Phenology and Dispersal of *Henosepilachna pustulosa* (Kôno) at Thistle Stands near a Potato Field in Sapporo[1)]

By

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(*With 6 Text-figures and 6 Tables*)

In *Henosepilachna vigintioctomaculata* complex (Hv-complex), two major groups, *H. vigintioctomaculata* (Motschulsky) (Hv)[2)] and *H. pustulosa* (Kôno) (Hp)[2)] are found in Japan (Katakura 1974 b). Under field conditions the former depends principally on potato while the latter on thistles. But feeding experiments proved that while Hv could not grow with thistle, Hp fed on both plants and their larvae successfully grew with both plants virtually without difference (Watanabe and Sakagami 1948, Kurosawa 1953, Yasutomi 1954, Watanabe and Suzuki 1965, Hinomizu 1976, etc.). Under field conditions Hp has occasionally been recorded from potato together with Hv (Inoue 1952, Yasutomi 1952, Kurosawa 1953, Sakagami and Yamaguchi 1954, Katakura 1976). But how Hp behave when it lives in thistle stands near potato fields has yet not been studied. This problem seems important not only for clarification of the Hv-complex but also for the study of adaptation of phytophagous insects to new host plants in general. The present paper deals with the phenology and dispersal of adult Hp in the area where a potato field was set up near thistle stands.

The work was carried out for two years, 1974 and 1975. Although methods and results varied between two years in minor aspects, the similar tendencies were recognized so that the descriptions are given mainly on the basis of results in 1975, with some references to those in 1974 when necessary.

Before going further I wish to express my sincere gratitude to Dr. Shôichi F. Sakagami for his pertinent guidance through the present study, and to Prof. Mayumi Yamada for his reading through the manuscript. Cordial thanks are also due to Mr. Haruo Katakura for his continuous advices throughout the course of the work, and to Mr. K. Nakamura, Entomological Laboratory, Kyoto University, who kindly allowed me to cite his unpublished data.

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1) Contributions to the knowledge of *Henosepilachna vigintioctomaculata* complex, VI.
2) Usage of these scientific names and abbreviations follows Katakura (1974 a, b).

Area studied and Method

The studied area is situated at Misumai Arboretum belonging to Hokkaido University, about 15 km southwest of the center of Sapporo. The surveyed field was chosen in the area where a small stream was running through a larch afforestation mixed with some broad leaf and coniferous trees (Fig. 1, A$\sim$B). The gallery forest consisted of broad leaf trees. Undergrowth was uniform and thick especially in larch afforestation, consisting of bamboo-grass about one meter high. The survey area, about 150 m long, was conveniently divided into five zones ($Z_1\sim Z_5$). There were abundant thistles along the stream, especially in Z_2, and Hp (all Hp belonged Sapporo Form or type P-III in Katakura 1974 b) lived on their leaves. Watanabe and Suzuki (1965) reported that about 94% of Hp larvae taken from Misumai could complete their development with potato. Therefore, the studied

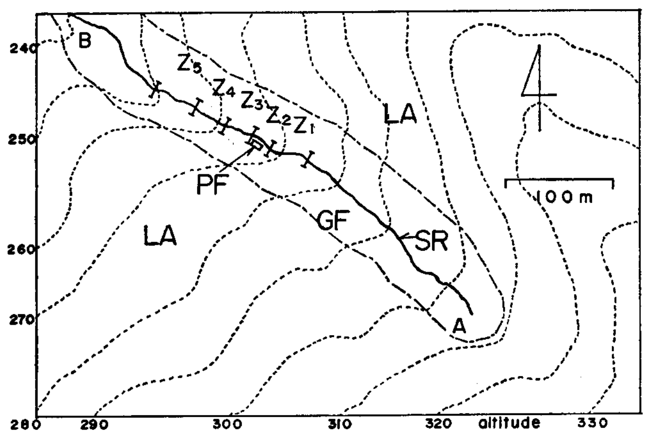

Fig. 1. The survey field showing five zones ($Z_1\sim Z_5$). SR. small stream, GF. gallery forest, LA. larch afforestation, PF. potato field.

local population seems to show a relatively high acceptability for potato. A small area was chosen in Z_2 adjoining thistles and 54 stocks of potato were cultivated there from May to September (Fig. 2). When potatoes sprouted in late May, Hp had already fed actively on thistles and oviposited on the leaves. The observations were made from 10 May to 4 October about every week. At each daily observation all adults were picked up from leaves of food plant and marked individually with five color paints. The marked individuals were gently liberated on the leaves where they were caught. Individual numbers in each zone were recorded at each observation, males and females separately. Furthermore, individual numbers were recorded in Z_2 for both thistle stands and potato fields separately. Thistle stocks were distinguished individually in all zones with vinyl tapes bearing respective number marks. In Z_2, thistle stands consisted of 26

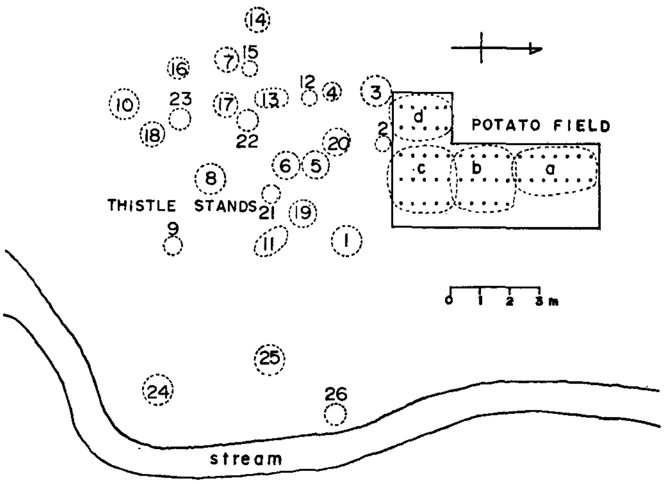

Fig. 2. Schematic representation of Z_2. Thistle stands: Each stock is shown by numbers. Dotted circles or ellipes are the extent covered by leaves of each stock. Potato field: Each dot represents one stock. Dotted circles are stock groups.

groups of stocks (Fig. 2). Potato field was also divided into four groups of stocks (a$\sim$d). Therefore, in all zones individuals were recorded at every stock in thistle stands and potato field separately.

Results and Discussions

1. Phenology

All five zones combined, 162 post hibernating adults (*HA*) and 225 newly emerged adults (*NA*) were confirmed by periodical census. Fluctuation of individual number at each zone was in general as follows: some individuals were continuously observed from May to early August, in early August individuals once decreased to a very low level followed by a burst in mid or late August (Fig. 3). In Z_2 fluctuation of individual number was bimodal with peaks in May to June and August. The first peak was composed of *HA* and the second one of *NA*. Such bimodal phenology of P-III was also confirmed in some other populations observed near Sapporo (Katakura 1976). In some of these cases, however, both peaks were a little earlier than in Misumai, about ten days in both seasons (Katakura unpub.). Time lag in Misumai was presumably brought by the delayed snow thawing compared with Sapporo. Individual number was most abundant in Z_2 in both *HA* and *NA*, occupying 50.4% and 41.6% of all individuals respectively. This was probably caused by the highest abundance of thistles there. In *HA* newly marked number reached the upper asymptote in mid July,

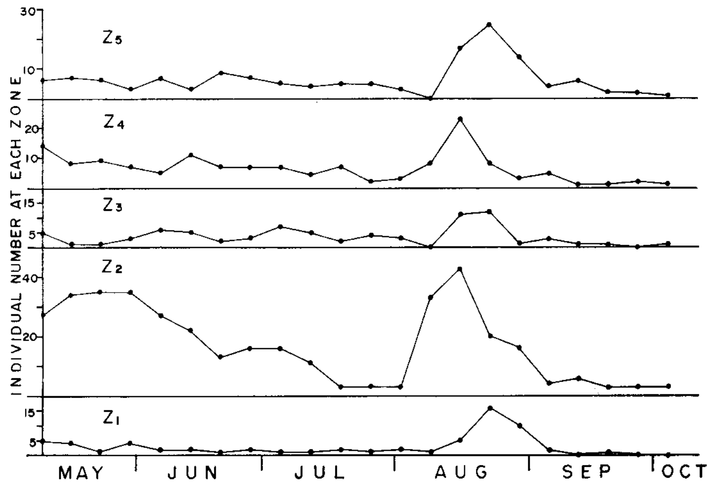

Fig. 3. Seasonal fluctuation of adult numbers at each zone.

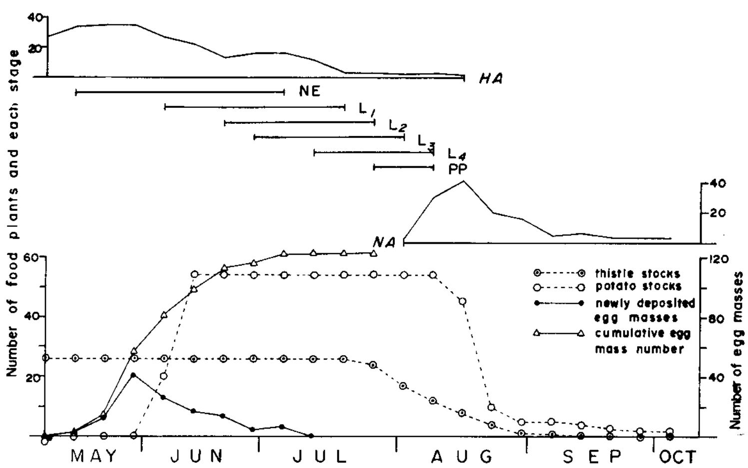

Fig. 4. Top. Sequence of each stage in Z_2. Bottom. Seasonal fluctuation of numbers of thistle and potato stocks as well as of numbers of newly laid egg masses and their cumulative curve. *HA*: Post hibernating adults, *NA*: Newly emerged adults, NE: Newly laid egg masses, L: Larvae of *n*th instar, PP: Pupae.

suggesting the deaths of most individuals. At that time thistle consumption by both adults and larvae attained a notable degree. In mid July many larvae of 1st~4th instars were found on thistle leaves (Fig. 4). The 4th instar larvae first observed on 12 July. They must feed on thistle and pupate till mid August, when virtually all thistles withered. If many *HA* survived to late July they would feed on much thistles and would threaten the survival of the new generation by food shortage. Therefore, alternation of generations in P-III is well synchronized with the growth of thistles. The cumulative number of *NA* attained the upper asymptote in mid September when adults began to hibernate.

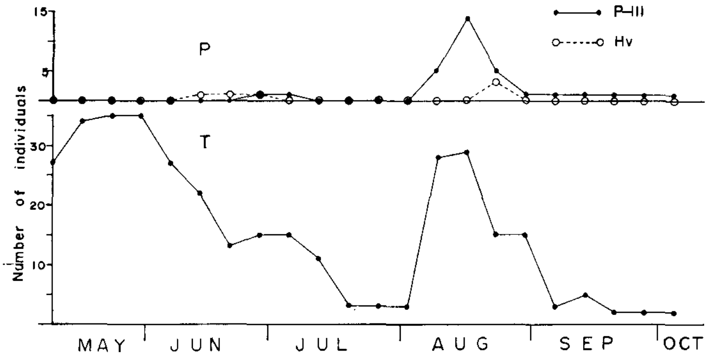

Fig. 5. Seasonal fluctuation of adult numbers of P-III and Hv in Z_2. P: Potato field, T: Thistle stands.

In Z_2 thistle stands and potato field were separately censused. Seasonal fluctuation of individual number of P-III on thistles had two peaks, May and August (Fig. 5). On the other hand, few individuals were observed at potato field adjacent to thistle stands during May to early August and only one peak by *NA* was confirmed in late August. A few individuals of Hv (belonged type V-II in Katakura 1974 b) were also observed in potato field. Total number of P-III was higher both in *HA* and *NA* on thistles than on potatoes. In *NA*, however, cumulative number at potato field was about equal to those of Z_1 or Z_3. In 1974, more potato stocks were planted than in 1975 and *NA* number at potato field were higher than those of any of other four zones. This indicates concentration of *NA* in August in the limited potato field because of food shortage. As shown in Fig. 4 over 70% of thistle stocks withered in Mid August, while potato stocks survived till late August. Therefore, the August peak in potato field was certainly an outcome of the dispersal of individuals from thistles forced by food scarcity. The thistle rosettes appeared since early August when the main stems withered, but their tissues were so soft that were not eagerly consumed by *NA*. For instance, all 26 thistle stocks (except five ones) in Z_2 issued rosettes but the ratio of number consuming them to total number observed in Z_2 were only 4/27 (16 August), 1/11 (24 Aug.), 2/15 (30 Aug.). On 16 August 14 individuals were observed in potato field. Therefore, *NA* in Z_2 seemed to feed more on potato leaves than on thistle rosettes when the former were abundant. In other zones, however most *NA* were observed on thistle rosettes or still survived thistle stocks. In Z_5 on 24

August more than a half of 25 individuals concentration on one rosette and one suvived thistle stock.

Oviposition on thistle in Z_2 had a peak in late May (Fig. 4). Cumulative numbers of egg masses attained 123 in Z_2. In potato field seven egg masses were confirmed from late June to mid July. As shown in Fig. 5 four individuals of Hv, one *HA* female, two *NA* females and one *NA* male were observed on potato field. Their provenances are unknown. The nearest potato field infested by Hv was about 500 m distant, no *Schizopepon bryoniaefolius* fed by Hv (cf. Katakura 1975) were found within the survey area. Only one female of P-III/*HA* consuming potato leaves was confirmed from May to August. Two and six pupae were confirmed respectively on 9 and 16 August in potato field. As both Hv and P-III were found in the area and two forms are distinguishable one another only by adults, the exact numbers of egg masses and pupae of P-III could not be determined. Potato leaves were ready to be consumed since early June, but at that time oviposition peak on thistle leaves was already passed over (Fig. 4). Consequently, few individuals of P-III laid eggs on potato leaves. This phenologic discrepancy between P-III and potato makes realization of a high density of P-III on potato difficult.

Summarizing, seasonal phenology of P-III is well adjusted to the availability of thistles. Dispersal is to some extent caused by the relative abundance of food plants as described in the next section.

2. Dispersal

Among all marked adults, 97 (59.9%) of *HA* and 64 (28.4%) of *NA* were rediscovered at least once (Table 1). The rediscovery ratios are relatively higher

Table 1. Rediscovery of individually marked adults in all five zones.

		HA			*NA*		
		♀	♂	Total	♀	♂	Total
No. indiv. marked		82	80	162	110	115	225
No. indiv. rediscovered *n* times	*1*	15	17	32	22	28	50
	2	13	15	28	5	5	10
	3	11	5	16	2	2	4
	4	3	5	8	0	0	0
	5	2	1	3	0	0	0
	6	2	2	4	0	0	0
	7	0	3	3	0	0	0
	8	0	3	3	0	0	0
Rediscovery	No.	46	51	97	29	35	64
	Ratio (%)	56.1	63.8	59.9	26.4	30.4	28.4
Rediscovery twice or more	No.	31	34	65	7	7	14
	Ratio (%)	37.8	42.5	40.1	6.4	6.1	6.2

than in other similar experiments with various insects. The maximum rediscovery times were eight in *HA* and three in *NA*. Rediscovery times and ratio of *NA* were less than those of *HA*. The number of *NA* rediscovered twice or more was less than one fourth of those in *HA*. This may be in part due to the scarcity of thistles in autumun, which makes the discovery around host plants difficult, and also caused by the sedentary nature of the species when the host plant is abundant from spring to early summer. On 14 June and 20 July some dead adults were found on thistle leaves and on 27 September and 4 October some adults attaching to a fallen dead leaf were discovered. Therefore, the undiscovered marked individuals might partly die in *HA* and partly enter in hibernation in *NA*. At a downward area about 100 m distant from Z_5 there were several thistle stocks. Imigration to this uncensused area from the studied area is possible. But about 23% of marked individuals were rediscovered three times or more. This may favor the rarity of too distant emigration from the studied area.

Among rediscovered *HA* adults, only one female showed dispersal P⇀P (= marked in potato field and rediscovered there) (Table 2). It is obvious that this female ♀139 had lived on thistle so that real dispersal was T⇀P⇀P. On the other

Table 2. Comparison of numbers dispersal type T→T and T→P in *HA* and *NA*

			HA			*NA*		
			♀	♂	Total	♀	♂	Total
Redis-covered *n* times	*1*	Total number	15	17	32	22	28	50
		T→T	14	17	31	18	22	40
		T→P	0	0	0	0	3	3
		P→P	1	0	1	4	2	6
		P→T	0	0	0	0	1	1
	2	Total number	13	15	28	5	5	10
		T→T→T	13	15	28	5	4	9
		P→P→P	0	0	0	0	1	1

hand, one fifth of once rediscovered *NA* adults showed dispersal involving potatoes. From the overwhelming high ratio of egg masses found on thistles than on potatoes (123: 7) in Z_2 and the discovery of Hv/*NA* only in potato field, nearly all *NA* adults rediscovered in potato field must have emerged on thistles, therefore dispersal types P⇀T, P⇀P, and P⇀P⇀P must be actually T⇀P⇀T, T⇀P⇀P, T⇀P⇀P⇀P. In 1974, too, T⇀P occured only 5% in total *HA* but about 22% in *NA*, showing an increased dispersal from thistle to potato in *NA*. Furthermore, as far as only the first rediscovery is concerned T⇀P was not recorded in *HA* but attained 17% in *NA*, apparently caused by the scarcity of host plant.

As shown in Table 3, 17.5% of rediscovered individuals in *HA* and 46.8% in *NA* were found on the same stocks at each census. This higher ratio in *NA* may

Table 3. Degree of conservatism to their food plants in *HA* and *NA*.

		HA			*NA*		
		♀	♂	Total	♀	♂	Total
Total number rediscovered		46	51	97	29	35	64
Redisocvered on same stock	No.	12	5	17	15	15	30
	Ratio (%)	26.1	9.8	17.5	51.7	42.9	46.8
Rediscovered on different stock	No.	19	26	45	11	18	29
	Ratio (%)	41.3	51.0	46.4	37.9	51.4	45.3

indicate that amount of thistles decreased in autumn and individuals once found out the host plant by chance might not discover other one near there compared in spring so that not leave there for a few weeks. On the other hand, 46.4% of rediscovered *HA* and 45.3% of *NA* were found on different stocks at each census. There were six individuals which were rediscovered four or more times and on five or more different stocks in Z_2 and its adjacent zones. All of them belonged to *HA* and their dispersal courses are shown in Fig. 6. Percentage ratios described above and these dispersal courses show frequent short distance dispersals of adult P-III in Misumai. The higher ratio of dispersal of males than females in *HA* may relate to search for the mating partner. Extent of dispersal in rediscovered individuals is shown in Table 4. Most individuals dispersed intrazonally or between two adjacent zones. Individuals dispersed over more than a zone (transzonal) were less than 20% in both *HA* and *NA*. Percentage ratio of individuals dispersed transzonally were especially low in *NA*. But the rediscovery ratio of *NA* was also low so that far reaching dispersal from the emerged point is not excluded.

Table 4. Extent of dispersal in *HA* and *NA*

			HA			*NA*		
			♀	♂	Total	♀	♂	Total
Total number rediscovered			46	51	97	29	35	64
Dispersal pattern	intrazonal	No.	32	28	60	24	28	52
		Ratio (%)	69.6	54.9	61.9	82.8	80.0	81.3
	interzonal between adjacent zones	No.	7	13	20	3	4	7
		Ratio (%)	15.2	25.5	20.6	10.3	11.4	10.9
	transzonal	No.	6	11	17	2	3	5
		Ratio (%)	13.0	21.6	17.5	6.9	8.6	7.8
	ditto within a week	No.	2	6	8	2	2	4
		Ratio (%)	4.3	11.8	8.2	6.9	5.7	6.3

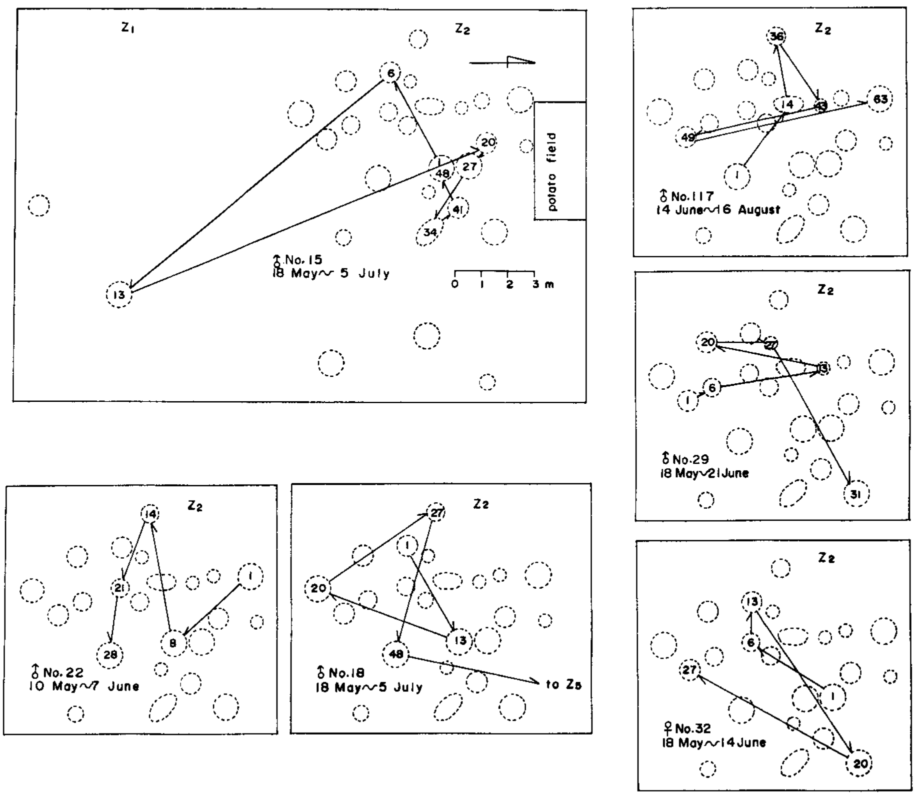

Fig. 6. Interstock dispersal of six *HA* individuals in thistle stands with marking dates. Dotted circles and ellipes are thistle stocks of Z_2 and a part of Z_1. Arrows show dispersal courses. Numerals are days after marking.

According to Nakamura (unpub.) in a Hp/*HA* population in Kyoto about 75% of adults were rediscovered in spring at the points where they were marked in the last autumn. But as host plants were abundant before hibernation in Kyoto, dispersal pattern of *NA* might be different from that in Misumai. Individuals dispersed transzonally within a week were less than 10% in both *HA* and *NA*. Consequently long distance dispersal within a short duration seems less frequent than interstock dispersal. Subsequent rediscovery courses of individuals involving transzonal dispersal are shown in Table 5. The maximum dispersal distance was given by ♀69 in *HA* from 31 May to 7 June over two zones about 100 m distant for each other. Except this individual and ♂159 in *NA* most transzonal dispersal required one week or more. Most individuals in Table 5 dispersed with a directionally, for instance, ♂3—$Z_2 \rightarrow Z_4 \rightarrow Z_5$, ♀8—$Z_2 \rightarrow Z_3 \rightarrow Z_5$, ♀12—$Z_2 \rightarrow Z_4 \rightarrow Z_5$, ♂48—$Z_5 \rightarrow Z_3 \rightarrow Z_2$, etc.. Possibly some adults in the studied area gradually

Table 5. Dispersal courses of some individuals dispersed over one zone. $Z_1 \sim Z_5$. zone symbols. Z_n-n: stock number n in zone Z_n. * Transzonal dispersal during more than a week. ** Transzonal dispersal within a week. n. Frequency of rediscovery.

				May				June				July				August		
	n	♀♂	No.	10	18	24	31	7	14	21	28	5	12	20	27	2	9	16
	1	♀	87				Z_2-7				Z_5-4							
		♂	35*		Z_1-1		Z_5-9											
		♀	69**			Z_2-21	Z_2-12	Z_5-10										
		♂	3		Z_2-3			Z_4-9		Z_5-8								
	2	♂	34		Z_2-17	Z_2-5					Z_5-11							
		♂	39		Z_4-1					Z_2-14	Z_1-4							
		♂	48*		Z_5-4	Z_3-4	Z_2-5											
		♂	70*			Z_1-7	Z_1-6		Z_4-10									
HA		♂	80			Z_5-4				Z_2-14		Z_2-14						
		♀	8		Z_2-5	Z_2-1		Z_3-3						Z_5-11				
	3	♀	26		Z_2-17			Z_2-12	Z_2-6		Z_4-5							
		♀	88				Z_2-13	Z_1-7							Z_3-6		Z_4-3	
		♂	57			Z_2-6				Z_4-8	Z_4-8			Z_4-5				
	4	♂	60*			Z_2-11	Z_2-19	Z_2-18	Z_4-8		Z_5-1							
	6	♀	12*		Z_2-5		Z_2-14	Z_4-2				Z_4-4	Z_4-5	Z_4-5	Z_5-4			
	7	♂	18*		Z_2-7		Z_2-6	Z_2-10	Z_2-14			Z_2-8		Z_5-4		Z_5-2		Z_5-2
	8	♂	54*			Z_2-3	Z_2-8	Z_4-3	Z_3-3			Z_4-1	Z_4-9		Z_4-9	Z_4-9	Z_4-9	

						August				September		
	n	♀♂	No.	2	9	16	24	30	6	13	20	27
		♀	88*			Z_4-2	Z_2-1					
		♀	178*				Z_2-4	Z_5-6				
NA	*1*	♂	152				Z_2-2					Z_4-9
		♂	159**				Z_5-1	Z_4-7				
	2	♂	167*				Z_1-4	Z_1-3	Z_3-6			

emigrated to the other area, extending the distribution. Concerning a Hv/*HA* population in Kyoto, Iwao et al. (1963) reported that rediscovery ratio of marked insects was relatively high (40–50%) in a week after the release and once fixed to a small range they moved only less than 2 m within a week. Nakamura (unpub.) also said that most adults of Hp/*HA* population in Kyoto remained within a narrow area of 40～50 m in diameter and long dispersal across a valley was exceptional. From these results the sedentary nature seems common to both Hv and Hp.

Individuals marked in the autumn 1974 and rediscovered in the spring 1975 are shown in Table 6. In 1974 observations were made from 4 June to 21 September about every week. The final check was made on 20 October. At each daily observation all adults were picked up from leaves of food plant and marked with distinct color paints specifying zones, Z_1 white, Z_2 vermilion, Z_3 green, Z_4 pink, Z_5 blue, respectively. The marked individuals were again gently liberated on the leaves where they were found. Furthermore, in Z_2 adults observed in potato field were marked with yellow color to distinguish from those on thistles.

Table 6. Number of individuals marked in 1974 autumn and rediscovered in 1975 spring as well as the points of rediscovery. Z_2T. thistle stands in Z_2. Z_2P. potato field in Z_2.

Marked at		Z_1	Z_2T	Z_2P	Z_3	Z_4	Z_5
No. marked in 1974		27	176	61	8	51	42
Rediscovered on 10 May 1975	No.	2	7	6	0	3	1
	place	Z_4-2	Z_2T-6 Z_3-1	Z_2T-3 Z_3-1 Z_4-1 Z_1-1	—	Z_2T-1 Z_4-2	Z_2T-1
Rediscovered on and after 18 May 1975	No.	5	10	8	0	3	3
	place	Z_2T-1 Z_4-3 Z_5-1	Z_2T-7 Z_3-1 Z_4-1 Z_5-1	Z_2T-7 Z_3-1	—	Z_2T-1 Z_4-2	Z_2T-1 Z_4-1 Z_5-1

Some adults observed in Z_2, both *HA* and *NA*, were marked individually by a piece of numbered paper sticked on the left elytra. Concerning *HA* 30 males and 30 females were collected on 1 and 3 June from thistles in Z_2. They were individually marked and liberated on 3 and 4 June on thistles of Z_2 according to the numerical order, Nos. 1～3 of both sexes on thistle stock 1, Nos. 4～6 on 2, etc., to stock 10. Concerning *NA*, 50 males and 67 females were collected during 10～25 August from thistle field of Z_2 and liberated on thistles on 15 and 27 August as in the case of *HA*, Nos. 1～3 on stock 1, Nos. 4～6 on 2, etc.. As shown in Table 6 only less than 10% (except Z_1) of individuals marked in 1974 were rediscovered in 1975. This low ratio may be caused partly by removal of color paints and partly by far reaching dispersal before and after hibernation. Although about 26% of individuals marked at Z_2 in 1974 were redisocvered in potato field, individuals immigrated into potato field in 1975 were only one. This suggests that the acceptance of potato leaves by some *NA* adults in 1974 did not evoke immigration into potato field by *HA* in 1975. Hibernation site and mortality during hibernating period are unknown, but most individuals rediscovered at Z_2 in 1975 had been marked at the same zone in 1974. Therefore, at least some individuals seem to hibernate near the point where they emerged and appear at the same point in the next year.

Consequently, the life of Hp depends highly on natural food plant, thistles. Cultivation of potato field near thistle stands caused immigration of some *NA* but virtually no *HA* adults there, nevertheless the Misumai population possesses a high potato acceptability (Watanabe and Suzuki 1965). Oviposition on potato leaves was very scarce, though this may depend in part on the absence of favorable potato leaves in oviposition period. It may be interesting to offer potato leaves to *HA* at the time soon after hibernation by an accelerated cultivation. In spite of their ability to complete the development with potato given artificially, their life history under field conditions highly depends on thistle life cycle, showing a conservative attachment to their native habitat. Therefore, as discussed by Sakagami and Yamaguchi (1954), a mere conservatism to isolated suitable habitats may act at least partly as a factor inhibiting adult dispersal into potato fields. However, in the present study *NA* invaded in the potato field and consumed more potato than thistle rosettes, at least in Z_2. This seems to indicate that conservatism to their host plant of P-III is cannot be maintained throughout the annual cycle. Katakura (1976) suggested that prereproductive isolation between P-III and V-II in potato field is at least partly controlled by a time lag in the appearance of post hibernating adults. In the present study, too, an important external factor inhibiting invasion of P-III/*HA* into potato field was the delay of sprouting of potato leaves compared with the appearance of P-III/*HA*. Hinomizu (1976) reported that mean potato consumption of P-III/*HA* was 0.2 and 50 even in *NA* reared with potato throughout the larval stage against 96.8% in Hv. This indicates that food preference of adult Hp is basically determined genetically even though larval conditioning can modify phenotypic expression to some extent. Genotypic preference for thistles, which must phenotypically be accelerated by inevitable conditioning by means of temporal synchronization between appearance of P-III and thistle, may lower the possibility of invasion into potato field at least for *HA*. The fact that only one *HA* was found consuming potato leaves in the present study despite frequent dispersal between thistle stocks, supports this assumption. In spite of a high acceptability of potato in P-III larvae, adult P-III generally prefers thistles and oviposits on them. As described above this genotypic preference for thistle by adult P-III may also be an important factor inhibiting invasion of *HA* into potato field. Therefore, the time lag between P-III and sprouting of potato seems important to prevent invasion into potato field extrinsically, which is further reinforced by other internal factor, genotypic preference, larval conditioning and possibly by a general sedentarism.

Under the operation of this factor complex P-III could not form a stable potato population in natural conditions at least in Sapporo and the vicinity, even with its high potato acceptability verified experimentally. For realization of such population temporal synchronization between life cycle of P-III and potato may be necessary.

Summary

1. Phenology and dispersal of *Henosepilachna pustulosa* (Kôno) (P-III: Sapporo form) feeding on thistles were studied under field conditions, by cultivating potatoes near thistle stands in Misumai Arboretum of Hokkaido University.

2. Seasonal fluctuation of individual numbers showed a bimodal type in thistle stands, the first peak in May to June composed of post hibernating adults and the second peak in August of newly emerged adults.

3. Virtually no invasion into potato field was observed from spring to mid summer but a considerable number of adults invaded into potato field in late summer, in parallel with withering of thistles.

4. Dispersal occurred mostly between thistle stocks being distant 50 m or less.

5. The most important external factor inhibiting invasion of P-III into potato field seems time lag between sprouting of potato leaves and appearance of post hibernating adult insects, which is reinforced by some internal factors such as, genotypic preference, larval conditioning to thistles, and a general sedentarism.

References

1) Single asterisked: Papers written in Japanese.

2) Double asterisked: Ditto, with English summary.

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