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**Stage-specific mortality, fecundity, and population changes in *Cassida rubiginosa*
(Coleoptera: Chrysomelidae) on wild thistle**

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Abstract *Cassida rubiginosa* Müller (Coleoptera: Chrysomelidae), one of the most conspicuous defoliators of thistle weeds, is capable of severely damaging thistle leaves; however, populations rarely reach sufficient density for effective thistle control under natural conditions. To investigate the impact of natural mortality factors on *C. rubiginosa* populations, life table studies were conducted between 1996 and 1998 in Kanazawa, Japan. Egg mortality, mortality in early larvae, and lost fertility contributed strongly to total generational mortality in every year studied. Egg mortality was primarily attributable to parasitism by wasps of the genus *Anaphes*, and the impact of predation and egg inviability was small. Mortality factors that affected the larval and pupal stages were largely unknown. Under field conditions, females only realized approximately 8.1–13.7 % of their potential fecundity, varying from 36.0 to 61.4 eggs per individual. Since annual changes in lost fertility exhibited a similar pattern to those in generational mortality, fertility loss might be the key factor driving *C. rubiginosa* populations. These results suggest that reproduction is the most important process that determines the level and fluctuation of the *C. rubiginosa* population.

Keywords life tables • mortality factors • tortoise beetle • survivorship • weed management

Introduction

Cassida rubiginosa Müller (Coleoptera: Chrysomelidae) is widely distributed in the Palearctic region of Europe and Asia (Zwölfer and Eichhorn 1966) and in North America (Barber 1916). 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 nutans* L., in cereals and pastures (Bacher and Schwab 2000; Kok 2001; Ward and Pienkowski 1978a). *Cassida rubiginosa* is capable of severely damaging thistle leaves. However, previous studies have shown that the populations rarely reached sufficient density for effective thistle control in Europe and North America (Ang and Kok 1995; Bacher and Schwab 2000; Ward and Pienkowski 1978b). Understanding the demographic traits of the species, such as mortality and fecundity, is therefore critical for the augmentation of naturally occurring *C. rubiginosa* populations to higher densities (Bacher and Schwab 2000).

Various abiotic and biotic factors affect fecundity and mortality in the different developmental stages of *C. rubiginosa*. Abiotic factors such as extreme temperature, rainfall, and severe wind have been reported to be associated with declines in fecundity (Kosior 1975) and increases in the mortality of eggs, early larvae, and overwintering adults (Kosior 1975; Spring and Kok 1999). Biotic factors such as parasitism (Ang and Kok 1995; Ward and Pienkowski 1978b) and predation (Bacher et al. 1999; Kosior 1975; Schenk and Bacher 2002; Ward and Pienkowski 1978b) are known to affect larval survival in the field. These multiple factors are likely to influence stage-specific mortalities and fecundity in the beetle, with different effects on the population dynamics of *C. rubiginosa*. However, few studies have quantified fecundity and stage-specific

mortalities and their relative impact on the population dynamics of *C. rubiginosa* under natural conditions (Kosior 1975).

The construction of a life table is the method most commonly used in studies of insect population dynamics, and it allows us to quantitatively assess the mortality factors (Bellows et al. 1992; Carey 2001; Harcourt 1969). *Cassida rubiginosa* is suitable for the life table study because the species spends its whole life cycle on the thistle leaves. Therefore, counts of each developmental stage on host plants provide a sound basis for the life table. Comparison of life table parameters among populations under different habitats can provide important insights into the dynamics of *C. rubiginosa* populations.

The objective of the present study was to construct comparable life tables for *C. rubiginosa* in a natural habitat. We conducted population censuses of different life-history stages (egg, first-instar larvae, fifth-instar larvae and adults) to estimate mortality rates in each stage, and laboratory experiments to measure potential fecundity, a necessary parameter for constructing complete life tables (Jenner et al. 2010; Toepfer and Kuhlmann 2006). Then we built three life tables to (1) examine the significance of stage-specific mortality rates in the total generation mortality and (2) determine which components contributed the most to annual variation in the total mortality and population growth rate. Such analysis will identify factors limiting *C. rubiginosa* population densities, and provide an essential background for developing measures to enhance their densities for effective weed control in natural conditions.

Materials and methods

Study site

The study site was located in Yuwaku, Kanazawa, Central Japan (36°48'N, 136°76'E), at an altitude of ca. 220 m. Mean annual temperature is 13.1 °C and annual rainfall is 2500 mm. A study plot (30 × 50 m) was established in a valley of the Yunokawa Stream, both sides of which were steep slopes covered with deciduous secondary forests containing 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 was covered with 1–2 m of snow from late December to early April.

Insects and plants

Cassida rubiginosa is univoltine (Kosior 1975; Ward and Pienkowski 1978a). In the study site, overwintered adults began to emerge from hibernation in early April (Koji and Nakamura 2006). Females laid oothecae that consisted of about 10 eggs on the undersurface of thistle leaves. Oviposition occurred from late April to July, with a peak from mid-May to mid-June. Larvae passed through 5 instars and pupated on the plant. New adults emerged in early July and disappeared at the end of August when they began estivation. Beetle longevity was substantial, and many individuals overwintered more than once.

Two perennial thistle species, *Cirsium matsumurae* Nakai and *Cirsium kagamontanum* Nakai, grow in the study area. *Cassida rubiginosa* occurred mainly on

C. matsumurae and occasionally on *C. kagamontanum*. These 2 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, increased 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. The abundance of *C. matsumurae* in the study site decreased each year (338, 294, 247, 168 shoots in 1996–1999, respectively); however, it was not significantly different for *C. kagamontanum* (177, 180, 194, 165 shoots in 1996–1999, respectively) (Koji and Nakamura 2002).

Population census

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

Adult populations were studied using mark-recapture techniques. All thistle plants in the study plot were individually examined to catch the adult beetles. On initial capture, each beetle was given a unique color code of 4 dotted points on the elytra by using lacquer paint. Capture date, place, generation, gender, and body size were recorded before releasing the beetle back onto the plant on which it was captured. Newly emerged adults can be distinguished from overwintered adults by their soft and pale-green body surfaces. Total numbers of overwintering and newly emerged adults in each year were estimated using the Jolly–Seber method (Jolly 1965; Seber 1973).

The numbers of egg batches and fifth-instar larvae were recorded separately for

each plant on each census date. Each egg batch was marked by attaching a small numbered tag to the leaf. To prevent double counting, fifth-instar larvae were marked with white lacquer paint by dotting a small point on the abdominal fecal shields.

Estimation of stage-specific mortality

Approximately 3 weeks after the first observation, the egg masses were taken to the laboratory and dissected under a microscope to count the number of eggs per mass and to assess mortality. At the study site, *C. rubiginosa* eggs were subjected to 4 main sources of mortality: parasitism by wasps, arthropod predation, inviability, and unknown causes. Eggs attacked by parasitic wasps were identified by debris left in the eggshells after the emergence of the wasps. The effects of predation could be observed as badly destroyed egg masses. The eggs that remained unhatched and shriveled were categorized as inviable. The egg masses that disappeared without any trace were regarded as being dislodged because of unknown causes.

On the basis of the estimated numbers of newly hatched larvae, fifth-instar larvae, and new adults, mortality was calculated for the stages of early larvae (first to fifth instars) and late larvae (fifth instar to adult). The mortality 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 (Koji and Nakamura 2006).

Estimation of potential and realized fecundity

To calculate the potential progeny values of the population, the potential fecundity of

field-collected *C. rubiginosa* was measured under laboratory conditions (20°C, with a light regime of L14:D10). Post-hibernation adults were collected on *C. matsumurae* at a site adjacent to the field study plot on May 5, 1996. At this time, adult females had reached reproductive maturity and had just started oviposition (Koji and Nakamura 2006). Twenty-seven mating pairs were separated, and each pair was kept individually in a transparent polystyrene container (8.0 × 15.3 × 3.0 cm), the bottom of which was lined with moistened filter paper. Each pair was provided a sufficient amount of fresh leaves of *C. matsumurae* throughout the experiment. All egg masses laid in the container were collected every 2 to 3 days and were dissected under a microscope to determine the number of eggs per mass. The experiment lasted until most females died or stopped depositing eggs (120 days of the total rearing period). The total number of eggs laid by each female over the course of the experiment was used to calculate mean potential fecundity. The potential progeny values of the population were obtained for each year by multiplying the density of overwintered females by the mean potential fecundity.

The fecundity realized under natural conditions was calculated as the number of observed eggs divided by female population size. Lost fertility, potential minus realized fecundity, was incorporated into the life tables to account for the impact that incomplete egg laying has on population change (Bellows et al. 1992; Jenner et al. 2010).

Construction of life tables

We constructed three life tables that referred to the fate of a cohort of eggs laid in 1996, 1997, and 1998. In the life tables, number of individuals was converted to the density

per 100 *C. matsumurae* shoots (i.e., the number of individuals divided by the number of shoot in the respective years and multiplied by 100). Mortality attributable to specific factors was expressed as apparent mortality, marginal mortality, and intensity of mortality (k -values), according to the method described in Bellows et al. (1992). Apparent mortality (q_x) is the ratio of the number dying (d_x) in stage x to the number entering (l_x) the same stage. When multiple mortality factors act simultaneously, the marginal attack rate (m_x) is a useful measure because it calculates the proportion of individuals of a particular stage that would be killed by a single factor if it were acting alone (Bellows et al. 1992). If there is only 1 identified mortality factor or if multiple mortality factors operate sequentially without overlap, then the marginal death rate equals apparent mortality. When factors operate contemporaneously and there is no information on the interactions between those factors, the marginal death rate is calculated as: $m_x = 1 - (1 - q)^{q_i/q}$, where q_i is the apparent mortality caused by the i th factor and q is the stage mortality rate caused by all factors (Elkinton et al. 1992). The k -value is the intensity of mortality in each stage, and is a measure of mortality that is independent of individual numbers, i.e., $k_x = -\log(1 - m_x)$ (Van Driesche and Bellows 1996). The k_x values are expressed as percentages of the total generational mortality K , which is the sum of all k_x values (Haye et al. 2010; Jenner et al. 2010; Toepfer and Kuhlmann 2006). Thus, $100k_x/K$ shows the contribution of a single mortality factor to the generational mortality of *C. rubiginosa*. The components of mortality investigated in this study were egg mortality, mortality in early larvae, mortality in late larvae, overwintering mortality in adults, sex ratio in overwintered adults, and lost fertility. Here, “mortality” is used in a broad sense to cover any loss in a given population, whether this loss results from direct mortality, from dispersal, or from reduced fecundity

(Morris 1957). Egg mortality was further separated into sub-components of mortality by parasitism, predation, inviability, and other unknown factors.

Life table analysis

Since the population process has many components, the key factor analyses were carried out in two steps. First, we focused on the population losses, and assessed the relative importance of individual mortality factors as determinants of the annual changes in generational mortality. The total mortality and stage-specific k -values were plotted for a set of 3 consecutive life tables, and the k -value that best tracked total mortality was regarded as the key factor (Varley and Gradwell 1960). Second, we conducted a similar analysis in order to determine the relative contribution of the population gains (by reproduction and recruitment of old-age adults) and losses (by mortality) to the population growth of *C. rubiginosa*. Information on population growth was given by the net reproductive rate of increase (R_0), which was calculated from the density of eggs in the second generation divided by those in the first generation (Southwood and Henderson 2000). The adult recruitment rate (B) was derived from the ratio of the number of all reproductive adults to those overwintered once. The logarithms of R_0 , B , potential fecundity (F), and total survival (expressed as the negative logarithm of the total mortality, i.e., $S = -K$) were plotted and the synchronization of the fluctuations was visually compared. To examine the effect of variation in plant abundance on the insect population growth, the rate of the yearly change in plant resources (r_{pl}) was also incorporated as a separate factor (Yamada 1995). The r_{pl} value was derived as log ratio of the number of *C. matsumurae* shoots in year n to those in

year $n + 1$.

To detect the stage(s) at which density dependent stabilization is occurring, we compared the temporal variability of population density among different life stages (Kuno 1991). Population variability was represented by the standard deviation of log-transformed densities (Gaston and McArdle 1994). Reduced variability in the stage implies the operation of some regulatory processes, which involve one or more density dependent components. On the other hand, increased variability implies that density-independent destabilization or disturbance acts during the stage (Hanski 1990; Kuno 1991). Densities of overwintered adults in year n were obtained from two values; total number of thistle shoots in year n and those in year $n - 1$. By analyzing the population variability in adult density obtained from the two values, we were able to evaluate the effect of changes in plant abundance from the pre- to the post-hibernation period on the population stability of *C. rubiginosa*.

Results

Stage-specific mortality

Stage-specific life tables are presented for 3 generations of *C. rubiginosa* in Table 1. The total mortality of *C. rubiginosa* from eggs to the reproductive season varied only slightly between 1996 and 1998, ranging from 99.5 to 99.9 %.

Egg mortality was generally high, ranging from 76.4 to 84.0 % of apparent mortality. Eggs of *C. rubiginosa* were heavily parasitized by wasps, and parasitism

accounted for 61–67 % of egg loss (shown as marginal mortality in Table 1). Our concurrent field survey showed that the main parasitoid that attacked egg batches collected in areas adjacent to the study site was a species of the genus *Anaphes* (Hymenoptera: Mymaridae). Mortality attributable to arthropod predation accounted for 11–16 % of the marginal mortality. Sucking predators (*Nabis apicalis* Matsumura [Heteroptera: Nabidae] and *Piocoris varius* (Uhler) [Heteroptera: Lygaeidae]) and ground beetles (*Dicranoncus femoralis* Chaudoir [Coleoptera: Carabidae] and other carabids) were also observed attacking egg masses of *C. rubiginosa*, and they seemingly played a major role in predation (and the partial dislodgement) of the egg masses.

Losses during the early larval (first to fifth instars) and late larval (fifth instar to adult) stages were high, and the mortality in these age intervals ranged from 80.4% to 86.2% and from 49.5% to 84.8%, respectively. *Nabis apicalis*, *P. varius*, *D. femoralis*, and *Polistes anelleni* Saussure (Hymenoptera: Vespidae) were observed attacking *C. rubiginosa* larvae. However, contribution of these factors to mortality in these age intervals of *C. rubiginosa* remained unknown.

The overwintering mortality of new adults in the winters of 1996–1997, 1997–1998, and 1998–1999 was 70.2%, 66.0%, and 83.7%, respectively (Table 1). In Yuwaku, however, a substantial number of old-age adults overwintered more than twice (Koji and Nakamura 2006). Therefore, the estimated densities of overwintered adults were higher than those of new adults in the prehibernation period (Table 1).

Potential and realized fecundity

At the end of the laboratory experiment, 9 females had survived, but their reproductive

activity was minimal (Fig. 1). The mean oviposition period of *C. rubiginosa* in the laboratory was 92.0 ± 5.6 (SE) days ($n = 27$). An average of 41.6 ± 2.9 (maximum 81) oothecae were laid per individual female over a 120-day period. The mean number of eggs per batch was 10.73 ± 0.09 (range, 1–22; $n = 1124$). The potential fecundity of *C. rubiginosa* females in the laboratory averaged 446.8 ± 34.5 eggs and ranged from 142 to 929 eggs. The potential progeny value derived from the density of reproductive females was 59871 (1997), 52722 (1998), and 35744 (1999) (Table 1).

In the field, only 8.1–13.7% of the potential fecundity value was realized (Table 1). The realized fecundities were 61.4, 52.0, and 36.0 in 1997, 1998, and 1999, respectively. As shown in Table 1, this lost fertility accounts for 24.2–26.0% of the generational mortality.

Relationships of fecundity and mortality to population dynamics

The distribution of k -values across different life stages is shown in Table 1. Egg mortality, mortality in early larvae, and lost fertility contributed strongly to the total generational mortality in every year studied, whereas the influences of late-larval mortality and adult overwintering mortality on the total mortality varied among the years. In 1997, the contribution of late-larval mortality was high (21.2%), but this stage suffered less mortality in 1996 and 1998 (8.5% and 10.9%, respectively). Adult overwintering mortality accounted for 18.6% of the generational mortality in 1998, but losses in this stage were lower in 1996 and 1997 (15.0% and 12.1%, respectively).

Annual changes in the generational mortality (K) and its components (k_x) are shown in Fig. 2a. Visual comparison revealed that lost fertility contributed the most to

the changes in the generational mortality throughout the study period. In addition, mortality in egg and adult overwintering stages tended to change in a pattern similar to that of the generational mortality. Mortality in the early larvae stage and the sex ratio in overwintered adults remained at the same levels throughout the study period. Patterns of the egg mortality caused by parasitism, predation, inviability, and unknown factors were very similar to that of total egg mortality, so the key factor responsible for variation in egg mortality was unidentified (Fig. 2b).

The net reproductive rate (R_0) of 1.44 indicated growing populations in 1996, whereas the rates in 1997 and 1998 were less than 1.0, indicating declining populations. Annual changes in the $\log-R_0$ and its components are shown in Fig. 3. Total survival (S) was most closely associated with the variation in population growth rate, indicating mortality is the major factor causing *C. rubiginosa* population change. Variation in plant abundance was not the key factor in driving insect population change.

The annual change in population density in each life stage, together with its standard deviation, are shown in Fig. 4. Population variability was lowest (0.084) for the egg stage of the first generation (i.e., variability for the period from 1996 to 1998, upper graph). The variability gradually increased until late larval stages and then decreased in the new adult (0.161). Population variability increased from new adult to overwintered adult. Overwintered adult densities obtained from total number of thistle shoots in the post-hibernation period showed a slightly lower variability (0.221) compared with those obtained from the number of thistle shoots in the pre-hibernation period (0.276), implying that variation in plant abundance stabilized the adult population density. The variability further decreased after old-age adults and/or immigrants recruited to the population (0.154). The variability in the egg density in the

second generation (i.e., variability for the period from 1997 to 1999, lower graph) was high (0.235), because of an extremely low density in 1999. The reason for the low egg density in 1999 was unknown.

Discussion

Here, we have presented the life tables for *C. rubiginosa* in its native habitat and provided quantitative information on the relative importance of stage-specific mortality rates for the generational mortality of the beetle. Such information will serve as a reference for future life tables when studying populations of *C. rubiginosa* on thistle weeds in different types of habitat.

Stage-specific mortality

Egg mortality was high throughout the study period and was one of the key contributors to the generational mortality. A mymarid wasp of the genus *Anaphes*, the main factor of egg mortality, was often observed to attack the newly laid egg batches of *C. rubiginosa*. *Anaphes pannonica* Soyka and *Oomyzus gallerucae* Fonscolombe (Hymenoptera: Eulophidae) have been reported to be parasitoids of *C. rubiginosa* eggs in Europe (Besuchet 1960; Girault 1914), whereas no egg parasitoids were observed in North America (Ang and Kok 1995; Tipping 1993; Ward and Pienkowski 1978b). In Europe, egg mortality could be attributed to physical factors such as temperature, wind, and rain (Kosior 1975). In the present study, however, the impact of egg inviability (presumably

affected by climatic factors) on mortality was small.

The larval and pupal stages were the most vulnerable immature life stages of *C. rubiginosa*, and early larval mortality accounted for 18.3–24.6% of the generational mortality. While the fifth instar larvae showed the largest population fluctuation over the three study years, new adult changed rather in counterbalance with the fifth instar larvae. Furthermore, population variability decreased from fifth instar larvae (0.188) to new adult (0.161). These results imply the operation of some regulatory processes in the late-larval and pupal stages, which might involve density dependent mortality by predation and/or parasitism. However, in this study, mortality factors that affect the larval and pupal stages are largely unknown. In Europe and North America, predation by spiders (Araneae), predatory bugs (Hemiptera: Reduviidae, Pentatomidae, and Nabidae), chrysopids (Neuroptera: Chrysopidae), and coccinellid and carabid beetles (Coleoptera: Coccinellidae and Carabidae) was observed (Bacher et al. 1999; Kosior 1975; Olmstead and Denno 1993; Ward and Pienkowski 1978b). In Switzerland, Schenk & Bacher (2002) estimated that the paper wasp *Polistes dominulus* Christ (Vespidae) was responsible for 99.4% of the predation on *C. rubiginosa* larvae. In this study, while generalist predators such as predatory bugs, carabids, and paper wasps were observed attacking *C. rubiginosa* larvae in the field, it was rarely possible to accurately identify the causes of death in these stages. In North America, 6 species of parasitoids have been identified from the larvae and pupae of *C. rubiginosa* (Ang and Kok 1995; Olmstead 1996; Tipping 1993; Ward and Pienkowski 1978b). Parasitoid fauna and its influence on *C. rubiginosa* larval mortality have not been elucidated in this study, so further investigation is required.

Adult overwintering mortality varied among the years and contributed

12.1–18.6% to the overall generational mortality. Since population variability increased from new adult to overwintered adult, winter survival disturbed and destabilized the population density. Although the reason for annual variation in winter mortality is unknown, one possibility is the difference in weather conditions during the hibernation period. Widely fluctuating temperatures in the fall and spring are often responsible for overwintering mortality among insects (Leather et al. 1993; Lee 1989; Milner et al. 1992). Spring and Kok (1999) suggested that fluctuating winter temperatures combined with the inability to access preferred hibernating locations (leaf litters) might result in high winter mortality in *C. rubiginosa*.

In spite of overwintering mortality, the estimated densities of overwintered adults were higher than those of new adults in the prehibernation period. Apparently, this high density of overwintered adults was due to the recruitment of old-age individuals. Koji and Nakamura (2006) observed that a substantial number of *C. rubiginosa* adults overwintered more than twice and accounted for 37.8–67.4% of the total number of reproductive adults. Since densities of total overwintered adults showed a lower variability (0.154) than those of adults who had overwintered once (0.221), density-dependent adult recruitment stabilized the population density during the post-hibernation period. However, results of the key factor analysis indicated that adult recruitment is a less important factor in determining population changes.

Potential and realized fecundity

Cassida rubiginosa demonstrated a high mean fecundity of 446 eggs per female in the laboratory. This result is comparable with those of similar studies conducted in North

America (Ward and Pienkowski 1978a) and in Europe (Kosior 1975), which reported a potential of 851 and 244 eggs per female, respectively. It is acknowledged that a potential fecundity estimate in this study was only obtained from a single rearing experiment and did not take into account the annual changes in beetle fecundity. The physiological state of reproductive females was not necessarily the same and potential fecundity might differ from year to year.

Despite the high fecundity in the laboratory, the realized fecundity under field conditions was shown to be far lower than its potential, reaching only 8.1–13.7% of the potential fecundity. Lost fertility was the most important population reduction factor, contributing 24.2–25.9% to the overall generational mortality. Furthermore, since annual changes in the lost fertility exhibited a similar pattern to those in the generational mortality, fertility loss was the key factor driving *C. rubiginosa* populations. These results suggest that reproduction is the most important process that determines the level and fluctuation of the population. Great reductions in fertility have been observed in many phytophagous insects (Bellows et al. 1992; Haye et al. 2010; Jenner et al. 2010; Toepfer and Kuhlmann 2006), and may be attributed to adult emigration, early adult death (Hutchison and Hogg 1985), inhibition of egg laying due to weather (Courtney & Duggan 1983), and/or the female response to host plant quality (Preszler and Price 1988) or the density of conspecifics (Nakamura and Ohgushi 1981; Ohgushi 1996; Ohgushi and Sawada 1985). Ohgushi and Sawada (1985) found that female movement while searching for the oviposition site and egg resorption were the primary factors causing the density-dependent reduction in reproduction of the thistle-feeding ladybird beetle, *Henosepilachna niponica* (Lewis) (Coleoptera: Coccinellidae). However, a density-dependent reduction in reproduction seems unlikely for *C. rubiginosa*, since

population variability increased from overwintered adult to egg. The primary factors reducing fertility in *C. rubiginosa* are not understood and must be investigated using experimental and/or long-term population studies. Such information may lead to the development of strategies to enhance *C. rubiginosa* densities for effective weed control in natural conditions.

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Table 1 Stage-specific life table of *Cassida rubiginosa* during the study period

Stage/Factor	1996-1997						1997-1998						1998-1999					
	l_x	d_x	$100q_x$	m_x	k_x	$100k_x/K$	l_x	d_x	$100q_x$	m_x	k_x	$100k_x/K$	l_x	d_x	$100q_x$	m_x	k_x	$100k_x/K$
Egg	5716						8227						6132					
Parasitism		2812	49.2	0.61	0.40	11.5		3955	48.1	0.62	0.42	10.8		3102	50.6	0.67	0.48	11.4
Predation		389	6.8	0.12	0.06	1.6		492	6.0	0.11	0.05	1.3		493	8.0	0.16	0.08	1.8
Inviability		570	10.0	0.17	0.08	2.3		1094	13.3	0.23	0.12	3.0		892	14.5	0.27	0.14	3.3
Unknown		596	10.4	0.18	0.09	2.4		1004	12.2	0.22	0.11	2.7		664	10.8	0.21	0.10	2.4
Subtotal		4367	76.4					6545	79.6					5151	84.0			
First instar larva	1349						1682						981					
Unknown		1163	86.2	0.86	0.86	24.6		1353	80.4	0.80	0.71	18.3		840	85.6	0.86	0.84	20.0
Fifth instar larva	186						329						141					
Unknown		92	49.5	0.49	0.30	8.5		279	84.8	0.85	0.82	21.2		92	65.2	0.65	0.46	10.9
Adult emerged	94						50						49					
Unknown ^a		66	70.2	0.70	0.53	15.0		33	66.0	0.66	0.47	12.1		41	83.7	0.84	0.79	18.6
Overwintered adult	28						17						8					
Overwintered adult + immigrant ^b	285						207						140					
Sex ratio (% females)		151 (47.0)	53.0	0.53	0.33	9.4		89 (56.8)	43.0	0.43	0.24	6.3		60 (56.8)	42.9	0.43	0.24	5.8
Adult female	134						118						80					
Potential progeny	59871						52722						35744					
Lost fertility		51644	86.3	0.86	0.86	24.6		46590	88.4	0.88	0.93	24.2		32861	91.9	0.92	1.09	25.9
Realized progeny	8227						6132						2883					
Net reproductive rate (R_0)	1.439						0.745						0.470					
Total mortality, %	99.5						99.8						99.9					
Generational mortality (K)	3.5						3.9						4.2					

l_x , number entering stage x (number of individuals per 100 shoots); d_x , number dying in stage x; q_x , apparent mortality; m_x , marginal mortality; k_x , intensity of mortality; $100k_x/K$, % of generational mortality

^a q_x was obtained from the ratio of the number of marked individuals to those recaptured in the following reproductive season

^b Including beetles overwintered once, twice, and three times (Koji and Nakamura 2006)

Figure captions

Fig. 1 Survivorship curves for *Cassida rubiginosa* females (*closed circles*) and mean (\pm standard error) number of eggs laid per female per day (*open circles*) under laboratory conditions

Fig. 2 Fluctuations in individual mortalities (*k*-values) with **a** total mortality (*K*) and **b** egg mortality of *Cassida rubiginosa* over 3 years. L1, first instar larvae; L5, fifth instar larvae

Fig. 3 Annual changes in the components of the net reproductive rate of increase (R_0) (*open circles*). *S*, total survival ($= -K$); *F*, potential fecundity; *B*, adult recruitment rate. Note that the same *F* value was assumed throughout the study period. Annual changes in the rate of yearly changes in the number of thistle shoot (r_{pl} , *closed circles*) are also shown

Fig. 4 Annual changes in population density (number per 100 shoots) in each life stage of *Cassida rubiginosa*. L1, first instar larvae; L5, fifth instar larvae. Densities of overwintered adults in year *n* were obtained from two values, total number of thistle shoots in year *n* (*closed circles*) and those in year *n* – 1 (*open circles*). Variability of population density (expressed as SD log density for a 3-year period) is shown in parentheses

Fig. 1

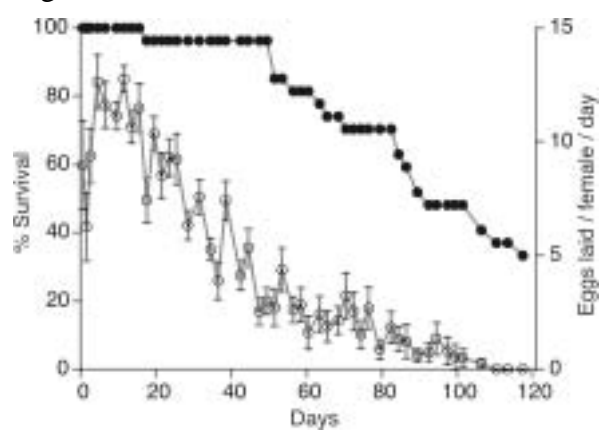


Fig. 2

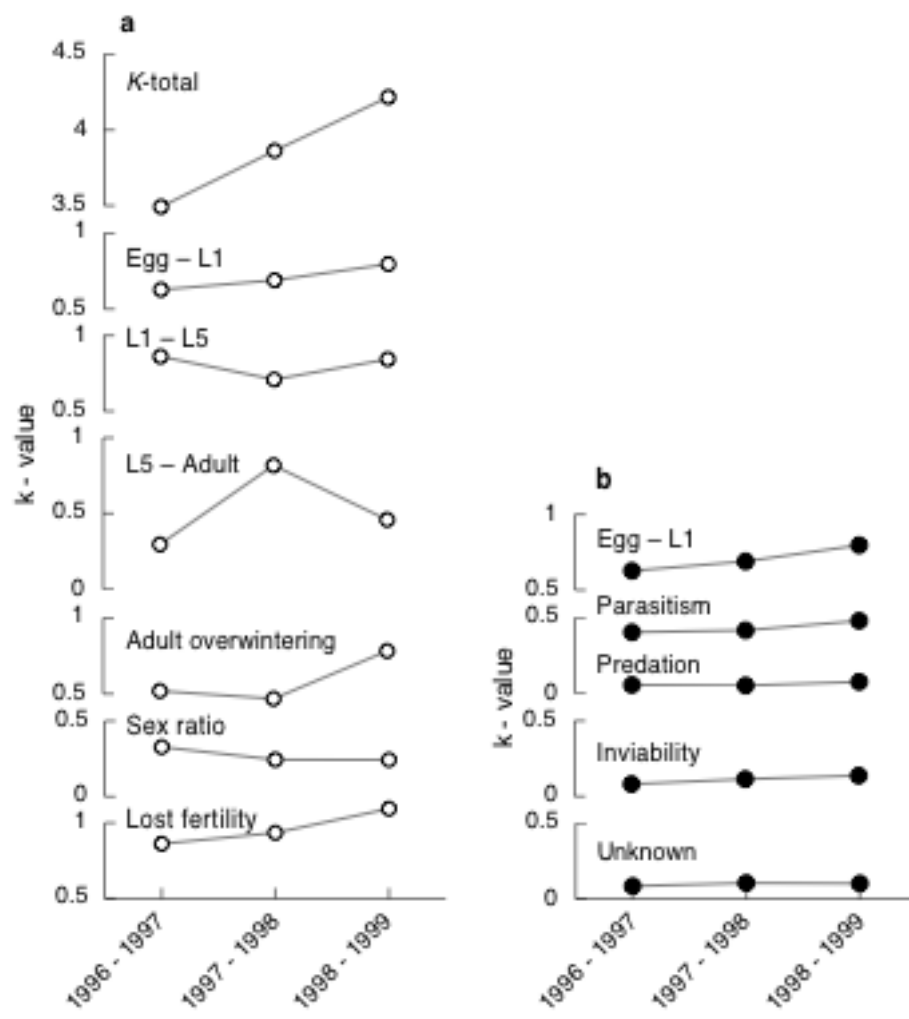


Fig. 3

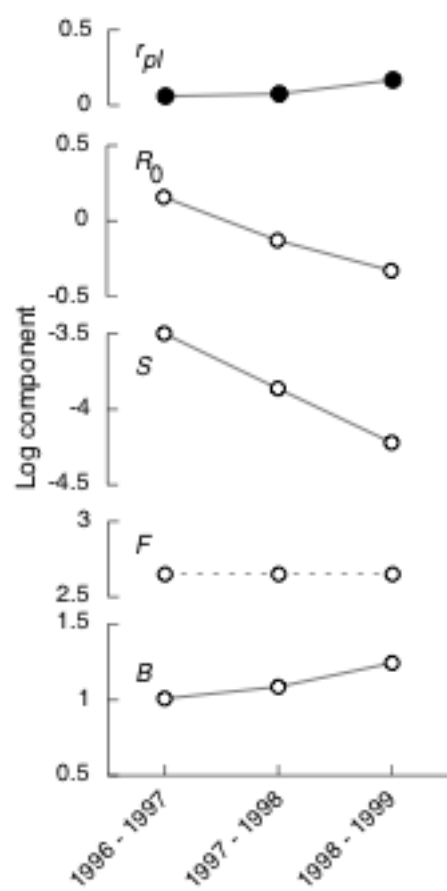


Fig. 4

