Res Popul Ecol (1999) 41:161–167

ORIGINAL ARTICLE

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A host shift from wild blue cohosh to cultivated potato by the phytophagous ladybird beetle, *Epilachna yasutomii* (Coleoptera, Coccinellidae)

Received: May 22, 1998 / Accepted: January 13, 1999

Abstract Life history traits of the phytophagous ladybird beetle *Epilachna yasutomii* were compared between a nonpest population feeding on wild blue cohosh and a pest population feeding on cultivated solanaceous crops, mainly potato. Newly emerged adults of the nonpest population entered diapause early in midsummer when blue cohosh withered, while adults of the pest population were found in tomato and eggplant fields until late autumn. The pest population had larger females, a higher population growth rate, a shorter larval developmental period, and reduced longevity of overwintered females, compared with the nonpest population. ANOVA indicated that all these life history traits were influenced by the food plant, and that the number of eggs laid per female and the longevity of overwintered females were also affected by the population type. These findings suggest that the life history pattern of *E. yasutomii* changed to high fecundity with a short life span from low fecundity with a long life span as a result of the host shift from wild blue cohosh to cultivated solanaceous crops.

Key words Adult longevity · Berberidaceae · Fecundity · Host suitability · Life history traits

Introduction

Many workers have studied host plant shift by phytophagous insects from the point of view of sympatric speciation or evolution of life history traits (e.g., Tauber and Tauber 1989; Bush and Smith 1997; Jiggins et al. 1997). From this aspect, life history traits of ladybird beetles of the genus *Epilachna* have also been studied among populations depending on several different host plants (Katakura et al. 1989; Nishida et al. 1997; Ueno et al. 1997). In addition, the study of host shift from wild plants to cultivated crops is important to understand the life history traits of nonpest and pest populations (Ito 1978; Tabashnik 1983). In general, abundance of the plants and animals and their interactions are thought to be more variable in time and space in an agricultural cropping system than in the natural ecosystem (Ferro 1987; Risch 1987; Gliessman 1990). Insects exhibit genetic variation within a species or a population with respect to life history traits. Many insects that have successfully colonized an agricultural ecosystem, and thereby become major pests, are thought to show more genetic variation in some traits such as host range, host plant suitability, diapause response, and insecticide resistance, which permits them to adapt well to agricultural cropping systems (Via 1990; Gould 1991). Understanding how the life history traits of a nonpest population change with a host shift from wild plants to cultivated crops is very important for reducing the injury level by pest insects or the pest population density in crop fields (Ito 1978; Tabashnik 1983).

In Japan, phytophagous ladybird beetles of the genus *Epilachna* feed not only on cultivated solanaceous crops but also on some wild native plants, for example, *Cirsium* thistle (Asteraceae), *Caulophyllum robustum* (Maxim.) (Berberidaceae), "blue cohosh," and *Scopolia japonica* Maxim. (Solanaceae), "deadly nightshade" (Katakura 1997). Potato cultivation increased in the mountainous area of central Honshu in the 1930s (Umemura 1984), and thereafter *Epilachna* ladybird beetles extended their range from wild vegetation to crop fields. Shirai and Morimoto (1997) compared life history traits of *Epilachna niponica* Lewis between a nonpest population depending on wild thistle and a pest population feeding on cultivated solanaceous crops. Their study revealed that the pest population had a higher population growth rate, a shorter larval developmental period, and larger females than the nonpest population. However, beetle acceptance of the potato as a host plant did not differ throughout the larval and adult stages between the nonpest and pest populations.

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Epilachna yasutomii Katakura, a close relative to *E. niponica*, is an appropriate model for such a comparative study between nonpest and pest populations, because the pest population of *E. niponica* in crop fields is very restricted in distribution and the phenology of wild thistles is quite similar to the overall phenology of solanaceous crops (Shirai and Morimoto 1997). In contrast, *E. yasutomii* has become a major pest in wide area of Kanto and Tokai districts, central Honshu (Katakura 1981, 1997). In the nonpest population of *E. yasutomii* associated with blue cohosh or deadly nightshade, adults disappear early in the midsummer when the wild host plants wither (Shirai 1988, 1991). Thus, there may be clearer differences in life history traits between the nonpest and pest populations of *E. yasutomii* than in the case of *E. niponica*.

In the present study, we compared life history traits between two *E. yasutomii* populations in the southern parts of Nagano Prefecture: a nonpest population depending solely on blue cohosh and a pest population feeding on potato, tomato, and eggplant. As in the previous study (Shirai and Morimoto 1997), a field census and two laboratory comparisons were conducted. First, the life history traits of the populations reared on the current host plant in the field were compared (nonpest population reared on blue cohosh vs. pest population reared on potato). Second, beetle acceptance of the potato as a host plant was compared between the two populations (nonpest population reared on potato vs. pest population reared on potato). The latter comparison was made to verify whether the current acceptability of the potato depends on the previous experience of the *E. yasutomii* population with use of the potato as a host plant.

Materials and methods

Study site and insect collection

Nonpest population. This population lived on a small community (~70 × 30m) of blue cohosh in stands of Japanese cedar (*Cryptomeria japonica* D. Don) in Nakatachi, Minami-shinano village, Nagano Prefecture (880m above sea level). Blue cohosh sprouts from early April, its leaves are fully expanded in May, and it withers between late July and mid-August. No other host plant species suitable for *E. yasutomii* was found in this area.

Pest population. Akasawa (Minami-shinano, 550m above sea level) is a small mountain village, 1.2km from Nakatachi, where potato, eggplant, tomato, and other vegetables are cultivated on a small scale from spring to autumn. Potatoes sprout in mid-April and are harvested by late July. Eggplant and tomato leaves were blasted by frost in early November. No other wild host plants of *E. yasutomii*, such as blue cohosh or deadly nightshade, were found in the forest near these crop fields. The location of the study site has been described by Shirai (1994). We collected 40 pairs of overwintered adults of *E. yasutomii* from each population on May 2, 1989, for laboratory experiments, and the pronotal width of females was measured.

Seasonal occurrence of the beetles

At Nakatachi, the numbers of *E. yasutomii* adults and egg masses on blue cohosh leaves were counted by 11 field censuses from April 8 to November 11, 1990. At Akasawa, the numbers of adults and egg masses were also counted on potato plants from April 8 to July 30, and on eggplant and tomato plants around the potato field from August 20 to November 11, 1990. Censuses were always carried out in the afternoon for 30min by a visual counting method.

Adult survival and oviposition

For each population, one pair of overwintered adults collected from the field was transferred to a plastic dish (9cm in diameter, 4.5cm deep) and supplied with either blue cohosh or potato leaves. These dishes were checked daily for the number of eggs laid and adult survival. The leaves were replaced with fresh ones every 1 or 2 days, and the experiment was terminated on October 6. The number of eggs per egg mass (egg mass size) and hatchability were determined for the egg masses that were not cannibalized by adult beetles. The intrinsic rate of natural increase (r) and the net reproductive rate (R_0) were calculated from the female survival data (lx) and the number of new females born per female every 2 days (mx). Hatchability, survivorship and developmental period in immature stages were employed as shown in Tables 1 and 2.

Survival and development during the immature stages

Six hatched larvae from this experiment were transferred to a plastic dish (9cm in diameter, 4.5cm deep) and reared on leaves of their parent's food plants. A fresh leaf was added to the dish every 1 or 2 days until the third instar and daily during the fourth instar. After emergence, 20 new female adults were randomly selected for pronotal width measurement.

Active period of newly emerged females

Prepupae and pupae of *E. yasutomii* were collected from potato plants at Akasawa on June 25, 1989, and from blue cohosh plants at Nakatachi on July 22, 1989. When adults emerged, 30 unmated females were transferred individually to plastic dishes (9cm in diameter, 4.5cm deep) and supplied with black nightshade (*Solanum nigrum* L.) leaves. Feeding activity and summer diapause were recorded daily for 150 days after emergence. The leaves were replaced with fresh ones every 1 or 2 days. We used 30 days as the summer diapause period of *E. yasutomii* in accordance with the study of *E. niponica* (Shirai and Morimoto 1997).

All laboratory studies were conducted at the National Institute of Agro-Environmental Sciences

Table 1. Comparison of oviposition traits between the Nakatachi nonpest and Akasawa pest populations of *Epilachna yasutomii*

Food plant	Number of eggs laid per female (mean ± SD) (*n*)	Egg mass size (mean ± SD) (*n*)	Hatchability (%) (mean ± SD) (*n*)
Nonpest population			
Blue cohosh	70.6[b] ± 65.6 (20)	18.8[a] ± 5.6 (26)	88.0[a] ± 18.3 (26)
Potato	194.4[a] ± 90.3 (20)	22.8[a] ± 3.5 (40)	94.7[a] ± 6.8 (40)
Pest population			
Blue cohosh	127.3[ab] ± 84.3 (20)	18.8[a] ± 7.8 (30)	87.7[a] ± 15.6 (30)
Potato	241.8[a] ± 142.4 (20)	21.5[a] ± 3.2 (37)	92.2[a] ± 8.8 (37)

Means followed by different letters (a,b) in the same column are significantly different at the 5% level (Kruskal–Wallis's test, Dunn's multiple comparison). Rearing condition: 23°C, 16L:8D

Table 2. Comparison of development during the immature stages between the Nakatachi nonpest and Akasawa pest populations of *E. yasutomii*

Food plant	Survival rate (%) (mean ± SD) (*n*)	Developmental period (days) (mean ± SD) (*n*)
Nonpest population		
Blue cohosh	88.0[a] ± 15.4 (12)	25.7[ab] ± 1.4 (12)
Potato	74.1[a] ± 15.9 (12)	24.9[bc] ± 1.8 (12)
Pest		
Blue cohosh	89.9[a] ± 10.9 (12)	27.6[a] ± 1.4 (12)
Potato	80.0[a] ± 13.3 (12)	23.6[c] ± 1.1 (12)

Means followed by different letters (a,b,c) in the same column are significantly different at the 5% level (Kruskal–Wallis's test, Dunn's multiple comparison). Rearing condition: 23°C, 16L:8D

Table 3. Female body size in terms of the pronotal width of wild and laboratory-reared adults in the Nakatachi nonpest and Akasawa pest populations of *E. yasutomii*

Food plant	Pronotal width (mean ± SD) (*n*)
Wild beetles	
Nonpest population	3.20[b] ± 0.16 (40)
Pest population	3.41[a] ± 0.17 (40)
Laboratory-reared beetles	
Nonpest population	
Blue cohosh	3.15[b] ± 0.14 (20)
Potato	3.31[ab] ± 0.22 (20)
Pest population	
Blue cohosh	3.17[ab] ± 0.16 (20)
Potato	3.29[a] ± 0.18 (20)

Means followed by different letters (a,b) are significantly different at the 5% level by Mann–Whitney U test for wild beetles and by Kruskal–Wallis's test, Dunn's multiple comparison for laboratory-reared beetles. Rearing condition: 23°C, 16L:8D

(NIAES), Tsukuba, under 23°C and 16L:8D conditions. Potato and black nightshade were grown in the greenhouse. Blue cohosh plants were collected every 10 or 14 days from Nakatachi, and the leaves were kept in a sealed plastic box at 5°C. Five pairs of adults from each population were deposited as voucher specimens at the Laboratory of Insect Systematics, NIAES.

Results

Seasonal occurrence of adult beetles

The seasonal occurrence of *E. yasutomii* beetles and host available periods for the two populations are outlined in Fig. 1. In the Nakatachi nonpest population, overwintered adults emerged in early May and laid eggs between mid May and early July. Newly emerged adults abounded in late July, but none appeared at this site after late August. In the Akasawa pest population, overwintered adults were present and oviposition was observed in early May. Newly emerged adults appeared in early July, and were found in the eggplant and tomato fields after the potato was harvested in early July. The adults were found again in October after a temporary decrease in number in late August. The Akasawa pest population showed slightly earlier oviposition and appearance of new adults, and longer active periods by the new adults, compared with the Nakatachi nonpest population.

Body size of female adults

Table 3 shows the body size of wild and laboratory-reared females. In the wild females, the body size of the pest population was significantly larger than that of the nonpest population. Among the laboratory-reared females, the body size of the pest population reared on potato was also significantly larger than that of the nonpest population reared on blue cohosh. There was no significant difference in body size between nonpest and pest populations reared on potato. Two-way ANOVA indicated that the body size of laboratory-reared females was significantly influenced by the food plant (Table 4).

Oviposition traits

Table 1 shows the number of eggs laid per female, egg mass size, and egg hatchability in two populations reared on blue cohosh or potato leaves. The pest females reared on potato

Table 4. Two-way ANOVA describing the effects of food plant and population on life history traits of *E. yasutomii*

Comparison	Female body size	Number of eggs laid per female	Developmental period in the immature stages	Female longevity
Food plant	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Population	NS	$0.01 < P < 0.05$	NS	$P < 0.01$
Food × population	NS	NS	$P < 0.01$	$P < 0.01$

Data were transformed to log χ before use in two-way ANOVA

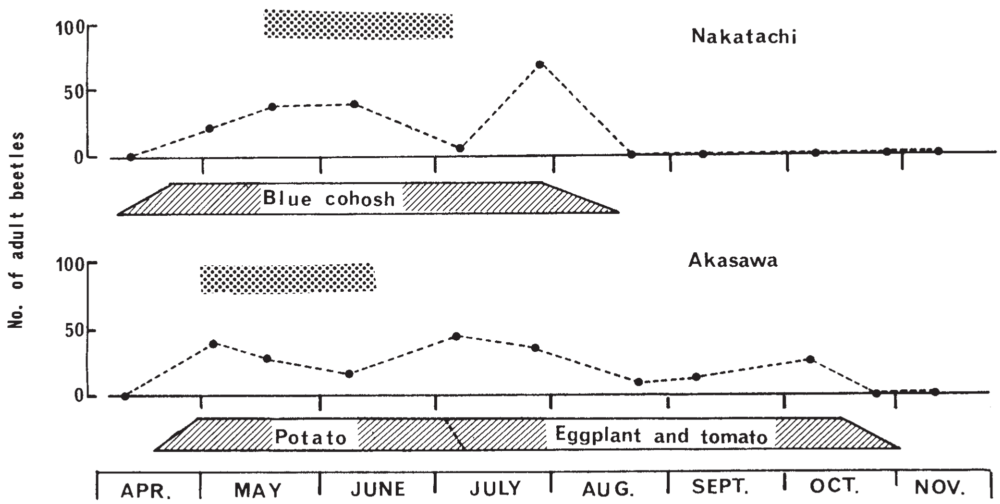

Fig. 1. Seasonal occurrence of adult beetles of *Epilachna yasutomii* of the Nakatachi nonpest (*upper graph*) and Akasawa pest (*lower graph*) populations in 1990. The number of beetles represents the number of adults counted during a 30-min period; both sexes are pooled. The *dotted area* shows the oviposition period

laid a significantly threefold larger number of eggs than the nonpest females reared on blue cohosh, but there was no significant difference in the number of eggs laid between the two populations reared on potato. Two-way ANOVA indicated that egg production was significantly influenced by both food plant and population type (Table 4). There was no significant difference in egg mass size or hatchability in any of the comparisons (Table 1).

Survival and development in the immature stages

Table 2 shows the survival rate and developmental period in the larval and pupal stages when reared on potato or blue cohosh leaves. No comparison revealed any significant difference in survival rate. The pest population reared on potato had a significantly shorter developmental period than the nonpest population reared on blue cohosh. There was no significant difference in developmental period between nonpest and pest populations reared on potato. Two-way ANOVA indicated that the developmental period was influenced by the food plant and by the food plant × population interaction (Table 4).

Female survival and oviposition schedule

Figure 2 and Table 5 show the survival and oviposition schedule of females and the reproductive characteristics and longevity of overwintered females, respectively. The oviposition schedule of the pest reared on potato was closely similar in overall oviposition period and peak period of oviposition to that of the nonpest reared on blue cohosh, although the former laid a much larger number of eggs than the latter. Of the nonpest females reared on blue cohosh, 55% were still surviving at the end of the experiment on October 6, while none of the pest females reared on potato remained alive by late July (Fig. 2); nonpest females on blue cohosh survived significantly longer than pest females on potato (Table 5). Both populations reared on potato had identical survival and oviposition patterns. Although 10% of the nonpest females on potato survived until the end of the experiment, longevity did not differ significantly between nonpest and pest populations reared on potato (Table 5). Two-way ANOVA indicated that longevity of females was significantly influenced by both food plant and population type, and by food plant × population interaction (Table 4).

The values of r and R_0 for the nonpest beetles reared on blue cohosh were 0.138 and 24.8, respectively, which were considerably lower than the corresponding values for the pest insects reared on potato (0.223 and 56.9). The values of r and R_0 for the pest on potato were both about 1.5 fold higher than those of the nonpest on potato (0.161 and 38.5) (Table 5).

Active period of newly emerged females

Table 6 shows the feeding activity periods and proportion of individuals exhibiting summer diapause for newly emerged

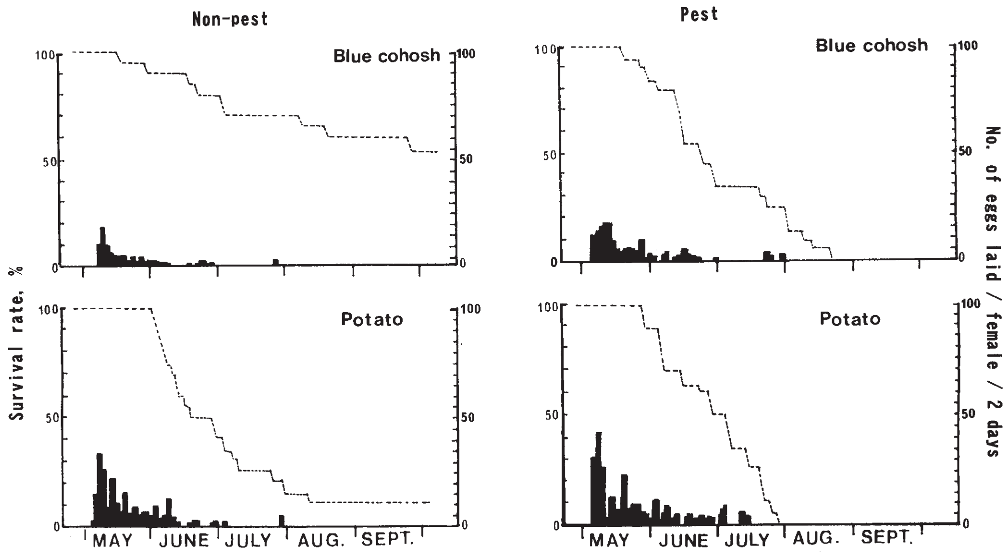

Fig. 2. Survival and oviposition schedules of the Nakatachi nonpest (*left*) and Akasawa pest (*right*) populations of *E. yasutomii* reared on blue cohosh (*upper graphs*) or potato leaves (*lower graphs*). The *histogram* shows the number of eggs laid per female every 2 days; the *dotted line* shows the survivorship curve for females

Table 5. Reproductive parameters and female longevity in the Nakatachi nonpest and Akasawa pest populations of *E. yasutomii*

Food plant	Intrinsic rate of natural increase, r^1	Net reproductive rate, R_0^1	Female longevity (days) mean ± SD $(n)^2$
Nonpest population			
Blue cohosh	0.1379	24.8	134.0[a] ± 67.5 (20)
Potato	0.1605	38.5	71.4[b] ± 51.9 (20)
Pest population			
Blue cohosh	0.1450	30.4	61.5[b] ± 29.6 (20)
Potato	0.2226	63.1	58.0[b] ± 17.3 (20)

[1] Values were calculated from the *lx–mx* curve data in Fig. 2
[2] Means followed by different letters (a,b) in the same column are significantly different at the 5% level (Kruskal–Wallis's test, Dunn's multiple comparison)

females. There was no significant difference in the periods from emergence to hibernation and the proportion in summer diapause. None of the females from the nonpest population, however, underwent summer diapause; two females from the pest population (6.7%) resumed feeding after cessation of feeding for more than 30 days.

Discussion

Life history traits of nonpest and pest populations

In the field, clear differences between the nonpest and pest populations were found in body size of females (Table 3) and seasonal occurrence of adult beetles (Fig. 1). The larger body size in the pest population was in accord with results for *E. niponica* (Shirai and Morimoto 1997). Larger body size favors the pest population living in artificially disturbed crop fields, because larger adults of *E. niponica* beetles survive better (Ohgushi 1996). A clear difference in seasonal occurrence of adult beetles was found, especially between summer and autumn. In the *E. yasutomii* population feeding on deadly nightshade, adults entered diapause in midsummer when deadly nightshade withered (Shirai 1988). Similarly, in the *E. yasutomii* population in the present study, newly emerged adults seemed to enter diapause in synchronization with early withering of the host plant. In the pest population, some individuals appeared in crop fields between September and October. A longer active period of females from the pest population was also observed in the laboratory, although the difference between the nonpest and pest populations was not significant (Table 6). Thus, some newly emerged adults are likely to extend their active periods when *E. yasutomii* shifts to cultivated solanaceous crops, which can be used as host plants until autumn. Extended active periods following host shift to cultivated crops have also been reported for the codling moth, *Cydia pomonella* L. (Ferro et al. 1974; Riedl 1983) and the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Hsiao 1978, 1986). Prolonged active periods of adults greatly favor rapid extension of the distribution area (Hare 1990).

In the laboratory, the number of eggs laid per female, developmental period in immature stages, and longevity of overwintering females significantly differed between the

Table 6. The periods from emergence to hibernation and proportion of individuals exhibiting summer diapause in the newly emerged females of the Nakatachi nonpest and Akasawa pest populations of *E. yasutomii*

Population[1]	Food plant	No. tested	Periods from emergence to hibernation (days) mean ± SD[2]	Proportion of individuals exhibiting summer diapause (%)[3]
Nonpest	*Solanum nigrum*	30	39.9[a] ± 17.6	0.0[a]
Pest	*Solanum nigrum*	30	48.7[a] ± 16.5	6.7[a]

[1] Rearing condition: 23°C, 16L:8D
[2] Nonsignificance at 5% level (Mann–Whitney U-test)
[3] Nonsignificance at 5% level (χ^2-test)

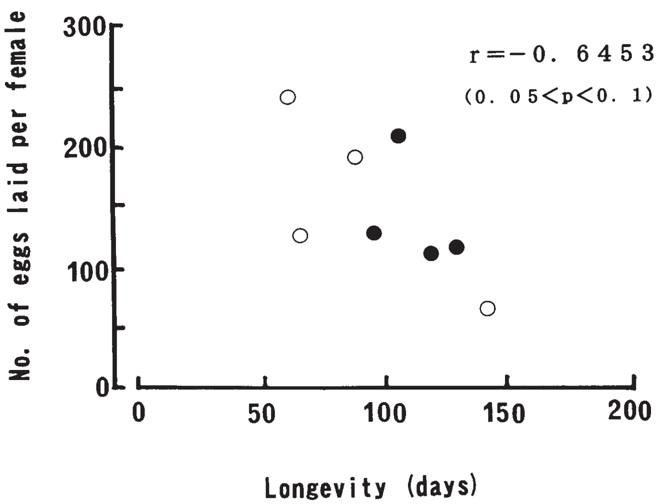

Fig. 3. Relationship between longevity and egg production in overwintered females of *E. yasutomii* (*open circles*) and *E. niponica* (*solid circles*). (Data for *Epilachna niponica* are from Shirai and Morimoto 1997)

nonpest and pest populations. Higher fecundity and shorter developmental periods are apparently favorable characteristics in an agricultural cropping system where insects suffer from much artificial disturbance, such as the potato harvest. This finding was in good accord with the result for *E. niponica* (Shirai and Morimoto 1997).

The longevity of females seems to involve a negative correlation with their egg production. With *E. niponica*, nonpest females reared on wild thistle tended to live longer than pest females reared on potato, although there was no significance between these longevities (Shirai and Morimoto 1997). When the data for *E. niponica* and *E. yasutomii* were pooled, there tended to be a negative correlation between longevity of the overwintered females and the number of eggs laid per female (Fig. 3). In the *E. yasutomii* population depending on deadly nightshade, 10%–14% of adults could overwinter twice (Shirai 1988). Similarly, in our *E. yasutomii* population on blue cohosh, a considerable number of adults seemed to overwinter twice, because 55% of the overwintered females in the nonpest population reared on blue cohosh were still surviving at the end of the experiment on October 6 (Fig. 2). In addition, two-way ANOVA indicated that differences in both egg production and female longevity were significantly influenced by population type (Table 4). It is thought that the *E. yasutomii* population had exhibited low fecundity with a long life span while existing on wild host plants, but its life history pattern changed to high fecundity with a short life span following a host shift to potato. This supports the hypothesis (Ito 1978) that an insect pest population that becomes successfully established in artificially disturbed crop fields has high mortality and a compensatory high reproductive rate.

Change in host acceptance of the potato

When reared on potato leaves, the value of R_0 increased 1.5 fold more in the pest population of *E. yasutomii* than in the nonpest population. However, there was no significant difference in any trait between the nonpest and pest populations reared on potato, which was in accord with the results obtained for *E. niponica* (Shirai and Morimoto 1997). Thus, it is considered that whether an *E. yasutomii* population had previously used potato as its host plant did not influence the current acceptability of potato.

Unlike the case for *E. niponica*, two-way ANOVA in the present study indicated that egg production and female longevity were significantly influenced not only by the food plant but also by the population type (Table 4); these two traits are genetically controlled. So far, there have been few reports that host acceptability changed as a result of host shift from wild plants to cultivated crops. With the Colorado butterfly, *Colias philodice eriphyle* Edwards, Tabashnik (1983) compared oviposition preference and larval survival between a nonpest population feeding on wild leguminous plants and a pest population depending on cultivated alfalfa. He concluded that there was no genetic difference controlling host plant use between the two populations because two-way ANOVA did not indicate any genetic influence.

The same conclusion was also reached in a study on host shift from wild solanaceous plants to potato by the Colorado potato beetle. Previously, Radcliffe (1982) cited the host shift of this species from wild plants to potato in North America as a rare case of adaptive coevolution in phytophagous insects and plants. However, two-way ANOVA (host plant × population) indicated that any interpopulation difference in life history traits (larval survival rate, body size, and tendency to diapause) was influenced only by the food plant factor (Horton et al. 1988). This conclusion was also supported by the observation that a local population of Colorado potato beetle, which had been isolated from potato for more than 40 years, preferred potato to a wild solanaceous plant (horse nettle) (Mena-Covarrubias et al. 1996). It is assumed that the Colorado butterfly and Colorado potato beetle could invade and become established in cultivated crop fields without any major physiological or behavioral change because the host changes occurred between closely related plant species within a single family (Tabashnik 1983; Hare 1990).

Significant genetic influence on adult longevity of *E. yasutomii* may result from reduced host acceptance of blue cohosh by the pest population. The pest population reared on blue cohosh was considerably shorter lived despite low egg production (Tables 1 and 5). Leaves of blue cohosh contain a number of characteristic secondary metabolites, such as caulosaponin (saponin), aporphine and quinolizidine (alkaloids), and citrullol (steroid) (Gibbs 1974). Pest populations that adapted well to potatoes may have rapidly lost the ability to thrive on blue cohosh. With *E. niponica*, no genetic influence was indicated between the nonpest and pest populations (Shirai and Morimoto 1997). This change may be because the pest population of *E. niponica* depended not only on solanaceous cultivated crops but also on wild thistle near the crop field, and the overall phenology of the nonpest population was almost identical to that of the pest population. Moreover, thistle leaves may contain fewer secondary metabolites that reduce survival and reproduction of *Epilachna* beetles, although we did not conduct any chemical analysis.

When we compare the life history traits of populations living on different host plants, including the comparison between wild plants and cultivated crops, we need to evaluate further the quality factor of host plants, resource availability in time and space (Jiggins et al. 1997), and the behavioral response to different host plants (Futuyma and Peterson 1985).

Acknowledgments We thank Dr. Takayuki Ohgushi (Kyoto University) for his valuable comments on an earlier draft of the manuscript. Cordial thanks are also given to two anonymous referees for constructive criticism on the manuscript.

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