

Mass Exploitation of *Panax japonicus*, An Allochthonous Food Plant, by the Ladybird *Henosepilachna vigintioctomaculata*:
A Curious Epiphenomenon in Food Preference
(Coleoptera: Coccinellidae)¹

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Among three host races of *Henosepilachna vigintioctomaculata*, adults of two races distributed in Hokkaido show a mass feeding on *Panax japonicus* which is not their natural host plant. Causes of the mass feeding were analysed. Results suggested that feeding incitant factor(s) are produced by a mass effect, and that feeding stimulant(s) in leaves of the plant make the ladybirds continue to feed. The other race distributed in Honshu did not represent the mass feeding, probably due to insusceptibility to the stimulants. Although the ladybird could grow with the plant, the adults reared with it in larval stage did not show much shift in their food preference.

INTRODUCTION

Henosepilachna vigintioctomaculata (MOTSCHULSKY) (hereafter Hv) is a famous pest of potato *Solanum tuberosum* (P, Solanaceae). Together with closely related species occurring in Japan it forms a sibling species complex, the *Henosepilachna vigintioctomaculata* complex, which varies in both morphology and food habit. In the course of previous food choice tests for adults to clarify geographic variations of food preference in the complex (HOSHIKAWA, 1983 a, b), a curious phenomenon was detected in Hv as to their response to *Panax japonicus* (T, Araliaceae), which is a subsidiary host of a species of the complex but not consumed by Hv in natural conditions. Among three host races of Hv divided by trends of the variation, one race distributed in Honshu (fpA-1) seldom fed on T irrespective of experimental conditions. On the other hand, two other races distributed in Hokkaido (fpA-2, 3) consumed T as much as their principal host plant, P or *Schizopepon bryoniaefolius* (Cucurbitaceae), once they started feeding; nevertheless their preference for T was far inferior to those for the principal hosts. This phenomenon, much consumption despite low preference, was called "Panax burst" (HOSHIKAWA, 1983 b). Moreover, feeding on T seemed to relate with a kind of aggregation effect, i.e. adults of fpA-2 or fpA-3 rarely fed on T as in fpA-1 when tested isolately, although they devoured much T when grouped. Although feeding on T by Hv has never been observed under field conditions, elucidation of the Panax burst may help us to fuller understand the complicated food habits of the *Henosepilachna vigintioctomaculata* complex.

¹ Contributions to the knowledge of *Henosepilachna vigintioctomaculata* complex. XV.

In this paper, *T* consumption by Hv is described with special reference to its aggregation effect; causes of *Panax* burst are considered based on results of some preliminary tests, and "host status" of *T* for Hv is weighed from various aspects including host suitability.

MATERIALS USED

Provenances of materials used are tabulated below:

Sample code	Locality	Date	Plant from which collected
Rishiri & Rebun Islands (fpA-3)			
III-L:	Lake Kushu, Rebun	VI-24, 1979	<i>P</i>
III-M:	Motochi, Rebun	IX-23, 1977	<i>K</i>
III-K:	Kabuka, Rebun	VII-3, 1878	<i>P</i>
III-O:	Oshidomari, Rishiri	VII-3, 1978	<i>P</i>
Hokkaido (fpA-2)			
II-Y	Yûchi, Wakkanai	VII-4, 1978	<i>P</i>
II-H:	Hiroshima-chô, near Sapporo	VII-2, 1977	<i>P</i>
II-N:	Nopporo, near Sapporo	VII-22, 1979	<i>P</i>
Honshu (fpA-1)			
I-K:	Kusô-domari, Shimokita Pen.	VIII-22, 1977	<i>K</i> + <i>G</i>
I-W:	Wakinosawa, Shimokita Pen.	VII-23, 1978	<i>P</i>
I-A:	Kita-Nojiri, Aomori	VIII-12, 1979	<i>E</i>

In the above list, *K*, *G*, *E* are *Cucurbita moschata*, *Arctium Lappa*, and *Solanum melongena*, respectively. Methods are described below together with results obtained as several kinds of test were involved.

RESULTS AND DISCUSSION

An aggregation effect in T consumption

Changes in T consumption by adult density

To confirm the aggregation effect in *T* consumption by Hv, a simple test was carried out using the above ten samples. The adults, which had been reared in masses with *P* before the test for about 1–9 weeks, were solitarily transferred in plastic boxes (15×8×3 cm) with moist filter paper on the bottoms and given there *T* or *P* leaves alternately every 24 hr. The test was started with one adult in each box. Then, their number in a box was successively doubled by lumping together adults in two boxes, always at change from *P* to *T* leaves.² Feeding areas by adults in respective boxes were measured by tracing the feeding marks with section paper.

Some representative results in Fig. 1 show a distinct difference between fpA-2 and 3 from fpA-1. In the former, means of *T* consumption drastically increased as the number of adults in a box increases, until attaining plateaux at eight or more adults. In the latter, however, feeding amounts remained invariably negligible. Besides the

² Because of sample shortage this procedure was adopted. Similar results had been obtained in a preliminary test with II-H, in which boxes with various density were prepared simultaneously.

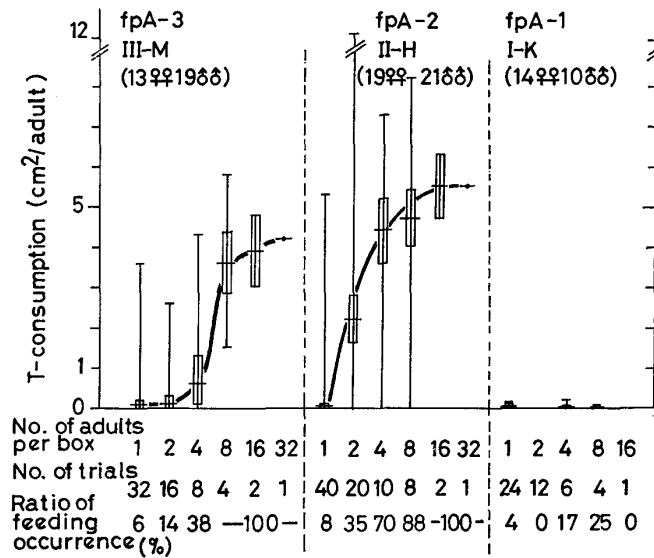


Fig. 1. Changes of consumption of *Panax japonicus* (*T*) according to the density of adult *Henosepilachna vigintioctomaculata* in a box, given by means, SD's and ranges of feeding area per adult. Race and sample code (p. 496) are at top with number of adults used in parenthesis. Further explanations in the text.

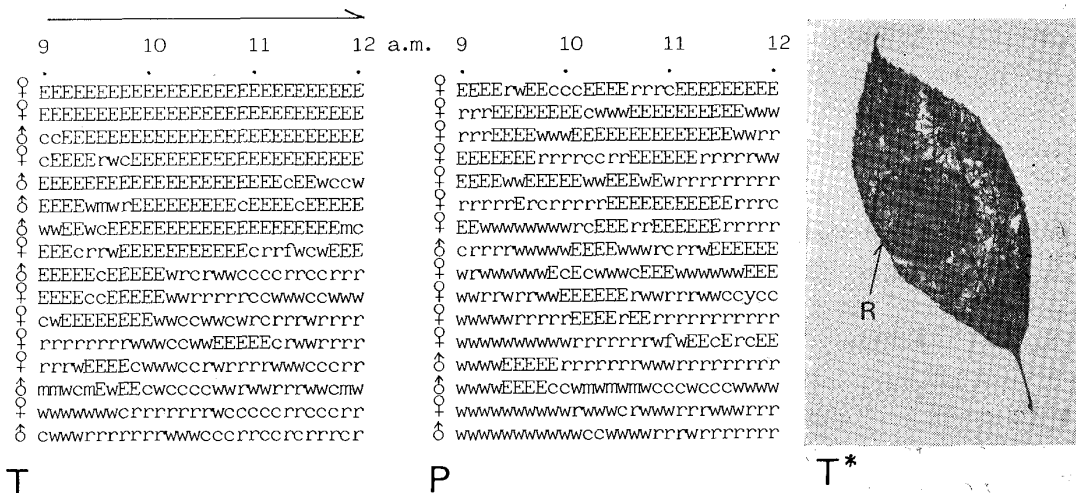


Fig. 2. Comparison of feeding continuity between *Panax japonicus* (*T*) and *Solanum tuberosum* (*P*). *T* and *P*: behavior sequences of adult *H. vigintioctomaculata* on *T* and *P* leaves, respectively. E: eating, r: resting, w: walking, c: self-grooming, f: intentional flying, m: intentional mating, y: "yawning" (extending abdomen with slight opening of elytra). *T**: feeding trace on a *T* leaf. Once "Panax burst" had started, an adult continued to feed even isolated from other adults. R: a part covered by the petri dish.

results shown in Fig. 1, II-Y, II-N, III-K and III-O revealed mass feeding such as II-H or III-M, while I-W and I-A behaved similar to I-K. Judging from all results obtained, the difference between curves for III-M and II-H in Fig. 1 should be a fluctuation by test conditions, not representing a distinction between fpA-2 and fpA-3. The adults, who consumed much *T* in a group, scarcely fed on *T* when isolated again.

Therefore, the change in *T* consumption can not be explained by prior feeding experience, but only by a kind of aggregation effect.

Figure 1 also shows variation ranges in *T* consumption as well as the ratio of trials in which feeding was observed. The density-related changes of mean *T* consumption in III-M and II-H chiefly depend on the ratio of feeding occurrence rather than gradual changes of feeding amount, i.e. these beetles tended to behave alternatively, either devouring much *T* or rejecting it completely, under mid-density condition.

Behavior under condition of Panax burst

In most cases of *Panax* burst occurring in the previous tests, feeding on *T* began approximately 10–18 hrs after *T* had been given. Behaviors of 16 adults of II-Y marked individually with “LIQUID PAPER” (Liquid Paper Co., U.S.A.) were pursued for three hours starting from 12 hr after *T* had been offered (Fig. 2, T). As a control, behaviors of adults from the same population, which had been starved for 12 hr and given *P* leaves, were simultaneously observed during 3 hr (Fig. 2, P). A difference in feeding continuity is obvious between the two groups. Once *Panax* burst has started, feeding tended to continue for a long time. In the control (Fig. 2, P), the mean of total duration for feeding behavior amounted to only 59 out of 180 min (s.d.=40) despite starvation, while that under *Panax* burst was 92 min (s.d.=68). Two top mentioned females in Fig. 2, T incessantly continued feeding throughout the three hours. These results suggest that *T* contains certain feeding stimulant(s) which force(s) Hv (fpA-2, 3) into continuous feeding. The adults under *Panax* burst continued to feed even though isolated individually by being cautiously covered with small petri dishes (37φ×15 mm) in all ten trials (Fig. 2, T*). Therefore, the aggregation effect should act in an early phase of *Panax* burst. No leadership by a particular adult was recognized; i.e. the individuals who attacked *T* at first differed from each other during three trials of the mass feeding.

Some preliminary experiments concerning the mechanisms of Panax burst

The question of what cues raise the aggregation effect and subsequent *Panax* burst can be considered along two lines. One is behavioral interactions among individuals (group effect) and the other is indirect ones through environmental conditioning, i.e. intervention of any substances, by many individuals (mass effect) (CHAUVIN, 1950). The absence of any direct interactions among adults in observations described above favors the occurrence of some mass effect in the present case.

Feeding on treated T leaves

Assuming any environmental conditioning under mass rearing, *T* leaves were treated as follows: (i) coated with excreta from other adults, (ii) allowed to be consumed in a small area by other adults, (iii) scratched many times with a knife, for ca. 10 mm² section, and (iv) coated with “*T* juice,” i.e. homogenized fluid made from *T* leaves. These leaves were given to adults of II-N individually isolated in plastic boxes (5×6×1.5 cm) for 24 hr.

Results (Table 1) show that treatments (ii) and (iii) were effective in raising the ratio of feeding occurrence, while (i) and (iv) did not much affect the ratio. A discrepancy between (ii) or (iii) and (iv) is curious. If chemical cues contained in *T* leaves raised the ratio in treatments (ii) and (iii), treatment (iv) should also bring the same result, unless rapid degeneration of the substances concerned is assumed. Another possibility is physical changes on the surface of the *T* leaf, feeding marks or scratches

Table 1. Feeding on leaves of *Panax japonicus* (*T*) with various treatments by adult *Henosepilachna vigintioctomaculata* (fpA-2) isolated individually

Kind of treatments on <i>T</i> leaves	No. of trials (A)	No. of observed feeding (B)	B/A (%)	<i>t</i> -value ^a
	50	3	6	—
(i) Coated with excreta	32	5	16	1.37
(ii) Partially consumed	32	14	44	3.68 ^b
(iii) Scratched	32	12	38	3.27 ^b
(iv) Coated with <i>T</i> juice	32	6	19	1.71

^a Difference in the ratio B/A from the control.^b Significant at 1% risk.

themselves, acting as a feeding incitant (HIRANO, 1971), although *T* leaves do not seem to be particularly tough and rough compared with the principal host plants of *Hv*. Anyhow, as shown in treatments (ii) and (iii), occasional feeding by some adults accelerates feeding by other adults, which then results in mass feeding on *T*. Similar cases are known in larvae of some lepidopterans and a sawfly on their natural host plant (reviewed by MORIMOTO, 1972).

Panax burst by mixed sample of fpA-1 and fpA-2

To clarify why fpA-1 does not develop *Panax* burst, a mixed sample consisting of I-A (10♀♀5♂♂; fpA-1) and II-N (10♀♀5♂♂; fpA-2) and a pure II-N sample (19♀♀11♂♂) were compared as for *T* consumption. Feeding amounts for 24 hr were 47.2 and 42.9 cm² in the mixed sample, and 88.7 and 79.4 cm² in the pure one, suggesting fpA-1 scarcely fed on *T* even under this condition.³ The lack of *Panax* burst in fpA-1, therefore, is not caused by the absence of "leaders" to start feeding, but probably caused by inability to respond either to the feeding stimulant or, less probably, the factor(s) acting as feeding incitant for fpA-2 and fpA-3. Occurrence of feeding deterrent in *T* leaves which is valid only to fpA-1 should not be the case, since I-A consumed *P* leaves coated with "*T* juice" as much as those coated with "*P* juice" (HOSHIKAWA, unpublished).

Panax burst under field conditions

As mentioned above, *T* feeding by *Hv* has never been observed under field conditions. To confirm whether *Panax* burst occurs or does not occur in the field, two masses of adults from II-N were kept in a net cage covering a natural stand of *T* grown in Kobetsuzawa and Nopporo, in and near Sapporo City, for 24 hr on July 24–25, 1979. In both cases *T* were fairly heavily consumed, i.e. 84 cm²/59 adults and 80 cm²/35 adults, respectively. Thus, *Panax* burst can take place in the field provided many individuals casually gather or are gathered on *T*.

Summarizing, *Panax* burst is tentatively interpreted as follows: *Panax* burst is released by production of factor(s) acting as feeding incitant by a mass effect and continuous feeding of *Hv* (fpA-2, 3) caused by feeding stimulant(s) in *T* leaves.

³ TOMIOKA (personal communications) observed a distinct individual variation in *T* acceptability of fpA-1 which I have never detected, in adults collected in Hirosaki City, Aomori. Since he continued to give only *T* leaves for several days, the feeding threshold might have dropped due to a long-time starvation in his tests.

Table 2. A comparison of larval development of *Henosepilachna vigintioctomaculata* reared with *Panax japonicus* (*T*) and *Solanum tuberosum* (*P*) under 23–24°C, 18L–6D

Sample	Food	No. of larvae tested	Mortality ^a (%)	Duration ^a (days)	Emergent adults		
					No. (♀/♂)	Body weight (mg) ♀	♂
I-B ^b	<i>T</i>	40	56.7±25.5	30.4±2.5	5/ 7	24.4±4.5	23.1±6.7
I-A ^c	<i>T</i>	100	71.8±20.0	27.6±1.3	14/ 9	27.6±2.9	24.9±2.1
	<i>P</i>	27	14.9± 0.8	22.2±0.8	12/11	37.1±3.7	35.9±3.2
III-L	<i>T</i>	132	82.0±15.2	29.1±1.1	13/16	27.2±3.4	24.9±4.4
	<i>P</i>	23	12.9± 5.4	21.9±0.9	11/ 9	44.9±3.7	41.8±2.3

^a Since hatching until emergence.

^b Issued from adults collected in Kammata near Takine, Fukushima Pref., on *Chrysosplenium japonicum*, V-7, 1979.

^c Reared in September, 1979, others in July, 1979.

Second, the reason why Hv in Honshu (fpA-1) do not develop *Panax* burst is due to their insusceptibility to the feeding stimulants.

"Host status" of *T* for Hv

Comparison of development of larvae reared with T or P

Host suitability of *T* for Hv was examined by rearing tests. Eggs produced by adult samples were reared with either *T* or *P* leaves under 23–24°C, 18L–6D, putting ca. 10–20 larvae in each plastic box (15×8×3 cm), the bottom of which was covered with moist filter paper. Unfortunately, the outbreak of a disease during tests destroyed most of the samples, particularly all of fpA-2. The results are summarized in Table 2.

In both fpA-1 (I-A, I-B) and fpA-3 (III-L), *T* was inferior to *P* as a food plant in all indices: mortality, duration for development and body weight of emerged adults. In *T* cultures, mortalities tended to be high in both first and fourth (final) instar larvae. Delay of growth in *T* cultures was about a week, most of which was caused by the prolonged larval period. Although *P* cultures of I-A produced relatively small adults, it was probably due to the poor conditions of *P* leaves available, since they were reared in autumn when *P* was withering. On the other hand, there was no significant difference in the indices between fpA-1 and fpA-3, despite a clear difference in food preference (HOSHIKAWA, 1983 b). Larvae in *T* culture were pale in ground color, rather whitish with a slight greenish tint, whereas those in *P* culture were normally yellowish white or yellow.

About three weeks after emergence, some of the females, which issued from *T* cultures and reared with only *T* leaves also in adult stage, laid egg masses, from which some larvae hatched out. The number of hatched larvae/number of eggs laid were 8/9, 8/10 and 14/17. Under normal conditions with long day photoperiod, the females lay a mass of ca. 20–30 eggs, about two weeks after emergence (MAKI et al., 1964). This casual observation suggests that *T* is inferior to normal hosts also for ovarian development. The hatched larvae could not be reared for seasonal restriction of food supply. Anyhow, Hv can scarcely grow with *T*. TOMIOKA (personal communications) also experienced a high mortality in *T*-cultured Hv and obtained 16 adults.

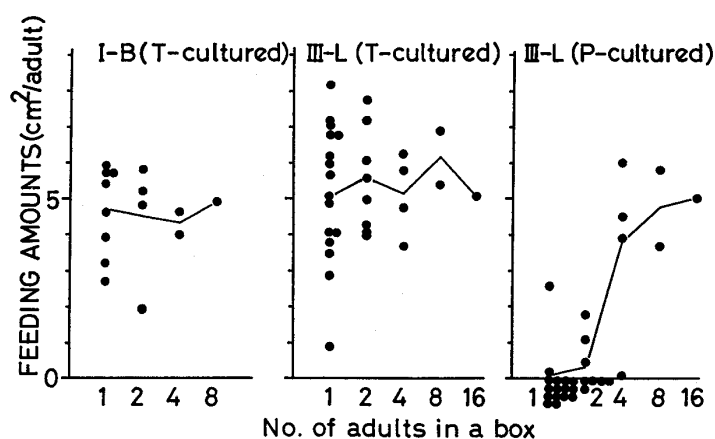


Fig. 3. A comparison of *T* consumption between *T*-cultured and *P*-cultured *H. vigintioctomaculata*. *P*-cultured III-L shows an aggregation effect as in field samples shown in Fig. 1, while both *T*-cultured III-L and I-B do not represent any density-related change.

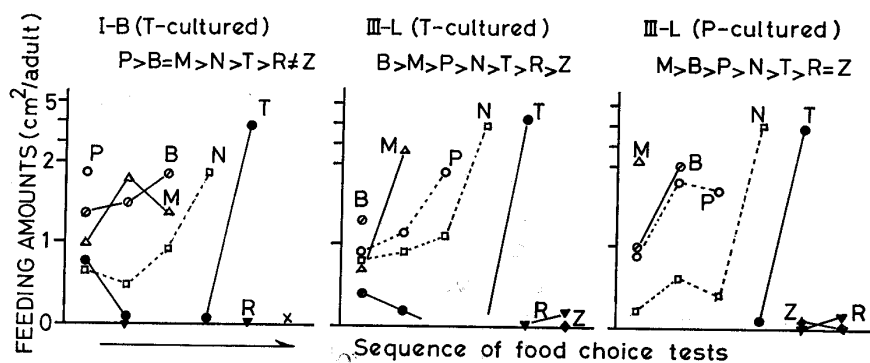


Fig. 4. Food preferences of *T*-cultured *H. vigintioctomaculata*, by repeating food choice test with removal of most preferred plant (HOSHIKAWA, 1983 a). Preference orders obtained are given at the top. *T*-cultured I-B (race: fpA-1) shows a trend similar to fpA-3 (*P*-cultured III-L) despite normal fpA-1 never eating *T* as much. *T*-cultured and *P*-cultured III-L are similar to each other in their preference, suggesting *T* feeding in larval stage did not much affect adult preference. Plant code: T, *Panax japonicus*; P, *Solanum tuberosum*; B, *S. nigrum*; M, *S. megacarpum*; N, *Schizopepon bryoniaefolius*; R, *Caulophyllum robustum*; Z, *Breea setosa*. ×: no intake.

Food preference of *T*-cultured *Hv*

Adults issued from the above *T* cultures were examined, together with those from *P* cultures as a control, as to their food preference by two consecutive tests. The first test was that described in section I-1, in which changes of *T* consumption by adult densities were compared. *T*-cultured adults were constantly given *T* leaves throughout the test. The second test was food choice for adults, described in a previous paper (HOSHIKAWA, 1983 a), in which preferences to seven species plants were examined by repeating food choice with successive removal of the top ranked plant consumed.

Results of the first test (Fig. 3) show that *T* consumption in *T*-cultured adults, both III-L (fpA-3) and I-B (fpA-1), were constantly high irrespective of adult densities. *T* acceptability of *T*-cultured adults was evidently raised. The aggregation effect as

shown in Fig. 1 disappeared, suggesting that the feeding incitant(s) produced by a mass effect are unnecessary for *T* consumption by *T*-cultured adults. Despite the high *T* acceptability, their preference did not much change as shown in the second food choice test (Fig. 4). Not only was *T* less preferred than solanaceans (*P*, *B*, *M*) and a cucurbitacean (*N*), but also feeding amounts on *T* decreased in early trials of the food choice test. Trends in preference of *T*-cultured I-B were similar to that with *Panax* burst (e.g. *P*-cultured III-L in Fig. 4) as for *T* consumption, representing much feeding on *T* at the fifth trial of food choice test. The similarity implies that fpA-1, which could be insusceptible to the feeding stimulant(s) (cf. II-2), turned to be susceptible to it by rearing with *T*. Thus, geographic variation in *T* preference of Hv is of a delicate nature; as physiological bases of the variation, race-specific response to feeding stimulant or incitant, are easily changed by *T* rearing during only one generation.

Summarizing, 1) Hv can scarcely grow with *T*. 2) Females reared with *T* can lay hatchable eggs and 3) *T*-cultured adults do not represent much shift in their food preference despite an evident rise in their *T* acceptability.

"Host status" of *T*

T can not be a host plant of Hv for the following reasons, though Hv can grow with *T*.

(1) To utilize *T*, adults are necessary to aggregate on *T*—Judging from the habits of Hv, such is unlikely to occur under field conditions.

(2) Even if Hv grow up on *T*, their food preference does not much change—Under changeable environmental conditions there is no guarantee of continuous utilization of *T* by a given population.

(3) Low host suitability of *T* for Hv.

Among these (3) might be able to be excluded since it may be changed by selection. However, (2) is important, in considering the evolution of food habit of Hv. It contrasts with some previous results of similar tests with allied species; for instance, the thistle feeder *H. pustulosa* shifts its adult preference when reared with potato or *Caulophyllum rubustum* in larval stage (HINOMIZU, 1976; HOSHIKAWA, unpublished). In conclusion, there is little possibility that Hv had utilized or will utilize *T* as a host plant. The problem why a geographic variation exists in the *T* preference of Hv still remains a puzzle.

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