

Kontyû, Tokyo, 52 (4): 605-614. December 25, 1984

Host-race Formation and Speciation in the *Henosepilachna vigintioctomaculata* Complex (Coleoptera, Coccinellidae)

III. Geographic Variation of Food Preference in the Thistle Feeder, *H. pustulosa**

Kazuo HOSHIKAWA

Institute of Low Temperature Science,
Hokkaido University, Sapporo, 060 Japan

Abstract Food preference of *Henosepilachna pustulosa* was examined by food choice tests using eleven species of plants. Local samples tested covered the whole distribution area of the species. Based on the geographic variation of food preference, the species was divided into two races: fpB-1 distributed south in Honshu and the Oshima Peninsula of Hokkaido, and fpB-2 north in the mainland of Hokkaido. As to the preference for *Caulophyllum robustum*, the latter showed a distinct cline with increasing preference southward, while the former exhibited constantly low preference. This geographic discontinuity of the variation occurs in the Oshima Peninsula, approximately between Yakumo and Oshamanbe, where neither *Cirsium* nor *Caulophyllum* depending populations have been discovered despite the occurrence of these host plants.

Among various species or forms of the *Henosepilachna vigintioctomaculata* complex (hereafter abbreviated as the Hv complex), the thistle feeder *H. pustulosa* (KÔNO), which is endemic to Japan, shows a large morphological variation in the elytral shape. Since its discovery by WATANABE and SAKAGAMI (1948), the local variation of this character has been reported by many authors, especially YASUTOMI (1966) and KATAKURA (1977, 1981). On the other hand, the food habit, another variable feature of the species pointed out by WATANABE and SAKAGAMI (1948) and SAKAGAMI and YAMAGUCHI (1954), has not been completely clarified as yet, though many fragmentary pieces of information have been accumulated. KUROSAWA (1953) found a population in Sapporo depending on the blue cohosh *Caulophyllum robustum*.** YASUTOMI (1974) described that several samples from Hokkaido preferred this plant while some samples from Honshu did not. IWAO (1959) observed individual variations of potato acceptability in populations near Kyoto, and HINOMIZU (1976) examined the potato acceptability in several populations in Hokkaido. These studies on the food habits of *H. pustulosa* were reviewed by KATAKURA *et al.* (1977).

* Contribution to the knowledge of *Henosepilachna vigintioctomaculata* complex. XVI. In this paper, the thistle feeding *Henosepilachna* is tentatively treated as a single species, though KATAKURA (1981), based on morphological studies, divided it into two species, *H. pustulosa* and *H. niponica*.

** Misidentified as *Thalictrum integilobum* in the original paper.

The present paper clarifies the geographic variation of food preference in *H. pustulosa*, which corresponds to fpB in the preliminary classification of food-preference type if the Hv complex (HOSHIKAWA, 1983 a). The process of race differentiation in fpB will be discussed in a forthcoming paper, together with undescribed host races of the Hv complex, fpC-fpG.

The plant names in the text are abbreviated as follows:

R: *Caulophyllum robustum* MAXIM., *Y*: *Chelidonium japonicum* THUNB., *T*: *Panax japonicus* C. A. MEYER, *A*: *Cirsium* spp., *G*: *Arctium Lappa* L., *Z*: *Breea setosa* (BIEB.) KITAM., *H*: *Scopolia japonica* MAXIM., *M*: *Solanum megacarpum* KOIDZ., *P*: *S. tuberosum* L., *B*: *S. nigrum* L., *N*: *Schizopepon bryoniaefolius* MAXIM.

Materials and Methods

A total of 56 samples from 38 populations of fpB were subjected to food choice tests for adults (FCTA: step-wise food choice tests with removal of the most preferred plant in each step) and for larvae (FCTL: continuous feeding on leaf discs of various plants). The source of these samples are given in Fig. 1 and Appendix. Main tests used 9 spp. of plant (*R*, *Y*, *T*, *H*, *B*, *P*, *N*, *A*, *G*), but *H* or *Y* was not available in some cases. *M* and *Z* were included only in some tests. *A* used for both FCTA and FCTL was probably *C. kamtschaticum* LEDEB. Further details of these tests were described in a previous paper (HOSHIKAWA, 1983 a).

Results

The food-preference type of fpB is generally characterized by (1) high preference for *A*, *Z*, and *M*, and (2) virtual rejection of *G*, *B*, and *T*. The preference for *R*, *N*, or *H* shows distinct geographic variation. The other two plants, *Y* and *P*, occupy middle ranks in the preference order. The details of food choice tests are as follows (see also Appendix).

1. Adults

Figs. 1 and 2 depict the geographic variation of the adult food preference. Among eleven plant species tested, the preference for *R* varied remarkably. *R* was scarcely eaten by samples from Honshu (Nos. 61, 55, 304 in Fig. 1) and the Oshima Peninsula (No. 32), being ranked the 6–7th in preference order (Fig. 2). On the other hand, among the samples from Hokkaido excluding the Oshima Peninsula, the *R* preference exhibited a distinct gradient, which may be called the *Caulophyllum* cline. *R* was eagerly devoured by southern samples in this cline, showing the top rank of preference (e. g. Nos. 27, 19 in Fig. 1), while it was consumed only a little by northern samples, being ranked 5–7th (e. g. No. 5). Samples from localities between these extremes showed intermediate preference for *R* (No. 13). Thus, *R* preference differed drastically between Chihase (No. 27) and Ohnuma (No. 32). This gap of variation is associated with a vacant zone (Fig. 1, V) of approximately

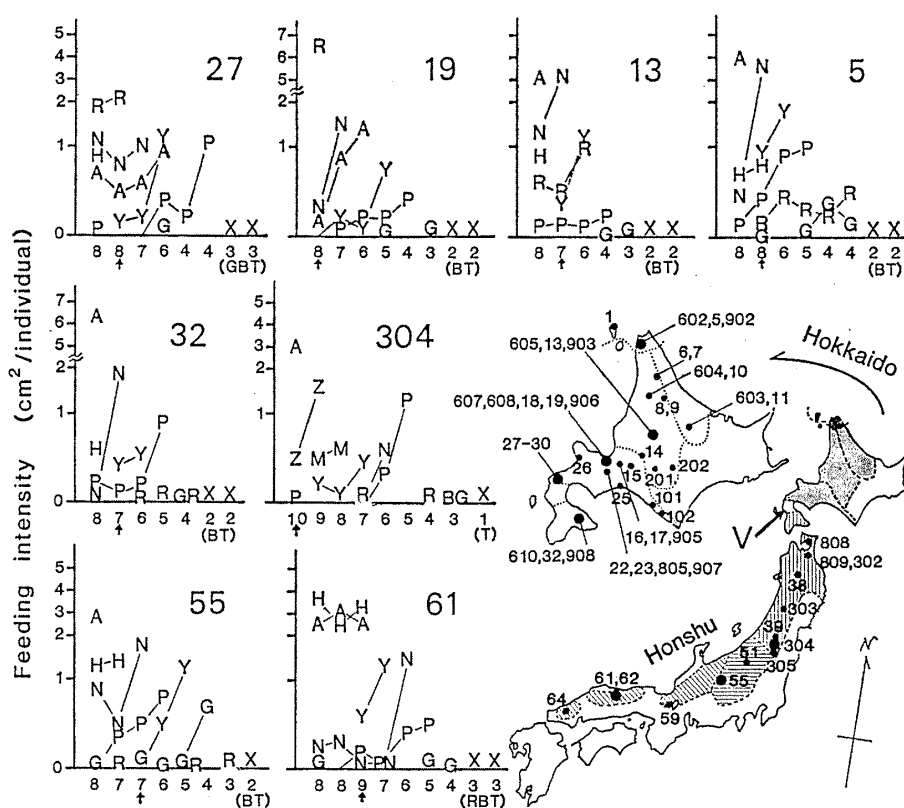


Fig. 1. Results of food choice test for adults (FCTA) with fpB populations (Nos. 5, 13, 19, 27, 32, 304, 55, and 61). Plant codes are given in p. 607. Ordinate: feeding intensity, i. e. the leaf area consumed. Abscissa: number of plant species offered in consecutive tests (arrow indicates addition of Y). x: no intake (refused plants in parentheses). The map shows sample localities, the distribution area of each morphological form of *H. pustulosa* based on KATAKURA *et al.* (1977). V: the vacant zone (explanation in text). Locality name, collection date, and host record for each sample are given in Appendix.

35 km in distance, between Yakumo and Oshamanbe, where neither *A* nor *R* feeders have been discovered despite the occurrence of both *A* and *R* (KATAKURA, 1981). Samples with a higher *R* preference tended to show a somewhat lower preference for *A*, in which *A* was often less preferred than *N*.

In most samples from Hokkaido, *N* was consumed as much as *A* and occupied the 2nd–3rd rank in preference order, while in samples from Honshu, *N* was less consumed than *A* and ranked 3rd–5th. The southernmost samples (No. 61, 64) particularly showed a lower *N* preference than the northern populations. In contrast, *H* preference was higher in southern samples, especially in Nos. 61, 64.

Excluding the plants of which preference varied geographically (*R*, *N*, *H*), a virtually stable preference order was obtained as $A > Y \geq P > G > B \neq T$. That is, *T* was completely refused by all samples in FCTA. Mature leaves of *B* were never consumed, though its flowers, buds, and very young leaves were often ingested slightly. Rejection of *B* characterizes fpB, which was not observed in other races

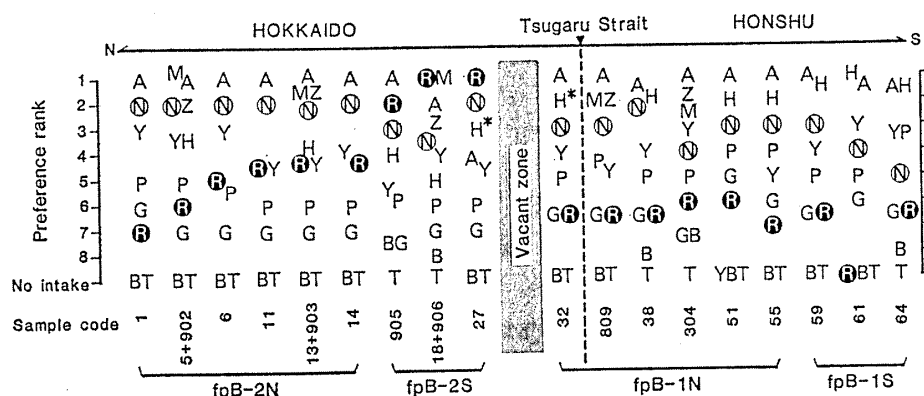


Fig. 2. Geographic variation in food preference of adults of fpB. Preference ranks obtained by FCTA are arranged according to localities from north (left) to south (right). Each column shows preference ranks of 9 spp. of tested plants, e. g. $A \geq H \geq N > Y > P > G = R > B \neq T$ in No. 38. For lack of leaves, *H* was not included in some tests or it was available only in the first step for several samples (*H**). In each of the three examples, the results of two samples are pooled (see also Appendix).

of the Hv complex. Most samples usually nibbled *G* only a little, but samples from mountainous regions in Honshu (Nos. 39, 51, 55) occasionally consumed about $3/4$ cm² per adult. This trend must be further confirmed because the feeding intensity on *G* varied erratically in other samples. Although the rank of *G* is slightly higher in the Honshu than in the Hokkaido samples (Fig. 2), it is merely a result of the variation in preference to *R*. There was no actual increase in the feeding amount of *G* in the southernmost samples (e. g. No. 61). Similarly, judging from the feeding intensities, there were no consistent geographic tendencies in the preference for *P* and *Y*. Rejection of *Y* by No. 51 should not be the characteristic of the population, because the larvae ate *Y* as those from the adjacent areas did.

Z and *M* were offered only to limited samples. *Z* seemed to be preferred slightly less than *A* in most cases. *M* was preferred very much by samples from Hokkaido while slightly less by those from Honshu. The data are insufficient to see geographic variations, if any, in the preference for *Z* and *M*.

To summarize, the variation was distinct and discontinuous in *R* preference, continuous and slight in *N* or *H* preference, and virtually absent in *P*, *Y*, *B* or *T* preference. Thus, fpB is divided into two "geographic" races by the differentiation in *R* preference:

fpB-1: Populations distributed to the south of the vacant zone.

fpB-2: Those distributed to the north of the vacant zone.

These are "geographic" races but not "host" races in a strict sense, because the northern fpB-1 and the northernmost fpB-2 are so similar in food preference that they could not be separated on this basis (HOSHIKAWA, 1983 a). These "geographic" races may be further divided into host races as follows, although the distinction is rather arbitrary due to continuous variations.

- fpB-1S: Samples from southwestern Honshu (e. g. Nos. 64, 59)
 fpB-1N: Those from central-northern Honshu and the Oshima Peninsula of Hokkaido (Nos. 55, 808, 32)
 fpB-2S: Those from southern Hokkaido excluding the Oshima Peninsula (Nos. 27, 15, 18, 101)
 fpB-2N: Those from northern Hokkaido (Nos. 14, 201, 1)

Among these four races, fpB-2S is peculiar by its extremely high *R* preference. This *R* preference becomes gradually lower northward, forming the *Caulophyllum* cline in fpB-2.

2. Larvae

General trends in the food preference of larvae immediately after hatching are summarized in Fig. 3B as in a previous paper (HOSHIKAWA, 1983 b), together with four typical results of FCTL (Fig. 3, A). Geographic tendencies of the preference ranks obtained by FCTL are shown in Fig. 4.

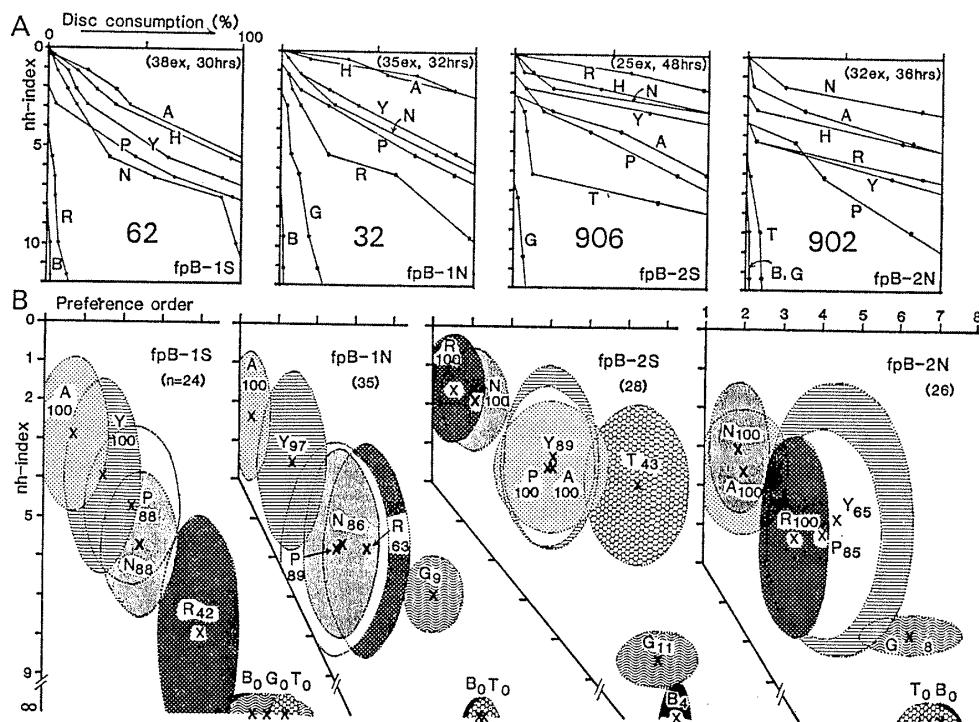


Fig. 3. A: Results of food choice test for larvae (FCTL). B: Preference order and consumption speed for each plant in FCTL. Center of each ellipse (x) shows means, and horizontal and vertical axes indicate standard deviations of ranks in preference order and consumption speed represented by nh-index (number of larvae \times hours required to consume half of leaf disc/100), respectively. Numerals in ellipses are percentages of the tests in which more than half of the leaf disc was consumed. *M* and *H* were omitted as they were not offered in all tests. Several samples, fpB-1S (59, 61, 62, 64), fpB-1N (32, 38, 39, 51, 55), fpB-2S (18, 19, 906, 25, 27), and fpB-2N (5, 902, 11, 13, 903, 14) are lumped together.

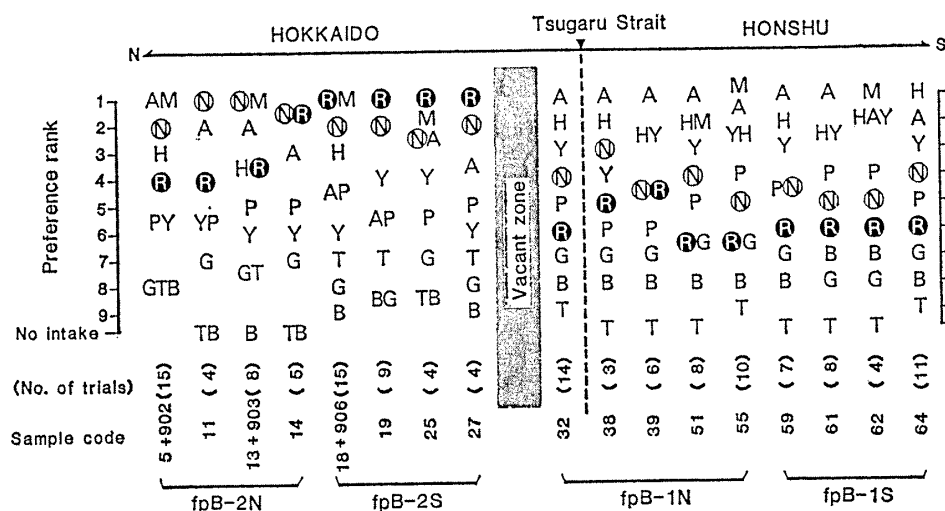


Fig. 4. Geographic variation in food preference of larvae immediately after hatching. Preference orders obtained by FCTL were averaged for each population (cf. HOSHIKAWA, 1983 a), and arranged by the same way as in Fig. 2.

In the preferences for *R*, *N*, and *H*, geographic tendencies similar to those in FCTA were observed in FCTL. *R* preference varied as fpB-2S > fpB-2N > fpB-1N > fpB-1S (Fig. 3, B), with a cline in fpB-2 and a gap between fpB-2S and fpB-1N (Fig. 4), though *R* in fpB-2 took slightly higher ranks than in FCTA. It should be noted that the northern fpB-1N (Nos. 32, 38, 39) tended to show higher *R* preferences than the southern fpB-1N and fpB-1S. *N* preference was fpB-2N = fpB-2S > fpB-1N = fpB-1S, while *H* preference was fpB-1 > fpB-2. The low *A* preference in fpB-2S was comparable to the *Y* or *P* preference (Fig. 3, B).

A remarkable difference from FCTA is seen in the *T* preference. *T* discs were frequently consumed more than half the area in fpB-2S (43% of tests), despite no acceptance by any adult. Ignoring the consumed amount, the frequencies of *T* feeding among populations of fpB-1S, -1N, -2S, -2N, were 3/24, 3/35, 19/28, 7/26, respectively. Only fpB-2S tended to accept *T*, and the others virtually rejected *T* as in FCTA.

No consistent geographic tendency was observed in the preference of *P* or *B*. *B* discs of mature leaves were refused almost completely, and only occasionally nibbled a little (13/24, 9/35, 13/28, 5/26 in fpB-1S, -1N, -2S, -2N, respectively), though some larvae of No. 19 once consumed more than half the disc. *Y* preference tended to decrease in the northern samples, as shown by the ratios of tests in which the disc was consumed more than half (100, 97, 89, 65% in fpB-1S, -1N, -2S, -2N, respectively). This trend was not found in FCTA. On the contrary, *G* preference may be lower in fpB-1S despite the rank varied slightly among different samples, being about the 7-8th (Fig. 4). *G* disc was nibbled in 6/24, 27/35, 18/28, 14/26 in fpB-1S, -1N, -2S, -2N, respectively, and rarely consumed more than half in the last three groups. *M* was tested only for limited samples. It was preferred

by all samples tested as shown in Fig. 4.

Thus, the discontinuity of variation in *R* preference between fpB-2S and fpB-1N was recognized also in FCTL. The trends of variation in the preference of other plants were mostly similar to those in FCTA. However, two additional tendencies were observed in FCTL: (1) a northward decline of *Y* preference and (2) an increased *T* preference in fpB-2S. The latter is of particular interest not only because *T* is definitely refused by the other races of fpB, but also because *T* is a subsidiary host of an allied species *H. yasutomii* (fpD). Besides the difference in the methods to evaluate the preference, causes of these discrepancies between the results of FCTL and FCTA should be in part epigenetic, because hatching larvae without feeding experience were used in FCTL, while adults that might have been conditioned by previous feeding were used in FCTA. Epigenetic changes in food preference could be important in the process of food niche shift.

Discussion

Under natural conditions, most populations of fpB depend on *A*. Some local populations utilize *R*, *H*, and *M*, and occasionally invade *P*-fields or *Z*-thickets. The preference orders generally reflect the host range in the field except that *N* and *Y* were more preferred than *P* despite they have never been recorded as hosts in the field. Why *N* and *Y* are not utilized as host plants by fpB? *Y* should not be a host of fpB by the following reasons: (i) its low suitability as food as shown by high mortality of larvae reared on it,* and (ii) *Y* (HARA and KANAI, 1959) and fpB overlap in distribution only in a narrow area of central Honshu. The high *Y* preference despite its low suitability may not be contradictory in such distributional relationships. At present, it is difficult to interpret the discrepancy concerning *N*. The consumption rate for *N* might have been overestimated in FCTA because of its thin leaves, but this can not explain the high *N* preference in FCTL (Fig. 4). Since *N* sprouts later than *A* in spring in Sapporo (HINOMIZU, *et al.*, 1978), the phenological difference between the insect and the plant is a possible factor involved, but *P* sprouting as late as *N* is to some extent utilized in the field. Presumably some unknown physiological factors are involved.

The variability in *P* preference of *H. pustulosa* was pointed out by IWA0 (1959) and HINOMIZU (1976). The present study could not detect such variability by either FCTA or FCTL. *P* preference may vary so slightly that it could not be detected by the present methods. Irregular fluctuations in the feeding amount or feeding rate for *P* in FCTA or FCTL might be in part due to the variability noted by IWA0 (1959).

Although *H. pustulosa* (fpB) was collected on *R* from various localities in Hokkaido (Kami-Otoineppu, Chitô, Kamuikotan, several places in Sapporo and the

* Only one deformed male emerged out of 65 larvae from a population in Sapporo, when *Y* was given through their larval period.

suburbs, and Mt. Yôtei), populations undoubtedly breeding on *R* are restricted to the southern part of the mainland, in the suburbs of Sapporo and on Mt. Yôtei. Other northern populations utilize *R* as a food plant only for newly emerged adults in late summer or autumn (HOSHIKAWA, unpublished), forming a cline in the host utilization for *R*.

In contrast to the host races of fpA (HOSHIKAWA, 1983 b), the races of fpB are neither separated from one another by apparent geographic barriers such as straits nor correspond to the morphological forms. Although *H. pustulosa* (fpB) is divided into seven distinct morphological forms by their elytral shape (KATAKURA, 1977), the food preference varies continuously through three or four morphological forms. This continuity is, however, broken off at the vacant zone, which is also a boundary for morphological forms. To the north of the vacant zone, i. e., at the southern end of the *Caulophyllum* cline, there are fpB-2S populations with high *R* preference, and they utilize both *A* and *R* as principal hosts ("two-niche situation" in MAYNARD SMITH, 1966). To the south of the vacant zone, on the other hand, there are two sympatric species, the *A* feeder (fpB-1N) and the *R* feeder (fpC, fpD). This situation suggests the importance of the *Caulophyllum* cline and of the vacant zone in the process of speciation of the Hv complex, fpB, fpC, fpD. etc. The process of race differentiation in fpB will, therefore, be discussed in relation to other forms, fpC-fpG, in a forthcoming paper.

Acknowledgement I wish to express my sincere gratitude to Professor Shôichi F. SAKAGAMI for his reading the manuscript.

References

- HARA, H. & H. KANAI, 1959. *Distribution maps of flowering plant in Japan, II*. 96pp+100pls. Inoue Shoten, Tokyo.
- HINOMIZU, H., 1976. Influence of food plants in larval stage on the host plant preference of adult lady beetles, *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). *Kontyû, Tokyo*, **44**: 93-101.
- HINOMIZU, H., KATAKURA, H., HOSHIKAWA, K., KIMURA, T., & S. NAKANO, 1981. Life cycle relations between the phytophagous ladybird *Henosepilachna pustulosa* (KÔNO) and its food plants in and near Sapporo. *New Entomol.*, **30**: 11-18.*
- HOSHIKAWA, K., 1983 a. Host-race formation and speciation in the *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). I. Host-plant ranges and food-preference types. *Kontyû, Tokyo*, **51**: 254-264.
- , 1983 b. *ditto*. II. Geographic variation of food preference in *Henosepilachna vigintioctomaculata*. *Kontyû, Tokyo*, **51**: 339-350.
- IWAO, S., 1959. Some experiments on the host-plant preference in a phytophagous ladybeetle, *Epilachna pustulosa* KÔNO, with special reference to its individual variation. *The Insect Ecology* **8**: 10-21.**
- KATAKURA, H., 1977. A review of the *Henosepilachna vigintioctomaculata* complex, phytophagous lady beetles. *The Insectarium*, **14**: 80-87.*
- , 1981. Classification and evolution of the phytophagous ladybirds belonging to *Hen-*

- osepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae). *J. Fac. Sci., Hokkaido Univ.*, (VI) **22**: 301-378.
- KATAKURA, H., HINOMIZU, H., HOSHIKAWA, K., & T. KIMURA, 1977. Problems and methods on the food habits of *Henosepilachna vigintioctomaculata* complex. *Seibutsu Kyôzai*, **12**: 61-92.*
- KUROSAWA, T., 1953. Notes on the food plants of *Epilachna pustulosa* KÔNO. *Ôyô-Kontyû*, **9**: 12-15.*
- MAYNARD SMITH, J., 1966. Sympatric speciation. *Amer. Nat.*, **100**: 637-650.
- SAKAGAMI, S. F. & Y. YAMAGUCHI, 1954. Some experiments on the food-habit of two puzzling species of ladybirds, *Epilachna pustulosa* KÔNO and *E. vigintioctomaculata* MOTSCHULSKY (Coleoptera, Coccinellidae). *Jour. Fac. Sci., Hokkaido Univ.*, (VI) **12**: 120-132.
- WATANABE, C. & S. SAKAGAMI, 1948. Contributions to the knowledge of *Epilachna pustulosa* KÔNO (Coleoptera: Coccinellidae). *Matsumushi*, **2**: 96-106.**
- YASUTOMI, K., 1966. Classification and bionomics on *Epilachna vigintioctomaculata* complex. *Kontyû to Shizen (Nature and Insects)*, **1**: 17-19.*
- , 1974. Food habits and its differentiation (*Henosepilachna vigintioctomaculata* complex, etc.). In ÔSHIMA (ed.). *The Behaviour and Adaptation of Insects*, p. 271-285. Baifukan, Tokyo.*

* In Japanese, ** In Japanese with English summary

Appendix

Sources of samples and the results of FCTA not represented in Fig. 2 are listed here. Sample code: locality name (cf. Fig. 1), date in parentheses, plant from which the sample was collected/plant used as food for rearing, number of individuals used for FCTA (♀♀/♂♂), and preference order. Samples were collected in 1976-'83; Nos. 1-64 in 1977, and Nos. 602-610, 805-809, 101-102, 201-202, 303-305 in 1976, '78, '81, '82, '83, respectively.

HOKKAIDO excluding OSHIMA PENINSULA fpB-2N: **1**: Lake Kushu, Rebun Is. (VI/15) A/A (0/1). **602**: Hama-Yûchi, Wakkanai (IX/1) A/A (8/8) A > N > R > P > G > B ≠ T. **5**: Yûchi, Wakkanai (VI/14) A/A (10/5) A > N > Y > H* > P > R > G ≠ B, T. **902**: do. (VI/18) A/A (10/10) M ≧ A > Z = N > H > P > R. **6**: Kami-Otoineppu (VI/13) A/A (11/4). **7**: do. (IX/10) A/A (7/4) A > N > R ≠ P, G, B, T. **604**: Kita-Moshiri, near Nayoro (IX/12) A/A (8/6) A > N ≧ R ≧ P > G > B ≠ T. **10**: do. (VI/14) A/A (3/3) A > N > R. **8**: Chitô, near Nayoro (IX/10) A/A (13/11) A > N > R > P ≧ G ≠ B, T. **9**: do. (IX/10) R/R (5/2) A ≧ N = R > P > G ≠ B, T. **603**: Kami-Shirataki, near Kamikawa (IX/3) A/A (8/8) A > R ≧ N > P > G > B ≠ T. **11**: do. (VI/13) A/A (6/4). **605**: Kamuikotan, near Asahikawa (VIII/14) A/A (9/9) A > R = N > P > G > B ≠ T. **13**: do. (VI/16) A/A (5/8) A > N > H* > R = Y > P > G ≠ B, T. **903**: do. (VI/19) A/A (6/2) A > M = Z > N > H = R > P. **14**: Lake Katsurazawa, Mikasa (VI/17) A/A (6/5). **202**: Shintoku (VI/20) A/A (7/8) A > M > N > R > P > G ≠ B, T. **201**: Shimukappu (VI/20) A/A (15/16) A = M > N > R = P > G > B ≠ T.

fpB-2S: **15**: Tsugitate, Kuriyama chô (IX/5) Z/Z (13/12) A > N > R > P > G ≧

$B \neq T$. 101: Nohya, near Shizunai (V/5) A/A (3/2) $R > M > Y \geq N > Z > A > H > P > G \neq T$. 102: Mitsuishi (VI/18) $A/P + A$ (2/3) $M > R > H^* = Z > N = A > P \neq T$. 16: Nopporo, near Sapporo (VIII/23) A/A (10/10) $A > R > N > P > B \geq G \neq T$. 17: *do.* (VIII/23) P/P (2/4) $A > P \geq N$. 905: *do.* (VI/20) A/A (7/6). 25: Tomakomai (VI/19) A/A (5/5) $A \geq R > N > P = Y > G \neq B, T$. 607: Kobetsuzawa, Sapporo (VII/23) A/A (8/12) $R > A > N > P = G \neq B, T$. 608: *do.* (VII/23) R/R (8/12) $R > N \geq A > P > G \neq B, T$. 18: *do.* (VI/23) A/A (5/4) $R > A > N \geq Y > P > G > B \neq T$. 19: *do.* (VI/23) R/R (3/2) $R > N > A > Y \geq P > G \neq B, T$. 906: *do.* (VI/10) R/R (7/6) $M = R > A > Z > N > H > P$. 22: Nakanosawa, Sapporo (VII/26) A/A (8/7) $R = A > N$. 23: Mt. Hakkenzan, Sapporo (VIII/7) R/R (5/4) $R > N > A \geq P \neq G, B, T$. 805: *do.* (VIII/31) $R + A/R + A$ (15/15) $R > Z = A > P$. 907: *do.* (VI/12) R/R (5/5) $R > M > N > Z = A > P \neq T$. 26: Tomari, Shakotan Pen. (IX/20) A/A (6/5) $A > R > N > P > G \neq B, T$. 27: Chihase, near Mt. Kariba (VI/5) A/A (11/6). 28: Harauta, near Mt. Kariba (VI/5) A/A (1/0) $R > A$. 29: Shimamaki, near Suttsu (VI/5) A/A (1/0) $R > A$. 30: Yubetsu, near Suttsu (VI/4) A/A (2/2) $A \geq R > N$.

OSHIMA PENINSULA and HONSHU. fpB-1N: 610: Ohnuma, near Hako-date (VIII/11) A/A (9/9) $A > P \geq N > G \geq R > B \neq T$. 32: *do.* (V/25) A/A (10/9). 908: *do.* (VII/11) A/A (10/11) $A > H^* > Z > M = N > P > R$. 808: Ohminato, Aomori Pref. (VII/23) A/A (2/2) $A > N = M > P = Y > R \neq G, B, T$. 809: Noheji, Aomori Pref. (VII/23) A/A (10/16). 302: *do.* (VII/18) A/A (10/12) $A = Z = M > N > Y = P > R \geq G \neq B, T$. 38: Tamagawa, Tazawako chô, Akita Pref. (VI/2) A/A (12/3). 303: Nozoki, Okachi Touge, Yamagata Pref. (VII/11) A/A (0/1) $A = M > N > P \neq R, G, B, T$. 39: Zaô Onsen, near Yamagata (V/12) A/A (9/8) $A > H = N \geq Y > P > G > R \neq B, T$. 304: Itaya Touge, near Fukushima (VII/10) A/A (13/6). 305: Tsuchiyu Onsen, near Fukushima (VII/9) A/A (2/1) $A > M > N > Y > P > R \neq G, B, T$. 51: Doai, near Mt. Tanigawa (V/18) A/A (6/7). 55: Shimashima, near Matsumoto (V/17) A/A (16/10).

fpB-1S: 59: Seriu, Kyoto (V/16) A/A (9/7). 61: Mitoku, near Kurayoshi (V/14) A/A (12/12), 62: *do.* (V/14, 15) H/H (7/4) $H > A = Y > P > N > R \neq G, B, T$. 64: Tsuwano, Shimane Pref. (V/12) A/A (16/14).