



Host-plant specificity limits the geographic distribution of thistle feeding ladybird beetles

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Abstract

The relationships between two phytophagous ladybird beetle species, *Epilachna pustulosa* Kôno and *E. niponica* Lewis (Coleoptera, Coccinellidae), and their main host plants, thistles (*Cirsium* spp., Asteraceae) were investigated in Oshima Peninsula, southern Hokkaido, northern Japan. *Epilachna pustulosa* was found feeding on *Cirsium kamtschaticum* in the northernmost part of the peninsula, whereas *E. niponica* was confined to the Ohno Plain and adjacent areas in the southernmost part, and occurred mainly on *C. alpicola*. No thistle feeding epilachnines were found in the middle part of the peninsula despite the abundance of another thistle species, *C. grayanum*. Both beetle species showed lower adult preference and reduced growth performance on *C. grayanum* compared to their respective host plants under laboratory conditions. We concluded that the distribution of thistle feeding epilachnines in Oshima Peninsula was principally determined by the availability of appropriate host plants.

Introduction

Every species is restricted to a particular geographic range. In many cases, geographic barriers to dispersal such as mountain ranges, or regions of abrupt environmental change such as the edges of deserts, often mark the boundaries of species (Gaston, 1990; Cox & Moore, 1993; Brown et al., 1996; Futuyama, 1997). The effect of interspecific relationships on distribution is also important. While there are a large number of ecological and biogeographical studies focused on how predation and competition affect the distribution of species (Cox & Moore, 1993; Begon et al., 1996; Futuyama, 1997), the effect of food resources on distribution seems to have been rather poorly investigated, although the effect is certainly more straightforward, at least in certain groups of animals that depend on a limited diet. This may be true for phytophagous insects, a majority of which are known to be oligophagous, utilizing only a particular group of plants as food (Strong et al., 1984). It appears likely

that their geographic distribution is largely controlled by the availability of appropriate food plants. However, empirical evidence that supports this implicit assumption is scarce (but see, Zwölfer & Romstöck-Völkl, 1991).

In the present paper, we will demonstrate that the distribution of two species of phytophagous ladybird beetles is virtually determined by the availability of particular species of food plants.

Background information

Epilachna pustulosa and *E. niponica* are closely related phytophagous ladybird beetles belonging to the *E. vigintioctomaculata* species complex (Katakura, 1981, 1997). Both species are endemic to Japan, occurring mainly on wild thistles (*Cirsium* spp.). *Epilachna pustulosa* is distributed in Hokkaido except for the southern and eastern parts, and *E. niponica* in southern Hokkaido and Honshu (Figure 1). Around

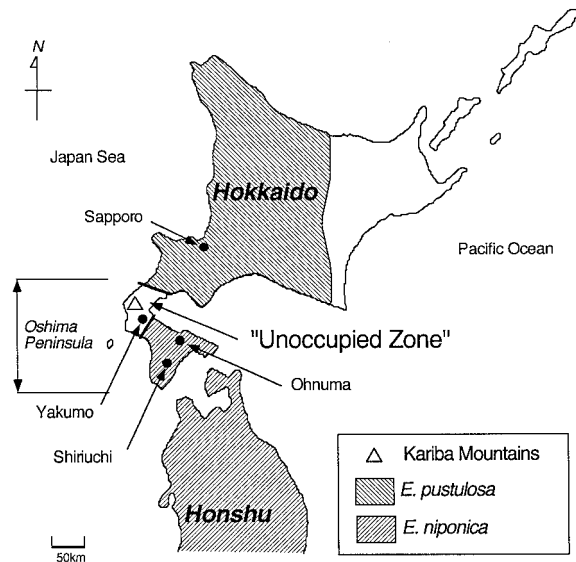


Figure 1. Distributions of *Epilachna niponica* and *E. pustulosa* in northern Japan based on Katakura (1981). Solid circles are sampling sites of epilachnines and/or thistles used in the experiments.

the neck of Oshima Peninsula in southern Hokkaido, there is an area where neither beetle occurs despite the abundance of thistles (Katakura, 1981). The north-western part of this 'unoccupied zone' coincides with the Kariba Mountains, but other parts do not have any distinct geographic barriers. Climatic factors cannot explain the absence of the ladybird beetles in the 'unoccupied zone', because the climate is not very different in the adjacent northerly and southerly areas where the ladybird beetles occur. Moreover, predators or competitors of epilachnines do not appear to be overly abundant within this zone.

The thistle flora of Oshima Peninsula is different from that of the rest of Hokkaido (Koizumi et al., 1997). Most parts of Hokkaido are dominated by *C. kamschaticum* or closely related forms, whereas Oshima Peninsula harbors a more diverse thistle flora comprising *C. grayanum*, *C. alpicola* and other thistle species. This difference in thistle flora between the peninsula and other parts of Hokkaido might explain the absence of thistle-feeding epilachnines in the unoccupied zone. To test this possibility, we investigated the relationship between thistles and the ladybird beetles on Oshima Peninsula. We also performed laboratory experiments to assess the suitability of three abundant species of thistles (*C. kamschaticum*, *C. grayanum* and *C. alpicola*) for the ladybird beetles.

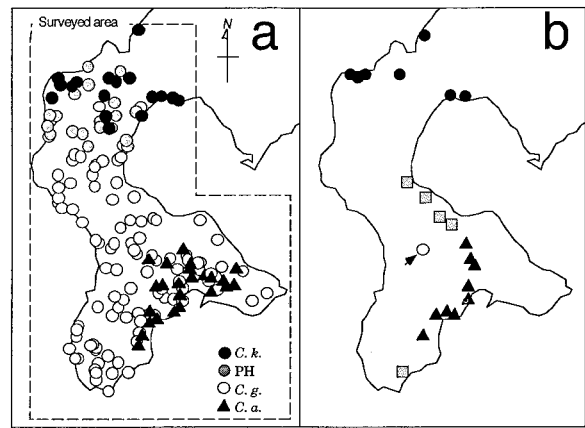


Figure 2. Distributions of common thistle species (a) and thistle feeding epilachnine beetles (b) in Oshima Peninsula, southern Hokkaido, northern Japan. a: *C. k.*, *Cirsium kamschaticum*; *C. g.*, *C. grayanum*; *C. a.*, *C. alpicola*; PH, putative hybrid populations between *C. kamschaticum* and *C. grayanum* (based on Koizumi et al., 1997). b: solid circles, *Epilachna pustulosa* collected on *C. kamschaticum*; solid triangles, *E. niponica* collected on *C. alpicola*; an open circle, *E. niponica* on *C. grayanum*. Hatched boxes are the sites where no thistle feeding epilachnines were found in the present study, but where previous records report the presence of *E. niponica*.

Material and methods

Field survey. Field surveys were carried out from spring to autumn, 1994 and 1995 (Koizumi et al., 1997). The surveyed area covered the whole range of Oshima Peninsula including the unoccupied zone (Figures 1 and 2). At each site, we gathered information about thistle species and *Epilachna* beetles. Identification of thistle species followed that of Kadota (1995).

Laboratory studies. We examined the acceptability and preference of adult beetles, and performance of larvae for the three species of thistles (*C. kamschaticum*, *C. alpicola*, *C. grayanum*) common in Oshima Peninsula. All the experiments and rearing were carried out under a controlled regime of L16:D8 at 20 °C in 1995.

Insects. Posthibernating adults of *Epilachna pustulosa* were collected on *C. kamschaticum* in Sapporo, north of Oshima Peninsula, where this species was a dominant thistle. Adults of *E. niponica* were collected on *C. alpicola* in Shiruichi, the southernmost part of Oshima Peninsula, where *C. alpicola* and *C. grayanum* were common. These beetles and their

progeny were used for the experiments. The collection sites are shown in Figure 1.

Plants. Three thistle species transplanted to an experimental field on the campus of Hokkaido University from Sapporo (*C. kamschaticum*) and from the southern part of Oshima Peninsula (Ohnuma, *C. alpicola*; Yakumo, *C. grayanum*) were used for the experiments. The original sites of these thistles are also shown in Figure 1.

Acceptability and preference of adult females. Host acceptability of adult beetles for the three thistle species was determined using no choice tests, while host preference was tested in choice assays. Experienced adult females collected from host thistles in the field were used for both assays. They were fed on alternative food plants, *Scopolia japonica* (Solanaceae) and/or *Solanum japonense* (Solanaceae; cf., Katakura, 1981; Katakura & Hosogai, 1997), for more than 1 week before the experiments started in order to diminish the possible influence of feeding experience before collecting. When the same beetles were used repeatedly in different feeding tests, they were fed on *S. japonica* and/or *S. japonense* for more than 24 h prior to each experiment to minimize the influence of preceding tests. The general procedure common to both no choice and choice tests is summarized as follows.

Leaves were used within two days after being picked, and were punched by a circular punch press in order to make leaf disks (3.1 cm diameter, 7.45 cm²). Leaf disks were placed in a transparent plastic cage (15 cm diameter and 5 cm depth polypropylene cage for choice tests; 8.0 × 15.3 × 3.0 cm styrene cage for no choice tests) whose bottom was covered by moist filter paper. Two leaf disks cut from the same plant were used for each trial as a set, one disk being placed on the face of the leaf and another one on the back. Two or three sets of leaf disks were used according to the purpose of the experiment. A female beetle was released in the center of the cage and was allowed to feed on the leaf disks for 24 h. The consumed leaf area was measured with the aid of image processing software (NIH Image ver. 1.55) after being photocopied and scanned into a computer.

No choice test. Host acceptability was examined by offering leaf disks of one species of thistles for 24 h. Two sets of leaf disks from the same species of thistles were offered to each beetle. Acceptance of the three

thistle species by each beetle species was tested in the following order:

E. pustulosa: *C. kamschaticum*, *C. alpicola*, *C. grayanum*.

E. niponica: *C. alpicola*, *C. kamschaticum*, *C. grayanum*.

A total of 15 *E. pustulosa* and 13 *E. niponica* females were measured for host acceptability.

Three-way choice test. Three sets of leaf disks (one set for each of the three thistle species) were offered to each beetle. After 24 h, leaf disks were removed and the areas eaten were measured. The test was repeated three times for each beetle. A total of 15 *E. pustulosa* and 15 *E. niponica* females were separately tested for the three host choice assay.

Two-way choice test. In the three-way choice tests described above, one of the thistles offered to beetles was a species not normally encountered by the insects under natural conditions because of the limited distribution of the plants (*C. alpicola* for *E. pustulosa*, and *C. kamschaticum* for *E. niponica*). In the two-way choice tests, we examined beetle preference for only those thistle species that they might encounter under natural conditions: *C. kamschaticum* and *C. grayanum* for *E. pustulosa*; *C. alpicola* and *C. grayanum* for *E. niponica*. Two sets of leaf disks (one set each for two thistles) were offered to each beetle in the two-way test. A total of 15 *E. pustulosa* and 13 *E. niponica* females were separately tested for the two host choice assay.

Host-related performance. Performance of larvae on the three species of thistles was examined by rearing larvae from hatching to emergence. Egg masses were gathered daily from posthibernating females kept individually in the laboratory (10 females each for both *E. pustulosa* and *E. niponica*). They were fed on picked *S. japonense* leaves in order to reduce possible maternal effects on the larval performance. In order to equalize the genetic background of beetles among food conditions, we made three sets of newly hatched larvae, each containing three individuals, from a single egg mass, and reared these sets on leaves of the three different species of thistles. Three sets of larvae from each female were tested. Each set of larvae was reared together in a transparent styrene cage (8.0 × 15.3 × 3.0 cm), the bottom of which was covered with moist filter paper. A sufficient amount of fresh leaves was provided throughout the experiment. As a measure of

performance, the eclosion percentage (i.e., percentage of individuals reaching adulthood) was calculated for the offspring of each female. Furthermore, the number of days required from hatching to adult eclosion and the pronotum width (a body size index) were recorded for individuals that reached adulthood.

Results

Association between *Epilachna* beetles and thistles in Oshima Peninsula

Seven species of thistles belonging to the genus *Cirsium*, and one *Breea* species were confirmed in Oshima Peninsula (Table 1). Dominant species of thistles changed from the northern part of the peninsula to the southern part (Koizumi et al., 1997; Figure 2a). *Cirsium kamtschaticum* was abundant in the northernmost part of the peninsula. This species was replaced by the southerly distributed *C. grayanum* around the southern slopes of the Kariba Mountains (cf., Figure 1). Between the distribution ranges of the two species, there was a zone occupied by populations of thistles with unique stem bases and stem pubescens, and floral characters intermediate between *C. kamtschaticum* and *C. grayanum*. These populations are here treated as putative hybrid populations between *C. kamtschaticum* and *C. grayanum* (cf., Koizumi et al., 1997). In the southernmost part of the peninsula, *C. alpicola* occurred sympatrically with *C. grayanum*. Five other species (*C. pendulum*, *C. aomorense*, *C. pectinellum*, *C. yezoense* and *B. setosa*) were not abundant, but not rare in the peninsula. They were often sympatric with one or two of the dominant species.

The distribution of epilachnine beetles in the surveyed area is shown in Figure 2b, which includes the data obtained by the present study and previous ones (Katakura, 1981; Tomioka, 1985). Although the ladybird beetles have been collected on five *Cirsium* and one *Breea* species of thistles (Table 1), the distribution of the beetles coincided well with those of particular species of *Cirsium* as follows (compare Figures 2a and 2b):

Epilachna pustulosa was obtained at seven sites in the northern part of the peninsula, all feeding on *C. kamtschaticum*. Their distribution limit on the Japan Sea side seems to lie around the western foot of the Kariba Mountains, and coincided well with the area where dominant thistles changed from

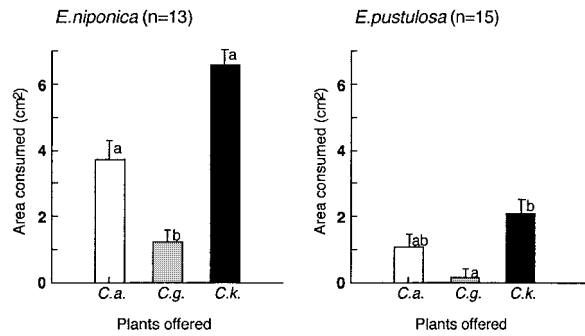


Figure 3. Mean leaf area of three thistle species (*C. a.*, *Cirsium alpicola*; *C. g.*, *C. grayanum*; *C. k.*, *C. kamtschaticum*) consumed by *Epilachna niponica* (left) or *E. pustulosa* (right) in no choice tests. Vertical lines represent 1 SE. Bars with same letters are not significantly different ($P > 0.05$) by Scheffé method following two-way ANOVA without replication.

C. kamtschaticum to the putative hybrids between *C. kamtschaticum* and *C. grayanum*. On the Pacific side as well, their occurrence was restricted to the area where *C. kamtschaticum* was predominant.

Epilachna niponica was obtained at ten sites in and near Ohno Plain in the southernmost part of the peninsula. At these sites, *E. niponica* occurred mainly on *C. alpicola*; at eight sites on *C. alpicola*, and one site on both *C. alpicola* and *Breea setosa*. We found *E. niponica* solely on *C. grayanum* in only one site. This site (Assabu, indicated by an arrow in Figure 2b) was located about 10 km from the nearest known site of *C. alpicola*.

Previous records of *E. niponica* in Hokkaido were also restricted to the southernmost part of the peninsula (Katakura, 1981; Tomioka, 1985) and included places where we could not confirm the occurrence of thistle feeding epilachnine beetles (Figure 2b). Unfortunately none of these previous records specified the species of thistles from which *E. niponica* was collected.

Host acceptability, preference and performance

No choice test. Both *E. pustulosa* and *E. niponica* showed a significant difference in mean consumed areas between the three thistle species (Figure 3, two-way ANOVA without replication, d.f. = 2, *E. niponica*, $F = 11.006$, $P < 0.001$, *E. pustulosa*, $F = 15.064$, $P < 0.001$). *Epilachna niponica* and *E. pustulosa* showed the same host acceptance ranking with both consuming thistles in the order *C. kamtschaticum* > *C. alpicola* > *C. grayanum*. We note, however, that differences in consumed areas were not statistically

Table 1. Survey results for the Oshima Peninsula. Given are the total number of sites where each thistle species was found and the number of sites where the thistle was infested by *Epilachna* beetles. Data based on Koizumi et al. (1997) and the current study

Thistle species	Number of sites where thistle found	Number of sites where thistle infested		% of infestation (sites infested/found)
		<i>E. pustulosa</i>	<i>E. niponica</i>	
<i>Cirsium kamschaticum</i>	18	7	0	38.9
<i>C. pectinellum</i>	2	0	0	0.0
Putative hybrids between				
<i>C. kamschaticum</i> and	19	0	0	0.0
<i>C. grayanum</i>				
<i>C. grayanum</i>	102	0	1	1.0
<i>C. pendulum</i>	3	0	0 ^a	0.0
<i>C. aomorense</i>	8	0 ^a	0 ^a	0.0
<i>C. yezoense</i>	12	0	0	0.0
<i>C. alpicola</i>	24	0	9	37.5
<i>Breca setosa</i>	6	0	1 ^b	16.7

^aThere are previous records of infestation.

^b*E. niponica* was collected not only on *B. setosa* but also on *C. alpicola* at this site.

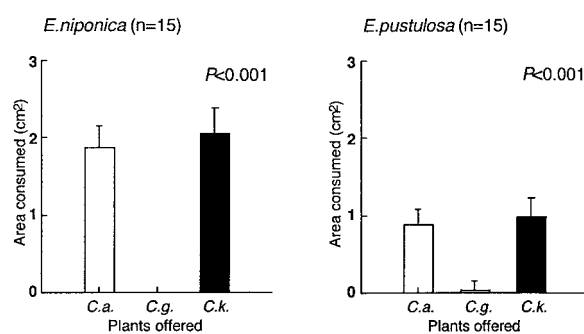


Figure 4. Mean leaf area of three thistle species (*C. a.*, *Cirsium alpicola*; *C. g.*, *C. grayanum*; *C. k.*, *C. kamschaticum*) consumed by *Epilachna niponica* (left) or *E. pustulosa* (right) in three-way choice tests. Vertical lines represent 1 SE.

significant for some pairwise comparisons ($P > 0.05$, Scheffé method following two-way ANOVA without replication, Figure 3).

Three-way choice test. The consumed leaf areas of three successive tests were pooled for each beetle before statistical analyses. Statistically significant preferences were observed for both beetle species (Figure 4, MANOVA (Manly, 1993), d.f. = 2, *E. niponica*, $F = 123.000$, $P < 0.001$, *E. pustulosa*, $F = 29.433$, $P < 0.001$). Both species showed very similar patterns of preference for the three thistle species tested, preferring *C. kamschaticum* (host plant of *E. pustulosa*) and *C. alpicola* (host plant of *E. niponica*) to *C. grayanum*.

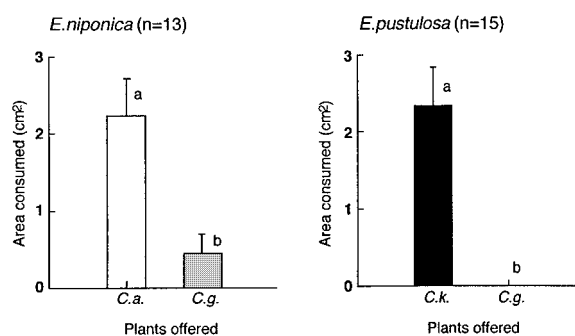


Figure 5. Mean leaf area of thistle species (*C. a.*, *Cirsium alpicola*; *C. g.*, *C. grayanum*; *C. k.*, *C. kamschaticum*) consumed by *Epilachna niponica* or *E. pustulosa* in two-way choice tests. Vertical lines represent 1 SE. Bars with same letters are not significantly different ($P > 0.05$) by MANOVA (Manly, 1993).

Two-way choice test. Both *E. niponica* and *E. pustulosa* showed statistically significant preferences for their primary host plant in their respective ranges (Figure 5, MANOVA, d.f. = 1, *E. niponica* for *C. alpicola* over *C. grayanum*, $F = 9.673$, $P = 0.009$; *E. pustulosa* for *C. kamschaticum* over *C. grayanum*, $F = 22.319$, $P < 0.001$).

Host-related performance. Eclosion rate, development time from hatching to eclosion, and pronotum width for males and females all showed significant host plant-associated effects in both *E. niponica* and *E. pustulosa* (Table 2). The performance of *E. niponica* larvae reared on *C. grayanum* was significantly

Table 2. Means \pm SEs for developmental traits of *Epilachna niponica* and *E. pustulosa* reared on three species of thistles. Sample sizes (n) are given in parentheses. Means and SEs of eclosion rates were for 10 replicates of each food condition

Insects	Species reared on*	Eclosion percentage	Developmental time (days)	Pronotum width (mm)	
				Female	Male
<i>E. pustulosa</i>	<i>C.k.</i>	84.5 \pm 3.0 ^a	31.34 \pm 0.25 ^a (76)	3.51 \pm 0.01 ^a (36)	3.34 \pm 0.02 ^a (38)
	<i>C.g.</i>	22.2 \pm 7.8 ^b	39.55 \pm 1.20 ^b (20)	3.05 \pm 0.06 ^b (11)	2.93 \pm 0.05 ^b (9)
	<i>C.a.</i>	54.4 \pm 11.4 ^{ab}	34.61 \pm 0.48 ^c (51)	3.36 \pm 0.03 ^c (20)	3.21 \pm 0.03 ^c (31)
<i>E. niponica</i>	<i>C.k.</i>	76.7 \pm 6.7 ^a	32.60 \pm 0.27 ^a (67)	3.95 \pm 0.02 ^a (30)	3.79 \pm 0.03 ^a (38)
	<i>C.g.</i>	68.8 \pm 3.6 ^b	35.16 \pm 0.37 ^b (63)	3.71 \pm 0.05 ^b (28)	3.67 \pm 0.03 ^b (35)
	<i>C.a.</i>	95.0 \pm 1.8 ^a	32.44 \pm 0.29 ^a (86)	4.00 \pm 0.02 ^a (42)	3.83 \pm 0.02 ^a (44)

**C.k.*: *C. kamtschaticum*; *C.g.*: *C. grayanum*; *C.a.*: *C. alpicola*.

All the traits were significantly influenced by thistle species as follows: Eclosion rate (non-parametric tests for multiple comparisons, Sokal & Rohlf, 1995, d.f. = 2), *E. niponica*, $P = 0.001$; *E. pustulosa*, $P = 0.001$; days from hatching to adult eclosion (one-way ANOVA, d.f. = 2), *E. niponica*, $F = 22.724$, $P < 0.001$; *E. pustulosa*, $F = 55.136$, $P < 0.001$; pronotum width (one-way ANOVA, d.f. = 2), *E. niponica*, female, $F = 32.768$, $P < 0.001$, male, $F = 10.421$, $P < 0.001$; *E. pustulosa*, female, $F = 58.313$, $P < 0.001$, male, $F = 49.495$, $P < 0.001$. Numerals with the same letters are not significantly different ($P > 0.05$, non-parametric tests for multiple comparisons, or Scheffé method following one-way ANOVA).

worse than that for larvae reared on the other two thistles (i.e., lower eclosion rate, delayed growth, and smaller body size). However, these traits did not differ between *E. niponica* reared on *C. kamtschaticum* and *C. alpicola* (Table 2). The performance of *E. pustulosa* was also worst for larvae reared on *C. grayanum* (Table 2). Moreover, developmental time was significantly shorter and body size larger for *E. pustulosa* reared on *C. kamtschaticum* than *C. alpicola*. Eclosion rate was also higher, but not significantly so (Table 2). The performance of *E. pustulosa* and *E. niponica* on the three thistle species therefore showed the following tendencies: *E. niponica*: *C. kamtschaticum* = *C. alpicola* > *C. grayanum*; *E. pustulosa* (excluding eclosion rate): *C. kamtschaticum* > *C. alpicola* > *C. grayanum*.

Discussion

Relationships between phytophagous insects and their food plants have long been a subject of keen interest in various fields of ecology and evolutionary biology, and an enormous number of studies have been made on various aspects of insect-plant relationships (Strong et al., 1984; Hunter et al., 1992; Bernays & Chapman, 1994; Cappuccino & Price, 1995; Mayhew, 1997). However, the relationships of phytophages and their food plants on a geographic scale have been relatively ignored. The present study demonstrates that ecological rather than topographical or physical factors limit

the distribution of thistle feeding epilachnines on Oshima Peninsula. Although thistles are common everywhere in Oshima Peninsula, those species appropriate for the persistence of ladybird beetles are restricted to particular regions. The occurrence of thistle feeding beetles in the peninsula is thus primarily determined by their ability or inability to utilize three dominant species of thistles, *C. kamtschaticum*, *C. grayanum* and *C. alpicola*. Thus, the beetles absence in the middle region of Oshima Peninsula is due to the paucity of the thistles *C. kamtschaticum* and *C. alpicola* and the dominance of the low ranking host *C. grayanum*.

Naturally, the above interpretation requires further critical testing. First, in the present study we did not examine the relationship of *E. pustulosa* with the putative hybrid thistles between *C. kamtschaticum* and *C. grayanum*. *Epilachna pustulosa* occurs in the area north of the Kariba Mountains feeding on *C. kamtschaticum*, but it was not found in the southern slope where the putative hybrid thistles were also common (Figure 2). If our hypothesis is correct, then we predict that *E. pustulosa* preference and performance on the 'hybrids' should be lower than that on *C. kamtschaticum*.

Second, the relationship between *E. niponica* and *C. grayanum* is still not completely understood. *Epilachna niponica* do not usually utilize *C. grayanum*, although this thistle species is abundant throughout the range of *E. niponica* (Figure 2). However, *E. niponica* has the ability to utilize *C. grayanum* under laboratory

conditions (Figures 3 and 4; Table 2). Furthermore, populations feeding only on *C. grayanum* apparently exist in the field (Figure 2b). *E. niponica* can utilize *C. grayanum* under certain conditions. Why it does not do so more extensively must still be resolved.

Third, because we used experienced females in our feeding assays, the differences found in the present study could be due to conditioning and/or maternal effects. Although we tried to reduce these possibilities, it is therefore not certain that the host acceptance, preference and performance differences of the beetles on alternative thistles represent environmental or underlying genetic variation.

Recent studies have dealt with various novel aspects of adaptation in phytophagous insects (Cobb & Whitham, 1993; Mopper et al., 1995; Mopper, 1996). For a thorough understanding of the factors responsible for the origin and persistence of the unoccupied zone of thistle feeding epilachnines in Oshima Peninsula, it will be necessary to conduct more intensive studies focusing on the interaction between variation in quantity and quality of each thistle species and the corresponding physiological ability of *Epilachna* beetles at the deme level.

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