Intimidating courtship and sex differences in predation risk lead to sex-specific behavioural syndromes

Chang S. Han [a, b, *], Piotr G. Jablonski [b, c, *], Robert C. Brooks [a]

[a] Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, NSW, Australia
[b] Laboratory of Behavioral Ecology and Evolution, School of Biological Sciences, Seoul National University, Seoul, South Korea
[c] Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland

ARTICLE INFO

Behavioural correlations between mating behaviour and antipredator behaviour are expected when sexual behaviour increases predation risk. However, the correlation would be different between males and females, particularly when the sexes experience different levels of predation risk. Here, we tested this idea using a water strider species, *Gerris gracilicornis* (Heteroptera: Gerridae). *G. gracilicornis* males employ an unusual intimidating courtship strategy capitalizing on predator behaviours and female response to predators. Since mounted females are more vulnerable than males to predatory attacks from below, we predicted that changes in female mating behaviours across predation contexts (boldness in a mating context) should be associated with female antipredator behaviours (boldness in a nonmating context), but that the correlation would be weaker for male mating behaviours. In a series of behavioural assays, we measured water striders' (1) mating behaviour in the absence of predators, (2) mating behaviour in the presence of predation risk, (3) boldness in the mating context (changes in female mating behaviour after predator attacks) and (4) boldness in the nonmating context. We found that females behaved more cautiously around predators in both the mating and nonmating contexts. We also found that females' boldness in the mating context was significantly correlated with their boldness in the nonmating context. In contrast to females, antipredator behaviour of males in the nonmating context did not correlate with their boldness in the mating context. Thus we suggest that sex differences in boldness across predation contexts appear to cause sex-specific behavioural syndromes.
© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Over the last decade, a number of empirical studies have reported that individuals of the same population differ consistently in their behaviour (Bell, Hankison, & Laskowski, 2009). The repeatable parts of animal behaviour are often also correlated with each other across traits (Garamszegi, Markó, & Herczeg, 2012). These correlations are referred to as 'behavioural syndromes' (Dingemanse & Dochtermann, 2013; Dingemanse, Dochtermann, & Nakagawa, 2012; Dochtermann & Dingemanse, 2013; Sih, Bell, & Johnson, 2004a, 2004b). Behavioural syndrome studies have made great progress studying traits such as aggressiveness, boldness towards predators and activity in a novel environment (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Yet, in spite of considerable research interest in behavioural syndromes, it remains unclear how sexual selection impacts their evolution (Schuett, Tregenza, & Dall, 2010), particularly the correlation between sexual and nonsexual behaviours (but see Han & Brooks, 2013, 2014, 2015). Because survival and reproductive success form the two major components of fitness, sexual selection can cause the emergence of a behavioural syndrome that is inherited via linkage disequilibrium (see review of Bell, 2007; van Oers, de Jong, van Noordwijk, Kempenaers, & Drent, 2005; Sih et al., 2004b). But how traits such as courtship behaviour and response to courtship relate to other nonsexual behaviours has received far less attention (but see Han & Brooks, 2013, 2014, 2015; Logue, Mishra, McCaffrey, Ball, & Cade, 2009).

Our understanding of behavioural syndromes involving antipredator behaviour has mostly come from studies of associations between predator avoidance or evasion and aggressiveness or exploration (see reviews Dingemanse & Réale, 2005; Sih & Bell, 2008). It remains unknown, however, whether this general

* Correspondence: C. S. Han, Behavioural Ecology Department of Biology, Ludwig-Maximilians University of Munich, Großhaderner Str. 2, 82152 Planegg-Martinsried, Germany; P. G. Jablonski, Laboratory of Behavioral Ecology and Evolution, School of Biological Sciences, Seoul National University, Gwanak-gu, Seoul, 151-742, South Korea.
E-mail addresses: hcspol@gmail.com (C. S. Han), piotrjab@behecolpiotrsangim.org (P. G. Jablonski).

behavioural syndrome of antipredator behaviour directly extends to mating behaviour. When sexual behaviour increases predation risk experienced by males, females or both sexes due to conspicuous sexual communication (Endler, 1980; Gwynne, 1989; Lima & Dill, 1990; Magnhagen, 1991), it is reasonable to expect the evolution of correlations between sexual behaviour and antipredator behaviour. First, life history trade-offs can explain the emergence of the behavioural correlation (Biro & Stamps, 2008; Réale et al., 2010; Stamps, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007; Wolf & Weissing, 2010). Because of trade-offs between survival and reproduction, individuals active in mate search could tend to invest more in reproduction than in survival, and they are predicted to be less cautious towards predation threats (Roff, 2002). In addition to this view, a state-dependent explanation (Dingemanse & Wolf, 2010; Sih et al., 2015; Wolf & Weissing, 2010) also predicts the correlation between sexual behaviour and antipredator behaviour.

Regardless of whether sexual behaviour is positively or negatively correlated with risk-taking behaviour, the behavioural correlation between them is generally expected to be similarly expressed in both sexes (see Pruitt & Riechert, 2009; Sprenger, Dingemanse, Dochtermann, Theobald, & Walker, 2012). Although males' sexual behaviours (e.g. courtship) and females' sexual behaviours (e.g. preference) are not functionally equivalent, genetic covariation between male sexual trait and female preference may develop similar structures of correlations between sexual behaviours and antipredator behaviours in both sexes (see Fowler-Finn & Rodríguez, 2015), especially when sexual behaviours of both sexes are influenced by predation risk (see below). However, it is also possible that the correlation between sexual behaviour and antipredator behaviour differs between the sexes when males and females experience different returns from sexual behaviour and different forms and intensities of predation risk (e.g. Fresneau, Kluen, & Brommer, 2014). For example, when only males suffer an increased predation risk due to the presence of conspicuous displays (Andersson, 1994), we could expect the correlation between mating behaviour and antipredator behaviour in males but not in females. That is, males more active in reproduction are predicted to be less cautious to predators, whereas females would express their mating behaviours regardless of the level of predation they experienced. Likewise, we also expect correlations between sexual behaviour and antipredator behaviour in females when they suffer predation risk during mating.

Males of one Asian water strider species, *Gerris gracilicornis* (Heteroptera: Gerridae), employ an unusual courtship strategy (i.e. intimidating courtship, Han & Jablonski, 2009, 2010) that capitalizes on predator behaviour and female response to predators (i.e. a form of sensory exploitation, Han & Jablonski, 2010). A male mounted on a female produces courtship signals by repeatedly tapping the water surface until the female exposes her genitalia for intromission (Han & Jablonski, 2009), and these ripples can attract predatory aquatic insects such as notonectids (Hemiptera, Notonectidae). Because a mounted female is more susceptible than the male to predatory attack by notonectids approaching from below the water surface, courtship ripples are a form of threat males use towards females (Han & Jablonski, 2010). In response to male intimidating courtship, *G. gracilicornis* females protrude their genitalia and permit the courting male's attempt to copulate (Han & Jablonski, 2009). When the female allows the male to copulate, he ceases signalling. In a predator-free environment, females can delay intromission to terminate mounting males' mating attempts by resistance because males can be more easily thrown off if their genitalia are not inserted. Thus mating of *G. gracilicornis* is determined by females. However, in the presence of predators, females are not able to delay intromission because the ripple signals attract predators and the female is more vulnerable because of the mating

position (Han & Jablonski, 2010). Since female water striders become more sensitive to males' intimidating courtship ripples in the presence of predators (Han & Jablonski, 2010), the variation in the female's latency to genitalia protrusion can be regarded as a flexible mating strategy of females in response to predation risk. Similarly, since courtship signalling by males can increase male mating success more when predators are present (Han & Jablonski, 2010), males may intensify their courtship signals to increase the chance of attracting predators. Thus, contextual variation in male courtship in response to predation risk can also be regarded as a flexible mating strategy of males.

In this species, we predicted that the correlations between sexual and nonsexual responses to predation risk will be sex-specific because of the sex-specific effect of being sensitive to predators on their fitness. Because mating females, unlike males, are at a considerably greater risk of predation (Arnqvist, 1989; Fairbairn, 1993; Han & Jablonski, 2010; Rowe, 1994), we predicted that females should be more cautious to the predation risk in a mating context than males, and that female boldness to predation in a mating context could also be associated with their boldness in a nonmating context. That is, more risk-prone females (boldness in a nonmating context) are predicted to be less sensitive to intimidating courtship ripples of males (boldness in a mating context).

We predicted that, in contrast to females, sexual selection on boldness in a mating context should result in males being less cautious to predators than females. This is because males improve their mating success when they increase the risk of attracting predators by courting more intensely. We also predicted that this may lead to male boldness across mating and nonmating contexts being more weakly correlated than in females. That is, the change in male courtship intensity in response to the threat of predation (boldness in a mating context) is predicted not to be related to males' activity under predation risk (boldness in a nonmating context).

To examine sex differences in boldness correlations across mating and nonmating contexts, we measured antipredator behaviours and mating behaviours (male courtship intensity and female response to male courtship) of males and females in the absence/presence of a predator. Although *G. gracilicornis* males' sexual behaviours (e.g. courtship intensity) and females' sexual behaviours (e.g. female response to male courtship) are not functionally equivalent, the expressions of both sexual behaviours are affected by the level of predation (Han & Jablonski, 2010). Thus they could be considered as the same responses towards predators in a mating context. Based on the behavioural data, we also calculated an index of boldness in a mating context to quantify how the mating behaviour was affected by the experience of predatory attack. Then we compared boldness correlations across mating and nonmating contexts (i.e. syndrome structures) of males and females using structural equation modelling (SEM) and model comparison based on the Akaike information criterion (AIC).

METHODS

Collection and Rearing

Overwintered *G. gracilicornis* (130–150 individuals) were collected at Cheonseong Mountain, South Korea, and transported to the laboratory. They were then separated into two rectangular plastic containers filled with water (40 × 50 cm, water depth 5 cm) according to sex, and frozen crickets, *Gryllus bimaculatus*, were given as food every day. Pieces of floating Styrofoam were provided as resting sites. To avoid variation in each individual's mating experience, we let individuals of both sexes copulate randomly once a day after placing one male and one female in a small