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Seasonal Fluctuation, Age Structure, and Annual Changes in a Population of *Cassida rubiginosa* (Coleoptera: Chrysomelidae) in a Natural Habitat

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ABSTRACT *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae) has attracted considerable interest as a potential biological control agent against thistle (Asteraceae: Cardueae) weeds, but population characteristics of this species are not well understood. We conducted an intensive mark–recapture study from 1996 to 1999 in Yuwaku, Kanazawa, Japan, to estimate adult population parameters such as population size, longevity, movement activity, reproductive rate, and winter survival. Overwintered adults began to emerge from hibernation in early April and actively moved among host plants until early May. Thereafter, adult dispersal activity decreased until late June, and the number of beetles gradually declined. New adults were active for only 2 to 3 wk after emergence and began aestivation at the end of August. Despite low reproductive rates per generation, the overwintering population was stable at a high density. Beetle longevity was substantial, and many individuals overwintered more than once. The age structure of adult beetles was responsible for the high stability of the population and low reproductive rate.

KEY WORDS *Cassida rubiginosa*, demographic traits, mark–recapture, population stability, reproductive rate

Cassida rubiginosa Müller (Coleoptera: Chrysomelidae) is widely distributed in the Palearctic Region of Europe and Asia (Zwölfer and Eichhorn 1966) and North America (Barber 1916). This species is suitable for the study of population dynamics because 1) large and sluggish adult beetles are easily monitored by the mark–recapture study; 2) adults, eggs, larvae, and pupae occur exclusively on leaves of host plants, ensuring construction of life tables; and 3) the host plant, thistle (Asteraceae: Cardueae), grows in patches and its abundance and spatial distribution are easy to evaluate. This species has attracted considerable interest as a potential biological control agent against notorious weeds such as creeping thistle, *Cirsium arvense* (L.) Scop, and musk thistle *Carduus thoermeri* Weinmann, in cereals and pastures (Palij and Kelpikova 1957; Harris and Zwölfer 1971; Ward and Pienkowski 1978; Ang and Kok 1995; Spring and Kok 1997, 1999; Bacher and Schwab 2000; Kok 2001), but quantitative population studies on the species are rather limited, especially in the natural habitat (Kosior 1975).

In Japan, where there are nine Cardueae genera, the genus *Cirsium* has a unique and diverse flora (Kitamura 1937, Kadota 1995). Most of the 64 species of *Cirsium* in Japan are endemic and grow in natural environments such as open grassland, forest margin, and streamside (Kadota 1995). As in Europe and North America, numerous insect herbivores feed on *Cirsium* in Japan (Zwölfer 1973, Kaihara et al. 1997). One of the unique attributes of the Japanese thistle-herbivore fauna is the predominance of indigenous ladybird beetles of genus *Epilachna* (Coccinellidae: Epilachninae). Since mid-1970s, many field studies have been conducted on the population dynamics of *Epilachna niponica* Lewis, revealing characteristics of population fluctuation and regulating mechanisms (Nakamura and Ohgushi 1979; Ohgushi and Sawada 1985, 1998; Shirai 1987; Koji and Nakamura 2002). However, *C. rubiginosa*, another dominant herbivore on Japanese thistles, has been ignored.

From 1996 to 1999, we studied populations of *C. rubiginosa* as well as *E. niponica* feeding on two wild thistles, *Cirsium matsumurae* Nakai and *Cirsium kagamontanum* Nakai in Yuwaku, on the outskirts of Kazawaza, Japan. These beetle populations are interesting from two standpoints. First, populations reach such a high density that host plants are often defoliated. Second, there is a rich insect fauna on thistles, especially on *C. matsumurae*: in total, 64 species,

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mostly leaf-eating species, were recorded on the leaf and stems of *C. matsumurae* (Kaihara et al. 1997). Among the leaf-chewing guild of thistles, *C. rubiginosa* and *E. niponica* were predominant, and two chrysomelids, *Altica cirsiicola* Ohno and *Lema cirsiicola* Chujo, were also common. Examining the difference in population dynamics and resource utilization patterns among these herbivore species provides a good arena for studying interspecific interactions in a phytophagous insect community. As an initial step toward clarifying the population dynamics of *C. rubiginosa*, we describe the adult population parameters of *C. rubiginosa* obtained by mark-recapture studies, such as seasonal changes in number, sex ratio, and movement activity as well as annual population changes, longevity, age structure, and reproductive rate.

Materials and Methods

Study Site. Yuwaku is located at an elevation of 220 m above sea level. Mean annual temperature is 13.1°C and annual rainfall is 2,500 mm. A study plot (30 by 50 m) was established in a valley of Yunokawa stream, both sides of which were steep slopes covered with deciduous-leaved secondary forests with *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 to 2 m of snow from late December to early April.

Host Plant. Two perennial thistle species, *C. matsumurae* and *C. kagamontanum*, grow on the bank of the stream and on sandy deposits accumulated behind check dams for erosion control. *C. rubiginosa* occurs mainly on *C. matsumurae*, and occasionally on *C. kagamontanum*. These two species show a largely similar pattern in phenology of shoot growth. The new rosettes sprouted in early April. They began shoot growth in mid-April, increasing rapidly in size, and reached full height (i.e., 100–150 cm and 55–116 cm for *C. matsumurae* and *C. kagamontanum*, respectively) in mid-July. Thereafter, flower stalks were extended until September and flowered over 3 mo. The host plant abundance in the study site decreased each year from 338 shoots (in 1996) to 168 shoots (in 1999) for *C. matsumurae*, but it was not significantly different in *C. kagamontanum*, varying from 165 shoots (in 1999) to 194 shoots (in 1998). Annual changes in population size of the thistle plants are given in Koji and Nakamura (2002).

Insect. *C. rubiginosa* is univoltine (Palij and Klepikova 1957, Kosior 1975, Ward and Pienkowski 1978, Spring and Kok 1999). Adults hibernate and first occur on host plants in early spring. Females laid eggs in small clusters that are surrounded by and glued with a brown lamellar secretion (oöthecae) on the under-surface of thistle leaves. Larvae passed through five instars and pupated on the plant. As with most species of Cassidinae, all instars carry abdominal shields made of exuviae and fecal material, which are thought to protect the larvae mechanically against enemies (Eisner et al. 1967, Olmstead 1996, Müller 2002). New

adults emerge in summer and enter hibernation by late autumn in leaf litter on the forest floor.

Census Methods. Mark-recapture censuses of beetles were conducted 25 times from April to September in 1995. From 1996 to 1998, censuses were performed at 1–3-d intervals from April to August and at intervals of 5 d thereafter (in total 70, 64, and 52 times for 1996–1998, respectively). In 1999, we censused overwintered adults at 5-d intervals from April to July (17 times). 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 by using lacquer paint. Capture date, place, generation, sex, body size, and reproductive maturation level of females were recorded before release to the plant on which they were captured. On subsequent censuses, marked adults were recaptured, but individuals copulating or ovipositing were checked visually without recapturing. Newly emerged adults can be distinguished from overwintered adults by their soft and pale green body surfaces. By viewing the abdomen, reproductive maturation status of females was estimated and categorized into two levels (0, nongravid; 1, gravid) in 1996 or three levels (0, nongravid; 1, weakly gravid; 2, heavily gravid) in 1997–1999.

Estimation of Population Parameters. For each census, the population size (\hat{N}_i) and survival rate ($\hat{\phi}_i$) were estimated using the basic Jolly-Seber model for open populations (Jolly 1965, Seber 1973). Because the values calculated using Jolly-Seber method are estimates, it is possible for them to fall outside realistic ranges ($\hat{\phi}_i > 1.0$ or $B_i < 0$). In such cases, values of 1.0 and 0 were taken as the best biologically realistic estimates (Sutherland 1996). Based on $\hat{\phi}_m$, the mean value of $\hat{\phi}_i$, mean length of residence time (L) was derived by $L = 1 / (1 - \hat{\phi}_m)$. The minimum estimate of residence time (MLR) also was 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. Adult dispersal was estimated from the mean distance traversed per day. Distance moved was compared between sexes by Wilcoxon rank sum test (Sokal and Rohlf 1994). The total population size (N_C) was computed using the sum of estimated recruitments to the population (ΣB_i). Using these estimates, population density per *C. matsumurae* shoot, sex ratio, reproductive rate per generation (R), and population variability also were obtained. In this article, R is defined as the number of new adults produced per overwintered adult. R and sex ratio were obtained from two values, N_C and total number of marked beetles (n_C). Sex ratio before and after winter was compared by a G-test (Sokal and Rohlf 1994). Population variability was represented by the standard deviation of log-transformed densities (Gaston and McArdle 1994). Survival rate of new adults to the reproductive season was derived from the ratio of the number of marked individuals to those recaptured in the following reproductive season. All statistical tests

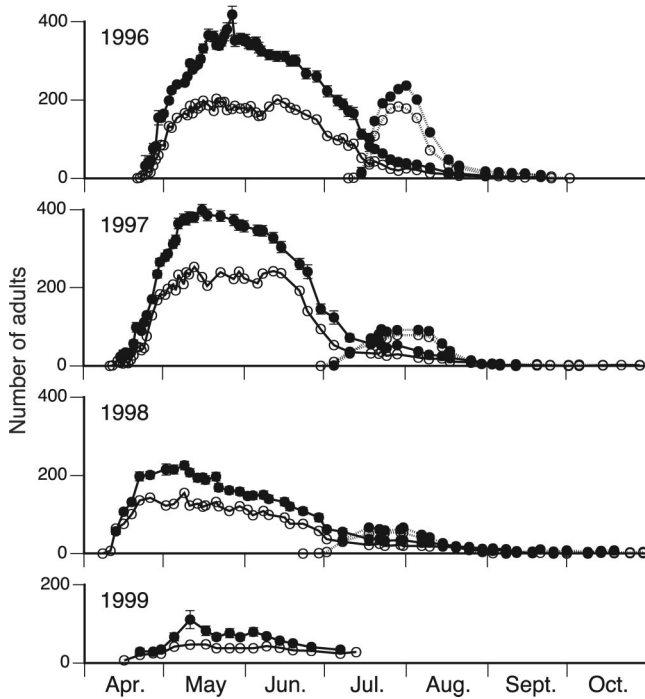


Fig. 1. Seasonal change in the number of adult *C. rubiginosa*. Vertical bars show standard error. ●, number of adults estimated by the Jolly-Seber method; ○, number of adults observed. Solid and dotted lines show overwintered and new adults, respectively. In 1999, only overwintered adults were censused.

were carried out using JMP version 5.1.1 for Mac (SAS Institute 2004).

Results

Seasonal Change in Adult Number. Fig. 1 indicates the seasonal change in the number of overwintered

and new adults in each year. Overwintered adults emerged from hibernation from mid- (1997–1999) to late (1996) April. The number increased until early May and was relatively constant for nearly 1.5–2 mo (early May–mid-June) and then decreased consistently until late August. New adults began to emerge

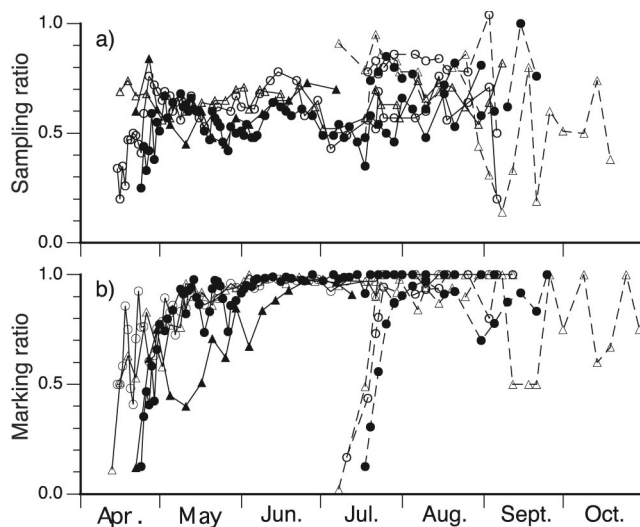


Fig. 2. Seasonal change in (a) sampling ratio and (b) marking ratio of adult *C. rubiginosa* in 1996 (●), 1997 (○), 1998 (△), and 1999 (▲). Solid and broken lines show overwintered and new adults, respectively. See text for explanation of the ratios.

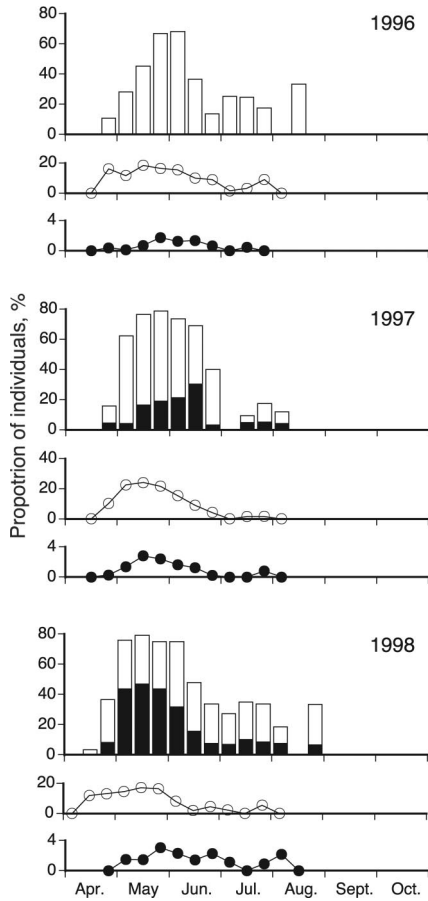


Fig. 3. Seasonal change in the reproductive activity in overwintered females of *C. rubiginosa*. Bar chart shows the proportion of gravid individuals. Open and filled columns show level 1 (light) and 2 (heavy) in gravid level, respectively. In 1996, gravid level 2 was not distinguished. Line graph shows the proportion of reproductive females that were mating (○) or ovipositing (●) when they were observed.

from early (1997 and 1998) to mid-July (1996). Their number increased and peaked in early August and then quickly decreased and disappeared toward the end of August.

Sampling and Marking Ratios of Adults. Sampling ratio, i.e., the observed number of adults divided by the estimated number of the Jolly-Seber method (\hat{N}_t), was constant throughout the seasons at around 0.6 and 0.8 for overwintered and new adults, respectively (Fig. 2a). For new adults, the ratio was constant from July to August at around 0.8 and then markedly fluctuated from September to October, as the population decreased in number. Marking ratio, derived by the Jolly and Seber method as the proportion of marked individuals to \hat{N}_t , rapidly increased to >90% as the census progressed (Fig. 2b). High values in marking and sampling ratios guarantee the accuracy of adult population parameters such as \hat{N}_t and those mentioned below.

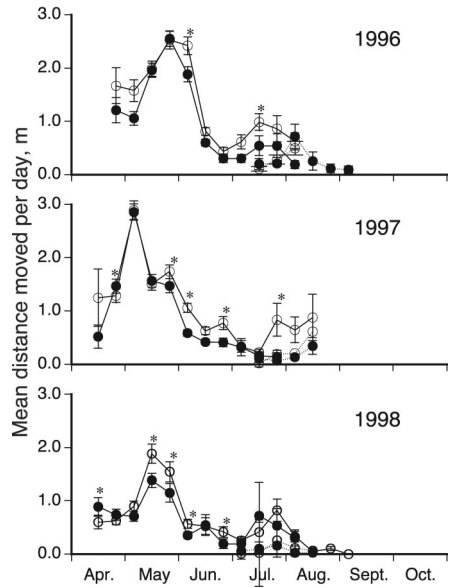


Fig. 4. Seasonal change in the mean distance moved per day by adult *C. rubiginosa*. The mean and standard error for each 10-d period was presented. Solid and broken lines show overwintered and new adults, respectively. For periods with an asterisk, a significant difference was detected between male (●) and female (○) (Wilcoxon rank sum test, $P < 0.05$).

Reproductive Season. Fig. 3 represents the seasonal change in the proportion of females that were gravid, copulating, and ovipositing when they were observed. For 1996–1998, copulation was observed 966, 950, and 404 times, respectively. Copulation frequency peaked previous to oviposition periods, from mid-April to mid-May, and consistently decreased until August. Oviposition was observed 65, 83, and 57 times for 1996–1998, respectively. Oviposition occurred from late April to July with a peak from mid-May to mid-June. The proportion of gravid females increased from late April to mid-May and was constant at $\approx 80\%$. The proportion decreased from mid-June to mid-July and then was relatively stable at 20–30% until late August.

Dispersal Activity. Seasonal changes in adult dispersal activity in study site, as expressed by the mean distance traversed per day were calculated for each 10 d period (Fig. 4). The mobility of overwintered adults increased gradually from the beginning of the season, reaching a peak from early to late May. The movement activity decreased to a low level as the season advanced, thereafter slightly increasing again in mid- to late July. Distance moved was greater in females than in males. The dispersal activity of new adults was low at around 0–0.5 m per day.

Figure 5 shows the seasonal change in the accumulated number of overwintered adults that were captured for the first time in each 10-d interval. Beetles with a mark applied in the previous years (143, 121, and 46 beetles in total from 1997 to 1999, respectively)

Table 1. Total number of marked (n_C) and estimated (N_C) beetles, proportion of females (%F) and population density during the study period

	n_C				%F	N_C				Density ^a
	Male	Female	Unknown	Total		Male	Female	Unknown	Total	
Overwintered adult										
1995	221	283	5	509	56.2					
1996	316	359	0	675	53.2	346.6	412.6	0	759.2	54.3
1997	384	365	5	754	48.7	444.9	394.0	0	838.9	47.0
1998	189	256	0	445	57.2	220.8	290.5	0	511.3	56.8
1999	77	106	0	183	57.1	102.0	134.1	0	236.1	56.8
New adult										
1995	9	35	1	45	79.5					
1996	119	175	0	294	59.5	126.2	189.5	0	315.7	60.0
1997	50	85	3	138	63.0	54.7	94.2	0	145.9	62.8
1998	35	65	0	100	65.2	34.3	85.8	0	120.1	71.4

^a N_C per shoot for both sexes combined.

occurred in mid-April to late May, whereas those without a mark (611, 386, and 171 in total from 1997 to 1999, respectively) occurred from April to June. Most of the latter were assumed to be immigrants from outside the study site, because dispersal activity of the newly emerged beetles was low (Fig. 4) and marking ratio was high the previous autumn (>80%; Fig. 2b). Later in the season (mid May-late June), whereas the number of overwintered beetles was relatively constant at ≈200 (1996-1997) or ≈150 (1998) (Fig. 1), those of nonmarked immigrants rapidly decreased (Fig. 5), indicating a lower immigration and/or emigration rate compared with earlier in the season.

Annual Change in Population Size. Total population size of overwintered adults (male and female combined) ranged from 236.1 (1999) to 838.9 (1997), whereas that of new adults ranged from 120.1 (1998) to 315.7 (1996) (Table 1). Population density per

shoot of overwintered adults ranged from 1.41 (1999) to 2.85 (1997) and that of new adults ranged from 0.49 (1998) to 0.93 (1996).

Age Structure. According to marking codes, overwintered adults consist of three generations: beetles overwintered once, twice, and three times. Table 2 shows total number of overwintered adults with different overwintering times. Individuals that overwintered twice or more occupied 67.4, 37.8, 62.0, and 58.7% of the total number of marked beetles for 1996-1999, respectively.

Sex Ratio. The percentage of females in captured individuals (n_C) was 48.7-57.2% for overwintered and 59.5-79.5% for new adults (Table 1). Female proportion in overwintered adults was slightly lower than that of new adults at emergence the previous year (but not statistically significant except 1997: $G = 9.90$, $df = 1$, $P < 0.01$ for 1997; $G = 1.27$, $df = 1$, $P = 0.259$ for 1998; and $G = 1.36$, $df = 1$, $P = 0.245$ for 1999), implying that adult mortality from emergence to the reproductive season occurred more in females than in males. The sex ratios derived by estimated population size (N_C) gave similar tendencies. The values were 47.0-56.8% and 60.0-71.4% for overwintered and new adults, respectively. Female proportion was lower in overwintered adults than in new adults at emergence the previous year ($G = 16.01$, $df = 1$, $P < 0.01$ for 1997; $G = 1.42$, $df = 1$, $P = 0.234$ for 1998; and $G = 7.64$, $df = 1$, $P < 0.01$ for 1999) (Table 1).

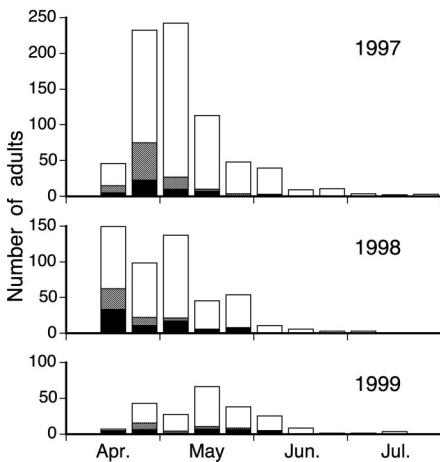


Fig. 5. Seasonal change in the total number of overwintered adult *C. rubiginosa* that were caught for the first time in each 10-d period. Filled column, adults marked in the season before last year; hatched column, adults marked in the previous season; open column, adults without a mark.

Table 2. Age structure of overwintered adult *C. rubiginosa*

Yr	Overwintering time of marked beetle ^a			No mark	Total
	3	2	1		
1995				509	509
1996		97	47	531	675
1997	2	52	89	611	754
1998	4	71	46	386	507
1999	7	20	19	171	217

^a Distinguished by individual codes.

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

	$\hat{\phi}_m$		L		MLR ^a	
	Male	Female	Male	Female	Male	Female
Overwintered						
1996	0.970	0.968	33.1	31.5	30.5 ± 25.6	29.7 ± 27.9
1997	0.965	0.970	28.5	33.0	26.4 ± 27.6	29.5 ± 28.8
1998	0.969	0.970	32.5	33.4	30.2 ± 31.9	31.3 ± 36.5
1999	0.954	0.964	21.6	28.1	16.7 ± 19.8	17.9 ± 21.7
New adult						
1996	0.952	0.942	20.8	17.3	14.5 ± 10.7	12.6 ± 11.0
1997	1.000	0.957		23.1	21.1 ± 10.5	18.0 ± 14.6
1998	1.000	0.955		22.3	18.9 ± 13.1	19.7 ± 19.4

^a Mean ± S.D.

Daily Survival and Length of Residence. The mean survival rate per day, $\hat{\phi}_m$, was consistently high (>0.94) throughout the census years (Table 3). There was little difference in $\hat{\phi}_m$ between the sexes or among the years. The average MLR value of overwintered adults was 16.7–30.5 and 17.9–31.3 for males and females, respectively (Table 3). The maximum of MLR was 138 d (1996), 195 d (1997), and 210 d (1998). For new adults, the maximum MLR was 14.5–21.1 and 12.6–19.7 for males and females, respectively. The mean duration of residence (L) derived from the Jolly–Seber method was 1–10 d longer than MLR (Table 3).

Survival Rate of New Adults to the Reproductive Season. The S_w value for both sexes combined was 0.227 (1995/1996), 0.303 (1996/1997), 0.341 (1997/1998), and 0.165 (1998/1999) (Table 4). Male S_w was, on the whole, higher than the female value. Table 5 summarizes the number of adults that emerged in year 1 and that were recaptured in the reproductive season of years 3 and 4. The proportion of adults overwintered twice was 8.5% (1995/1997), 7.7% (1996/1998), and 3.8% (1997/1999). The numbers, however, are undoubtedly underestimated because of mark loss and emigration.

Reproductive Rate per Generation, R , and Stability of Population Size. R derived from n_C was 0.43 (1996), 0.18 (1997), and 0.22 (1998). The estimates from N_C were 0.42 (1996), 0.17 (1997), and 0.23 (1998). Population variability was 0.073 and 0.161 for overwintered and new adults, respectively.

Table 4. Survival rate of adult *C. rubiginosa* from emergence to following spring (S_w)

	1995–1996	1996–1997	1997–1998	1998–1999
Male	0.667	0.361	0.420	0.200
Female	0.114	0.263	0.294	0.147
Total	0.227*	0.303	0.341	0.165

* Significantly different between the sexes (G -test; $P < 0.05$).

Table 5. Proportion of adult *C. rubiginosa* that overwintered twice and three times determined from mark–recapture data

Yr of emergence	No. emerged in the first year ^a	No. recaptured in the third year (% overwintered twice)	No. recaptured in the fourth year (% overwintered three times)
1995	613	52 (8.5)	4 (0.7)
1996	905	70 (7.7)	7 (0.8)
1997	524	20 (3.8)	

^a Number of individuals emerged in year 1 + no-marked overwintered beetles in year 2.

Discussion

C. rubiginosa is capable of severely damaging thistle leaves, but populations rarely reached sufficient density for effective thistle control under natural conditions (Ward and Pienkowski 1978, Ang and Kok 1995, Bacher and Schwab 2000). Studies of the life history and demographic traits of the species are critical for the development of effective management strategies for thistle control.

Seasonal Changes in Adult Population Parameters. Intensive mark–recapture study revealed the adult population characteristics of the species such as seasonal changes in number, sex ratio, and movement activity. Overwintered adults began to emerge from hibernation in early April and actively moved among thistle plants until early May. During this period, many immigrants were recruited from outside the study site (Fig. 5). Later in the season (mid May–late June), whereas the number of beetles was relatively constant (Fig. 1), adult dispersal activity decreased along with a decrease in reproductive activities (Figs. 3 and 4), resulting in fewer immigrants (Fig. 5).

It should be noted that the movement activity of overwintered adults temporarily increased from July to August. In Poland, *C. rubiginosa* was observed migrating from the meadows in which it fed and reproduced to nearby forests where it spent the winter under leaf litter (Kosior and Klein 1970). Although we did not conduct a census in the forest surrounding the study site, the temporary increase in movement distance of overwintered adult in summer seems to suggest migration to a hibernating location.

New adults occurred for only 2 to 3 wk after emergence (Table 3) and disappeared toward the end of August (Fig. 1). New adults of *C. rubiginosa* occurred until early November in Virginia (Ward and Pienkowski 1978) or until early October in southern Poland (Kosior 1975). Compared with these places, the Yuwaku population has a very hot summer (4 to 5°C higher in monthly average temperature). Low activity and quick disappearance of new adults strongly imply an aestivo-hibernal dormancy in this population.

Annual Population Changes. The population was characterized by high density of overwintered adults and low variability in annual population density for both overwintered (0.073) and new (0.161) adults.

Throughout the study period, the number of *C. matsumurae* shoots decreased because of flooding and the vegetation change in succession (Koji and Nakamura 2002), and the population size of *C. rubiginosa* also exhibited a decreasing trend for both overwintered and new adults. Thus, population density per thistle shoot was very stable, showing an exceptionally high stability for herbivorous insect population (Hanski 1990).

Survival rate of new adults to the reproductive season was higher for males than females (Table 4), resulting in lower female proportion in overwintered adults (Table 1). There were no clear differences between sex in the daily survival and duration of residence for overwintered and new adults (Table 3). Thus, female-biased mortality occurred during hibernating period. The reason of lower winter survival for females is unknown.

Despite a low reproductive rate per generation, the population of overwintered beetle was stable at a high density. Because new adults were sedentary and had high levels of marking and sampling ratios, underestimation of the reproductive rate is unlikely. Apparently, high stability of overwintered adult was because of the longevity of adults. Kosior (1975) reported that the maximum longevity in the Ojców, Poland, was 45 and 24 mo for females and males, respectively. In Yuwaku, a substantial number of individuals overwintered more than twice. The age structure of adult beetles was responsible for the high stability of a population with a low reproductive rate. Further analysis will be necessary to examine the role of reproductive and mortality processes in producing high stability in the population.

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