



BRILL

Behaviour 160 (2023) 337–355

Behaviour
brill.com/beh

High incidence of leg autotomy in urban crickets

Takashi Kuriwada*, Seiya Shindome, Yuki Tomita and Motohiro Kawanishi

Kagoshima University, Faculty of Education, Department of Science Education,
Laboratory of Zoology, Korimoto1-20-6, Kagoshima 890-0065, Japan

*Corresponding author's e-mail address: kuriwada@edu.kagoshima-u.ac.jp

ORCID iD: Kuriwada: 0000-0002-1055-191X

Received 27 June 2022; initial decision 18 August 2022; revised 21 December 2022;
accepted 9 January 2023; published online 6 February 2023

Abstract

Predation is an important selection pressure affecting animals. Predation has both consumptive and non-lethal effects. Because it is often difficult to estimate the extent to which non-lethal effects occur, we focused on autotomy as an indicator of non-lethal effects occurring in urban habitats. Autotomy is expected to indicate that individuals have escaped from predators. The incidence of leg autotomy in the cricket *Dianemobius nigrofasciatus* was compared between urban and rural habitats. The incidence of autotomy was higher in urban than in rural habitats. Failure to moult and conspecific aggressive interactions were not the main factors contributing to the incidence of autotomy in these crickets. The ease of autotomy and risk-taking tendencies did not differ among habitats. These results indicate that the incidence of autotomy reflects predation failure, and the non-lethal effects of predation are more likely to occur in urban habitats.

Keywords

Orthoptera, limb loss, anti-predatory response, urbanization, *Dianemobius nigrofasciatus*.

1. Introduction

Currently, more than half of the global human population lives in urban environments (United Nations, 2018), and urban areas are experiencing constant expansion and growth. Urbanisation exerts various biotic and abiotic effects owing to disturbances from human activities such as noise and light pollution, habitat fragmentation, invasive species introduction, toxic chemical emissions and climatic change (Parris, 2016; Johnson & Munshi-Smith, 2017). The negative impacts of urbanisation on organisms have been investigated in various taxa (Alberti, 2015; Alberti et al., 2017). Such strong

selection pressures force organisms to adapt, emigrate, or become extinct (McKinney, 2006). Phenotypic and adaptive changes in traits in response to urbanisation have also been documented (Lambert et al., 2021). The difference in selection pressure between urban and non-urban areas is important for predicting the possibility of adaptation to urban environments.

Predation is one of the most important selection pressures, because it is directly linked to the death of prey animals. Predation has not only lethal or consumptive effects but also non-lethal or non-consumptive indirect effects. The risk of predation or threat experience causes morphological, physiological, and behavioural changes in prey animals (Werner & Peacor, 2003). For example, cues from predatory crayfish shift habitat use by the freshwater snail, *Physa acuta*, from mid-depth to the water surface (Kawaguchi & Kuriwada, 2020). Predator-induced change also has an impact on population dynamics and community structure (Werner & Peacor, 2003). Therefore, differences in the direct and indirect effects of predation between urban and rural environments are important for understanding adaptive evolution in urban environments.

In urban areas, substantial habitat modification and introduction of invasive species change species composition and predator abundance. A meta-analysis by Eötvös et al. (2018) showed that predation rates for birds were significantly higher in rural habitats than in urban habitats. Although Eötvös et al. (2020) used dummy caterpillars to show that predation pressure decreases from rural to urban habitats, there is limited information on the effect of predators on urban invertebrates. Invertebrates are strongly influenced in their behaviour by ambient temperature. Because locomotor performance is also affected by temperature (Deere & Chown, 2006), predator avoidance will change depending on the ambient temperature. Temperatures in urban habitats are generally higher than those in rural habitats owing to the heat island effect (Parris, 2016). Therefore, in ectothermic animals, not only differences in predator composition, but also temperature would affect predation pressure.

Autotomy is an anti-predatory defence in which individuals sacrifice part of their body to escape predators (Fleming et al., 2007; Lagos, 2017; Sugiyura, 2020). Autotomy of the legs results in the loss of locomotor organs, which has an enormous impact on subsequent behaviour and fitness components, such as foraging ability, predatory avoidance, reproductive performance, and body conditions. For example, Bateman & Fleming (2005)

showed decreased escape speed and number of jumps in the escape sprint, mating success, and longevity in field crickets, *Gryllus bimaculatus*, in addition to physical injury due to the loss of body parts. Because some insect species use their hind legs in male-male contests, autotomy of the hind legs means permanent loss of a sexually selected weapon (Embets et al., 2016). Thus, autotomy has a serious impact on subsequent behaviour and physiological conditions. Therefore, a comparison of the incidence of autotomy between rural and urban environments may provide important information regarding the differences in indirect predation effects between the two environments.

We compared the incidence of autotomy between urban and rural habitats using the band-legged ground cricket, *Dianemobius nigrofasciatus*. Crickets autotomize their hind limbs when they are nipped (Matsuoka & Ishihara, 2010; Matsuoka et al., 2011) and inhabit both rural and urban environments, such as city parks, gardens and grass fields (Orthopterological Society of Japan, 2016). Because autotomized limbs are not regenerated in Orthoptera (Bateman & Fleming, 2005), autotomy will affect the individuals for the rest of their lives. This cricket exhibits behavioural and life history plasticity depending on the incidence of leg autotomy. Autotomised crickets grow faster, reduce body size (Matsuoka & Ishihara, 2010), and call more frequently (Matsuoka et al., 2011). This plasticity can be considered as one of the non-consumptive effects, and this change may spill over into the population dynamics and other surrounding species by affecting reproduction and predatory avoidance. The difference in the incidence of autotomy between urban and rural habitats indicates that the frequency of non-lethal effects also differs.

However, differences in predation pressure and/or predation failure, as well as differences in the ease of autotomy in each habitat, may cause differences in the incidence of autotomy among habitats. Indeed, the ease of tail autotomy differs among habitats in some lizards (Cooper et al., 2004; Brock et al., 2015). The cost of autotomy is expected to be higher in urban habitats, where food will be less available and thermoregulation will be more difficult because of the phenomena of heat islands and reduced availability of shelters. Therefore, urban individuals may be less likely to autotomize their legs than rural individuals. In addition, if more risk-taking individuals exhibit relatively higher predation risk, differences in the personality among

the habitats will cause differences in the incidence of autotomy. Indeed, Australian water dragons, *Intelligama lesueurii*, from semi-natural populations were significantly bolder than those from natural populations (Baxter-Gilbert et al., 2019). Boldness is positively associated with tail autotomy in the male water anole, *Anolis aquaticus* (Talavera et al., 2021). Finally, autotomy can be caused by factors other than predation (Emberts et al., 2019). For example, failure to moult (stick insect (*Didymuria violescens*), Maginnis, 2008; coreid bugs, Emberts et al., 2016), intraspecific aggression (geckos (*Mediodactylus kotschy* and *Hemidactylus turcicus*), Itescu et al., 2017), and damage associated with wounded body parts (leaf-footed cactus bug (*Narnia femorata*), Emberts et al., 2020) are often known to cause autotomy.

Therefore, the following three laboratory experiments were conducted to determine the relative importance of these factors in the incidence of autotomy. First, we experimentally examined whether urban crickets are less likely to autotomize their legs than rural crickets. Second, if urban individuals exhibit higher boldness than rural individuals, the higher boldness would reflect a higher incidence of autotomy. Thus, we compared boldness between urban and rural crickets as the latency to emergence from a shelter. Finally, autotomy can occur by moulting failure and conspecific aggressive interactions, in addition to predation. The extent to which autotomy occurs outside predation is not well understood. Therefore, we estimated the incidence of autotomy caused by conspecific interactions and moulting failure.

2. Material and methods

2.1. Study species

The band-legged ground cricket, *Dianemobius nigrofasciatus* (Matsumura) (Orthoptera: Trigonidiidae), is a native species widely distributed in Japan, Korea, northern China and Siberia (Orthopterological Society of Japan, 2016). In Japan, they are commonly found around crop fields, weedy river margins, and lawns between 30°N and 44°N (Masaki, 1972; Matsuda et al., 2019). In southern Japan, including Kagoshima Prefecture, adults emerge in summer and produce non-diapause eggs, whereas those of the next generation emerge in autumn and produce diapause eggs (Masaki, 1972). Adults are common from late June to early August and late September to November in the bivoltine areas, and are occasionally observed in January (mean temperature in Kagoshima City in January is 8.7°C). This cricket can call at

temperatures below 15°C (T. Kuriwada, personal observation). The crickets mainly live on the ground and under grass, and are often found in urban parks and vacant lots with little vegetation. They emit calling songs at night during the summer season and during the day in autumn (T. Kuriwada, personal observation).

2.2. Capture and maintenance of individuals

Individuals of *Dianemobius nigrofasciatus* were collected from six sites (Figure 1; three urban and three rural habitats) in Kagoshima City from late June to early July (summer) and from early October (autumn) in 2019. As urban sites, we chose habitats along highways with four or more lanes. For rural sites, we chose habitats that were not on busy roads or faced forests. The ratio of impermeable surfaces was calculated as the percentage of the area of artificial structures and paved roads on the satellite imagery of Google Maps out of an area of 100 m around the centre of the study sites (Figure 1).

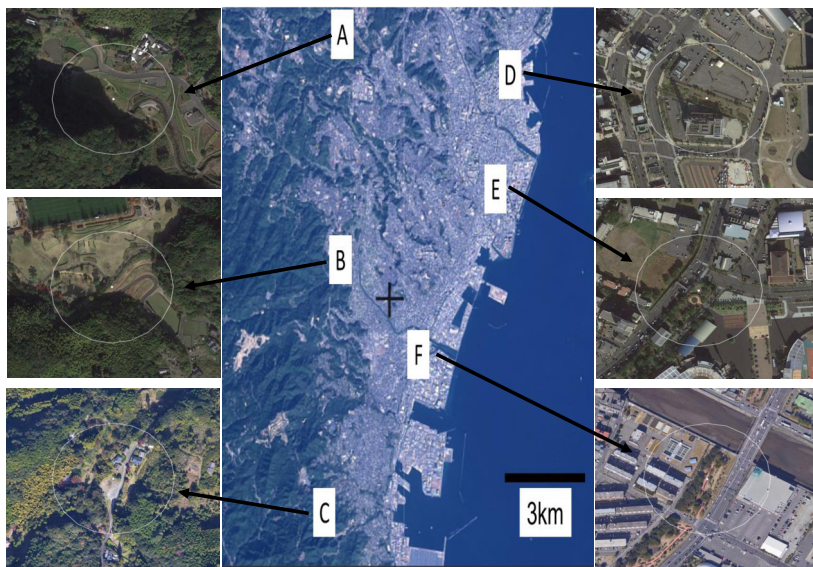


Figure 1. Maps showing the location of the three rural (A–C) and three urban (D–F) sites in Kagoshima city. E and C indicate the sites with the most and least incidences of automotony, respectively. Maps from the Geospatial Information Authority of Japan website were used as base maps (<https://maps.gsi.go.jp/#12/31.534506/130.512543/&base=ort&ls=ort&disp=1&vs=c1j0h0k0l0u0t0z0r0s0m0f1>). The 6 photos around the map are Google Earth image of the survey sites. The circle has a radius of 100 m from the centre of the survey sites.

Table 1.

Outline of each survey site.

Habitat ID	Habitat type	Survey date	Area of survey site (m ²)	Percentage of impermeable surface	Traffic noise (mean ± SD) (dB)
A	Rural	7/6: 10/3	1300	11.0	47.6 ± 3.6
B	Rural	6/25: 10/4	2000	7.8	52.9 ± 5.9
C	Rural	6/25: 10/4	300	7.6	48.5 ± 5.2
D	Urban	6/25: 10/3	3500	82.4	60.6 ± 4.2
E	Urban	7/6: 10/3	2300	65.0	61.1 ± 3.0
F	Urban	7/6: 10/4	5300	72.7	61.7 ± 3.5

Habitat ID letters correspond to the symbols in Figure 1.

QGIS (QGIS Development Team, 2021) was used to calculate the area of the artificial structures and paved roads in a circle with a radius of 100 m. River surface area was excluded from the calculations. The ratio of impermeable surfaces in the urban habitats was larger than that in the rural habitats (Table 1; urban: 65.0–82.4%; rural: 7.6–11.0%). We measured the noise levels at each site as the peak sound pressure level using a sound level meter (GM-1351; Benetech, Shenzhen Jumaoyuan Science and Technology, Shenzhen city, P.R. China) by pointing in four different directions on the ground surface at the sampling sites to use the noise level as an indicator of urbanisation. Noise levels were measured four times at each site during each season. The noise level in the urban habitats was higher than that in the rural habitats (Table 1; urban: 61.10 ± 3.56 dB (mean ± SD); rural: 49.64 ± 5.47 dB, $\chi^2 = 15.24$, $df = 1$, $P < 0.0001$).

We chose similar grassy areas as the study sites across all sites. In particular, individuals were mainly collected from areas with a mixture of turfgrass and bare ground. We walked through the grass and open fields to find the crickets, and the crickets were captured using a capture device made by cutting the bottom of a two-litre plastic bottle and attaching a centrifuge tube to a spout. The survey time per survey site was approximately 60–100 min (four investigators). The collected crickets were brought to the laboratory and kept in separate containers for each site (17 cm width × 11 cm depth × 12.5 cm height) at 26–28°C under a photoperiod of 16:8 h (L:D). The container included cardboards for shelter, soil in a 200 ml plastic cup as a water source, and excess rabbit food (Marukan, Osaka, Japan) and cat chow (Purina, Kobe, Japan) as food sources. Crickets were used in subsequent experiments.

Five to nine days after the measurements of the incidence of autotomy, the crickets were collected again for body size measurements. To eliminate the effect of autotomy on body size, we only sampled adult crickets that had not autotomised any limbs. The collected crickets were preserved in 70% ethanol for body size measurements. The head width, including the compound eyes, was measured as an index of body size according to a previously described method (Masaki, 1972; Matsuda et al., 2019), using a digital microscope (3R-MSUSB401, 3R Solution, Tokyo, Japan).

2.3. Measurement of the incidence and latency of autotomy

The developmental stage of the crickets (i.e. adult or nymph) and whether any of the crickets had already autotomised a leg (i.e., incidence of autotomy) were recorded immediately after the above-mentioned sampling.

To examine whether there was an individual difference in the ease of autotomy between the sites, the latency to autotomy of crickets was compared using an artificial stimulus between the sites with the highest (E in Figure 1) and lowest (C in Figure 1) incidences of autotomy based on the above-mentioned field survey. To minimise the number of crickets for which autotomy was induced, we narrowed down the sites to be tested. The experiment was conducted approximately 14 days after sampling in Autumn (13:30–15:10). The crickets were individually placed in plastic pouches (6.0 × 8.5 cm) to render them immobile, and then the right or left hind femur was nipped with a medical tweezer until the cricket autotomised the nipped leg. Almost all of the crickets autotomised seconds after being grabbed with tweezers. The point of autotomy was between the trochanter and femur (Figure 2). Latency to autotomy was recorded using a stopwatch. All experiments were performed by one of the authors (TK), using as much pressure as possible. The artificial stimulus was applied once per individual.

2.4. Measurement of boldness

To quantify the boldness of individuals among the sites, we measured individual latency to emergence when placed within a safe shelter in a novel environment (Hedrick, 2000; Hedrick & Kortet, 2006; Fisher et al., 2015). We collected adult crickets with no visible physical defects from the above-mentioned six sites between 10:00–11:30 on 29 (sites B, C and F) and 31 (sites A, D, and E) October and 6 (sites A, D and E) and 7 (sites B, C and F) November 2019. The collected crickets were maintained at each site

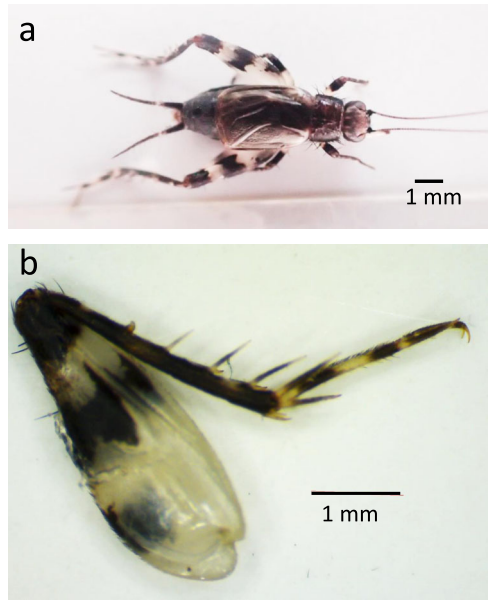


Figure 2. Overall image from dorsal view of male *Dianemobius nigrofasciatus* (a) and autotomised hind leg (b).

in a net bag (50 × 35 cm) with wet cotton. Two to four hours after collection (13:00–15:00), behavioural trials were conducted in a temperature-controlled room (20°C ± 2°C) under fluorescent lights (because the crickets of autumn generation emit calling songs in daylight; T.K., personal observation). According to data from the Japan Meteorological Agency, the temperature of the experiment was the approximate temperature under the field conditions of Kagoshima City. A focal individual was placed in an experimental vial (a clear plastic vial (diameter 3.0 cm × height 7.5 cm) covered with a layer of packing tape) with a lid and placed upright in an experimental arena (17 cm width × 11 cm depth × 12.5 cm height; Figure 3a). The cricket inside the vial was allowed to habituate to the environment for 2 min. After the habituation period, the vials were carefully placed lengthwise in the arena and the lid was removed. The time at which the cricket's head first emerged from the vial was recorded to the nearest 0.1 s using a stopwatch. If the crickets did not emerge in 3 min (180 s), the trial was stopped and the data were treated as censored data. The trial order for each site was conducted in a counterbalanced sequence.

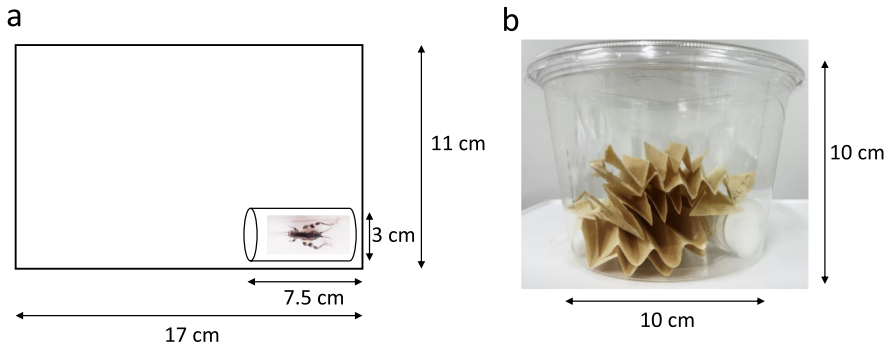


Figure 3. Schematic view of measurement hiding behaviour (a) and an image of rearing container under the predator free conditions. The rearing container contains folded filter papers for shelter and a cotton-plugged water vial.

2.5. Incidence of autotomy under the predator-free and high-density conditions

Between 33 and 50 adult crickets were collected from the above-mentioned six sites on 1 (sites A and B) and 2 (sites C–F) July 2020 and reared under the above-mentioned conditions. F_1 progenies were used in subsequent experiments. Fifty hatchlings were reared in a plastic container (10 cm diameter, 10 cm height) at 26–28°C under a photoperiod of 16:8 h (L:D). The temperature was set to allow for comparison with a previous study (Masaki, 1972). Approximately half of adult individuals emerge after 40 days at 27°C (Masaki, 1972). The crickets were supplied with filter paper for shelter, cotton-plugged water vials, excess cat chow, and rabbit food (Figure 3b). After 40 days, the surviving individuals, developmental stage (i.e., adult or nymph), and the incidence of autotomy were noted. Five to six replicates per site of the experiment were conducted.

2.6. Statistical analyses

All statistical calculations, including the following analyses, were conducted using R 4.0.3 software (R Core Team, 2020). Descriptive statistics of the results are presented as mean \pm SD.

To examine the difference in the incidence of autotomy and developmental stage between urban and rural sites, a generalised linear mixed model (GLMM) using the lmer function in lme4 in version 1.1.14 (Bates et al., 2015). For GLMMs using a binomial distribution, dispersion ratio was calculated using the “performance” package version 0.10.0 to test for overdis-

persion of the data. If the dispersion ratio is much higher than 1, it indicates overdispersion. In the case of a large degree of overdispersion, GLM with the pseudo-likelihood method was conducted. For GLMMs using gamma and normal distributions, plots of standardised residuals against fitted values were checked to examine nonconstant variance. A clear trend in the plot indicates heteroscedasticity (Crawley, 2005). In the case of GLMM using a normal distribution, the Shapiro–Wilk normality test was also performed.

Because the response variables were binary variables, we used GLMMs, assuming a binomial error distribution and logit link function. Site ID was treated as a random effect, and the explanatory variable was habitat type (i.e., urban or rural). Sex and nested temporal variables (i.e., season/sampling days) were chosen as covariates. In the GLMM for the incidence of autotomy, only adults were used in the analysis because nymphs include individuals at various stages, from young to old, and the incidence of autotomy is rare. The incidence of autotomy of nymphs was analysed using Fisher's exact probability test. A likelihood ratio test was used to evaluate the statistical significance of each coefficient in the models. The dispersion ratio of the models of incidence of autotomy and adult:nymph ratio were 1.04 and 1.33, respectively.

In the analysis of body size, because the response variables could be assumed to have a Gaussian distribution, GLMMs with a Gaussian error distribution and identity link were used. Site ID was treated as a random effect, and the explanatory variables were habitat type (i.e., urban or rural), sex, and nested variables (i.e., season/sampling day). There was no significant deviation from normality ($p = 0.25$), and there was no trend in the plot of residuals with the fitted value.

We examined the difference in latency to autotomy between the sites with the highest and lowest incidences of autotomy using a GLMM with gamma error and log link. The gamma distribution was adopted because the response variable was the time to the occurrence of uncensored events (Crawley, 2005). No trend was observed in the plot of the residuals with the fitted values.

To examine the effect of habitat type on the amount of time to emerge from a refuge, Cox proportional hazards regressions, a type of survival analysis with censored data, were conducted using “survival” package version 3.2.13 because the data of individuals that did not emerge until after 3 min were treated as censored data (Dalgaard, 2002).

Survival rate and developmental stage were analysed using GLMMs with binomial error distributions and logit links because the response variables were binary variables. The random effect was site ID. Habitat type was used as the explanatory variable. However, the dispersion ratio of the survival rate model was 13.57, indicating high overdispersion. Therefore, we conducted a GLM with a quasi-binomial distribution to address the overdispersion. The dispersion ratio in the developmental rate was 1.24. The difference in the incidence of autotomy between the rural and urban crickets was compared using Fisher's exact probability test.

3. Results

3.1. Results of the field survey

We sampled 471 crickets from three urban and three rural sites in summer and autumn. The hind legs tended to be missing more often than the middle and front legs (80 of 92 autotomised crickets = 87.0%, $p < 0.001$, binomial test). There were few autotomised crickets (including adults and nymphs) with two or more missing legs (four crickets). The percentages of autotomized nymphs in urban and rural habitats were 7.1% (9/127) and 6.1% (3/49), respectively ($p = 1.0$ with Fisher exact probability test). The incidence of autotomy in adult crickets in urban habitats was significantly higher than in rural habitats (Figure 4: $\chi^2 = 4.84$, $df = 1$, $p = 0.028$). The incidence of autotomy in adult males was significantly higher than that in adult females (autotomised males, 35; intact males, 62; autotomised females, 45; intact females, 153; Figure 4; $\chi^2 = 6.87$, $df = 1$, $p = 0.0087$). The nested variable between the season and sampling day had no significant effect on the incidence of autotomy ($\chi^2 = 2.62$, $df = 2$, $p = 0.27$). The adult:nymph ratio of the urban habitats was significantly lower than that of the rural habitats (Table 2; $\chi^2 = 4.15$, $df = 1$, $p = 0.042$). The nested variable between season and sampling day had a significant effect on the adult: nymph ratio (Table 2; $\chi^2 = 7.94$, $df = 2$, $p = 0.019$).

There was no significant difference in head width between urban and rural sites (Table 3: $\chi^2 = 2.23$, $df = 1$, $p = 0.14$). The head width of males was significantly smaller than that of females (Table 3: $\chi^2 = 162.68$, $df = 1$, $p < 0.0001$). The crickets were larger in summer than in autumn (Table 3: $\chi^2 = 20.94$, $df = 1$, $p < 0.0001$).

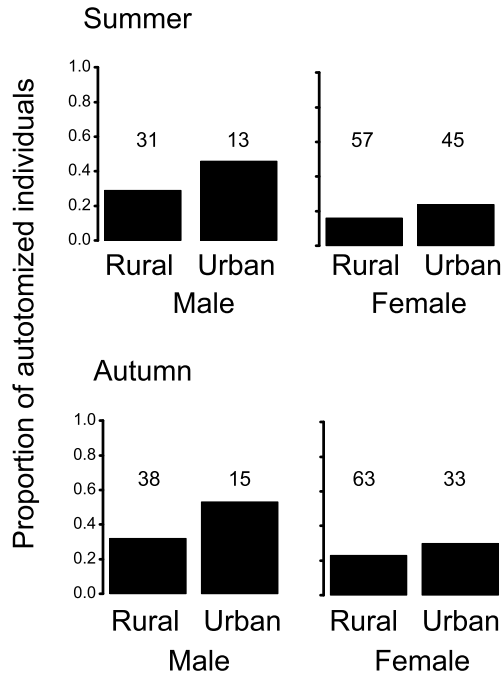


Figure 4. Difference in the proportions of autotomised individual *D. nigrofasciatus* between the urban and rural habitats. Black bars indicate autotomised individuals. The number above the columns indicates the sample size.

3.2. Latency to autotomy

There were no differences in the latency to autotomy of the crickets between the sites with the highest (Figure 1E) and lowest (Figure 1C) incidences of

Table 2.

The number of nymphs and adults of *D. nigrofasciatus* in both urban and rural habitats.

Season	Site	Adult		Nymph		
		♂	♀	♂	♀	Unknown sex
Summer	Urban	13	45	8	8	10
	Rural	31	57	1	2	0
Autumn	Urban	15	33	26	53	22
	Rural	38	63	15	21	10

Unknown sex, nymphs that have not grown enough to identify the sex.

Table 3.Head width of adult *D. nigrofasciatus* in both urban and rural habitats.

Season	Site	Sex	Mean \pm SD (mm)	Sample size
Summer	Urban	♂	1.56 \pm 0.053	24
	Rural	♂	1.60 \pm 0.064	29
	Urban	♀	1.71 \pm 0.067	49
	Rural	♀	1.72 \pm 0.070	56
Autumn	Urban	♂	1.55 \pm 0.092	27
	Rural	♂	1.54 \pm 0.065	29
	Urban	♀	1.66 \pm 0.077	49
	Rural	♀	1.68 \pm 0.089	45

autotomy (highest male: 2.75 ± 2.70 s, $N = 12$; highest female: 2.53 ± 2.44 s, $N = 19$; lowest male: 1.93 ± 1.39 s, $N = 15$; lowest female: 3.38 ± 4.81 s, $N = 16$; $\chi^2 = 0.0023$, $df = 1$, $p = 0.96$), nor were there differences between the sexes ($\chi^2 = 1.51$, $df = 1$, $p = 0.22$). All individuals autotomised their legs in response to artificial stimuli.

3.3. The amount of time to hiding behaviour

There were no significant differences in the amount of time to emerge from a refuge between the urban and rural crickets (urban males: 72.36 ± 80.02 s, $N = 44$; rural males: 80.94 ± 79.55 s, $N = 47$; urban females: 73.39 ± 77.08 s, $N = 49$; rural female: 82.65 ± 80.62 s, $N = 48$; $\chi^2 = 0.12$, $df = 1$, $p = 0.72$) and between the sexes ($\chi^2 < 0.0001$, $df = 1$, $p = 0.96$).

3.4. Incidence of autotomy under the predator-free and high-density conditions

There was no significant relationship between the survival rate during the 40 days and habitat type (urban: 0.42 ± 0.30 , $N = 16$; rural: 0.36 ± 0.22 , $N = 16$; $t_{31} = 1.39$, $p = 0.18$). The developmental stage was not significantly different between the urban and rural habitats (adult rate in urban: 0.23 ± 0.18 ; rural: 0.13 ± 0.14 ; $\chi^2 = 0.76$, $df = 1$, $p = 0.38$). The incidence of autotomy at 40 days was 3 in over 336 individuals ($\approx 0.89\%$) in the urban sites, and 3 in over 291 individuals (about 1.03%) in the rural sites. There was no significant difference in the incidence of autotomy between urban and rural sites (Fisher's exact probability test; $p = 0.86$).

4. Discussion

The incidence of autotomy was higher in urban habitats than in rural habitats. If this result is caused by predation, there are three possible explanations. One possibility is that the predation pressure in urban habitats is higher than that in rural habitats. If this is applicable, it would be possible to estimate predation pressure by using the incidence of autotomy. Because it is practically difficult to estimate predation pressure, if the incidence of autotomy can be used as an alternative indicator of it, then various studies on predator–prey interactions can be developed. The second possibility is that the high incidence of autotomy was due to high predation failure. Urban organisms are often non-native species that do not engage in predator–prey interactions on an evolutionary time scale, and predators may not be able to respond effectively to the predatory avoidance of prey animals. Furthermore, human disturbance often interrupts the foraging behaviour of insectivorous birds in urban habitats (Murison et al., 2007). The third possibility is that urban habitats may be a benign environment for crickets, because even autotomized individuals can survive in their habitats. Autotomized house crickets, *Acheta domesticus*, have been shown to have increased susceptibility to predators (Bateman & Fleming, 2006a). Therefore, the higher incidence of autotomy in urban habitats may be due to crickets surviving for a long time after the leg autotomy. To examine these three possibilities, comparisons of predator compositions and predator–prey interactions between urban and rural habitats are needed.

Because autotomy occurs outside of predation, we examined this possibility: 1) the ease of autotomy in urban crickets is higher than that in rural crickets, 2) the tendency of risk-taking behaviour of urban crickets is higher than that of rural crickets, 3) failure to moult in urban crickets is higher than that in rural crickets, and 4) the aggressive interaction of urban crickets is higher than that of rural crickets. We examined whether these four factors affected the incidence of autotomy. First, the latency to autotomy by the artificial stimulus did not significantly differ between the sites with the highest and lowest incidences of autotomy. Therefore, Factor 1 does not have a major impact on the difference in the incidence of autotomy. Second, there was no significant difference in hiding behaviour. Therefore, Factor 2 did not have a strong effect on the difference in the incidence of autotomy. Finally, there was a low incidence of autotomy (approximately 1%) under high population density and predator-free conditions. Therefore, Factors 3 and 4 did not have

strong effects on the difference in the incidence of autotomy. These results might be considered because the incidence of autotomy mainly reflects predation failure in the habitat.

However, the results of these laboratory experiments should be considered limited because of the large differences between the field environments and laboratory conditions. The fact that the null hypothesis was not rejected does not indicate that the effect of this factor is equal between habitats. In addition, other factors that were not examined in our study may have influenced the incidence of autotomy. For example, non-predatory entrapments, such as tree saps/resins, can also cause autotomy (Maginnis, 2008). A comprehensive list of the factors that can cause autotomy will be developed, and each factor should be examined.

Autotomy causes behavioural and life-history changes in *D. nigrofasciatus*. Matsuoka et al. (2011) showed that autotomy induces active calling behaviour in male *D. nigrofasciatus*. In such cases, the form and direction of the sexual selection may change. If the genetic and/or phenotypic qualities of offspring are enhanced by sexual selection, population dynamics are affected by these changes (Candolin, 2019; Candolin & Wong, 2019). Furthermore, the developmental time of autotomized *D. nigrofasciatus* is significantly shorter than that of intact individuals (Matsuoka & Ishihara, 2010). In urban habitats, approximately half of the males autotomized their hind legs, and the males showed faster growth. Intrinsically, females have shorter developmental period than males (Matsuoka & Ishihara, 2010), but the reduced difference in developmental period may cause a discrepancy in reproductive timing. Such behavioural and life history changes associated with autotomy may spill over into population dynamics at various spatial scales.

Other effects of autotomy include the loss of mobility and energy (Bateman & Fleming, 2005). Because urban environments have a higher ambient temperature and fewer shelters, thermoregulation is more difficult in urban habitats. Although autotomy itself does not change thermoregulatory behaviour in the field crickets *G. assimilis* (Díaz-Ricaurte et al., 2022), decreased locomotor performance will increase the severity of thermoregulation. It is important to investigate the impact of behavioural changes and constraints associated with autotomy on thermoregulation. Furthermore, crickets grow better when they forage for both animal and plant matter (Ogita et al., 2021), but carnivores would need to have higher mobility to catch prey

or to search for dead animals. Given the reduction in locomotor performance by autotomy, foraging efficiency and intra- and interspecific competition will also be affected by autotomy.

It should be noted that urban sites were closer to the ocean than were rural sites. It is possible that proximity to the ocean, such as predator composition and wind strength, rather than the urban environment itself, may promote the incidence of autotomy. Because urban cities often develop along waterfront areas, confounding factors may also need to be considered to understand the evolution of urban environments.

In this study, the incidence of autotomy was higher in males than in females in a field survey. Although females are unlikely to autotomize their legs compared to males in other cricket species (Bateman & Fleming, 2006b, 2008), there was no significant difference in the ease of autotomy between males and females in the present study. As male mating behaviour in various taxa is conspicuous for predators (Andersson, 1994), male *D. nigrofasciatus* may also have a higher predation risk than females. However, in other crickets *G. bimaculatus*, 36% of individuals autotomized in the wild, and there was no difference between the sexes (Bateman & Fleming, 2005). Alternatively, *D. nigrofasciatus* males were smaller than the females. Potential predators can easily prey on males because of their convenient size.

Differences in predation pressure may be an important factor for understanding adaptive evolution in urban environments. The present study showed that the incidence of autotomy is higher in urban habitats, possibly because of predation. Differences in predation pressure on invertebrates between urban and rural habitats has not been well documented, although rigorous verification is still needed of the present results. It will be interesting to investigate how the non-lethal effects of autotomy affect individual behaviour and spill over into population dynamics and community structures in urban environments.

Acknowledgements

We thank Dr. Naoki Matsuda and Dr. Hideharu Numata for providing valuable information regarding *Dianemobius nigrofasciatus*. We would like to thank Editage (www.editage.com) for the English language editing. The manuscript has been significantly improved based on the comments of two anonymous reviewers and the associate editor. The funding for this study was

partially supported by the Special Budget of the Ministry of Education, Culture, Sports, Science, and Technology (MEXT; Establishment of Research and Education Network on Biodiversity and Its Conservation in the Satsuman Islands) and the Japan Society for the Promotion of Science (JSPS) KAKENHI Grant Number 19K21244 (TK). The manuscript has been significantly improved based on the comments of two anonymous reviewers.

References

- Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. — *Trends Ecol. Evol.* 30: 114–126.
- Alberti, M., Correa, C., Marzluff, J.M., Hendry, A.P., Palkovacs, E.P., Gotanda, K.Y., Hunt, V.M., Apgar, T.M. & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. — *Proc. Natl. Acad. Sci. USA* 114: 8951–8956.
- Andersson, M. (1994). *Sexual selection*. — Princeton University Press, Princeton, NJ.
- Bateman, P.W. & Fleming, P.A. (2005). Direct and indirect costs of limb autotomy in field crickets, *Gryllus bimaculatus*. — *Anim. Behav.* 69: 151–159.
- Bateman, P.W. & Fleming, P.A. (2006a). Increased susceptibility to predation for autotomized house crickets (*Acheta domestica*). — *Ethology* 112: 670–677.
- Bateman, P.W. & Fleming, P.A. (2006b). Sex and the single (-eared) female: leg function, limb autotomy and mating history trade-offs in field crickets (*Gryllus bimaculatus*). — *Biol. Lett.* 2: 33–35.
- Bateman, P.W. & Fleming, P.A. (2008). An intra- and interspecific study of body size and autotomy as a defense in Orthoptera. — *J. Orthoptera Res.* 17: 315–320.
- Bates, D., Maechler, M., Bolker, B., Christensen, R.H.B., Singmann, H. & Dai, B. (2015). Package ‘lme4’: linear mixed-effects models using Eigen and S4 (version 1.1-7). — R Foundation for Statistical Computing, Vienna, available online at <https://cran.r-project.org/web/packages/lme4/lme4.pdf>.
- Baxter-Gilbert, J., Riley, J.L. & Whiting, M.J. (2019). Bold new world: urbanization promotes an innate behavioral trait in a lizard. — *Behav. Ecol. Sociobiol.* 73: 1–10.
- Brock, K.M., Bednekoff, P.A., Pafilis, P. & Foufloupoulos, J. (2015). Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? — *Evolution* 69: 216–231.
- Candolin, U. (2019). Mate choice in a changing world. — *Biol. Rev.* 94: 1246–1260.
- Candolin, U. & Wong, B.B. (2019). Mate choice in a polluted world: consequences for individuals, populations and communities. — *Philos. Trans. Roy. Soc. Lond. B: Biol. Sci.* 374: 20180055.
- Cooper, W.E., Pérez-Mellado, V. & Vitt, L.J. (2004). Ease and effectiveness of costly autotomy vary with predation intensity among lizard populations. — *J. Zool.* 262: 243–255.
- Crawley, M.J. (2005). *Statistics: an introduction using R*. — Wiley, Chichester.
- Dalgaard, P. (2002). *Introductory statistics with R*. — Springer, New York, NY.

- Deere, J.A. & Chown, S.L. (2006). Testing the beneficial acclimation hypothesis and its alternatives for locomotor performance. — *Am. Nat.* 168: 630-644.
- Díaz-Ricaurte, J.C., Guevara-Molina, E.C., Alves-Nunes, J.M., Serrano, F.C. & Hrnair, M. (2022). Linking body condition and thermal physiology in limping crickets: does limb autotomy incur costs concerning behavioral thermal tolerance? — *J. Exp. Zool. A.* 337: 393-402.
- Emberts, Z., St. Mary, C.M. & Miller, C.W. (2016). Coreidae (Insecta: Hemiptera) limb loss and autotomy. — *Ann. Entomol. Soc. Am.* 109: 678-683.
- Emberts, Z., Escalante, I. & Bateman, P.W. (2019). The ecology and evolution of autotomy. — *Biol. Rev.* 94: 1881-1896.
- Emberts, Z., St. Mary, C.M., Howard, C.C., Forthman, M., Bateman, P.W., Somjee, U. & Miller, C.W. (2020). The evolution of autotomy in leaf-footed bugs. — *Evolution* 74: 897-910.
- Eötvös, C.B., Magura, T. & Lövei, G.L. (2018). A meta-analysis indicates reduced predation pressure with increasing urbanization. — *Landsc. Urban Plan.* 180: 54-59.
- Eötvös, C.B., Lövei, G.L. & Magura, T. (2020). Predation pressure on sentinel insect prey along a riverside urbanization gradient in Hungary. — *Insects* 11: 97.
- Fisher, D.N., James, A., Rodríguez-Muñoz, R. & Tregenza, T. (2015). Behaviour in captivity predicts some aspects of natural behaviour, but not others, in a wild cricket population. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 282: 20150708.
- Fleming, P.A., Muller, D. & Bateman, P.W. (2007). Leave it all behind: a taxonomic perspective of autotomy in invertebrates. — *Biol. Rev.* 82: 481-510.
- Hedrick, A.V. (2000). Crickets with extravagant mating songs compensate for predation risk with extra caution. — *Proc. Roy. Soc. Lond. B: Biol. Sci.* 267: 671-675.
- Hedrick, A.V. & Kortet, R. (2006). Hiding behaviour in two cricket populations that differ in predation pressure. — *Anim. Behav.* 72: 1111-1118.
- Itescu, Y., Schwarz, R., Meiri, S. & Pafilis, P. (2017). Intraspecific competition, not predation, drives lizard tail loss on islands. — *J. Anim. Ecol.* 86: 66-74.
- Johnson, M.T. & Munshi-South, J. (2017). Evolution of life in urban environments. — *Science* 358: eaam8327.
- Kawaguchi, M. & Kuriwada, T. (2020). Effect of predator cue on escape and oviposition behaviour of freshwater snail. — *Behaviour* 157: 683-697.
- Lagos, P.A. (2017). A review of escape behaviour in orthopterans. — *J. Zool.* 303: 165-177.
- Lambert, M.R., Brans, K.I., Des Roches, S., Donihue, C.M. & Diamond, S.E. (2021). Adaptive evolution in cities: progress and misconceptions. — *Trends Ecol. Evol.* 36: 239-257.
- Maginnis, T.L. (2008). Autotomy in a stick insect (Insecta: Phasmida): predation versus molting. — *Florida Entomol.* 91: 126-127.
- Masaki, S. (1972). Climatic adaptation and photoperiodic response in the band-legged ground cricket. — *Evolution* 26: 587-600.
- Matsuda, N., Fujita, S., Tanaka, K., Watari, Y., Shintani, Y., Goto, S.G., Nisimura, T., Izumi, Y. & Numata, H. (2019). Robustness of latitudinal life-cycle variations in a cricket *Dianemobius nigrofasciatus* (Orthoptera: Trigonidiidae) in Japan against climate warming over the last five decades. — *Appl. Entomol. Zool.* 54: 349-357.

- Matsuoka, N. & Ishihara, M. (2010). Autotomy-induced life history plasticity in band-legged ground cricket *Dianemobius nigrofasciatus*. — Entomol. Sci. 13: 1-7.
- Matsuoka, N., Miyakawa, M. & Ishihara, M. (2011). Effect of hind-limb autotomy on calling and hiding behavior in the band-legged ground cricket, *Dianemobius nigrofasciatus*. — J. Ethol. 29: 209-213.
- McKinney, M.L. (2006). Urbanization as a major cause of biotic homogenization. — Biol. Conserv. 127: 247-260.
- Murison, G., Bullock, J.M., Underhill-Day, J., Langston, R., Brown, A.F. & Sutherland, W.J. (2007). Habitat type determines the effects of disturbance on the breeding productivity of the Dartford Warbler *Sylvia undata*. — Ibis 149: 16-26.
- Ogita, S., Tanaka, Y. & Kuriwada, T. (2021). Effect of diet on body size and survival of omnivorous crickets. — Entomol. Sci. 24: 347-353.
- Orthopterological Society of Japan (2016). The standard of Polyneoptera in Japan. — Gakken Plus, Tokyo (in Japanese).
- Parris, K.M. (2016). Ecology of urban environments. — Wiley, Chichester.
- QGIS Development Team (2021). QGIS geographic information system. — QGIS Association, Laax, available online at <https://www.qgis.org>.
- R Core Team (2020). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna.
- Sugiura, S. (2020). Predators as drivers of insect defenses. — Entomol. Sci. 23: 316-337.
- Talavera, J.B., Carriere, A., Swierk, L. & Putman, B.J. (2021). Tail autotomy is associated with boldness in male but not female water anoles. — Behav. Ecol. Sociobiol. 75: 44.
- United Nations (2018). World urbanization prospects, the 2018 revision. — United Nations, New York, NY.
- Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. — Ecology 84: 1083-1100.