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Number of Eggs Laid by *Pieris rapae crucivora*, Compared with *P. napi nesis*, in Sapporo (Lepidoptera: Pieridae)

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Synopsis The number of eggs laid by the cabbage white butterfly *Pieris rapae crucivora* BOISDUVAL, was estimated by three methods, adult chase, forced oviposition and dissection of ovaries. In Sapporo a female may deposit 600–800 eggs during her life span. The egg-laying activity of *P. rapae* differs from that of *P. napi nesis* FRUHSTORFER in the presence of a high peak in the period soon after emergence.

Pieris rapae is one of the best known insects in the life table studies (MOSS, 1933; MIYASHITA *et al.*, 1956; DEMPSTER, 1968; OSADA and ITÔ, 1974), but three points have been left unsolved, *i.e.* key factors for the mortality, adult longevity and the number of eggs laid by a female. On the last item the results differ among authors: 350, RICHARDS, 1940; 400, IWATA, 1967; 200–300, ITÔ *et al.*, 1975. Considering individual, seasonal and local differences in this widespread species, more reliable reports should be accumulated. The present paper deals with the number of eggs laid by *P. rapae crucivora* studied on the campus of Hokkaido University, in comparison with that by *P. napi nesis* (YAMAMOTO, 1978).

Before going further, we wish to express our sincere thanks to Prof. Shôichi F. SAKAGAMI, Institute of Low Temperature Science, Hokkaido University, for his kind guidance to the present study and to Prof. Mayumi YAMADA, Zoological Institute, Hokkaido University, for his reading through the manuscript.

Materials and Methods

The three procedures used in a previous study on *P. napi* (YAMAMOTO *op. cit.*) were applied to the present study, too. 1) Adult chase: The newly emerged females were liberated after being individually marked and chased by two observers during the active period, 1976. 2) RICHARD's method: The egg laying was observed with a laboratory-reared female two hours per day from 25th to 27th and 30th May in 1977. 3) Dissection of ovaries: Many females were dissected from June to October, 1977, and the number of mature and immature eggs stored in ovaries was counted.

The population on the University Campus is basically trivoltine with the partial and unsuccessful fourth generation. The adults of the first generation, G_1, fly from early May to late June, those of G_2 from late June to late July and of G_3 from early August to mid September (Fig. 1). The larvae on the Campus mainly feed on the predominant weed *Rorippa sylvestris* with the larvae of *P. napi.*

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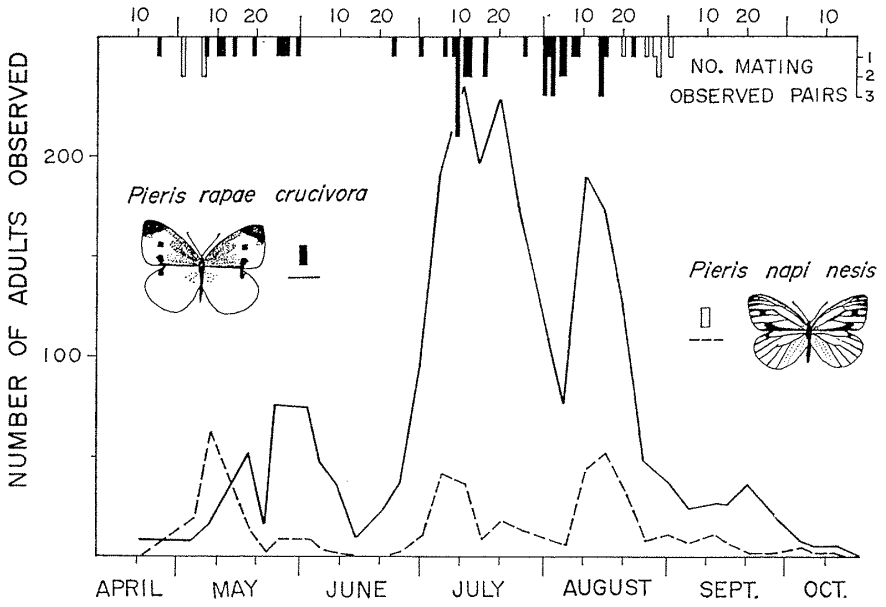

Fig. 1. Seasonal change of the number of adults observed of *P. rapae crucivora* and *P. napi nesis*, together with the number of pairs in copula observed (histograms from the top).

Results and Discussion

1. Burst of egg laying

As *P. rapae* females are less sedentary and more sensitive to observers than *P. napi* females, most marked females could not be chased more than three days. This made estimation of the exact number of eggs laid through their life span difficult, so that the number of eggs laid was inferred by comparing fragmentary data obtained from each adult chase for eleven females (3 ♀/G_1, 5/G_2, 3/G_3), whose daily life was successively traced more than two days. Fig. 2 shows fluctuation of the number of eggs daily laid by these females since emergence, excluding observations under adverse weather (low temperature, rain, *etc.*). At a glance it is obvious that the females burst into their egg-laying activity on the day after copulation, and that the number of eggs laid gradually decreases subsequently. TAKATA and ISHIDA (1957) also observed the egg-laying burst in the green house: The most vigorous egg laying on two to three days after emergence and the cessation of egg laying at about seven days old. Such an egg-laying burst in early flight period was not confirmed in *P. napi* reported previously (Fig. 2b).

2. A long chase after egg-laying burst

Three females were found dead on 10, 17 and 19 days old, respectively. One of them, No. 47, gave an additional information on the egg-laying activity during the latter half of the life span. She laid 453 eggs for ten days and died 19 days after emergence. Details of the egg laying are cited as follows: The female in copu-

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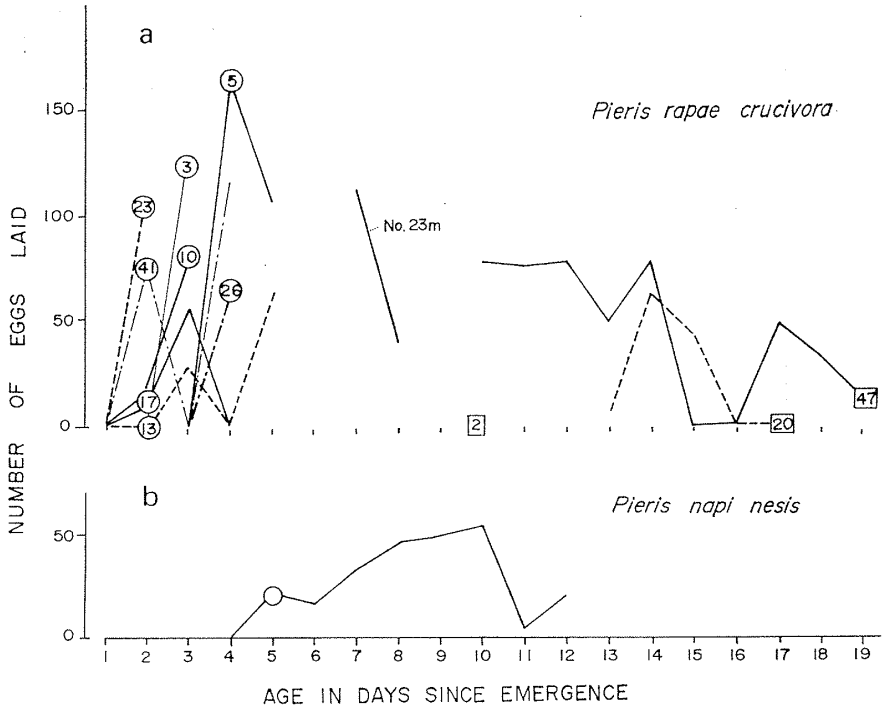

Fig. 2. The number of eggs laid by observed females, excluding the data taken under adverse weather. Broken lines=G_1, solid lines=G_2 and chain lines=G_3. Numerals in circles and squares represent the mark code of each female. Circles indicate copulation in the prior day, and three squares deaths of three females, Nos. $2/G_1$, $20/G_1$ and $47/G_3$. a. The results for eleven *P. rapae crucivora* females. b. The results for a single female of *P. napi nesis* from YAMAMOTO (1978, Table 1).

lation was marked and released in the afternoon Aug. 8th. Afterwards No. 47 was not traced until 16th because the other marked individuals had been chased. At 9: 19 on 17th August (10 days old), No. 47, who was just in oviposition, had been rediscovered. Her subsequent egg-laying activity is given in Table 1, together with weather conditions. The daily egg-laying rhythm had generally a peak in the morning, but was fairly affected by weather, *e.g.* complete cessation on Aug. 22nd and 23rd (due to a low temperature and a short insolation period), later start on Aug. 24th and 25th (due to a low temperature), *etc.* The number of daily laid eggs gradually decreased in due course. On 26th August after laying 13 eggs she died on the drive way by an accident.

3. *Inference of the egg-laying number by No. 47*

The total number of eggs laid by No. 47 in her life span can be estimated if the egg-laying number in the nine unobserved days was inferred based upon the weather conditions being important for oviposition. To know whether egg laying was made or not on each of these nine days, favorable conditions for egg laying are briefly discussed for both *P. rapae* and *P. napi* on emphasis of the maximum air temperature

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Table 1. Number of eggs laid and egg-laying duration of the female of *Pieris rapae crucivora*, No. 47, emerged and copulated on August 8th.

Date (Day age)	No. eggs laid (a.m./p.m.)	Total duration spent for egg laying (min.)	Insolation (h.)	Maximum air temperature (°C)	Remarks[1)]
Aug. 8 (1)	Emergence & copulation		2.7	23.8	−
9 (2)			5.5	24.8	+
10 (3)			2.9	22.1	−
11 (4)			8.2	24.1	+
12 (5)			2.6	23.8	−
13 (6)			5.5	20.8	−
14 (7)			10.6	22.6	+
15 (8)			5.8	21.9	−
16 (9)			11.7	22.9	+
17 (10)	78 (78/ 0)	19.75	10.6	24.2	
18 (11)	76 (76/ 0)	20.25	10.1	24.2	
19 (12)	78 (71/ 7)	26.50	8.3	27.5	
20 (13)	48 (48/ 0)	13.25	2.8	23.4	
21 (14)	79 (79/ 0)	25.00	3.6	23.8	
22 (15)	0		5.0	21.6	
23 (16)	0		2.7	22.0	
24 (17)	49 (37/12)	13.25	8.4	22.1	
25 (18)	32 (19/13)	15.50	7.4	21.1	
26 (19)	13 (13/ 0)	4.75	11.4	25.6	
Total	453	138.25			

1) +: egg-laying; −: not egg-laying condition.

and insolated period (*cf.* HIROSE, 1954) recorded by Sapporo Meteorological Observatory (see Table 1). In Fig. 3b the number of eggs laid is plotted to the maximum air temperature. The numerals given by each dot show the duration of insolated hours. The number of eggs shows a linear increase to the maximum air temperature except five deviated dots representing the burst of egg laying just after copulation in *P. rapae* (encircled by broken line). In the summer form of *P. rapae* egg laying was not made at the condition of 19.7°C/0.4 insolated hours, 21.6°C/5.0 hrs and 22°C/2.7 hrs but made at 20.9°C/4.4 hrs, 21.1°C/7.4 hrs and 21.1°C/13.2 hrs. This suggests that the females start oviposition even at less than about 22°C when the insolated period is longer than about 5.0 hrs, while the critical maximum air temperature seems to be about 18°C in the spring form. On the other hand, *P. napi* seems to have no such a critical air temperature within the limit of observations. The same favorable temperature is also obtained in Fig. 3a where egg-laying rate was plotted to the maximum air temperature. A female of *P. rapae* laid on the average about four eggs per minute between 22°C and 25°C in the summer form, and between 20°C and 23°C in the spring form. Under any thermal conditions within the limit of observations, *P. napi* laid two eggs, but the egg-laying rate of *P. rapae* dropped to this level at the thermal range out of 22°C–25°C in the summer form

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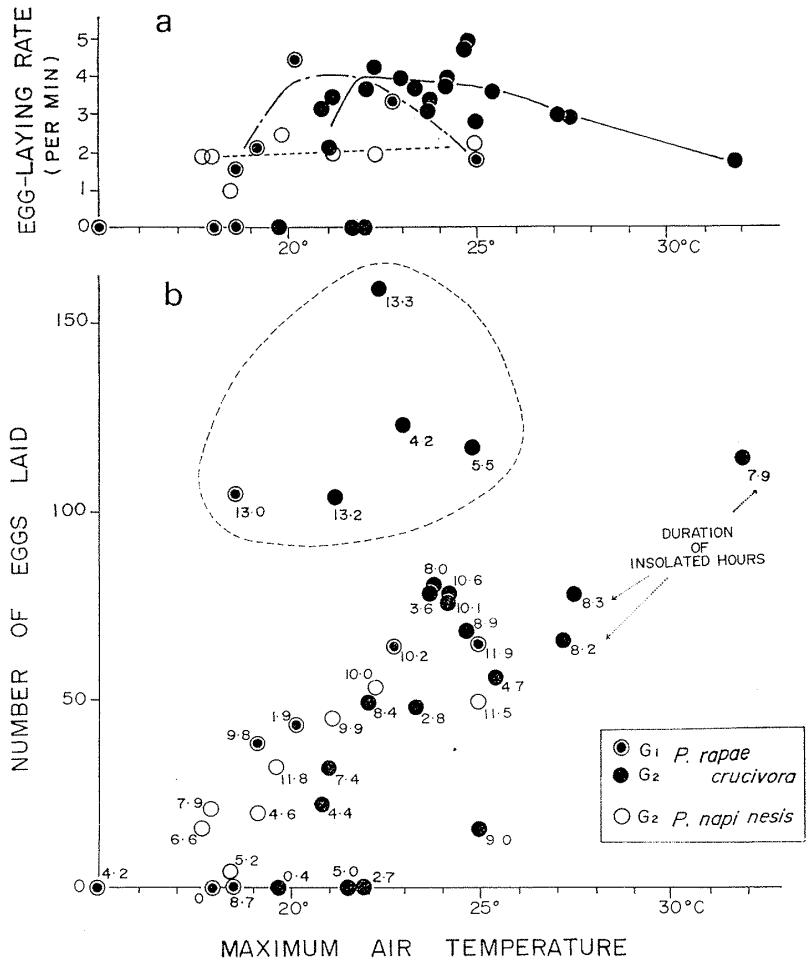

Fig. 3. The number of eggs laid (b) and the egg-laying rate (a) of *P. rapae crucivora* plotted to the maximum air temperature. Further explanations in the text.

and out of 20°C–23°C in the spring form.

In No. 47 four out of nine unobserved days were favorable for egg laying, while five unfavorable: 8th (emergence), 10th (a low temperature and a short insolation period), 12th and 13th (rainy), and 15th (as in 10th) (see remarks in Table 1). Assuming the same rhythm on these four probable egg-laying days, estimate of the total eggs laid is 634 ($=453+4\times453/10$), but actually may be more (about $800>453+78\times4$), considering egg-laying burst soon after copulation.

4. Egg laying within a flower pot

RICHARD's method was tentatively applied to a G_1 female which probably emerged between 9th and 14th May a week or so before the capture, judging both from scale wear on the abdominal dorsum (YAMAMOTO *op. cit.*) and a warm weather favorable for emergence. The behavior including oviposition was recorded every 30 seconds (Fig. 4). The average number of eggs was about 45 per day except for

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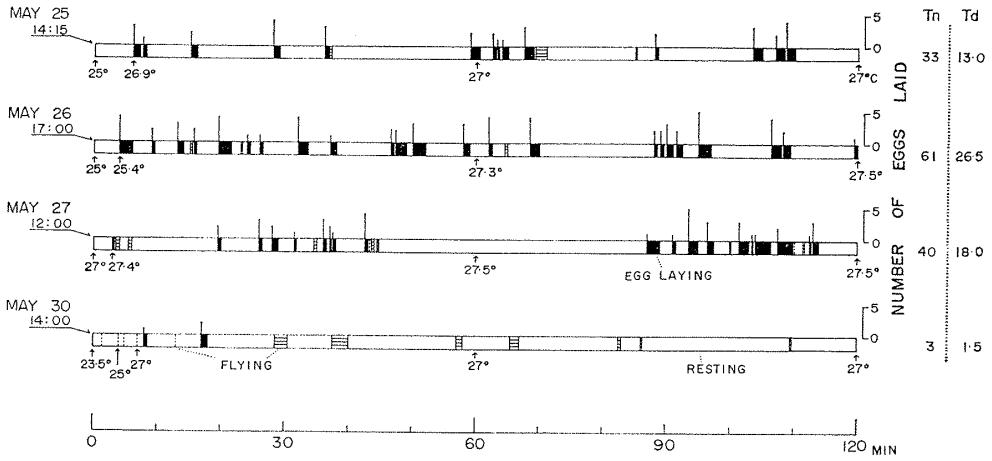

Fig. 4. The number of eggs laid by a particular female of *P. rapae crucivora* reared by RICHARD's method with durations of various activities exhibited. Tn: The total number of eggs laid. Td: The total duration for egg-laying.

the last experiment on 30th May (three eggs).

5. Comparison between RICHARD*'s method and natural conditions*

With the female of *P. napi* YAMAMOTO (*op. cit.*) obtained on the average 2.8 eggs/min. by RICHARD's method and 2.0 eggs/min. in natural conditions. He concluded that the RICHARD's method can be used for estimate of the egg-laying number in *P. napi.* In *P. rapae,* the result obtained by this method was compared with natural oviposition (Table 1). Although the duration for egg-laying was nearly similar (RICHARD's=13.0, 26.5 and 18.0: natural=19.75, 20.25, 26.50, 13.25 *etc.*), the egg-laying number by RICHARD's method (33, 61 and 40 eggs) was less than that under natural conditions (78, 76, 48, 79, . . . eggs). This means a lower egg-laying rate under forced conditions. The average egg number per minute was 2.3 (137/59.0) by RICHARD's method (Fig. 4), while 3.3 (453/138.25) in natural conditions (Table 1). This maladaptation to artificial conditions may have been caused by the trait of this species laying eggs one by one between flights in open field, while *P. napi*, having a higher egg-laying rate under artificial conditions, tends to lay eggs walking within small spaces of the dense foliage of *Rorippa.* Consequently, RICHARD's method seems inappropriate to obtain the reasonable estimate of the total number of eggs laid by *P. rapae.*

6. Number of ovarian eggs in unmarked females

Fig. 5 shows the seasonal change of the average number of oocytes stored in the ovaries of the females caught almost day by day and summed up for every five day period except for the spring season. In total, eight females were examined for G_1, 115 for G_2, 97 for G_3, and 52 for G_4. Decrease of the number of oocytes stored in ovaries of older females is probably due to prior ovipositions, though the decrease shown in Fig. 5 underestimates the real egg-laying number on account of

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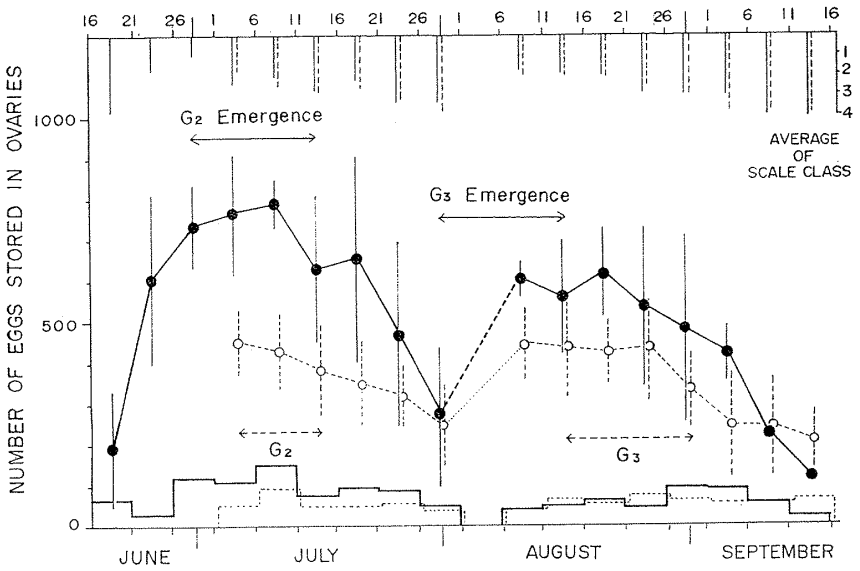

Fig. 5. Seasonal change of the average number of oocytes in the ovaries of unmarked females and S.D. (vertical lines), together with the number of mature eggs (histograms) and relative age (vertical lines from the top). Solid lines=*P. rapae crucivora*, broken lines=*P. napi nesis*.

intermingled age classes among females dissected within a single interval. Especially during the emergence period the decrease is not so much clear due to the presence of newly emerged females with many oocytes. But fresh females are distinguished from older ones by the captured date and the scale classes (YAMAMOTO *op. cit.*).

Table 2. Average number and S.D. of oocytes in ovaries of unmarked females of *Pieris rapae crucivora* for each scale class. Mature eggs are parenthesized.

Date \ Scale class		I	II	III	IV
July	1– 5	636 (49)±140	841 (86)± 29	772 (130)±162	859 (173)± 90
	6–10	810 (138)± 39	748 (164)	776 (156)± 76	/
	11–15	714 (50)	691 (94)±169	587 (59)±171	542 (54)±239
	16–20	759 (73)±181	768 (106)±185	596 (105)±240	226 (70)± 76 G_2
	21–25	532 (108)	/	560 (101)±273	382 (67)±179
	26–31	/	462 (60)±265	318 (54)±110	160 (33)± 75
Aug.	6–10	629 (9)± 16	568 (48)± 74	604 (84)	/
	11–15	526 (29)± 94	603 (62)±121	519 (59)±171	414 (46)±305
	16–20	635 (38)±161	612 (58)± 97	569 (77)±220	751 (159)
	21–25	/	436 (15)± 80	595 (51)±183	467 (63)±375
	26–31	/	637 (99)±273	488 (102)±219	349 (71)±157 G_3
Sep.	1– 5	/	/	419 (91)± 69	/
	6–10	/	/	/	214 (54)
	11–15	/	/	/	116 (20)

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The real number of eggs laid is approximated by the discrepancy of the average oocyte number between newly emerged females and old exhausted ones as shown in Table 2 by the number of oocytes of the females in each scale class for each interval. In G_2 the discrepancy of the average number between 810 (138=mature eggs) $\pm$39 (S.D.) and 160 (33)$\pm$75 is considered as an approximation of the average number of eggs actually laid, 650$\pm$106 (at 95% fiducial limit on the assumption of the normal distribution). The estimation for G_3 females is 513$\pm$204, less than that in G_2 females. For G_1 so few females were dissected that the obtained number, 689, is less reliable. The number of mature eggs is much higher in the earlier stage of a generation than in the later stage, especially in G_2 (Fig. 5, Table 2). And the average number of mature eggs is remarkably higher than that of the females taken in copula (24$\pm$31, n=14). This fact seems to imply a rapid maturation of eggs and a higher egg-laying activity at earlier flight period as suggested in previous sections.

7. Number of ovarian eggs in marked females

Marked females emerging from pupae collected in field were liberated in early July (G_2) and early August (G_3). Dissection of ovaries was made for recaptured females. Decrease of number of oocytes in G_3 females was obscure by the absence of older females examined. Fig. 6 graphically shows the pattern of egg decrease in G_2 females, compared with the result obtained for *P. napi* (YAMAMOTO *op. cit.*, Table 3). In G_2 decrease of number of oocytes between the youngest and oldest females was about 700 (*ca.* 800–*ca.* 100), which is similar to that obtained in previous sections. NORISS (1935) reported a similar value (843=eggs laid 356+ ripened 487) on the average of six females fed on a solution of cane-sugar solved in distilled water.

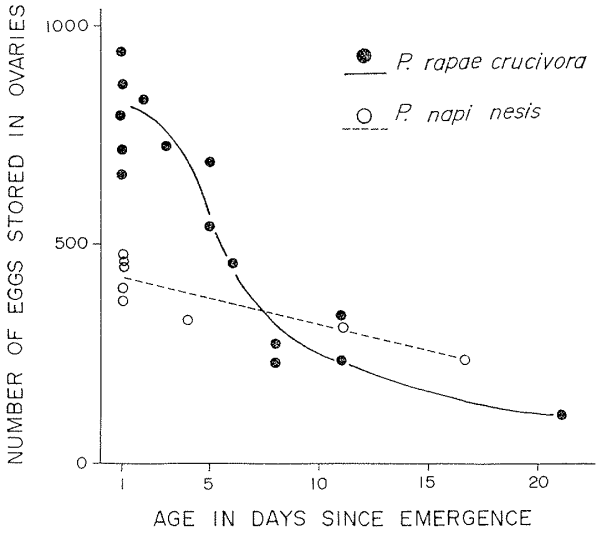

Fig. 6. Decrease of egg number in ovaries of *P. rapae crucivora* and *P. napi nesis* with the age after emergence.

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Conclusion

The difference of the number of eggs laid in G_2 between *P. rapae* and *P. napi* by the employed methods is tabulated as follows:

Method	*P. rapae*	*P. napi*	Ratio (r/n)
Adult chase	634–800	240–400	2.6–2.0
Dissection of ovaries			
of unmarked females	550–750	153–387	3.6–1.9
of marked females	700	250	2.8

P. rapae has a fecundity about three times as high as *P. napi*. Further the egg-laying curve of *P. rapae* has a high peak soon after copulation. The difference is expressed as two presumable curves given in Fig. 7.

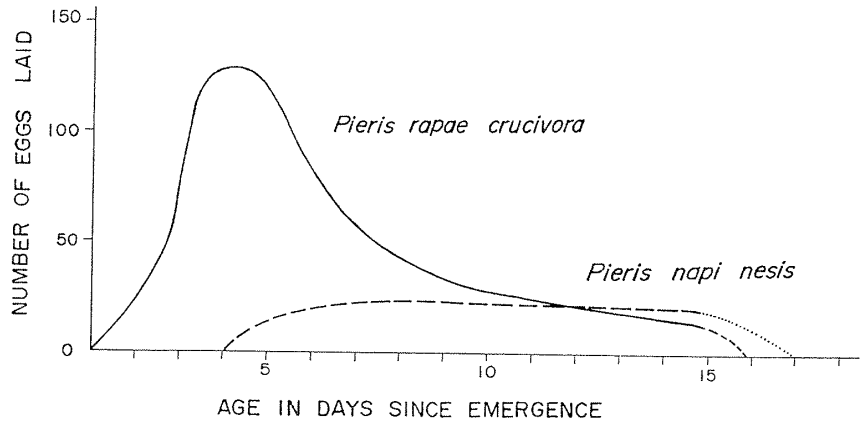

Fig. 7. Presumable curves showing egg-laying activity and age sequence in *P. rapae crucivora* and *P. napi nesis*.

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Postscript After the completion of the manuscript, a paper of Suzuki, Y. (Appl. Ent. Zool. 13: 312–313, 1978) was published. His result ensures our conclusion, viz. the oviposition curve of *P. rapae* (based on 13 females reared individually in plastic cages) has a peak at the age of 3-day-old and resembles the solid line of our Fig. 7. His rearing technique seems to have an advantage over the Richard's method.

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