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Abstract: Males of the seed bug *Togo hemipterus* are larger in size and have considerably larger front legs compared to females. This size discrepancy is likely related to the fact that males fight for food using their enlarged forelegs. A "hungry" bug, i.e. one previously without food, is expected to behave in a certain way when food is present. Here, we demonstrate that aggressive "fighting and chasing" behavior was frequently observed only between males under starvation conditions and became especially severe when food was present. *Togo hemipterus* males may adopt a resource-defense mating system that is beneficial for males because females aggregate near food when it is scarce. This strategy strongly suggests that the aggressive behavior acts as male-male competition. In a second set of experiments, aggressive behavior occurred between two small males, two large males, or one large and one small male. Fighting ensued mainly when large males were involved, and larger males won fights. Consequently, the male-biased sexual size dimorphism in *T. hemipterus* appears to be partially attributable to sexual selection favoring larger males.

Sexual Size Dimorphism and Aggressive Interactions under Starvation Conditions in the

Seed Bug *Togo hemipterus* (Heteroptera: Lygaeidae)

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Running head: Sexual size dimorphism and male aggressive behavior in the seed bug

ABSTRACT

Males of the seed bug *Togo hemipterus* are larger in size and have considerably larger front legs compared to females. This size discrepancy is likely related to the fact that males fight for food using their enlarged forelegs. A “hungry” bug, *i.e.* one previously
5 without food, is expected to behave in a certain way when food is present. Here, we demonstrate that aggressive “fighting and chasing” behavior was frequently observed only between males under starvation conditions and became especially severe when food was present. *Togo hemipterus* males may adopt a resource-defense mating system that is beneficial for males because females aggregate near food when it is scarce. This
10 strategy strongly suggests that the aggressive behavior acts as male–male competition. In a second set of experiments, aggressive behavior occurred between two small males, two large males, or one large and one small male. Fighting ensued mainly when large males were involved, and larger males won fights. Consequently, the male-biased sexual size dimorphism in *T. hemipterus* appears to be partially attributable to sexual selection
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KEY WORDS: sexual size dimorphism; aggressive behavior; starvation conditions; resource-defense mating system; male body size; *Togo hemipterus*

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INTRODUCTION

Many animals compete for limited resources, such as food, oviposition sites, mating sites, and mates, especially among males (reviewed in Thornhill and Alcock 1983; Andersson 1994). Consequently, males have developed various distinct traits as
25 “weapons” for use in male–male competition. Such weapons are observed in many animal taxa, from invertebrates to vertebrates (reviewed in Andersson 1994). Insects in particular have developed many distinct weapons, such as the long horn of horned beetles (Eberhard 1979, 1980; Otte and Stayman 1979; Burkhardt and de la Motte 1988), the enlarged mandibles of stag beetles (Otte and Stayman 1979), the long eye stalks of
30 stalk-eyed flies (McAlpine 1979; Burkhardt and de la Motte 1988; Wilkinson and Dodson 1997), and the enlarged forceps of earwigs (Moore and Wilson 1993; Radesäter and Halldórsdóttir 1993; Forslund 2000). Such traits often exhibit strong sexual

dimorphism, and females usually have smaller or rudimentary traits (reviewed in Thornhill and Alcock 1983; Eberhard and Gutiérrez 1991; Andersson 1994; Emlen and Nijhout 2000). Larger males with more developed traits are directly favored in male–male competition (reviewed in Thornhill and Alcock 1983; Andersson 1994).

Some species of Heteroptera have weapons that serve in male-male competition for limited resources. Some coreids have enlarged and spiny femora on the hind legs (Miller, 1971) while in some lygaeids similar morphological characteristics are seen on femor of the forelegs (Schuh and Slater 1995; Rodriguez 2000). In the case of coreids they are used in male-male interactions (Fujisaki 1980, 1981; Mitchell 1980; Miyatake 1993, 1995, 1997; Eberhard 1998), while Rodriguez (2000) noted in the lygaid *Scolopostethus affinis* both sexes could use the front legs to strike opponents although such aggressive interactions were rare.

Body size is a good predictor of resource-holding power (Parker 1974). When two contestants differ in fighting ability or resource-holding power, this asymmetry, if perceived by both contestants, should be used to settle contests. Escalated fighting should occur when the difference in the size of contestants is small (Maynard Smith and

Price 1973), and many studies have verified this hypothesis (*e.g.* Austad 1983; Wells
50 1988; Miyatake 1993).

We hypothesized that food may have a strong effect on competition in the
Lygaeidae, as they rarely display aggression when food is absent and only exhibit such
behavior when food is present (Himuro, unpublished data). If the presence of food is a
key cause of competition, a “hungry” bug, *i.e.* one previously without food, is expected
55 to behave in a certain way when food is present, and the level of starvation should
influence the strength of aggression. Preliminary observations have indicated that the
seed bug *Togo hemipterus* (Scott) exhibits two types of aggressive behavior: indirect
(chasing) and direct (fighting). In chasing behavior, one individual chases another while
shaking its own antennae. In fighting behavior, two individuals stand on their middle
60 and hind legs; raise their head, thorax, and forelegs; extend their forelegs horizontally;
and strike each other with the forelegs while shaking their antennae, similar to
observations of other lygaeids (*e.g.* Rodriguez 2000). They are ground-living and feed
on gramineous seeds such as *Oryza sativa* (L.), *Digitaria ciliaris* (Retz), and *Setaria*
viridis (L.) (Tomokuni et al. 1993).

65 We addressed several hypotheses in this study. First, we propose that strikingly
enlarged forelegs have developed mainly through sexual selection. Second, we expect
that aggressive behavior occurs mainly between males, the purpose of which is to
acquire mates and is mediated by the presence of food. Therefore, we first examined the
sexual size dimorphism of the forelegs and observed aggressive behavior between males,
70 between females, and between males and females under two levels of starvation (starved
for 0 or 10 days). In addition, we examined the effect of body size as an index of
resource-holding power on aggressive behavior and the outcome of contests. We sought
to determine why these individuals fight and to identify the main context of aggressive
behavior.

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MATERIALS AND METHODS

Insect Rearing

Adults of *T. hemipterus* were originally derived from wild females collected on the
campus of Kyoto University, Kyoto, western Japan (35°01' N, 135°46' E), on 21–22
80 July 2004, 14 November 2006, and 10 May 2007. Nymphs were reared in jars (0.43 L)

that contained moist sand to maintain suitable humidity; the openings were covered with nylon mesh. We provided distilled water and fresh brown rice as food every 4–5 days for all developmental stages of bugs. The bugs were maintained under a photoperiod of 16 h light:8 h dark (light: 07:00–23:00 h) at $25 \pm 2^\circ\text{C}$. After imaginal molt and cuticular
85 hardening, *i.e.* after the insect's body coloration blackened, we transferred bugs to jars (0.43 L) with wet cotton and brown rice. Five days later, we segregated bugs by sex to prevent mating prior to experiments. Individuals of the same sex and age were housed together for 20 days, with no more than five individuals per jar. Adult bugs were individually marked with a paint marker (Mitsubishi Paint Marker PX-21, Mitsubishi
90 Pencil Co., Ltd., Japan), and body length was measured using a stereomicroscope equipped with an ocular micrometer. The pre-reproductive period of this species is approximately 25 days at 25°C ; reproductive activity then continues for approximately 3 months (Himuro, unpublished data). In all experiments, we used sexually mature virgin individuals.

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Sexual Size Dimorphism of Morphometric Traits

To compare the morphometric traits of adult male and female *T. hemipterus*, we collected adults on the campus of Kyoto University on 16, 17, 30 April and 1 May 2002 and measured the morphometric traits of 254 males and 259 females. Measured parameters included body length (*i.e.* from the top of the head to the tip of the abdomen: as a indicator of body size), pronotum width, femur length and width of the right foreleg, and femur length of the right middle leg. If right legs were absent, we measured left legs.

Differences in Aggressive Behavior and Effects of Starvation by Sex

On the day prior to the start of the experiment, we transferred individual bugs to Petri dishes containing wet cotton and two grains of brown rice. On the following day, we removed the rice and starved the individuals for 0 or 10 days. The 10-day starvation period had no debilitating effect on *T. hemipterus* (Himuro, unpublished data). To examine aggressive behavior between males, between females, and between males and females, we placed two males and two females in a Petri dish (90 mm diameter, 20 mm depth) with one grain of brown rice and used a digital video camera (SONY DCR-PC120 NTSC, Sony Corporation, Japan) to record their behavior for 2 h

(10:00–12:00) under constant fluorescent light at $25 \pm 2^\circ\text{C}$ (starved for 0 days, $N = 11$; 10 days, $N = 13$). We examined the proportion of individuals that displayed aggressive behavior (chasing and/or fighting) and the proportion of successfully feeding individuals (the proportion of individuals that were able to feed on the grain of brown rice with no aggressive behavior under the control of a male).

Male Aggressive Behavior and Effects of Starvation and Body Size

The body length of field-collected males was 5.94 ± 0.02 mm (mean \pm 1 SE, $N = 254$) and ranged from 4.97 to 6.80 mm, with a unimodal distribution. For the purposes of subsequent experiments testing the effect of relative size, we regarded males with body lengths of 6.2–6.5 mm as large and those of 5.3–5.6 mm as small.

Two males were placed in a Petri dish (45 mm diameter, 20 mm depth) with one grain of brown rice, and their behavior was recorded for 2 h (10:00–12:00) with same procedures mentioned above. Three types of experiments were performed on bugs that had been previously subjected to three different food regimes (starved for 0, 5, or 10 days). First, two small males were used to examine aggressive behavior between small

males (starved for 0 days, $N = 16$; 5 days, $N = 13$; 10 days, $N = 13$). Second, two large
130 males were used to examine aggressive behavior between large males (starved for 0 days,
 $N = 14$; 5 days, $N = 16$; 10 days, $N = 16$). Finally, one large male and one small male
were used to examine aggressive behavior between small and large males (starved for 0
days, $N = 14$; 5 days, $N = 13$; 10 days, $N = 16$). We measured the proportion of
individuals that chased and fought, the frequency of chasing and fighting behavior, the
135 duration of fighting, and the outcome of chasing and fighting.

Which Is the Main Factor Causing Male Aggressive Behavior: Food or Female?

Two males that had been starved for 10 days were placed in a Petri dish (45 mm
diameter, 20 mm depth) and their behavior was recorded for 2 h (10:00–12:00) with
140 same procedures mentioned above. These males were subjected to four different
experimental regimes: (1) one grain of brown rice and one female ($N = 13$), (2) one grain
of brown rice ($N = 11$), (3) one female ($N = 13$), or (4) neither brown rice nor a female (N
= 14).

145 Analyses

We used Mann-Whitney *U*-tests to examine sexual size differences in their body length and pronotum width. Analysis of covariance (ANCOVA) was used to assess the relationships between body length and leg traits, with particular focus on sexual differences in the slopes of this relationship. The rationale for using ANCOVA was to
150 determine which sex was under higher sexual selection pressure.

The proportions of aggressive behavior in each group were compared using Fisher's exact probability test. For comparisons among more than three groups, sequential Bonferroni methods (Rice 1989) were applied after Fisher's exact probability test at the 5% significance level. The starvation level or sex of the opponent, which
155 affects the proportion of successfully feeding individuals, was analyzed using a log linear model. Likelihood ratio tests were used to examine the relationship between the level of starvation and the proportions of chasing and fighting individuals. The starvation level and experimental conditions (*i.e.* between small males, between large males, and between large and small males), which affect the frequencies of chasing and
160 fighting behavior and the duration of fighting behavior, were analyzed using ANCOVA.

Binomial tests were used to examine the effect of body size on the outcomes of chasing and fighting behavior. All analyses were conducted using JMP IN version 5 release 5.1.2 software (SAS Institute Inc. 2004).

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RESULTS

Sexual Size Dimorphism in Morphometric Traits

Males were significantly larger than females on all measured traits (Fig. 1, Table 1).

Males also had significantly larger front and middle legs; ANCOVA results indicated that the slopes of the relationships between body length and the linear femur length of the foreleg, the femur width of the foreleg, and the femur length of the middle leg were significantly greater in males than in females (sex effect: see in Table 1; body length effect: femur length of the foreleg, $P < 0.001$; femur width of the foreleg, $P < 0.001$; femur length of the middle leg, $P < 0.001$). Significant interactions were observed between sex and body length for the femur length and width of the foreleg but not for the femur length of the middle leg (Sex \times Body length interaction: femur length of the foreleg, $P < 0.001$; femur width of the foreleg, $P < 0.001$; femur length of the middle leg,

$P = 0.465$), *i.e.* the femur length and width of the foreleg increased more in males than in females with increases in body length.

180 Differences in Aggressive Behavior and Effect of Starvation by Sex

We placed two males and two females and examined aggressive behavior between males, between females and between male and female. Aggressive behaviors occurred primarily between males and did not appear to be lethal, nor were any puncture wounds observed. Aggressive behaviors between males tended to occur more frequently at the 185 10-day starvation level compared to 0 days of starvation. We did not observe any aggressive behaviors between females, and we rarely observed aggressive behaviors between males and females (Table 2). Under 10-day starvation, only two males chased a female and on only one occasion each. The proportion of successfully feeding individuals indicated that the sex of the opponent strongly affected male aggression (log 190 linear model; starvation level: $df = 1$, $\chi^2 = 0.355$, $P = 0.552$; sex of the opponent: $df = 1$, $\chi^2 = 38.431$, $P < 0.001$; Fig. 2). Males which controlled a brown rice allowed females to feed on the rice, meanwhile, they did not allow other males to feed on the rice both under

0-day and 10-day starvation levels (Fig. 2).

195 Male Aggressive Behavior and Effects of Starvation and Body Size

When both males were small, the starvation level and proportions of chasing and fighting were not significantly related (Table 3); however, when both males were large, the proportion of chasing and fighting individuals increased significantly with the severity of starvation (Table 3). When males were of unequal size, the proportion of chasing individuals was not significantly related to starvation level (Table 3); however, the proportion of fighting individuals increased significantly with the severity of starvation (Table 3).

The frequency of chasing behavior was not affected by the level of starvation or by male size relationships (ANCOVA; starvation level: $F = 0.48$, $P = 0.492$; experimental conditions: $F = 2.161$, $P = 0.127$; Table 3). The frequency of fighting individuals increased significantly with the severity of starvation (starvation level: $F = 4.22$, $P < 0.05$; experimental conditions: $F = 1.351$, $P = 0.274$; Table 3). The duration of fighting behavior was not affected by the level of starvation or experimental conditions

(starvation level: $F = 0.011$, $P = 0.919$; experimental conditions: $F = 0.612$, $P = 0.544$;

210 Table 3).

The proportions of aggressive behavior between large males (68.8 %, $N = 16$) and between small and large males (75.0%, $N = 16$) were significantly higher than that between small males (23.1%, $N = 13$) but did not differ significantly from one another (Fisher's exact probability test $P < 0.05$ with adjustment by the sequential Bonferroni

215 method). In male–male competition between large and small males, large males won all chasing and fighting events (binomial tests; chasing, starved for 0 days: $N = 29$, $P < 0.001$; 5 days: $N = 26$, $P < 0.001$; 10 days; $N = 75$, $P < 0.001$; fighting, starved for 5 days: $N = 9$, $P < 0.01$; 10 days: $N = 42$, $P < 0.001$).

220 Which Is the Main Factor Causing Male Aggressive Behavior: Food or Females?

Aggressive behavior occurred primarily in the presence of food (Fisher's exact probability test $P < 0.001$). The proportions of aggressive behavior in the presence of both food and females (46.2%, $N = 13$) and in the absence of females (54.5 %, $N = 11$) did not differ significantly ($P > 0.05$ using Fisher's exact probability test adjusted by the

225 sequential Bonferroni method). However, the proportion of aggressive behavior in the
absence of food was 0% regardless of whether a female was present (present: $N = 13$; not
present: $N = 14$) and varied significantly from treatments with food ($P < 0.05$). In the
absence of food, we observed mating in 5 cases of 13, whereas in the presence of food,
mating occurred in 7 cases of 13.

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DISCUSSION

In many insects, the body size of females is larger than that of males, probably
because of a high fecundity advantage for large females (Shine 1988; Honek 1993;
Andersson 1994). Teder and Tammaru (2005) showed that females were the larger sex in
235 >80% of 158 insect species from a variety of insect orders. However, *T. hemipterus*
exhibits male-biased sexual size dimorphism, in which males are significantly larger
than females in body size (Table 1). Sexual size dimorphism is presumably the result of
adaptation in response to a difference in the net selection pressures between the sexes
(Andersson 1994; Preziosi and Fairbairn 1996; Blanckenhorn 2000, 2005). A larger
240 body size is advantageous in male–male competition (Shine 1989; Andersson 1994;

Fairbairn 1997; Blanckenhorn 2005), and the male-biased sexual size dimorphism in *T. hemipterus* appears to be partially related to sexual selection favoring large males, as a larger body size is advantageous in aggressive behavior (both chasing and fighting).

Togo hemipterus males have proportionately larger forelegs than females (Fig. 1).

245 In contrast to the linear regression of femur length of the foreleg on body length, the slope of the linear regression of femur length of the middle leg on body length did not differ significantly between sexes, indicating that the male foreleg traits have developed through sexual selection and serve a distinct function in males, *i.e.* as “weapons” in male–male competition.

250 The two aggressive behaviors of *T. hemipterus*, *i.e.* chasing and fighting, occurred mainly between males and rarely between females or between males and females (Table 2). However, in other species of Heteroptera, fighting behavior occurs both between females and between males and females (Mitchell 1980; Eberhard 1998; Rodriguez 2000). In general, females are more likely to fight over food than are males because they
255 require more resources to produce eggs. However, *T. hemipterus* females rarely fought, even when they were starved (Table 2). These results strongly indicate that aggressive

behavior functions as male–male competition in *T. hemipterus*.

The proportion of successfully feeding individuals indicated that the sex of the opponent strongly affects male aggressive behavior. Males allowed females to feed (Fig. 260 2) and then often courted them and sometimes mated. Male *T. hemipterus* may use food as a nuptial gift, similar to other animal species (reviewed in Thornhill and Alcock 1983; Andersson 1994; Vahed 1998). Males of the lygaeid *Stilbocoris natalensis* also offer food to females as a nuptial gift (Carayon 1964), although *S. natalensis* males do not have enlarged forelegs and do not fight one another (Carayon 1964). Additional 265 experimental work is necessary to determine whether *T. hemipterus* indeed uses food as a nuptial gift. Recent study suggested that food may function as a counter-drug against male’s toxic seminal substances in *T. hemipterus* (Himuro and Fujisaki 2010).

We found that a larger body size is advantageous in male–male competition, such as chasing and fighting, indicating that body size is a good predictor of resource-holding 270 power (Parker 1974). We found that escalated fighting frequently occurred even when the difference in the body size of contestants was large. Furthermore, the difference in the body size of contestants had no effect on the duration of fighting behavior in *T.*

hemipterus. We did not examine the effects of the value of the resource to each contestant, which may have affected the pattern and duration of fighting behavior
275 (Enquist and Leimar 1987). In this assay, the insects were in a closed and limited space. Thus the frequency and the duration of aggressive behavior would be probably much higher than those in nature. It is needed to investigate the effects of the density of individuals and the size of space on their aggressive behaviors.

Aggressive behaviors occurred primarily when a large male was involved,
280 indicating that the benefit and/or cost arising from the aggressive behavior varies depending on body size. Smaller males may adopt a different strategy in male–male competition, as observed in several other animal species (reviewed in Shuster and Wade 2003).

The proportions of fighting and chasing individuals and the frequency of fighting
285 behavior increased with the severity of starvation (Table 3). Males fought only when food was present, regardless of whether a female was present. Therefore, the presence of food was clearly an extremely important factor in *T. hemipterus* competition. In contrast, the presence of a female did not appear to be a proximate factor affecting male

competition; instead, female presence may serve as an important ultimate factor in *T.*

290 *hemipterus* competition.

The distribution of females is thought to be primarily affected by resources, whereas the distribution of males should be primarily affected by the availability of females (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). This difference may be attributable to the fact that female reproductive success tends to be limited by
295 resources, whereas male reproductive success tends to be limited by access to females (Bradbury and Vehrencamp 1977; Emlen and Oring 1977). In the field, *T. hemipterus* feeds on graminaceous seeds, and the distribution and abundance of seeds tend to vary highly in space and time (Solbreck 1978; Solbreck and Pehrson 1979). Himuro (2009) demonstrated that *T. hemipterus* males attract females using sex pheromones, especially
300 when males feed on seeds. Consequently, *T. hemipterus* males might adopt a kind of resource-defense mating system that would be beneficial because females aggregate near food resources when they are scarce. In contrast, when food resources are abundant, females are more scattered throughout the habitat, forcing males to search for them. Thus, *T. hemipterus* males may adopt alternative mating strategies depending on the

305 distribution and abundance of food resources. This hypothesis was supported to some extent by our observation that the proportion of fighting and chasing males increased with increases in the severity of starvation. Moreover, such strategies may vary depending on male body size.

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REFERENCES

- Andersson M (1994) *Sexual Selection*. Princeton University Press, New Jersey.
- 320 Austad, SN (1983) A game theoretical interpretation of male combat in the bowl and
doily spider (*Frontinella pyramitela*). *Anim Behav* 31:59–73.
- Blanckenhorn WU (2000) The evolution of body size: what keeps organisms small? *Q
Rev Biol* 75:385–407.
- Blanckenhorn WU (2005) Behavioral causes and consequences of sexual size
325 dimorphism. *Ethology* 111:977–1016.
- Bradbury JW, Vehrencamp SL (1977) Social organization and foraging in emballonurid
bats. III. Mating systems. *Behav Ecol Sociobiol* 2:1–17.
- Burkhardt D, de la Motte I (1988) Big ‘antlers’ are favoured: female choice in stalk-eyed
flies (Diptera, Insecta), field collected harems and laboratory experiments. *J Comp
330 Physiol A* 162:649–652.
- Carayon J (1964) Un cas d'offrande nuptiale chez les Hétéroptères. *CR Acad Sci Paris*
259:4815–4818.
- Eberhard WG (1979) The function of horns in *Podischnus agenor* (Dynastinae) and

- other beetles. In: Blum MS, Blum NA (eds) *Sexual Selection and Reproductive*
335 *Competition in Insects*. Academic Press, New York, pp 231–258.
- Eberhard WG (1980) Horned beetles. *Sci Am* 242:124–131.
- Eberhard WG (1998) Sexual behavior of *Acanthocephala declivis guatemalana*
(Hemiptera: Coreidae) and the allometric scaling of their modified hind legs. *Ann*
Entomol Soc Am 91:863–871.
- 340 Eberhard WG, Gutiérrez EE (1991) Male dimorphisms in beetles and earwigs and the
question of developmental constraints. *Evolution* 45:18–28.
- Emlen DJ, Nijhout HF (2000) The development and evolution of exaggerated
morphologies in insects. *Annu Rev Entomol* 45:661–708.
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating
345 systems. *Science* 197:215–223.
- Enquist M, Leimar O (1987) Evolution of fighting behaviour: the effect of variation in
resource value. *J Theor Biol* 127:187–205.
- Fairbairn DJ (1997) Allometry for sexual size dimorphism: pattern and process in the
coevolution of body size in males and females. *Annu Rev Ecol Syst* 28:659–687.

- 350 Forslund P (2000) Male-male competition and large size mating advantage in European earwigs, *Forficula auricularia*. *Anim Behav* 59:753–762.
- Fujisaki K (1980) Studies on the mating system of the winter cherry bug, *Acanthocoris sordidus* Thunberg (Heteroptera: Coreidae) I. Spatio-temporal distribution patterns of adults. *Res Popul Ecol* 21:317–331.
- 355 Fujisaki K (1981) Studies on the mating system of the winter cherry bug, *Acanthocoris sordidus* Thunberg (Heteroptera: Coreidae) II. Harem defence polygyny. *Res Popul Ecol* 23:262–279.
- Himuro C (2009) Evolutionary ecology research about sexual conflict over reproduction in the seed bug *Togo hemipterus* (Heteroptera: Lygaeidae). PhD thesis. University of Kyoto, Kyoto, Japan (in Japanese).
- 360 Himuro C, Fujisaki K (2010) Mating experience weakens starvation tolerance in the seed bug *Togo hemipterus* (Heteroptera: Lygaeidae). *Physiol Entomol* 35:128–133.
- Honek A (1993) Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66:483–492.
- 365

Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18.

McAlpine DK (1979) Agnostic behavior in *Achias australis* (Diptera, Platystomatidae)

and the significance of eyestalks. In: Blum MS, Blum NA (eds) *Sexual Selection*

and *Reproductive Competition in Insects*. Academic Press, New York, pp

370 221–230.

Miller NCE (1971) *The biology of the Heteroptera*. EW Classey Ltd, Hampton.

Mitchell PL (1980) Combat and territorial defense of *Acanthocephala femorata*

(Hemiptera: Coreidae). *Ann Entomol Soc Am* 73:404–408.

Miyatake T (1993) Male-male aggressive behavior is changed by body size difference in

375 the leaf-footed plant bug, *Leptoglossus australis*, Fabricius (Heteroptera:

Coreidae). *J Ethol* 11:63–65.

Miyatake T (1995) Territorial mating aggregation in the bamboo bug, *Notobitus*

meleagris, Fabricius (Heteroptera: Coreidae). *J Ethol* 13:185–189.

Miyatake T (1997) Function morphology of the hind legs as weapons for male contests

380 in *Leptoglossus australis* (Heteroptera: Coreidae). *J Insect Behav* 10:727–735.

Moore AJ, Wilson P (1993) The evolution of sexually dimorphic earwig forceps: social

interactions among adults of the toothed earwig, *Vostox apicedentatus*. *Behav Ecol* 4:40–48.

Otte D, Stayman K (1979) Beetle horns: Some patterns in functional morphology. In:
385 Blum MS, Blum NA (eds). *Sexual Selection and Reproductive Competition in Insects*. Academic Press, New York, pp 259–292.

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. *J Theor Biol* 47:223–243.

Preziosi RF, Fairbairn DJ (1996) Sexual size dimorphism and selection in the wild in the
390 waterstrider *Aquarius remigis*: body size, components of body size and male mating success. *J Evol Biol* 9:317–336.

Radesäter T, Halldórsdóttir H (1993) Two male types of the common earwig: male-male competition and mating success. *Ethology* 95:89–95.

Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225.

395 Rodriguez SRL (2000) On the fore legs of seed bugs (Heteroptera: Lygaeidae): aggression and allometric scaling in *Scolopostethus affinis* Schilling. *J Kansas Entomol Soc* 73:6–10.

SAS Institute Inc (2004) JMP Start Statistics, 3rd ed. SAS Institute Inc, Cary, NC, USA.

Schuh RT, Slater JA (1995) True Bugs of the World (Hemiptera: Heteroptera):

400 Classification and Natural History. Cornell University Press, New York.

Shine R (1989) Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q Rev Biol* 64:419–461.

Shine R (1988) The evolution of large body size in females: a critique of Darwin's "Fecundity advantage" model. *Am Nat* 131:124–131.

405 Shuster S, Wade M (2003) Mating systems and strategies. Princeton University Press, Princeton, New Jersey.

Solbreck C (1978) Migration, diapause, and direct development as alternative life histories in a seed bug, *Neacoryphus bicrucis*. In: Dingle H (ed) Evolution of Insect Migration and Diapause. Springer-Verlag, New York, Heidelberg, Berlin, pp 195–217.

Solbreck C, Pehrson I (1979) Relations between environment, migration and reproduction in a seed bug, *Neacoryphus bicrucis* (Say)(Heteroptera: Lygaeidae). *Oecologia* 43:51–62.

- Teder T, Tammaru T (2005) Sexual size dimorphism within species increases with body
415 size in insects. *Oikos* 108:321–334.
- Thornhill R, Alcock J (1983) *The Evolution of Insect Mating Systems*. Harvard
University Press, Cambridge, Massachusetts.
- Tomokuni M, Yasunaga T, Takai M, Yamashita I, Kawamura M, Kawasaki T (1993) A
field guide to Japanese bugs—Terrestrial heteropterans. *Zenkoku Noson Kyoiku*
420 *Kyokai*, Publishing Co, Ltd, Tokyo, Japan (in Japanese).
- Vahed K (1998) The function of nuptial feeding in insects: a review of empirical studies.
Biol Rev 73:43–78.
- Wells MS (1988) Effects of body size and resource value on fighting behaviour in a
jumping spider. *Anim Behav* 36:321–326.
- 425 Wilkinson GS, Dodson GN (1997) Function and evolution of antlers and eye stalks in
flies. In: Choe JC, Crespi BJ (eds) *The Evolution of Mating Systems in Insects and*
Arachnids. Cambridge University Press, Cambridge, pp 310–328.

Tables

Table 1. Measurements of morphometric traits (mean \pm 1 SE) of *Togo hemipterus* males ($N = 254$) and females ($N = 259$) in the field

Morphometric trait	Males	Females	<i>P</i> -value
Body length (mm)	5.94 ± 0.02	5.90 ± 0.02	< 0.05 [†]
Pronotum width (mm)	1.31 ± 0.01	1.21 ± 0.00	< 0.001 [†]
Femur length of foreleg (mm)	1.87 ± 0.01	1.62 ± 0.01	< 0.001 ^{† †}
Femur width of foreleg (mm)	0.52 ± 0.00	0.47 ± 0.00	< 0.001 ^{† †}
Femur length of middle leg (mm)	1.55 ± 0.01	1.46 ± 0.00	< 0.001 ^{† †}

[†] *P*-values refer to Mann-Whitney *U*-tests.

^{† †} *P*-values refer to ANCOVA (Sex effect)

Table 2. Proportions of aggressive behavior between males, between females, and between males and females under two levels of starvation in *T. hemipterus*

Starvation level	Proportion of aggressive behavior (%)		
	Between males	Between females	Between males and females
0 days	18.2 (11) ab	0 (11) b	0 (11) b
10 days	61.5 (13) a	0 (13) b	15.4 (13) ab

Numbers in parentheses indicate sample size.

Fisher's exact probability test, $P < 0.001$.

Different letters indicate significant differences ($P < 0.05$) using Fisher's exact probability tests (adjusted by the sequential Bonferroni method).

Table 3. Effect of starvation on aggressive behavior between two small males, between two large males, or between one large and one small male of *T. hemipterus*

	Starvation level			P-value
	0 days	5 days	10 days	
Two small males				
Proportion of chasing individuals (%)	6.3 (16)	38.5 (13)	23.1 (13)	0.238
Frequency of chasing behavior	18 (1)	7.8 ± 1.5 (5)	7.0 ± 3.6 (3)	
Proportion of fighting individuals (%)	6.3 (16)	30.1 (13)	23.1 (13)	0.232
Frequency of fighting behavior	2.0 (1)	1.5 ± 0.3 (4)	7.7 ± 1.8 (3)	
Duration of fighting behavior (s)	9.2 ± 3.8 (2)	12.1 ± 1.7 (6)	8.0 ± 1.0 (23)	
Two large males				
Proportion of chasing individuals (%)	7.1 (14)	37.5 (16)	56.3 (16)	< 0.01
Frequency of chasing behavior	1.0 (1)	6.0 ± 1.3 (6)	3.0 ± 0.6 (9)	
Proportion of fighting individuals (%)	0 (14)	31.3 (16)	56.3 (16)	< 0.01
Frequency of fighting behavior	0 (0)	3.4 ± 1.4 (5)	2.3 ± 0.6 (9)	
Duration of fighting behavior (s)	—	7.0 ± 0.9 (17)	8.6 ± 1.1 (20)	
One large and one small male				
Proportion of chasing individuals (%)	57.1 (14)	46.2 (13)	68.8 (16)	0.385
Frequency of chasing behavior	3.6 ± 1.4 (8)	4.5 ± 2.2 (6)	6.8 ± 2.0 (11)	
Proportion of fighting individuals (%)	0 (14)	23.1 (13)	50 (16)	< 0.01
Frequency of fighting behavior	0 (0)	3.0 ± 2.0 (3)	6.4 ± 2.6 (8)	
Duration of fighting behavior (s)	—	6.7 ± 1.0 (9)	7.9 ± 0.8 (42)	

Values are mean ± 1 SE (sample sizes).

P-values refer to likelihood ratio tests.

Figure captions

Figure 1. Relationships between body length and leg traits (femur length of foreleg, femur width of foreleg, and femur length of middle leg) of males (closed symbols) and females (open symbols) of *Togo hemipterus*.

Figure 2. The proportion of successfully feeding males and females of *T. hemipterus* at two levels of starvation (0 and 10 days). Bars indicate ± 1 SE.

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