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ORIGINAL ARTICLE

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Patterns in the autotomized adults of two sympatric, closely related grasshopper species in their natural habitat

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Abstract Insects have various defense responses to natural enemies, including autotomy. Detailed knowledge of autotomy patterns and frequencies in the wild is required to make reliable inferences concerning the fitness benefits and costs of the consequences of autotomy. However, few quantitative surveys have been conducted on the frequency of autotomized insects in the wild. Here, I examined data on autotomy in adult *Parapodisma tanbaensis* and *Parapodisma subastris* grasshoppers, which are sympatric, closely related species, collected over two consecutive years at three field sites in Kyoto, Japan. To investigate what traits were related to the frequency of autotomized adults, I recorded the species, sex, body size, and hind leg status after sampling adults because, according to previous research, these four parameters can be used to make predictions about the frequency of autotomized adults in the wild. There was a significant interaction effect between grasshopper sex and the sampling season on the frequency of autotomized adults and a non-linear increase in the frequency of autotomized adults as the season advanced. However, there were no significant effects caused by species or body size. Thus, a sexual difference existed in the occurrence and disappearance of autotomized adults in the wild as the season advanced. The ecological and evolutionary factors and mechanisms causing this pattern are discussed.

Keywords Autotomy · Body size · Inefficient predator · Insect defense · Sexual difference

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Introduction

Insects have various defense responses to natural enemies (Edmunds 1974), including autotomy, which is the voluntary shedding of a body part. It usually occurs in response to predation and can allow an insect to escape from a predator (Bateman and Fleming 2011; Juanes and Smith 1995). Autotomy is found in many taxa (Arnold 1984; Juanes and Smith 1995; Maginnis 2006; Fleming et al. 2007) and has evolved many times independently (Bateman and Fleming 2005), which suggests that there is frequently a strong selective advantage in the loss of a body part (Fleming et al. 2007). While the loss of a body part by autotomy can benefit an individual's chance of survival by allowing the insect to escape from attacking predators, it has many costs because of the loss of the resources in the body part and also the loss of function associated with the body part, which affect long-term survival and reproduction (Maginnis 2006; Bateman and Fleming 2009). There are no clear taxonomic patterns regarding the incidence of autotomy and, in fact, a high degree of variability has been seen among taxa. Thus, the incidence of autotomy may reflect environmental processes acting upon individual taxa rather than simple phylogenetic patterns alone (Juanes and Smith 1995; Fleming et al. 2007). To make more reliable inferences concerning the fitness benefits and costs of the consequences of autotomy, detailed knowledge of the frequency of autotomy in a species or population in the wild, including their annual and spatial variations, is required (Smith and Hines 1991).

Insects may autotomize labial palps, legs, antennae, caudal lamellae, and stingers (Fleming et al. 2007). Autotomy in insects in the wild has been investigated extensively only in Odonata larvae and Orthoptera adults (Fleming et al. 2007). In Odonata, the aquatic larvae possess three leaf-shaped caudal lamellae that form an important surface for gas exchange and also aid in swimming (Fleming et al. 2007). In Texas, USA,

~50.0% of *Ischnura posita* larvae were reported to be missing at least one caudal lamella or regenerating one caudal lamella (Robinson et al. 1991). In a papyrus swamp in western Uganda, Africa, 56% of *Proischnura subfurcatum* larvae were reported to be missing at least one gill (Apodaca and Chapman 2004). In a small temporary fishless pond near Antwerp, Belgium, ~90% of *Lestes viridis* larvae were reported to be missing at least one caudal lamella and ~20% were missing all three lamellae (Stoks 1998). In orthopteran insects, hind legs, which are used for jumping (Bennet-Clark 1990; Bateman and Fleming 2005), may be lost through autotomy (Dixon 1989; Bateman and Fleming 2005). Adults lacking a hind leg due to autotomy not only show reduced speeds but also perform fewer jumps during an escape (Bateman and Fleming 2005, 2006). Approximately 20% of adults of the bush cricket *Scudderia texensis* in southern Oklahoma, USA (Dixon 1989) and ~35% of adults of the field cricket *Gryllus bimaculatus* in Pretoria, South Africa, were reported to be missing at least one hind leg (Bateman and Fleming 2005). In central Florida, USA, 29.8% of the semiaquatic grasshopper *Paroxya atlantica* individuals were reported to be missing a hind leg, while none were missing both hind legs (Bateman and Fleming 2011). In Kentucky, USA, 11.9% of male adult cave crickets (*Hadenoecus subterraneus*) were reported to have lost their hind leg(s) and 12.8% of female adults had lost theirs (Chandoo et al. 2013). On the isle of Langeoog in Germany, 14.4% of male and 9.6% of female adult Cepero's groundhoppers, *Tetrix ceperoi*, captured in their habitat were reported to have lost their hind leg(s) (Hochkirch et al. 2007). However, there have been few long-term quantitative surveys on the patterns and frequencies of autotomy in insects. Most assessments have consisted of only a single or within-year samplings of insects, and the traits of the insects related to the frequency of autotomy have rarely been examined (Dixon 1989; Robinson et al. 1991; Stoks 1998; Bateman and Fleming 2005, 2011; Fleming et al. 2007; Hochkirch et al. 2007).

The grasshoppers *Parapodisma subastris* and *Parapodisma tanbaensis* (Orthoptera: Catantopidae) are distributed in the Kinki District of Honshu Island, Japan, and are often observed to exhibit the loss of a hind leg(s) in the wild (Miura and Ohsaki 2007). Miura and Ohsaki (2015) suggested that the mortality caused by the emergence of the parasitoid fly *Blaesoxipha japonensis* (Diptera: Sarcophagidae) from adult *P. subastris* grasshoppers could be one of the costs of autotomy because *P. subastris* adults lacking a hind leg are more frequently killed by the emergence of this parasitoid fly than intact adults. In contrast to *P. subastris*, *P. tanbaensis* adults lacking a hind leg(s) and intact adults did not differ in the mortality caused by the emergence of *B. japonensis* (Miura and Ohsaki 2015), although the distribution of these two *Parapodisma* species is sympatric in the Kinki District (Miyatake and Kanô 1992; Miura 2003; Miura and Ohsaki 2007). However, it remains unknown what traits and/or factors may be related to the frequency of hind leg loss in these *Parapodisma* adults in the wild.

Previous experiments showed that some organismal traits are related to the occurrence of autotomy. Thus, I focused on four such traits in these *Parapodisma* grasshoppers, sex, body size, collection season, and species identity. First, the sex of the adult grasshoppers could be related to the occurrence of autotomy because of the differences in behavior and physiology between the sexes (Fleming et al. 2007; Hochkirch et al. 2007). For example, males look for females for mating and perform a display for the females (Hochkirch et al. 2007). Such male-specific behavior will attract not only females of the same species but also predators. Thus, the frequency of males missing a hind leg would be expected to be higher than that of females in the wild.

Second, the body size of individuals could directly and/or indirectly affect the occurrence of autotomy (Fleming et al. 2007; Bateman and Fleming 2008). More frequent predator attacks occur on larger prey, as predicted by the optimal foraging theory, causing a higher frequency of large autotomized adults. However, larger prey may show a lower frequency of autotomized adults because larger animals can rely on armor or retaliation (kicking, biting or struggling), which are much more effective responses than autotomy (Bateman and Fleming 2008), when predators attack them. In addition, larger animals may incur a greater cost of locomotion after losing a leg because of the greater body mass (Bateman and Fleming 2008). Because body size is often related to other traits, such as sex and species, it may be indirectly correlated to the frequency of autotomized individuals. To remove this indirect effect, we considered the body sizes of both *Parapodisma* species in the statistical analysis.

Third, the frequency of autotomized individuals differs depending on their age (Schoener 1979; Fleming et al. 2007) because limb regeneration appears to be rare or incomplete in orthopteran insects (Bateman and Fleming 2008). In addition, mating experiences can increase the occurrence of autotomy, as shown by the mated females of the field cricket *G. bimaculatus*, which lose more legs than the virgin females, while there was no significant difference between virgin and mated males (Bateman and Fleming 2006). Thus, the frequency of *Parapodisma* autotomized adults could be predicted to increase as the season advanced.

Fourth, the frequency of autotomized individuals differs among grasshopper species (Fleming et al. 2007). The abiotic and biotic factors, as well as the ecological mechanisms, that influence the autotomy of *Parapodisma* species could differ between the species even if their distribution is sympatric. For example, the species-specific nutritional needs of various polyphagous insect herbivores (Behmer and Joern 2008), or the reproductive interference among them (Gröning et al. 2007), could cause them to prefer different microhabitats or plant uses, resulting in habitat segregation even if their distribution is sympatric (Miura and Ohsaki 2015). Not only food plants and abiotic conditions, but also natural enemies, could differ among the microhabitats. As indicated by the difference in adult mortality caused by *B. japonensis* between *P. subastris* and *P. tanbaensis* (Miura and Ohsaki 2007), the fate of autotomized individuals could differ between these *Parapodisma* species (Miura and Ohsaki 2015).

I recorded the four traits mentioned above, and the conditions of the hind legs of *P. tanbaensis* and *P. subastris* adults in the wild, by simultaneously sampling them for two consecutive years at three locations in Kyoto, Japan, and then I examined the answers to the following questions: (1) Does the frequency of autotomized adults differ between the sexes? Is the frequency of autotomized males higher than that of autotomized females?; (2) Does the body size of adults influence the likelihood of autotomy? For example, do larger adults show a higher likelihood of autotomy?; (3) Does the frequency of autotomized adults increase as the adults age or as the season advances?; and (4) Does the frequency of autotomized adults differ between these two species? Finally, I discuss the factors and mechanisms related to the observed patterns and frequencies of autotomized adults in these two *Parapodisma* species from ecological and evolutionary perspectives.

Methods

Study species and sampling

P. tanbaensis and *P. subastris* are univoltine, overwinter as eggs, and feed on a wide range of dicotyledonous plants (Miyatake and Kanô 1992; Miura and Ohsaki 2004). *P. tanbaensis* occurs only in the Kinki District, whereas *P. subastris* occurs in the Kinki and Tohkai Districts, Honshu Island, Japan (Miyatake and Kanô 1992). In Kyoto (in the Kinki District), adult grasshoppers of both species occur from July to October (Miura 2003; Miura and Ohsaki 2007). For orthopteran insects, the lack of a hind leg(s) occurs in the natural habitat (Dixon 1989; Bateman and Fleming 2005; Hochkirch et al. 2007; Miura and Ohsaki 2007), and limb regeneration appears to be rare or incomplete (Bateman and Fleming 2008). Limb regeneration has not been observed in either of the *Parapodisma* species studied here (Miura, personal observation). Because *Parapodisma* adults are brachypterous (Miyatake and Kanô 1992), they retreat from the natural enemies they encounter only by jumping and/or walking. Thus, the functions of hind legs in the movement of *Parapodisma* grasshopper adults may be more important than their functions in macropterous grasshopper adults (Miura and Ohsaki 2015).

Parapodisma adults were captured once a month in 2001and 2002 from July to October in three locations (Kibune, Kumogahata, and Mt. Hiei) in Kyoto. After looking for *Parapodisma* adults and carefully capturing them using a net, I identified the species and measured the prothorax length using a caliper as an index of body size (Miura and Ohsaki 2007, 2014, 2015). The grasshoppers were generally captured individually. There were no hind legs of grasshoppers remaining in the net after they were captured. The details of the procedures have been described previously in Miura (2003) and in Miura and Ohsaki (2007, 2015).

Statistical analysis

The loss of hind leg(s) in grasshopper was a categorical variable, with intact grasshoppers ranked as zero and ones lacking hind leg(s) ranked as one. Grasshopper species and sex were also categorical variables Grasshopper body size was a continuous variable. Month was also a continuous variable that allowed the examination of whether the frequency of autotomized adults changed based on the capture time. I examined whether the frequency of autotomized individuals increased as the seasons advanced. I designated the sample data from July as “15 days”, the sample data from August as “45 days”, and the sample data from September as “75 days” (Miura and Ohsaki 2014, 2015). Because few insects were captured in October, the data from October were combined with those from September in the statistical analysis. JMP version 12.2 was used for all statistical analyses (SAS Institute, Cary, NC, USA, 2015).

The factors related to the hind leg loss in each *Parapodisma* grasshopper species were examined using a generalized linear model with a binomial error distribution and a logit link function. In this analysis, I selected the generalized linear model based on overdispersion tests and intervals, and Firth’s bias-adjusted estimates were included in the model specifications (SAS Institute, Cary, NC, USA, 2015). To focus on the factors in questions, I examined four main effects (month, grasshopper species, grasshopper sex, and body size), six interaction effects between the main effects, and one quadratic term, month, which was examined to determine whether the frequency of autotomy changed linearly or non-linearly as the season advanced.

Results

The quadratic term of month and the interaction between sex and month were significant (Table 1). The significance of the former (Table 1) suggests that the frequency of autotomy changed non-linearly as the season advanced (Fig. 1). In total, 7.9% of 126, 5.2% of 153, and 13.2% of 114 adults were missing a hind leg in July, August and September, respectively. The significance of the interaction between sex and month (Table 1) suggests that the frequency of autotomy differed between the sexes as the season advanced. In total, 2.7% of 73, 2.0% of 50, and 11.1% of 27 male adults were

Table 1 Factors related to the loss of hind legs in two *Parapodisma* species

Factor	*df*	χ^2	*P*	Coefficient (SE)
Month	1	3.357	0.067	0.0190 (0.01044)
Species	1	1.757	0.185	
Sex	1	2.752	0.097	
Size	1	0.115	0.735	
Month × month	1	4.218	0.040	0.0010 (0.00046)
Species × month	1	1.682	0.195	
Sex × month	1	4.409	0.036	
Size × month	1	2.025	0.155	
Sex × species	1	2.776	0.096	
Size × species	1	0.343	0.558	
Size × sex	1	0.000	1.000	

The results were examined using a generalized linear model with a binomial error distribution and logit link

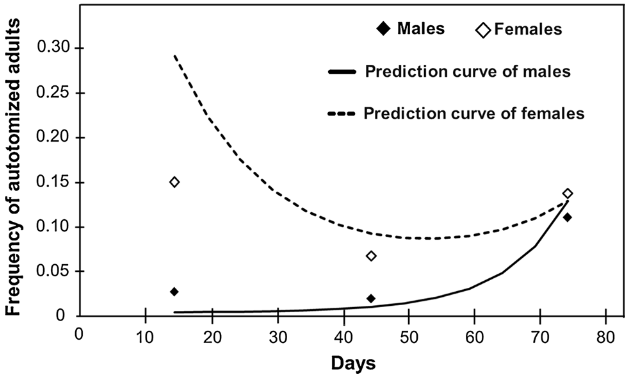

Fig. 1 The relationship between the month and the frequency of autotomized adults. The predicted curve in males shows $y = 1/[1 + \exp(5.207791 + 0.029283x - 0.000977x^2)]$, while the predicted curve in females shows $y = 1/[1 + \exp(-0.464562 + 0.104957x - 0.000977x^2)]$. Both formulas were calculated using a generalized linear model

missing a hind leg in July, August, and September, respectively, while 15.1% of 53, 6.8% of 103, and 13.8% of 87 female adults were missing a hind leg in July, August, and September, respectively (Fig. 1). The significant differences between species and between sexes are listed in Tables 1 and 2.

Discussion

As the season advanced, the frequency of autotomized adults differed between the sexes and changed non-linearly (Table 1; Fig. 1). However, there were no significant effects of body size or species identity as main effects or interaction effects on the frequency of autotomy (Table 1). These results suggested that the seasonal sexual difference of autotomy in *P. subastris* and *P. tanbaensis* adults was important in the wild. Thus, affirmative answers to Questions 2 and 4 were not supported, while affirmative answers to 1 and 3 were only partly supported based on the statistical results (Table 1). Below, I discuss the factors and mechanisms causing these results in the context of understanding the ecology and evolution of autotomy in the wild.

Generally speaking, the frequency of autotomized adults in a population is determined by two processes: the rate of occurrence of autotomized individuals in a population and the rate of disappearance of autotomized individuals from the population (Harris 1989). Because predator attack is widely considered to be a major cause of the loss of a hind leg in orthopteran insects (Bateman and Fleming 2006), it could be related to these two processes. In the former process, the production of autotomized adults is based on attacks by predators against intact adults. In the latter process, the loss of autotomized adults from the population is based on their death by predation. Therefore, we need to pay attention to the factors and mechanisms in both processes that led to the present results, and we need to discuss the mechanisms that influenced the frequency of autotomized adults, which changed non-linearly and according to the insect's sex as the season advanced (Fig. 1).

Intact adults of different sexes can be attacked at different rates because predator discovery rates can also differ based on the prey's sex. In Montana, USA, male adult grasshoppers were two to three times more vulnerable to avian predators than females in a study using a tethered-grasshopper method (Belovsky et al. 1990). Belovsky et al. (1990) proposed that avian predators discovered males more frequently owing to the frequency of behaviors, such flying, hopping, and walking, that differed between males and females. Although the predator attack rate was not estimated, Hochkirch et al. (2007) found a higher frequency of autotomized male Cepero's groundhopper, *T. ceperoi*, than females partly because of the male adults' courtship display, which involved visual signals for females performed on the bare ground (Hochkirch et al. 2006). These same behaviors may result in the disappearance of autotomized adults. In the present study, such grasshopper behaviors might not have been the cause of the greater rate of predator attack against *Parapodisma* male adults than female ones, because the male adults of *P. tanbaensis* and *P. subastris* do not perform courtship displays for females and female-specific behaviors are unknown (Miura, personal observation).

As the season advanced, the frequency of autotomized adults changed non-linearly, and the pattern of the change was different between the sexes (Table 1). The frequency of autotomized male adults increased gradually as the season advanced (Fig. 1), which could answer Question 3. However, the frequency of autotomized female adults did not gradually increase, and the frequency in August was lower than those in July and September, and the frequency in July was lower than that in September (Table 1; Fig. 1). This suggested that the directions of the mechanisms and factors affecting the frequency of autotomized females changed depending on the season. Such mechanisms or factors could be related to the processes of occurrence and/or disappearance of autotomized individuals. Some biological mechanisms of predators at the individual or community level could explain these patterns of change. At the level of individual predators, predator preference or attack ability could be changed. For example, in the early season, the predator's food conservatism and neophobia (Marples and Mappes 2011) could result in a delay in their acceptance and consumption of a new type of prey, which would be the autotomized adults in the present study. After attacking the females, the predators could not consume them completely. In the late season, the predator's experience, which is known to have an impact on prey choice (Exnerová et al. 2007, Lindström et al. 2001), could result in the consumption of the autotomized adults. At the community level, the composition of predators could change (Mappes et al. 2014). Such mechanisms could have influenced the occurrence and disappearance of autotomized *Parapodisma* females differently from *Parapodisma* males in the present study.

When considering predator attacks on prey, we need to pay attention to the differences in prey defense strategies against predators. For example, even if the predator attack rates against intact males and females were the same, a higher frequency of autotomized females than autotomized males could be found if the autotomized females could more easily escape from predation, while autotomized males could be consumed totally after predator attacks. It is important to consider the types of predators because a field population suffering predation by a 100% effective predator will have no autotomized individuals (Schoener 1979; Medel et al. 1988; Vervust et al. 2009; Bateman and Fleming 2011). It is possible that after intact adults are attacked by predators, autotomized females use more effective defense tactics than autotomized males. The same results could occur if autotomized females could more easily escape from predators than autotomized males.

At the individual prey level, their experience with being attacked or the existence of predators in the past could induce another level of defense responses. Thus, past experiences of prey with predators may influence the prey's ability to escape. For example, the grasshopper *Melanoplus femurrubrum* reared from a nymphal stage under chronic risk of spider predation showed an improved physical escape performance as adults by altering their jumping technique (Hawlena et al. 2011). This suggests that the non-lethal effects of predators could influence the behaviors and physiology of grasshoppers because of the long-lasting physiological stress induced by the persistent risk of predation (Hawlena et al. 2011). If *Parapodisma* male nymphs in the wild more frequently encounter predators than *Parapodisma* female nymphs, then these experiences may result in the male intact adults escaping from predation without autotomy more successfully than female adults. Consequently, a higher frequency of autotomized females than of autotomized males could be found in the wild even if the attack rates are the same between intact male and female adults. Because of the many possible complex mechanisms and multiple factors causing the ultimate frequency patterns of autotomized individuals, we will need to perform many experiments and assessments in the future to explain the presently observed patterns.

There were no significant effects of the species or size of *Parapodisma* grasshoppers on the frequency of autotomized adults in the wild (Table 1). Thus, the ecological mechanisms involving the differences between these species and among sizes do not have important effects on the frequency of autotomized adults. Thus, autotomy in these *Parapodisma* species did not primarily depend on certain mechanisms and factors, such as using microhabitats to create differences in abiotic conditions, food plant use, or vulnerability against predators and parasitoids (Miura and Ohsaki 2015). With regard to size, as above, predators and prey defense responses appeared to have little influence on the frequency of autotomized adults. In future studies, we need to

Table 2 *Parapodisma* adults of each species and sex sampled per month

Month	*P. tanbanensis*		*P. subastris*	
	Female	Male	Female	Male
July	29 (17.2)	50 (4.0)	24 (12.5)	23 (0.0)
August	58 (5.2)	39 (2.6)	45 (8.9)	11 (0.0)
September	53 (9.4)	22 (13.6)	34 (20.6)	5 (0.0)
Total	140 (9.3)	111 (5.4)	103 (13.6)	39 (0.0)

The figures in parentheses represent autotomized adults (%)

examine how sexual differences in ecological mechanisms and factors, and the experiences of, and learning by, *Parapodisma* grasshoppers of predator existence and attacks affects autotomy in the wild.

In the present research system, the disappearance of the autotomized adults from *Parapodisma* grasshopper populations could be caused by the parasitoid fly *B. japonensis* (Miura and Ohsaki 2015); therefore, this effect should also be investigated. *P. subastris* adults lacking hind legs were more frequently killed by *B. japonensis* than intact adults in their natural habitat, and the host mortality caused by *B. japonensis* could be one of the future costs of autotomy in *P. subastris* adults (Miura and Ohsaki 2015). Thus, the presence of *B. japonensis* might influence whether an intact adult *Parapodisma* grasshopper autotomizes its hind leg. *Parapodisma* adults that had experienced attacks and the presence of *B. japonensis* differed in the manner of autotomy compared with unexperienced adults. Of course, the attacking experiences of *B. japonensis* on intact and autotomized *Parapodisma* adults might also change their manner of attack. In a future study, it will be important to test whether the experiences of *Parapodisma* nymphs and adults with attacks or the existence of *B. japonensis* could influence the decision and/or ability to undergo autotomy.

The main future experiments will address some of these issues by examining two hypotheses. The first one is that predators attack female adults more easily than male ones, and the other is that the defense strategies of females, compared with those of males, after predator attack enable the females to more efficiently escape from predation. First, the encounter and attack rates of predators can be examined in the wild using tethered intact adult grasshoppers in their natural habitat (Belovsky et al. 1990) by determining the rate at which tethered adults lose a hind leg. Using dummies of grasshoppers is also useful for estimating the attack rates of predators, as shown by many successful studies (Joiris et al. 2010; Low et al. 2014; Mappes et al. 2014; Molleman et al. 2016; Niskanen and Mappes 2005; Remmel and Tammaru 2009; Roslin et al. 2013; Tvardikova and Novotny 2012). Second, the time to autotomize the hind leg(s) of these *Parapodisma* grasshoppers can be measured by gripping the hind leg firmly using forceps in the laboratory (Bateman and Fleming 2006). This could be useful to examine the relationships between autotomy and other prey defense responses, and that between the sexes in *Parapodisma* species and non-lethal attacks or mating experiences. The predator's experience of attacking prey and the prey's experience of being attacked by the predator in the past could influence the behaviors of both prey and predator through learning. These experimental test data, combined with the field data, could help clarify the function of autotomy and stimulate further research on the significance of ecological interactions in anti-predator or parasitoid defenses.

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Compliance with ethical standards

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Conflict of interest The authors declare that they have no conflict of interest.

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