Comparison of Population Dynamics of Two Pierid Butterflies, *Pieris rapae crucivora* and *P. napi nesis*, Living in the Same Area and Feeding on the Same Plant in Sapporo, Northern Japan[1)]

By

Michiya Yamamoto

Zoological Institute, Hokkaido University

(With 25 Text-figures and 24 Tables)

The aim of the present study is to compare the population trends of two closely related pierid butterflies, *Pieris rapae crucivora* Boisduval and *P. napi nesis* Fruhstorfer, living in the same area and feeding on the same plant. *P. rapae crucivora* is a well known pest of cultivated crucifers and one of the most predominant butterflies throughout the lowlands of Japan. *P. napi nesis* feeds almost exclusively on wild crucifers and abundant only in the northern Japan. On the studied area, however, the larvae of both species mainly feed on the exotic weed, *Rorippa sylvestris* (L.) Besser. Under this rather exceptional situation, *P. rapae crucivora* is more abundant than *P. napi nesis*. The elucidation of how the relative abundance of these co-habitants is maintained is the main purpose of this study. Many previous studies on population ecology of insects have dealt with a single pest species. The comparison of two species, one being a pest and the other not, living in the same area involves some interesting aspects so far relatively ignored, e.g. relative abundance and qualification for pest. Main efforts of the study were concentrated to estimate the number of eggs laid per female and to construct the life tables of two species. The former involves also the information on the activity range of adults and the latter the results of key factor analysis.

Materials and methods

1. *Distribution of the three pierid butterflies*: In Japan there occur three common *Pieris* species, being closely related each other and all with the Northern

1) This paper constitutes a part of the doctoral thesis presented to the Faculty of Science, Hokkaido University.

Palaearctic elements, *P. rapae*, *P. napi* and *P. melete*.[1] *P. rapae* is a Holarctic species of the Eurasian origin and lately has invaded by accidents Australia and New Zealand. The populations of East Asia including Japan are regarded as ssp. *crucivora* Boisduval. *P. napi* is a Northern Palaearctic species with its southern limit of distribution in Japan. The populations of Honshu and Hokkaido are respectively classified in ssp. *japonica* Shirôzu and *nesis* Fruhstorfer. The world distribution of two species mentioned above is shown in Fig. 1. The third species, *P. melete* Mènétriès is the southernmost representative, showing a Japan-China-Himalayan distribution. These three species exhibit a complete sexual isolation for one another (Suzuki *et al.* 1977) and the larvae are segregated by the difference of food plants (Hiura 1973, Ohsaki 1978), though the adults are found

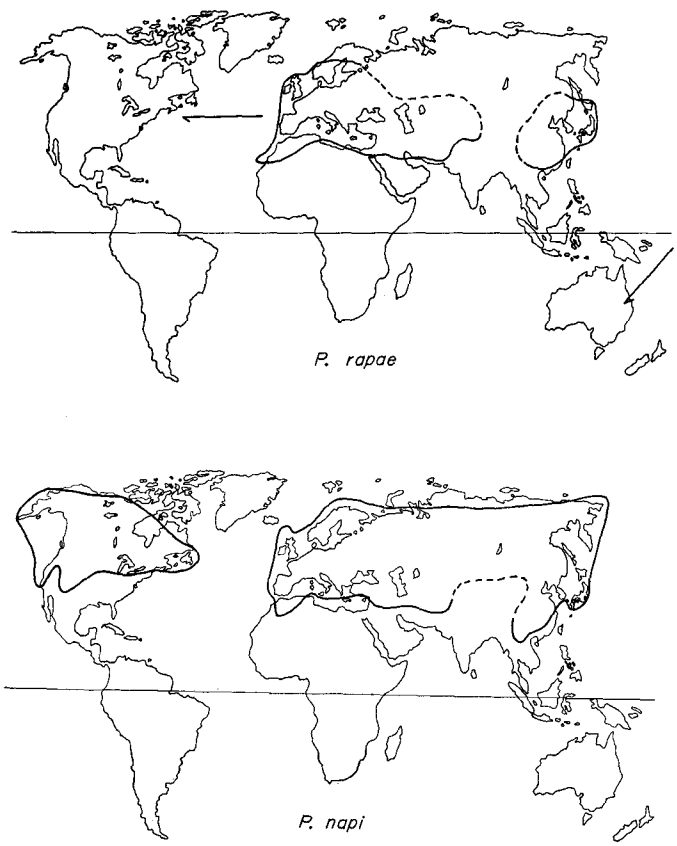

Fig. 1. World distribution of *P. rapae* and *P. napi* (cf. Hiura 1979).

1) Recently the genus *Artogeia* has been adopted for these species by some authors (e.g. *Artogeia rapae*, *A. napi* and *A. melete*).

Table 1. Rank order of five top butterfly species at four localities in Japan. Jûgoshima (JM), western Hokkaido (Yamamoto 1977); Utsunomiya, eastern Honshu (Gôda 1969); Kyoto, western Honshû (Morisita 1967); Hirao, southern Japan (Kawabata 1976). Gradient: Relative dominance according to latitudinal change.

	JM	Utsunomiya	Kyoto	Hirao	Graident
Colias erate	1	4	15	11	N>S
Pieris rapae	2	1	2	1	N=S
P. napi	3	46	-	-	N≫S
Lycaena phlaeas	4	7	12	21	N>S
Everes argiades	5	5	4	7	N=S
Ypthima argus	8	2	1	2	N<S
Eurema hecabe	-	3	3	8	N<S
Neope goschkevitschii	17	28	5	9	?
Zizeeria maha	-	11	7	3	N<S
Papilio xuthus	-	19	21	4	?
Parnara guttata	-	12	6	5	N<S

Table 2. Predominant butterfly species in and near Sapporo expressed by Ps (species prosperity index, Morisita 1967) and N (total number of indivudals observed in 1973), Jo (Jozankei), JM (Jûgoshima) and UC (the campus of Hokkaido University). H: Habitat type preferred (O=open-land, W=woodland, Ow, Ow, oW=intermeidates).

Jo (28.6=mean frequency)				JM (46.1)				UC (91.0)			
Species	Ps	(N)	H	Species	Ps	(N)	H	Species	Ps	(N)	H
Pieris napi	1.046	(479.0)	OW	*Colias erate*	1.762	(665.5)	O	*Pieris rapae*	3.132	(1,229.5)	O
P. rapae	0.674	(301.5)	O	*Pieris rapae*	1.621	(503.0)	O	*Colias erate*	2.180	(778.5)	O
Colias erate	0.375	(161.0)	O	*P. napi*	1.051	(384.0)	OW	*Pieris napi*	0.550	(231.5)	OW
Araschnia burejana	0.104	(60.5)	W	*Lycaena phlaeas*	0.255	(112.5)	O	*Lycaena phlaeas*	0.239	(132.5)	O
Brenthis ino	0.087	(58.5)	W	*Everes argiades*	0.202	(193.0)	OW	*Everes argiades*	0.142	(112.0)	OW
Lycaena phlaeas	0.079	(55.0)	O	*Ochlodes venata*	0.095	(89.0)	Ow	*Ochlodes venata*	0.066	(94.0)	OW
Papilio machaon	0.070	(54.5)	Ow								
Aglais urticae	0.076	(53.5)	W								
Everes argiades	0.040	(38.0)	OW								
Inachis io	0.081	(34.5)	oW								
Thoressa varia	0.026	(34.5)	W								
Argyronome ruslana	0.050	(29.5)	Ow								
Ochlodes venata	0.035	(27.5)	Ow								
Total		1,387.5				1,947.0				2,578.0	
%		79.5				84.5				96.5	

interminglingly on flight. *P. rapae crucivora* is abundant throughout Japan and recently introduced in Okinawa (Osada and Ito 1974). This species occupies the top or second rank in many local butterfly assemblages (Table 1). *P. napi* and *P. melete* behave oppositely in the latitudinal relative abundance, the former more abundant in the northern areas and the latter in the southern areas. In the areas in and near Sapporo the two pierid butterflies *P. rapae crucivora* and *P. napi nesis*, are predominant species together with *Colias erate* Esper (Table 2), both being triboltine with a similar phenology. Adults of *P. rapae crucivora* prefer openlands and insolated areas. *P. napi nesis* is eurytopic but prefers rather shaded areas, though more abundant in woodlands (Yamamoto 1977). The two forms are henceforth abbreviated as *Prc* and *Pnn*.

2. *Census procedures*: Census methods adopted are tabulated below, together with the years in which the respective survey was carried out:

Survey for:	Method	Year
Adult number	Belt transect census	1972, '73 '74
	Collecting for 0.5 hours	1977, '78
	Capture-recapture method	1974
Number of eggs laid by a single female	Adult chase	1975, '76
Census of immature stage	Quadrat method	1974
Number of pupa and adult emergence	Counting along the walls of buildings	1974 '79

Further details about the procedures are explained in the sections concerned.

3. *Area studied*: The campus of Hokkaido University (UC) used for the studies (Fig. 2) consists of three different habitats for the two species.

Crop field of wheat, potato, beet, corn and bean.....Areas along B~D and a part of areas along A~B in the map.

Abandoned areas with weeds.....Areas along A~B and E~F.

Patches of wood, the undergrowth of which sparsely involves *Cardamine leucantha* O.E. Schulz, an original larval food plant of *Pnn*.....Areas along D~E.

Census belt for adults was about 4.6 km running from A through B, C and D to F (Fig. 2, arrow). In total 34 quadrats were set on the area to study the floral composition (Fig. 2, open circles). About 15 of these quadrats (Fig. 2, double circles) in A~C were also used to construct the life tables of immature stage. Several stations for caputre-recapture method were set in A to C. Marked butterflies were released at a single spot (Fig. 2, cross) in the evening. Adult chase was carried out throughout the area of UC to clarify the number of eggs laid by a single female and activity range of adult butterflies.

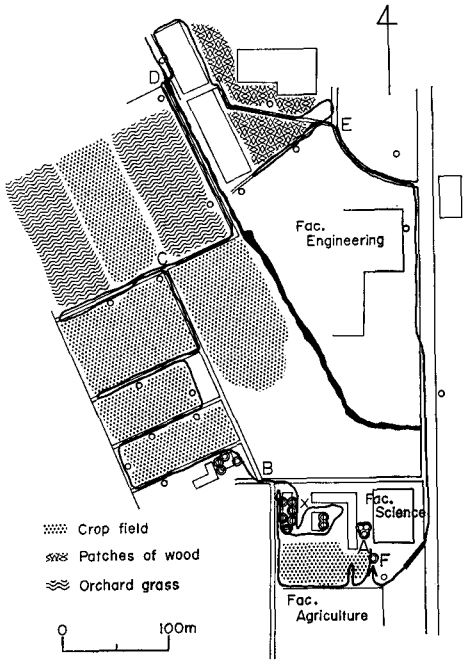

Fig. 2. Map of the campus of Hokkaido University. Open circles: Quadrats used for study of floral composition. Double circles: Quadrats used for the studies of both floral composition and immature life tables. Cross: Releasing point for capture-recapture method.

4. *Larval food plants*: As given introductively, *Prc* mainly feeds on cultivated crucifers, while *Pnn* on wild crucifers. But in western Hokkaido the clear-cut segregation of food plants between two species is obscure due to the existence of a common food plant, *Rorippa sylvestris*. In and near Sapporo, the main food plants of *Prc* are *Brassica oleracea* var. *capitat*, *Raphanus sativus* and *Rorippa sylvestris*, and of *Pnn Cardamine leucantha* and *Rorippa sylvestris*. Especially in the area surveyed, crop crucifers have not been abundantly cultivated and the wild crucifers mentioned above were scarce except *Rorippa sylvestris*. Consequently both species are now highly dependent upon the exotic mustard, *Rorippa sylvestris*. This weed was first found and recorded by Okuyama (1963) at Ofune in Tokyo. In Hokkaido Sakagami and Fukuda (1973) incidentally reported in their wild bee survey at UC in 1959 the weed as *Rorippa* sp. in the list of plants predominantly visited by bees. Hasegawa (1966) reported the weed as a common larval food plant between the two pierid species. Later it has spread everywhere in and near Sapporo and is extending its range to northern Hokkaido, though less common in Honshu and eastern Hokkaido. Coexistence of the two pierid species found in and near Sapporo had not appeared until this weed species grew abundantly.

Results and discussions

Adult number of a given generation, n, produced in the area is given by the following equation:

$$N_{a(n)} = N_{f(n-1)} N_{e(n)} S_{e(n)} S_{l(n)} S_{p(n)} S_{a(n)}$$

in which N_a=adult number, N_f=female number, N_e=number of eggs laid by a single female within a limited area, S_e=survival rate of egg, S_l=survival rate of larva, S_p=survival rate of pupa, S_a=successful rate of emergence and n=generation number. To clarify factors causing the fluctuation of adult number in UC, exact estimation of all these items is necessary. N_e is obtained by combining egg number per female in her life span with her staying duration (or survival duration) within UC. Obviously the area may receive some immigrating adults while lose some adults by emigration. Immigration is negligible in the present study because of less habitats for two species in the surrounding areas out of UC, whereas emgiration is intense.

The results are divided into four parts, number of adults (for estimation of N_a and N_f), number of eggs per female (for estimation of N_e used in combination with the next item), activity range of adults, and life tables of two species (for estimation of S_e, S_l, S_p and S_e). The related discussions are given in each section.

1. The number of adults

The number of adults was estimated by combining the caputre-recapture method and belt transect census, both bearing some merits and demerits. The capture-recapture method is theoretically most reliable but in practice its efficiency is often low in comparison with the effort expended. On the other hand, the belt transect census is rather easily practicable, but it is not easy to estimate the absolute density from the obtained relative abundance. Further, both methods should be repeated to cover the variation range caused by diurnal, seasonal and annual change of the number (Frazer 1973, Yamamoto 1975). In the present study, these defects were partially, even though not completely, removed by the combined use of two complementary methods.

1.1. *Comparison between belt transect census method and capture-recapture method*: Before dealing with the individual number obtained as relative abundance, the discrepancy between the real and the observed individual number must be discussed based upon the result obtained by the capture-recapture method, which was carried out in parallel with the belt transect method. In adult census made in 1974 any individuals of two species on the wing or at rest within 10 m width of both sides of the census course were registered without collecting. Certain individuals difficult to specify at distance were captured and liberated after identifying species and sex. In the capture-recapture method adults marked with lacquer paint were collected and registered along the census route, together

Table 3. Adult number obtained by capture-recapture method in G_h of *P. rapae crucivora*. Other explanations in text.

Date	n_i	R_i	m_i	m_{hi}			
V 17	31	26	—	$h=1$			
18	47	45	7	7	2		
19	44	42	5	1	4		
·						3	
21	45	40	9	2	1	6	4
22	41	38	6	0	2	0	4
Total	208	191	27	10	7	6	4
				r_i			
VI 12	14	13	—	$h=1$			
13	29	27	3	3	2		
14	27	23	8	0	8		
·						3	
16	23	17	11	0	4	7	
Total	93	80	22	3	12	7	
				r_i			

with unmarked ones. Release was made at Point × (Fig. 2) in the evening in order to secure natural dispersal of marked adults. Though releasing was made from a single point, random mingling of marked individuals with unmarked ones seemed to be assured due to high dispersal ability of these species. The results obtained by capture-recapture method are shown in Tables 3~5 on *Prc* and 6~8 on *Pnn*. Symbols adopted from Iwao (1971) are: n_i=number of individuals sampled at the time i, R_i=number of individuals marked and released at the time i, m_i= number of marked individuals in n_i, m_{hi}=number of individuals recaptured at the time i after last marked at the time h and r_i=total number of individuals recaptured in R_i. The result from adult chase described later (Section **3**) suggests that UC-population is thought to be open, i.e. allowing dilution and disappearance of some adults. The number of individuals in open population can be estimated by Jolly-Seber's method given by the following equation:

$$N_i = \frac{n_i+1}{m_i+1}\left(\frac{R_i+1}{r_i+1}z_i+m_i\right)$$

in which N_i=total number of individuals at the time i, z_i=number of individuals marked before i and thereafter recaptured at the time i. Results of calculation

Table 4. Adult number obtained by capture-recapture method in G_1 of *P. rapae crucivora*.

Date	n_i	R_i	m_i	m_{hi}														
VI 24	15	10	—															
·				$h=1$														
27	26	25	2	2														
·					2													
29	64	60	11	4	7	3												
30	58	57	23	2	3	18	4											
VII 1	62	62	32	1	1	12	18	5										
2	62	61	29			5	5	19	6									
3	61	60	26				3	6	17	7								
4	57	57	31			1	1	3	10	16								
·											8							
12	79	78	6						2	2	2	9						
13	81	72	17							1	1	15	10					
14	74	71	26								1	12	13	11				
15	38	33	14					1				2	1	10				
·															12			
17	44	40	8										2	3	3	13		
18	59	55	12										1	4	1	6	14	
19	82	79	23									3	2	5	2		11	15
20	89	84	23										2	1	1	2	6	11
Total	951	904	283	9	11	36	27	29	29	19	4	32	21	23	7	8	17	11
				r_i														

except the data indicating a lower recaptured number ($m_i \leq 4$) were plotted against the number of adults censused on the same day (Fig. 3). The correlation coefficient value is $0.798 > 0.497$ (=95% fiducial limit) in *Prc* and $0.785 > 0.514$ in *Pnn*. Although a linear relation is allowed in both cases, an exponential expression using log. estimted number seems more suitable ($r=0.810$ in *Prc* and 0.846 in *Pnn*) by underestimation of too many adults over counting ability. Anyhow, the occurrence of significant correlation between observed and estimated number allows to use the former to analyze fluctuation within the same species. But as fluctuation of individual number varies between two species, a proper correction must be made on account of the different coefficient between two regression functions (Fig. 4):

Prc ..... log Y=0.00513 X+1.98
Pnn ..... log Y=0.0112 X+1.58

in which Y=number of individuals estimated by capture-recapture method and X= number of individuals censused. The real abundance of two species reverses at the

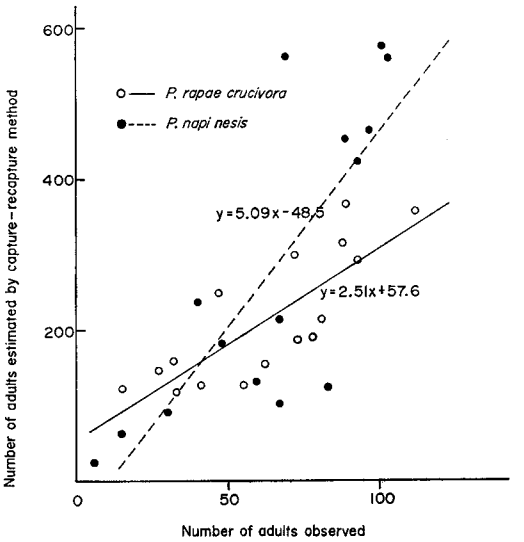

Fig. 3. The relation between the observed and the estimated number of adults.

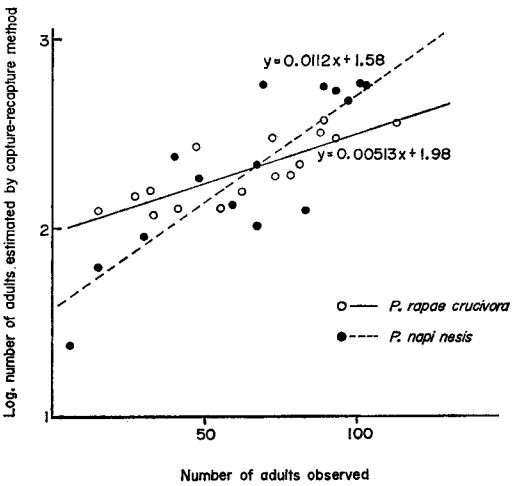

Fig. 4. The relation between the number of adults observed and the logarithmic number of adults estimated based upon capture-recpature method.

Table 5. Adult number obtained by capture-recapture method in G_2 of *P. rapae crucivora*.

Date	n_i	R_i	m_i	m_{hi}															
VIII 5	69	67	—																
·				$h=1$															
9	78	68	13	13	2														
10	67	65	20	4	16	3													
11	63	60	33	5	12	16	4												
12	66	61	26	2	5	5	14												
·								5											
20	53	47	3					3	6										
21	55	53	11						11	7									
22	30	28	14						7	7									
·											8								
27	57	55	8						2	3	3	9							
28	51	49	4							1	2	1							
·													10						
30	37	37	3									2	1	11					
31	43	36	4							1		1	1	1					
·															12				
IX 4	25	22	1												1	13			
5	31	27	6							1						5			
·																	14		
11	13	12	0															15	
12	13	10	2													1		1	16
13	13	11	1													1			
Total	764	708	149	24	33	21	14	3	20	13	5	4	2	1	1	7	0	1	0
				r_i															

point of 70 individuals observed. These different coefficients may be caused by a different ratio of active individuals counted at 10:30–census to total number occurring on the same day.

Duration of stay of particular adult (DSA) within studied area with 95% fiducial limit was obtained from the mean interval between marking and the last

Table 6. Adult number obtained by capture-recapture method in G_h of *P. napi nesis*.

Date	n_i	R_i	m_i	m_{hi}			
V 17	37	31	—	$h=1$			
18	59	58	3	3	2		
19	45	43	1		1		
·						3	
21	23	16	2	1		1	4
23	13	13	1				1
Total	177	161	7	4	1	1	1

r_i

Table 7. Adult number obtained by capture-recapture method in G_1 of *P. napi nesis*.

Date	n_i	R_i	m_i	m_{hi}												
VI 29	11	9	—	$h=1$												
30	20	19	1	1	2											
VII 1	35	35	7		7	3										
2	55	53	10	1	1	8	4									
3	60	59	17		1	3	13	5								
4	58	58	9				2	7								
·									6							
12	93	81	2				1		1	7						
13	102	79	11				1			10	8					
14	87	77	17							7	10	9				
15	62	60	15							2	4	9				
·													10			
17	43	35	18							4	3	4	7	11		
18	37	32	8									3	3	2	12	
19	34	31	12							1	1	1		2	7	13
20	42	33	8								1			1	2	4
Total	739	661	135	2	9	11	17	7	1	24	19	17	10	5	9	4

r_i

Table 8. Adult number obtained by capture-recapture method in G_2 of *P. napi nesis.*

Date	n_i	R_i	m_i	m_{hi}												
VIII 5	14	12	—													
·				$h=1$												
9	50	44	1	1	2											
10	59	56	4		4	3										
11	84	82	11	1	3	7	4									
12	69	66	18		4	4	10									
·								5								
20	116	107	1		1				6							
21	71	65	14					1	13	7						
22	42	37	5						2	3						
·											8					
27	63	57	0									9				
28	52	42	8						3		1	4				
·													10			
30	47	39	8									1	7	11		
31	63	52	8								1	1	2	4		
·															12	
IX 4	14	10	1												1	13
5	25	19	4												2	2
Total	769	688	83	2	12	11	10	1	18	3	2	6	9	4	3	2

r_i

recapture date for each generation, post-hibernating generation (G_h), the 1st generation (G_1) and the 2nd generation (G_2):

	Prc		*Pnn*	
	Total	Female	Total	Female
G_h	1.93±0.29(44*)	3.00±2.43(3)	1.71±1.03(7)	3.00 (2)
G_1	3.36±0.43(177)	2.75±1.60(8)	2.53±0.45(92)	3.92±2.21(14)
G_2	3.57±0.52(192)	2.00 (2)	3.14±1.01(65)	4.00±4.50(4)

*=number of individuals recaptured

These figures are used to avoid double counts of the same individuals on estimating total adults emerged on UC.

Table 9. Diurnal change of the number of adults observed.

	Prc									*Pnn*								
Time	7:30~			10:30~			14:30~			7:30~			10:30~			14:30~		
Date	♂	♀	?	♂	♀	?	♂	♀	?	♂	♀	?	♂	♀	?	♂	♀	?
V 5	3			2	3	3		2	8	4			15	4	1		3	17
9				10	5	3	5	4	1				42	17	4	31	11	3
15	23	18	5				7	6	2	12	12	1				5	6	
19				25	21	5							9	4				
26	23	21	1	41	19	16	30	14	2	3	1	1	5	4		1	1	
VI 3	12	8	5	41	19	15	2	2		2	2	1	4	4	1			0
6	10	6	3	25	15	7	23	7	7			1	2	2		1		
11				18	10	5	20	1	3				1					0
22	3	3		15	6	3						0			0			
26	23	8	5	24	6	7	7	3	4	1		1	1	1	1	1		
VII 1	86	36	10	77	9	10	45	4	3	7	1	1	6	4	1	5	2	
6				147	29	14	124	8	8				23	19		14	11	2
12	230	114	19	193	20	23	174	8	14	34	11	2	22	15		15	4	
16	235	94	34	148	21	23	105	4	13	4	6		4	5		7	2	
21	115	45	12	180	31	18				3	8		9	9				
26				143	14	15	53		1				5	9		4	3	
VIII 6	74	25	6	71	4	4	24	1			3		3	3		1	1	
11				139	39	13	90	9	1				30	14		9	8	
21	15	8		98	22					12	7		18	14				
26	12	1	6	40	8		10		1	6	6		4	4		5	1	
IX 1	1	5	1	34	3					6	4		7	4				
6	6	1		15	6	3	9	2		1	2		4	3		2	4	
13				13	13	1	14	2					7	4		6	3	
21	7	2		22	13	3	20	3	1			1		2		1	1	

1.2.. *Diurnal change of the number of adults observed*: Diurnal change of the number of individuals observed was studied by belt transect census made three times per day (early morning 7:30~, late morning 10:30~, early afternoon 14:30~, each time about 1.5 hrs.) at A~F, UC in the active season of 1973 (Table 9). Both species are very similar in diurnal activity and phenology. In spring (G_h) a high activity is exhibited in late morning to early afternoon, especially early May (*Pnn*) and late May (*Prc*). In both species G_1 in early summer indicates a high activity in the early and late morning. Especially *Prc* females were abundant in the first census. The diurnal activity of G_2 in late summer resembled that of G_h, that is, a high activity was shown in the 2nd and 3rd censuses. This phenological change of the diurnal activity in *Prc* was reported by Hirose (1954), too. To standardize the difference of relative abundance among seasons and between species, census time with most abundant individuals observed should be adopted. In the present case and 2nd (10:30) census is used as representative for the relative abundance.

1.3. *Seasonal change of the number of adults observed*: Fig. 5C shows the number of individuals observed by adult census made from 10:30 everyday in the

flight season of two species, 1974. G_h adults appear from middle April to late June, G_1 from early July to early August and G_2 from early August to early September. Pupae of G_3 hibernate and emerge in the next spring, i.e. $G_h = G_3$. Phenology of

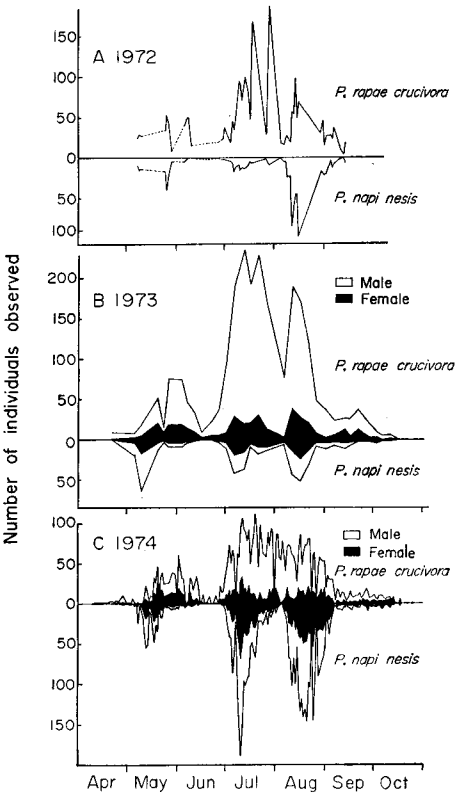

Fig. 5. Seasonal fluctuation of the adult number of species censused in 1972 ~ 1974.

two species is very similar, both characterized by trivoltinism, pupal hibernation and male predominance. Seasonal fluctuation of the adult number mainly depends upon that of males. Cumulative number of adults counted at 10:30-census is shown for each generation as follows:

	Prc		*Pnn*	
	Total	Females	Total	Females
G_h	758 (49 days)	260 (37 d.)	451 (33 d.)	175 (29 d.)
G_1	2,662 (33 d.)	457 (42 d.)	1,738 (39 d.)	663 (36 d.)
G_2	1,718 (43 d.)	366 (40 d.)	2,269 (43 d.)	840 (41 d.)

Considering the different DSA within the census area between species and among generations (p. 213), estimated total number of adults in one generation is given by

accumulation of estimated number during a generation divided by the average DSA of individuals for each generation concerned.

		Total	Females
In *Prc*			
	G_h	2,911 (2,530~3,425)	1,280 (707~6,673)
	G_1	2,539 (2,251~2,912)	1,659 (1,049~3,966)
	G_2	1,844 (1,610~2,159)	?
In *Pnn*			
	G_h	1,042 (650~2,621)	425
	G_1	1,834 (1,557~2,231)	560 (358~1,284)
	G_2	2,030 (1,533~2,988)	661 (309~?)

In G_h and G_1 population a higher abundance of *Prc* than *Pnn* is indicated in both males and females. *Prc* in G_1 was numerically superior to that of *Pnn*, though a higher and acuter increase of the latter species is seen in early July (Fig. 5C). In G_2 *Pnn* showed a higher estimated number than *Prc*, but the relation is obscure in females due to inaccurate estimation of the average DSA. Totally the relation of abundance between these two species and among generations is shown as follows: *Prc*; $G_h > G_1 > G_2$. *Pnn*; $G_2 > G_1 > G_h$. *Prc*$\gg$*Pnn* in spring (G_h), *Prc*>*Pnn* in early summer (G_1) and *Prc*<*Pnn* in late summer (G_2). Whether this relation is annually maintained or not is discussed in the following section.

1.4. *Annual change of the adult number in two species*: Unfortunately the annual fluctuation of adult number was not continuously traced beyond three years. The comparison of Figs. 5 and 6, both given by unconnected number, suggests a gradual drop of the predominance of *Prc* from 1972 to 1974 possibly followed by a stable state until 1979, though seasonal pattern of fluctuation of individual

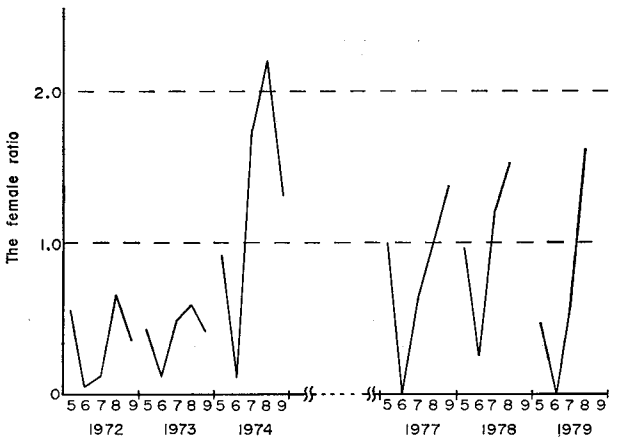

Fig. 6. The annual fluctuation of the female ratio between two species (*Pnn*/*Prc*).

number seemed to change annually. For *Prc* the post-hibernating pupae were collected in April from 1975 to 1979 (for 1974, in the preceeding November) and the emergence of adults was checked (Table 10). The result also seems to suggest a gradual decrease of *Prc* adults, mentioned above.

Table 10. The number of post-hibernating pupae of *P. rapae crucivora* collected in April (in the preceeding November in 1974). The number of emergence given in parentheses.

Section \ Year	1974	'75	'76	'77	'78	'79	Total
Aa	0	3 (3)	3 (3)	1	1 (1)	0	8 (7)
Ab	1	17 (6)	19 (9)	8 (6)	21 (6)	14 (3)	79 (30)
Ac	3 (3)	0	0	4 (3)	2	1	7 (3)
Bd	1	7 (2)	4 (2)	0	0	3	14 (4)
Be	1 (1)	4	1	2	1 (1)	1 (1)	9 (2)
Total	6 (4)	31 (11)	27 (14)	15 (9)	25 (8)	19 (4)	

2. The number of eggs laid per female

It is difficult to estimate the fecundity of insects which, as in many butterflies, lay eggs one by one, not in batch between flights (Kurata 1955, Iwata 1967). Even for such the commonest species as *P. rapae* the estimated number of eggs laid per female differs among authors: 350, Richards 1940; 400, Iwata 1967; 200~300, Itô *et al.* 1975. These authors do not mention how the fecundity was determined. Recently the fecundity of *Prc* higher than so far reported was shown under both laboratory (Suzuki 1978) and natural conditions (Yamamoto and Ohtani 1979). These two results were very similar each other in both the number of eggs laid and the daily laying pattern. The number of eggs laid per female of *Pnn* except G_h was reported by Yamamoto (1978). In the present section the number of eggs laid per G_h-female and the difference among some localities are discussed based upon the dissection of overies.

2.1. *The number of eggs laid by a G_h-female*: A total of 35 *Prc* females and 28 *Pnn* females collected on UC from May to late June, 1978 were dissected. The results obtained are shown in Table 11, together with the results of G_1 and G_2 in the same year for each age class classified by condition of scale detachment. The relative age was distinguished into four classes by decrease of the areas covered with scales on abdominal dorsum (I. zero, the dorsum completely covered with scales, II. more than a half covered, III. less than a half covered, IV. nearly exposed). The number of eggs laid is approximately estimated by the discrepancy of the average oocyte number between newly emerged females and old exhausted ones. The results obtained show a similar number of eggs laid by G_h- and G_1- female in respective species, though the average female size is different among generations. The number of eggs laid per female of UC-population is summarized,

Table 11. Number of oocytes in dissected ovaries with the number of mature eggs in parentheses and S.D. at UC in 1978.

Age class / Date	I	II	III	IV
Prc				
V 1~10	**792(24)**	—	709(89)±114	812(76)± 90
11~20	—	695(123)	701(114)±123	616(133)± 40
21~31	822(46)± 16	900(126)± 53	657(103)± 47	—
VI 1~10	—	674(114)	513(89)	—
11~20	814(70)	—	—	107(27)
21~30	—	—	298(58)	**144(16)**
VI 21~30	**1,064(96)**	938(154)±235	—	—
VII 1~10	847(104)±119	1,122(194)	654(70)	—
11~20	796(12)	850(169)± 78	998(174)	—
21~31	—	615(71)±125	451(81)±125	**158(54)**
VIII 1~10	667(51)± 42	511(51)± 71	456(72)±221	—
11~20	437(53)± 18	560(75)± 96	489(129)	—
21~31				
Pnn				
V 11~20	**523(59)**	477(72)± 53	500(77)± 57	472(69)± 41
21~31	—	449(76)±227	490(86)± 45	380(92)± 84
VI 1~10	—	—	378(78)± 68	**268(28)**
VII 1~10	**480(55)± 88**	525(85)± 59	569(97)± 64	—
11~20	—	369(41)±137	494(54)±116	233(47)±178
21~31	—	386(98)	319(59)± 41	159(29)± 43
VIII 1~10	475(37)± 34	436(73)±139	372(68)	—
11~20	434(66)± 55	353(60)±117	269(37)± 98	449(46)
21~31	—	379(67)± 92	309(53)± 10	—
IX 1~10	—	172(46)	273(37)± 49	**172(28)**

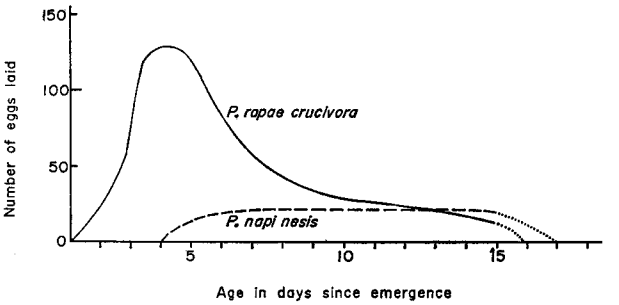

Fig. 7. Presumable laying curves of *P. rapae crucivora* and *P. napi nesis* and age sequence.

together with the result reported previously (Yamamoto and Ohtani *op. cit.*):

	G_h	G_1	G_2
Prc	600~800	600~800	300~700
Pnn	2 0~400	200~400	200~400

Prc has a fecundity about three times as high as *Pnn*. Further the laying curve of *Prc* has a high peak soon after copulation. The difference is expressed as two presumable curve given in Fig. 7 (cited from Yamamoto and Ohtani *op. cit.*).

2.2. *The difference of egg number among localities*: To know the local difference of the number of eggs laid, *Prc* females collected in three districts of southern Japan, Fukuoka City, Yamaguchi City and Osaka City in early spring, 1978, were dissected.

Locality	Fukuoka	Yamaguchi	Osaka
Date	IV 4	IV 5	IV 10
No. females dissected	12	12	8
Age class II		1,128(48*)	
III	884(62)±167**	774(48)± 71	771(95)± 87
IV	371(43)	784(56)±103	678(38)±115

*=number of eggs matured
**=S.D.

Table 12. Number of oocytes in ovaries of *P. napi nesis* collected near Sapporo.

Age class / Date	I	II	III	IV
Jozankei				
V 11~20	634 (90)	—	—	—
21~31	—	534 (56) ± 12	443 (59)	—
VI 1~10	—	—	423 (46) ±144	331 (41) ±126
11~20	546 (66)	390 (62) ± 20	—	276 (76)
21~30	—	—	332 (44)	236 (20)
VII 1~10	—	606 (126)		
11~20	—	401 (73) ±113	455 (89) ±162	—
21~31	474 (106)	368 (71) ± 73	214 (66) ± 95	134 (16) ± 79
VIII 1~10	164 (20)	—	205 (29) ± 52	122 (32) ± 33
11~20	—	309 (37) ± 67	242 (23) ± 96	150 (27) ± 89
21~31	—	426 (34) ± 59	234 (38) ±128	154 (29) ± 63
IX 1~10	—	—	318 (46) ± 82	154 (17) ± 72
11~20	—	—	—	236 (36) ±110
Hakkenzan				
V 11~20	504 (0)	425 (13) ± 67	349 (31) ± 63	—
21~31	—	—	491 (63) ± 10	—
VI 1~10	—	—	472 (58) ± 84	247 (63) ±111
21~30	596 (4)	—	—	340 (40) 68
VII 1~10	510 (38) ±116	533 (80) ±132	564 (44)	336 (64) ±130
11~20	354 (50)	371 (51) ± 12	258 (50)	184 (0)
21~31	—	442 (10)	184 (29) ± 18	174 (23) ±119
VIII 1~10	—	—	146 (10)	—
11~20	—	184 (52)	203 (19) ±106	117 (13) ± 27
21~31	—	—	344 (59) ±102	195 (31) ± 66
IX 1~10	—	—	—	227 (19) ± 10

Although most of these females were assumed to be relatively old, the number of oocytes was of the same order to that found in young UC females. This suggests a higher biotic potential of the females of populations in southern Japan.

In *Pnn* the dissection of ovaries was made with the populations collected at Jozankei (96 females) and Hakkenzan (65) near Sapporo where the larvae feed on *Cardamine leucantha* (Table 12). The decrease of the average oocyte number between newly emerged females and old exhausted ones was similar to the results obtained on UC (Section **2.1.**), but these mountains populations may be bivoltine because newly emerged females were not found in late August when UC-population issues G_2 adult.

The different density of eggs laid in a particular area is caused not only by the different number of eggs laid per female during the life span but also by the different DSA within the area, dispersal ability of females, and number of laying females within the area. This problem is discussed in the next section.

3. Flight activity range of adults

Adult chase or the continuous chase of the particular individual was made in 1975 and 1976 also to know the activity range in adult stage of two species. A total of 15 males and 26 females in *Prc* (Yamamoto unpubl.), and one male and six females in *Pnn* were marked soon after emergence or copulation and followed day to day till their disappearance, everyday continuously from start of activities in the morning to roosting in the evening as far as possible. For *Prc* Ohsaki (1978) reported sedentariness in males and nomadic tendency in females. These tendencies were supported by Kobayashi and Takano (1978), too. As for *Pnn* no study has hitherto been published on this problem. Fig. 8 shows the regressive oviposition of *Pnn*-G_1-No. ♀9 (June 13, 9:00~23, 13:53). The individual made a slight

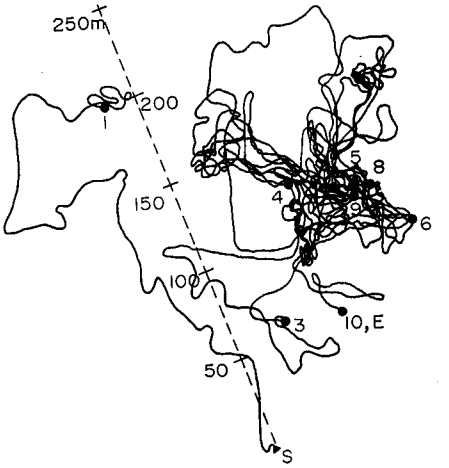

Fig. 8. The flight activity of *P. napi nesis* G_1 ♀9. Closed circles: Roosting sites on successive observation days as given by numerals. S and E: Start and the end of observations.

emigration from emergence site, then regressively oviposited there.

Although both *Prc* and *Pnn* have a high flight activity, especially in males (Ohtani and Yamamoto unpubl.), actual dispersal distance is not so large due to the regressive tendency. This tendency may cause sedentariness of *Prc* males and *P. napi japonica* as reported by Ohsaki (*op. cit.*)

3.1. *The sedentary tendency*: The sedentary tendency can be expressed by the duration of stay within a particular area, DSA, a higher value of which indicates a higher sedentariness. For this purpose each individual record was divided by nine concentric circles, $C_n(n=1\sim9)$, the center of which is the release point and the diameter is $n\times100$ m each. By this way the daily activity pattern of any individual can be expressed numerically irrespective of actual course of movement. DSA of an individual within each concentric circle was defined as the period till the first day of emigration with and/or without return from the circle concerned. Fig. 9 shows the average DSA within each concentric circle of activity range in all individuals chased. DSA was longer in males than in females in *Prc*. Between two species, *Pnn* was more sedentary than *Prc* in G_1-females.

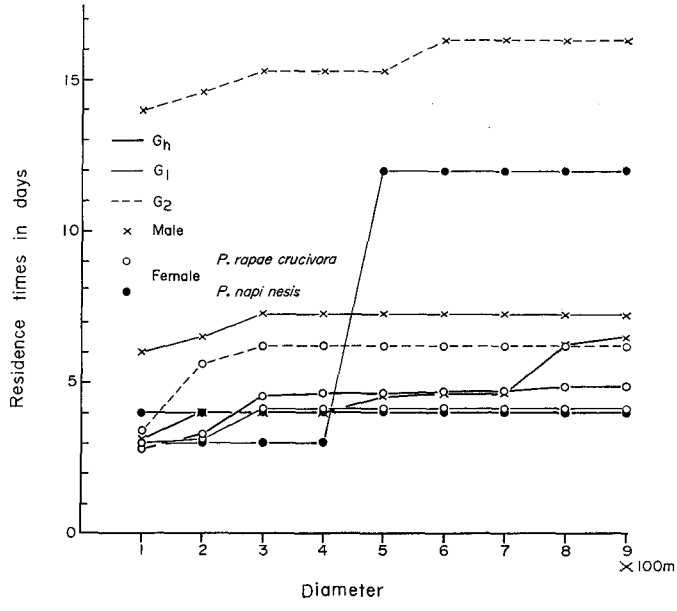

Fig. 9. Mean DSA in days within each area (C_n, $n=1\sim9$).

3.2. *Comparison in females*: In spring both species have a similar DSA with a limited area, while in G_1 a higher sedentariness of *Pnn* is recognized. Although no *Pnn*-G_2-females were chased, their DSA is probably equal or higher than G_1,

judging from the result of capture-recapture method (cf. Section **1.1.**). A higher sedentariness of *Pnn*-females mentioned above affects the estimation of the number of eggs laid within a limited area. Probably the large difference between two species on the number of eggs laid per female during the life span would not be proved if studied within a limited area for a higher sedentariness of *Pnn*-females. Based upon the presumable curves of laying pattern (Fig. 7), the cumulative number of eggs by a single female is calculated as follows:

Age in days	1	2	3	4	5	6	7	8	9	10	11	12	13
Prc	0	20	80	205	325	415	475	525	565	600	630	660	···
Pnn	0	0	0	0	30	60	90	120	150	180	210	240	···

Within the studied area belonging to the circular area of 900 m in diameter, *Prc* may lay 200~300 eggs and *Pnn* about 30 eggs during the first 4~5 days of their DSA in G_h. But in G_1 the sedentariness of Pnn-female is three times higher than in *Prc*. This decreases the interspecific diffrrence and *Pnn*-female may lay 240 eggs for 12 days in the circular area of 500~900 m in diameter, while *Prc*--female the same number of eggs in G_h, 200~300 for 4~5 days in the same area. In G_2 females of *Prc* stay there for 6~7 days but lay only 300~400 eggs due to the lower fecundity per female than in G_h and G_1. The number of eggs laid by a female within the studied area of UC is thus assumed as follows:

	G_h	G_1	G_2
Prc	200~300	200~300	300~400
Pnn	30~40	200~400	200~400

4. The life tables of two species

The last problem concerns preparation of the life table for each generations, decrease of the number of individuals through successive developmental stages; egg, 1st to 5th instar (L_1~L_5), pupa (P) till the adult (A). Population studies on *P. rapae* have been carried out extensively in the countries where this species behaves as pest of the cultivated crucifers; England (Moss 1933, Richards 1940, Demspter 1967, 1968), Canada (Harcourt 1966), the United States (Pimentel 1961, Parker 1970) and Japan (Miyashita *et al.* 1956, Osada and Itô 1974, Itô *et al.* 1975, Hasui 1977). Osada and Itô (*op. cit.*) summarized these results: Mortality of *P. rapae* is commonly high at three developmental stages, L_1, L_5 and pupa, caused by the adverse weather (rainfall and wind), predators (paper wasps and birds) and hymenopteran parasitoids. At the area studied in the present study the amount of cultivated crucifers is so negligible that *Prc* highly depends upon the other larval food plants, particularly *Rorippa sylvestris* as clarified by adult chase for the females (Table 13). *Pnn* is also highly dependent upon *R. sylvestris*, though some amount of *Cardamine leucantha*, an original larval food plant, was found at the northern part of UC. As *R. sylvestris* received the majority of eggs laid by both species except *Prc*-G_2, changes of the numbers of immatures on this plant could explain

Table 13. Number of eggs laid by individually marked females on various larval food plants. Rs: *Rorippa sylvestris*. As: *Armoracia susticana*. So: *Sisymbrium officinale*. Ra: *Raphanus sativus*. Bc: *Brassica campestris*. Rr: *Raphanus raphanistrum*. Ri: *Rorippa islandica*.

Code number of female \ Plants received eggs		Rs	Ar	So	Ra	Bc	Rr	Ri
G_h	*Prc*, '75 7	40						
	'76 b1	11	2					
	10	5						
	13	198						
	15	21						
	21	11						
	23	106						
	22	1	5					
	20	143						
	Total (%)	446 (98.5)	7 (1.5)					
	Pnn, '76 7	64						
	9	221		11				
	'77 1	18						
	Total (%)	303 (96.4)		11 (3, 6)				
G_1	*Prc* '76 3	124						
	5	267	2		8			
	10	66		4		24	2	
	17	25	2	63		22	1	
	22	15						
	23	12	2	113		12	5	
	Total (%)	509 (66.3)	9 (0.8)	180 (23.4)	8 (1.0)	58 (7.5)	8 (1.0)	
	Pnn '78 3	27 (96.4)		1 (3.6)				
G_2	*Prc* '76 26	50		2		1	10	
	41	161	3	2			4	14
	47	446		4		1		2
	Total (%)	657 (93.9)	3 (0.4)	8 (1.1)		2 (0.3)	14 (2.0)	16 (2.3)

the most, if not all, aspects of fluctuation of the number of adults. For this purpose, 14 quadrats (1×1 m) in spring, 16 in early summer and 15 in late summer were set at an area around the University buildings not so highly frequented or disturbed by men as the crop fields. In 1974 within these quadrats, 25 smaller quadrats (20×20 cm) were set and the numbers of individuals found therein were counted everyday, each stage separately. A needle stick was used to seek the individuals attaching on the underside of the leaves. Head width of both species was used to distinguish the instars:

Instar	L_1	L_2	L_3	L_4	L_5
Head width in mm.	0.5	0.5~1.0	1.0	1.5	2.0

Eggs, larvae and pupae are very alike between species, but can be distinguished by the following characters:

	Color		Shape	
	Prc	*Pnn*	*Prc*	*Pnn*
Egg	creamy	whity	rounder at the cephalic pole	thinner at the cephalic pole slightly larger
Larva	yellowish green	dark green	rod-like	flatter
Pupa	without dark patches	with dark patches	stumpy	slender

Other auxiliary characters are summarized, together with some ecological notes:

	Prc	*Pnn*
Egg (E)	Laid singly on the underside of leaves	As in *Prc* but often several eggs laid jointly on the upperside of leaves
	No particular preference on positions of food plant	With preference for shaded parts, i.e. lower leaves or positions
L_1	Often migrating to younger leaves near the point of hatching	Very sedentary, remaining on the leaves where laid
	First lighter green, later yellowish	First darker green, later whitish
	Solitary	Often gregarious when oviposited jointly
L_2	Often found on the uppersides of leaves	Not found on the uppersides of leaves
L_3	Mostly found on the uppersides of leaves	〃
L_4	〃	〃
L_5	After completion of feeding, leaving the food plant for pupating site	Not emigrating in post feeding period
Pupa(P)	Pupation mostly at shaded place near food plant, especially on walls of buildings in the present study	Pupation mostly on stalks of food plant.

As pupae of *Prc* were mostly found on the walls of the buildings nearby, not within the quadrats, the number of pupae found on the walls was counted everyday, and the decrease of individual number in the stage later than post feeding period (PPP) was estimated based upon this census.

4.1. *Decrease of individual number after PPP stage*: L_5/*Prc* was studied by releasing larvae marked with color ink at three distances, 1 m (balck), 2 m (red) and 3 m (blue) from the definite point of the wall. The migration was clearly orientated (Table 14), which caused increase of individual number invading into a quadrat as described later (p. 227). The survival rate of post-migration individuals

Table 14. Migration to pupating sites by marked 5th instar larvae of *P. rapae crucivora*. *=releasing

Marked with	Black					Red					Blue				
Found / Date	on wall	at 1m	2m	3m	No. ndi-viduals newly marked	wall	1m	2m	3m	No. indi-viduals newly marked	wall	1m	2m	3m	No. indi-viduals newly marked
IX 16		*			12			*		12				*	12
17	1	4	1		12			9		11				7	10
18	5	7			16	2		8		17				9	17
19	9	11			5	2		12	1	6				15	6
20	6	3			4	1		12		4			3	10	4
21	8	5	1		8	6		5		7				6	7
22	5	4	1			8		5	1		5			5	
23	5	3	2			6		2	1	3	1	1		3	2
24	4	2	2			2		2			1	1		3	
25	2	1										1		3	
26	2	1			4	1				4				2	3
27		1											1		

Table 15. The number of individuals of *P. rapae crucivora* found dead on the building walls at various stages.

Site censused \ Stage	PPP	PP	P	Unsuccessful emergence	No. emergence
G_1					
Aa	0	2	1	0	0
Ab	3	4	7	1	4
Ac	1	1	5	0	2
Bd	5	0	1	0	1
Be	2	1	2	0	0
Total	11	8	16	1	7
G_2					
Aa	5	1	0	0	0
Ab	66	14	10	0	0
Ac	17	8	10	0	1
Bd	128	25	20	0	3
Be	18	1	5	0	0
Total	234	49	45	0	4
G_3					
Aa	22	1	0	0	3
Ab	28	19	19	1	6
Ac	11	10	15	0	0
Bd	6	6	9	0	2
Be	2	1	4	0	0
Total	69	37	47	1	11

can be estimated by the census on the walls at each surveyed section (Table 15). Considering total number of individuals found dead as the number of individuals survived from PPP to adults (A) is given (PP=pre-pupa, P=pupa, unsuccessful emergence in parentheses):

	PPP	PP	P	A	A/PPP
G_1	43	32	24	7(1)	0.1628
G_2	377	143	49	4(0)	0.0106
G_3	165	96	59	10(1)	0.0606

The survival rate emergence/PPP was thus 16.3% (G_1), 1.06% (G_2) and 6.06% (G_3).

In *Pnn* intense collection of pupae and parasite cocoons was made only for G_2, 1979, to reinforce the insufficient result in G_2 of 1974 (Table 16). The survival rate adults/pupae was 49.2% (unsuccessful emergence was 25.0%), and total survival rate emergence/pupae was 36.9%, both higher than in *Prc*.

Table 16. The number of G_2 dead individuals of *P. napi nesis* collected in 1979.

Stage / Site censused	PPP	P	Unsuccessful emergence	No. emergence
Ab I	15	8	1	5
Ab II	26	2	1	1
Ab III	32	5	2	9
Ac IV	9	9	1	3
Boe	1	0	0	1
Bon	1	6	3	5
Boo	0	3	0	0
Total	84	33	8	24

4.2. *Decrease of individual number till the last instar*: Seasonal fluctuation of the individual number of two species is given in Figs. 10 (*Prc*) and 11 (*Pnn*) for each developmental stage. Three generations of both species are clearly segregated. A higher abundance of *Prc* than *Pnn* is found in all immature stages. In these figures, however, difference of duration among stages is not considered. As the figures show the fluctuation of the number of individuals × days, a longer lasting stage obviously causes a higher total number than a real number by accumulation. To correct this the individual number must be divided by the duration of the respective stage (Table 17). The durations obtained in the field conditions do not much deviate from those obtained in the laboratory conditions (Fig. 12). The number of calculated individuals is that expected at the middle of respective stage (Itô and Murai 1977), assuming a uniform intra-stage mortality rate. But this assumption cannot stand for some stages (Figs. 13 and 14) in which the decrease, i.e. disappearance, was higher in the earlier period of the stage. This is particularly conspicuous in L_1 where disappearance was highest in the first day, i.e. just

after hatching from eggs. In such a case the corrected number of individuals × days overestimates the real number at the middle of the stage. Using the average survival duration of each stage (Table 18), the number of individuals entering the concerned stage is estimated (Table 19), but disappearance and migration of larvae make the exact estimation difficult. Disappearance of L_1 and some L_2 is caused by both their death and overlook, whereas increase of individual number in the later instars (L_4 and L_5) is caused by immigration from other feeding places (Section **4.1.**). Only the numbers of eggs and L_3 can be regarded as reasonable approximation to the real number of individuals survived within the quadrats. Considering both disappearance of L_1 and immigration of the older larvae, Table 20 was prepared by the records of particular individuals entering the stage concerned, together with the result in the Section **4.1.** The total survival rate until emergence was estimated by multiplying the survival rate from egg stage to L_5 by that from PPP to emergence:

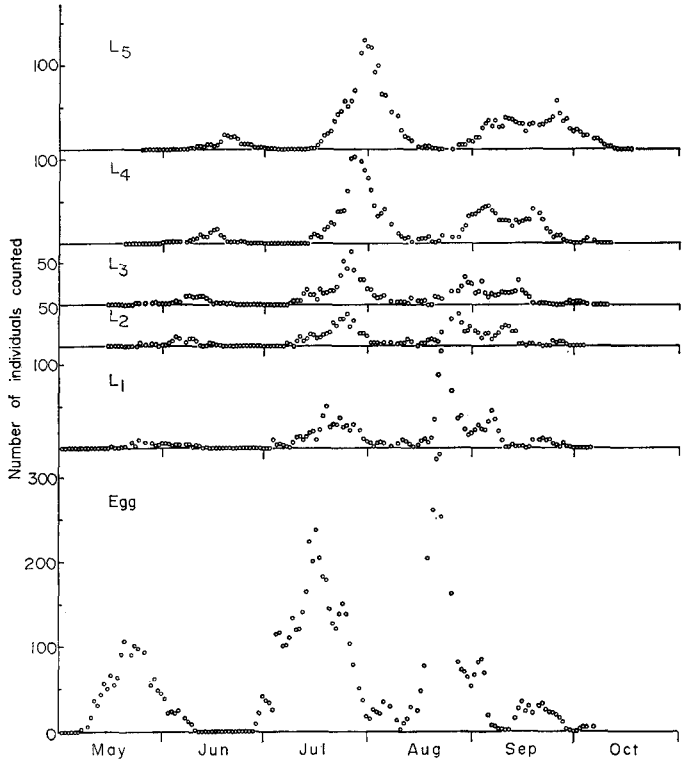

Fig. 10. Fluctuation of individual number of *P. rapae crucivora* in each developmental stage, Egg, L_1, L_2, L_3, L_4 and L_5.

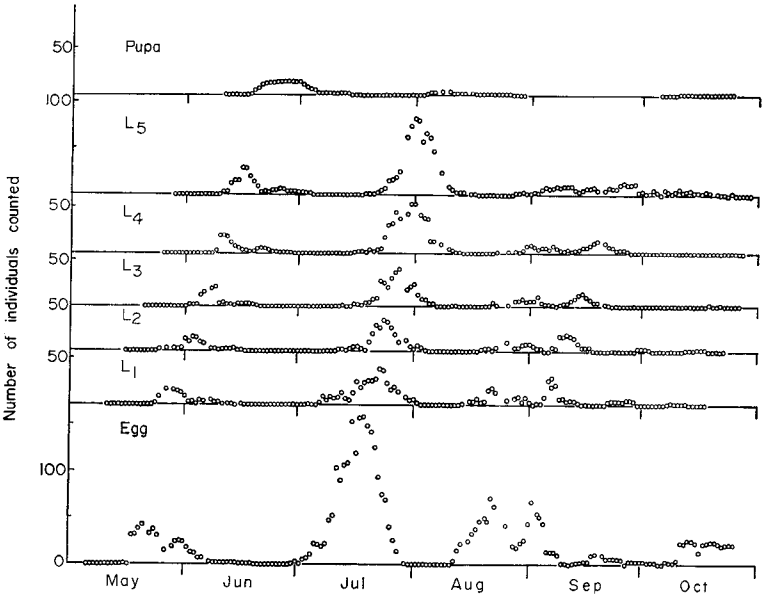

Fig. 11. Flucutation of individual number of *P. napi nesis* in each developmental stage.

Table 17. Duration of each developmental stage in days passed until the next stage in field conditions (asterisked figures in laboratory conditions).

Generation	G_1			G_2			G_3		
Stage	N	$\bar{x}$ S.D.	Total duration	N	$\bar{x}$ S.D.	Total duration	N	$\bar{x}$ S.D.	Total duration
Prc Egg	26	8.54±1.24		52	4.92±1.06		81	4.01±1.05	
L_1	7	3.29±1.89	11.83	32	3.17±0.88	8.09	44	3.07±0.70	7.08
L_2	5	2.80±0.84	14.63	35	2.34±0.97	10.43	40	2.53±0.85	9.61
L_3	19	3.42±1.26	18.05	35	2.71±1.30	13.14	35	2.60±0.81	12.21
L_4	16	3.63±1.09	21.68	33	2.79±0.82	15.93	24	4.04±1.04	16.25
L_5	7	5.86±1.35	27.54	19		20.14	22	4.41±1.26	20.66
PP	4	1.0	28.54	0			—		
P	6	9.17±1.47	37.71	3	11.33±2.08	31.47	—		
Pnn Egg	22	7.95±1.76		48	4.98±1.12		49	4.06±1.01	
L_1	23	5.61±1.73	13.56	23	3.30±0.88	8.28	29	3.31±1.07	7.38
L_2	21	5.00±1.45	18.56	35	2.46±1.01	10.74	16	3.56±0.73	10.93
L_3	21	4.52±1.44	23.08	19	2.42±0.84	13.16	18	3.39±0.98	14.32
L_4	15	3.53±0.92	26.61	19	2.79±0.71	15.95	19	4.26±0.99	18.58
L_5	8	5.38±0.74	31.99	14	3.64±1.08	19.59	12	4.92±1.38	23.50
PP	11	1.27±0.47	33.26	38*	0.71±0.46	20.30	32*	1.34±0.70	24.84
P	9	12.56±1.59	45.82	42*	7.38±0.73	27.68	11*	228.62±6.86	253.46

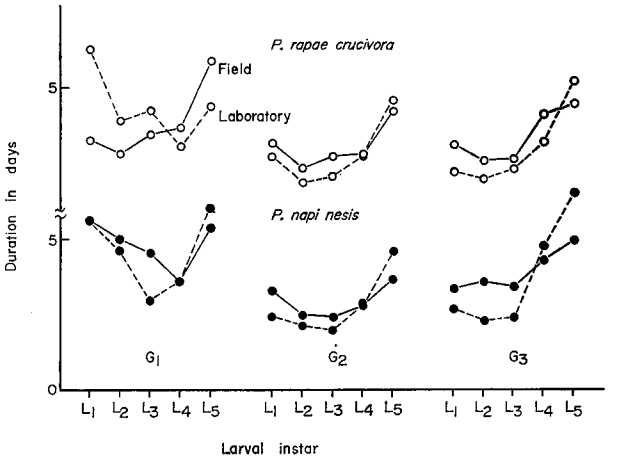

Fig. 12. Relation of stage duration in days in field and laboratory conditions.

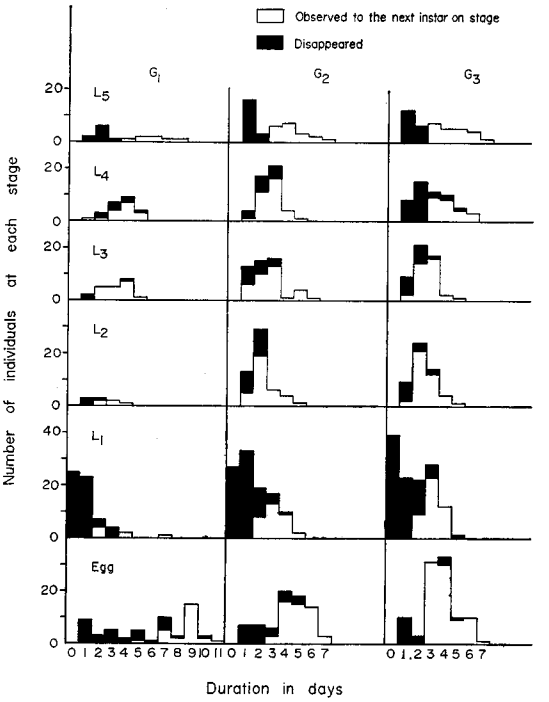

Fig. 13. Daily change of individual number of *P. rapae crucivora* within a particular stage.

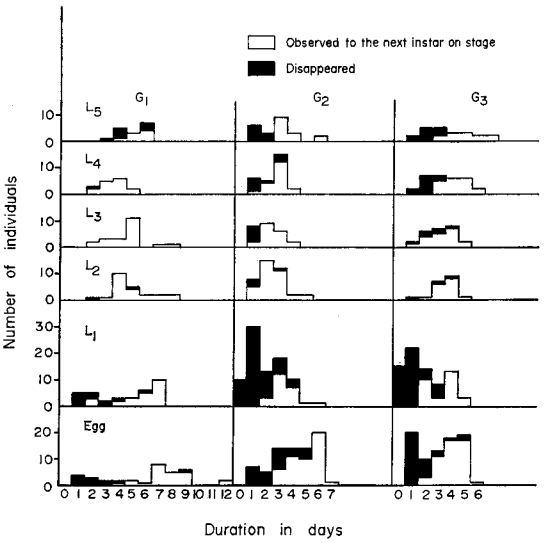

Fig. 14. Daily change of individual number of *P. napi nesis* within a particular stage.

Table 18. Apparent average duration in days passed until transfer to the next stage or disappearance or death within each stage by 95% fiducial limit.

Generation	G_1		G_2		G_3	
Stage	N	$\bar{x}$ S.E.	N	$\bar{x}$ S.E.	N	$\bar{x}$ S.E.
Prc Egg	57	5.95±0.85	74	4.15±0.37	98	3.65±0.28
L_1	37	1.73±0.42	81	2.12±0.26	86	2.37±0.23
L_2	9	2.11±0.81	53	2.08±0.26	52	2.31±0.26
L_3	22	3.23±0.61	50	2.42±0.36	50	2.30±0.25
L_4	24	3.50±0.45	47	2.60±0.85	52	2.96±0.40
L_5	16	3.63±1.20	38	2.68±1.77	40	3.03±0.64
Pnn Egg	35	6.11±1.07	76	4.21±0.39	81	3.12±0.35
L_1	34	4.53±0.81	73	2.21±0.29	60	2.35±0.34
L_2	23	4.87±0.66	39	2.36±0.34	19	3.42±0.43
L_3	21	4.52±0.66	25	2.08±0.27	25	2.08±0.46
L_4	16	3.43±0.51	28	2.46±0.36	29	3.52±0.51
L_5	16	5.00±0.55	23	2.74±0.63	22	3.64±0.08

Table 19. The individual number in each stage with the range of 95% fiducial limit in parentheses.

Generation	G_1	G_2	G_3
Stage			
Prc Egg	285 (249~332)	969 (890~1, 065)	821 (763~887)
L_1	65 (53~ 86)	275 (246~ 314)	404 (369~447)
L_2	43 (32~ 71)	219 (195~ 250)	219 (197~246)
L_3	37 (31~ 45)	264 (230~ 310)	207 (186~232)
L_4	36 (32~ 41)	463 (422~ 512)	301 (264~348)
L_5	42 (31~ 62)	590 (485~ 753)	357 (295~453)
Pnn Egg	84 (71~102)	462 (424~ 509)	325 (292~366)
L_1	33 (28~ 40)	185 (163~ 213)	100 (87~117)
L_2	22 (20~ 26)	111 (97~ 130)	58 (50~ 65)
L_3	26 (23~ 30)	161 (143~ 185)	48 (42~ 56)
L_4	36 (31~ 42)	218 (190~ 255)	56 (54~ 60)
L_5	40 (36~ 45)	280 (228~ 363)	65 (54~ 84)

Table 20. Life tables of two species. x: Developmental stage. d_x: Individual number dead within the stage. $100q_x$: Mortality rate in the stage concerned. Asterisked figures: Corrected based upon the data in 1979.

Generation	G_1			G_2			G_3		
x	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$	l_x	d_x	$100q_x$
Prc Egg	244	184	75.4	891	483	54.2	674	308	45.7
L_1	60	25	41.7	408	141	34.6	366	141	38.5
L_2	35	9	25.7	267	25	9.4	225	33	14.7
L_3	26	4	15.4	242	30	12.4	192	30	15.6
L_4	22	6	27.3	212	24	11.3	162	36	22.2
L_5	16	7	43.8	188	164	87.2	126	81	64.3
P	9	6	66.7	24	22	91.7	45	37	82.2
Adult	3			2			8		
Total			98.9			99.8			98.9
Pnn Egg	64	17	26.6	455	215	47.3	230	114	49.6
L_1	47	9	19.1	240	63	26.3	116	47	40.5
L_2	38	2	5.3	177	24	13.6	69	9	13.0
L_3	36	3	5.3	153	11	7.2	60	11	18.3
L_4	33	2	6.1	142	25	17.6	49	18	36.7
L_5	31	17	54.8	117	113	96.6	31	28	90.3
P	14	5	35.7	4	3*	25.0*	3	3	100.0
Adult	9			1*			0		
Total			85.9			99.7*			100.0

	Prc	*Pnn*
G_1	1.07%	14.06%
G_2	0.22	0.32
G_3	1.13	0.0

Consequently the number of emerged adults is:

	Prc	*Pnn*
G_1	2.6 (≒3)	9*
G_2	1.99(≒2)	1.48(≒1)**
G_3	7.68(≒8)	?

*=observed number
**=corrected by pupal survival rate obtained from 1979's result

Mortality rate is shown in Table 20 as 100 q_x. Death number, d_x, is equal to the decrease of the number from one stage to the next. Stage-specific mortality rate can be estimated by counting the number of individuals dead within the stage, too (Table 21). Two mortality rates obtained from these different calculations are similar for each other, which favors the validity of the life tables obtained. In Table 20, deaths of L_1 within a day after hatching are entered d_x of E.

Table 21. Mortality rate (M) in each developmental stage of two species, obtained from individual records. D: Number of individuals dead. S: Number of individuals molted to the next stage.

Generation	G_1			G_2			G_3		
Stage	D	S	M	D	S	M	D	S	M
Prc Egg	31	26	54.4	22	52	29.7	17	81	17.3
Unfound after hatching	30		31.6	20		14.4	14		12.6
L_1	27	38	41.5	38	81	21.9	45	52	46.4
L_2	12	24	33.3	10	69	12.7	9	53	14.5
L_3	7	27	20.6	7	49	12.5	8	43	15.7
L_4	12	23	34.3	16	35	21.4	19	27	41.3
Pnn Egg	15	22	37.1	28	48	36.8	32	49	39.5
Unfound after hatching	5		11.6	16		14.7	17		21.5
L_1	9	29	23.7	37	56	39.8	29	33	46.8
L_2	2	24	8.7	9	45	16.7	12	29	29.3
L_3	2	22	8.3	7	43	14.0	8	30	21.1
L_4	1	21	4.5	12	39	23.5	12	21	36.4
L_5	17	14	54.8	42	4	91.4			
P	5	9	35.7	4	0	100.0			

Three factors, the number of females (Section **1.3.**), the number of eggs laid (Section **3.2.**) and totally survival rate obtained from these life tables determine the fluctuation of adult numbers of the next generation observed on UC in 1974, that is, *Prc*>*Pnn* between species and $G_1>G_2$ in *Prc* and $G_1<G_2$ in *Pnn*. Only mean values of each factor were multiplied as follows, for example, G_1-*Prc* estimation was made from $1{,}280\times250\times0.0107$:

In *Prc*

	Number of adults		
	Observed (0)	Estimated (E)	D*
G_1	2,539	3,424	34.9
G_2	1,844	1,376**	25.4

In *Pnn*

G_1	1,834	2,091	14.0
G_2	2,030	538	73.5

*=% ratio of deviation $|0-E|/0$
**=corrected by 66.3% dependence on *Rorippa sylvestris*

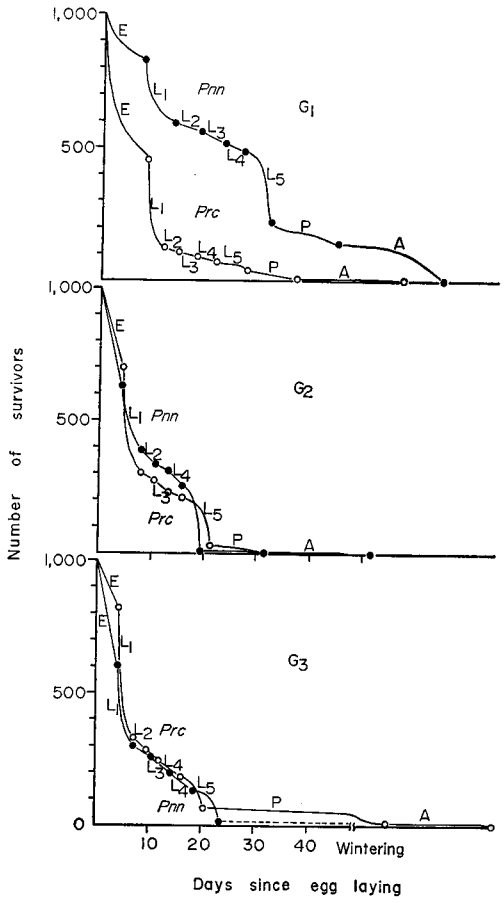

Fig. 15. Survivorship curves for three generations of *P. rapae crucivora* and *P. napi nesis*.

Except *Pnn*-G_2 observed and estimated figures don't deviate so much for each other, judging from the correlation coefficient between adult numbers obtained by census and capture-recapture method. The high deviation in *Pnn*-G_2 was probably caused by the overlook of some pupae which are more difficult to discover than *Prc* by their habit of pupating in the foliage of food plant (p. 224). Crowded weeds in summer season probably accelerate difficulty for discovering the pupae.

From the obtained survivorship curves (Fig. 15), those of female adults (Suzuki 1978) and age-specific birth rate (Fig. 7), the net reproductive rate per generation, R_o, generation time, T, and intrinsic rate of natural increase, r, were calculated between generations and between species as follows (for example of Prc-G_2 in Table 22):

	Prc			*Pnn*		
	R_0	T	r	R_0	T	r
G_1	3.709	42.19	0.0311	22.038	54.21	0.0571
G_2	0.764	34.53	−0.0078	0.505	40.76	−0.0168

where $r = \frac{\ln R_o}{T} = \frac{\ln \sum l_x m_x}{T}$. r would be higher in *Prc* than *Pnn* under

Table 22. Daily number of survived individuals inferred from Fig. 15 and Table 20 in G_2-female of *P. rapae crucivora*. x: Age in days. m_x: Age-specific birth rate.

x	l_x	d_x	m_x	x	l_x	d_x	m_x
0-1	1,000	136	-	26-27	7.2	1	-
- 2	864	136	-	-28	6.2	1	-
- 3	728	135	-	-29	5.2	1	-
- 4	593	135	-	-30	4.2	1	-
- 5	458	89	-	-31	3.2	1	-
- 6	369	28	-	-32	2.2	0	0
- 7	341	26	-	-33	2.2	0	20
- 8	315	15	-	-34	2.2	0	60
- 9	300	14	-	-35	2.2	0	125
-10	286	14	-	-36	2.2	0	120
-11	272	11	-	-37	2.2	0	90
-12	261	11	-	-38	2.2	0	60
-13	250	12	-	-39	2.2	0.2	50
-14	238	14	-	-40	2.0	0.3	40
-15	224	13	-	-41	1.7	0	35
-16	211	18	-	-42	1.7	0	30
-17	193	18	-	-43	1.7	0	30
-18	175	18	-	-44	1.7	0	25
-19	157	55	-	-45	1.7	0.3	25
-20	102	75	-	-46	1.4	0.2	20
-21	27	1	-	-47	1.2	0.2	10
-22	26	1	-	-48	1.0	0.2	5
-23	25	1	-	-49	0.8	0.5	0
-24	24	1	-	-50	0.3	0	0
-25	23	1	-	-51	0.2	0.3	0
-26	22	14.8	-	-52	0.2		

laboratory conditions due to higher fecundity of *Prc* (cf. Southwood *et. al.* 1974), while higher in *Pnn* than *Prc* under field conditions in the present study. Most previous reports estimated r in experimental conditions in which the difference of the total survival rate among compared species was ignored.

4.3. *Mortality factors*: In Table 20 the high mortality rate in two species appears at three developmental stages. The first high mortality occurs in the early stage of L_1, which has already been recognized by the life tables prepared for the populations feeding on cultivated crucifers and is caused both by adverse weather and insect predators. The second one appears in L_5, caused partly by a parasitoid wasp, *Apanteles glomeratus*. The third one in pupal stage is caused partly by another parasitoid wasp, *Pteromalus puparum* which seems more serious in *Prc* than *Pnn*. In addition to these well-known mortality factors, other factors are shown in detail in Table 23 in which cases of deaths are individually mentioned. But d_x of $L_1 \sim L_4$ in Table 20 is much higher than deaths actually observed. Most cases of these disappearance seem to be caused by tabulated predators and unknown nocturnal predators (Dempster 1967). On the deaths at stages after L_5 the result in Table 23 seems to reflect the real relative importance. The kinds of predators would be different according to the food plant species and localities surveyed, though a fairly high mortality is caused by them, especially at early developmental stage by insect predators (about 48% in E, 59% in L_1 of *Prc* while 33% in L_1 of *Pnn*) and later stage by vertebrate predators (the most cases of disappearance may be caused by them, i.e. 26% in PPP and 19% in PP of *Prc*, though not surveyed in *Pnn*).

4.4. *The relation between mortality rate and population density*: Nextly the relation between these mortality factors and population density is thought by key-factor analysis (Morris 1963a, Kuno 1973, Southwood and Reader 1976, Podoler and Rogers 1975, Ito and Murai *op. cit.*). The logarithmic number of individuals determined at a given developmental stage is plotted to that at the next stage. Then equation of the regression line and the correlation coefficient, r, are calculated. From the coefficient of the regression line, b, the relation between mortality rate and population density can be suggested, that is, density-dependent when $b<1$, density-independent when $b=1$ and inverse density-dependent when $b>1$. Density-dependent mortality can regulate a population within a stable range, acting intensely at high densities but weakly at low densities (cf. Roughgarden 1971, May *et al.* 1974, Stubbs 1977). On the other hand, density-independent and inverse density-dependent mortality would ultimately increase the density if not accompanied with density-dependent mortality. In the present paper key factors mean those which cause density-dependent mortalities. In this method r^2 is called the coefficient of determination, being used as the standard of the rate of the change of dependent variables affected by the change of independent variables. The scatter diagrams (Figs. 16 ~ 24) show the relations between egg and L_1 (E-L_1), L_1-L_2,

Table 23. The number of individuals the deaths of which were directly observed. Asterisked items were obtained not from the quadrat-survey.

Generation		G_1	G_2	G_3
Stage	Mortality factors			
Prc Egg	.....	24(%)	69(%)	54(%)
	Predacious mites	4(16.7)	39(56.5)	28(51.9)
	Detached from leaves	20(83.3)	6(8.7)	14(25.9)
	Unfertilized		17(24.6)	9(16.7)
	Eaten by older larvae		7(10.2)	3(5.5)
L_1	.....	2	4	11
	Spider mite	1(50.0)	2(50.0)	7(63.6)
	Unsuccessful molting			1(9.1)
	Disease		1(25.0)	
	Spider			1(9.1)
	Mishandled		1(25.0)	1(9.1)
	Detached from leaves			1(9.1)
	Unknown	1(50.0)		
L_2	.....		5	1
	Unsuccessful molting		3(60.0)	
	Unknown		2(40.0)	1(100.0)
L_3	.....	1	1	3
	Unsuccessful molting			2(66.7)
	Unknown	1(100.0)	1(100.0)	1(33.3)
L_4	.....	1	7	8
	Unsuccessful molting		1(14.3)	4(50.0)
	Disease	1(100.0)		
	Unknown		6(85.7)	4(50.0)
L_5	.....	3	46	7
	Apanteles glomeratus	2(66.7)	29(63.0)	
	Spider			1(14.3)
	Dermapteran			1(14.3)
	Unknown	1(33.3)	17(37.0)	5(71.4)
PPP.*	.....	11	234	69
	Apanteles glomeratus	6(54.5)	159(67.9)	19(27.5)
	Disappearance	5(45.5)	47(20.1)	30(43.5)
	Spider		4(1.7)	13(18.8)
	Disease		24(10.3)	7(10.2)
PP*.	.....	8	49	37
	Disappearance		8(16.3)	10(27.0)
	Unsusccessful pupation	8(100.0)	41(83.7)	27(73.0)
P.*	.....	16	44	47
	Pteromalus puparum	10(62.5)	14(31.8)	11(23.4)
	Other parasitoid waps	2(12.5)	1(2.3)	5(10.6)
	Disappearance	4(25.0)	23(52.3)	29(61.7)
	Disease		5(11.4)	
	Drying		1(2.2)	2(4.3)
P.	.....	5		
	Pteromalus puparum	2(40.0)		
	Artifacts	3(60.0)		

Table 23. (Continued)

Generation		G_1	G_2	G_3
Stage	Mortality factors			
Emergence*.	.....	1(%)		1(%)
	Unsuccessful emergence	1(100.0)		
	Wing undeveloped			1(100.0)
Adult.*	.....	2	2(%)	1
	Adverse weather	1(50.0)		
	Sparrow	1(50.0)		
	Traffic accident			1(100.0)
	Artifacts		1(50.0)	
	Spider		1(50.0)	
Pnn Egg	.....	1	14	25
	Predacious mites			13(52.0)
	Detached from leaves		3(21.4)	5(20.0)
	Unfertilized	1(100.0)	11(78.6)	6(24.0)
	Eaten by older larvae			1(4.0)
L_1	.....		5	1
	Spider mite		2(40.0)	
	Mishandled			1(100.0)
	Unknown		3(60.0)	
L_2	.....	-	-	-
L_3	.....	1	1	1
	Unsuccessful molting		1(100.0)	
	Spider	1(100.0)		
	Unknown			1(100.0)
L_4	.....		10	2
	Unsuccessful molting		2(20.0)	
	Apanteles glomeratus		3(30.0)	
	Carabid bettle			1(50.0)
	Unknown		5(50.0)	1(50.0)
L_5	.....		46	1
	Apanteles glomeratus		42(91.3)	1(100.0)
	Unknown		4(8.7)	
PPP	.....		84	
	Apanteles glomeratus		77(91.7)	
	Disease		7(8.3)	
P*.	.....		33	
	Pteromalus puparum		20(60.0)	
	Other parasitoid wasps		5(15.2)	
	Disease or drying		6(18.2)	
	Diptera (Tachinidae)		2(6.0)	
P.	.....		4	1
	Pteromalus puparum		2(50.0)	
	Other parasitoid wasps		2(50.0)	1(100.0)
Emergence.*	.....		8	
	Wing undeveloped		8(100.0)	

L_2-L_3, L_3-L_4, L_4-L_5, L_5 and pre-pupa (L_5-PP), prepupa and pupa (PP-P) and pupa and adult (P-A). The mortality factors for each stage are inferred as follows:

Stage	Symptom	Principal mortality factors	Generations*	
			Prc	*Pnn*
E-L_1	Disappearance	Detached and fallen from leaves by adverse weather (not distinguished from L_1 deaths just after hatching)	1	
	Darkened	Unfertilized	2	1,2
	Shrivelled	Sucked by spider mites	2,3	3
	Leaf, to which E attached, eaten	Eaten by older larva with leaf		
L_1-L_2	Dead without molting	Unsuccessful molting		
	Disappearance	Predators (mainly spider mites and spiders)	1,2,3	
	Darkened	Disease, etc.		
L_2-L_5	Disappearance	Predators (insects and birds)	3	1,3
	Dead without molting	Unsuccessful molting	2,3	2
	Changing yellowishly	Disease	1	
L_5-PP	Accompanied with parasitoid coccoons	*Apanteles glomeratus*	1,2	2
	Disappearance	Predators (birds and spiders)	3	
PP-P	Disappearance	Predators (birds)		
	Dead without pupation	Unsuccessful pupation	1,2,3	
P-A	Disappearance	Predators (birds)	2,3	
	With small emergence holes	*Pteromlaus puparum*	1	2
	With large emergence holes	Hymenoptera (Ichneumonidae) and Diptera (Tachinidae)		
	Darkened	Disease		
	Dried up	Unknown factor		
A	Dead without emergence, though with pigmented wing	Unsuccessful emergence	1,3	

*=generations affected more than 50%

Although the influence of these mortality factors cannot be expressed quantitatively yet, some comments are given on the mode of action of these factors based upon the values of b at particular stages of each generations.

Prc:

E-L_1 (Fig. 16): In the course of the census deaths of L_1 were frequently observed within a day after hatching. Possibly deaths in L_1 are likely to appear as a lasting influence of mortality factors during egg stage. Density-dependent relation in G_1 and G_2 is possibly caused by concentration of predators, especially in spring in the areas of high egg densities, which are usually well insolated.

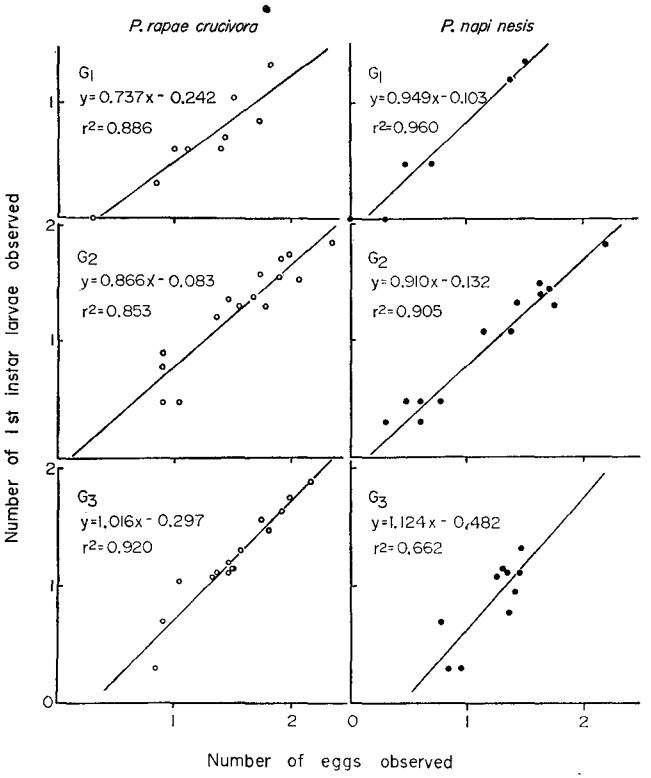

Fig. 16. Relation of the number of eggs and 1st instar larvae (L_1).

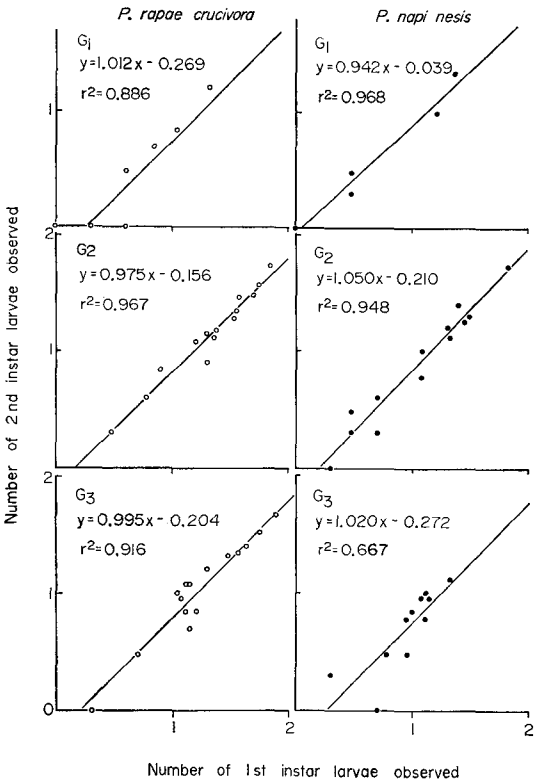

Fig. 17. Relation L_1-L_2.

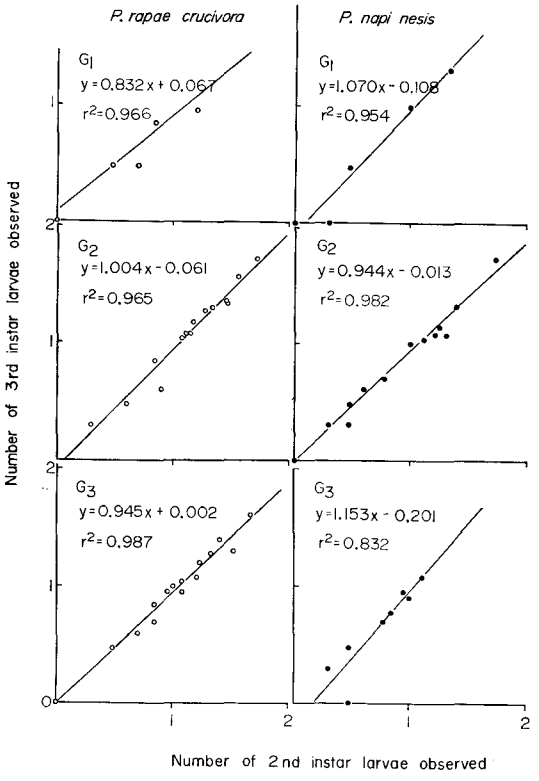

Fig. 18. Relation L_2-L_3.

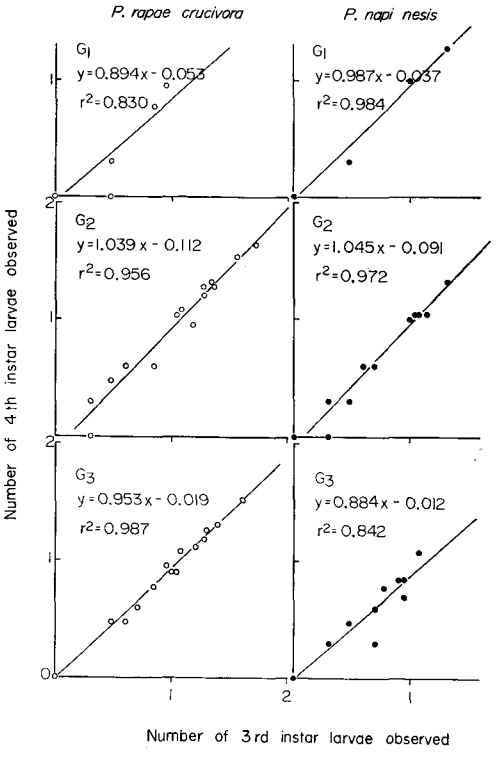

Fig. 19. Relation L_3-L_4.

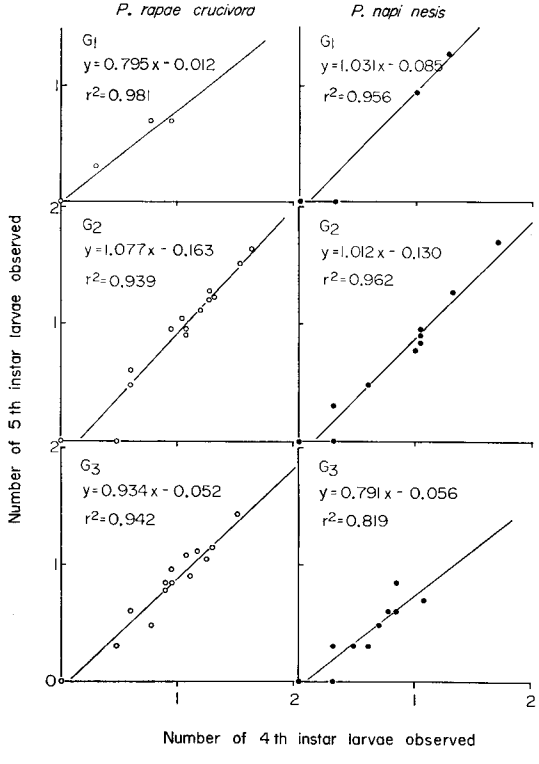

Fig. 20. Relation L_4-L_5.

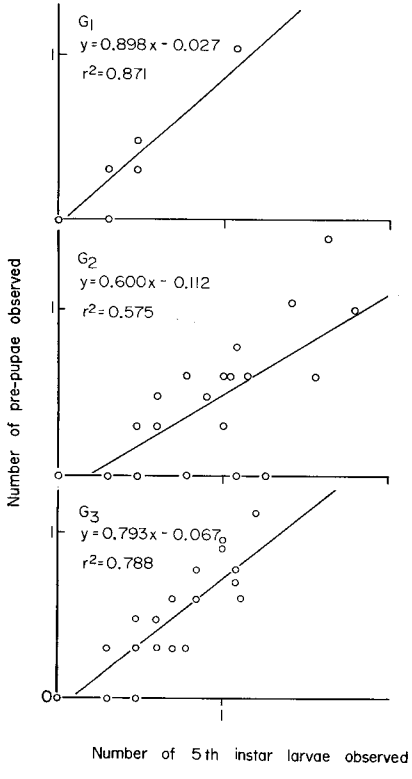

Fig. 21. Relation L_5-PP in *P. rapae crucivora*.

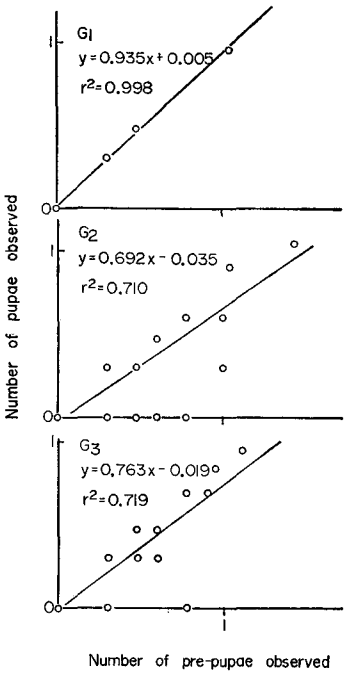

Fig. 22. Relation PP-P in *P. rapae crucivora*.

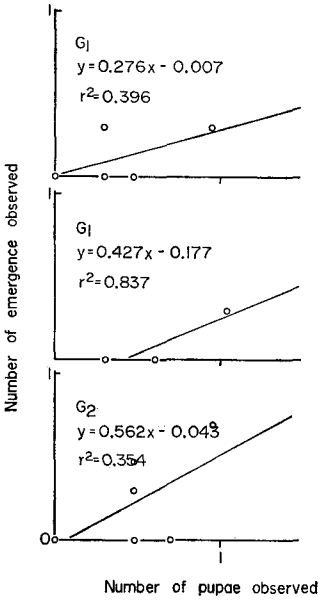

Fig. 23. Relation P-A in *P. rapae crucivora*.

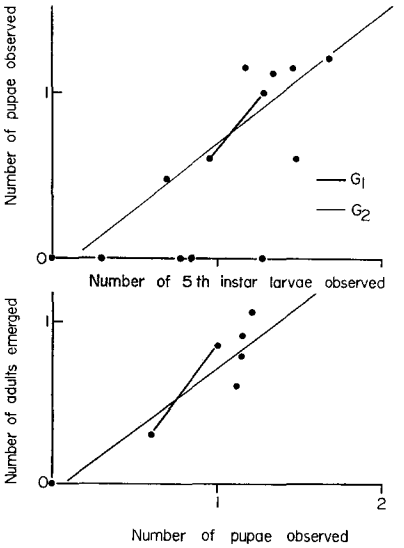

Fig. 24. Relation L_5-P and P-A in *P. napi nesis*. G_1 from two points.

L_1-L_2 (Fig. 17): Mortality rate is high, but seemingly governed by density-independent factors. The migration of L_1 to adjacent leaves may cause randomness of prey during this stage.

L_2-L_3 (Fig. 18), L_3-L_4 (Fig. 19) and L_4-L_5 (Fgi. 20): Mortality factors in these stages seem to act density-independently except in G_1, L_4-L_5 at which density-dependent influence is suggested.

L_5-PP (Fig. 21): Highly density-dependent except G_1 due to the high incidence of attack by *Apanteles glomeratus* which lays eggs in L_2 (Sato 1976).

PP-P (Fig. 22): Density-dependent stage except G_1, mainly by unsuccessful pupation, being caused by lack of food source at late larval stage.

P-A (Fig. 23): Highly density-dependent by the parasitoid wasp, *Pteromalus puparum*, and predation by birds which tend to forage continuously at favorable sites, the latter being particularly serious by immobility of pupae.

A- : Unsuccessful emergence is assumed to be caused by adverse weather (density-independent), but reliable data are not yet sufficient.

Pnn:

E-L_1 (Fig. 16), L_1-L_2 (Fig. 17), L_2-L_3 (Fig. 18), L_3-L_4 (Fig. 19) and L_4-L_5 (Fig. 20): Density-independent in contrast to *Prc* because of sedentarily remaining on the underside of the leaves until L_4.

L_5-P (Fig. 24): By the absence of migration, this stage is not subdivided in two stages as in *Prc*. Inverse density dependence in G_1 suggested by the value of

Table 24. Regression equations between two developmental stages.

Generation		G_1	G_2	G_3
Stage				
Prc	E-L_1	y=0.7371x−0.2417	y=0.8663x−0.0843	y=1.0156x−0.2971
	L_1-L_2	y=1.0117x−0.2691	y=0.9745x−0.1562	y=0.9947x−0.2040
	L_2-L_3	y=0.8318x+0.0668	y=1.0044x−0.0610	y=0.9448x+0.0022
	L_3-L_4	y=0.8936x−0.0534	y=1.0390x−0.1118	y=0.9534x−0.0187
	L_4-L_5	y=0.7952x−0.0117	y=1.0773x−0.1625	y=0·9338x−0.0521
	L_5-PP	y=0.8980x−0.0268	y=0.6002x−0.1116	y=0.7927x−0.0672
	PP-P	y=0.9348x+0.0050	y=0.6922x−0.0346	y=0.7631x−0.0192
	P-A	y=0.2760x−0.0068	y=0.4271x−0.1766	y=0.5618x−0.0426
Total		y=0.1071x−0.0073	y=0.1874x−0.3674	y=0.2995x−0.2655
Pnn	E-L_1	y=0.9491x−0.1034	y=0.9104x−0.1324	y=1.1237x−0.4816
	L_1-L_2	y=0.9415x−0.0387	y=1.0496x−0.2104	y=1.0195x−0.2716
	L_2-L_3	y=1.0700x−0.1082	y=0.9437x−0.0125	y=1.1530x−0.2009
	L_3-L_4	y=0.9869x−0.0366	y=1.0451x−0.0908	y=0.8841x−0.0123
	L_4-L_5	y=1.0305x−0.0852	y=1.0121x−0.1297	y=0.7913x−0.0563
	L_5-P	y=1.2263x−0.5681	y*=0.7952x−0.1119	—
	P-A	y=1.3672x−0.5220	y*=0.7662x−0.0613	—
Total		y=1.6314x−1.9377	y*=0.5685x−0.4818	—

*=Corrected based upon the data in 1979

b is possibly caused by gregarious habit. G_2 is density-dependence as in *Prc* due to the parasitism by *Apanteles glomeratus*.

P–A (Fig. 24): A high value of b in G_1 is not so reliable as calculated from the data of only two quadrats. A density-dependent tendency in G_2 is probably

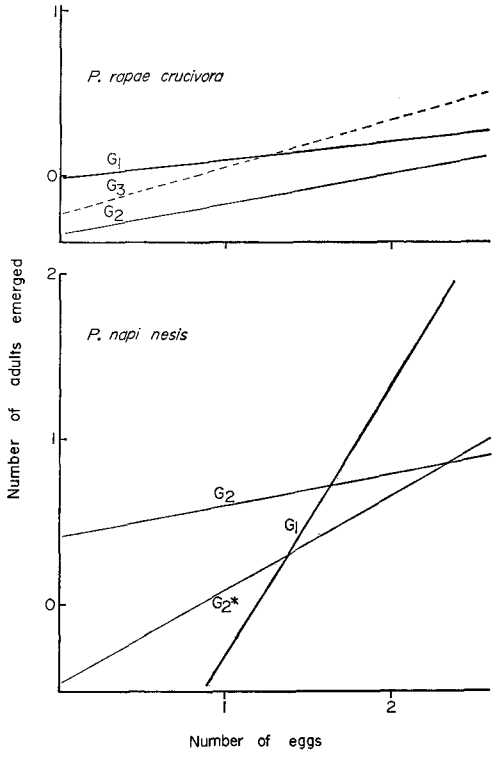

Fig. 25. Relation E-A. G_2*: Corrected based upon the data in 1979.

caused by depredation would not so high as *Prc* by the pupal sites covered with snow in this species.

Total regression equations between E-A were estimated as given in the last column of Table 24. A higher density-dependent mortality in *Prc* than in *Pnn* is also shown in Fig. 25. In summarization, key factors are parasitism by *Pteromalus puparum* and predation by birds at P-A stage both in *Prc* and *Pnn*.

Concluding remarks

Two related pierid species feed on a common food plant, *Rorippa sylvestris* on the University Campus. This plant was introduced to Hokkaido from Europe

before several decades (Itô, personal communication). Previously *Pnn* has mainly fed on *Cardamine leucantha* in woodlands, while *Prc* on cultivated crucifers. Such populations feeding on *Cardamine* in shaded areas are still kept in woodlands near Sapporo (Jozaneki and Hakkenzan). Since the proliferation of *R. sylvestris*, both species would begin to adopt this exotic plant as larval food. Its dense foliage would have allowed *Pnn* to live in open area, though females of *Pnn* do not lay eggs on the poor foliage of *Rorippa* at highly insolated areas. This makes habitat segregation between two species obscure, especially in adults, though *Prc* still prefers open area and *Pnn* shaded areas. For these pierid species inhabiting UC, *R. sylvestris* has an overwhelming importance than other crucifers, cabbages, radishes, etc., by its stability as a food source. It is perennial, abundantly grows in high density and constantly bears fresh and soft leaves preferred by young larvae. Different adult abundance between species and among generations, i.e. $G_h > G_1 > G_2$ in *Prc* $G_h < G_1 < G_2$ in *Pnn*, *Prc* $\gg$ *Pnn* in G_h, *Prc* > *Pnn* in G_1 and *Prc* < *Pnn* in G_2 was probably maintained in 1974 by following main factors:

G_h ·····	*Prc*	$\gg$	*Pnn* ·····	unknown
	$\vee$		$\wedge$	
G_1 ·····	*Prc*	>	*Pnn* ·····	different fecundity
	$\vee$		$\wedge$	
G_2 ·····	*Prc*	<	*Pnn* ·····	different mortality rate
	⋮		⋮	
	different mortality rate		different mortality rate between G_h and G_1, but different fecundity between G_1 and G_2	

Further, these two pierid species are different in the following aspects as elucidated in the present study:

	Prc		*Pnn*
Eggs			
Size	—	<	—
Number	—	>	—
Larvae and pupae			
Sedentariness	—	<	—
Density-dependence in mortality	—	>	—
Adults			
Generation time	—	<	—
Body size	—	>	—
r under laboratory conditions	—	>	—
Dispersal ability of females	—	>	—

Various features in the mode of life shown above can be interpreted by the *r*- and *K*- selection theory (MacArthur 1960, Pianka 1970, Southwood *et al.* 1974, Southwood 1977). The ecological strategy of a given species will be determined by

the degree of the stability of its habitat, i.e. *K*-selection more prevailing in permanent and predictable habitat and *r*-selection in temporal and unpredictable habitat. But such the generalization is not always appropriate for the present case in which two related pierid species recently began to depend upon a new common food source, *R. sylvestris* (cf. Young and Muyshondt 1972, Sterns 1976). Although *Prc* may be originally *r*-strategist and *Pnn* *K*- strategist, their ecological status on UC is still uncertain because they have barely adopted recently the new mode of life, for *Prc* the adoption of perennial food plant, for *Pnn* the life in open-land. But a hesitating prediction could be presented on the future of two species as to their relative abundance. Density-dependent mortality, which acts more intensely in *Prc* than in *Pnn*, would cause proportional increase in mortality rate or decrease in fecundity as population increase (Stubbs *op. cit.*). To avoid the density-dependent mortality, the egg density should be lowered. As far as the butterflies are concerned, decrease of egg density does not necessarily require the decrease of the number of eggs laid per female. A low egg density without decreasing the number of eggs laid per female could be realized either by a high dispersal ability or by a sparse oviposition by females as actually adopted by *Prc*. On the other hand, *Pnn* shows a tendency to increase the egg density within an area by its sedentary nature and concentration of eggs. These differences of life mode will cause increase of *Pnn* up to a certain population density relative to that of *Prc*, the limit of which could be clarified only by further analysis.

Summary

Population studies on two related pierid species, *Pieris rapae crucivora* (*Prc*) and *P. napi nesis* (*Pnn*) living in the same habitat and feeding on the same food plant were carried out on the campus of Hokkaido University from 1972 to 1979. Main results are:

1. The number of adults counted by belt transect census related exponentially with that estimated by the caputre-recapture method, i.e. the absolute density of adult butterflies can be estimated by combining the capture-recapture method and belt transect census.

2. Dominance of *Prc* in earlier years followed by increase of *Pnn* since 1974 was inferred.

3. In 1974 abundance of adults among three generations (post-hibernating generation=G_h, 1st generation=G_1 and 2nd generation=G_2) was $G_h>G_1>G_2$ in *Prc* while $G_2>G_1>G_h$ in *Pnn*.

4. The number of eggs laid per female in *Prc* was twice or thrice as many as in *Pnn*, that is, 600~800 in *Prc* and 200~400 in *Pnn*.

5. Duration of stay of adult butterflies within a limited area was longer in males than in females in *Prc*. Between two species, *Pnn* was more sedentary than *Prc* in G_1-females.

6. Total survival rate obtained from the results of life tables was: *Prc*-G_1;

1.07%, -G_2; 0.22%, -G_3; 1.13%, *Pnn*-G_1; 14.06% and -G_2; 0.32%.

7. Female number, number of eggs laid per female and total survival rate elucidated a considerable part of the fluctuation of the adult number estimated on the studied area in 1974.

8. The estimated intrinsic rate of natural increase, *r*, was higher in *Pnn* than in *Prc*, though considerably fluctuated among generations.

9. Considering the relations between mortality rate and density, the influence of density-dependent mortality was more intense in *Prc* than in *Pnn*.

Acknowledgements

I wish to express my sincere thanks to Prof. Shôichi F. Sakagami, Institute of Low Temperature Science, Hokkaido University, for his kind guidance to the present study and Prof. Mayumi Yamada, Zoological Institute, Hokkaido University, for his reading through the manuscript. Particular appreciation is due to Mr. Takeshi Ohtani, Zoological Institute, Hokkaido University for his unselfish help at tedious field surveys of adult chase. Cordial thanks are also due to all members of the staff of the Experimental Farm, Faculty of Agriculture, Hokkaido University, especially to Prof. Fumiji Kita for his allowance of butterfly census and other activities, and to Prof. Kôji Itô, Graduate School of Environmental Research, Hokkaido University, for his valuable advices on the larval food plant, *Rorippa sylvestris*.

References

Dempster, J.P. 1967. The control of *Pieris rapae* with DDT. I. The natural mortality of the young stages of *Pieris*. J. appl. Ecol. **4**: 485–500.

——— 1968. The control of *Pieris rapae* with DDT. II. Survival of the young stages of *Pieris* after spraying. *Ibid.* **5**: 451–475.

Frazer, D.G. 1973. Estimating butterfly numbers. Biological conservation **5**: 271–276.

Gôda, K. 1969. The seasonal distribution of the butterflies at Yanagida, Utsunomiya. Insecto Utsunomiya **20**: 9–19. (In Japanese)

Harcourt, D.G. 1966. Major factors in survival of the immature stages of *Pieris rapae* (L). Canad. Ent. **98**: 653–662.

Hasegawa, J. 1966. Seasonal variation of fore-wing length in *P. melete* and *P. napi nesis*. Coenonympha **18**: 343–345. (In Japanese)

Hasui, H. 1977. On the seasonal variability of survivorship curves and life tables of *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae). Jap. J. Ecol. **27**: 75–82. (In Japanese)

Hirose, K. 1954. Weather conditions and daily activity of *Pieris rapae crucivora*. Shin Konchû **7**: 33–39. (In Japanese)

Hiura, I. 1973. Butterflies migrate across the sea (in Japanese). iv+200 pp. Aoki, Tokyo.

——— 1979. An outline of genus *Pieris*. Acta Rhopalocerologica **3**: 1–19 .(In Japanese)

Itô, Y. and M. Murai 1977. On the research method for animal ecology (in Japanese). iv+558 pp. Kokinshoin, Tokyo.

———, Sakiyama, M. and M. Osada 1975. Population dynamics of *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae), an introduced insect pest in Okinawa. II. Features of the population dynamics based on the results of one-year survey. Jap. J. appl. Ent. Zool. **19**: 29–34.

Iwao, S. 1971. Estimstion of animal populations by caputre-recapture method. Biological Science (Tokyo) **23**: 14–22. (In Japanese)

Iwata, T. 1967. Large eggs. In M. Morisita and T. Kira (eds.), Natural history – Ecological studies, Ch. VIII, p. 211–248 (in Japanese). Chuokoron-sha, Tokyo.

Kawabata, M. 1976. The species composition and the seasonal change of butterflies in the suburbs of Fukuoka – A record. Physiol. Ecol. Japan **17**: 359–363. (In Japanese)

Kobayashi, S. and S. Takano 1978. Survival rate and dispersal of the adults of *Pieris rapae crucivora* Boisduval. Jap. J. appl. Ent. Zool. **22**: 250–254.

Kuno, E. 1973. Statistical characteristics of the density-dependent population fluctuation and the evaluation of density-dependence and regulation in animal populations. Res. Popul. Ecol. **15**: 99–120.

Kurata, M. 1955. A study on the egg size, egg number on a food-leaf and the larval growth with reference to determine each instar of *Luehdorfia puziloi inexpecta* Sheljuzhko. New Entomol. **4**: 23–26.

MacArthur, R. 1960. On the relative abundance of species. Amer. Natur. **94**: 25–36.

May, R.M., Conway, G.R., Hassell, M.P., and T.R.E. Southwood 1974. Time delays, density-dependence and single-species oscillations. J. Anim. Ecol. **43**: 747–770.

Miyashita, K., Itô, Y. and A. Gotoh 1956. Study on the fluctuation of egg and larval popultions of common cabbage butterfly and the factors affecting it. Studies on the mortality rate and behavior of field population of agricultural pest insect (3rd rept.). Jap. J. appl. Ent. **12**: 50–55. (In Japanese)

Morisita, M. 1967. The seasonal distribution of the butterflies in the suburbs of Kyoto. In M. Morisita and T. Kira (eds.), Natural history – Ecological studies, Ch. IV, p. 94–132 (in Japanese). Chuokoron-sha, Tokyo.

Morris, R.F. 1963a. pp. 30–37 in The dynamics of epidemic spruce budworm populations. (ed. R.F. Morris), Mem. Ent. Soc. Canada **31**.

Moss, J.E. 1933. The natural control of the cabbage caterpillars, *Pieris* spp. J. Anim. Ecol. **2**: 210–231.

Ohsaki, N. 1978. In pursuit of pierid populations: Adaptive strategies on the three related pierid species. Shizen **389**: 56–67. (In Japanese)

Okuyama, S. 1963. Concerning two naturalized plants. Jour. Jap. Bot. **38**: 256.

Osada, M. and Y. Itô 1974. Population dynamics of *Pieris rapae crucivora* Bosiduval (Lepidoptera: Pieridae), an introduced insect pest in Okinawa. I. Winter-spring generations. Jap. J. appl. Ent. Zool. **18**: 65–72.

Parker, F.D. 1970. Seasonal mortality and survival of *Pieris rapae* (Lepidoptera: Pieridae) in Missouri and the effect of introducing an egg parasite, *Trichogramma evanescens*. A. Entomol. Soc. Amer. **63**: 985–994.

Pianka, E.R. 1970. On *r*- and *K*-selection. Amer. Natur. **194**: 592–597.

Pimentel, G. 1961. Natural control caterpillar populations on cole crops. J. Econ. Entomol. **54**: 889–892.

Podoler, H. and D. Rogers 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. **44**: 85–114.

Richards O.W. 1940. The biology of the small white butterfly (*Pieris rapae*), with special reference to the factors controlling its abundance. J. Anim. Ecol. **9**: 243–288.

Roughgarden, J. 1971. Density-dependent natural selection. Ecology **52**: 453–468.

Sakagami, S.F. and H. Fukuda 1973. Wild bee survey at the campus of Hokkaido University. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **19**: 190–250.

Sato, Y. 1976. Experimental studies on parasitization by *Apanteles glomeratus* L. (Hymenoptera: Braconidae). I. Parasitization to different species of genus *Pieris*.

Appl. Ent. Zool. **11**: 165–175.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. **46**: 337–365.

———, May, R.M., Hassel, M.P., and G.R. Conway 1974. Ecological strategies and population parameters. Amer. Natur. **108**: 791–804.

——— and P.M. Reader 1976. Population census data and key factor analysis for the viburnum whitefly, *Aleurotrachelus jelinekii* (Frauenf.), on three bushes. J. Anim. Ecol. **45**: 313–325.

Stearns, S.C. 1976. Life-history tactics: A review of the ideas. Q. Rev. Biol. **51**: 3–47.

Stubbs, M. 1977. Density dependence in the life-cycles of animals and its importance in *K*- and *r*-strategies. J. Anim. Ecol. **46**: 677–688.

Suzuki, Y. 1978. Adult longevity and reproductive potential of the small cabbage white, *Pieris rapae crucivora* Boisduval (Lepidoptera: Pieridae). Appl. Ent. Zool. **13**: 312–313.

———, Nakanishi, A., Shima, H., Yata, O., and T. Saigusa 1977. Mating behaviour of four Japanese species of the genus *Pieris* (Lepidoptera: Pieridae). Kontyû **45**: 300–313.

Yamamoto, M. 1975. Notes on the methods of belt transect census of butterflies. J. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. **20**: 93–116.

——— 1977. A comparison of butterfly assemblages in and near Sapporo City, northern Japan. *Ibid.* **20**: 621–646.

——— 1978. Number of eggs laid by *Pieris napi nesis* Fruhstorfer (Lepidoptera, Pieridae) in Sapporo, northern Japan. New Entomol. **27**: 61–66.

——— and T. Ohtani 1979. Number of eggs laid by *Pieris rapae crucivora*, compared with *P. napi nesis*, in Sapporo (Lepidoptera: Pieridae). Kontyû **47**: 530–539.

Young, A.M. and A. Muyshondt 1972. Biology of *Morpholyphemus* (Lepidoptera: Morphidae) in El Salvador. J. New York Entomol. Soc. **80**: 18–42.