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Life History Traits of Pest and Non-Pest Populations in the Phytophagous Ladybird Beetle, *Epilachna niponica* (Coleoptera, Coccinellidae)

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Abstract. Life history traits of the phytophagous ladybird beetle, *Epilachna niponica* were compared between a non-pest population feeding on wild thistle and a pest population feeding on cultivated solanaceous crops, mainly potato. The pest population had larger females, a higher population growth rate, a more continuous oviposition schedule, and a shorter developmental period in the immature stages, compared with the non-pest population. The two populations showed no clear differences in phenology from spring to autumn, egg mass size, hatchability, and larval survival rate. Significant differences were found in number of eggs laid per female during the first and second periods, and in the developmental period of the immature stages. These life history traits were influenced primarily by food plant. A higher fecundity and shorter immature period appear to be readily altered by the host shift from thistle to potato.

Key words: host shift, host suitability of potato, oviposition schedule, wild thistle.

Introduction

Comparison of the life history traits of populations of related species or conspecific populations living under different environmental conditions is important for understanding the evolution of reproductive strategies or other life history traits (Price 1984). In particular, comparing the life history traits of conspecific populations on wild and cultivated plants will reveal how the life history of non-pest populations change with host shift from wild species to cultivated crops (Ito 1978). However, the life history traits of conspecific pest and non-pest populations have been compared only for the Colorado potato beetle, *Leptinotarsa decemlineata* Say (Hsiao 1978; Horton et al. 1988) and *Colias* butterfly (Tabashnik 1983), because it is very difficult to find the original host of a pest population, or a non-pest population which depends solely on wild native host plants (Turnipseed and Kogan 1976; Kim 1993).

In Japan, phytophagous ladybird beetles of the genus *Epilachna* have local distributions not only on cultivated solanaceous crops but also on some wild native plants (e.g. thistle, blue cohosh and deadly nightshade; Katakura 1981; Nakamura 1983). Though the potato was introduced into Japan in the 16th or 17th century, its cultivation did not increase in the mountainous area of central Honshu until 1930 (Umemura 1984). Therefore, the relationship between potatoes and *Epilachna* ladybirds is an appropriate model for a comparative ecological study between non-pest and pest insect populations.

With *Epilachna niponica* Lewis, Iwao and Machida (1961) suggested that the inter-population difference in adaptation to potato may depend on the history of potato acting as host plant, because adult beetles reared on potato in the larval stages showed a significant preference for potato leaf over those reared on thistle (see also Iwao 1959). This implies that the host shift from thistle to potato was accompanied by adaptive changes in the pest population to utilize potato. Many workers have studied non-pest *E. niponica* populations feeding on thistle (e.g. Nakamura and Ohgushi 1979; Ohgushi and Sawada 1981; Sawada and Ohgushi 1994; Ohgushi 1996). However, no further studies have been carried out for pest *E. niponica* populations as suggested by Iwao and Machida (1961).

In the present study, we evaluated life history traits of two *E. niponica* populations that are distributed in Shiga prefecture; a non-pest population depending solely on wild thistle and a pest population feeding mainly on cultivated

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solanaceous crops (potato, eggplant and tomato). Two comparisons were made in the laboratory to elucidate changes in life history traits due to the host shift from wild thistle to cultivated potato. First, the life history traits on the current host plant in the field were compared (non-pest population reared on thistle vs. pest population reared on potato). Second, the host suitability of potato was compared between the two populations (non-pest population reared on potato vs. pest population reared on potato). The latter comparison was made to determine whether the host acceptability of potato depends on experience that the *E. niponica* population has previously used potato as a host plant.

Materials and methods

Study sites and collection

Non-pest population: Kawadodani (Ibuki town, Shiga prefecture, 500 m above sea level; Fig. 1) is a mountain stream at the foot of Mt. Ibuki, where *E. niponica* lives on wild thistle of the genus *Cirsium* growing along the stream. There were no cultivated plants around the site, the nearest potato field was in Joheiji village, about 2 km away. In three field censuses taken on April 27, May 3 and May 11, 1985, only one individual of *E. niponica* was found on April 27 in the Joheiji potato field. We collected 30 pairs of overwintered adults from young thistle leaves in Kawadodani on April 27, 1985 and used them as a non-pest population which had never fed on potato.

Pest population: Tsubakizaka (Yogo town, Shiga prefecture, 290 m above the sea level; Fig. 1) is a small mountain village about 30 km northwest from Kawadodani, where potato, eggplant and tomato are cultivated on a small scale from early spring to late autumn. *E. niponica* coexisted with *E. vigintioctomaculata* Motschulsky in these fields. *E. niponica* was also found on thistle plants (genus *Cirsium*) around the solanaceous crop fields. We collected 50 pairs of overwintered adults of *E. niponica* from potato plants just after budding, on April 27, 1985. We used them as a pest population feeding primarily on cultivated solanaceous crops. The pronotal width of female adults collected from both populations were measured. Three pairs of adults collected from each population were deposited as voucher specimens at the Laboratory of Insect Systematics, National Institute of Agro-Environmental Sciences, Tsukuba.

Phenology

At Kawadodani, the number of *E. niponica* adults on thistle plants was estimated about every two weeks from mid-April to mid-November, 1985. At Tsubakizaka, *E. niponica* adults on potato plants were also counted biweekly until late July. After the potatoes were harvested, censuses were performed biweekly until mid-November on eggplants and tomato plants around the potato field. Censuses at both sites were always carried out in the afternoon for 30 minutes by a visual counting method.

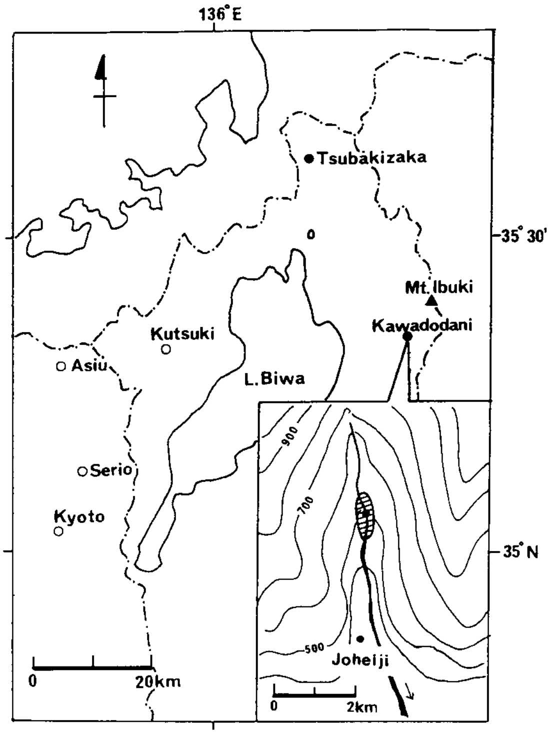

Fig. 1. Locations of the *Epilachna niponica* populations in the present study (●) and in other studies (○).

Adult survival and oviposition

For each population, pairs of overwintered adults collected from the field were transferred to a plastic dish (9 cm diameter, 4.5 cm deep) and supplied with either fresh thistle or potato leaves. These dishes were checked daily for the number of eggs laid and adult survivorship. The leaves were replaced with fresh ones every one or two days, and the experiment was terminated on September 30. The number of eggs per egg mass was recorded for every egg mass laid by the females. Hatchability was examined using egg masses which were saved from cannibalism by adult beetles.

The intrinsic rate of natural increase (r) and the net reproductive rate (R_0) were calculated from the female survivorship data (l_x) and the number of new females born per female every two days (m_x). The sex ratio of the newly emerged adults was regarded as 1 : 1.

Survival during the immature stages

Ten to twelve hatched larvae from the above experiment were transferred to a plastic dish (15 cm diameter, 6 cm deep) and reared on leaves of their parent's food plants. A fresh leaf was added to the dish every one or two days until the third instar, and daily during the fourth instar. After emergence, twenty new female adults were randomly selected for pronotal width measurement.

Summer diapause of newly emerged females

Prepupae and pupae of *E. niponica* were collected from thistle plants at Kawadodani and from potato plants at Tsubakizaka on July 7, 1990. When the adults emerged, thirty unmated females were transferred individually to a plastic dish (9 cm diameter, 4.5 cm deep) and supplied with fresh thistle leaves (Kawadodani population) or eggplant leaves (Tsubakizaka population). Feeding activity and summer diapause were recorded for 150 days after emergence. We defined summer diapause for individuals showing the following sequence of feeding activity: feeding intensely after emergence→cessation of feeding for more than 30 days→resumption of feeding. We used a 30 day period since this is the summer diapause period of *E. vigintioctomaculata*, which shows a clear summer diapause from mid-summer to early autumn in the field (Shirai 1991).

All laboratory studies except for the summer diapause study were conducted at the National Research Institute of Vegetables, Ornamental Plants and Tea, Mie in 1985 under constant conditions of 25°C and 16L8D. The summer diapause of newly emerged females was tested at the National Institute of Agro-Environmental Science, Tsukuba in 1990 under 23°C and 16L8D conditions. Potatoes and eggplants cultivated on each experimental farm, and thistles grown near each institute, were used as food plants.

Results

Phenology of adult beetles

The phenology of *E. niponica* beetles and their host plants for the two populations is outlined in Fig. 2. The number of both sexes were pooled. In the Kawadodani non-pest population, overwintered adults emerged in mid-April, and the population peaked in early to mid-May. The largest number of newly emerged beetles were found in late July, and after a temporary decrease in August they entered hibernation by mid-November. The phenology of the Tsubakizaka pest population showed a similar pattern to that of the non-pest population. After the potatoes were harvested by late July, newly emerged adults were found in the neighboring eggplant and tomato fields.

Body size of female adults

Table 1 shows the body size of wild and laboratory-reared

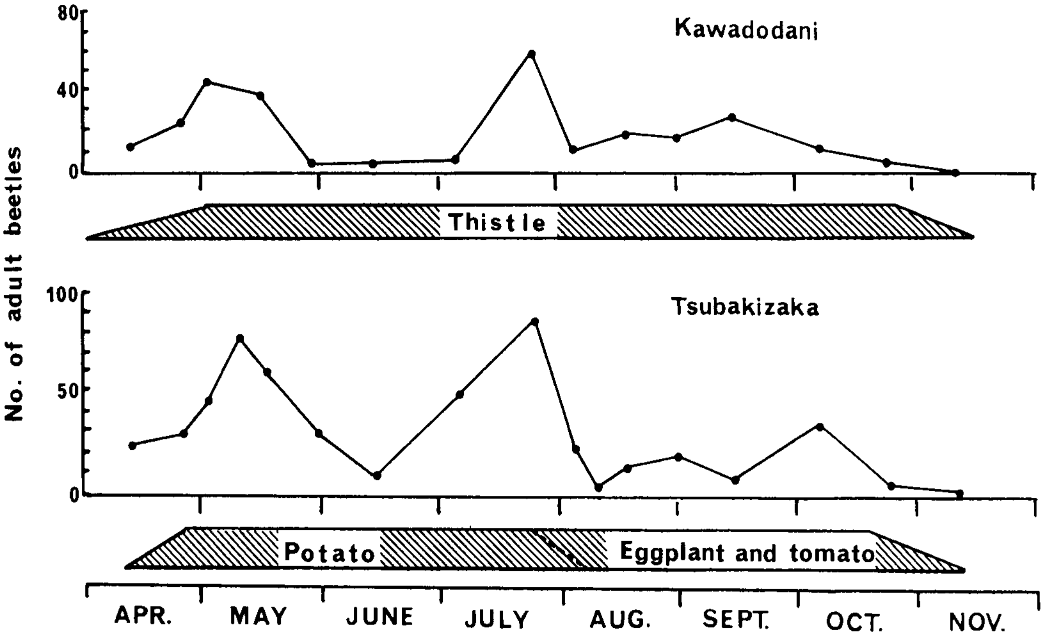

Fig. 2. Seasonal changes in the number of adult beetles of *E. niponica* at the Kawadodani non-pest (above) and Tsubakizaka pest populations (below) in 1985. The number of beetles represents the number of adults counted during a 30 minute period.

Table 1. Female body size in terms of the pronotal width of wild and laboratory-reared adults in the Kawadodani non-pest and Tsubakizaka pest populations of *Epilachna niponica*.[1]

Population Food plant	Pronotal width (mm) mean ± SD (*n*)
Wild beetles	
Non-pest	3.59±0.21 (33)[b]
Pest	3.77±0.17 (46)[a]
Laboratory-reared beetles[2]	
Non-pest	
Thistle	3.60±0.09 (20)[a]
Potato	3.66±0.11 (20)[a]
Pest	
Thistle	3.43±0.09 (20)[b]
Potato	3.63±0.13 (20)[a]

[1] Means followed by different letters are significantly different at the 5% level by Mann-Whitney *U* test for the wild beetles, and by Kruskal-Wallis's test, Dunn's multiple comparison for the laboratory reared beetles.

[2] Rearing conditions: 25°C, 16L8D.

females. For wild beetles, the body size of the pest population was significantly larger than that of the non-pest population. In laboratory-reared beetles, there were no significant differences in two comparisons (non-pest on thistle vs. pest on potato, and non-pest on potato vs. pest on potato). However the pest population on thistle was significantly smaller than any of the other insect-host treatments. Two-way ANOVA analysis indicated that the body size of laboratory-reared females was significantly influenced by both food plant and population, and by their interaction (Table 2).

Oviposition traits

Table 3 shows the number of eggs laid per female, egg mass size and egg hatchability when two populations were reared on thistle or potato leaves. The oviposition period was divided into two periods; the first period, April 28 to July 13 and the second period, July 14 to September 30, since the oviposition schedule was dichotomized when the beetles were reared on thistle leaves (Fig. 3). During the first period, pest females on potato laid a significantly larger number of eggs than non-pest females on thistle, but there was no significant difference between the two populations on potato. Conversely, during the second period, non-pest females on thistle laid a significantly larger number of eggs than pest females on potato. The pest females on potato laid about a two-fold larger total number of eggs than non-pest females on thistle, although the difference was not significant because of large individual variations within each population. Also, there was no significant difference in egg numbers between non-pest on potato and pest on potato. Two-way ANOVA analysis indicated that egg production was influenced only by the food plant (Table 2). There were no significant differences in egg mass size or hatchability in any of the comparisons (Table 3).

Survival and development in the immature stages

Table 4 shows the survival rate and developmental period in the larval and pupal stages with thistle or potato leaves. No experimental setups showed any significant difference in survival rate. However, the pest population on potato had a significantly shorter developmental period than the non-pest on thistle. This difference was due to the larval developmental period, since the pupal period was almost equal (from 8.5 to 9.2 days) in the four treatments. There was no significant difference in developmental period between non-pest on potato and pest on potato. Two-way ANOVA analysis indicated that developmental period was influenced by the food plant and by the food plant × population interaction (Table 2).

Female survival and oviposition schedule

Figure 3 and Table 5 show the survival and oviposition schedules of females, and the reproductive parameters of two populations, respectively. The non-pest population on thistle laid eggs continuously from late April to mid-May, thereafter ceased oviposition for about one month, and then sporadically laid a small number of eggs from July to September. Twenty percent of females on thistle were still surviving at the end of experiment on September 30. The pest population on potato showed a pattern of continuous oviposition from late April to late July. None

Table 2. Two-way ANOVA describing the effects of food plant and population on life history traits of *E. niponica*.[1]

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

[1] Data were transformed to logχ before use in two-way ANOVA.

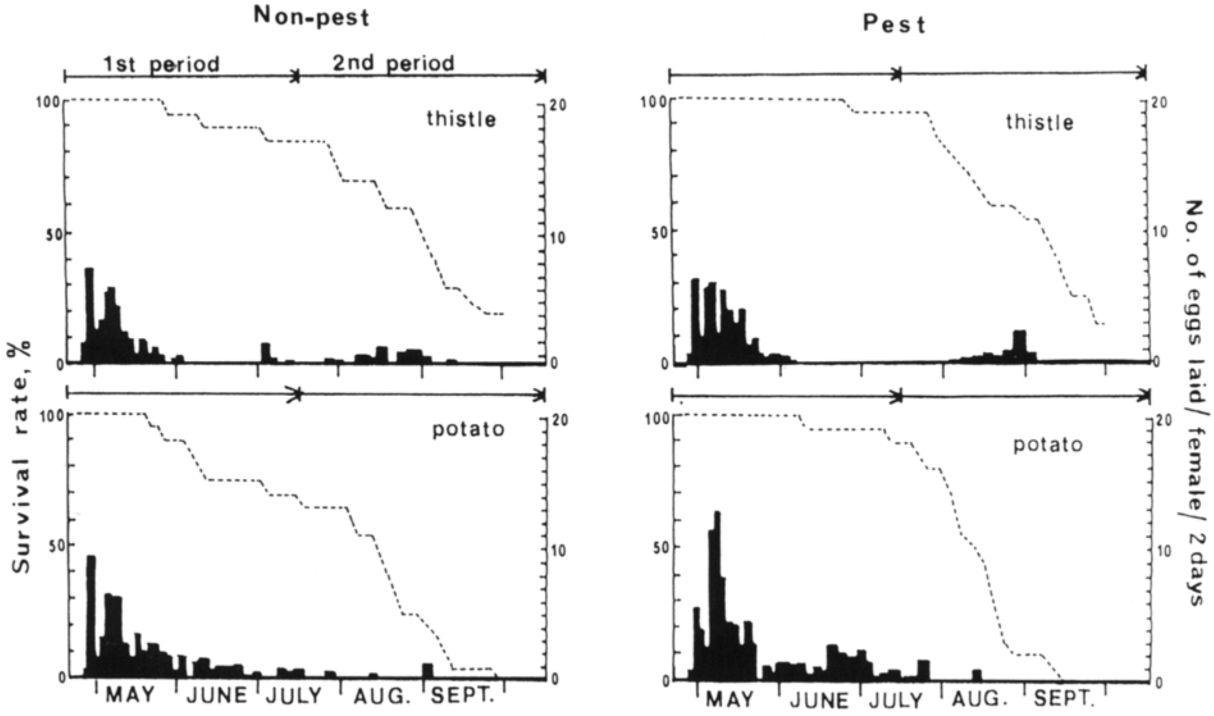

Fig. 3. Survivorship and fertility schedules of the Kawadodani non-pest (left) and Tsubakizaka pest (right) of *E. niponica* reared on thistle (above) or potato leaves (below). The histogram shows the number of eggs laid per female every two days, and the dotted line the survivorship curve for females.

of the pest females remained alive at the end of experiment, though the difference in survival rate was not significant between the two populations (0% vs. 20%; Fig. 3). The values of r and R_0 of non-pest on thistle were 0.125 and 31.8, respectively, which were considerably lower than the corresponding values for pest on potato (0.144 and 56.9; Table 5). Comparing non-pest on potato and pest on potato, the two populations showed almost identical survival and oviposition patterns; all of the non-pest females on potato died by the end of experiment (Fig. 3). The values of r and R_0 of pest population on potato were both slightly higher than those of non-pest on potato (Table 5).

Summer diapause of newly emerged females

The two populations showed almost identical feeding activity patterns for newly emerged females (Fig. 4). They

Table 3. Comparison of oviposition traits between the Kawadodani non-pest and Tsubakizaka pest of *E. niponica* .[1,2]

Population Food plant	Number of eggs laid per female			Egg mass size mean±SD (n)	Hatchability (%) mean±SD (n)
	First period[3] mean±SD (n)	Second period[3] mean±SD (n)	Total period mean±SD (n)		
Non-pest					
Thistle	95.9± 65.4 (20)^{a}	17.4±20.7 (16)^{a}	113.3± 74.4 (20)^{a}	23.3±5.6 (104)^{a}	88.9± 9.5 (24)^{a}
Potato	130.8±139.7 (20)^{ab}	2.8± 2.9 (12)^{ab}	133.6±135.8 (20)^{a}	20.1±7.2 (128)^{a}	85.7± 9.6 (15)^{a}
Pest					
Thistle	99.6± 74.0 (20)^{ab}	20.9±33.1 (19)^{a}	120.5± 86.6 (20)^{a}	23.4±6.4 (104)^{a}	89.6± 8.6 (29)^{a}
Potato	212.3±155.2 (20)^{b}	2.0± 4.8 (18)^{b}	214.2±150.2 (20)^{a}	22.6±4.9 (187)^{a}	81.1±11.7 (16)^{a}

[1] Means followed by different letters in the same column are significantly different at the 5% level (Kruskal-Wallis's test, Dunn's multiple comparison).

[2] Rearing conditions: 25°C, 16L8D.

[3] First period: April 28 to July 13, Second period: July 14 to September 30.

Table 4. Comparison of development during the immature stages between the Kawadodani non-pest and Tsubakizaka pest populations of *E. niponica*.[1,2]

Population Food plant	Replication	Survival rate (%) mean±SD	Developmental period mean±SD
Non-pest			
Thistle	13	78.8± 9.8^{a}	31.7±1.5^{ab}
Potato	12	78.4±19.1^{a}	29.8±1.0^{bc}
Pest			
Thistle	13	85.6±11.2^{a}	32.6±1.5^{a}
Potato	12	74.2±14.4^{a}	28.7±0.9^{c}

[1] Means followed by different letters in the same column are significantly different at the 5% level (Kruskal-Wallis's test, Dunn's multiple comparison).

[2] Rearing conditions: 25°C, 16L8D.

fed intensely on each food plant for 20 to 30 days after emergence, and then most individuals ceased feeding for about 50 days, thereafter resuming feeding. There was no significant difference in the proportion of individuals entering summer diapause between the non-pest (82.8%) and pest populations (86.7%; Fig. 4). Feeding activity patterns of both populations from the laboratory conditions were in accord with the phenology of new adults in the field (Fig. 2).

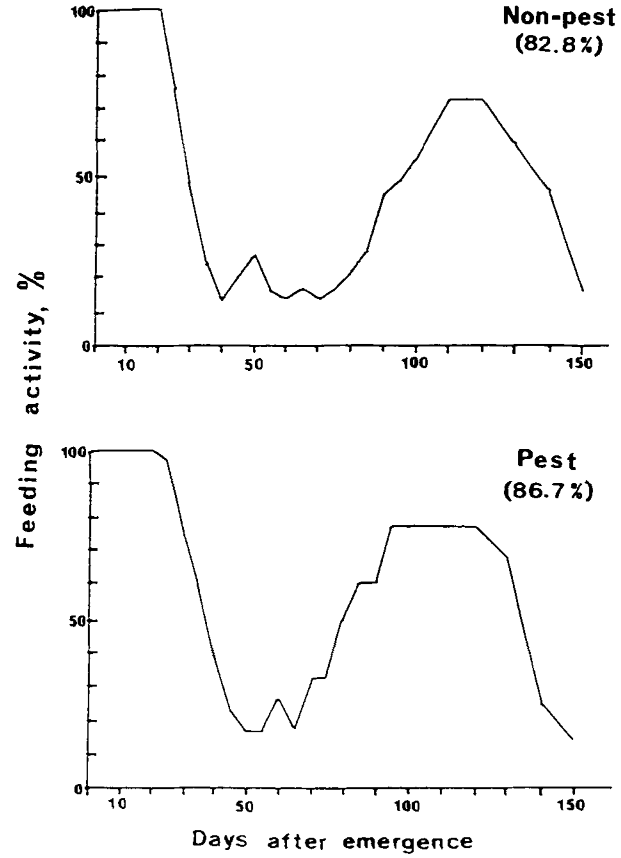

Fig. 4. Pattern of feeding activity of newly emerged females of the Kawadodani non-pest and Tsubakizaka pest of *E. niponica*. Vertical axis shows the percentage of individuals feeding on a leaf each day. Proportion of individuals exhibiting summer diapause is indicated in parentheses.

Discussion

Phenology of local populations

Whether phytophagous insects are able to invade and successfully colonize new cultivated crop fields mainly depends on the following three factors: (i) synchronization of crop phenology with insect life history, (ii) host plant preference, and (iii) host plant suitability for high egg production and survival during immature stages (Hodkinson and Hughes 1982; Ferro 1987). When soybean was introduced into South America in the 20th century, many species of noctuid moths and stink bugs living on wild leguminous plants were able to invade new cultivated crop without temporal restraint because of synchronization of crop phenology with these insect's life histories (Kogan 1991).

Table 5. Reproductive parameters in the Kawadodani non-pest and Tsubakizaka pest populations of *E. niponica*.

Population Food plant	Intrinsic rate of natural increase, r[1]	Net reproductive rate, R_0[1]
Non-pest		
Thistle	0.1253	31.8
Potato	0.1234	34.6
Pest		
Thistle	0.1257	39.9
Potato	0.1437	56.9

[1] Values were calculated from the l_x-m_x curve data in Fig. 3.

In the Kawadodani non-pest population, *E. niponica* was found on thistles from early spring to late autumn until fresh thistle leaves were blasted by frost. If the Kawadodani population invaded potato fields, they could readily use this crop for oviposition, since potato has already germinated by late April. Although potatoes are harvested by late July, just before and after the emergence of new adults, newly emerged adults are able to move to the neighboring eggplant and tomato fields. Thus *E. niponica* could use these crops as host plants till late autumn. The phenology of thistle is in good accord with the overall phenology of solanaceous crops including potato, tomato and eggplant (Fig. 2). Hence, a non-pest population feeding on thistle could easily shift to a potato or other solanaceous crop field without temporal restraint.

In both Kawadodani and Tsubakizaka, most adult beetles are presumed to enter summer diapause (Fig. 2). The diapause was also confirmed by laboratory experiments (Fig. 4). Censuses in potato and thistle plants at Tsubakizaka for three years (1980 to 1982) also suggest that most of the newly emerged adults of *E. niponica* enter diapause in mid-summer (T. Hozumi, unpublished data). The summer diapause was also observed in other thistle-feeding *E. niponica* populations at Kutsuki, Shiga (Ohgushi and Sawada 1981) and the Botanical garden of Kyoto University, Kyoto (Sawada and Ohgushi 1994; Ohgushi and Sawada 1995; see Fig. 1 for locations). On the other hand, the thistle-feeding *E. niponica* populations at Asiu, Kyoto (Nakamura and Ohgushi 1979) and Ohshika, Nagano (Shirai 1987, 1991) did not enter summer diapause; newly emerged adults decreased gradually in number after emergence, and entered hibernation by mid-October.

Summer diapause is an important trait for comparing the evolution of seasonality in life history among insect populations (Masaki 1980). Our studies on *E. niponica* populations suggest a geographical difference in the summer diapause in newly emerged adults. In *E. yasutomii* (Katakura), a close relative of *E. niponica*, a population on deadly nightshade, *Scopolia japonica* Maxim. at Takatoh, Nagano, entered early hibernation without a summer diapause when the deadly nightshade had already withered in the early summer (Shirai 1988, 1991). However, in all of the *E. niponica* populations studied here, host thistles supplied ample fresh leaves till autumn. This suggests that the summer diapause of *E. niponica* does not depend primarily on host plant phenology. The differences observed in summer diapause are possibly dependent on micro-climatic conditions or subtle differences in host plant conditions. For example, there was a difference in summer diapause between an introduced population (Sawada and Ohgushi 1994; Ohgushi and Sawada 1995) and its source population (Nakamura and Ohgushi 1979).

Life history traits in non-pest and pest populations

Significant differences between the non-pest reared on thistle and the pest reared on potato were found in number of eggs laid per female during the first and second periods, and the developmental period in the immature stages. These life history traits were influenced primarily by food plant (Table 2), and a higher fecundity and shorter immature period appear to be readily altered by switching host plants from thistle to potato.

In the field, body size of pest females was larger than that of non-pest females. In the laboratory-reared females, no significant difference was found between the non-pest on thistle and the pest on potato, although the pests on thistle were significantly smaller than others. Furthermore, two-way ANOVA analysis indicated effects not only of food plant but also of population. This suggests that female body size is influenced by both environmental and genetic factors.

Rearing on potato leaves tended to accelerate larval developmental speed and enlarge the body size of females compared with rearing on thistle leaves. Thus potato is a nutritious host plant suitable for the larval development in *E. niponica*. Among the life history traits of the pest on potato, the concentration of egg production in the early season (the first period in Fig. 3) and the shorter immature period must give rise to high population growth in fields where potatoes are harvested by mid- to late July, before and after new beetles emerge. Likewise, a larger body size favors the pest population living in artificially disturbed cultivated crop fields, because larger adults of *E. niponica* survived better during hibernation (Ohgushi 1996).

Change in host acceptability to potato

The present study showed no significant differences in any life history traits between non-pest and pest reared on potato leaves. Therefore, it is concluded that whether an *E. niponica* population has once used potato as its host plant did not influence the host acceptability to potato, and that the current suitability of potato observed in the pest Tsubakizaka population did not increase through a process of adaptation to potato. In addition, the present study showed no evidence for any gradual changes in host plant preference due to host shift from thistle to potato as suggested by other studies (Iwao 1959; Iwao and Machida 1961), since both larvae and adults of the two populations fed well on potato leaves.

The results from the present study were consistent with some conclusions from the studies on host suitability of cultivated crops for pest and non-pest conspecific populations in the Colorado potato beetle, *Leptinotarsa decemlineata* (Hsiao 1978; Horton et al. 1988), Colorado butterfly, *Colias philodice eriphyle* Edwards (Tabashnik 1983), and bruchid beetle, *Zabrotes subfasciatus* Boh. (Pimbert 1985). Non-pest populations of the Colorado potato beetle and the Colorado butterfly showed a high host acceptability to cultivated potato or alfalfa, respectively. Non-pest bruchid beetles from wild legumes also significantly preferred cultivated legumes and laid a larger number of eggs on cultivated crops. It is assumed that these three species are able to invade and have established in cultivated crop fields without any major physiological or behavioral changes because the host changes occurred within a single plant family, the *Solanaceae* or *Leguminoceae* (Hare 1990). Despite the host change between different plant families, Compositae (thistle) to

Solanaceae (potato), the present study indicated the high host suitability of potato for non-pest *E. niponica*. A phylogenetic analysis suggested that *E. niponica* may be derived from an ancestral species that fed on solanaceous or cucurbitaceous plants (Katakura 1981). The non-pest Kawadodani *E. niponica* may be evidence of maintenance of the ancestral species adaptation to its host, alluded to previously.

Further study will be required to fully understand the differences observed in the number of eggs laid by the two populations. The total number of eggs laid by the pest females on potato was 1.6-fold greater than the number laid by non-pest females on potato, though the difference was not statistically significant. In addition, out of all the life history traits studied, the number of eggs laid per female showed the largest individual variation and the greatest discrepancy between the non-pest and pest on potato. Tabashnik et al. (1981) suggested that a high degree of individual variation in oviposition preference may play an important role for the butterfly, *Colias eurytheme* Boisduval, in host shift to new plant species. Via (1990) and Kim (1993) also reported that many natural insect populations having large individual variation in life history traits were efficiently adapted to agro-ecosystems and established in cultivated crop fields. Therefore, it is necessary to continuously monitor any changes in both the mean number of eggs laid per female and its individual variance, using populations artificially introduced from wild thistle to cultivated potato in experimental fields.

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