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ORIGINAL RESEARCH PAPER

Mortality effects of the parasitoid flesh fly *Blaesoxipha japonensis* (Diptera: Sarcophagidae) in relation to body size of the adult grasshopper *Parapodisma tanbaensis* (Orthoptera: Catantopidae)

Kazumi Miura · Naota Ohsaki

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Abstract Body size is a significant factor for organisms because it has a profound effect on almost all of their physiological, life-history, ecological, and evolutionary traits. Sexual size dimorphism (SSD) is one of the sources creating intraspecific variation in body size. In general, female adults are larger than male adults in insects. Whereas much research has examined the significance of male competition and fecundity as causes of SSD in insects, relatively less is known about the effects of parasitoids on host insect size. To investigate the effects of the parasitoid fly *Blaesoxipha japonensis* Hori on the body size of the adult grasshopper *Parapodisma tanbaensis* Tominaga et Kanô, we examined the relationship between adult host size and host mortality rate caused by *B. japonensis* when adult grasshoppers captured in the field were reared in the laboratory. The results showed that females were larger than males and that the host mortality rate caused by *B. japonensis* was inversely related to host size in females, whereas there was no significant relationship between male size and host mortality rate. These results suggest that the effect of this parasitoid on host body size is one factor favoring the female-biased SSD in this adult grasshopper.

Keywords Differential plasticity hypothesis · Host–parasitoid interaction · Host size · Sex-specific plasticity · Sexual size dimorphism

Introduction

Body size is a key trait of organisms because it has profound effects on almost all of their physiological, life-history (Brown et al. 2004), ecological (Cohen et al. 2005), and evolutionary (Blanckenhorn 2005) traits. Sexual size dimorphism (SSD), a systematic difference in size between males and females of a species, is one source creating intraspecific variation in body size. The direction and magnitude of SSD vary considerably among taxa (Blanckenhorn 2005; Stillwell et al. 2010). In general, female adults are larger than male adults in insects (Honěk 1993; Teder and Tammaru 2005). Many researchers have examined the significance of male competition and fecundity as causes of SSD in insects (Blanckenhorn 2005; Fairbairn et al. 2007). Large females generally have higher fecundity, and this may favor larger body size (Fairbairn et al. 2007; Hochkirch and Gröning 2008). On the other hand, large males often have greater mating success in male–male competition and female choice, and this may favor larger body size (Blanckenhorn 2005).

Insect herbivores are attacked by taxonomically diverse natural enemies, which represent an important and ubiquitous cause of herbivore mortality (Hawkins et al. 1997). Among such enemies of herbivores, parasitoids are an

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K. Miura (✉)
Center for Ecological Research, Kyoto University, Hirano 2, Otsu, Shiga 520-2113, Japan
e-mail: blaesoxipha@yahoo.co.jp

Present Address:
K. Miura
Angewandte Zoologie/Ökologie der Tiere, Institut für Biologie, Freie Universität Berlin, Haderslebener Str. 9, 12163 Berlin, Germany

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

Present Address:
N. Ohsaki
Yamagata University, 1-4-12 kojirakawa, Yamagata 990-8560, Japan

important component in the terrestrial community (Hawkins et al. 1997). Parasitoids can influence or regulate host populations and affect the structure of ecological communities (Godfray 1994; Hawkins 1994; Otterstatter et al. 2002). As potential regulators of their host populations, parasitoids are intensively used in biological control (Godfray 1994; Hawkins et al. 1997). They can select for or against host traits (Godfray 1994; Gross 1993; Vincent and Bertram 2010; Wagner 1996; Zuk et al. 1993, 1995), and within a host species, parasitoids may attack larger individual hosts more often (Godfray 1994), probably due to a positive relationship between host size and the fitness of the parasitoid because of greater resources for the parasitoids (Godfray 1994; Otterstatter 2004; Visser 1994). However, few researchers have examined the mortality effects of parasitoids on the body size of hosts that display SSD.

We examined how parasitism pressure by the parasitoid flesh fly *Blaesoxipha japonensis* Hori (Diptera: Sarcophagidae) changes depending on host body size of *Parapodisma tanbaensis* Tominaga et Kanô (Orthoptera: Catantopidae) in the field. As in most insect species, female adults are larger than males in *P. tanbaensis* (Miura 2003; Miura and Ohsaki 2007). *B. japonensis* uses *P. tanbaensis* as a host (Miura 2003). Miura and Ohsaki (2007) examined how *B. japonensis* used *P. tanbaensis* and *P. subastris* Huang (Orthoptera: Catantopidae) as hosts; however, little is known about the effect of *B. japonensis* on the SSD in the host (Miura 2003; Miura and Ohsaki 2007). To determine whether size-related mortality in adult *P. tanbaensis* was caused by *B. japonensis* in the field, we collected adult grasshoppers from the field and reared them in the laboratory. The grasshoppers were allowed to complete their lifespan, and the occurrence of death caused by *B. japonensis* was recorded.

Materials and methods

Study species

The host grasshopper *P. tanbaensis* is distributed in the Kinki District, Honshu Island, Japan. It is brachypterous, univoltine, overwinters in the egg stage, and feeds on a wide range of dicotyledonous plants (Miyatake and Kanô 1992). In Kyoto, adult grasshoppers occur from July to October (Miura and Ohsaki 2007). The parasitoid fly *B. japonensis* is distributed in Japan, China, and far-eastern Russia (Pape 1994). Many *Blaesoxipha* species parasitize acridid grasshoppers (Pape 1994). *B. japonensis* is a gregarious parasitoid that parasitizes fifth-stadium *Parapodisma* nymphs and adults of both *P. tanbaensis* and *P. subastris* from July to September in Kyoto (Miura 2003; Miura and Ohsaki 2007). In a previous study, we found that approximately 10 % of *P. tanbaensis* collected from the field were killed by *B. japonensis* (Miura and Ohsaki 2007).

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 host tissue becomes liquified just before emergence of this parasitoid larva from the host (Miura, personal observation). As in other *Blaesoxipha* flies (Rees 1973), it appears that *B. japonensis* females place the larvae on the host body surface, and the larvae burrow into the host body and then feed on the hemolymph and/or fat body.

Examining adult-stage specimens is useful for determining body size in insects, because the skeletal growth of an insect stops at the final molt and does not change during the adult stage. In contrast, many noninsect organisms continue to grow after reproductive maturity, and sex-specific patterns of growth or survival after maturity can alter body size with age (Fairbairn et al. 2007).

Sampling and rearing methods

Once a month from July to October 2001–2002, we captured adult *Parapodisma* grasshoppers in the field at three sites (Kibune, Kumogathata, and Mt. Hiei) in Kyoto Prefecture, Japan, using a net. In the laboratory, we identified the species and measured the prothorax length with a caliper and used the length as the index of body mass, as it was significantly correlated with body mass in the hosts captured in 2002 (Kendall's coefficient of rank correlation; females $\tau = 0.195$, $p = 0.025$, $n = 66$; males, $\tau = 0.380$, $p = 0.0001$, $n = 53$). All hosts were killed when egressing *B. japonensis* larvae pupated and emerged. Female hosts from which *B. japonensis* larvae egressed had not laid eggs after capture. Fifth-instar nymphs did not attain adulthood when parasitized by *B. japonensis* (Miura, unpublished data). It took <8 days for *B. japonensis* larvae to egress from the captured hosts (Miura 2003). Thus, hosts were assumed to have been parasitized after adult eclosion, when *B. japonensis* larvae egressed. Details of sampling and rearing procedures in our study were previously reported by Miura and Ohsaki (2007).

Statistical analysis

To examine the relationship between host mortality and body size, we used a generalized linear model (GLM) with a binomial error distribution and a logit link function. We selected the GLM with overdispersion tests and intervals and with Firth bias-adjusted estimates in the specification of the fitted model in JMP version 9.03 (SAS Institute, Cary, NC, USA). Either survival, or death caused by

Table 1 Relationship between various factors and host mortality rate caused by *Blaesoxipha japonensis*

Factor	*df*	χ^2	*P* value
Year	1	0.000	1.000
Month	1	0.000	1.000
Location	2	1.504	0.472
Host sex	1	0.881	0.348
Body size	1	0.610	0.435
Month × year	1	0.000	1.000
Location × year	2	3.669	0.160
Host sex × year	1	2.172	0.141
Body size × year	1	4.042	0.044
Location × month	2	0.647	0.724
Host sex × month	1	0.000	1.000
Body size × month	1	0.000	1.000
Host sex × location	2	0.031	0.984
Body size × location	2	0.000	1.000
Body size × host sex	1	3.306	0.069

B. japonensis in each individual host, was treated as the dependent variable. We used month as a continuous variable because host mortality rate changes according to the time of capture. We specified collection dates in July as day 15, those in August as day 45, and those in September as day 75. Because few hosts were captured in October, data from that month were combined with those from September for statistical analysis.

At first, we examined a model of five main effects (year, month, location, body size, host sex) and ten first-order interaction effects between main effects. We found a significant effect of the interaction between year and body size and a marginally significant effect of interaction between host sex and body size (Table 1). Therefore, we examined data for each host sex by year.

Results

In all, 111 male and 140 female adults were captured. Females were larger than males: mean standard error (SE): female 7.11 mm (0.032 mm); male 5.60 mm (0.028 mm); 12 % of 58 male adults and 11 % of 74 female adults captured in 2001 and 2 % of 53 male adults and 4 % of 66 female adults captured in 2002 were killed by *B. japonensis*. Host mortality in 2001 was negatively correlated with female host body size [coefficient (SE) −2.62 (1.30), Table 2], whereas in 2002, there was no significant relationship between female host size and host mortality: coefficient (SE) 0.27 (1.64), Table 2; there was no relationship between male host body size and mortality rate in either year: in 2001, coefficient (SE) −0.010 (2.10); in 2002, −0.54 (2.90), Table 2. As body size of female hosts in 2001 increased, the mortality rate decreased according to the relationship $Y = 1/(1 + \mathrm{e}^{-(-2.62X + 16.27)})$ (Fig. 1).

Table 2 Relationship between female and male host mortality rate caused by *Blaesoxipha japonensis* and various factors during each year

Factor	*df*	χ^2	*P* value	Coefficient (SE)
Female				
2001				
Month	1	0.000	1.000	
Location	2	0.219	0.896	
Body size	1	6.712	0.010	−2.62 (1.30)
Location × month	2	1.055	0.590	
Body size × month	1	0.000	1.000	
Body size × location	2	0.000	1.000	
2002				
Month	1	0.000	1.000	
Location	2	0.000	1.000	
Body size	1	0.000	1.000	0.27 (1.64)
Location × month	2	0.000	1.000	
Body size × month	1	0.000	1.000	
Body size × location	2	0.000	1.000	
Male				
2001				
Month	1	0.000	1.000	
Location	2	0.000	1.000	
Body size	1	0.000	1.000	−0.010 (2.10)
Location × month	2	2.557	0.279	
Body size × month	1	0.000	1.000	
Body size × location	2	0.000	1.000	
2002				
Month	1	0.000	1.000	
Location	2	1.123	0.570	
Body size	1	0.000	1.000	−0.54 (2.90)
Location × month	2	0.000	1.000	
Body size × month	1	0.000	1.000	
Body size × location	2	0.000	1.000	

SE standard error

Discussion

Our findings suggest that host mortality caused by *B. japonensis* favors the female-biased SSD of *P. tanbaensis* adults. Larger female hosts can have advantages over smaller females against attack by a parasitoid. For example, larger hosts may notice the approach of *B. japonensis* with more sensitive ears (Bailey 1998), escape to greater distances by jumping away, and have stronger mechanical defenses, such as kicking (Vincent and Lailvaux 2008),

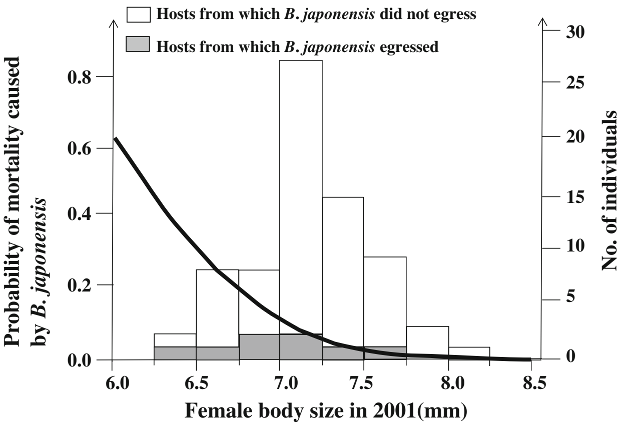

Fig. 1 Distribution of body size of females from which *Blaesoxipha japonensis* did and did not emerge. All females were collected in 2001. The curve ($Y = 1/(1 + e^{-(-2.62X + 16.27)})$ shows the relationship between the probability of host female mortality caused by *B. japonensis* and body size of females based on the generalized linear model in 2001 (Table 2)

thus enabling them to escape (Blanckenhorn 2005). Higher immunity levels in larger hosts (Ryder and Siva-Jothy 2001) may enable them to more easily kill *B. japonensis* larvae in their bodies. On the other hand, smaller adults have evolutionary advantages of early emergence, rapid body heating, and rapid escape (Blanckenhorn 2005).

The strength and direction of selection in the wild often varies considerably from year to year (Siepielski et al. 2009). Our findings show that the host mortality rate caused by *B. japonensis* did not significantly differ during the course of the collection season or among sites (Table 1). This suggests that spatial and annual temporal differences in host mortality rates were small in our study. On the other hand, the interaction between year and host body size was significant (Table 1) and signs of correlation coefficients for female body size differed between 2001 and 2002, although the coefficient in 2002 was not significant (Table 2). In male grasshoppers, signs of coefficients in both years were similar were not significant (Table 2). These findings suggest that selection pressure on body size does not always operate in the same direction in this host grasshopper. However, the higher rate of mortality caused by this parasitoid suggests a good estimate of selection pressure this parasitoid exerts (Hawkins 1994), even if significantly higher mortality rarely occurs. To confirm the host-size-related selection by *B. japonensis*, further research is necessary using an experimental test of choice by *B. japonensis* between large and small hosts.

Sex-specific phenotypic plasticity in response to environmental conditions has been identified as one source of intraspecific variation in the magnitude and direction of SSD (Bonduriansky 2007; Fairbairn 2005; Hu et al. 2010; Mikolajewski et al. 2013; Stillwell et al. 2010; Teder and Tammaru 2005). In our study, dead female adults from which *B. japonensis* emerged were smaller than those from which *B. japonensis* did not emerge, whereas this tendency was not found in males (Table 2). Fifth-instar nymphs did not attain adulthood when parasitized; however fifth-instar nymphs from which *B. japonensis* egressed were captured in the fifth stadium, and similarly, adults from which *B. japonensis* egressed were captured in adulthood (Miura unpublished data). It took <8 days for *B. japonensis* larvae to egress from adult grasshoppers after capture (Miura 2003). The grasshoppers are assumed to have been parasitized after their adult eclosion, when *B. japonensis* larvae egressed. Even if hosts infested as nymphs are able to allocate greater resources to growth (Sequeira and Mackauer 1992), our results suggest that the emergence of *B. japonensis* from adult grasshoppers can cause sex-specific differences in host body size and could promote the female-biased SSD of this adult grasshopper.

Grasshoppers are hosts to a number of parasitoids and internal parasites (Greathead 1963; Laws 2009; Laws and Joern 2012; Rees 1973). In Japan, some parasitoids have been reported to use grasshoppers as hosts (Miura 2003; Miura and Ohgushi 2010; Shima 1999). Because we obtained only *B. japonensis* from these adult grasshoppers in the study areas during the study period, the dominant mortality factor affecting grasshopper body size was *B. japonensis*. In a 3-year survey in a tall-grass prairie in Kansas, USA, female adults of *Orphulella speciosa* (Scudder) and *Melanoplus keeleri* (Thomas) parasitized by dipterans were larger than unparasitized ones (Laws and Joern 2012). Future studies should examine which parasitoids or parasites can evolutionarily influence the adult size of *Parapodisma* grasshoppers in other areas, although there was no significant difference in body size between nematode-infested and uninfested adult female grasshoppers, *Melanoplus dawsoni* (Scudder) (Laws 2009).

Although it would be adaptive for *B. japonensis* to use only female hosts due to the greater resources for them, our results showed there was no intersexual difference in mortality rate caused by *B. japonensis* (Table 1). Multiple different mechanisms may be involved in causing the higher mortality rates of male or the lower rates of female hosts (Krasnov et al. 2005). First, it may cost *B. japonensis* less to access male hosts because of the differences in the fine habitat use and behaviors for searching for a mate between host sexes (Krasnov et al. 2005). Second, mating females may be less vulnerable to invasion by *B. japonensis* larvae than nonmating females, because mating females are shielded from parasitoids by males mounting on their back. Third, because weaker immune responses in males are common in insects (Schmid-Hempel 2005), the male adult grasshopper cannot kill *B. japonensis* larvae in their bodies as frequently as females do. Future study is needed to examine these different possible mechanisms.

In general, female adults of the Orthoptera order are larger than males (Hochkirch and Gröning 2008). There have been many studies on the relationship between body size and mating success (del Castillo et al. 1999; del Castillo 2003; Koning and Jamieson 2001) and between body size and fecundity (Gwynne 1982; Simmons 1988). However, little is known about the effect of parasitoids on host SSD. Our study suggests that host mortality caused by *B. japonensis* results in larger body size of female hosts. This suggests that *B. japonensis* can be a selective pressure for larger female hosts. Future study is required to examine whether or not the mortality effects of *B. japonensis* on host SSD are stronger than the effects of fecundity or mating success in host SSD, because the strength or direction of this selection on host size in the wild can vary.

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