SHORT COMMUNICATION

Role of body size in dominance interactions between male water striders, *Aquarius paludum*

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Abstract Water striders are a model system for the study of sexual size dimorphism, but the effect of body size on the dominance relationship between individuals has not been experimentally tested. In 34 staged contests between males of the water strider *Aquarius paludum*, we determined the effect of body size difference between contestants on the outcome of the aggressive interactions. In contests between a large and a small male, the larger individuals won the interactions significantly more often than expected by chance. This is the first experimental evidence for the importance of body size in pair-wise contests among water striders.

Keywords Male–male competition · Sexual size dimorphism · *Aquarius paludum* · Gerridae

Introduction

Dominance relationships are often determined by the body size of individuals (Archer 1988; Francis 1988). Higher ranked individuals have better quality habitats, food, and

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mates. Therefore larger size in males should be favored by natural selection in all these contexts due to intense male–male competition, especially in polygamous mating systems and/or territorial mating systems. Unless opposing selection is involved, this may lead to male-biased sexual dimorphism. However, when opposing selection is involved then even in polygamous mating systems, which typically favor larger males, female-biased sexual dimorphism may evolve.

Water striders provide a good example. There is substantial evidence of selection mechanisms that favor smaller males (Arnqvist 1989; Blanckenhorn et al. 1995; Fairbairn 1990, 1993; Rowe 1994; Watson et al. 1998), leading to female-biased sexual size dimorphism (SSD). Yet, water strider males are polygamous and they compete with each other for access to mates and food and defend their territories in some species (Wilcox and Ruckdeschel 1982; Rubenstein 1984; Vepsalainen and Nummelin 1985a, b; Nummelin 1987; Jablonski 1996; Jablonski and Scinski 1999). This should, as in other animals, produce selection towards larger males at the stage of aggressive interactions for mates, territories, and food, all of which involve repelling intruders. However, there is little behavioral evidence for the hypothetical large-size advantage in dominance interactions as an indicator of natural selection for larger size (assuming that dominance increases access to resources). Although Jablonski (1996) showed that body size of a territory owner in comparison to intruders may affect territory size in one species, we are not aware of studies that experimentally address the role of body size in dominance interactions among water striders.

The aim of this study is to determine how dominance relationships among males are affected by body size difference between two opponents in *Aquarius paludum*. The report also presents previously undescribed postures in

water striders used by individual males to visually appear larger (taller) than an opponent.

Materials and methods

The water strider *A. paludum* is widely distributed in Asia and Europe in lentic water bodies. We used males of *A. paludum* from a large artificial pond on the campus of the Seoul National University, Korea. After collecting, we separated them according to the body length. We used individuals from the extreme lower and upper 30% of the natural size distribution as experimental small and large individuals, respectively. With digital images from a fixed digital camera (Sony A100), body size of live water striders was measured using Image J program. All animals were individually marked on the thorax with enamel paints and placed in two rectangular plastic containers (40×50 cm) in order to experience dominance relationships with only similar-sized opponents. Hence, the experience of all experimental individuals prior to the test was the same: all experienced interactions with only similarly sized opponents.

In the experiment, we measured the effect of body size on the dominance relationship between two interacting males. We conducted 34 tests, in which the behavior of individuals was closely watched and the outcome of interaction scored. In each test, two individuals were observed in a glass container (40×40 cm) filled with water (10 cm in depth). During the first 3 min, the two individuals were allowed to adapt to the new environment and to recognize each other. After the adaptation period, in order to provoke the interaction, we delicately touched the water surface, imitating the presence of a prey and attracting both males. The two males reacted to the ripples created in this way by approaching and attempting to grasp the "prey," and by behaving aggressively towards each other. This method allowed both animals to remain at the same level with respect to the "ownership" of the resource, which is known to affect the outcome of aggressive interactions (e.g., Davies 1978).

We compared the outcome of these interactions between two treatments: "same-size" and "different-size" treatment. The size difference between the two opponents in the same-size treatment (1.3 ± 0.3 mm, $n = 17$; mean $\pm$ standard error) was significantly smaller ($t_{32} = 10.7, P < 0.001$) than the difference between the two opponents in the different-size treatment (8.0 ± 0.6 mm, $n = 17$). The latter corresponds to approximately 6% of average body length of the smaller male. For the same-size treatment, 17 pairs of same-size individuals were matched (nine pairs of small males and eight pairs of large males). For the different-size treatment, one large and one small individual were paired ($n = 17$ pairs). For each dyad, we classified the outcome of a provoked aggressive interaction as either "focal individual winning," if the focal individual moved forward or stayed in the place of interaction, or "focal individual losing," if this individual turned away and left the site where the interaction took place.

The outcomes of interactions were determined within 3 s after the two individuals approached the site of origin of the surface vibrations. In this way, we avoided classifying behaviors that might have been elicited by causes other than the competition. The focal individual was either the larger one in the different-size treatment or a randomly chosen one (from among two) in the same-size treatment. The focal individual was scored as dominant if it was the "winning" individual. We used χ^2 statistics to determine whether treatment affects the proportion of interactions in which the focal individual was dominant.

Results

In 11 tests of the different-size treatment, the larger individual moved forward and repelled the smaller one, in 3 tests the larger individual stayed put and the smaller retreated, and in 3 tests it was the larger one who retreated. In the same-size treatment, 2 focal males moved forward, 3 males stayed put, and 12 males moved backward, leaving the site where the interaction took place. In consequence, the treatment had a significant effect on the outcome of the dyadic interaction ($\chi^2 = 6.0$, $df = 1$, $P = 0.014$; Fig. 1), and the winning interactions in the different-size treatment occurred significantly more often than theoretical null expectation of 50% ($\chi^2 = 7.1$, $df = 1$, $P = 0.008$; Fig. 1). The frequency of winning by the focal male in the same-size treatment was not different from 50% ($\chi^2 = 2.9$, $df = 1$, $P = 0.09$; Fig. 1), but it was relatively smaller than
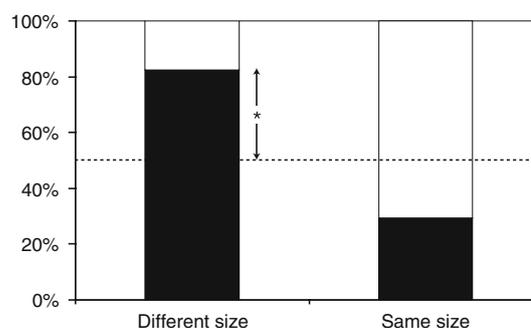

Fig. 1 Proportion of the interactions in which the focal male was the dominant (*black bar*) in all interactions in different-size ($n = 17$) and same-size ($n = 17$) treatments. In the different-size treatment, the focal individual was always the larger of the two opponents. In the same-size treatment, the focal individual was randomly chosen from the two males in each test. The *dotted horizontal line* indicates the theoretical random expectation

null expectation because in some interactions neither of the males won or retreated and there was no clear winner. After removing these tests ($n = 6$) from the analysis, the frequency of winning by the focal male in the same-size treatment was clearly not different from 50% ($\chi^2 = 0.82$, $df = 1$, $P = 0.37$), indicating that males tended to move backward and did not behave aggressively in the interaction with the same-size opponent. Within the same-size treatment there was no difference between trials with small and those with large individuals paired for the test ($\chi^2 = 0.48$, $df = 1$, $P = 0.49$) in the frequency of winning by the focal individual.

Direct observations indicated that the interacting water striders may change their body posture in response to an approaching competitor from a typical posture (Fig. 2a) to a "standing up" posture in which the body is elevated high above the water surface (Fig. 2b, Video S1 in the ESM). In this posture an individual appears taller than the approaching intruder, and the longer his legs are, the taller the individual can stand. Since larger body size is correlated with longer legs (Hungerford and Matsuda 1960), larger individuals are able to look taller in such a posture than small-bodied individuals.

Discussion

The experiment demonstrated that larger individuals are dominant in contests over resources. We are not aware from the literature of such a direct experimental evidence of the body size effect in water striders. Although we used only vibrations mimicking prey, we see no reason why the same effect should not be present in contests over other resources such as territories or mates. There was a possibility that some "non-aggressive" individuals lost interest, rather than losing the fight, because the vibration stimulation was very short, and there was no real prey involved. Even if this might have happened, we see no reason that the probability of "losing interest" would differ between the smaller and the larger males.

Because *A. paludum* live in a lentic habitat and a great proportion of males are wingless in the summer generation, they do not have the opportunity to leave for a different habitat with a smaller number of dominant competitors. Hence, our results indicate that smaller males may face more difficulties in securing vital resources, which may create selection towards larger male size. If body size also affects dominance among females, then larger body size will be favored in either sex if individuals experience competition over the resources. Such a selection would contribute to the evolutionary mechanisms that shape the level of SSD according to the differential-equilibrium model by Blanckenhorn (2000 and Blanckenhorn et al. 2007), where SSD is an outcome of diverse selective pressures that counterbalance each other in a sex-specific manner, leading to a different body size in males than females.

Our results indicate that in the context of resource defense, the selection for larger size may contribute to this model as one of such counterbalancing selection forces. Among the variety of selective forces, fecundity selection on females (Preziosi et al. 1996), mechanical constraints on pairing (Fairbairn et al. 2003), and loading constraint
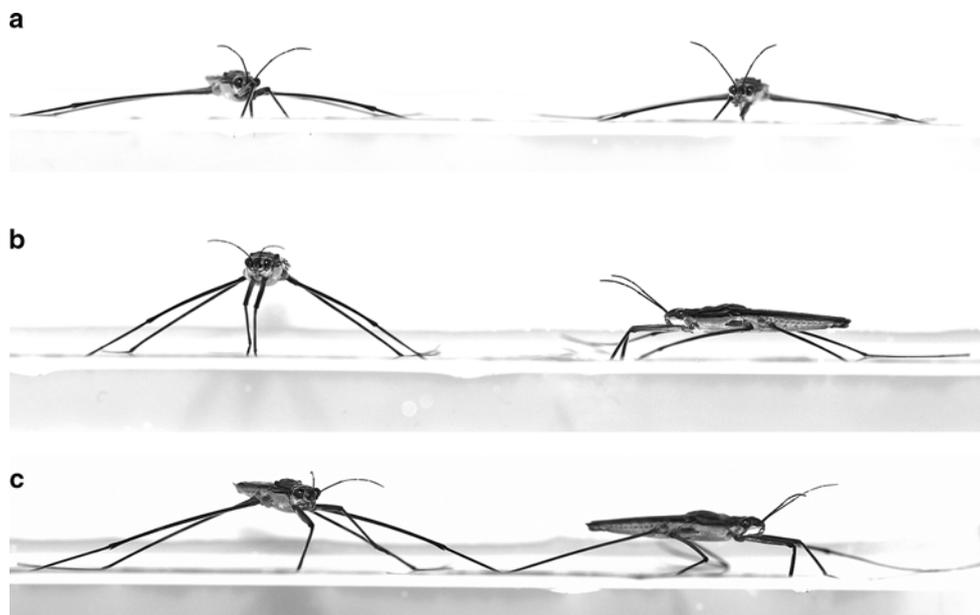

Fig. 2 An example of two interacting individuals next to each other when no "standing up" posture is present (**a**) and when the "standing up" posture is used (**b**, **c**). Photo by C.S. Han

(Fairbairn 1990, 1993) have been considered as the mechanisms leading towards female-biased SSD in water striders. Additionally, post-copulatory mate-guarding was regarded as critical in the evolution of SSD in water striders by affecting the male body size (Fairbairn 1993) relative to the female. It was proposed that in water strider species with a long guarding period, SSD increases because females may prefer smaller males who can reduce the energetic cost of pairing during which females carry males on their backs (Fairbairn 1993). Additionally, in some situations male size may evolve convergently to a certain optimal female-biased sexual size ratio because the kinematics of the males' initial mate-grasping behavior depends on male size relative to the female he tries to mate with (Han et al., unpublished data). While in the latter situation no counterbalancing selection is required to explain the precise maintenance of a specific SSD, in the former scenario some counterbalancing selection forces towards larger body size of males should operate to evolutionarily maintain the species-specific SSD.

Our study suggests that, in addition to such opposing selection forces as have already been proposed (Fairbairn 1990, 1997, 2007), one of the counterbalancing mechanisms may be the advantage of large size in direct ("contest") competitions for resources. Furthermore, since competing individuals of A. paludum used the "standing up" posture, which exaggerates the height (Fig. 2b, Video S1 in ESM), we hypothesize that this exaggerated behavior may amplify the size difference between competitors and that it may affect the dominance relationship between individuals. A similar posture was also observed by females when approached by mate-seeking males (Han and Jablonski, personal observation). In the future, detailed studies are necessary to assess the functions of the standing-up posture during individual interactions and consequently how this behavior affects morphological evolution such as SSD, body size, and leg length.

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