

Oviposition site selection by herbivorous beetles: a comparison of two thistle feeders, *Cassida rubiginosa* and *Henosepilachna niponica*

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Abstract

In insects that feed on plants in both adult and larval stages, it is often difficult to distinguish oviposition preference from adult feeding preference, because oviposition can occur at or in proximity to feeding sites. In the present study, characteristics of oviposition site selection of two beetle species, *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae) and *Henosepilachna niponica* (Lewis) (Coleoptera: Coccinellidae), were investigated in the field and laboratory, with particular attention to relationships with adult feeding sites. In the field, distances between adult feeding scars and egg masses differed for *C. rubiginosa* and *H. niponica*, with the former being very small and the latter averaging 24.6 cm. The same tendencies for the distances between adult feeding scars and egg masses of the two beetle species were confirmed in cages in which only female beetles were released. *Cassida rubiginosa* restricted egg laying to host plants in the field and to leaves in laboratory assays. On the other hand, *H. niponica* placed 8% of egg masses on plants adjacent to host plants in the field and often placed eggs on artificial substrates rather than leaf discs in laboratory assays. These results suggest that oviposition and female feeding sites are virtually inseparable in the case of *C. rubiginosa*, while *H. niponica* females do not necessarily keep to host plant leaves as oviposition substrates and they tend to oviposit at some distance from their feeding sites. Results are discussed in relation to proximate and ultimate causes of host selection behavior.

Introduction

In phytophagous insects, especially those showing complete metamorphosis, mobility in the neonate larval stages is generally much lower than that in the adult stage. Consequently, host plant selection by holometabolous insects depends largely on the oviposition preference of adult females. An accurate evaluation of oviposition preference therefore is essential for understanding current host plant selection and the evolution of host plant specificity.

Host selection or host specificity of phytophagous insects has often been discussed in the context of optimal oviposition theory (i.e., the preference–performance

linkage; Jaenike, 1978). In the optimal oviposition theory, it is predicted that oviposition preference should correspond with host suitability for offspring development, because females are assumed to maximize their fitness by maximizing offspring performance. However, the existing data for this seemingly plausible prediction range from a good correspondence between oviposition preference and larval performance (Leather, 1985; Via, 1986; Denno et al., 1990; Hamilton & Zalucki, 1993; Briese, 1996) to very poor correspondences (Courtney, 1981; Jaenike, 1989; Kibota & Courtney, 1991; Hornor & Abrahamson, 1992; Underwood, 1994). Reasons why oviposition preference and larval performance might not be correlated have been discussed by Thompson (1988), Courtney & Kibota (1990), and Mayhew (1997, 2001). One of the possible factors responsible for a poor preference–performance correspondence would be that the adult female sometimes does not have access to information about the quality of the plant as food for her offspring. This is especially true if the adult female either

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does not feed at all, as in Lepidoptera, or does not feed on the same plant tissue that the larva feeds on.

On the other hand, in many phytophagous insects, such as herbivorous beetles, adult females feed on the plant tissue on which their offspring will also feed. In the context of optimal oviposition theory, one may expect that such insects can examine directly and accurately the quality of their larval food through adult feeding, and that a good correspondence between oviposition preference and larval performance will eventually be realized. However, the quality of food resources for ovipositing females as well as for larvae should be considered at the same time. Recent arguments on host specificity of phytophagous insects have focused on adult performance on respective hosts from the viewpoint of optimal foraging (Stephens & Krebs, 1986), as an alternative hypothesis to understand oviposition preference. Based on the optimal foraging theory, phytophagous females may maximize their fitness by staying on hosts that give the highest adult performance in terms of longevity and fecundity, even if the success of their offspring on these particular hosts is sacrificed to some extent (Jaenike, 1986; Scheirs et al., 2000, 2004; Mayhew, 2001; Scheirs & De Bruyn, 2002).

The interpretation of oviposition preference of phytophagous insects based on the optimal foraging theory necessarily takes adult feeding preference into account, and a few empirical studies have dealt with oviposition and adult feeding preference as independent characters (Scheirs et al., 2000, 2004; Scheirs & De Bruyn, 2002). However, in insect groups using plants during both adult and larval stages, in particular in insects such as many chrysomelid beetles of which adults and larvae are ectophagous herbivores feeding on the same plant species and females lay eggs on the plant surface, it may often be difficult to distinguish oviposition preference itself from female feeding preference. It even is uncertain whether substantial oviposition preference exists among such insects. Therefore, investigation of the relationship between oviposition and adult feeding preference would be useful to get a better understanding of host selection in insects of which adults also depend on plants.

In the present study, we investigated characteristics of oviposition site selection by the two herbivorous beetle species, *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae) and *Henosepilachna niponica* (Lewis) (Coleoptera: Coccinellidae), with particular attention to the relationships with feeding sites of females. Both beetle species are ectophagous specialists of thistles (*Cirsium* spp.; Asteraceae), and lay eggs on the surface of host plant leaves under natural conditions. Based on results obtained through field observations and laboratory experiments, we addressed two questions: (i) do both beetles oviposit near feeding sites, and (ii) do ovipositing

females of both beetles exhibit the same degree of fidelity to host leaves?

Materials and methods

Insects and plants

Both *C. rubiginosa* and *H. niponica* are univoltine species specialized on thistles, and have a similar life cycle. Post-hibernating adults appear in early spring (late April to early May) and start oviposition after a short period of feeding. Oviposition continues until mid-summer. Females lay eggs usually on the undersides of the leaves of their food plants; *C. rubiginosa* lay an ootheca consisting of about 10 eggs, while *H. niponica* lay about 20–30 eggs at a time in one mass. Hereafter, we refer to an ootheca or an egg mass of the two beetle species simply as ‘egg mass’. *Cassida rubiginosa* females usually lay one to a few egg masses per day, whereas *H. niponica* females lay one egg mass every few days under laboratory conditions (N Fujiyama, unpubl.). Under natural conditions, egg masses of *H. niponica* are generally deposited in low density, due to increased female dispersal as egg densities increase (Ohgushi, 1999). Similarly, population densities of *C. rubiginosa* are usually low under natural conditions, although density-dependence of female reproductive behavior has not been investigated (Bacher & Schwab, 2000; Koji & Nakamura, 2006). Adults and larvae of both species are ectophagous and feed on the same plant species. Due to low mobility, larval activity is virtually restricted to the plant or the cluster of plants on which egg masses were originally laid. New adults begin to emerge in late July, and they enter hibernation in autumn.

In the southwestern area of Hokkaido, the northernmost island of Japan, the main host species of *C. rubiginosa* is *Cirsium grayanum* (Maxim.) Nakai and *Cirsium alpicola* Nakai, two abundant thistles in the area, while *H. niponica* is confined almost exclusively to *C. alpicola* (Koizumi et al., 1999). Consequently, these two beetle species often co-occur, especially on *C. alpicola* in this area.

Field observations

Distance between eggs and adult feeding sites. Field observation was conducted at Hekirichi, Hokuto (41°53'N, 140°34'E) for *C. rubiginosa* on 14 July 2005, and at Shiriuchi, Kamiiso (41°38'N, 140°21'E) for *H. niponica* on 17 July 2005. The distance (in cm) between an observed egg mass and the nearest feeding scar by adult beetles on host plants was measured along plant surfaces that beetles could have walked on. Feeding scars by *C. rubiginosa* adults are oval holes of an almost regular size (about 4 × 8 mm), although they are often difficult to distinguish from those by congeneric beetles. Egg masses of *C. rubiginosa* can be

easily identified based on their shape and the typical dark brown color of the ootheca. On the other hand, feeding scars by *H. niponica* adults can be accurately distinguished from those left by other herbivores, because epilachnine beetles scrape the leaf surface, leaving the epidermis of one side with a lace-like appearance (cf. Howard, 1941), and *H. niponica* is the only epilachnine species that occurs on thistles in this area (Koizumi et al., 1999). The appearance of egg masses of *H. niponica* is somewhat similar to those of other co-occurring carnivorous ladybird species, such as *Coccinella septempunctata brucki* Mulsant and *Harmonia axyridis* (Pallas), but still can be identified based on the larger egg size and its relatively loose assemblage as a mass. At the Hekirichi site, among the two target beetle species, *C. rubiginosa* occurred as the only species among related thistle-feeding chrysomelid beetles. Furthermore, no other herbivores that make feeding scars similar to those by *C. rubiginosa* adults were encountered in this site. On the other hand, at the Shiriuchi site, although distribution of both of the target beetle species was confirmed at the same time, occurrence of another thistle-feeding species, *Cassida vibex* L., was also confirmed (N Fujiyama, K Togashi, S Kikuta & H Katakura, unpubl.). Therefore, accurate identification of feeding scars by *C. rubiginosa* was impossible at this site, and, thus, we did not carry out the observations for *C. rubiginosa* at the Shiriuchi site. In addition, for both beetle species, we tried to avoid counting very old feeding scars, of which the color of the edge had turned from greenish to brown although such scars were rarely found. A rough estimate showed that the area damaged by adult feeding scars on each host plant growing at the two sites was very small (less than 5% of the total leaf area, at most).

For each beetle species, a total of 30 egg masses were investigated. In the case of *C. rubiginosa*, observations were conducted on *C. grayanum* and *C. alpicola* until the number of egg masses found added up to 30, from either plant species, because adult females do not show particular feeding preference between these two hosts, at least under laboratory conditions (N Fujiyama, unpubl.). Data of *H. niponica* were exclusively collected on *C. alpicola*. It should be noted that the number of females responsible for the 30 egg masses observed under natural conditions was unknown.

Distribution of egg masses on host and non-host plants. Distribution of egg masses was observed at the same time and location as the field measurement mentioned above. For each beetle species, a total of 15 host plant individuals (for *C. rubiginosa*, eight and seven plants of *C. grayanum* and *C. alpicola*, respectively; for *H. niponica*, 15 plants of *C. alpicola*) with more than one egg mass of the target

beetle species were investigated. First, the number of egg masses on each host plant individual was recorded. Then, all leaves of plants other than the hosts growing within a radius of 1 m from each host plant individual were carefully checked for presence/absence of egg masses. The number of egg masses on non-host plant leaves was also recorded.

Distance between eggs and adult feeding sites in cages

The above-mentioned field measurement of the distance between eggs and feeding scars probably included feeding scars made by male beetles, which are impossible to discriminate from those made by females. Therefore, similar observations were carried out in an experimental garden on the Hakodate Campus, Hokkaido University of Education (41°47'N, 140°45'E), mainly in order to confirm the reliability of the observations under natural conditions. A total of four cages made of cheesecloth (2 × 2 × 2 m) were prepared, and two cages each were assigned to each of the respective beetle species. A *C. alpicola* individual having several shoots was transplanted at the center of each cage. As mentioned above, it was impossible to know how many female beetles were responsible for the egg masses observed under natural conditions. Therefore, we released three female beetles per cage (i.e., a total of six females were used for each beetle species) considering the normal density of beetles on a host individual under natural conditions, and allowed them to feed and oviposit repeatedly on the host plant. Females collected at the Shiriuchi site were released into the cages in mid-July 2005. In the case of *H. niponica*, sexes of adult beetles can be easily determined by the naked eye, based on morphology of the sixth visible abdominal sternite, while external morphology of male and female beetles of *C. rubiginosa* is almost identical except for an incomplete sexual size dimorphism (Ward & Pienkowski, 1978). Therefore, sexes of *C. rubiginosa* were roughly determined based on mating behavior under mass rearing conditions, and then females were selected after confirmation of at least one oviposition in the laboratory.

Presence of egg masses on the host plants was checked twice per week. If an egg mass was found, the distance from the egg mass to the nearest feeding scar was recorded. After the measurement of the distance, egg masses were immediately and gently wiped out with 70% EtOH to avoid possible effect of egg density on oviposition behavior of female beetles (Ohgushi & Sawada, 1985). No apparent physical damage on leaf surface by this treatment was found. Observations were continued until the number of egg masses of respective beetle species summed up to more than 30 when egg masses in the two cages were added together. Basically, any artificial treatment or observation

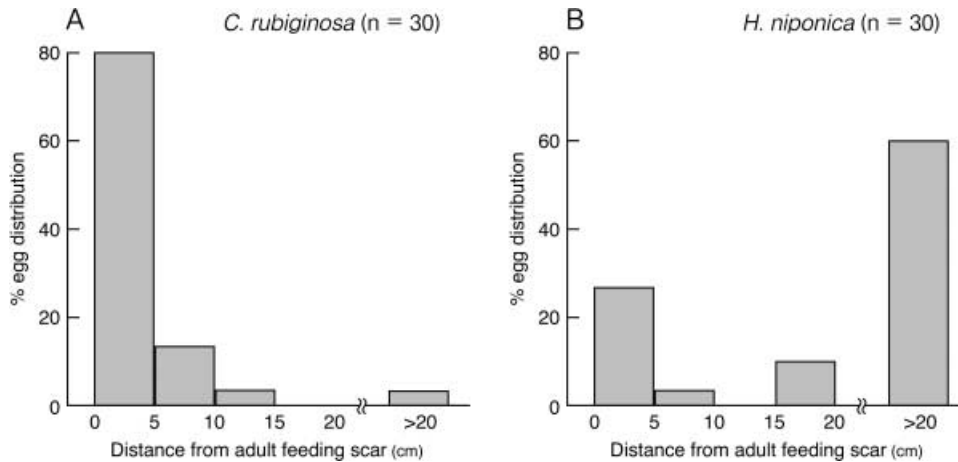


Figure 1 Frequency distribution of egg masses of two thistle-feeding beetle species, (A) *Cassida rubiginosa* and (B) *Henosepilachna niponica*, at different distances from adult feeding scars under natural conditions.

activity did not appear to cause significant change of female behavior, because similar tendencies to that in the field were observed in the cages (see Results).

Oviposition substrate selection in the laboratory

As an oviposition chamber, a transparent cylindrical plastic case (8 cm in diameter \times 2 cm high) was used. The bottom of the case was lined with moist filter paper, and the cap of the case was punched with holes in a circle with a diameter of 6 cm and filled again with filter paper from the inside to provide ventilation. A disc of *C. alpicola* leaf (4 cm in diameter) was put on a plastic stage that was placed at the center of the case, enabling beetles to access the leaf disc from both the front and back sides of the leaf. A female beetle was released into the chamber and was allowed to feed on the leaf disc and oviposit for 24 h. Then, the position of egg masses in the chamber was recorded according to different substrates, that is, host plant leaves and other artificial materials (i.e., plastics of the walls of the chamber and surface of the stage, and filter papers on the bottom and top inside the chamber). Fifteen female beetles each of *C. rubiginosa* and *H. niponica*, collected at the Shiriuchi site in early June 2005, were investigated simultaneously in a single rearing room under a controlled regime of L16:D8 at 20 °C. At most 10 instances of oviposition were repeated for each female beetle.

For each beetle species, data from 15 females was pooled, and the observed egg distribution was compared with expected values of random distribution of egg masses calculated based on the surface areas of substrates in the oviposition chamber by χ^2 -test. In addition, distribution of egg masses was compared between the beetle species by χ^2 -test.

Results

Field observations

Distance between oviposition and adult feeding sites. Because egg masses of *C. rubiginosa* tended to concentrate on particular host plant individuals, we could find 30 egg masses on three plant individuals each of *C. grayanum* (13 egg masses) and *C. alpicola* (17 egg masses). The distance (mean \pm SE) from adult feeding scars was somewhat larger on *C. alpicola* (4.9 ± 1.92) than on *C. grayanum* (2.3 ± 0.62). However, because this difference was not statistically significant (Mann–Whitney U-test: $U = 124$, $P = 0.57$), we pooled data from the two different host species. All egg masses of *C. rubiginosa* were found less than 20 cm away from adult feeding scars, except for one case on *C. alpicola*, that was 32.5 cm from the nearest adult feeding site (Figure 1A, Table 1). Of the egg masses, 80% was found within 5 cm from adult feeding scars (Figure 1A). For *H. niponica*, 30 egg masses were found across 12 *C. alpicola*

Table 1 Distance (mean \pm SE; cm) between egg masses and the nearest adult feeding scars on host plants of two thistle-feeding beetle species, *Cassida rubiginosa* and *Henosepilachna niponica*, in the field and in the cage experiment

	No.	Mean \pm SE	Range (min.–max.)
Field site			
<i>C. rubiginosa</i>	30	3.8 ± 1.13	0.5–32.5
<i>H. niponica</i>	30	24.6 ± 3.54	0.1–60.0
Cage			
<i>C. rubiginosa</i>	40	4.4 ± 0.64	1.0–20.0
<i>H. niponica</i>	30	21.7 ± 2.88	1.5–54.0

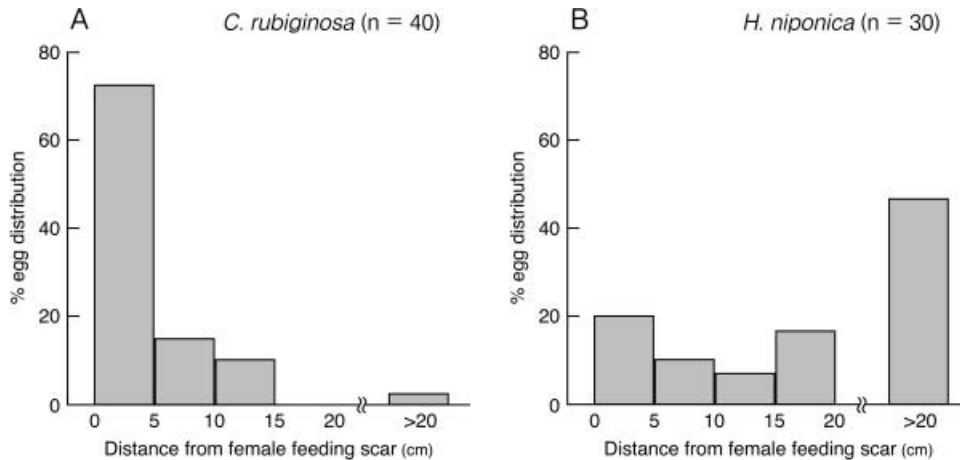


Figure 2 Frequency distribution of egg masses of two thistle-feeding beetle species, (A) *Cassida rubiginosa* and (B) *Henosepilachna niponica*, at different distances from female feeding scars in the cage experiment.

plants. In contrast to *C. rubiginosa*, egg masses were scattered over a wider range, and 60% of the egg masses were more than 20 cm apart (60 cm at the most; Table 1) from adult feeding sites (Figure 1B). The mean distance between egg masses and adult feeding scars of *H. niponica* was significantly larger than that of *C. rubiginosa* (Mann–Whitney U-test: $U = 691$, $P = 0.0001$; Table 1).

Distribution of egg masses on host and non-host plants. Many kinds of plants other than host plants, such as herbs of the Urticaceae, Umbelliferae, and Asteraceae, vines of the Actinidiaceae, Fabaceae, and Vitaceae, and grasses and ferns, grew around the host plants. In some cases, vines had twisted around thistles. None of 48 egg masses of *C. rubiginosa* were found on plants other than the hosts. On the other hand, three egg masses out of 36 egg masses (8.3%) of *H. niponica* were found on plants other than thistles, two on *Heracleum dulce* Fisch. (Umbelliferae) and one on *Lysichiton camtschatcense* (L.) Schott. (Araceae).

Distance between oviposition and adult feeding sites in cages

The results of the cages were similar to those of the field observations. For *C. rubiginosa*, a total of 40 egg masses were observed during the 1-week census (i.e., in two observation rounds). A total of 72.5% of egg masses of *C. rubiginosa* were found within 5 cm of female feeding scars, and fewer eggs were found as the distance from the feeding scars increased (Figure 2A). For *H. niponica*, a total of 30 egg masses were found within 3 weeks (i.e., in five observation rounds); 46.7% of egg masses were confirmed at a distance of more than 20 cm from female feeding scars (54 cm at the most; Table 1), and there was no tendency for

egg masses to be found in proximity to female feeding scars (Figure 2B). Again, the mean distance between egg masses and adult feeding scars of *H. niponica* was significantly larger than that of *C. rubiginosa* (Mann–Whitney U-test: $U = 1059$, $P < 0.0001$; Table 1).

Oviposition substrate selection in the laboratory

A total of 126 and 62 egg masses were produced by *C. rubiginosa* and *H. niponica* females, respectively. The cumulative number of times that each female oviposited ranged from 3–10 for *C. rubiginosa*, and 2–7 for *H. niponica*. For both beetle species, the distribution of egg masses was biased to oviposition on the host plant leaves and was significantly different from a random distribution (for *C. rubiginosa*: $\chi^2 = 804.15$, d.f. = 1, $P < 0.0001$; for *H. niponica*: $\chi^2 = 23.7$, d.f. = 1, $P < 0.0001$) (Figure 3). There was also inter-specific difference in the tendency to oviposit on host plant leaves ($\chi^2 = 104.91$, d.f. = 1, $P < 0.0001$); all of the egg masses of *C. rubiginosa* were laid on the host plant leaves, while 65.3% of egg masses of *H. niponica* were laid on substrates other than the leaves (Figure 3).

Discussion

Both in the field and in the cages, the distances between adult feeding scars and egg masses differed significantly between *C. rubiginosa* and *H. niponica*; most egg masses of *C. rubiginosa* were found in proximity to the adult feeding sites, while egg masses of *H. niponica* were scattered over a wide range. It is possible that we missed some of the feeding scars by beetles in these measurements, because many beetles show signs of sample feeding (or test bite) behavior, resulting in subtle feeding scars before substantial

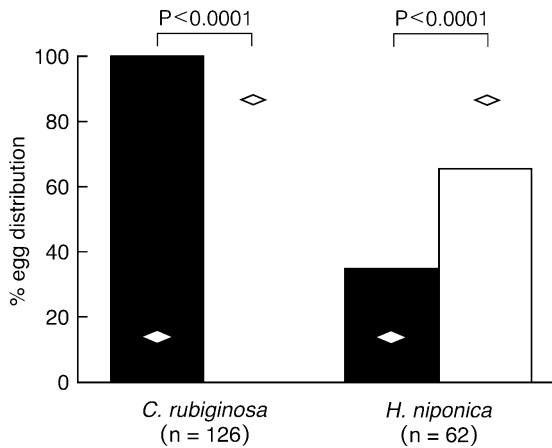


Figure 3 Oviposition substrate selection by two thistle-feeding beetle species, *Cassida rubiginosa* and *Henosepilachna niponica*, under laboratory conditions. Solid and open bars indicate percentage of egg masses laid on host plant leaves and other substrates, respectively. Lozenges indicate expected values of random distribution of eggs calculated based on the surface areas of substrates in the oviposition chamber. Both distributions are significantly different from random distribution (χ^2 -test: $P < 0.0001$).

feeding takes place (Harrison, 1987; Henderson et al., 2004). However, it has been also reported that sample feeding is more frequent on non-host plants, and most cases of this behavior on hosts will eventually lead to substantial feeding (Harrison, 1987; Henderson et al., 2004). Therefore, possible bias due to omission of such subtle feeding scars in the data for *H. niponica* would be negligible, because all observations and experiments in the present study were conducted with normal host plant (for *C. rubiginosa*, virtually no bias is expected because the positions of feeding scars and egg masses were very close to each other). Concerning the oviposition substrate selection in the field and laboratory, *C. rubiginosa* females laid their eggs strictly on host plants and host plant leaves, while egg masses of *H. niponica* were sometimes distributed on non-host plant leaves or artificial substrates. Our results suggest that oviposition by *C. rubiginosa* occur strictly on host plant leaves in proximity to the female feeding sites, while *H. niponica* females tend to oviposit at some distance from their feeding sites and do not keep to the host plant leaves as oviposition substrates.

When low mobility in neonate larvae of holometabolous herbivorous insects is taken into account, strict oviposition on host plant leaves observed in *C. rubiginosa* would be essential and appears to have been shaped as an adaptive trait. Nonetheless, the fact that most egg masses were found in proximity to the adult feeding sites is noteworthy, suggesting that oviposition sites and female feeding sites

are virtually inseparable in this species. In such cases, strict oviposition on larval foods can inevitably occur concomitantly with adult feeding activity, if females lay eggs only near their own “dining tables”. In any case, with the close relationship between oviposition and adult feeding sites, it is more plausible that adult performance on the host has taken an important role in determining host specificity (Jaenike, 1986; Scheirs et al., 2000, 2004; Scheirs & De Bruyn, 2002). Further investigations based on the optimal foraging theory as well as from the view point of optimal oviposition are indispensable to elucidate how the host specificity of *C. rubiginosa* has been shaped. On the other hand, it has been suggested that females of *H. niponica* show a particular behavior in selection of oviposition sites, that is, a tendency to oviposit after some movement from their feeding sites. At the same time, *H. niponica* females appeared to not necessarily keep to the host plant leaves as oviposition substrates in the field and laboratory. Probably as a consequence of these behavioral characteristics of females, some portion of *H. niponica* eggs will occasionally be laid on non-host plants in proximity to hosts under natural conditions, as documented in the present study. As here, oviposition on non-host plants has also been observed in other epilachnine beetles including tropical ones (N Fujiyama, pers. obs.), this behavior might be a common feature across herbivorous coccinellids. Another implication of this finding is that such “careless” oviposition may have played some role in the evolution of host-use pattern of this group. Of course, larvae that hatch from the eggs on non-host plants observed in the present study could probably not develop on these plants, because plants from Araceae and Umbelliferae are currently not included in host range even if all herbivorous ladybirds in the subfamily Epilachninae are considered (Schaefer, 1983). Nonetheless, in an evolutionary perspective, this behavior might provide a potential chance to oviposit on what appears to be a novel host plant. The fact that many herbivorous ladybird beetles are associated with climbing plants (Schaefer, 1983; Kobayashi et al., 1998; Katakura et al., 2001), such as those belonging to the Actinidiaceae, Cucurbitaceae, Fabaceae, Vitaceae, and Asteraceae, may support this scenario, because accidental oviposition on novel hosts should be more frequent when the normal and the novel host plants are twisted together.

Concerning *H. niponica*, 60% of the egg masses in the field and approximately half of the egg masses in the cages were found at distances of more than 20 cm from the adult feeding scars. Additionally, the mean distance between egg masses and adult feeding scars of *H. niponica* was more than 20 cm. Because length and width of *C. alpicola* leaves are usually less than 20 cm, it means that most egg masses more than 20 cm away from adult feeding sites were

oviposited on leaves that had no feeding damage, although we did not pay attention to this during our observations. It has been reported that prior herbivory by conspecifics (Haukioja & Neuvonen, 1985; Brown & Weis, 1995; Van Zandt & Agrawal, 2004), as well as by other herbivores (Agrawal, 1999; Wise & Weinberg, 2002; Van Zandt & Agrawal, 2004) often causes a reduction of leaf quality in terms of larval food resources (Karban & Baldwin, 1997; Awmack & Leather, 2002). Furthermore, it is also possible that feeding by beetles induces several kinds of plant defense (Karban & Baldwin, 1997), including emission of volatile plant chemicals that attract natural enemies (Takabayashi & Dicke, 1996; Dicke & van Loon, 2000; Fatouros et al., 2005). Therefore, if a reduction of leaf quality or any plant defenses occur at the leaf level in thistle plants, oviposition on undamaged leaves by *H. niponica* females will be adaptive. Alternatively, this behavior might be phylogenetically constrained in herbivorous ladybird beetles. In fact, the two beetle species studied here belong to different families. Herbivorous ladybirds (the subfamily Epilachninae) are considered to have evolved from carnivorous coccinellids (Hodek & Honek, 1996), whereas the family Chrysomelidae is a herbivorous clade belonging to the essentially herbivorous superfamily Chrysomeloidea. Furthermore, within the Coccinellidae, according to morphological characteristics, a close relationship between the subfamilies Epilachninae and Coccinellinae is inferred (Hodek & Honek, 1996). Therefore, some behavioral characteristics of herbivorous ladybirds may have been shaped under constraints of its carnivorous ancestry. For instance, in the aphidophagous coccinellid *H. axyridis* (belonging to the Coccinellinae that is possibly a sister group of the Epilachninae; Hodek and Honek, 1996), a tendency to oviposit at more than 10 cm distance from adult feeding sites (i.e., aphid colonies) was also observed, and its advantage in avoiding predation by conspecific non-sibling larvae was suggested (Osawa, 1989). At present, it is not clear whether oviposition behavior of *H. niponica* has a similar effect in avoiding predation. In any case, a comparison of larval performance on leaves with/without adult feeding damage and additional field observations, focusing on the role of natural enemies, are indispensable in future studies to evaluate the significance of oviposition site selection behavior of *H. niponica*.

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