ORIGINAL ARTICLE

Kazumi Miura · Naota Ohsaki

The cost of autotomy caused by the parasitoid fly *Blaesoxipha japonensis* (Diptera: Sarcophagidae): an interspecific comparison between two sympatric grasshopper host species

Abstract In insects, while much is known about how autotomy, the loss of a host's hind leg(s), affects locomotion, mating and escape from predators, little is known about the effects of such loss on mortality caused by a parasitoid fly in natural habitat. We tested to see if host mortality caused by the parasitoid fly, *Blaesoxipha japonensis*, was related to the presence or absence of a hind leg(s) in two closely related, sympatric grasshopper species, *Parapodisma tanbaensis* and *P. subastris*. After capturing adult grasshoppers of both species in the same three locations simultaneously for 2 years, we assessed whether *B. japonensis* caused the death of a host by rearing these captured grasshoppers until they died. The results showed that autotomy significantly affected the mortality caused by *B. japonensis* in *P. subastris* adults, but not in *P. tanbaensis* adults. This suggests that the increased mortality caused by parasitoids can be one of the costs of autotomy in *P. subastris* in its natural habitat, and that the mortality effect caused by *B. japonensis* in autotomized adults may differ based on behavioral, physiological, and/or ecological factors that differ between these two sympatric *Parapodisma* species.

Keyword Body size · Closely related species · Host–parasitoid interactions · Immunity · Vegetation structure

K. Miura
Center for Ecological Research, Kyoto University, Hirano 2, Otsu, Shiga 520-2113, Japan

N. Ohsaki
Laboratory of Insect Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan

Present address:
K. Miura (✉)
Environmental Ecology Research Group, Department of Environmental Science, University of Eastern Finland, P.O. Box 1627, 70211 Kuopio, Finland
E-mail: blaesoxipha@yahoo.co.jp; kazumi.miura@uef.fi

Present address:
N. Ohsaki
Yamagata University, 1-4-12 Kojirakawa, Yamagata 990-8560, Japan

Introduction

Autotomy is the self-amputation of a limb or other appendage, often as a reflexive action and along a predetermined breakage plane (Juanes and Smith 1995; Bateman and Fleming 2005). Autotomy has evolved independently many times, and has been observed in many taxa (Bateman and Fleming 2005). The loss of a part of the body incurs costs related to survival and reproduction. It is assumed autotomy may also generate long-term costs as a result of compromised locomotion and ability to escape from predators (such as reduced mobility, balance, sprint speed, or locomotory ability), reduced ability to forage or mate, lowered social status, loss of fat stores through loss of tissue, or death (Stoks 1999; Bateman and Fleming 2005). The amount of evidence related to the costs of autotomy continues to mount (Dixon 1989; Juanes and Smith 1995; Stoks 1999; Bateman and Fleming 2005, 2006, 2008, 2009; Clause and Capaldi 2006; Maginnis 2006; Fleming et al. 2007; Slos et al. 2009).

In insects, parasitoid attacks occur in various taxa (Godfray 1994; Hawkins et al. 1997) and are one of the greatest biotic sources of mortality for insect herbivores (Hawkins et al. 1997). Some host traits are under selection pressure by parasitoids (Gross 1993; Zuk et al. 1993, 1995; Wagner 1996). However, the effects of parasitoids on autotomy in hosts are unknown. Miura and Ohsaki (2007) found that autotomized adult *Parapodisma subastris* and *P. tanbaensis* (Orthoptera: Catantopidae) that had been attacked by the parasitoid fly *Blaesoxipha japonensis* (Diptera: Sarcophagidae)

experienced higher mortality rates than were observed in intact adults in their natural habitat. *B. japonensis* larva egress through a hole made in the dorsal region of the intersegmental membrane between the head and thorax of a host grasshopper, causing host death. Thus, increased host mortality caused by *B. japonensis* could be one of the costs of autotomy for these two grasshopper species in their natural habitat. Autotomized adults may be less effective in attempting to remove the parasitic larvae deposited on their body surface than intact adults because the autotomized adults lacked hind leg(s) (Miura and Ohsaki 2007) and the host grasshopper on which *B. japonensis* deposits larvae may use its hind leg(s) to dislodge the deposited larvae (Danyk et al. 2000). Until now, we have not examined to see if this was one of the costs in each grasshopper species and whether there was an interspecific difference in the cost between *P. tanbaensis* and *P. subastris* adults.

Interspecific comparison has been extensively used in research in the fields of ecology and evolution (Endler 1986; Harvey and Pagel 1991). In particular, interspecific comparisons between closely related species allow the identification of factors and mechanisms underlying a biological phenomenon because of the basic assumption that closely related species share more phenotypic similarity and more similar responses to environmental factors than less closely related species (Endler 1986; Harvey and Pagel 1991). That is, the trait differences among closely related species are likely to be caused by fewer differences of factors or mechanisms among such species compared with the trait differences among more distantly related species. Moreover, because *P. subastris* and *P. tanbaensis* in our study are distributed sympatrically, they may share the same biotic and abiotic factors more frequently in their natural habitat than would allopatrically distributed and closely related species (Vogelweith et al. 2014). Thus, the interspecific comparison in our study between two closely related species, *P. tanbaensis* and *P. subastris*, should be advantageous during attempts to estimate the underlying factors or mechanisms generating their differences in autotomy.

In this study, we investigated the relationship between host mortality caused by *B. japonensis* and the condition of the hind legs in *P. tanbaensis* and *P. subastris* adults in their natural habitat. We simultaneously collected adults of both grasshopper species from the same locations and reared them in our laboratory. We allowed the collected grasshoppers to complete their lifespan and recorded the occurrence of death caused by *B. japonensis*. We examined whether host mortality caused by *B. japonensis* in the autotomized adults was higher than that in intact adults in each grasshopper species. Finally, we discuss the factors or mechanisms causing the difference in the host mortality between intact and autotomized adults and between the two species.

Methods

Study species

The adults of the two grasshopper species, *P. tanbaensis* and *P. subastris,* are brachypterous (Miyatake and Kanô 1992). Both species 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, both adult grasshopper species occur from July to October (Miura and Ohsaki 2007) and are distributed sympatrically (Miyatake and Kanô 1992; Miura 2003; Miura and Ohsaki 2007).

In orthopteran insects, a lack of hind leg(s) has been reported to occur in natural habitats (Dixon 1989; Bateman and Fleming 2005; Hochkirch et al. 2007; Miura and Ohsaki 2007), and juveniles may be able to cover the cost of loss of a leg by regenerating it in successive instars. However, limb re-generation appears to be rare or incomplete in orthopteran insects (Bateman and Fleming 2008). *P. tanbaensis* and *P. subastris* adults are often observed to lack a hind leg (Miura and Ohsaki 2007), and leg regeneration has not been observed (Miura, personal observation). Because the hind legs are used for jumping in orthopteran insects (Bennet-Clark 1990; Bateman and Fleming 2005) and because *Parapodisma* adults are brachypterous, the hind legs of *Parapodisma* grasshopper adults might be more important functionally than those of macropterous grasshopper adults for moving away from natural enemies that they encounter.

The parasitoid fly *B. japonensis* occurs in Japan, China, and Far East Russia (Pape 1994). Many *Blaesoxipha* species parasitize various grasshopper species (Pape 1994; Miura 2003; Miura and Ohgushi 2010). *B. japonensis* is a gregarious parasitoid that parasitizes fifth-stadium *Parapodisma* nymphs and adults of both *P. tanbaensis* and *P. subastris* in Kyoto (Miura 2003).

B. japonensis larvae egress through a hole made in the dorsal region of the intersegmental membrane between the head and thorax of the dead grasshopper host (Miura, personal observation). The internal organs of the host body tissue become liquefied immediately before the emergence of *B. japonensis* (Miura, personal observation). The processes of host use by other *Blaesoxipha* flies (Rees 1973) suggest that the larvae of *B. japonensis* can be placed on the host body surface and then feed on the hemolymph and/or fat body after they burrow into the host body (Miura and Ohsaki 2014).

Sampling and rearing methods

Once a month, we captured *Parapodisma* adults in 2001 and 2002 from July to October in each of three loca-

tions: Kibune, Kumogahata, and Mt. Hiei in Kyoto. After looking for *Parapodisma* adults and carefully capturing them using a net, we identified the species and measured the prothorax length in our laboratory with a caliper as the index of body size. The presence or absence of the hind leg(s) of adults of both *Parapodisma* species was recorded. The grasshoppers were captured almost individually. In the net, there was no hind leg of grasshopper after being captured. So, it seemed that they had no trouble in losing their hind legs during the sweeping attempts we made to capture them. Captured *Parapodisma* adults were assumed to have been parasitized after adult eclosion, when *B. japonensis* larvae egressed. It took less than 8 days for *B. japonensis* larvae to egress from the captured hosts (Miura 2003; Miura and Ohsaki 2014); therefore, the *B. japonensis* adults appear to emerge quite quickly after infestation of the host. Miura and Ohsaki (2007) explained the details of the sampling and rearing procedures used in our study.

Statistical analysis

We set the value for "injury" in intact hosts as zero, the value in hosts lacking one hind leg as one, and the value in hosts lacking both hind legs as two, as a ranked variable. Host body size was a continuous variable. The other factors except "month" were categorical variables. Month was a continuous variable because we examined to see if the host mortality rate caused by *B. japonensis* might have changed with late season capture. We examined the sampled data of July as those of 15 days, the sampled data of August as those of 45 days, and the sampled data of September as those of 75 days for these statistical analyses. Because few hosts were captured in October, the data from October were combined with those from September for statistical analysis. The categorical choice of either a dead host caused by the emergence of *B. japonensis* or a surviving host of each individual was treated as the dependent variable. We used JMP version 9.03 for all statistical analyses (SAS Institute, Cary, NC, USA, 2011).

We assessed the relationships between the host mortality caused by *B. japonensis* and other factors using a generalized linear model (GLM) with a binomial error distribution and a logit link function. In this analysis we selected the GLM with overdispersion tests and intervals and with Firth bias-adjusted estimates in the model specification (SAS Institute, Cary, NC, USA, 2011). We assessed the data in each host species separately because we did not examine the interaction effect between the injury and the other factors because degrees of freedom were lacking. First, we examined a model that had six main effects (year, month, location, body size, host sex, and injury) and 15 first-order interaction effects between the main effects in *P. tanbaensis*. Second, we examined a model that had six main effects (year, month, location, body size, host sex, and injury) and 10 first-order interaction effects between the main effects (except in-

jury) in *P. subastris* because degrees of freedom were lacking.

Results

In 2001, 76 *P. tanbaensis* and 40 *P. subastris* were collected in Kibune, 16 and 21, in Kumogahata, respectively, and 40 and 34 on Mt. Hiei, respectively. In 2002, 85 *P. tanbaensis* and 34 *P. subastris* were collected in Kibune, 19 and 4 in Kumogahata, respectively, and 15 and 9 on Mt. Hiei, respectively. These totaled to 251 *P. tanbaensis* and 142 *P. subastris* individuals.

In *P. tanbaensis*, injury type was not significant, while there was a significant interaction effect between year and body size, and between host sex and body size (Table 1). In *P. subastris*, injury type was significantly related to host mortality ($\chi^2_2 = 7.407$, $P = 0.025$) and there were no significant interaction effects ($P > 0.60$) for any factors. That is, if one considers the factors of year (Y), month (M), host sex (H), and body size (B), as well as for the interactions of $Y \times M$, $Y \times H$, $Y \times B$, $M \times H$, and $M \times B$, then $df = 1$, $\chi^2 = 0.000$, and $P = 1.000$. Similarly, for location (L), $L \times B$, $M \times L$, and $Y \times L$, $df = 2$, $\chi^2 = 0.000$, and $P = 1.000$. The exceptions were injury type (I), $L \times H$, and $H \times B$, where $df = 2, 2$ and 1, $\chi^2 = 7.407, 0.426$ and 0.204, and $P = 0.025, 0.808$ and 0.651, respectively.

In *P. tanbaensis*, 7.3 % of the 232 intact adults and 10.5 % of the 19 adults lacking one hind leg were killed by *B. japonensis*, respectively (Table 2). In *P. subastris*, 1.6 % of the 128 intact adults, and 7.7 % of the 13 adults lacking one hind leg, and 100 % (one of one adult) lacking both hind legs were killed by *B. japonensis* (Table 2). Thus, autotomized adults incurred higher mortality caused by *B. japonensis* than intact adults of *P. subastris*, whereas those of *P. tanbaensis* did not incur higher mortality.

Discussion

Autotomy is a widespread anti-predator behavior with future costs including reduced mating success and survival that also provides an organism with obvious escape benefits (Fleming et al. 2007; Slos et al. 2009). The present study suggests that *P. subastris* adults lacking hind leg(s) were more frequently killed by *B. japonensis* than intact ones in their natural habitat, and that host mortality caused by *B. japonensis* could be one of the future costs of autotomy in *P. subastris* adults. Autotomy is considered to have an effective escape function against attack by predators (Bateman and Fleming 2005), and recent studies suggest that defenses that are effective against predators are not as effective against parasitoids (Gentry and Dyer 2002; Barbosa and Caldas 2007; Smilanich et al. 2009). Accordingly, defense against parasitoids might be less effective in autotomized adults when they are compared with intact adults. That

Table 1 Relationship between various factors and mortality caused by *Blaesoxipha japonensis* in *Parapodisma tanbaensis* adults in a generalized linear model

Factor	df	χ^2	P value
Year (Y)	1	0.000	1.000
Month (M)	1	0.000	1.000
Location (L)	2	2.649	0.266
Host sex (H)	1	2.225	0.136
Injury type (I)	1	0.000	1.000
Body size (B)	1	1.464	0.226
$Y \times M$	1	0.000	1.000
$Y \times L$	2	2.075	0.354
$Y \times H$	1	2.847	0.092
$Y \times I$	1	0.000	1.000
$Y \times B$	1	4.903	0.027
$M \times L$	2	1.952	0.377
$M \times H$	1	1.098	0.295
$M \times I$	1	3.020	0.082
$M \times B$	1	0.394	0.530
$L \times H$	2	0.000	1.000
$L \times I$	2	0.929	0.629
$L \times B$	2	0.000	1.000
$H \times I$	1	0.000	1.000
$H \times B$	1	6.038	0.014
$B \times I$	1	0.000	1.000

Table 2 Number of adults lacking a hind leg(s) in *Parapodisma tanbaensis* and *P. subastris* adults captured at each site, and the mortality caused by *Blaesoxipha japonensis* in the two grasshoppers

	P. tanbaensis		*P. subastris*	
	Female	Male	Female	Male
Intact	127 (7.1 %)	105 (7.6 %)	89 (1.1 %)	39 (2.6 %)
Missing one leg	13 (15.4 %)	6 (0.0 %)	13 (7.7 %)	0 (0.0 %)
Missing two legs	0 (0.0 %)	0 (0.0 %)	1 (100 %)	0 (0.0 %)
Total	140 (7.9 %)	111 (7.2 %)	103 (2.9 %)	39 (2.6 %)

The values in parentheses are the percentages of grasshopper adults whose death was caused by *B. japonensis*

is, an effective predator avoidance response involving autotomy might have resulted in enhanced susceptibility to the parasitoid, although there have been no reports of differences in behavior or physiology between intact *P. subastris* adults and ones lacking hind leg(s) during the process of host use by *B. japonensis*.

The results of the present interspecific comparison between the two grasshopper species suggests that some mechanism(s) and factor(s) affecting the process of host use by *B. japonensis* from the search for a host until emergence from the host differ between the two host species. The condition of the hind legs in *P. subastris* adults was related to the adult mortality, whereas that in *P. tanbaensis* adults was not (Table 1). No significant factor or interaction effect was observed in *P. subastris*, whereas significant interaction effects were found between year and body size, and between host sex and body size, in *P. tanbaensis* (Table 1). Thus, some factor(s) related to host mortality caused by *B. japonensis*, such as physiological or behavioral trait(s), or ecological factor(s), might differ between these two host grass-

hopper species. Below, we will discuss two such possible factors: immune responses in the host grasshopper, and vegetation composition and structure in the habitat.

While immunity is often thought of in the sense of genetic or physiological immunity, insects often exhibit behavioral immunity (Roode and Lefèvre 2012). First, *P. subastris* adults lacking hind leg(s) may have weaker behavioral immune responses against *B. japonensis* than adults of *P. tanbaensis* or than intact adults in either species. Immune response often differs between closely related species and is dependent on various factors (Zuk et al. 2004) such as age (Chun et al. 1995; Rolff 2001; Doums et al. 2002; Hillyer et al. 2005), spatial location (Berggren 2009; Vogelweith et al. 2013a), and sex (Rolff 2001; Schmid-Hempel 2005). In our study, the adult age, spatial location, and annual variations in adults of both grasshopper species appeared to not be related to host mortality caused by *B. japonensis*, except for the significant interaction between year and body size in *P. tanbaensis* (Table 1). No indication of a sexual difference in the immune responses was observed in *P. subastris* adults. However, some difference may exist in *P. tanbaensis* between the sexes in the immunological responses, depending on host sex and body size (Table 1); for example, as Miura and Ohsaki (2014) reported, *B. japonensis* caused less mortality in larger female adults, whereas the mortality was independent of male body size. Stronger behavioral (Lee et al. 2008) and physiological (Vogelweith et al. 2013b) immune responses in larger lepidopteran larvae and physiological immune responses in larger house crickets (Ryder and Siva-Jothy 2001) have been reported, and further research will be needed to clarify whether physiological and behavioral immune response differences cause the body-size-dependent sexual differences in the host mortality caused by *B. japonensis*.

Autotomized damselfly (*Lestes viridis*) larvae show possibly reduced immune responses compared with intact ones, because of reduced phenoloxidase activity (Slos et al. 2009). Phenoloxidase is a key component of immune responses in insects, and catalyses melanin formation to encapsulate pathogens (Slos et al. 2009). Autotomy in insects could also lead to lower foraging by the autotomized insects (Stoks 1998, 1999), low nutritional status (Moret and Schmid-Hempel 2000; Siva-Jothy and Thompson 2002), as well as energy limitation and the reallocation of resource reserves, resulting in reduced immune responses. Thus, phenoloxidase activity in autotomized grasshoppers could also be reduced, although perhaps transiently (Slos et al. 2009). Therefore, even if *B. japonensis* larvae infested a host grasshopper before the loss of a hind leg by autotomy, reduced host immune responses could lead to a higher survival rate and/or greater growth of *B. japonensis* larvae in a subsequently autotomized host than in an intact one. Therefore, autotomized adults could incur higher mortality caused by *B. japonensis* than intact ones.

Second, *B. japonensis* may more frequently encounter *P. subastris* adults lacking hind leg(s) than intact adults

or adults of *P. tanbaensis*. The vegetation composition and structure can affect parasitoid prevalence in grasshoppers (Laws and Joern 2012). Searching for better foodplants, microclimate, and mates can differ between sexes and between species (Krasnov et al. 2005; Walker and Allen 2014). Sometimes, the parasitism rates in closely related oligophagous insect herbivores depend on their host plants (Ohsaki and Sato 1990, 1994; Sisterson and Gould 1999; Oppenheim and Gould 2002; Pélissié et al. 2009). Habitat segregation or difference in plant use among closely related polyphagous species can occur although their food habits are polyphagous, partly because of reproductive interference among them (Gröning et al. 2007). Additionally, species-specific nutritional needs among closely related polyphagous insect herbivores (Behmer and Joern 2008) can cause them to prefer different microhabitats, although a predation risk can alter species-specific nutritional needs (Hawlena and Schmitz 2010). The vegetation composition (total grass biomass) and structure (canopy height and spatial variability in canopy structure) can affect the behaviors of grasshoppers, because grasshopper species density differs according to the characteristics of vegetation (Joern 2004, 2005). In particular, vegetation structure can affect the success of grasshoppers attempting to escape from predators and parasitoids, and may also affect their ability to regulate body temperature and to maintain water balance (Joern 2004). Thermoregulation is a critical activity that affects food processing, nutrient acquisition rates, and the potential to fend off pathogens (Joern 2004).

In the present study, the seasonal, spatial, and annual variation of the vegetation in the habitat may not have been related to the host mortality caused by *B. japonensis* in adults of either grasshopper species, except for the significant interaction between year and body size in *P. tanbaensis* (Table 1). Rather, sex and body size are importantly related to the behavior of intact and autotomized grasshoppers (Table 1). Autotomized insects must respond to two conflicting demands, the needs to forage and to escape from predators (Stoks 1999). After autotomy, larvae of the damselfly *Lestes sponsa* changed their behaviors and used a complex microhabitat to seek refuge from predators (Stoks 1999). Thus, *Parapodisma* grasshopper adults in our study might have differentially selected microhabitats for escape space and for thermoregulation depending on the body size of each species, as well as on hind leg condition, and sex. These factors could lead to autotomized *P. subastris* adults being more frequently attacked and killed by *B. japonensis* than intact ones.

In addition, it has recently been proposed that host plants affect the level of immunity of insect herbivores (Ojala et al. 2005; Karimzadeh and Wright 2008; Vogelweith et al. 2011), as well as their non-immunological defenses (Parker et al. 2011), such as plant-mediated resistance of insect herbivores against pathogens and parasitoids. Insect herbivores often defend themselves against their enemies not only by feeding on high-quality host plants (Ojala et al. 2005; Karimzadeh and Wright 2008; Vogelweith et al. 2011) but also by storing secondary metabolites obtained from their host plants in their bodies (Sword 2001; Singer and Stireman 2003; Smilanich et al. 2011). Thus, the difference in the food plants between intact and autotomized adults or between the two grasshopper species studied here could have influenced the immune responses against *B. japonensis*. We should perform combined studies of the host insect's immune response and the structure or composition of plant species in the habitat to examine whether plant-mediated immune traits in adults of *Parapodisma* species could affect the mortality in them caused by *B. japonensis*.

Little is known about the effect of parasitoids on autotomized insects. However, our methods using *Parapodisma* and *Blaesoxipha* species are useful for making a detailed interspecific and intraspecific comparisons among *Parapodisma* species to aid in the investigation of the effects of parasitoids on autotomized hosts and for identifying the environmental factors and ecological mechanisms responsible for the patterns observed in the present study. Fourteen *Parapodisma* species occur in Japan (Miyatake and Kanô 1992) with interspecific (Miyatake and Kanô 1992) and intraspecific (Tatsuta et al. 2001) variation in their respective morphological traits. Some parasitoids, including *Blaesoxipha* species, have been reported to use grasshoppers as hosts in Japan (Shima 1999; Miura 2003; Miura and Ohgushi 2010). Thus, the experimental tests and field data in our study system can be helpful for clarifying the function of autotomy in these species' natural habitat, and for stimulating further research on the significance of ecological interactions in host defense against parasitoids.

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