Host plant suitability of a recently naturalized thistle *Cirsium vulgare* (Asteraceae) for a phytophagous ladybird beetle, *Epilachna pustulosa* (Coleoptera: Coccinellidae)

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The phytophagous ladybird beetle, *Epilachna pustulosa* Kôno occurs mainly on the thistle *Cirsium kamtschaticum* Ledeb. In recent years, we have confirmed feeding and oviposition by *E. pustulosa*, and some degree of larval development of this beetle, on a naturalized congeneric thistle, *Cirsium vulgare* (Savi) Tenore. In this study, we assessed the host suitability of *C. vulgare* for *E. pustulosa*, using larval rearing and simple food choice tests, by comparing the performance on, and preference for, their legitimate host *C. kamtschaticum*. All experiments were initiated in July, when the utilization of *C. vulgare* by *E. pustulosa* became obvious. For larval performance, *E. pustulosa* showed a lower eclosion rate, shorter developmental duration and smaller body size when reared on *C. vulgare* than on *C. kamtschaticum*. *Cirsium vulgare* appeared to be a less adequate larval food than *C. kamtschaticum*. Adult feeding preference was altered seasonally; females preferred *C. kamtschaticum* to *C. vulgare* in a food choice test conducted in early July, whereas they showed the opposite preference in tests conducted in mid and late July. The utilization of *C. vulgare* by *E. pustulosa* appeared to be induced by qualitative deterioration of *C. kamtschaticum* leaves in July, which resulted in increased dispersion of adult beetles.

Key words: adult preference; *Cirsium vulgare*; *Epilachna pustulosa*; larval performance; naturalized plants.

INTRODUCTION

Phytophagous insects may encounter unfamiliar plants by range expansion or habitat alternation of either the plants or the insects, or both. In some situations, phytophagous insects will utilize unfamiliar plants as novel hosts; this proceeds according to the chemical similarity of the plants to those normally utilized by the insects, rather than according to close taxonomic relatedness (Renwick 1989).

Oviposition by phytophagous insects on plants that are poor or unsuitable for larval performance has been repeatedly reported (Chew 1977; Rausher

1979; Courtney 1981; Wiklund 1981; Thompson 1988; Renwick 1989; Jaenike 1990; Thompson & Pellmyr 1991; Bernays & Chapman 1994; Larsson & Ekbom 1995; Mayhew 1997). In most of these cases, the plants involved were recently added to the habitat, and thus the insects presumably did not have sufficient time to evolve behavioral avoidance or physiological adaptation to these new plants (e.g. Wiklund 1975; Chew 1977; Rodman & Chew 1980; Legg *et al.* 1986; Thompson 1988; Larsson & Strong 1992).

Although such maladaptive host utilization occurs, encounters with unfamiliar plants can also provide an opportunity for host shifts or host-range expansion for the insects (Bernays & Chapman 1994). Therefore, novel associations between insects and plants with known histories are the best arena to investigate the significant question concerning the diet breadth evolution of phytophagous insects, that is, how novel potential
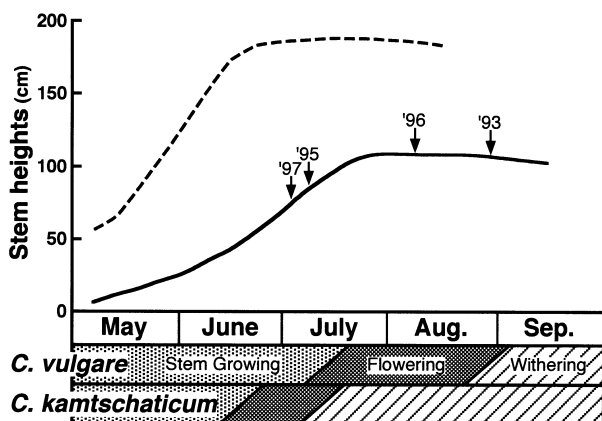
Fig. 1. Seasonal changes in stem heights (upper) and the periods of flowering and withering (lower) for *Cirsium vulgare* (——) and *C. kamtschaticum* (– – –) (N. Fujiyama, unpubl. data, 1999). The first observed utilizations (feeding or oviposition) of *C. vulgare* by *Epilachna pustulosa* in the successive years from 1993 to 1997 are indicated with arrows.

hosts can influence the diet breadth or host utilization patterns of these insects.

The phytophagous ladybird beetle, *Epilachna pustulosa*, occurs mainly on the thistle *Cirsium kamtschaticum* in and near Sapporo, Hokkaido, northern Japan (Katakura 1981). In recent years, we have confirmed feeding and oviposition by *E. pustulosa*, and some degree of larval development of this beetle, on a recently naturalized congeneric thistle *Cirsium vulgare* in the Sapporo area (Fig. 1). The utilization of *C. vulgare* was observed only from mid-summer to early autumn (July to September), and was observed only when this plant was growing in and near the habitats where *E. pustulosa* fed on *C. kamtschaticum*.

In the present study, we aim to assess the host suitability of *C. vulgare* as a novel host plant for *E. pustulosa*. Comparisons involving performance on, and preference for, their legitimate host, *C. kamtschaticum*, were carried out. On the basis of the results, we offer possible ecological interpretations for the novel association between *E. pustulosa* and *C. vulgare*.

BACKGROUND INFORMATION

Epilachna pustulosa is a univoltine coccinellid species endemic to Hokkaido (Katakura 1981). In

the Sapporo area, posthibernating adults appear in early May and start oviposition in late May. Oviposition continues until mid-July. Females lay eggs in egg masses usually on the underside of the leaves of their food plants. Larvae start to emerge in early June. Adults and larvae feed on the same plant species. Because of the low mobility of the larvae, larval development is usually restricted to the plant or cluster of plants on which the eggs were laid. New adults start to emerge in early August and they enter hibernation by late September.

The legitimate host of *E. pustulosa*, *C. kamtschaticum*, is a perennial wild herb and is the most abundant and prevailing species of thistle in Hokkaido (Kadota 1995). This thistle species grows nearly everywhere in forest margins, stream sides and grassy fields as an assemblage of a few to more than 15 clonal shoots (=clone; cf. Fujiyama & Katakura 1997).

Cirsium vulgare is a recently naturalized species of European origin (Matuki & Ito 1960; Ito *et al.* 1987) and occurs in disturbed habitats (Grime 1979). The invasion of this plant to Japan was firstly confirmed in Hokkaido, and the date of invasion is believed to have been around 1950 (Matuki & Ito 1960). This thistle species is biennial and populations appear to be short-lived (van Leeuwen 1981).

The general phenologies of the two thistles in the Sapporo area are as follows (Fig. 1): most clones of *C. kamtschaticum* and *C. vulgare* sprout in late April, soon after the disappearance of the snow cover. *Cirsium kamtschaticum* grows rapidly to June and reaches approximately 2 m in height; it blooms from June to July. *Cirsium vulgare* grows gradually to approximately 1 m until August, and blooms from July to late August. *Cirsium kamtschaticum* withers by August, whereas *C. vulgare* retains its leaves until September.

METHODS

In 1997, we compared larval performance of *E. pustulosa* on the two thistle species, *C. kamtschaticum* and *C. vulgare*. In 1998, we conducted food choice tests in order to assess adult preference of the beetle for the two thistles. All experiments were initiated in July, when utiliza-

tion of *C. vulgare* by *E. pustulosa* became obvious in the field (Fig. 1).

All experiments were carried out under a controlled regime of L16 : D8 at 20°C.

Rearing of larvae

In order to obtain egg masses for rearing, we collected two posthibernating adult females on 5 July 1997 at Hoshioki, located in the western suburbs of Sapporo. One individual was feeding on *C. vulgare* and the other was feeding on *C. kamtschaticum*. Both females were sexually mature and had copulated before collection (cf. Katakura 1982). After they were brought back to the laboratory, each female was fed the alternative food plant *Solanum japonense* Nakai (Solanaceae) (cf. Katakura 1981) in a transparent styrene cage (8.0 cm × 15.5 cm × 3.0 cm), the bottom of which was covered with moist filter paper. Rearing of larvae and food choice tests (see below) were also carried out in cages that were identical with respect to size and humidity. Egg masses laid by the two females were gathered every day.

Two sets of newly hatched larvae, each containing five individuals from a single egg mass, were reared on either *C. vulgare* or *C. kamtschaticum*. Ten replicate sets of offspring (from six egg masses) were collected from each female. Consequently, a total of 100 larvae (50 from each female) were reared on the two thistle species.

During the rearing period (mid-July to late August), we used leaves from several clones of *C. vulgare* growing on the campus of Hokkaido University (located in the northern part of Sapporo), and those from a clone of *C. kamtschaticum* transplanted into an experimental garden of Hokkaido University in the spring of 1994 from Sankakuyama (located in the western suburbs of Sapporo). From mid-July, *C. kamtschaticum* was approaching the withering stage (cf. Fig. 1), and yellowing of older leaves was observed from August. However, because older instar larvae of *E. pustulosa* have sufficient mobility to move from one leaf to another, at least within a single thistle clone, we intentionally selected intact and green leaves of the two thistles as larval food, especially for *C. kamtschaticum*. A sufficient amount of leaves was provided at intervals of 1 or 2 days until the third instar, and leaves were provided every day during the fourth (final) instar stage.

Larvae were reared until emergence. Larval survival and developmental stages were checked daily. The number of individuals reaching each developmental stage, the developmental duration (the number of days required from hatching to adult eclosion), and the pronotum width (a body size index) of newly emerged adults were recorded.

Food choice tests

For the food choice tests conducted in 1998, we did not use the beetles from Hoshioki, because another field census was being conducted there (N. Fujiyama *et al.*, unpubl. data, 1998). Instead, posthibernating adult females collected from *C. kamtschaticum* at Sankakuyama were used. These beetles were probably naive to *C. vulgare*, because we have never confirmed the presence of this thistle species at Sankakuyama.

The collected beetles were fed *S. japonense* leaves for more than 1 week before the experiments started, in order to diminish the possible influence of a feeding experience before collection. When the same beetles were used repeatedly in different feeding tests, they were fed *S. japonense* leaves for more than 24 h prior to each test, in order to minimize the influence of the preceding tests.

Two pieces of leaf (approximately 20 cm², each from different thistle species) were placed in the cage at a distance of approximately 2–4 cm from each other. We released a female beetle into the cage and allowed it to feed on the leaf pieces for 24 h. Thirteen to 15 replicates using different females were carried out simultaneously in each choice test. The consumed leaf area was measured with the aid of image processing software (NIH Image, ver. 1.59; National Institute of Health, Bethesda, MD, USA) after the data were scanned into a computer. The existence of a feeding preference (i.e. difference in feeding amounts) was examined by a type of MANOVA (Manly 1993), as a lack of independence was suspected between the consumed areas on the two leaf pieces offered to each beetle (cf. Fujiyama & Katakura 2001).

In the food choice tests, we used leaves from a single clone of *C. vulgare* and *C. kamtschaticum*, both of which were growing on the campus of

Hokkaido University. The choice tests were repeated three times on different dates in July.

RESULTS

Larval performance

Results are summarized in Table 1. The eclosion rate was significantly lower when the larvae were reared on *C. vulgare* than when they were reared on *C. kamtschaticum* (Wilcoxon's signed ranked tests: for offspring from the female caught on *C. vulgare*, $n = 10$, $T_s = 0$, $P = 0.005$; for offspring from the female caught on *C. kamtschaticum*, $n = 10$, $T_s = 11$, $P = 0.120$; for both offspring pooled, $n = 20$, $T_s = 15$, $P = 0.001$). For the number of individuals reaching adulthood, a *G*-test detected no significant interaction between larval derivation and the thistle species that was used as larval food (d.f. = 1, $G = 3.66$, $P > 0.05$). Death of larvae on *C. vulgare* occurred mainly in the first and fourth (final) instar periods (63.5% and 20.3% of the total mortality, respectively), whereas on *C. kamtschaticum*, larval death mainly occurred in the first and second instar periods (71.4% and 14.3%, respectively) (Fig. 2).

Two-way ANOVAs detected highly significant differences for the effect of larval food, both on developmental duration and pronotum width (Table 2). Shorter developmental duration and smaller body size were achieved when larvae were reared on *C. vulgare* than when they were reared on *C. kamtschaticum* (Table 1). For both of these two developmental traits, there were no significant interactions between larval derivation and the thistle species that was used as larval food (Table 2).

Adult preference

In the first food choice test conducted in early July, posthibernating adult females of *E. pustulosa* significantly preferred *C. kamtschaticum* over *C. vulgare* (Fig. 3a). However, in the following two tests, conducted in mid and late July, females exhibited the opposite preference, namely, they significantly preferred *C. vulgare* over *C. kamtschaticum* (Fig. 3b, c).
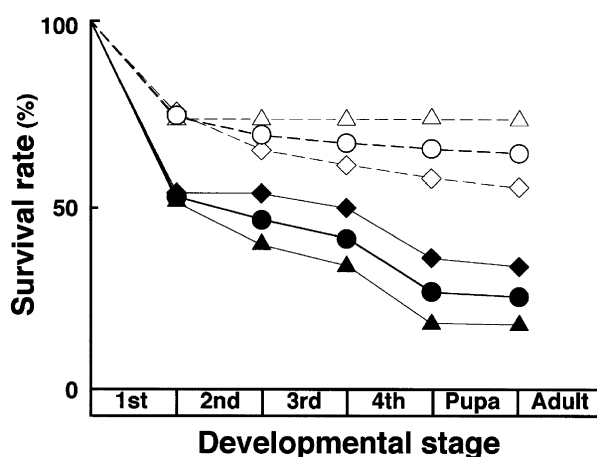
Fig. 2. Percentage survival of *Epilachna pustulosa* reared on *Cirsium vulgare* (closed symbols) and *C. kamtschaticum* (open symbols). Cv offspring, the mother was caught on *C. vulgare*; Ck offspring, the mother was caught on *C. kamtschaticum*. (▲ △), Cv offspring; (◆ ◇), Ck offpsring; (● ○), pooled.

Table 1 Developmental traits [mean ± SE (*n*)] of *Epilachna pustulosa* reared on *Cirsium vulgare* and *Cirsium kamtschaticum*

Reared on	Derivation[†]	Eclosion rate (%)	Developmental duration in days	Pronotum width (mm) Female	Male
C. vulgare	Cv	18.0 ± 4.67 (10)	33.89 ± 0.696 (9)	3.16 ± 0.016 (4)	3.04 ± 0.029 (5)
	Ck	34.0 ± 7.33 (10)	33.59 ± 0.569 (17)	3.15 ± 0.061 (9)	3.04 ± 0.053 (8)
	Pooled	26.0 ± 4.61 (20)	33.69 ± 0.436 (26)	3.15 ± 0.042 (13)	3.14 ± 0.034 (13)
C. kamtschaticum	Cv	74.0 ± 7.33 (10)	35.76 ± 0.474 (37)	3.38 ± 0.024 (21)	3.21 ± 0.024 (16)
	Ck	56.0 ± 9.33 (10)	36.75 ± 0.435 (28)	3.30 ± 0.040 (15)	3.23 ± 0.030 (13)
	Pooled	65.0 ± 6.13 (20)	36.19 ± 0.332 (65)	3.35 ± 0.023 (36)	3.22 ± 0.019 (29)

[†]Cv, the mother was caught on *C. vulgare*; Ck, the mother was caught on *C. kamtschaticum*.

Table 2 Two-way ANOVAs on developmental traits of *Epilachna pustulosa* reared on *Cirsium vulgare* and *Cirsium kamtschaticum*

Source	Developmental duration d.f.	SS	F	Pronotum width d.f.	SS	F
Food	1	0.083	17.364***	1	0.058	37.478***
Mother	1	0.001	0.287	1	0.001	0.509
Food × Mother	1	0.007	1.494	1	<0.001	0.189
Sex	1	0.013	2.630	1	0.034	21.978***
Error	86	0.414		86	0.132	

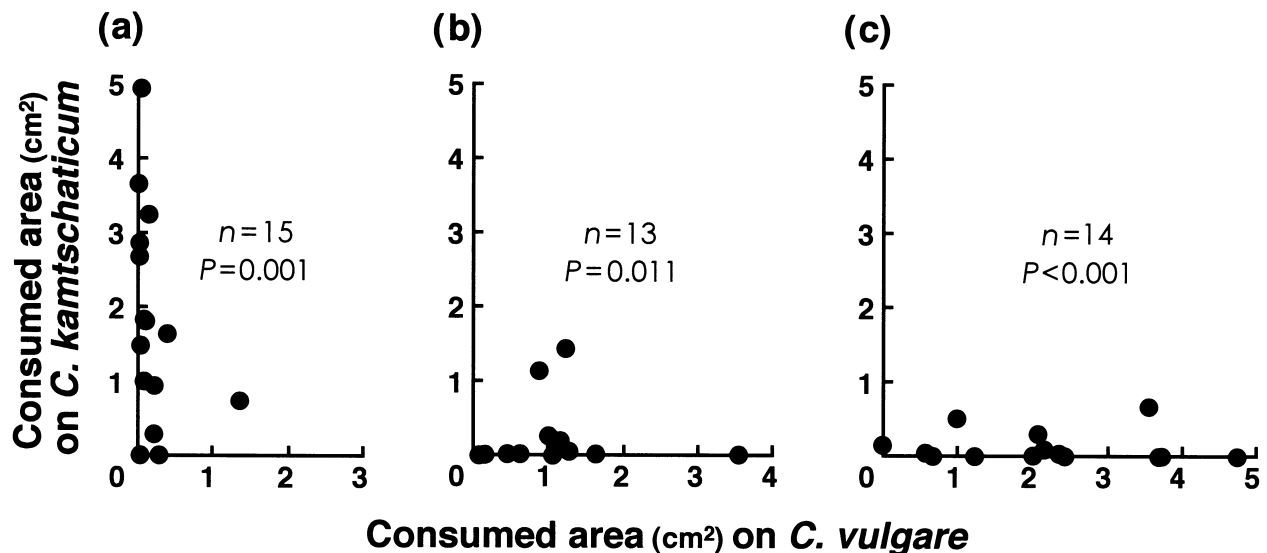Data were log-transformed before the analyses. ***$P < 0.001$.

Fig. 3. Choices by posthibernating adult *Epilachna pustulosa* females for *Cirsium vulgare* and *Cirsium kamtschaticum* examined on different dates in July. **(a)** 6 July 1998; **(b)** 22 July 1998; **(c)** 31 July 1998. Each dot represents the actual area (in cm²) consumed by each beetle. Analyzed by MANOVA (Manly 1993). A significant difference indicates the existence of a preference for thistle leaves, as determined by a larger leaf area consumed.

DISCUSSION

Suitability of *C. vulgare* as a larval food for *E. pustulosa*

Epilachna pustulosa showed a lower eclosion rate, a shorter developmental duration and a smaller body size when reared on *C. vulgare* than on *C. kamtschaticum* (Table 1). Thus, with respect to the eclosion rate and body size, *C. vulgare* is a less adequate larval food for *E. pustulosa* than *C. kamtschaticum*. Furthermore, death in the fourth instar larval period was more frequent on *C. vulgare*

than on *C. kamtschaticum* (Fig. 2). In *C. vulgare*, the existence of some accumulative toxic components or a shortage of some nutrients that are necessary for pupation may occur.

In contrast, an observed shorter developmental duration on *C. vulgare* could be interpreted as indicating the superiority of this thistle species, at least with respect to this particular trait. However, in the present study, larval rearing was carried out from July to August. In this season, although we intentionally selected hearty leaves of *C. kamtschaticum* for the *E. pustulosa* larvae, the *C. kamtschaticum* leaves were approaching the with-

ering stage (cf. Fig. 1); thus, some qualitative deterioration of the leaves could be expected. Indeed, in previous rearing experiments conducted in earlier seasons under the same regime (Fujiyama & Katakura 1997; Koizumi *et al.* 1999), larval performance of *E. pustulosa* on appropriate *C. kamtschaticum* plants was somewhat better than that observed in the present study, with regard to all three developmental traits examined, with shorter developmental duration ranging from 31.3 to 34.9 days. Therefore, the relatively short developmental duration on *C. vulgare* does not necessarily show its superiority as a larval food.

Therefore, it can be assumed that *C. vulgare* is less adequate than *C. kamtschaticum* as a larval food for *E. pustulosa*, especially when the suitability of the two thistle species throughout the season is considered.

Proximate factors for utilization of *C. vulgare* by *E. pustulosa*

In the food choice tests, female beetles preferred *C. vulgare* to *C. kamtschaticum* in the latter half of July, whereas the opposite preference was observed in the first half of July (Fig. 3). This alternation of food preference was probably caused by the qualitative deterioration of *C. kamtschaticum* leaves later in the season. Such seasonal qualitative deterioration of *C. kamtschaticum* leaves will enhance dispersion of *E. pustulosa* adults from this plant. Additionally, frequent adult dispersal later in the season may be caused by increased conspecific egg density on *C. kamtschaticum* (cf. Ohgushi 1999), or by other changes in leaf quality induced by feeding damage caused by *E. pustulosa* and other herbivores (cf. Reznik 1991).

Under such circumstances, the possibility of incessant influx of these dispersing *E. pustulosa* adults on *C. vulgare* is expected to be very high, because in this season, *C. vulgare* is more vigorous and probably more intact; the plant will also have none, or at least fewer ladybird beetle eggs on it than will *C. kamtschaticum*. Additionally, *C. vulgare* achieves its maximum plant size in late July (Fig. 1). Visual cues as well as olfactory cues from *C. vulgare* may, in part, give rise to the utilization of this thistle by *E. pustulosa*.

Utilization of *C. vulgare* by *E. pustulosa* as an adaptive phenomenon

As mentioned earlier, *C. vulgare* is considered to be a less suitable food source for *E. pustulosa* development. The observed alternation in adult food preference (Fig. 3) may indicate that *E. pustulosa* cannot discriminate *C. vulgare* from its legitimate host, *C. kamtschaticum*, using species-specific cues for thistles. It is probable that *E. pustulosa* are utilizing *C. vulgare* by cues for selection of more appropriate *C. kamtschaticum* clones remaining in later season, without gaining any benefits (or even incurring costs) (cf. Wiklund 1975; Chew 1977; Rodman & Chew 1980; Legg *et al.* 1986; Thompson 1988; Larsson & Strong 1992).

Alternatively, the utilization of *C. vulgare* may somehow increase the total fitness of *E. pustulosa*. The utilization of *C. vulgare* always occurred late in the season (Fig. 1) and was rather subsidiary. Because *C. kamtschaticum* is less available due to the normal process of withering by August (Fig. 1), it is also possible that such subsidiary utilization of *C. vulgare* contributes to an increase in the net number of reproductive adults for the following year. Although we have not confirmed incidence of complete larval development of *E. pustulosa* on *C. vulgare* under natural conditions, the shorter developmental duration on *C. vulgare* may be favorable for increasing the number of newly emerged adults, especially for eggs oviposited in late season, despite the higher mortality rate observed on this thistle (cf. Table 1).

To determine whether the utilization of *C. vulgare* by *E. pustulosa* is adaptive or maladaptive, total fitness should be compared under natural conditions between populations utilizing *C. kamtschaticum* exclusively and those utilizing both *C. kamtschaticum* and *C. vulgare*. In any case, the novel association between *E. pustulosa* and *C. vulgare* provides a rare opportunity for studying the current diet breadth evolution of phytophagous insects.

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