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Preference-performance linkage in a herbivorous lady beetle: consequences of variability of natural enemies

Abstract We investigated the relationship between oviposition preference and offspring performance in a herbivorous lady beetle *Epilachna pustulosa* on two co-occurring plant species, thistle *Cirsium kamtschaticum* and blue cohosh *Caulophyllum robustum*, in 1994 and 1995. The relative importance of bottom-up effects by host plants and top-down effects by natural enemies on offspring performance were determined using field and laboratory experiments. In both years, egg density on blue cohosh was significantly higher than on thistle. A laboratory experiment demonstrated that larval survival from hatching to adult emergence was significantly higher, and developmental period shorter when larvae were reared on blue cohosh compared to thistle. The positive preference-performance linkage varied between years in the field. Top-down effects had a different impact on larval survival on the two host plant species. Arthropod predators, a lady beetle *Harmonia axyridis* and an earwig *Forficula mikado*, considerably depressed immature survival on thistle, while they were negligible on blue cohosh. Although the lack of effective predation increased larval survival on blue cohosh, it led to defoliation due to increased larval feeding late in the season. Because of severe intraspecific competition, old larvae had significantly lower survival on blue cohosh than on thistle. In 1994, as larval survival decreased due to defoliation on blue cohosh, the overall survival rate was significantly higher on thistle than on blue cohosh. This survival pattern was opposite to that found in the laboratory experiment. In contrast, in 1995, the increase in predatory lady beetles on thistle caused greater larval mortality. Thus, the overall survival was significantly lower on thistle than on blue cohosh, although severe intraspecific competition occurred on blue cohosh as it had in 1994. Consequently, the offspring performance on the two host plants is largely determined by the relative importance of arthropod predation determining larval survival on thistle and host plant defoliation reducing late larval survival on blue cohosh. These results indicate the important role of spatial and temporal variability of natural enemies on the preference-performance linkage of herbivorous insects.

Key words Bottom-up and top-down effects · Enemy-free space · *Epilachna pustulosa* · Oviposition preference · Offspring performance

Introduction

The relationship between oviposition preference and growth, survival, and reproduction of offspring has been a central issue in the study of the evolution of insect-plant interactions (Thompson 1988; Thompson and Pellmyr 1991). An evolutionary logic predicts that oviposition behavior should be favored by natural selection to lay eggs on plant species or plant parts on which offspring fitness is maximized. The preference-performance linkage has recently been explored in terms of host plant selection or site selection on a plant, revealing a positive correlation between oviposition preference and offspring performance (Whitham 1980; Rausher 1982; Via 1986; Damman and Feeny 1988; Singer et al. 1988; Craig et al. 1989; Minkenberg and Ottenheim 1990; Ohgushi 1992, 1998; Kouki 1993; Nylin and Janz 1993). For example, ovipositing females of a willow-galling sawfly *Euura lasiolepis* have a strong oviposition preference for long shoots of young and vigorous willows associated with a high larval survival (Craig et al. 1989).

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On the other hand, in some herbivorous insects there is a poor correlation between preference and offspring performance, irrespective of quality of oviposition site for the offspring (Thompson 1988; Courtney and Kibota 1990). A poor preference-performance correlation may be brought about by oviposition onto introduced host plants and relative shortage of suitable plants or plant parts (Thompson 1988), or constraints of life history characteristics such as a short lifespan available for oviposition and a poor capacity for directed flight (Underwood 1994; Larsson and Ekbom 1995). This weak correspondence may also result from the effects of natural enemies on larval survival (Courtney 1988; Thompson 1988; Denno et al. 1990; Valladares and Lawton 1991).

A number of studies investigating the relationship between oviposition preference and offspring performance have been conducted in the absence of natural enemies under laboratory conditions (see references in Thompson and Pellmyr 1991). These studies have largely focused on effects of plant quality as the primary determinants of offspring performance. However, the ranking of performance, based on growth and survivorship, in the absence of the enemies of an insect can differ from the ranking in the presence of enemies in the field (Thompson 1988). For example, Denno et al. (1990) demonstrated that females of a willow-feeding leaf beetle, *Phratora vitellinae*, avoided *Salix viminalis* as an oviposition host despite high larval performance on that host, because larvae were defenseless against some predators when raised on this salicylate-poor willow. In the context of multitrophic interactions (Price et al. 1980), we need to determine the relative importance of direct and indirect effects by natural enemies on offspring performance to understand the preference-performance linkage more exactly (Bernays and Graham 1988; Gross and Price 1988; Valladares and Lawton 1991).

In a herbivorous lady beetle *Epilachna niponica* (Lewis), feeding on a thistle *Cirsium kagamontanum* (Nakai) in central Japan, the oviposition preference among individual plants has a strong association with offspring lifetime fitness, and the preference-performance linkage is of crucial importance in determining population stability (Ohgushi 1995, 1998). *Epilachna pustulosa* (Kono), a closely related species, is distributed widely in Hokkaido, the northernmost island of Japan. It has one generation a year, and overwinters at the adult stage. *E. pustulosa* often utilizes two host plant species, thistle, *C. kamtschaticum* (Lodeb.), and blue cohosh, *Caulophyllum robustum* (Maxim.), when the two plant species occur sympatrically (Katakura 1981; Kimura and Katakura 1986).

The main objective of this study was to compare the relationship between oviposition preference and offspring performance of *E. pustulosa* on the two host plant species, occurring in the same area. In particular, we ask how top-down effects by natural enemies and bottom-up effects by host plant quality govern offspring performance on each host species.

Materials and methods

Study site

This study was conducted in 1994 and 1995 on an isolated population of *E. pustulosa* at Hoshioki, which is located 12 km northwest of Sapporo City, Hokkaido. In the study area, the lady beetle feeds on leaves of both host plant species: thistle *C. kamtschaticum* and blue cohosh *C. robustum*. The thistle grows in two discrete monospecific patches 10 m apart from each other, consisting of 76 and 69 individual plants in 1994 and 1995, respectively. Fifty meters from the thistle patches, blue cohosh grows in understory vegetation of broad-leaved deciduous trees. There were 54 and 50 individual plants in 1994 and 1995, respectively. Thistle grows rapidly, sprouting in late April, reaching its full size of about 200 cm by July, and flowers from late June to early July. Throughout the flowering season, old leaves become senescent. On the other hand, blue cohosh sprouts in early May, reaching 50 cm at maturity, and flowers in early June. The aboveground parts of both plants die back to the ground at the end of each growing season.

The lady beetle

Overwintering adult females emerge from hibernation in early May and begin to lay eggs in clusters on the undersurface of leaves of host plants. Larvae pass through four instars. Adults eclose from mid-July until mid-August, and they enter hibernation by early October.

Population census

In 1994 and 1995, population censuses of *E. pustulosa* were conducted at intervals of 1–2 days from early May to early October by which time all adults had entered hibernation. All individuals of thistle and blue cohosh in the study sites were carefully examined for egg batches and the number of eggs in each batch was counted. To facilitate following the fate of individual eggs, each egg batch was marked by attaching a small numbered tag to the leaf. The number of hatched larvae was obtained by counting the empty egg shells that remained on the leaves after hatching.

All fourth-instar larvae were individually marked using lacquer paint to determine the number of larvae that entered the last instar stage. Adult beetles were also individually marked with a system of four small dots of lacquer paint on their elytra. Newly marked adults were released immediately on the plant where they had been captured. Subsequent capture history (date and place) was recorded for individual beetles.

Oviposition preference

Oviposition preference was measured by determining the egg density per leaf mass of host plants. Since plant size differs significantly between thistle and blue cohosh, to compare oviposition preference, egg density was expressed as the number of eggs laid per dry weight of total leaves of each plant. Dry weight (g) of the total number of leaves of an individual plant was given by the following equations (Hinomizu et al. 1981; N. Fujiyama, personal communication): $W_L = 0.369W$ and $\log W = 1.13\log(H \times B_1 \times B_2) - 4.86$ ($r = 0.90$) for *C. kamtschaticum*; $W_L = 0.50W$ and $\log W = 0.66 \log(H \times B_1 \times B_2) + 0.17$ ($r = 0.99$) for *C. robustum*; where W and W_L represent dry weight of individual plant and total leaves, respectively, and H, B_1, and B_2 are the height, maximum width, and minimum width of a plant, respectively.

Offspring performance

In the field, offspring performance was measured by stage-specific survival rates. Egg survival was estimated as the ratio of the number of hatching to deposited eggs. Early larval survival from first to fourth instar was calculated as the ratio of the number of fourth-instar larvae to that of larvae hatched. Late larval survival from fourth instar to adult emergence was calculated as the ratio of the number of adults emerged to that of fourth-instar larvae. Adult survival from emergence to the reproductive season was estimated as the ratio of the number of marked adults which were recaptured in the following spring to that of marked adults which newly emerged in summer.

We conducted a laboratory experiment to determine effects of leaf quality on larval survival, developmental period, and adult size. Nine egg batches were collected from the field in late May 1995. To remove effects of genetic heterogeneity, newly hatched larvae from each egg batch were divided equally into two groups. One group was reared on thistle and the other on blue cohosh. Larvae of each group were reared until adult emergence in a separate plastic cup (13 cm in diameter and 6 cm in depth) with a plastic lid and were kept under constant conditions of 23°C and 16 h light:8 h dark in an environmental chamber. Ample amounts of fresh leaves of each of the host plants were offered every day. Adult size from the anterior edge of the head to the posterior edge of the elytra was measured to the nearest 0.05 mm using a vernier caliper.

Field experiment to exclude arthropod predation

To determine effects of arthropod predators on larval survival in the field, we conducted a cage experiment for predation exclusion. Five plants of each of thistle and blue cohosh were randomly selected and caged with nylon organdy on 15 June 1995. In addition, concentric rings of Tanglefoot were placed around the base of the caged plants. Twenty and 10 newly hatched larvae were placed on a leaf of each caged thistle and blue cohosh, respectively. We counted the number of larvae that were alive on 20 July, at which time all larvae had reached the fourth-instar stage. Larval survival from hatching to fourth instar was used to compare caged and noncaged plants.

Estimation of leaf damage to host plants

We visually estimated leaf damage of individual plants by adults and larvae of the lady beetle at each census. Each plant was classified into one of five categories based on the proportion of leaf area eaten. We transformed the degree of leaf herbivory to a percentage of leaf consumption.

Statistical analyses

Egg density on blue cohosh and thistle was compared by the Mann-Whitney U-test, as was larval survival on caged and noncaged plants. The chi-square test was used to determine whether stage-specific survival rates of the lady beetle on the two host species were significantly different. Differences in survivorship curves on thistle and blue cohosh were analyzed by a nonparametric comparison of the associated survival distribution functions (Pyke and Thompson 1986). The analyses were conducted with SAS procedure LIFE-TEST (SAS 1990).

Results

Oviposition preference

Egg density per gram of blue cohosh leaf was significantly higher than that on thistle in both years (Mann-Whitney U-test; $U = 86$, $P < 0.0001$ for 1994; $U = 40$, $P = 0.021$ for 1995; Fig. 1).

Offspring performance

Survivorship curves on thistle and blue cohosh differed significantly (logrank test; 1994: $\chi^2 = 10.03$, $df = 1$, $P = 0.0015$; 1995: $\chi^2 = 459.81$, $df = 1$, $P < 0.0001$; Fig. 2). Egg survival and early larval survival were significantly lower on thistle than on blue cohosh (Table 1). Conversely, late larval survival was significantly higher on thistle than on blue cohosh. This trend was consistent in the two years. In addition, adult survival until the reproductive season was significantly higher on thistle than on blue cohosh in 1994 (27.7% vs 4.2%, $\chi^2 = 12.33$, $df = 1$, $P = 0.0004$). Overall survival from egg to adult emergence varied between years, being significantly higher on thistle than on blue cohosh in 1994 but lower in 1995.
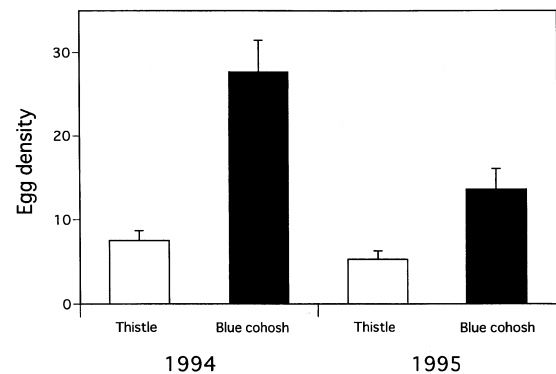

Fig. 1 Mean values of egg densities in terms of resource availability (number of eggs per gram dry weight of total leaves of an individual plant) on thistle and blue cohosh (*vertical bars* SE)
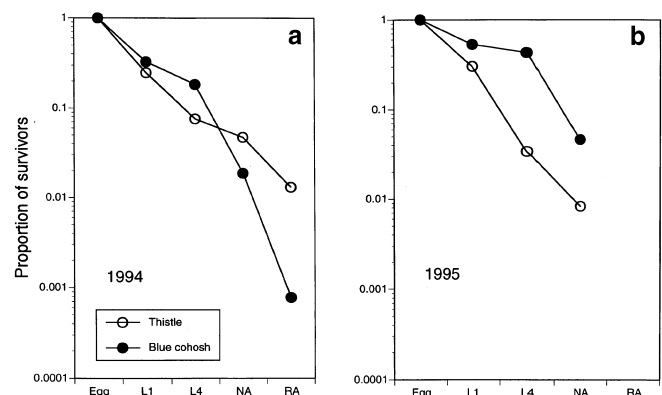

Fig. 2a,b Proportion of survivors at different life stages on thistle (*open circles*) and blue cohosh (*closed circles*) throughout life stages: *L1* first-instar larva, *L4* fourth-instar larva, *NA* newly emerged adult, *RA* reproductive adult in the following spring

Table 1 Stage-specific survival rates of *Epilachna pustulosa* on thistle and blue cohosh

Stage	Year	Percent survival rate (n)		df	χ^2	P
		Thistle	Blue cohosh			
Egg	1994	24.7 (5996)	32.8 (2564)	1	60.14	<0.0001
	1995	30.4 (3247)	53.5 (602)	1	121.02	<0.0001
Early larva	1994	30.9 (1481)	55.8 (841)	1	139.85	<0.0001
	1995	11.3 (987)	81.1 (322)	1	581.05	<0.0001
Late larva	1994	62.0 (458)	10.2 (469)	1	269.32	<0.0001
	1995	24.3 (112)	10.7 (261)	1	11.42	0.0007
New adult	1994	27.7 (284)	4.2 (48)	1	12.33	0.0004
Egg-new adult	1994	4.7 (5996)	1.9 (2564)	1	38.83	<0.0001
	1995	0.8 (3247)	4.7 (602)	1	47.90	<0.0001

Top-down effects on larval performance

Two predominant arthropod predators were found during the immature stage: the larvae of a predatory lady beetle *Harmonia axyridis* (Pallas) and the nymphs of an earwig *Forficula mikado* (Burr). The earwig feeds on early instar larvae, while the predatory lady beetle attacks both early and late larvae. Their numbers increased from late June and reached a peak in mid-July on thistle, but they were negligible on blue cohosh throughout the season (Fig. 3). Note that the relative abundance of the two predator species changed greatly between years; the majority of predators were earwig nymphs in 1994 while the predatory lady beetle larvae became predominant in 1995. The average density of these two predators in July was significantly higher on thistle than on blue cohosh (Table 2).

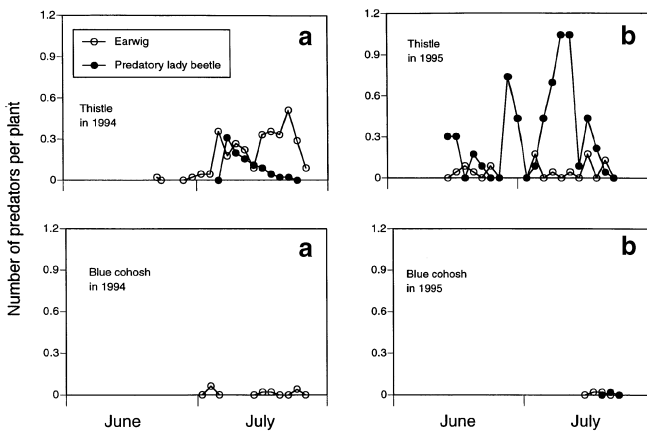The predator exclusion experiment demonstrated that effects of arthropod predation on larval survival differed between the two host plants (Fig. 4). On thistle, caged larvae had a significantly higher survival rate than noncaged larvae that were exposed to arthropod predators ($U = 7$, $P = 0.012$). On the other hand, there was no difference between caged and noncaged larvae on blue cohosh ($U = 11$, $P = 0.754$). Furthermore, caged larvae had a significantly lower survival rate on thistle than those on blue cohosh ($U = 0$, $P = 0.009$).

Bottom-up effects on larval performance

A laboratory experiment illustrated that the two host plants had different effects on larval performance. First, the survival rate from first instar to adult emergence was significantly higher on blue cohosh than on thistle. This was mostly the result of increased first-instar survival on blue cohosh (Table 3). Second, the developmental period until adult emergence was significantly shorter on blue cohosh than on thistle (Table 4). However, adult
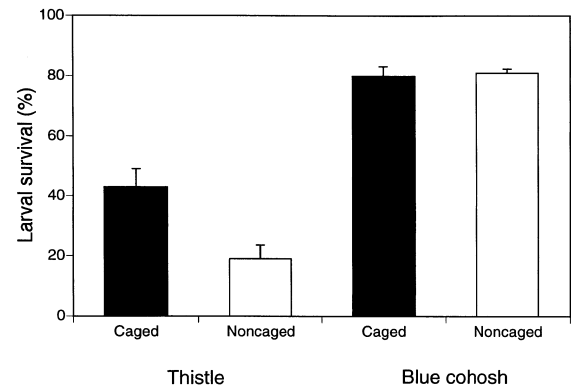

Fig. 3 Seasonal changes in density of arthropod predators (nymphs of the earwig *Forficula mikado* and larvae of the predatory lady beetle *Harmonia axyridis* per individual plant) on thistle (**a,c**) and blue cohosh (**b,d**) in 1994 (**a,b**) and 1995 (**c,d**)

Fig. 4 Mean (+SE) values of larval survival during a period from hatching to fourth instar on caged and noncaged plants of thistle and blue cohosh (thistle $n = 100$ and 2564, blue cohosh $n = 50$ and 602, for caged and noncaged plants, respectively)

Table 2 Density (mean ± SE number per shoot in July) of an earwig *Forficula mikado* and a predatory lady beetle *Harmonia axyridis* on thistle and blue cohosh

Predator	Year	Thistle	Blue cohosh	U	P
Forficula mikado	1994	3.17 ± 0.75	0.15 ± 0.09	491	<0.0001
	1995	0.57 ± 0.15	0.04 ± 0.03	332	0.0069
Harmonia axyridis	1994	0.89 ± 0.25	0	744	0.0098
	1995	4.13 ± 0.80	0.02 ± 0.02	147.5	<0.0001

Table 3 Stage-specific survival rates of *E. pustulosa* on thistle and blue cohosh in a laboratory experiment

Stage	Thistle		Blue cohosh		df	χ^2	P
	n	Survival rate (%)	n	Survival rate (%)			
First instar	56	67.9	56	94.6	1	13.19	0.0003
Second instar	38	92.1	53	94.3	1	0.18	0.6719
Third instar	35	97.1	50	96.0	1	0.08	0.7787
Fourth instar	34	88.2	48	95.8	1	1.69	0.1930
First instar to adult emergence	30	53.6	46	82.1	1	10.48	0.0012

Table 4 Developmental period from hatching to adult emergence and size of adult *E. pustulosa* at emergence on thistle and blue cohosh in a laboratory experiment

	Thistle		Blue cohosh		U	P
	n	Mean $\pm$ SE	n	Mean $\pm$ SE		
Developmental period (days)	30	30.6 $\pm$ 0.65	46	21.1 $\pm$ 0.28	7	< 0.0001
Male size (mm)	12	6.20 $\pm$ 0.07	21	6.25 $\pm$ 0.08	143	0.195
Female size (mm)	18	7.15 $\pm$ 0.07	25	7.20 $\pm$ 0.08	121.5	0.779
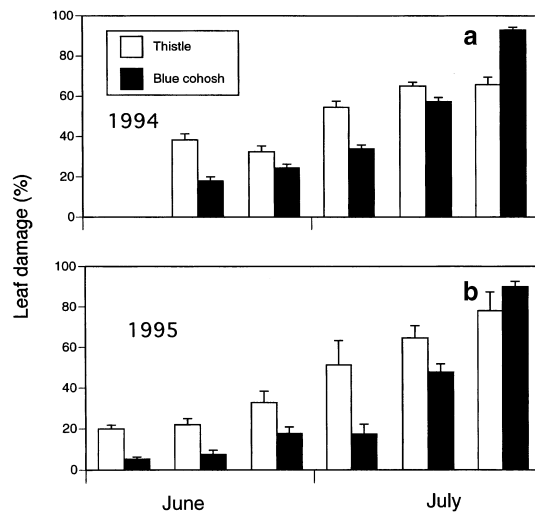
Fig. 5a,b Mean (+SE) values of seasonal changes of leaf damage by beetle feeding. Leaf damage is expressed as the percentage consumption of total leaf area

size at emergence in both sexes did not differ between the two host plants.

In the field, leaf damage of thistle was consistently higher than that of blue cohosh early in the season. However, blue cohosh was quickly defoliated by larval feeding after mid-July (Fig. 5), when fourth-instar larvae peaked in numbers. On the other hand, defoliation was not observed on thistle in 1994, although severe leaf damage occurred on some plants in 1995.

Discussion

Oviposition preference

Ovipositing females moved freely among patches of thistle and blue cohosh in the study area (Yamaga 1995).

Although the two host plant species were both accessible to ovipositing females of *E. pustulosa*, there was a strong oviposition preference for blue cohosh. Blue cohosh is an understory species and favors a dark environment, which suggests that blue cohosh is less apparent to insect herbivores. Nevertheless, blue cohosh is preferred by ovipositing females of the lady beetle. In the laboratory also, blue cohosh is preferred over thistle by individual females for oviposition (H. Katakura, personal communication).

Top-down effects on offspring performance

The differential impact of natural enemies on larval survival on the two hosts was clearly illustrated by the predator-exclusion experiment. The impact of arthropod predators on larval survival was high on thistle, but insignificant on blue cohosh. Such low predation on blue cohosh has also been reported in the southeastern part of Sapporo City (Kimura and Katakura 1986). Two factors may contribute to this low predator density on blue cohosh. First, few alternative prey are available on this species. During the study period, the only other prey we observed feeding on blue cohosh were negligible numbers of lepidopteran larvae and aphids. We saw no signs of herbivory by other insects. Lack of alternative prey insects probably inhibited the maintenance of a large predator population. Second, there may be lack of suitable habitats for the predatory lady beetle and the earwig on blue cohosh. These predators prefer open areas, while blue cohosh grows principally in the dark understory of hardwood forests.

Arthropod predation was also demonstrated to reduce immature survival and thus adult density of *E. niponica* feeding on thistle in central Japan. This was demonstrated by a field cage experiment (Ohgushi and Sawada 1985) and a population introduction experiment (Ohgushi and Sawada 1998). The introduced population

of *E. niponica* reached such a high density that it defoliated the thistles, just as *E. pustulosa* did on blue cohosh in this study. In contrast, there was no defoliation in the source area. This dramatic increase in population density was caused by increased larval survival due to the absence of effective predators (Ohgushi and Sawada 1998). Similar patterns have been seen in biological control studies that have shown that natural enemies attacking immature insect pests can suppress population densities far below outbreak levels (Huffaker 1971; Huffaker and Messenger 1976; Murdoch et al. 1985; McClure 1986).

Bottom-up effects on offspring performance

In the laboratory, larval performance was higher on blue cohosh compared to thistle. This is strengthened by the results of the cage experiment, which demonstrated that larval survival on blue cohosh was significantly higher than on thistle when the impact of natural enemies had been removed.

Coupled with high-quality food, the absence of natural enemies on blue cohosh allowed larvae to reach such a high density that complete host plant defoliation frequently occurs after mid-July. This causes severe intraspecific competition among old larvae for limited food resources. As a result, late larval survival on blue cohosh was significantly lower than that on thistle in both years. Defoliation was accelerated because of the smaller biomass of blue cohosh. Hence, mortality of late larvae was mostly brought about by food shortage on highly damaged plants. Kimura and Katakura (1986) also showed that defoliation due to larval feeding was a main cause of mortality in *E. pustulosa* larvae on blue cohosh. On the other hand, arthropod predation on thistle prevented the larval density from reaching levels high enough to cause defoliation. Intraspecific competition at the larval stage due to host plant defoliation has been demonstrated in several herbivorous insects, such as the Colorado potato beetle *Leptinotarsa decemlineata* (Say) (Harcourt 1971) and the cinnabar moth *Tyria jacobaeae* (L.) (Myers and Campbell 1976; Dempster 1982).

Variable preference-performance linkage

E. pustulosa shows a positive correlation between oviposition preference and offspring performance under some conditions. We found that ovipositing females have a preference for blue cohosh compared to thistle in the field and that they perform better on blue cohosh than on thistle in the laboratory. The results of other studies demonstrate the same pattern. Hoshikawa (1984) conducted a laboratory preference test and also showed that females of *E. pustulosa*, collected from the suburbs of Sapporo, preferred blue cohosh over thistle. Ueno et al. (1997) also showed that *E. pustulosa* larvae per-

form better on blue cohosh than on thistle in the laboratory. They found that larvae on blue cohosh had significantly higher larval survival, shorter development times to adult emergence and larger body size in both sexes than those on thistle.

However, in the current study, the preference-performance linkage of *E. pustulosa* varied between years in the field. Oviposition preference for the two host plants was constant between years, but offspring performance varied. In 1994, the overall survival until adult emergence was significantly higher on thistle than on blue cohosh. This improved survival on thistle was maintained in the reproductive season in the next year. Conversely, in 1995, there was a significantly lower overall survival on thistle than on blue cohosh. Thus, the association between oviposition preference and offspring performance was negative in 1994 but positive in 1995.

The variable outcomes of the association between preference and performance were caused by year-to-year variation in larval survival, which is largely determined by natural enemies. The absence of effective predators on blue cohosh may indirectly reduce survival of late larvae, mediated by host plant defoliation and increased larval competition. Late larval mortality caused by food shortage contributed more to determining the overall survival rate than the increased survival of early larvae that were free from predation. Hence, overall survival was significantly lower on blue cohosh than on thistle. In 1995, increased predatory lady beetle feeding on both early and late larvae on thistle caused significantly higher mortality than the previous year. The predatory lady beetle is more effective in reducing larval survival than the earwig which feeds only on early instar larvae. As a result, overall survival was significantly lower on thistle than on blue cohosh. Moreover, late larval survival on blue cohosh was maintained at the same level as in 1994. Two factors protect larvae on thistle from the impact of host plant defoliation, compared to blue cohosh. First, thistle plants often produce rosette leaves in their basal part in mid-July, and late larvae tend to move to the newly emerged leaves, to avoid highly damaged leaves. There is no such regrowth of vegetative tissue in blue cohosh. Second, many larvae have already pupated when thistles became highly damaged, while old larvae peak in numbers on blue cohosh when defoliation occurs.

Valladares and Lawton (1991) pointed out that density-dependent reduction in larval success on more preferred plants by ovipositing females may mask a positive correlation between oviposition preference and offspring performance. This scenario is applicable to the situation in 1994. In *E. pustulosa*, ovipositing females laid more eggs on blue cohosh, a better host plant species in terms of larval performance. There is a two-fold advantage of blue cohosh for larval success. In addition to better quality, it also provides "enemy-free space" which enhances larval survival (Price et al. 1980; Jeffries and Lawton 1984; Bernays and Graham 1988; Denno et al.

1990). However, enemy-free space may also have disadvantages for offspring performance because of increased likelihood of density-dependent defoliation in preferred plants with a heavy egg load. Based on host plant quality, we predict that there should be a positive preference-performance relationship: in the absence of predators and natural enemies, blue cohosh is the preferred host and larval performance is higher on this species. However, in 1994, we found that while blue cohosh was preferred, larval performance was lower on this species because of high levels of intraspecific competition. In 1995, the expected preference-performance pattern was found because the high predation rate on thistle greatly reduced larval survival.

In general, the abundance of generalist predators such as predatory lady beetles is largely dependent on the abundance of alternative prey species on plants, which varies considerably in time and space (Andow and Risch 1985; Ohgushi and Sawada 1998). Ohgushi and Sawada (1998) showed that the density of *H. axyridis* feeding on *E. niponica* larvae on thistle varied greatly between years, probably depending on the abundance of other prey insects.

Why has such a strong preference for blue cohosh been maintained despite the conflicting selective pressures? For ovipositing females, the cues for plant quality are easy to detect and accurate predictors of oviposition site quality. In this context, ovipositing females feed on leaves before laying eggs, which may enable them to assess the quality of an oviposition site. Hence, *E. pustulosa* females can offer better host plants to offspring when they lay eggs. In contrast, it is difficult to predict the occurrence of natural enemies and their influence on intensity of intraspecific competition, since as highly mobile predators, such predators are not likely to provide predictable cues at the time of oviposition. On the other hand, offspring fitness is directly and indirectly affected by the natural enemies, independent of host quality. As a result, the preference-performance linkage may alter according to variable effects of natural enemies.

An alternative hypothesis is that, in most years at most sites, the advantages to ovipositing on blue cohosh outweigh the disadvantages. However, this is unlikely. Defoliation due to larval feeding is rather common and thus intraspecific competition is severe on blue cohosh (Kimura and Katakura 1986; H. Katakura, personal communication). Thus, high levels of intraspecific competition for limited resources may often exceed the advantage of the better quality of blue cohosh for larval performance.

Consequently, variable effects of natural enemies may be a key component in alternating the preference-performance linkage that is predicted by the quality of host plant species. This study emphasizes that we should incorporate variable multitrophic-level interactions into arguments on the association between oviposition preference and offspring performance in herbivorous insects.

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