it is more important for the species living in the unpredictable habitat to pass the worst conditions and to colonize new habitats via dispersing females. Thus, the population size fluctuated sharply in *P. rapae* (Fig. 1). *P. melete* and *P. napi*, on the other hand, live in the predictable habitat, in which eggs of large size are suitable even though the numbers are few. *P. melete* and *P. napi* may maintain their population levels stably by the reduction of mortality. Indeed, their population size was much more stable than that of *P. rapae* (Fig. 1).

SUMMARY

Three *Pieris* butterflies, *P. rapae*, *P. melete* and *P. napi*, are very different in the number of annual generations from each other even in the same area. The causes of such differences were investigated through field work in an area of their coexistence, and experiments in the laboratory.

The numbers of annual generations of *P. rapae, P. melete* and *P. napi* were estimated to be about 6, 3 and 3, respectively, in the study area. From the laboratory experiments, the threshold temperature for development of all three species were estimated at about 8°C. The total effective temperature accumulations of females were calculated as 370, 399 and 458 day degrees. The mean reproductive ages of adult females were 4.2, 6.2 and 6.3 days, respectively. Consequently, total generation times at 18°C for example were calculated as 41.2, 46.7 and 50.3 days, respectively.

The seasonal changes of daily mean air temperatures of larval habitats through all flight seasons were approximated from quadratic equations. For example, when the air temperature of the larval habitat of *P. rapae* is 23.7°C, those of *P. melete* and *P. napi* are 18.0°C and 19.0°C, respectively. So the total generation time of the three species are calculated as 27.3, 46.7 and 48.1 days, and the numbers of generations in a year were calculated to be 6, 3 and 3, respectively. This result agrees with the estimated numbers of generations in the field. That is, under the above conditions, *P. rapae* increases the generation number twice as much as *P. melete* by reducing the generation time by 41.5% (physiologically 11.8% and behaviourally 29.7%). Consequently, the differences of the generation numbers among the three species were mainly due to the differences in the air temperature of the larval micro-habitats, which were supported by the forewing length of butterflies of each generation and the differences in their photoperiodic responses for inducing pupal diapause. The difference in the air temperature of larval habitats may mainly depend on the differences of light preference in ovipositing females, i.e., *P. rapae* prefers sunny situations, whilst *P. melete* and *P. napi* prefer shaded situations.

The reduction of the generation time of 41.5% is equivalent to an increase of r_c from 0.113 to 0.193. If *P. rapae* increases the r_c with the same generation time as *P. melete, P. rapae* must increase the number of eggs 42.54 times, from 386 to 16420 eggs, when the numbers of eggs of *P. melete* and *P. napi* are 169 and 115. So, the finite rate of increase of *P. rapae* was higher by about 8.7×10^7 and 2.7×10^8 times as much as those of *P. melete* and *P. napi,* respectively, in a year. Thus, *P. rapae* may highten its reproductive potentiality due to the reduction of the generation time by both physiologic and behavioural means.

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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

III. 成虫による生息場所選択に関連した年間世代数の違い

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），の年間世代数は混生地においても著しく異なる。その原因を3種の混生地での野外調査と，室内実験から明らかにし，その適応的意義と3種の繁殖戦略を比較考察した。

調査地において，モンシロ，スジグロ，エゾは各々6，3，3世代と推定された。飼育実験の結果，発育零点はともに約8°C，雌の有効積算温度は，370，399，458日度，雌成虫の平均繁殖時間は4.2，6.2，6.3日と推定された。したがって，例えば18°C の温度条件下での各種の平均世代時間は，41.2，46.7，50.3日と計算される。

3種の幼虫の生息場所の平均気温の季節的変化は2次式で近似され，例えばモンシロの生息場所が23.7°C の時に，スジグロ，エゾの生息場所は18°C，19°C，3種の平均世代時間は27.3，46.7，48.1日となり，年間世代数は6，3，3と計算される。これは野外の推測世代数に一致する。幼虫の生息場所の温度の違いは，産卵の際に，モンシロは日向を，スジグロとエゾは日陰の産卵植物を選択するという産卵行動の違いに負っている。

つまり，上記の温度条件下で，モンシロはスジグロに比べ平均世代時間を生理的に11.8%（幼虫の発育期間で7.3%，平均繁殖時間で4.5%），行動的に29.7%，計41.5%短縮することにより，倍の年間世代数を獲得している。

3種の世代時間の違いが，主に幼虫生息場所の温度差に負うことは，3種の成虫の前翅長の季節的変化と，休眠誘起の光周反応の違いからも支持される。

モンシロの期間自然増加率はスジグロやエゾと比べて年間1億〜3億倍高かった。つまり，モンシロはスジグロに比べて世代時間を41.5%短縮して日当り r_c を0.113から0.193に上げている。これをスジグロと同じ世代時間のままで上げるとすると，産卵数を386から16420と42.54倍上げねばならない。

このように，モンシロは生理的にも行動的にも世代時間を短縮し，他の2種に比べて潜在的増加能力を高めている。