



## Predators induce conditions for size-dependent alternative reproductive tactics in a water strider male



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Alternative reproductive tactics (ARTs) are commonly associated with differences in morphological, physiological and behavioural traits. The morphological differences can be associated with differences between ARTs in effectiveness of sexual display but the relationship has rarely been documented. We tested it using the Asian water strider *Gerris gracilicornis* (Heteroptera: Gerridae), in which males have two ARTs: a signalling courtship tactic and a nonsignalling tactic. Many *G. gracilicornis* males employ an intimidating signalling courtship tactic capitalizing on predators' behaviours and female responses to predators. The males produce courtship ripple signals on the water's surface by vibrating their middle legs after mounting the female. In this study we found that smaller males more often adopted a non-signalling than a signalling courtship tactic. We hypothesized that smaller males with shorter middle legs and weaker muscles may not be able to produce ripples that are sufficiently strong to attract predators from a distance, and therefore sexual selection favours nonsignalling tactics in smaller but not larger males. We created a  $2 \times 2$  experimental design to test the contribution of male body size to the intimidation effect under different levels of predation risk. We showed that only large males' ripple signals had an intimidation effect on females. We also found that females suffered a higher predation risk when large, but not small, males mounted them. The signal intensity of large males was also stronger than that of small males. Hence, we suggest that size-dependent effectiveness of the intimidation signalling maintains the size-dependent reproductive tactics in *G. gracilicornis*.

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Alternative reproductive tactics (ARTs) are widely observed in inferior males which subvert the female's preference for high-quality males by adopting nondisplaying or sneak mating tactics (Gross, 1996; Oliveira, Taborsky, & Brockmann, 2008; Shuster & Wade, 2003). ARTs are also commonly associated with discrete morphological traits (reviewed in Brockmann, 2008). Large males may develop conspicuous ornaments adapted for male-male competition or sexual display, whereas small males may develop only rudimentary ornaments. When these individual differences in body size or ornaments relate to the differences in reproductive behaviour, morphological differences can contribute to the evolution of ARTs (Aubin-Horth, Dodson, & Sinervo, 2004; Brockmann, 2002; Gross, 1996; Magellan, Pettersson, & Magurran, 2005; Moczek & Emlen, 2000). Large males with fully developed ornaments are usually territorial, engage in male-male competition and

exhibit courtship displays to attract females. In contrast, small inferior males with rudimentary ornaments are usually non-territorial, parasitizing superior males' courtship efforts, and attempting to copulate without courtship displays.

If body size or ornament size affects the characteristics of the courtship signalling, then the morphological differences may cause differences in effectiveness of sexual displays, creating sexual selection for morphology-dependent ARTs. For example, male guppies, *Poecilia reticulata*, increased courtship display when their tail length, which appears to affect the effectiveness of the courtship signal, was increased by manipulation (Karino & Kamada, 2009; Karino & Kobayashi, 2005). In insects, large male *Drosophila* were more successful in a vibrational courtship as a result of their larger wing area (Ewing, 1964). When the courtship effectiveness is size dependent and courtship is costly to produce, alternative non-signalling tactics might evolve in small males. Despite the effect of body size on ARTs, the relationship between body size (morphological phenotype), effectiveness of courtship behaviour (behavioural phenotype) and ARTs (reproductive tactics) is still poorly

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understood (but see Malavasi, Lindström, & Sundström, 2001; Malavasi, Torricelli, Lugli, Pranovi, & Mainardi, 2003).

Sneaker tactics arise from fitness benefits when inferior males avoid engaging in costly courtship displays (Brockmann, 2008). For example, when females prefer high-quality males which perform an elaborate courtship display, inferior males may subvert female mate choice and enjoy a mating advantage by adopting a non-displaying coercive tactic with less investment in ornaments (reviewed in Brockmann, 2008; Taborsky, Oliveira, & Brockmann, 2008). The sneaker tactic can arise as a 'best-of-a-bad-job' strategy when the fitness of sneaker small males is higher than that of signalling small males (e.g. when sexual selection acts against small males performing ineffective courtship display with rudimentary ornaments).

Here we tested the relationship between body size, courtship effectiveness and ARTs in an Asian water strider, *Gerris gracilicornis*. The males of this species use coercion to mount a female and the biomechanics of these initial struggles lead to size-assortative mating initiation (Han, Jablonski, Kim, & Park, 2010). After mounting a female successfully, a male produces courtship ripples on the water's surface by vibrating his middle legs (Fig. 1; Han & Jablonski, 2009). This unusual courtship behaviour is a form of male intimidation because the courtship ripple signals from males riding on top of a female attract aquatic predators such as notonectids (Hemiptera, Notonectidae), and the female is more vulnerable to predation because she is beneath the male (Han & Jablonski, 2009, 2010). Therefore females appear to be 'intimidated' by this potential increase in predation risk, especially in habitats with high predation risk, which the females can detect based on the perceived unsuccessful attack attempts by predators (Han & Jablonski, 2010). Therefore, females rapidly submit to copulation, to which males respond by stopping the intimidation signalling (intimidating courtship; Han & Jablonski, 2010). Typically a male continues signalling as long as the female does not allow intromission (Han & Jablonski, 2008, 2010). In contrast to this intimidating courtship strategy of the majority of males, we noted that the very small males tended to produce no such courtship

ripple signals after mounting the female (see Results), suggesting an existence of an alternative nonsignalling strategy in this species.

We hypothesize that size-dependent effectiveness of courtship signals in inducing females to copulate (i.e. intimidating females) contributes to the evolution of a nonsignalling strategy in small males. It is possible that larger males with longer middle legs and stronger muscles are able to produce stronger ripples, which attract predators from further away (allometry hypothesis). If so, we predict that the females will not respond to the intimidation signalling by mounted smaller males as strongly as to the large males. However, regardless of the intensity of intimidating courtship ripples, females mounted by large and heavy males are predicted to be more susceptible to predators' attacks and, therefore, more susceptible to mating attempts from large males (weight hypothesis). Previous research on water striders has shown that a female in mating tandem incurs higher predation risks than a single female (Arnqvist, 1989; Fairbairn, 1993; Rowe, 1994). This is known to be due to either decreased mobility because of the weight of the male or increased visibility. However, none of the studies has tested how the size of mounting males affects the predation risk of females during mating. Given that heavy individuals are more vulnerable to predators due to decreased mobility or increased visibility (Arnqvist, 1989; Fairbairn, 1993; Rowe, 1994), we suggest that a female's predation risk is less affected by a small male than by a large male mounted on top of her.

Here, we tested this hypothesis by asking the following questions. (1) Do smaller males employ the nonsignalling strategy more often than large males, and is there a size threshold below which only the nonsignalling strategy is observed in males? (2) Do smaller males mounted on females increase the predation risk to the females less than larger males? (3) Is the signal intensity (amplitude of waves) of smaller males weaker than that of larger males? (4) Do females respond less to the signalling by smaller than by larger males?

## METHODS

### *Study Species and Rearing Conditions*

*Gerris gracilicornis* is widely distributed in East Asia with a mating season between March and June. Insects were collected in creeks in Gwanak Mountain near Seoul National University. Males and females were put in separate rectangular, plastic basins (40 × 50 cm) and were fed ad libitum daily with surplus frozen crickets, *Gryllus bimaculatus*. Pieces of polyethylene sheets were provided as rest sites. All animals were individually marked on the thorax with small dots of enamel paint.

Notonectids, *Notonecta triguttata*, generalist predators that attack small insects fallen on the water's surface, were used as predators for water striders in the experiment. They detect prey at a distance using water vibrations and disturbances produced by prey (Lang, 1980). Notonectids were collected at pools near rice fields in the Kimpo region, South Korea, and individually kept in transparent, plastic, cylindrical boxes (diameter 10 cm, height 15 cm). Each individual received one frozen *G. bimaculatus* every day but was starved for 3 days before experiments (see below).

### *Size Distribution of Signalling and Nonsignalling Males*

To distinguish nonsignalling from signalling males, we observed the courtship behaviour of 192 males when we put males and females together in a basin. We classified a male as a 'signalling' male when he produced courtship ripples by vibrating his middle legs while attempting to mate with females (described in Han & Jablonski, 2009) and as a 'nonsignalling' male when he did not



**Figure 1.** A mating pair of *Gerris gracilicornis* and a notonectid predator (*Notonecta triguttata*). The male mounting the female is producing courtship ripple signals with his middle legs stretched forwards, parallel to each other (see Han & Jablonski, 2009). The predator is approaching the pair in response to the male's ripple signals.

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