ORIGINAL ARTICLE

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Population dynamics of a thistle-feeding lady beetle *Epilachna niponica* (Coccinellidae: Epilachninae) in Kanazawa, Japan. 1. Adult demographic traits and population stability

Abstract Population dynamics of a thistle-feeding univoltine lady beetle, *Epilachna niponica* Lewis (Coleoptera: Coccinellidae), was studied from 1996 to 1999 in Yuwaku, Kanazawa, Japan. The lady beetles often reached such a high density level that food was depleted. The Jolly–Seber method was used for adult marking, release, and recapture data to estimate population parameters of adult number, daily resident rate, longevity, reproductive rate (R, the number of new adults produced per overwintered adults), and survival rate of new adults to the reproductive seasons (S_w). These estimates were compared with those of the Asiu, Kutsuki (A and F), and Kyoto populations, which were previously studied with similar methods and have similar intensities. Asiu and Kutsuki F populations remained at a rather low density with a low R, while Kutsuki A and Kyoto populations reached a high density where food depletion occurred with a high R value. The Yuwaku population often reached a food-depleting level as in the Kutsuki A and Kyoto populations. It also shared the short life span of overwintered adults (13.5 days) of other high-density populations; however, it showed much shorter longevity of new adults (36.6 days), much lower R (1.0–2.5), and higher S_w (43%–53%). In some traits the Yuwaku population was similar to the Asiu population: low R, high S_w, and low population variability (SD of log densities; 0.103 and 0.115 for overwintered and new adults, respectively, which were lowest among the populations).

Key words Natural population · Food plant depletion · Mark–recapture method · Adult life span · Overwintering rate · Reproductive rate

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Introduction

A herbivorous lady beetle, *Epilachna niponica* Lewis (hereafter referred to as EN), is a univoltine species and feeds on thistles in central-northern Honshu and southern Hokkaido in Japan (Katakura 1981). The species is a promising one for studying the process of speciation and population dynamics, because (1) it is distributed patchily and is remarkably variable among the local populations in morphology (adult size and elytral shape) and biology (host plants and food plant preference) (Katakura 1981, 1997), and (2) demographic techniques (mark–recapture of adult beetles and life table construction for immature stages) are easily applicable to EN (Nakamura and Ohgushi 1979; Nakamura 1983). Therefore, since the mid-1970s, the population dynamics of EN has been studied in many localities under different habitat conditions with similar census methods including intensive mark–recapture procedures and construction of life tables for 3–7 years, which makes quantitative comparison among the local populations possible (Ohgushi and Sawada 1981; Nakamura 1983).

Common characteristics of EN populations are summarized in two points: (1) EN populations showed an exceptionally high stability for herbivorous insect populations; and (2) every population was stabilized during the reproductive season (reviewed in Ohgushi 1998; Koji 1999). On the other hand, there is a remarkable interpopulation variation of EN in density and variability. The Asiu population living in a cool temperate climax beech forest in the northern part of Kyoto Prefecture remained at a relatively constant low density below the level where food depletion occurred (Nakamura and Ohgushi 1979, 1981, 1983). The Kutsuki F (Kijiyama) population living in temperate deciduous forests 15km east of the Asiu population (Ohgushi and Sawada 1981, 1985a; Ohgushi 1986, 1992) and two populations in village areas in Nagano Prefecture (Shirai 1987) also usually stayed at a low density. This stability is the result of two regulating mechanisms: (1) density-dependent dispersal of reproductive adults among host

plant patches (Nakamura and Ohgushi 1981; Ohgushi and Sawada 1985a), and (2) resorption of eggs in the female ovary promoted by deterioration of host plants (Ohgushi and Sawada 1985a; Ohgushi 1995).

In contrast, in the Kutsuki A (Nyudani), new adults defoliated some thistle plants in years of high density (Ohgushi and Sawada 1981). In the Kyoto population, which was artificially introduced from Asiu, new adults reached a very high density so that food was inadequate (Sawada 1984; Sawada and Ohgushi 1994; Ohgushi and Sawada 1995, 1998). Compared to the low-density populations, the two high-density populations had (1) much lower arthropod predation pressure in immature stages, (2) shorter reproductive life span, (3) lower survival rate from eclosion to reproductive season in adult stage, and (4) broader fluctuation in population size (Ohgushi 1986; Sawada and Ohgushi 1994; Ohgushi and Sawada 1997, 1998).

We studied an EN population feeding mainly on a thistle, *Cirsium matsumurae* Nakai (CM), in Yuwaku, Kanazawa. This population is interesting from two standpoints. First, the population often reached such a high density that CM was defoliated, which seems at least partly due to low arthropod predation pressure as is the case with other high-density populations. Second, and most typically, CM has a very rich insect fauna: a total of 64 species, mostly leaf-eating species, were recorded on the leaf and stems of the thistle (Kaihara et al. 1997; Kaihara 1999). Especially, the tortoise beetle *Cassida rubiginosa* Müller (CR) is as predominant as EN. Our study also considered the CR populations, which will be reported elsewhere.

The present study sought to identify the demographic traits of an EN population in intra- and interspecifically abundant condition. This article, the first in a series, reports the adult population parameters such as population size, sex ratio, survival rate, longevity, and reproductive rate, and compares them with those of other populations published in earlier studies.

Study sites and methods

Climate and vegetation

Yuwaku is located at an elevation of 220m above sea level. Mean annual temperature is 13.1°C, and annual rainfall is 2500mm. The study site was in a valley of the Yunokawa Stream, both sides of which were steep slopes covered with deciduous secondary forests with trees of *Alnus fauriei* Lév. et Vant., *Juglans mandshurica* Maxim. var. *sachalinensis* (Miyabe et Kudo) Kitamura, and *Cryptomeria japonica* (L. fil.) D. Don. The site is covered with 1–2m of snow from late December to early April.

Host plant

Two perennial thistle species, *Cirsium matsumurae* (CM) and *Cirsium kagamontanum* Nakai (CK), grow on the banks of the stream and on sandy deposits accumulated behind check dams for erosion control. These two species show a largely similar pattern in phenology of shoot growth. The new rosettes sprouted in early April soon after the disappearance of snow cover. They began shoot growth in mid-April, increasing rapidly in size, and reached full height in mid-July. Thereafter, flower stalks were extended until September, then flowered over 3 months. At the onset of the study in the spring of 1996, we individually numbered 134 CM and 59 CK plants found in a 30 × 50m area (main area). During the study period, some of the thistles, mostly CM, were washed away by floods due to heavy rain. To accommodate the loss, 10 (1998) and 21 (1999) additional CM plants and 2 (1998) and 1 (1999) CK plants found upstream of the main area were newly marked for the study (Table 1). All marked thistles were examined twice (April–July) or once (August–October) a month to record the size of the plants (height and number of shoots). Leaf damage by EN and other insects combined was also recorded by visual estimation of a 0–5 system as follows: 0, intact leaves;

Table 1. Annual changes in total number of thistle plants and shoots, mean number of shoots per plant, and mean height of shoots during the study period

	Cirsium matsumurae				*Cirsium kagamontanum*			
	1996	1997	1998	1999	1996	1997	1998	1999
Total number[a]								
Plant	134 + 0	125 + 0	115 + 10	102 + 21	59 + 0	54 + 0	52 + 2	45 + 1
Shoot	338 + 0	294 + 0	247 + 30	168 + 35	177 + 0	180 + 0	194 + 10	165 + 4
Number of shoots per plant[b]	2.5 ± 0.2 (1–14)	2.4 ± 0.2 (1–12)	2.2 ± 0.2 (1–12)	1.7 ± 0.1 (1–10)	3.0 ± 0.4 (1–12)	3.3 ± 0.4 (1–20)	3.8 ± 0.5 (1–20)	3.7 ± 0.6 (1–22)
Mean height of shoots, cm[b]	147.8 ± 5.2 (16–275)	121.6 ± 5.4 (7–249)	103.7 ± 4.6 (5–250)	100.6 ± 3.5 (6–202)	98.9 ± 6.0 (9–190)	111.6 ± 7.3 (3–208)	103.6 ± 7.9 (3–221)	55.6 ± 2.1 (5–140)
Mean level of defoliation[c]								
July	–	2.2 ± 0.1 (102)	3.2 ± 0.1 (229)	2.2 ± 0.1 (149)	–	1.2 ± 0.1 (50)	1.5 ± 0.1 (167)	1.1 ± 0.1 (153)
August	–	3.0 ± 0.9 (80)	4.0 ± 0.1 (205)	2.6 ± 0.1 (137)	–	1.6 ± 0.1 (48)	1.8 ± 0.1 (150)	1.4 ± 0.1 (147)

[a] Main area plus additional area (see text for explanation)
[b] Mean ± SE (range)
[c] Mean ± SE (*n*); values were evaluated on July 6, August 15 (1997), July 17, August 22 (1998), and July 8, August 4 (1999)

1, 1%–20%; 2, 21%–40%; 3, 41%–60%; 4, 61%–80%; 5, 81%–100%.

Adult

According to preliminary mark–recapture censuses in 1995 (25 times total), EN adults clearly preferred CM to CK for oviposition, so that most of the EN population in the study area was found on the former species. EN overwintered in the adult stage and emerged in early spring. Females laid eggs in clusters on the undersurface of thistle leaves. Larvae passed through four instars and pupated on the plant. New adults also fed on thistle leaves and, by late autumn, entered hibernation in leaf litter or soil near their host plants.

All thistle plants in the study plot were individually examined to catch the beetles. On initial capture, each beetle was given a unique color code of four dotted points on the elytra using lacquer paint. Capture date, place, sex, and body size were recorded before release to the plant on which they were captured. On subsequent censuses, marked adults were checked by sight without recapturing.

From 1996 to 1998, censuses were performed at 1- to 3-day intervals from April to August and 5-day intervals thereafter (in total 70, 64, and 52 times for 1996, 1997, and 1998, respectively). In 1999, we censused overwintered adults at 5-day intervals from April to July (17 times).

Total number ($\hat{N}_i$) and daily rate of residence ($\hat{\phi}_d$) on each census were estimated using the Jolly–Seber stochastic model, and mean length of residence time (L) and total number (N_G) of adults of each generation were also determined (Jolly 1965; Seber 1973; see also Nakamura and Ohgushi 1979). The term "residence" instead of "survival" is used for parameters $\hat{\phi}_d$ and L, because emigration and death cannot be distinguished here as the cause of loss. According to these estimates, population density per thistle shoot, sex ratio ($\%F$), reproductive rate per generation (R), population variability, and survival rate of new adults to the reproductive season (S_w) were also obtained. In this article, R is defined as the number of new adults produced per overwintered adult. R and $\%F$ were obtained from two values, N_G and total number of marked beetles (n_G). Population variability was represented by the standard deviation of log-transformed densities (Gaston and McArdle 1994). S_w was derived in three ways: the ratio of n_G to total number of individuals recaptured in the following reproductive season (S_{w1}, a minimum estimate), and the ratio between n_G (S_{w2}) or N_G (S_{w3}) in one generation and those in the following reproductive season. These three estimates inevitably include large errors because of loss of marks and movement of beetles between the study site and outside (see Results). Therefore, three methods were used in this article. Besides L, minimum estimate of residence time (MLR) was also estimated from the period between the first and last captures. For new adults, the period from eclosion to entering hibernation was tentatively regarded as the length of residence. In individuals that were captured only once, it was operationally treated as zero.

Results

Annual changes in host plant characteristics

The total number of CM plants and shoots decreased throughout the study period (see Table 1). Total number of plants and shoots in 1999 was about 76% and 50% of that in 1996, respectively. The variability in the total number of shoots during the study period was 2.0 fold in CM and 1.2 fold in CK (see Table 5, later in this article), and number of shoots per plant was varied from 1 to 14 (mean, 1.7–2.5) and from 1 to 22 (mean, 3.0–3.8), respectively. There were no differences in the number of shoots per plant among the years (Kruskal–Wallis test, $H = 3.73$, $P = 0.16$ in CM; $H = 2.89$, $P = 0.24$ in CK). Plant height decreased in CM due to the loss of large plants to flooding but was not significantly different in CK (Kruskal–Wallis test, $H = 33.27$, $P = 0.001$ in CM; $H = 1.69$, $P = 0.430$ in CK). Mean level of defoliation of CM was 2.2–3.2 in July and 2.6–4.0 in August. Defoliation level of CK was lower than CM for all years (Mann–Whitney U tests with sequential Bonferroni's correction of significance level: July 1997: $U = 978$, $P < 0.001$; August 1997: $U = 570$, $P < 0.001$; July 1998: $U = 3814.5$, $P < 0.001$; August 1998: $U = 2757$, $P < 0.001$; July 1999: $U = 6141$, $P < 0.001$; August 1999: $U = 15\,099$, $P < 0.001$).

Seasonal change in adult number

Figure 1 indicates the seasonal change in the number of overwintered and new adults observed (n_i) and that estimated by the Jolly–Seber method ($\hat{N}_i$). Overwintered adults emerged from hibernation from early April (1997–1999) to mid-April (1996). Their number increased until late April and then formed a plateau for nearly 1.5 months (early May–mid-June); most had died by the end of June. New adults began to emerge from late June (1997, 1998) to mid-July (1996). Their number increased quickly and peaked in mid- to late July, then they decreased gradually and disappeared at the end of October or early November to enter hibernation. The observed numbers of new adults temporarily declined from early August to middle/late September. Inactive adults were frequently found on the underside of withered host plant leaves, suggesting that this temporal drop is due to aestivation of new adults (see following).

Sampling and marking ratios of adults

Sampling ratio, derived by $n_i/\hat{N}_i$, was constant around 0.6 for both overwintered and new adults throughout the seasons except that the ratio for new adults dropped to 0.1 from mid-August to middle or late September, probably due to aestivation (Fig. 2a). Marking ratio, derived by the Jolly–Seber method as the proportion of marked individuals to $\hat{N}_i$, rapidly increased to >0.8 as the census progressed (Fig. 2b). The high level of marking and sampling ratios guarantees the accuracy of the adult population parameters such as $\hat{N}_i$ and those mentioned later.
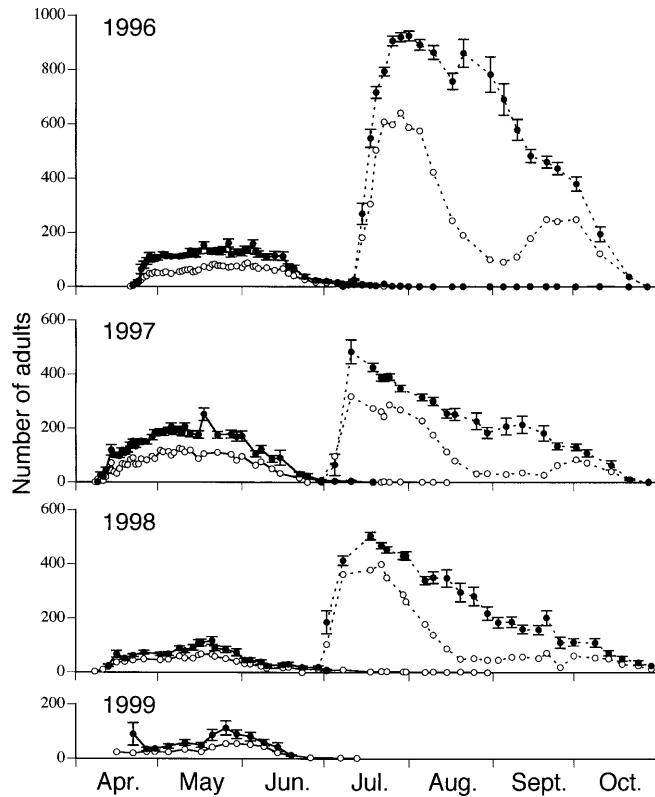
Fig. 1. Seasonal change in the number of adult *Epilachna niponica*. *Vertical bars*, standard error; ●, number of adults estimated by the Jolly–Seber method; ○, number of adults observed; *solid and dotted lines*, overwintered and new adults, respectively. In 1999, only overwintered adults were censused

Adult aestivation

Figure 3 shows the seasonal change in the number of marked adults emerging in July and early August, which were grouped by emergence date. The number of adults recaptured in each group decreased temporarily in late August–early September due to aestivation. The proportion of aestivating females was higher than that of males.

Sex ratio of adults

The percentage of females in n_G was 60.3%–70.6% for overwintered adults and 54.5%–66.2% for new adults (Table 2). Female proportion in overwintered adults was significantly higher than that of new adults at emergence the previous year (*G* test, $P < 0.02$ for every year except 1996 and 1998), implying that adult mortality from emergence to the reproductive season occurred more in males than in females. The sex ratios derived by N_G were 58.2%–66.9% and 55.0%–63.0% for overwintered and new adults, respectively, although there was no significant difference in after and before the hibernation (*G* test, $P = 0.12$–0.41) (Table 2). Based on the assumption that aestivation was terminated before late September, the sex ratio of new adult after aestivation was derived by the total number of marked beetles that were recaptured from late September to hibernation. The ratio slightly increased after aestivation, i.e., from 54.5% (at emergence; Table 2) to 60.8% in 1996, from 66.2% to 74.5% in 1997, and from 57.1% to 63.8% in 1998. The sex ratio increased from autumn to the following spring again in 1997–1998 (74.5%–78.9%) and 1998–1999 (63.8%–76.3%) but it did not increase in 1996–1997 (60.8%–54.9%).
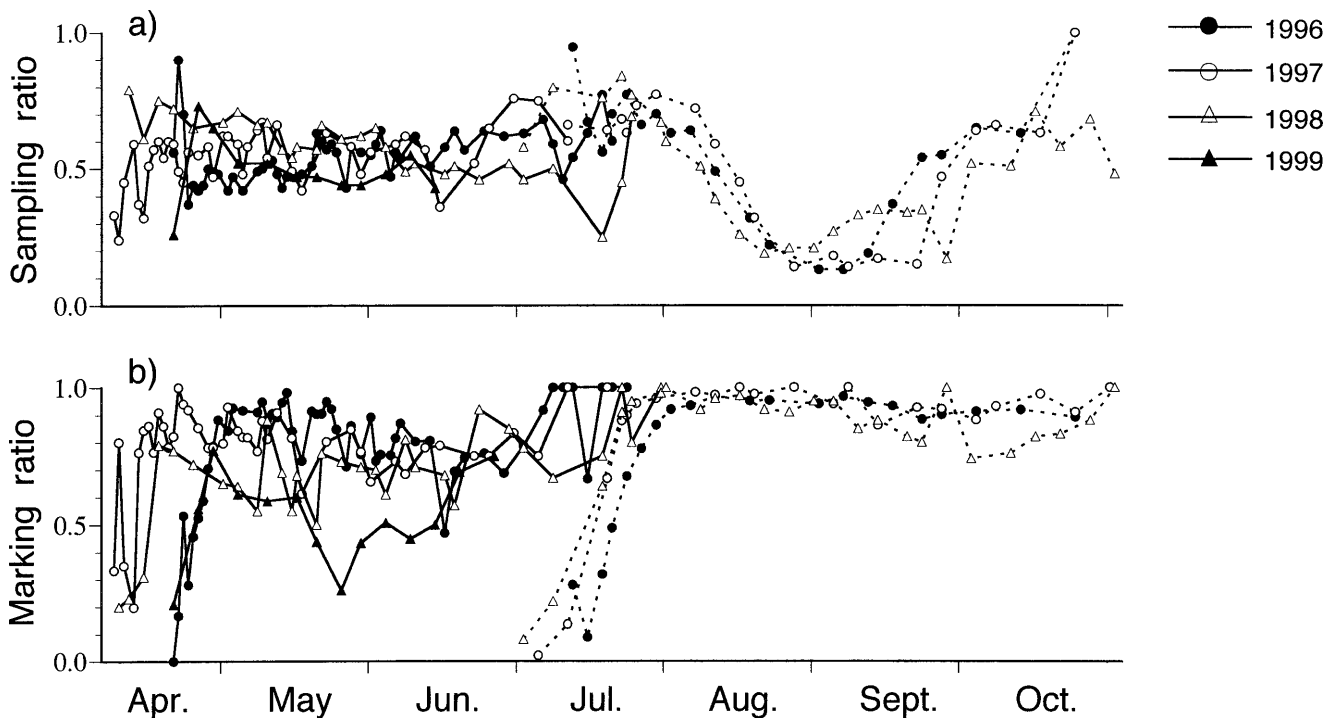

Fig. 2. **a** Seasonal change in sampling ratio, and **b** seasonal change in marking ratio of adult *E. niponica*. *Solid and broken lines*, overwintered and new adults, respectively (see text for explanation of the ratios)
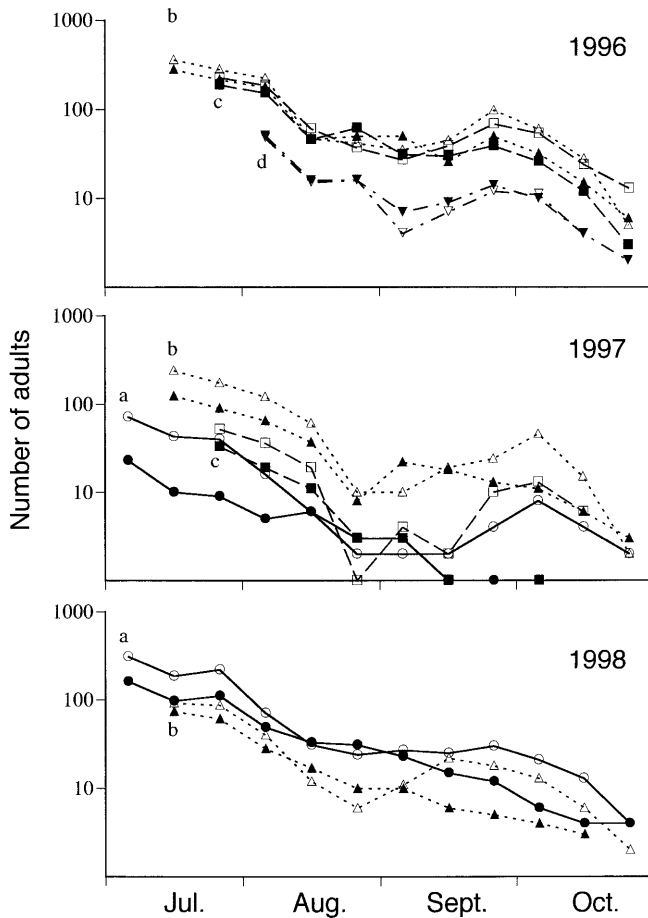
Fig. 3. Seasonal change in the number of marked adult *E. niponica* that emerged in July and early August and were recaptured in the following census. The adults were grouped according to emergence date: (*a*) 1–10 July, (*b*) 11–20 July, (*c*) 21–31 July, and (*d*) 1–10 August; the number of recaptures was totaled for each 10-day interval. *Open and closed symbols*, females and males, respectively

Figure 4 shows seasonal change in the proportion of females observed (n_i) and estimated ($\hat{N}_i$). Female ratios in both overwintered and new adults were around 0.6–0.8 throughout the seasons. The ratio obtained from n_i temporarily dropped from late August to September due to the higher proportion of aestivating female individuals (see Fig. 3).

Daily rate of adult residence, $\hat{\phi}_d$

Figure 5 shows the seasonal change in the survival rate converted every 10 days. In overwintered adults, the rate increased for the first 10 days, then gradually declined during the reproductive period (from May to mid-June). In 1998, when the reproductive season was earlier (late April) than the other 2 years, the decline in adult survival was also earlier, then slightly increased again in late May. There were no marked differences in the seasonal pattern between the sexes. In new adults, the rate was constantly high (about 0.8) until late September, then declined as individuals entered hibernation. As a result of aestivation, the survival rates from mid-August to early September were higher in
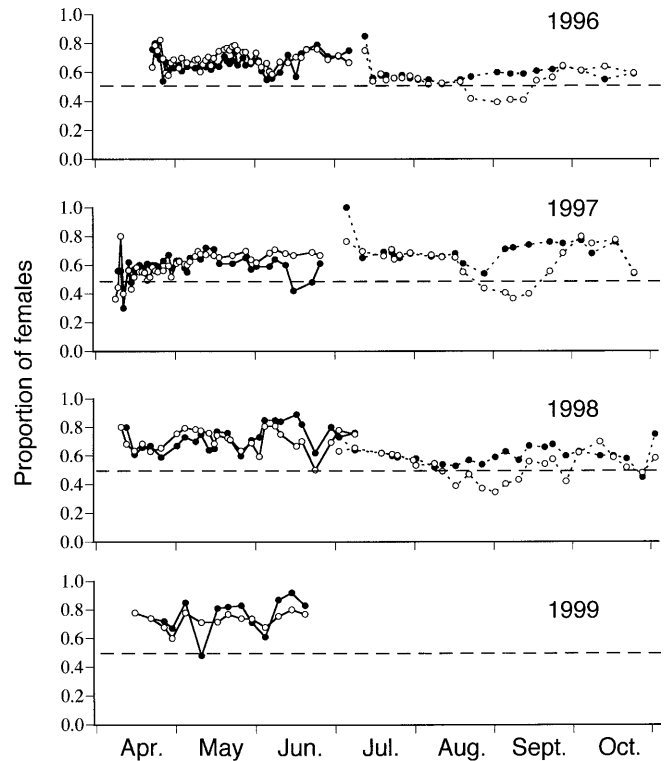

Fig. 4. Seasonal change in the proportion of females in adult *E. niponica* population. *Solid and dotted lines*, overwintered and new adults, respectively; *open and closed circles*, proportion of females observed and estimated by the Jolly–Seber method, respectively
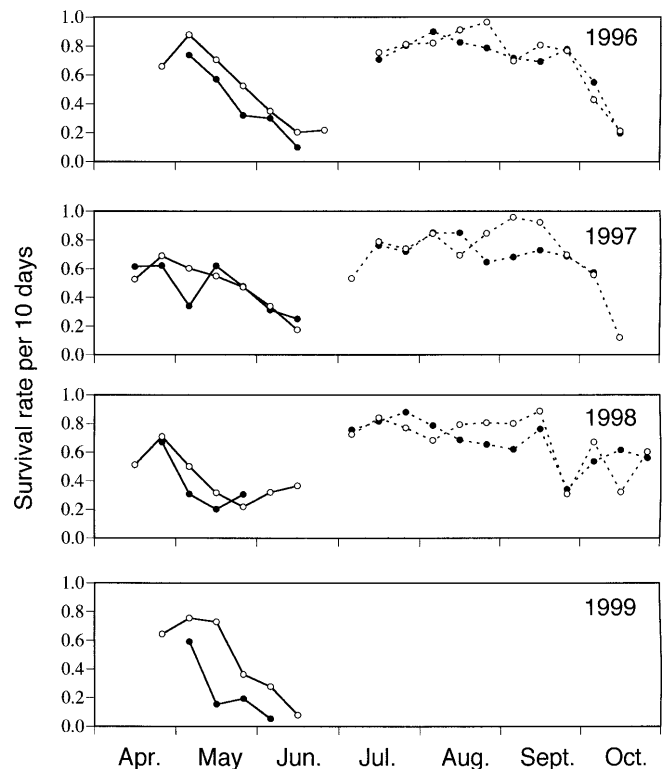

Fig. 5. Seasonal change in the survival rate per 10 days of adult *E. niponica*. *Solid and dotted lines*, overwintered and new adults, respectively: *open and closed circles*, females and males, respectively

Table 2. Total number of marked (n_G) and estimated (N_G) beetles, population density, proportion of females (%F), and reproductive rate (R) during the study period

	1995					1996				
	Male	Female	Unknown	Total	(%F)	Male	Female	Unknown	Total	(%F)
Overwintered adult										
n_G	124	213	13	350	(63.2)	169	281	52	502	(62.4)
N_G						252.1	350.9	–	603.0	(58.2)
Density[a]									1.78	
New adult										
n_G	94	161	30	285	(63.1)	590	707	15	1312	(54.5)
N_G						683.1	835.8	–	1518.9	(55.0)
Density[a]									4.49	
$R (n_G)$[b]									2.6	
$R (N_G)$[b]									2.5	

[a] N_G per shoot for both sexes combined
[b] Both sexes combined

Table 3. Annual changes in estimates of mean survival rate per day ($\hat{\phi}_m$), mean length of residence time (L), and the minimum length of residence (MLR) during the study period

	1996		1997		1998		1999	
	Male	Female	Male	Female	Male	Female	Male	Female
Overwintered adult								
$\hat{\phi}_m$	0.906	0.930	0.924	0.934	0.913	0.920	0.848	0.916
L	10.7	14.3	13.2	15.2	11.5	12.5	6.6	11.9
MLR[a]	12.1 ± 19.4	13.6 ± 18.7	11.5 ± 15.3	13.3 ± 19.4	9.8 ± 18.6	9.4 ± 14.4	3.5 ± 6.8	7.6 ± 13.7
New adult								
$\hat{\phi}_m$	0.973	0.976	0.966	0.972	0.970	0.970	–	–
L	36.9	40.9	29.4	35.1	33.2	33.8	–	–
MLR[a]	28.8 ± 26.2	33.0 ± 30.0	26.8 ± 27.8	30.8 ± 31.8	25.8 ± 25.0	29.0 ± 29.3	–	–

[a] Mean ± SD

females than in males. $\hat{\phi}_m$, the mean value of $\hat{\phi}_d$, was consistently very high (>0.9) throughout the census years (Table 3). There was little difference in $\hat{\phi}_m$ between the sexes or among the years (Table 3).

Length of adult residence time

The average minimum length of residence (MLR) value of overwintered adults was 9.8–12.1 and 9.4–13.6 for males and females, respectively (Table 3). For new adults, it was 25.8–28.8 and 29.0–33.0, respectively, showing a longer period for females than for males, but differences were not statistically significant (Mann–Whitney U test, $P > 0.05$ for all years and generations). MLR for both overwintered and new adults decreased during the study period (Kruskal–Wallis test, overwintered adults: $H = 80.74$, $P < 0.001$; new adults: $H = 6.52$, $P = 0.038$). The mean duration of residence (L) derived from the Jolly–Seber method was 1–8 days longer than MLR (Table 3).

Total number of adult residents, N_G, and adult density per thistle shoot

N_G for overwintered adults (male and female combined) ranged from 392.2 (1999) to 767.3 (1997), whereas that for new adults ranged from 782.9 (1997) to 1518.9 (1996) (see

Table 2). Population density per shoot for overwintered adults ranged from 1.69 (1998) to 2.61 (1997), and that for new adults ranged from 2.66 (1997) to 4.49 (1996).

Survival rate of new adults to the reproductive season, S_w

S_{w1} for both sexes combined was 0.103 (1996–1997), 0.064 (1997–1998), and 0.043 (1998–1999) (Table 4). S_{w2}, derived by n_G, was 0.470 (1996–1997), 0.549 (1997–1998), and 0.346 (1998–1999). S_{w3}, inferred by N_G, was 0.505 (1996–1997), 0.534 (1997–1998), and 0.431 (1998–1999). Female S_w, on the whole, was higher than the male value. Both S_{w2} and S_{w3} showed much higher value than S_{w1}. S_{w1} is a minimum estimate because of (1) loss of marks and (2) emigration of marked individuals from the study site (Fig. 6). The figure shows the seasonal change in the accumulated number of overwintered adults with a mark applied in the previous year and those without a mark that were captured for the first time each 10-day interval. The former (a total of 133 and 38 beetles in 1997 and 1998, respectively, as shown in Table 2) appeared in April and early May with a peak in mid-April, while the latter (a total of 484 and 216 in 1997 and 1998, respectively; see Table 2) appeared from April to June with a peak in May. Most of the latter were assumed to be immigrants from outside the study site because dispersal activity of the newly emerged beetles was very low (S. Koji,

1997					1998					1999				
Male	Female	Unknown	Total	(%F)	Male	Female	Unknown	Total	(%F)	Male	Female	Unknown	Total	(%F)
238	361	18	617	(60.3)	96	230	7	326	(70.6)	75	171	3	249	(69.5)
331.3	436.0	–	767.3	(56.8)	138.4	279.9	–	418.3	(66.9)	135.3	256.9	–	392.25	(65.5)
			2.61					1.69					2.33	
200	392	2	594	(66.2)	299	415	5	719	(57.7)					
289.8	493.1	–	782.9	(63.0)	354.9	555.0	–	909.9	(61.0)					
			2.66					3.68						
			1.0					2.2						
			1.0					2.2						

Table 4. Survival rate of adult *Epilachna niponica* from emergence to following spring (S_w)[a]

	1995–1996			1996–1997			1997–1998			1998–1999		
	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total
S_{w1}	0.138	0.174	0.182	0.102	0.103	0.103	0.040	0.077	0.064	0.024	0.058	0.043[c]
S_{w2}	–[b]	–[b]	–[b]	0.403	0.511	0.470[c]	0.480	0.587	0.549[c]	0.251	0.412	0.346[c]
S_{w3}	–[b]	–[b]	–[b]	0.485	0.522	0.505	0.478	0.568	0.534[c]	0.381	0.463	0.431[c]

[a] The portion of adults that overwintered more than twice is mentioned in the text
[b] Not estimated because n_G and N_G in 1995 (preliminary census) were too small
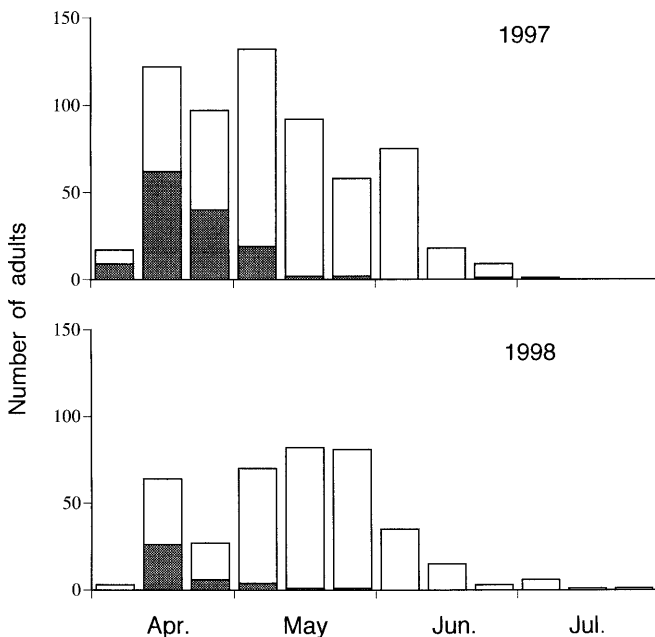[c] Significantly different between the sexes (G test, $P < 0.05$)

Fig. 6. Seasonal change in the total number of overwintered adult *E. niponica* that were caught for the first time in each 10-day period. *Hatched columns*, adults marked in the previous season; *open columns*, unmarked adults

unpublished data) and marking ratio was very high in the previous autumn (>0.9; Fig. 2b).

A small portion of adults overwintered more than once, which was confirmed by mark-recapture data, which for adults of each generation were 733, 1796, and 941 individuals for 1995, 1996, and 1997, respectively. These values are consistent with the number of new adults marked in year i and that of no-mark overwintered adults in year $i + 1$: 0.1% (1995–1997, 1 individual), 0.2% (1996–1998, 3 individuals), and 0.1% (1997–1999, 1 individual) of those overwintered twice. The figure, however, was undoubtedly underestimated because of mark loss and emigration.

Reproductive rate per generation, R, and stability of population size

R derived from n_G was 2.6 (1996), 1.0 (1997), and 2.2 (1998) (see Table 2). The estimates from N_G were 2.5 (1996), 1.0 (1997), and 2.2 (1998), showing a similar tendency. Population variability was 0.103 and 0.115 for overwintered and new adults, respectively.

Discussion

Characteristics of the Yuwaku population

The total number of CM shoots decreased each year during the study period (1996–1999) (see Table 1). This decrease was caused by the following two factors. (1) Flooding: CM grew mainly on the sand deposits, and flooding due to heavy rain washed away some of these plants growing along the watercourse. (2) Succession: a check dam was constructed

Table 5. Comparison of demographic traits among *E. niponica* populations with different habitat conditions in Japan

	Population (census period)				
	This study (1996–1999)	Asiu[a] (1974–1976)	Kutsuki site F[b] (1976–1980)	Kutsuki site A[b] (1976–1980)	Kyoto[c] (1975–1981)
Elevation, m	200	700	350	220	60
Mean annual temperature, °C	13.1	11.3			15.8
Habitat	Temperate secondary forest	Cool temperate climax forest	Temperate secondary forest	Temperate secondary forest	Botanical garden
Variability in the amount of food plants (fold)	2.0[d]	≈1.0	2.3	3.6	2.4
Longevity of female (L)					
Overwintered adult	13.5 ± 1.2	38.9 ± 5.0	21.5 ± 1.7	19.5 ± 2.9	25.7 ± 4.1
Newly emerged adult	36.6 ± 2.3	24.6 ± 0.7	41.8 ± 4.4	42.0 ± 5.3	74.7 ± 5.3
Density per shoot					
Overwintered adult	2.1 ± 0.2	0.7 ± 0.1	1.6 ± 0.4	1.1 ± 0.3	0.4 ± 0.1
Newly emerged adult	3.6 ± 0.5	1.0 ± 0.2	1.3 ± 0.3	5.9 ± 1.0	3.2 ± 0.4
Reproductive rate, R[e]	1.0–2.5	0.9–3.3	0.1–1.6	2.2–13.1	4.8–16.8
Survival rate of new adult, S_{w3} (S_{w1}), %[f]	43.1–53.4 (4.3–10.3)	66.3–82.0 (37.0–52.4)	108.6–166.3 (9.9–49.0)	12.0–38.5 (8.7–23.4)	6.1–36.4 (2.9–31.7)
Proportion of adults that overwintered twice, %	0.1–0.2	0.5–1.6	1.0–4.3	0	0
Population variability[g]					
Overwintered adult	0.103	0.143	0.271	0.290	0.304
New adult	0.115	0.169	0.300	0.170	0.170
Aestivation of new adult	Yes	No	Yes	Yes	Yes

[a] Nakamura and Ohgushi (1979, 1981)
[b] Ohgushi and Sawada (1981); Ohgushi (1986)
[c] Sawada (1984); Sawada and Ohgushi (1994)
[d] For *C. matsumurae* alone
[e] Derived from N_G
[f] For explanations of S_{w1} and S_{w3}, see text
[g] Standard deviation of log-transformed densities

in 1964 and sand deposits were formed in the late 1970s. CM, a colonizing species, was dominant on the sand deposits during the 1980's, but thereafter it decreased as the vegetation progressed. During the study period, CM was further replaced by grasses and the herbs *Miscanthus sinensis* Anderss., *Artemisia montana* (Nakai) Pamp. and by trees such as alders and willows. The population size of EN also exhibited a decreasing trend for both overwintered and new adults, reflecting the decreasing trend of the food resource (Table 2). During the study period, the EN population remained at a high level where food depletion occurred and showed high stability (Table 5). The decreasing trend in both host plant and EN population accelerated after this study. In fact, the population size of new EN adults in autumn of 1999 was by far the smallest ever. In 2000 and 2001, the host plant abundance continued to decrease, but there were still plenty of thistle leaves for the beetles in the site. However, EN population size in the study site decreased to an extremely low level (Koji, personal observation). The reason for the sudden crash of the EN population is unknown.

Comparison of demographic traits of Yuwaku population with other populations

Table 5 summarizes the demographic traits of Yuwaku and the other four populations studied by similar methods and having similar intensities. Asiu and Kutsuki F populations remained at a rather low density with a low reproductive rate, R, while Kutsuki A and Kyoto populations reached a high density where food depletion occurred with a high R value. The adult demographic traits of the Yuwaku population are compared with other populations next.

Life history

The Yuwaku population showed a fixed univoltine life cycle: overwintered adults were found in April–June and produced new adults in July–October. The number of new adults on the thistles decreased due to aestivation in late August to early September and recovered in mid-September. Aestivation was also found in other high-density populations located at low elevations where summer is very hot (Kutsuki A, Kyoto).

Sex ratio

The sex ratio of overwintered adults was higher than that of new adults at emergence the previous year (Table 2), as a result of higher S_w in females than in males (see Table 4). Such male-biased mortality was also suggested in Kutsuki (Ohgushi 1986) and Kyoto (Sawada and Ohgushi 1994) but not in Asiu (Ohgushi and Sawada 1995).

In Yuwaku, females had a higher aestivation rate than males (see Fig. 3). Differential survival between the sexes

may be related with the differential aestivation rates, if the adults entering aestivation during the hot summer had a better survival than those without aestivation. In other high-density populations, sex ratio in overwintered adults was also biased toward the female as in Yuwaku, but sexual difference in the aestivation rate was not found (Ohgushi 1986; Ohgushi and Sawada 1995).

Adult longevity

The mean L value of overwintered females in Yuwaku was shortest, 13.5 days, while the longest was the Asiu population, 38.5 days. That of the two lowland populations was 19.5 (Kutsuki A) and 25.7 (Kyoto) days, respectively. The short life span of overwintered adults and early reproduction in Kutsuki A and Kyoto populations were molded by natural selection through arthropod predation and heat stress in summer (Ohgushi 1991, 1998; Ohgushi and Sawada 1997). For new adults, the Asiu population, where new adults emerged last and entered hibernation earliest due to cooler temperature conditions, had the shortest L value, 24.6 days. Yuwaku was shortest (36.6 days) among the remaining populations.

Survival rate of new adults to the reproductive seasons

S_{w3} was more than 60% in the low-density populations, Asiu and Kutsuki F. S_{w3} in Kutsuki F was unnatural (>100%), probably due to a different rate of immigration or emigration of beetles in the study site. Among food plant-depleting populations, S_{w3} was low in Kyoto and Kutsuki A (6.1%–36.4% and 12.0%–38.5%, respectively) while in Yuwaku it was high (43.1%–53.4%). Although S_{w1} varied greatly among years in all populations, three high-density populations showed, on the whole, lower values of S_{w1} than those in Asiu and Kutsuki F. The proportion of adults that overwintered twice was high in Asiu and Kutsuki F, but low in Yuwaku, Kyoto, and Kutsuki A, the high-density populations.

Population density, reproductive rate per generation, R, and population variability

In the low-density populations, Asiu and Kutsuki F, average density of new adults per shoot of thistle was low (1.0 and 1.3, respectively) because of low overwintered adult density (0.7 and 1.6, respectively) and low R (0.9–3.3 and 0.1–1.6, respectively). The low R value was caused by large immature mortality by arthropod predation, especially by the earwig *Anechura harmandi* (Burr) (Nakamura and Ohgushi 1979; Ohgushi 1986; Ohgushi and Sawada 1985b). Survival rate of new adults to the next spring, S_w, was constantly high (S_{w3}, 66.3–82.0 and 108.6–166.3, respectively), but over-wintered adult density was low due to the low new adult density, as already mentioned.

In Yuwaku, new adult density was high (3.6), as in Kutsuki A (5.9) and Kyoto (3.2), as a result of high immature survival rate probably due to low predation pressure (Ohgushi 1986; Ohgushi and Sawada 1998; Koji, unpub-lished). However, the Yuwaku population was different from Kutsuki A and Kyoto populations in two aspects: first, overwintered adult density was highest (2.1) due to high S_w (43.1–53.4), and R was relatively low (1.0–2.5). Although overwintered adult density in Kutsuki A and Kyoto was low (1.1 and 0.4, respectively) due to low S_w (12.0–38.5 and 6.1–36.4, respectively), R was high (2.2–13.1 and 4.8–16.8, respectively). Second, In Yuwaku, the variability of annual population density was low for both overwintered (0.103) and new (0.115) adults because R and S_w were stable (2.5- and 1.2-fold variation, respectively), whereas in Kutsuki A and Kyoto, it was much higher for both overwin-tered (0.290 and 0.304, respectively) and new (0.170 and 0.170, respectively) adults, because R (6.0- and 3.5-fold, respectively) and S_w (3.2- and 6.0-fold, respectively) were much more variable than Yuwaku. It should be noted that the Yuwaku population often reached a food-depleting level but was more stable than Asiu and Kutsuki F, where effective density-dependent regulation mechanisms were found (Nakamura and Ohgushi 1981; Ohgushi and Sawada 1985a). The reproductive and mortality processes produc-ing a high stability in the Yuwaku population will be ana-lyzed in the next article.

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