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Short communication

Population differentiation in host-plant use in a herbivorous ladybird beetle, *Epilachna vigintioctomaculata*

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Introduction

Herbivorous insects that are polyphagous as a species often exhibit monophagy or oligophagy at the population level (Fox & Morrow, 1981). The difference among populations in host-plant use may arise either intrinsically from genetic changes and/or extrinsically from changes in ecological factors such as availability of host-plant species (Rausher, 1982; Tabashnik, 1983; Hare & Kennedy; 1986; Scriber, 1986).

Even when genetic changes are not involved initially, differential host use may lead to evolutionary divergence between populations. If local populations of a herbivore species use different host plants, the populations may diverge as each is subjected to natural selection for improved ability to use its own host species. Thus, variation in host-plant use between populations can reveal patterns of local adaptation and suggests the responses to past selective forces.

Epilachna vigintioctomaculata (Coleoptera, Coccinellidae, Epilachninae) is a likely candidate in which to detect differential adaptation. *Epilachna vigintioctomaculata* is one of the closely related herbivorous ladybird beetles (*E. vigintioctomaculata* complex) that has diversified greatly in external morphology and host-plant use in and around the Japanese Archipelago. *Epilachna vigintioctomaculata* mainly feeds on *Solanum tuberosum* L. (Solanaceae). Although some additional plants in the family Solanaceae are subsidiarily used by adult beetles, larvae develop almost entirely on *S. tuberosum* (Katakura, 1981). Some populations on Hokkaido (the main northern island of Japan) are found on *Schizopepon bryoniaefolius* Maxim. (Cucurbitaceae) but this host is not attacked on Honshu (the main central island). Such variation suggests geographical variation in host-plant use (Katakura, 1981), as the populations on Hokkaido have depended and persisted on *S. bryoniaefolius* since their discovery in 1951 (Katakura, 1981). Thus, the Hokkaido populations on *S. bryoniaefolius* and Honshu populations may be subject to differential selection on their respective host-plants.

Here we conduct reciprocal transplant experiments to test for growth performance differences between *E. vigintioctomaculata* collected from *S. bryoniaefolius* on Hokkaido and *S. tuberosum* on Honshu and determined whether the larvae from different populations exhibit differential adaptation to their own host-plant species.

Materials and methods

Epilachna vigintioctomaculata is univoltine. In June 1996, overwintered beetles were collected from *S. bryoniaefolius* and *S. tuberosum* at a suburb of Sapporo City, Hokkaido and Niigata City, Honshu, respectively. The beetles were maintained at 22 °C, 16L:8D in an incubator, and these conditions were used throughout the experiment. Beetles were supplied with fresh leaves from their native host plants every other day. Egg clutches oviposited by females were collected daily.

Newly hatched larvae from each egg clutch were divided into two equal groups. Half of the larvae were reared on *S. tuberosum* and the other half were reared on *S. bryoniaefolius*. The experiment was started with a total of 520 and 92 larvae from the Sapporo and

Table 1. ANOVAs to compare variations in larval period and pupal mass of *Epilachna vigintioctomaculata* from two populations reared on *Solanum tuberosum* or *Schizopepon bryoniaefolius*. r^2 shows the fit of the overall model

Source	Larval period				Pupal weight			
	d.f.	MS	F	P	d.f.	MS	F	P
Sex	1	0.001	0.204	0.6521	1	0.593	33.256	<0.0001
Host	1	1.240	250.640	<0.0001	1	0.954	53.492	<0.0001
Population	1	0.015	3.061	0.0809	1	2.64	148.072	<0.0001
Population × host	1	0.412	83.377	<0.0001	1	0.234	13.105	0.0003
Error	450	0.005			450	0.018		
r^2	0.421				0.340			

Niigata population, respectively. These larvae were reared individually in plastic cases supplied with a sheet of filter paper to maintain moisture. Fresh host-plant leaves were added to the cases every other day. Larval development was monitored daily to determine the period from egg hatch to pupation. Pupal mass was measured to the nearest 0.1 mg on a microbalance.

Larval period and pupal mass were log transformed prior to statistical analyses. Three-way ANOVAs were performed to test for sex, population, host, and population × host interaction effects on larval period and pupal mass. For the survivorship data, log-likelihood-ratio analysis was performed using population, host, and population × host interaction as factors.

Results and discussion

Females had greater pupal mass than males, however, the sexes did not differ in the lengths of their larval periods (Table 1). Beetles from Sapporo grew significantly larger and survived better than those from Niigata, regardless of which host plant they were reared on (Figure 1, Table 1). The larval period of the Sapporo population was shorter than that of the Niigata population, but the difference was not significant. For larval period and pupal weight, performance of beetles was higher on *S. tuberosum* than on *S. bryoniaefolius* (Figure 1, Table 1). For survivorship, significant host effect was not detected (Table 2).

Significant population × host interactions were observed for all three performance measures, indicating that each population was different in the way they responded to the host-plants (Figure 1, Table 1). Both populations had relatively shorter larval periods on their own host species; when reared on *S. tuberosum*, larvae from the Sapporo population had longer larval period than those from the Niigata population. When reared on *S. bryoniaefolius*, on the other hand, larvae from the Niigata population had longer larval period than those from the Sapporo population. For pupal weight, beetles from both population grew smaller on *S. bryoniaefolius*, however, the difference of pupal mass between the hosts was largest for the Niigata population. Both populations achieved higher survivorship on their own host-plants, although the difference between hosts was not significant when tested for each population (for Niigata: G=3.01, d.f.=1, P=0.0829, for Sapporo: G=2.82, d.f.=1, P=0.0933).

Table 2. Results of log-likelihood-ratio analysis for survivorship in a herbivorous ladybird beetle, *Epilachna vigintioctomaculata* reared on *Solanum tuberosum* or *Schizopepon bryoniaefolius*

Source	d.f.	G	P
Host	1	0.42	0.517
Population	1	69.5	<0.001
Population × Host	1	5.34	0.021

These growth performances were measured under identical conditions for the two populations, thus controlling most sources of nongenetic effects. Therefore, the significant population × host interaction, especially the one of crossing type obtained for larval period, suggests genetic differentiation of local populations due to adaptation to their host-plants. However, because parental beetles from the two populations were fed different host species, it is also possible that host-dependent maternal effects could have contributed to the differential response to host-plants. Little is known about host-dependent maternal effects in this species, and whether host-dependent

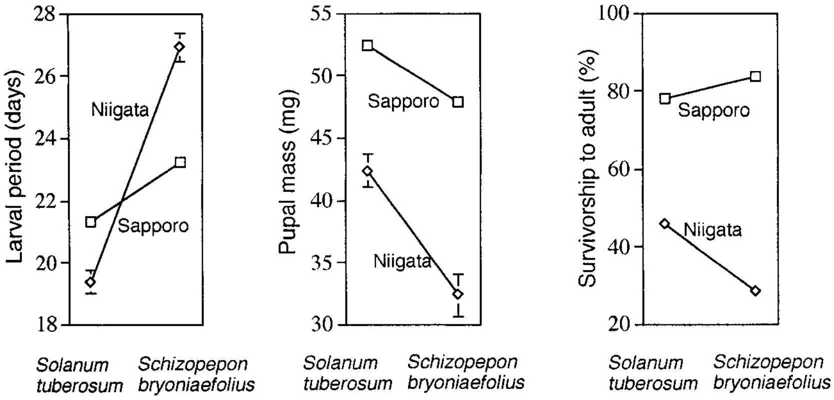

Figure 1. Percentage survival to adult (right) and adjusted least squares means for larval period (left)and pupal mass (middle) in a herbivorous ladybird beetle, *Epilachna vigintioctomaculata* from twopopulations reared on *Solanum tuberosum* or *Schizopepon bryoniaefolius*. Bars indicate standard errors.

maternal effects generate significant population × host interactions needs further examination.

Variation in host-plant use between populations can reveal patterns of local adaptation and suggests the responses to past selective forces. On the other hand, the process of evolutionary change is dependent on the amount of genetic variation maintained within the population. Within-populational genetic variation has been estimated for both populations studied (Ueno et al., 1999, unpubl.). Significant genetic variation was detected for larval period and pupal mass on *S. tuberosum* and *S. bryoniaefolius* for both the Niigata (Ueno et al., 1999) and the Sapporo population (Ueno et al., unpubl.). In addition, these studies detected positive or neutral genetic correlations between growth performance on *S. tuberosum* and analogous performance on *S. bryoniaefolius*. Therefore, the results shown in these studies suggest that within-populational genetic variation and covariation do not constrain, but rather facilitate, host-plant adaptation of *E. vigintioctomaculata*, at least to *S. tuberosum* and to *S. bryoniaefolius*. The genetic properties are thus consistent with the present results of differential local adaptation to use *S. tuberosum* in the Niigata and *S. bryoniaefolius* in the Sapporo population.

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