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Demography of the Heike firefly *Luciola lateralis* (Coleoptera: Lampyridae), a representative species of Japan's traditional agricultural landscape

Shinsaku Koji[1]*, Akinori Nakamura[1], Koji Nakamura[2]

[1]Center for Regional Collaboration, Kanazawa University, Kakuma, Kanazawa, 920-1192, Japan

[2]Division of Biodiversity, Institute of Nature and Environmental Technology, Kanazawa University, Kakuma, Kanazawa, 920-1192, Japan

*S. Koji, E-mail: shinsak1@hotmail.com, tel: +81-768-88-2568, fax: +81-768-88-2899

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Abstract Populations of the Heike firefly, *Luciola lateralis*, a representative species of Japan's traditional agricultural landscape (known as satoyama), have recently experienced rapid declines in many areas of Japan. Owing to the popularity of this firefly, many local communities have increased conservation efforts through the restoration of aquatic habitat complexes in satoyama. To provide fundamental parameters to predict population dynamics of the firefly, we conducted a mark–recapture study in restored paddy fields, and we estimated adult population parameters such as population size, survival, recruitment, sex ratio, and body size. We found that capture probability generally decreased as the season advanced, probably because of seasonal changes in detectability and/or firefly behavior. The daily survival rate of adults decreased over the season and may be related to a seasonal decline in adult body size. Adult population exhibited a highly male-biased sex ratio. Firefly abundance in the restored paddy fields doubled during the 4-year study period. Our analysis showed that adult detectability, recruitment, and survival rate are seasonally variable and could affect population size estimates obtained by a simple flash census. The mark–recapture technique can provide precise estimates of adult *L. lateralis* population characteristics and, thus, is a valuable method for predicting firefly populations and assessing the success of the restoration program.

Keywords Mark–recapture, Population size, Rice paddy field, Satoyama, Aquatic insects, Japan

Introduction

The traditional agricultural landscape of Japan, called satoyama, provided a variety of habitat types for wildlife and helped maintain the rich biodiversity of Japanese rural areas (Washitani 2001; Kobori and Primack 2003). The aquatic habitat complex, consisting of a network of paddy fields, ponds, and creeks connected to adjacent streams, harbored numerous aquatic organisms (Washitani 2001; Takeda et al. 2006). However, recent intensification of agriculture as well as the abandonment of paddy fields in rural areas have altered the rural wetland landscape drastically, threatening formerly common freshwater aquatic fishes, amphibians, and aquatic insects, including dragonflies, fireflies, and water beetles (Kadoya et al. 2009 and references therein). Declines in the populations of these species have prompted public interest in conserving and restoring biodiversity in satoyama (Washitani 2001; Takeda et al. 2006).

Fireflies (Coleoptera: Lampyridae) are among the most representative insects of Japanese satoyama (Kato 2001). The two species most familiar to the public, the Genji firefly (*Luciola cruciata* Motschulsky) and the Heike firefly (*L. lateralis* Motschulsky), have an exceptional life cycle that is intimately connected to aquatic habitats: Genji and Heike firefly larvae inhabit mainly creeks and paddy fields, respectively. Since these fireflies use both aquatic and terrestrial environments throughout their life cycles, conservation of fireflies would result in extensive conservation of biodiversity in the satoyama landscape (Takeda et al. 2006). In addition, the Genji and Heike fireflies, with their unique luminescence, have become the objects of exceptionally high social interest in Japan and have had a prominent influence on Japanese culture (Minami 1961; Ohba 1988; Mitsuishi 1996; Takada 2010). Therefore, these fireflies are regarded as appropriate flagship species to facilitate citizen participation in conservation of the satoyama landscape (Takeda et al. 2006).

In recent decades, firefly populations have declined rapidly in many areas of Japan, possibly because of the artificial modification of land and rivers, eutrophication and pollution of water environments, and habitat destruction caused by cementing of irrigation ditches (Ohba 1988; Mitsuishi 1996). As a result, many local communities have initiated conservation efforts for this firefly by restoring aquatic ecosystems in the satoyama landscape. Long-term population monitoring has also been conducted to assess the effects of restoration (Mitsuishi 1996; Yuma 2007; Matsuda et al. 2008).

Most numerical studies on firefly populations involve a simple flash counting method, i.e., counting illuminating individuals from a fixed observation point for a fixed duration (Hori et al. 1978; Yuma and Ono 1985; Lewis and Wang 1991; Cratsley and Lewis 2005; Takeda et al. 2006; Yuma 2007). Such a simple observation method provides significant information regarding long-term population fluctuations (Mitsuishi 1996; Yuma 2007; Matsuda et al. 2008) and habitat requirements of the firefly (Shibue et al. 1995; Takeda et al. 2006; Tomita et al. 2006). However, the population size determined by this method depends on population parameters such as discovery rate, adult recruitment, and survival (Yuma 2007). These parameters can vary across the season, as has been demonstrated for many insects (Stoks 2001b; Koji & Nakamura 2002; Schtickzelle et al. 2002; Tikkamäki & Komonen 2011; Kudô et al. 2011). Therefore, detailed demographic data, which can be obtained by the mark–recapture method, are required to verify the reliability of flash counting method for quantifying firefly population size. Although mark-recapture technique is laborious and time-consuming, if designed properly, it can provide fundamental parameters to predict the persistence of focal populations. Such quantitative demographic information is essential to the design and evaluation of firefly conservation plans.

In this study, we described the adult population parameters of *L. lateralis* in restored paddy fields. Hori et al. (1978) conducted a mark–recapture study on a population of *L. cruciata* and reported adult population parameters such as survival rate, population structure, recruitment, and dispersal. However, no such study has been conducted on *L. lateralis*, which has a life cycle that appears to be different from that of *L. cruciata* (Mitsuishi 1996). By using the mark–recapture method, we estimated seasonal changes in survival probability, recruitment, population size, sex ratio, and body size as well as annual population changes in a population of *L. lateralis*.

Material and methods

Study species

Luciola lateralis females lay eggs from June to August on mosses and moist surfaces of plants on

irrigation ditch walls and/or paddy field ridges (Minami 1961; Mitsuishi 1996). The newly hatched larvae drop into the water and prey on freshwater snails, most commonly *Austropeplea ollula* (Gould), *Physa acuta* Draparnaud, and *Semisulcospira libertina* (Gould). Larvae pass through four instars before hibernation. In spring, they resume feeding and molt once, then the fully grown larvae climb up the earthen bank and burrow underground, where they pupate. New adults emerge in June and fly above the rice fields and irrigation ditches before mating on suitable nearby lower vegetation. The adults do not feed and consume only moisture.

Study site

The study site (0.5 ha) was located in Kitadan Valley, Kanazawa, central Japan (36°32′N, 136°42′E) at an elevation of approximately 60 m. Mean annual precipitation at the nearby Kanazawa weather station is approximately 2500 mm, and mean annual temperature is 14.3 °C with a monthly range from 3.6 °C (February) to 26.6 °C (August). Both sides of the valley are steeply sloped and covered with deciduous secondary forests of *Quercus serrata* Murray and *Q. variabilis* Blume. According to interviews with local farmers, Kitadan Valley had been formerly managed as terraced paddies, but the paddy fields were abandoned in the mid-1980s. In 2002, the Kakuma Nature School of Kanazawa University and local volunteers began restoring of the valley to previous conditions. By 2003, five rice paddy parcels and six shallow ponds (i.e., parcels without rice culture) had been restored by resuming paddy cultivation. During the study period, restored parcels gradually increased from 23 (2005) to 38 (2008) (Table 1). No insecticides, herbicides, or fungicides were applied throughout the study period. The study site was divided into 10 (2005) to 13 (2008) sections, each of which included several restored parcels.

Mark–recapture survey

From 2005 to 2008, mark–recapture censuses of fireflies were conducted at 3- to 14-day intervals from June (late May in 2008) to August (Table 1). Each section was searched for illuminating adult fireflies from 8 PM to 10 PM, and all available individuals in each section were netted and kept in separate nylon

mesh bags. Captured fireflies were examined after all of the sections were surveyed, and capture date, section, sex, and body length (measured to the nearest 0.1 mm using calipers) were recorded for each individual. Each firefly was given a unique color code of four dots painted on the elytra using lacquer paint. The fireflies were then released in the section where they were captured. Throughout the study period, the same person conducted the mark–recapture censuses.

Data analysis

Population sizes were estimated for each year using the POPAN formulation of the Jolly–Seber model (Schwarz and Arnason 1996) as implemented in the MARK 5.1 program (White and Burnham 1999). POPAN estimates three primary parameters, survival probability (ϕ), capture probability (p), and proportional recruitment (*pent*). The derived parameters are daily recruitment (B_i), daily population size (N_i), and total population size (N_{tot}). The primary parameters may be constant (.), be sex-dependent (g), respond to time in factorial (t) or linear (T) manners, or display additive (g+t, g+T, …) or interactive (g*t, g*T, …) effects. Capture probability may also depend on daily relative humidity or air temperature (Ohba 1988; Yuma and Hori 1990). We used data for daily relative humidity and air temperature at 8 PM, which were recorded at the Kanazawa Local Meteorological Observatory (http://www.jma-net.go.jp/kanazawa/).

We first conducted a goodness-of-fit (GOF) test on the saturated model [ϕ (g*t) p (g*t) *pent* (g*t)] using the RELEASE program in MARK. The Jolly–Seber model assumes the independence of individuals and homogenous capture and survival probabilities among individuals regardless of previous capture history (Williams et al. 2002; Amstrup et al. 2005). Since the GOF test indicated a lack of fit of the models in 2006 and 2007, we computed a dispersion parameter, $\hat{c}$ (Lebreton et al. 1992), to account for the extra-binomial variation in these models. Next, we fitted progressively simpler models with different combinations of the parameters mentioned above. The values of the Akaike information criterion for small samples (AICc) (or the quasi-likelihood adjusted QAICc in the case of overdispersion) were used for model selection, and the model with the minimum AICc (or QAICc) value was chosen as the optimal model for inference (Lebreton et al. 1992; Burnham and Anderson 2002). We modeled survival and capture probabilities using a logit link function, proportional recruitment using a multinomial logit

link function (probabilities sum to 1), and population size using a log link function. The mean daily survival rate of fireflies (ϕ') was calculated as an arithmetic mean from estimated daily values, and the mean lifespan of fireflies (L) was derived as $L = -1/\ln \phi'$.

Adult body length was analyzed using a linear mixed-effects model with "sex" and "date at first capture" as factors and "year" as a random effect (Pinheiro and Bates 2000). The linear mixed model was fitted with the restricted maximum likelihood method using R 2.10.1 (R Development Core Team 2009).

Results

A total of 3544 fireflies were marked and observed 7214 times, meaning that each individual was captured an average of 2.04 times (Table 2). Females were recaptured less frequently than males (χ^2-test; 2005: $\chi^2 = 6.7$, $df = 1$, $P = 0.01$; 2006: $\chi^2 = 26.3$, $df = 1$, $P < 0.001$; 2007: $\chi^2 = 40.2$, $df = 1$, $P < 0.001$; 2008: $\chi^2 = 50.1$, $df = 1$, $P < 0.001$).

Goodness-of-fit tests indicated that the totally time-dependent model [ϕ (g*t) p (g*t) *pent* (g*t)] adequately fitted the data in 2005 and 2008 (2005: $\chi^2 = 138.90$, $df = 123$, $P = 0.155$; 2008: $\chi^2 = 77.36$, $df = 89$, $P = 0.806$). For data sets in 2006 and 2007, however, the GOF statistic showed a lack of fit (2006: $\chi^2 = 154.99$, $df = 115$, $P = 0.01$; 2007: $\chi^2 = 276.46$, $df = 154$, $P < 0.001$). To correct for this overdispersion, we used a dispersion parameter in the remaining analyses (2006: $\hat{c} = 1.348$; 2007: $\hat{c} = 1.795$).

According to the model selection results (Table 3), capture probabilities of the most parsimonious models were time-dependent in factorial (2006 and 2008) or linear (2007) manners or depended on relative humidity (2005). In 2006 and 2008, capture probabilities differed between sexes and were consistently higher in males (Fig. 1). Capture probabilities decreased from June to mid-July, despite considerable daily variation. In 2007, male capture probabilities were higher than female capture probabilities at the beginning of the season but gradually decreased to the same level as females as the season advanced. In 3 of the 4 study years (2006, 2007, 2008), daily survival probability showed a linear temporal trend, with lower survival later in the season (Table 3; Fig. 2). In 2005, a model that assumes

daily variation in survival probabilities outperformed the other models. In all years, a model that included an additive sex effect on survival probability was preferred over the other models. Daily survival probabilities were higher in males in 2005, 2007, and 2008 and higher in females in 2006 (Fig. 2). Mean life span (L) was 4.11–6.05 days and 3.65–5.65 days for males and females, respectively (Table 4). The period between the first and last captures ranged from 1 to 27 days for males and from 1 to 23 days for females. Proportional recruitment was time dependent in a factorial manner (Table 3) and differed between sexes in 2005, 2007, and 2008, with slightly higher recruitment in males.

The daily estimates of recruitment and population size are shown in Fig. 3. Adult fireflies first appeared at late May (2008) or mid-June (2005). Number of individuals increased until early July and then decreased consistently until mid-August. Males were consistently more abundant than females. Male and female population sizes followed a similar temporal pattern and exhibited a relatively constant sex ratio (approximately 70–80% male) throughout the flight season (Fig. 4). The estimated total population size (male and female combined) increased from 1302 (2005) to 2799 (2007) (Table 4). Total population sex ratios were male-biased; 70.5–75.9% of *L. lateralis* were males.

Luciola lateralis females were significantly larger than males ($F_{1, 3547} = 2190.45$, $P < 0.001$). Day of season significantly affected body length ($F_{1, 3547} = 122.10$, $P < 0.001$), and fireflies were smaller as the season progressed (Fig. 5). The relationship between body length and season was stronger for females than for males ($F_{1, 3547} = 33.94$, $P < 0.001$; Fig. 5).

Discussion

Seasonal changes in adult population parameters

The intensive mark–recapture study revealed adult population characteristics of the Heike firefly, *L. lateralis*, such as seasonal changes in number, sex ratio, and survival rate. The adult population peaked in late June and then decreased gradually until mid-August. Recruitment patterns were more gradual than they were in the closely related firefly *L. cruciata*, which appeared briefly from mid-June to mid-July (Hori et al. 1978; A. Nakamura unpublished data).

202 The model selection results showed that capture probabilities varied across the season. In 3 of the 4
203 study years (2006, 2007, and 2008), capture probabilities generally decreased as the season advanced.
204 The declining capture probability late in the season may be the result of lower detectability because of
205 denser ground cover vegetation or seasonal changes in firefly behavior, as exhibited in *L. cruciata* (Yuma
206 and Hori 1990) and several species of the genus *Photinus* (Lewis and Wang 1991; Cratsley and Lewis
207 2005). Yuma and Hori (1990) showed that the location of *L. cruciata* females shifted from lower
208 vegetation to tree canopy as the season advanced. Given that such a seasonal habitat shift is observed for
209 *L. lateralis*, it could affect capture probabilities.
210 In every year studied, body lengths of new adults decreased over the course of the season. The same
211 tendency was observed for several firefly species of the genera *Luciola* (Iguchi 2001; Ho et al. 2010) and
212 *Photinus* (Cratsley and Lewis 2005). Yuma (1981) examined the body size of *L. cruciata* larvae that
213 climbed up the bank of a river to pupate and suggested that larger larvae climbed earlier and smaller
214 larvae climbed later in the season. Seasonal variation in the adult body length of *L. lateralis* may also be
215 explained by different timing of larval climbing.
216 In 3 of the 4 study years (2006, 2007, and 2008), daily survival rates decreased continuously over the
217 season. Although the reason for this tendency is unknown, one possibility is the seasonal decline in adult
218 body size. Body size variation has been shown to affect the survival of many insect species (Palmer 1985;
219 Ohgushi 1996; Munguía-Steyer et al. 2010). *Luciola lateralis* is a capital breeder, an organism in which
220 adults depend entirely on resources derived from the larval period. Therefore, larger individuals that
221 emerged early in the season may have larger resource reserves and may survive longer than smaller
222 individuals. Causes and consequences of the seasonal variation in *L. lateralis* body size remain to be
223 determined.
224
225 Sex ratio
226
227 Mark–recapture data showed that total population sex ratios in *L. lateralis* were highly male-biased in
228 every year. Populations of diploid insects often exhibit significantly male-biased operational sex ratios
229 (Stoks 2001a and references therein), and several hypotheses have been proposed to explain this
230 phenomenon (e.g. Frey and Leong 1993; Nylin et al 1995; Maxwell 1998; Underwood and Shapiro 1999;

231 Stoks 2001a, b; Adamski 2004). For *L. lateralis* populations, a higher number of males may reflect sex
232 ratio differences at emergence, probably because of male-biased primary sex ratios or mortality
233 differences during preadult stages. Throughout the season, recruitment (i.e., number of new individuals in
234 the population from reproduction and/or immigration) was larger in males than in females. Because the
235 study site was well isolated from neighboring paddy fields and damp areas, the number of immigrants
236 from outside seems minimal, and recruitment values likely represent the number of newly emerged adults.
237 Male-biased adult recruitment also was found in the *L. cruciata* population in Kyoto, central Japan (Hori
238 et al. 1978). Yuma (1981) determined the sexes of *L. cruciata* larvae based on body length–weight
239 relationships and found male-biased (3:1) sex ratios in mature climbing larvae of the same population.
240 Moriya et al. (2009) reared field-collected *L. cruciata* climbing larvae until emergence as adults and
241 reported a male-biased (3:1) sex ratio in new adults. If *L. lateralis* has a male-biased sex ratio at adult
242 emergence, then the sex ratio must have shifted from even (1:1) toward male-biased during the period of
243 development. Further investigation will be needed to examine mortality differences between sexes during
244 the preadult stages.
245
246 Annual population changes
247
248 *Luciola lateralis* abundance in the restored paddy fields doubled during the 4-year study period. No data
249 were found that verified the occurrence of *L. lateralis* in the study site before rice paddy restoration.
250 However, the preliminary abundance survey in and around Kitadan Valley revealed that although *L.*
251 *lateralis* fireflies occurred mainly in paddy fields, a few individuals were also observed in nearby damp
252 areas (A. Nakamura unpublished data). Therefore, a low-density population of *L. lateralis* likely existed
253 in the study area prior to restoration activities and grew rapidly following restoration of the terraced rice
254 paddies. Shibue et al. (1996) examined the relationship between *L. lateralis* abundance and duration of
255 paddy fields abandonment, and indicated that length of abandonment affected negatively the firefly
256 abundance. These results suggest that rice cultivation is an important way to recover *L. lateralis*
257 abundance. Abundance and distributional patterns of aquatic fireflies have often been explained by
258 factors such as larval prey abundance (Ohba 1988; Mitsuishi 1996; Takeda et al. 2006; Tomita et al.
259 2006), ditch hydrological conditions (e.g., ditch width and current velocity) (Shibue et al. 1995, 1996),

water quality (e.g., pH and dissolved oxygen [DO]) (Takeda et al. 2006), water pollution by agrochemicals (Ohba 1988; Mitsuishi 1996), ditch structural conditions (e.g., artificial alterations and bankside vegetation cover) (Shibue et al. 1996; Takeda et al. 2006), riverbed conditions (e.g., dominance of gravel deposition) (Tomita et al. 2006), relative light intensity (Shibue et al. 1996), and rainfall amount (Yuma 2007). Takeda et al. (2006) examined the relative importance of environmental factors on *L. cruciata* and indicated that abundance increased with increasing pH, DO, and prey abundance and decreased with water depth and the proportion of artificially modified ditch length. Habitat requirements of the *L. lateralis* firefly are not well understood and must be investigated further to collect reliable information about key habitat variables affecting conservation of this firefly.

Implications for conservation

A firefly abundance survey by flash counting is a simple method for both professional and amateur observers and, if properly designed, provides a reliable estimate of relative population size (Yuma 2007). However, this commonly employed monitoring method may also be subject to errors, because discovery rate, adult recruitment, and survival were temporally variable for *L. lateralis*. In particular, results of the present study suggest two notable points for the *L. lateralis* abundance survey. First, capture probability declined later in the season and the flash census could underestimate population size. Therefore, to obtain comparable data from many sites by flash counting, observations must be conducted concurrently, preferably earlier in the season. Considering recruitment of adults throughout the season, monitoring should be extended over the entire flight period of the firefly. Second, capture probability was lower for females, implying a possible underestimation of female population size compared with male population size by the flash census method. For the duration of each nightly mating period, *L. lateralis* males emit flashes while in flight, whereas lighting females generally remain stationary on perches in lower vegetation (Mitsuishi 1996). Thus, more males were likely to be found than females, and sex ratios obtained from the flash count would overestimate the actual male-biased sex ratio. Capture probabilities must be considered in the estimate of the population sex ratio.

Hori et al. (1978) compared estimates of *L. cruciata* population obtained by the mark–recapture and flash census methods, and found the flash count underestimated the population size if the count exceeded

100. Given that such underestimation occurs for *L. lateralis* whose flash displays is weaker than *L. cruciata* (Minami 1961), reliable estimation of the large population requires the mark–recapture approach.

The present study revealed adult demographic factors such as survival and recruitment, which are temporally variable. The next step will be to gain a mechanistic understanding of *L. lateralis* demography to reliably predict the success of the restoration program. Future studies should explore underlining mechanisms of the male-biased sex ratio and seasonal variations in adult survival and body size. Furthermore, studies should address the role of reproductive and preadult mortality processes on population growth.

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Table 1 Total number of restored rice paddies and shallow ponds, number of sections, census period, and number of sampling events during the study period

Year	Number of rice paddies	Number of ponds	Number of sections	Census period	Number of sampling events
2005	15	8	10	Jun 14–Aug 18	39
2006	18	11	12	Jun 8–Aug 16	37
2007	22	13	13	Jun 2–Aug 16	36
2008	23	15	13	May 29–Aug 7	26

Table 2 Total number of marked beetles, number of releases after (re)capture, and percentage of recaptured individuals of *Luciola lateralis* during the study period

Year	Sex	Number of marked individuals	Number of releases after (re)capture	Number of recaptured individuals	Recapture ratio (%)
2005	Male	341	740	204	59.8
	Female	185	315	89	48.1
2006	Male	578	1250	341	59.0
	Female	327	525	135	41.3
2007	Male	775	1835	492	63.5
	Female	365	624	159	43.6
2008	Male	756	1619	415	54.9
	Female	217	306	60	27.6

Table 3 Summary of model selection statistics for survival rate (ϕ), recapture probability (p), proportional recruitment (*pent*), and total number of individuals (N) of adult *Luciola lateralis*

Year	Model[a]	(Q)AIC$_c$	Δ(Q)AIC$_c$	*np*
2005	$\phi_{g+t}\, p_{RH}\, pent_{g+t}\, N_g$	3334.42	0.00	66
	$\phi_t\, p_{RH}\, pent_{g+t}\, N_g$	3334.95	0.53	65
	$\phi_t\, p_{g+RH}\, pent_{g+t}\, N_g$	3335.25	0.84	66
	$\phi_{g+t}\, p_{g+RH}\, pent_{g+t}\, N_g$	3336.60	2.18	67
	$\phi_t\, p_{RH}\, pent_t\, N_g$	3336.61	2.20	65
2006	$\phi_{g+T}\, p_{g+t}\, pent_t\, N_g$	3579.23	0.00	55
	$\phi_{g+T}\, p_{g+t}\, pent_{g+t}\, N_g$	3580.46	1.24	56
	$\phi_T\, p_{g+t}\, pent_t\, N_g$	3581.14	1.91	54
	$\phi_{g*T}\, p_{g+t}\, pent_t\, N_g$	3581.33	2.10	56
	$\phi_T\, p_{g+t}\, pent_{g+t}\, N_g$	3582.39	3.16	55
2007	$\phi_{g+T}\, p_{g*T}\, pent_{g+t}\, N_g$	4004.95	0.00	36
	$\phi_{g*T}\, p_{g*T}\, pent_t\, N_g$	4005.30	0.34	36
	$\phi_{g*T}\, p_{g+T}\, pent_t\, N_g$	4005.87	0.92	35
	$\phi_{g*T}\, p_{g*T}\, pent_{g+t}\, N_g$	4006.81	1.85	37
	$\phi_{g*T}\, p_{g+T}\, pent_{g+t}\, N_g$	4007.72	2.76	36
2008	$\phi_{g+T}\, p_{g+t}\, pent_{g+t}\, N_g$	4416.03	0.00	52
	$\phi_{g+T}\, p_{g+t}\, pent_t\, N_g$	4416.43	0.40	51
	$\phi_{g+T}\, p_{g*t}\, pent_t\, N_g$	4417.24	1.21	52
	$\phi_{g+T}\, p_t\, pent_t\, N_g$	4417.87	1.84	50
	$\phi_{g*T}\, p_{g+t}\, pent_{g+t}\, N_g$	4418.06	2.03	53

Five best-supported models are shown in order of Akaike's information criterion (AIC$_c$) or AIC$_c$ adjusted for quasi-likelihood (QAIC$_c$). AIC$_c$-based (or QAIC$_c$-based) differences from the best model [Δ(Q)AIC$_c$] and number of estimated parameters (*np*) are also shown

[a]g = sex; *t* = time; T = linear trend of sampling date; RH = relative humidity; + = additive effect of two variables; * = effect of the interaction of two variables

Table 4 Annual changes in estimates of mean life span, population size (with lower and upper 95% confidence intervals), and proportion of males during the study period

Year	Mean life span (days)		Total population size		Proportion of males (%)
	Male	Female	Male	Female	
2005	4.11	3.65	945 (854–1037)	357 (309–406)	72.6
2006	4.66	5.65	1553 (1449–1657)	652 (577–726)	70.5
2007	6.05	5.52	2030 (1876–2183)	769 (679–860)	72.5
2008	5.86	3.95	1998 (1761–2235)	633 (506–760)	75.9

Figure legends

Fig. 1 Seasonal change in daily estimates (±95% confidence intervals) of capture probability for male (*filled circles*) and female (*open circles*) *Luciola lateralis.* In 2005, difference in capture probability by gender was not observed in the best-supported model

Fig. 2 Temporal changes in daily estimates (±95% confidence intervals) of survival probability for male (*filled circles*) and female (*open circles*) *Luciola lateralis*

Fig. 3 Estimates of daily recruitment (*left*) and population size (*right*) of male (*filled circles*) and female (*open circles*) *Luciola lateralis* using the best-supported model. Error bars indicate 95% confidence intervals

Fig. 4 Seasonal change in the proportion of males in adult *L. lateralis* populations. *Filled circles* and *filled triangles*, 2005 and 2006, respectively; *open circles* and *open triangles*, 2007 and 2008, respectively

Fig. 5 Relationships between date of first capture and body size in male (*filled circles*, *solid line*) and female (*open circles*, *dashed line*) *Luciola lateralis*. n = 3554 beetles in 4 years. Regression lines result from a linear mixed-effect model

Fig. 1

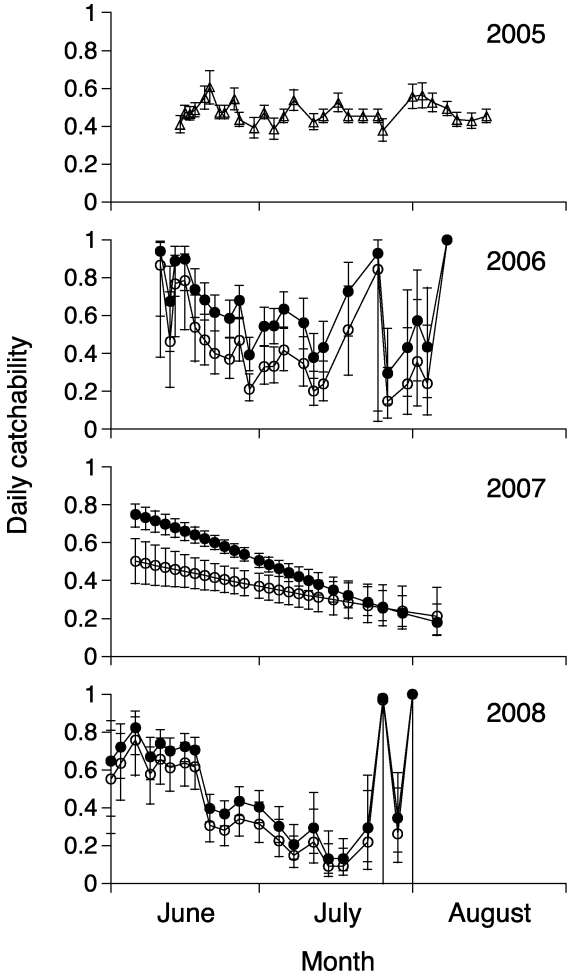
2005
2006
2007
2008
Daily catchability
0
0.2
0.4
0.6
0.8
1
June
July
August
Month

Fig. 2

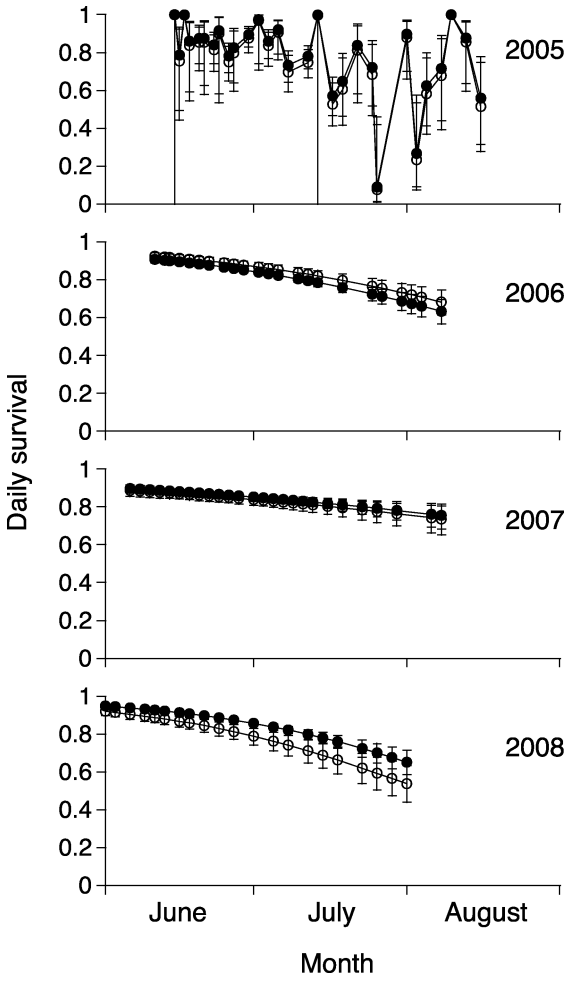
Daily survival
1
0.8
0.6
0.4
0.2
0
2005
2006
2007
2008
June
July
August
Month

Fig. 3

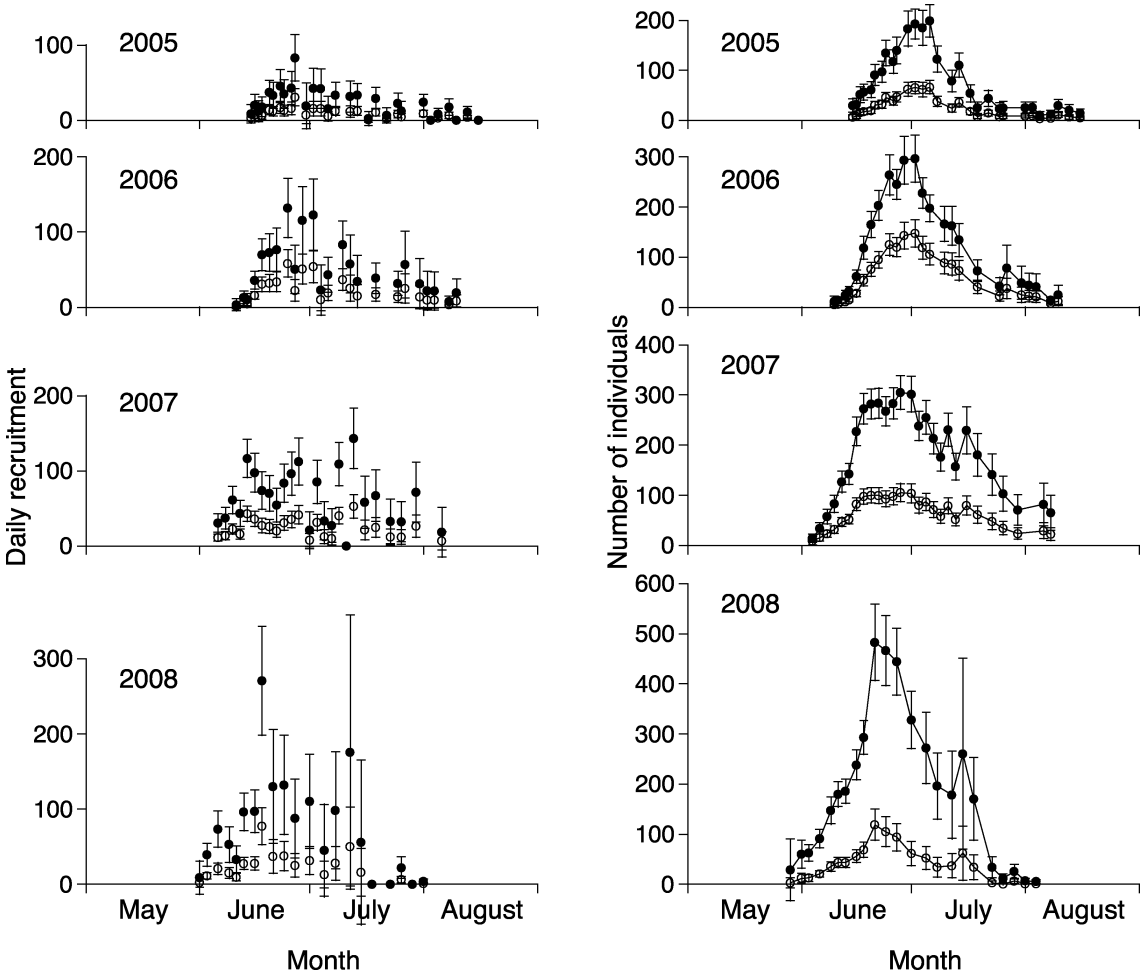
2005
2006
2007
2008
Daily recruitment
Number of individuals
May
June
July
August
Month

Fig. 4

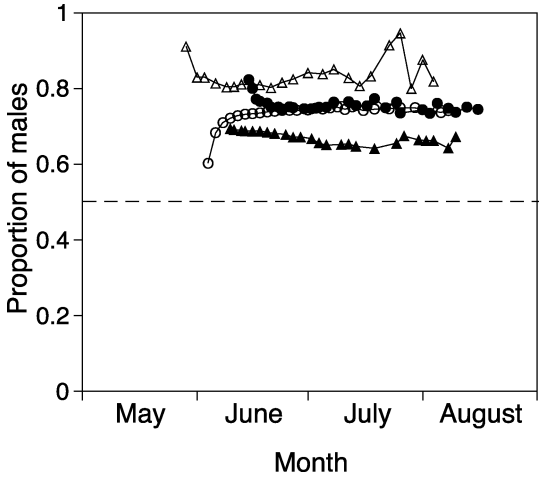
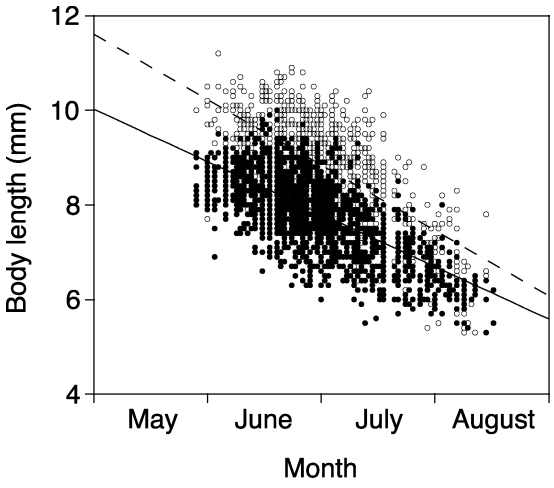
Fig. 5