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Evolution of individual variation in behaviour and behavioural plasticity under scramble competition

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In scramble competition mating systems, individual behaviours related to male–male competition are expected to be plastic across sociosexual environments. However, the evolutionary forces that shape individual differences in behavioural plasticity remain poorly understood. We measured behaviour associated with scramble competition in male water striders, *Tenagogerris euphrosyne*, in two social contexts. Male *T. euphrosyne* tend to mount other individuals or pairs indiscriminately and then dismount if their target is either another male or a mating pair. We measured the speed with which a focal male dismounted (i.e. his sensitivity to having made an inappropriate mounting) in each of these contexts. We quantified temporal consistency of dismount speed within each context, as well as individual variation in behavioural plasticity across contexts. We then estimated the effect of the behaviour and of plasticity on individual fitness in different sex ratio conditions. We found that individuals differed in their recognition sensitivity traits, and also in how plastic their sensitivity (i.e. dismount speed) was to context (mating status or sex). When we measured the mating success of each male within experimental groups kept at four different sex ratios, recognition sensitivity traits in both contexts interacted to influence mating success, and there were significant differences in linear selection on sensitivity traits between sex ratio treatments. We discuss how insensitive males evolve, and how individual variation in behavioural plasticity could be maintained by selection or environmental variability.

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Phenotypic plasticity, the potential of a given genotype to produce different phenotypes in different environmental conditions, provides a conceptual framework in which to study flexibility and complexity of morphological, physiological and behavioural traits (West-Eberhard 2003; DeWitt & Scheiner 2004; Pigliucci 2005). Because of its remarkable flexibility and reversibility, behaviour has profitably been understood as the ultimate form of plasticity (Ghalambor et al. 2010), and recent studies have considered individual behavioural differences in the framework of behavioural plasticity (Scheiner & Lyman 1989; Betini & Norris 2012; Dingemanse et al. 2012a, b). Most work on behavioural plasticity, however, has not focused on individuals, but on populations in different places or where different environmental conditions prevail (Nussey et al. 2007).

Individuals within a population can differ in their responsiveness to changing environmental conditions (I×E; Nussey et al. 2007). Most research on individual behavioural plasticity has tested behavioural change across time (temporal consistency/temporal plasticity; see Hagberg et al. 1991; Suomi et al. 1996; Dingemanse et al. 2002; Bell & Stamps 2004). But fewer studies have considered individual behavioural plasticity across different situations (i.e. contexts; see Morand-Ferron et al. 2011). For example, individual nutmeg mannikins, *Lonchura punctulata*, differ in their use of foraging tactics (producer versus scrounger; Morand-Ferron et al. 2011). Mannikins generally increased the scrounger tactic (resource exploitation) when the number of foods increased, but individuals differed in the extent of their foraging tactics across food abundance.

Individual behaviours associated with scramble competition are expected to be plastic across the sociosexual environments (e.g. mate density or operational sex ratio; Bretman et al. 2011). Scramble competition is a common mating system in animals (Ghiselin 1974; Thornhill & Alcock 1983; Andersson 1994), favouring traits that enable the competing sex (usually males) to find mates (females) rapidly and accurately (Schwagmeyer & Woontner 1986; Spritzer et al. 2005a, b). Sex ratio and population density can change the intensity of scramble competition, the best tactics for an individual to use, and the direction and the strength of selection on the underlying

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behavioural traits (Bertin & Cézilly 2003). Thus, individuals are expected to adjust their behaviour in response to social context. It remains unknown, however, whether behavioural traits involved in scramble competition are plastic across social contexts.

In this paper, we highlight two aspects of 'recognition sensitivity' in a male water strider *Tenagogerris euphrosyne* as important traits associated with scramble competition. In nature, *T. euphrosyne* is always found under male-biased sex ratios, but the strength of this male bias varies over short spatial and temporal scales. Mating initiation in water striders often comprises a forceful attempt by a male to mount the female (Spence & Anderson 1994; Arnqvist 1997). However, males often attempt to mate another male or mating pair (Sih & Watters 2005; Eldakar et al. 2009). Males that are poor at recognizing female mating status might waste time mounted on mating pairs, and males that fail to recognize when they are mounted on a male might likewise waste time and thus miss ephemeral chances to mate when single females become available. We quantified 'recognition sensitivity', the tendency to recognize potential mates (i.e. unmounted females) as opposed to inappropriate mates (i.e. other males or mating pairs), as the latency to dismount an inappropriate mate. We studied recognition sensitivity in two contexts: when a male mounts another male (i.e. sex sensitivity), or a mating pair (i.e. mating status sensitivity).

Despite the similar costs, sex sensitivity and mating status sensitivity might not be one and the same thing. Some males could be equally poor at recognizing their error and dismounting in the two contexts (recognizing sex and recognizing mating status), and others could equally be good in both contexts. Yet other males could be better in one context than another; that is to say, their mounting response might show a high level of plasticity between situations. Likewise, the responses of males who are poor in both situations and those who are good in both situations can be said to show low plasticity in recognition sensitivity.

Furthermore, in a species with a coercive mating system and scramble competition among males for access to reproductive females, the ability to distinguish single females from single males or mating females rapidly is crucial to male fitness. This ability might become more important as the sex ratio becomes more male-biased because increasing scramble competition places a fitness premium on the ability to distinguish, court, copulate with and then subsequently guard the relatively rare single females among a large number of single males. In the second part of this study, we explored how recognition sensitivity traits, measured under standard conditions in the first part of the study, influence subsequent mating success of males under four different sex ratios. We applied evolutionary selection analysis, as developed and applied by Lande & Arnold (1983), to explore the effects of both types of sensitivity on male mating success.

Given that a number of single males were present at more male-biased sex ratios, we predicted that sex sensitivity of males would be an important determinant of their mating success. But as males begin to mount females, the number of mating pairs increased and we predicted that mating status sensitivity would become important. Thus, under fluctuating population sex ratio conditions along the microhabitats of water striders, responses of males across two different social contexts (sex sensitivity context and mating status sensitivity context) cannot be canalized. Hence, we predicted that males would differ in their responses towards two different social contexts (sex sensitivity context and mating status sensitivity context, significant I×E) and selection on our two measures of recognition sensitivity would differ across different sex ratio conditions.

We tested for: (1) individual variation in recognition sensitivity within each of the two contexts (consistent individual differences); (2) whether sensitivity differs between the two contexts (i.e. population-level plasticity); and (3) whether there are individual differences in plasticity (i.e. individual-level plasticity or individual-environment interactions, I×E). To do so we used a form of reaction norm analysis (Nussey et al. 2007) to test for between-individual variance in recognition sensitivity traits and variation in individual behavioural plasticity (I×E) of recognition sensitivity to context (i.e. sex sensitivity versus mating status sensitivity trials). Given that scramble competition is thought to favour highly plastic, labile behaviour, we predicted that there would be little between-individual variation in recognition sensitivity, strong population -level plasticity of these measures to context, but little between-individual variation in this plasticity. Lastly, based on the measurements of males' recognition sensitivity, we explored (4) whether mating success of males differed between different experimental sex ratio treatments.

METHODS

Study Species and Rearing Conditions

Tenagogerris euphrosyne is the most common water strider species in eastern Australia, but behavioural studies of this species are scarce (but see Colvin et al. 2006). We used animals from two collection trips to Hacking River, Otford, New South Wales (−34° 11′, +151° 0′). In southern Australia, *T. euphrosyne* has a bivoltine life cycle (two generations per year) in which overwintered and post-diapause females (a first spring generation) produce a first summer generation, and females of a first summer generation reproduce directly and produce a second summer generation that overwinters. The first batch (i.e. the spring generation) was collected on 6 November 2010 and the second batch (i.e. the summer generation) was collected on 8 January 2011. Males, individually marked on the pronotum with enamel paints, were kept individually in small containers (10 × 15 cm), and females were kept in groups of up to 20 individuals per container (14 × 21 cm). The enamel marks have no detectable effects on survival or mating success (Ferguson & Fairbairn 2000). Frozen crickets (*Teleogryllus commodus*) and neriid flies (*Telostylinus angusticollis* and *T. lineolatus*) were given as food, and pieces of floating styrofoam were provided as resting sites.

Assays for the measurement of recognition sensitivity traits were performed in each male's home container. The water in the home container was changed 12 h before the start of an experimental trial. Experiments for the mating success were performed in a large tank (50 × 50 cm), and males were returned to their home container after the measurement of mating success. All individuals were released to the original habitat after the experiment was completed.

Measurement of Recognition Sensitivity Traits and Contextual Plasticity of Sensitivity

Although previous research on water strider species considered the mounting behaviour of the male on other males as an aggressive behaviour (e.g. Sih & Watters 2005; Eldakar et al. 2009), male mounting in *T. euphrosyne* did not appear aggressive or result in behavioural changes such as struggling or fleeing (C. S. Han, personal observation).

First, we screened each male for mating motivation by putting three single females in a male's home container. If he mounted at least one female within 5 min, we retained him for use in the subsequent experiment. Such a prescreening is necessary because it usually takes about 1–2 weeks after winter diapause or moulting to adulthood for males to become reproductively active (C. S. Han,

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