



## Differential frequency of autotomy in two colour morphs of the grasshopper *Atractomorpha lata* (Orthoptera: Pyrgomorphidae) on dense and sparse grass substrates

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**Abstract.** Background colour matching is considered highly effective in preventing the detection of an animal by visual predators. In a grasshopper species with green-brown polymorphism, a green morph on grass and a brown morph on bare ground or dead litter may be difficult for visual predators to distinguish from their respective backgrounds. However, few studies have examined the effects of background colour on the predation susceptibility of green and brown morphs of grasshoppers under natural conditions. In this study, the frequency of injuries including autotomy in the green-brown polyphenic grasshopper *Atractomorpha lata* was compared between two substrates: dense green grass and sparse grass (i.e., mixed cover consisting of 50% green grass and 50% bare soil or dead litter). More than half of injuries were hind-limb autotomy. The frequency of injuries was higher on dense grass for the brown morph than for the green morph, but on sparse grass it was higher for the green morph than for the brown morph. Because autotomy in orthopterans is almost always caused by birds, we conclude that background colour matching in *A. lata* functions as camouflage against predators with colour vision, such as birds.

### INTRODUCTION

In animals, body colour plays important roles in avoiding predation. In particular, background colour matching is considered highly effective for preventing the detection of an animal by visual predators (Cuthill, 2019). Although it is often thought to be intuitively obvious that predation is avoidable through camouflage including background matching (Stevens & Merilaita, 2009), this phenomenon has rarely been verified in natural habitats (e.g., Cook et al., 2012).

Green-brown polymorphism is widely shared across orthopteran insects (Rowell, 1972; Schielzeth, 2020). For example, a green morph on green grass and a brown morph on bare ground or dead litter may be difficult for visual predators to distinguish from their respective backgrounds (Pellissier et al., 2011; Heinze et al., 2022). Laboratory experiments using animals with green-brown polymorphism have demonstrated that each colour morph is difficult for visual predators to detect in different environments (Hidaka et al., 1959; Morey, 1990). However, little is known about how body colour differences affect the predation susceptibility of grasshoppers under natural conditions.

To clarify the adaptive significance of body colour, mortality rates have been compared between different body colour morphs in field experiments (Wiklund, 1975; Hazel et al., 1998; Cook et al., 2012). Notably, such experiments

can obscure the effects of body colour on mortality because deaths caused by colour-blind predators and diseases are typically included in total mortality rates. Therefore, it is important to investigate predation pressure only by predators with colour vision.

Among predators with colour vision, birds strongly impact grasshopper populations (Bryant, 1914; Joern, 1986). However, it is very difficult to quantify grasshopper predation by birds in the field (e.g., Bröder et al., 2023). Instead of directly observing predation, attempts have been made to estimate predation pressure from signs of attack, such as wounds on an insect's body. For example, when a butterfly is attacked by a bird or lizard and escapes without being eaten, scars or beak marks may be left on its wings. Due to the correlation between the proportion of individual butterflies with beak marks and butterfly mortality, this sign is considered a suitable indicator of predation pressure (Ide, 2006; Kiritani et al., 2013).

In grasshoppers, autotomy may be able to be used as an indicator of predation pressure instead of beak marks. Autotomy is the self-controlled loss of a body part at a predetermined breakage location (Emberts et al., 2019). Many orthopteran species use autotomy to escape predation when a body part is grasped (Fleming et al., 2007). The autotomy of the hind limb of a grasshopper occurs only when the animal is grasped around the joint between the femur

and tibia; grasping any other part of the limb and the body does not result in autotomy (Nishida, 2008). Therefore, the autotomy is primarily caused by predators that attempt to grab the limbs rather than the body when attacking grasshoppers. In an experiment in which quails, frogs, and praying mantises were used as predators to examine whether they would induce autotomy in grasshoppers, the quails frequently induced autotomy, while the frogs induced autotomy only once when they happened to bite the femur-tibia joint of a grasshopper, and the praying mantises never induced autotomy (Okada, unpubl. data, cited in Nishida, 2008). Consequently, it is reasonable to suppose that the predator that cause autotomy in orthopterans is bird.

In insects, autotomy does not only occur when a predator grabs a limb; it can also occur when moulting fails (Maginnis 2008), when the limbs are injured (Emberts et al., 2017), or when the limbs become stuck to a carnivorous plant (Krueger et al., 2023). In these cases, unlike the type of autotomy that occurs immediately after a predator attack, autotomy occurs several tens of minutes after the limbs become immobile (Emberts et al., 2020). Therefore, autotomy cannot be simply taken as evidence of a predator attack. However, if the frequency of autotomy due to causes other than predator attacks does not differ between treatments, the frequency of autotomy would reflect predation pressure. Indeed, among animals that exhibit autotomy, its frequency in natural populations varies according to predation pressure (Cooper et al., 2004). Therefore, the frequency of autotomy may serve as an indicator of bird predation pressure against orthopterans in the field.

In this study, we investigated whether the frequency of autotomy in the green-brown polymorphic grasshopper *Atractomorpha lata* (Motschoulsky) differs depending on their body colour, with the goal of determining whether background colour matching prevents predation of *A. lata*.

## MATERIAL AND METHODS

### Organisms

*Atractomorpha lata* (Orthoptera: Caelifera: Pyrgomorphidae) is a grasshopper that inhabits short grasses in northern China, Taiwan, the Korean Peninsula and most parts of Japan. In Japan, this species has one generation in a year, with adults appearing from late August to November, and exhibits sexual dimorphism, such that females are significantly larger than males. Adults of both sexes display green-brown body colour polymorphism (Fig. 1). Colour variation in this species is due to phenotypic plasticity, and the term “polyphenism” has been used as a refined terminology to distinguish environmentally induced phenotypic variation from genetically determined polymorphisms. *Atractomorpha lata* individuals tend to be brown when grown at high temperatures, but background colour does not affect their body colour (Tanaka, 2008). The temperatures of *A. lata* microhabitats are higher on bare soil and litter than on grass in sunny areas (Stoutjesdijk, 1980), such that body colour changes caused by temperature appear to provide cryptic colouration that matches the habitat (Tanaka, 2008). However, *A. lata* individuals do not actively choose a background that matches their own body colour (Ide, 2022).

### Field investigation

Grasshoppers were captured from 17 September to 2 December, 2019 on patches of either dense grass (height 5–30 cm; green



Fig. 1. Green (male) and brown (female) morphs of *Atractomorpha lata*.

grass with no visible bare soil; approximately 4 ha) or sparse grass (height < 10 cm; mixed cover consisting of 50% green grass and 50% bare soil or dead litter; approximately 400 m<sup>2</sup>) in rural Kurume, Fukuoka, southern Japan (Fig. 2). These patches were spaced 1 km apart in a rural landscape. The most commonly observed predators in these patches were birds such as bull-headed shrike *Lanius bucephalus* and meadow bunting *Emberiza cioides*. Each adult grasshopper was captured by placing a plastic container over it to prevent damage; it was then transported to



Fig. 2. Study area. (A) dense grass, (B) sparse grass.

the laboratory, where its sex and body colour were determined. Injuries (partial loss of limbs, antennae, and wings) were recorded, and body weight was measured using a digital balance with accuracy to the nearest 0.1 mg. More than half of injuries were hind-limb autotomy, which occurred at the trochanter-femur joint. Therefore, analyses were performed separately for the frequency of hind-limb autotomy alone and the frequency of all injuries including autotomy. *Atractomorpha lata* individuals rarely fly and are highly sedentary (Miyatake & Kano, 1992; Chung et al., 1997); therefore, it was assumed that no grasshoppers moved between the dense and sparse grass, and that injuries had occurred in the field where they were captured.

### Statistical analyses

Statistical analyses were conducted using R version 3.6.3 (R Core Team, 2020). To determine whether the colour morph proportion was biased in *A. lata*, a binomial test was performed. The proportion of colour morphs were compared between sexes and between substrates using Fisher's exact probability test. Body weight of *A. lata* was compared between colour morphs with Welch's *t*-test.

A generalised linear model with a binomial error structure was used to identify factors influencing the frequency of autotomy in *A. lata*; the state of the hind legs of each individual (i.e., both legs intact or one leg autotomised) served as the dependent variable, whereas body colour, capture substrate (dense or sparse grass), sex, and interactions among all factors served as independent variables. We also performed a similar analysis to identify factors influencing the frequency of injuries including autotomy, with presence or absence of injury as the dependent variable. The 'glm' function was used for these analyses. Model selection was performed using the 'dredge' function in the *MuMIn* package (Bartoń, 2023) to compare the Akaike information criterion (AIC) values of all potential candidate models and select the model with the lowest AIC value.

## RESULTS

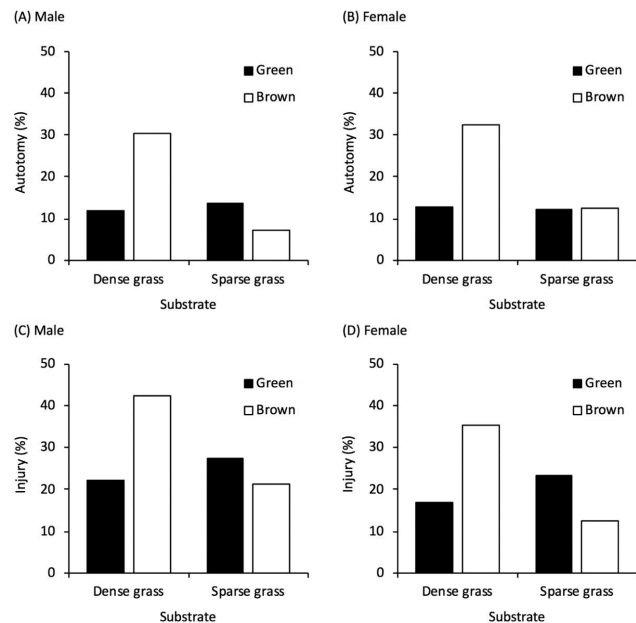
Overall, 1261 individual grasshoppers were sampled; of these, 1031 were found on dense grass and 230 were found on sparse grass substrates (Table 1). The green morph represented the majority of all grasshoppers collected on both substrates, and the proportions did not significantly differ between sexes (Fisher's exact probability test: dense grass:  $P = 0.900$ , sparse grass:  $P = 0.699$ ). The brown morphs of both sexes were slightly rarer on dense grass than on sparse

**Table 1.** Percentages of green and brown colour morphs of *Atractomorpha lata* captured on each substrate. Green morphs were always more than brown morphs (binomial test).

Sex	Substrate	N	Green morph (%)	Brown morph (%)	<i>P</i>
Male	Dense grass	518	93.6	6.4	< 0.0001
	Sparse grass	116	87.9	12.1	< 0.0001
Female	Dense grass	513	93.4	6.6	< 0.0001
	Sparse grass	114	86.0	14.0	< 0.0001

**Table 2.** Body weight measurements for green and brown colour morphs of *Atractomorpha lata* captured on each substrate. Data are presented as means  $\pm$  standard errors. Differences were evaluated using the Welch's *t*-test.

Sex	Substrate	Green morph (mg)	Brown morph (mg)	<i>t</i>	<i>df</i>	<i>P</i>
Male	Dense grass	91.7 $\pm$ 0.5	93.5 $\pm$ 1.8	1.014	37.18	0.317
	Sparse grass	91.9 $\pm$ 1.1	96.5 $\pm$ 4.3	1.027	14.73	0.321
Female	Dense grass	451.5 $\pm$ 4.5	453.6 $\pm$ 22.1	0.096	35.8	0.924
	Sparse grass	504.9 $\pm$ 9.9	472.9 $\pm$ 26.2	-1.146	19.50	0.266



**Fig. 3.** Proportions of individuals with hind-limb autotomy or with injuries (including autotomy) for the green and brown morphs of *Atractomorpha lata* on dense and sparse grass substrates. (A) autotomy of males, (B) autotomy of females, (C) injuries of males, and (D) injuries of females.

grass (Fisher's exact probability test: male:  $P = 0.048$ , female:  $P = 0.012$ ). Grasshopper weight did not significantly differ between colour morphs on either substrate (Table 2).

In total, 169 autotomised individuals were captured, all of which had only one hind leg missing. The total proportion of autotomised males was 13.1%. On dense grass, the proportion of autotomised males was higher for brown morph than for green morph, but on sparse grass it was higher for green morph than for brown morph (Fig. 3A). The total proportion of autotomised females was 13.7%. The proportion of autotomised females on dense grass was also higher for brown morph than for green morph, but on sparse grass it was similar between both morphs (Fig. 3B). The generalised linear model that best predicted the frequency of autotomy included body colour, substrate, and their interaction (AIC = 985.9; Table 3). Thus, the frequency of autotomy was significantly higher for brown morph than for green morph, on dense grass than on sparse grass, and the body colour with the higher frequency of autotomy differed between substrates. Sex was not selected as an independent variable for the best model, i.e., sex did not affect the frequency of autotomy.

The total proportions of individuals with injuries including autotomy were 24.0% for males and 18.8% for females. Among grasshoppers collected from dense grass, the proportions of injured individuals of both sexes were



**Table 3.** Summary of generalised linear model selection of the factors influencing the frequency of autotomy in *Atractomorpha lata*. Only variables included in the selected model are shown. The base category for each variable is shown in parentheses. SE – standard error.

Variable	Estimate	SE	z	P
Intercept	−0.7841	0.2634	−2.977	0.0029
Body colour (green)	−1.1761	0.2810	−4.186	<0.0001
Substrate (sparse grass)	−1.4131	0.6631	−2.131	0.0331
Body colour × substrate	1.4724	0.7025	2.096	0.0361

higher for the brown morph than for the green morph (Fig. 3C, D). On the contrary, it was higher for the green morph of both sexes on sparse grass. The generalised linear model that best predicted the proportions of injured individuals included body colour, substrate, sex, and interaction between body colour and substrate (AIC = 1299.9; Table 4). This indicated that the proportion of injured individuals was significantly higher for brown morph than for green morph, on dense grass than on sparse grass, for male than for female, and that the more frequently injured colour morph differed between substrates.

**Table 4.** Summary of generalised linear model selection of the factors influencing the frequency of injury in *Atractomorpha lata*. Only variables included in the selected model are shown. The base category for each variable is shown in parentheses. SE – standard error.

Variable	Estimate	SE	z	P
Intercept	−0.6120	0.2612	−2.342	0.0192
Body colour (green)	−0.9702	0.2644	−3.670	0.0002
Substrate (sparse grass)	−1.1513	0.5514	−2.088	0.0368
Sex (male)	0.3122	0.1391	2.244	0.0248
Body colour × substrate	1.4962	0.5806	2.577	0.0100

## DISCUSSION

### Autotomy as a proxy for predation pressure

It is reported that the frequency of autotomy in animals is influenced by various factors, including not only the detectability but also daily activity patterns and the intensity of male-male competition (Kuo & Irschick, 2016; Moura et al., 2023). In order to use autotomy as a proxy for predation pressure, it is necessary to control these factors. Therefore, we first examine whether autotomy and injuries are reliable indicators of predation pressure on the two colour morphs of *A. lata*.

When investigating autotomy frequencies at different sites, different predator faunas can be problematic. This is because the proportion of prey that die before autotomy varies according to predator's hunting efficiency, resulting in different frequencies of autotomy (Medel et al., 1988; Bateman & Fleming, 2011). Therefore, correlations between the frequency of autotomy and predation pressure may apply in only a limited number of situations; however, we compared prey living in habitat patches with similar predator fauna and prey conditions to increase the likelihood that the frequency of autotomy was a suitable proxy for predation pressure. Grasshoppers were collected from dense and sparse grass patches with low vegetation height,

located in close proximity to each other; therefore, both substrate types were assumed to share common predators.

The frequency of autotomy also varies according to the willingness of the prey to autotomise a body part, which varies based on characteristics such as body size and sex of prey (Dixon, 1989; Bateman & Fleming, 2006a, 2008). This would distort the relationship between predation pressure and the frequency of autotomy. For example, larger individuals tend to be reluctant to autotomise because they may be able to escape predators by kicking or biting (Bateman & Fleming, 2008). With regard to sex, males are reluctant to autotomise if autotomy would put them at a disadvantage in the competition for females (Dixon, 1989). Significant sexual differences in body size in *A. lata* confound these factors, making it difficult to predict which sex will have a higher frequency of autotomy. As a result, there was no difference in the frequency of autotomy between sexes, but the reason is unknown. Because multiple mechanisms may be involved, resulting in similar autotomy frequencies by chance, data for males and females should be analysed separately. When the sexes were separated, body size did not differ between *A. lata* colour morphs in either sex, suggesting that at least the willingness to autotomise a leg was similar between colour morphs.

If survival of autotomised individuals decreases (e.g., Bateman & Fleming, 2006b; Miura & Ohsaki, 2015), predation pressure may be underestimated. However, because grasshoppers change their behaviour to mitigate the negative effects of autotomy (Tsurui et al., 2014), the reduction in survival due to autotomy may not be significant. Furthermore, this study focuses on differences in predation pressure between colour morphs. If the survival of autotomised individuals of both colour morphs declines similarly, which would be likely, the difference in frequency of autotomy between colour morphs could be taken as reflecting differences in predation pressure.

All nymphs of *A. lata* are green when they hatch, but brown individuals appear in the late nymphal stage, and then the adult body colour does not change. If limb loss during green nymphal stages remain in adults, this could be a noise when investigating the relationship between adult body colour and predation pressure. However, because birds tend to be attack larger grasshoppers (Belovsky et al., 1990), it is unlikely that birds will induce autotomy in grasshopper nymphs. For example, in crickets, the proportion of individuals with injuries increased significantly after they became adults (Cherrill & Brown, 1997). Therefore, although injuries that are sustained during nymphal stage can remain in adulthood, it is reasonable to assume that most injuries on adult grasshoppers were sustained after they reached adulthood.

Because aggressive contests between *A. lata* males often occur (Fujimori, 1990), injuries other than autotomy may have been caused by male-male contests. Therefore, it is not always the case that the frequency of injuries in males reflects predation pressure. However, *A. lata* females are basically passive in the process of copulation and physical conflict between sexes and female-female aggression are

rarely observed (Fujimori, 1990; Muse & Ono, 1996), suggesting that it is appropriate to use injuries on females as an indicator of predation pressure.

As described above, using autotomy and injuries as proxies for predation pressure has multiple concerns, and comparing males and females is particularly inappropriate. However, in this study, it can be concluded that the frequency of autotomy and the frequency of injuries can generally be used as proxies for predation pressure.

### Influence of background colour matching on predation susceptibility

The results support the hypothesis that each colour morph of *A. lata* is cryptic to predators that have colour vision against different microhabitats. The frequency of autotomy was higher on dense green grass for both sexes of the brown morph; the frequency of autotomy for the male green morph was higher on the sparse grass substrate with partial coverage by brown soil or dead litter, although there was no difference between colour morphs in females. When considering all injuries including autotomy, the proportion of injured individuals was higher for green than for brown morph on sparse grass, also in females. In short, in both males and females, the brown morph was more likely to be attacked by predators on dense grass, while the green morph was more likely to be attacked on sparse grass. In other words, in environments with different background colours, different-colour morphs are less likely to be attacked in an environment that matches their body colour, thus favouring the occurrence of two different cryptic colour morphs within a population (Merilaita et al., 1999; Pellissier et al., 2011). Nonetheless, few studies have demonstrated that the orthopteran colour morph preyed upon more often differs among habitats according to colour.

Some previous studies that examined the predation susceptibility of (non-orthopteran) colour-polymorphic species in two sites with different background colours revealed higher predation rates in morphs that did not match the background colour, i.e., highly attacked colour morphs differed between the sites (Sims & Shapiro, 1983; Sandoval, 1994; McKillup & McKillup, 2002; Duarte et al., 2018), whereas others did not show such pattern (Edmunds & Grayson, 1991; Hazel et al., 1998; Rich et al., 2021). Many of these field studies examined prey survival or attack rates as indicators of attacks by any predator species, rather than focusing on specific predators. However, numerous predators do not have colour vision, and frequent predation by such species may prevent the detection of any camouflage effect achieved by background colour matching by the prey species. For example, in summer, a green swallowtail pupa morph had a higher survival rate than a brown morph on a green background and a brown morph had a higher survival rate on a brown background, whereas there was no difference in survival rates in winter (Wiklund, 1975). This finding appears to be related to the lack of colour vision in the small nocturnal mammals that were the main predators of these pupae in winter. In the present study, the frequencies of autotomy of green and brown grasshopper morphs were reversed between dense and sparse grass substrates,

perhaps because only the attacks by predators with colour vision (i.e., birds) were detected. In field studies examining predation rates of artificial prey models, the rank order of predation susceptibility between colour morphs is often reversed in different locations (Vignieri et al., 2010; Yamamoto & Sota, 2020; Otte et al., 2024), presumably because olfactory predators are implicitly eliminated and only visual predators attacked the models.

The rate at which colour-polymorphic prey species are attacked may be influenced by factors other than variation in conspicuousness among colour morphs. For example, predators may primarily consume the most abundant prey morph (Murdoch & Oaten, 1975; McKillup & McKillup, 2008), or predators may form search images for frequently encountered prey items, improving their ability to detect prey (Tinbergen, 1960; Dawkins, 1971). Such behaviour may lead to frequency-dependent prey choice. In the present study, the brown morph of *A. lata* was a minority in both substrates, with particularly low proportions on dense grass. Nonetheless, the frequency of autotomy was higher for the brown morph than for the green morph on dense grass, such that the brown morph was more frequently attacked by birds. Therefore, even if predators of *A. lata* engaged in frequency-dependent predation, it would have had little effect on the total predation pressure.

Animals with different body colours may have different body temperatures. In members of order Orthoptera, a higher degree of melanism is generally associated with higher body temperature due to solar radiation absorption (Forsman et al., 2002; Köhler & Schielzeth, 2020). Individuals with a high body temperature are active, such that melanised individuals may be able to quickly react and evade attacks (Civantos et al., 2004). Therefore, body colour may indirectly affect predation susceptibility through body temperature. For example, in two alpine grasshopper species, brown morphs were 1.5°C warmer than green morphs (Köhler & Schielzeth, 2020). If brown morphs of *A. lata* also have a higher body temperature than green morphs, then brown morphs would be expected to experience less predation, particularly on dense grass, where temperatures tend to be lower than those on bare soil or dead litter (Stoutjesdijk, 1980). However, it remains unknown whether body temperature differs between colour morphs in *A. lata*. The relationship between body colour and body temperature in *A. lata* should be investigated in a future study.

When comparing between substrates, grasshoppers were attacked more frequently on dense grass than on sparse grass. This may be because sparse grass offers greater complexity of background colour. Some studies have shown that visual background complexity make it difficult to detect prey (Merilaita, 2003; Dimitrova & Merilaita, 2010; Rowe et al., 2021). Sadiq & Kodandaramaiah (2023) found that colour diversity on the background impeded prey detection, and expected that green-brown dimorphic grasshoppers would have higher survival on backgrounds with both colours (e.g., grass and soil). The results of this study support this prediction.

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