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# Effects of behavioural type, social skill and the social environment on male mating success in water striders

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We examined the relative importance of individual differences in personality (activity and aggressiveness), social skill and the social environment (average activity and aggressiveness of the group, presence of hyperaggressive males) in determining the behaviour and mating success of males of the stream water strider, *Aquarius remigis*. Males that had a consistently more active–aggressive behavioural type had, on average, higher mating success largely because they spent more time active in microhabitats associated with acquiring mates. Some active–aggressive males, however, showed hyperaggressive behaviour, apparently attempting to mate forcibly with other males, or forcibly separate pairs, which was rarely successful. A higher tendency to be hyperaggressive was associated with reduced mating success (i.e. being hyperaggressive represents low social skill). The overall effect was thus stabilizing sexual selection on male activity and aggression. The social environment also had large effects on male behaviour and mating success. In particular, the presence of a keystone hyperaggressive male had strong negative effects on the mating success and general activity of other males in the pool. Notably, males with a more active–aggressive behavioural type maintained higher mating success than less active–aggressive males in the presence of a hyperaggressive male. Social plasticity (change in behaviour in response to changing social conditions) also depended on the male's behavioural type; males with a more active–aggressive behavioural type were more plastic.


The past decade has seen a surge of interest in behavioural syndromes (or 'animal personalities') characterized by (1) within-individual consistency in behaviour (i.e. individuals express a behavioural type) often across multiple contexts and (2) consistent differences among individuals in behavioural type (Reale, Reader, Sol, McDougall, & Dingemanse, 2007; Sih & Bell, 2008; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004). For example, in many species, individuals differ in their level of activity (Conrad & Sih, 2009; Sih, Kats, & Maurer, 2003), boldness (Hedrick & Kortet, 2012; Johnson & Sih, 2007), aggressiveness (Blumstein, Petelle, & Wey, 2013; Johnson & Sih, 2005), exploration tendency (Dingemanse, Both, Drent, Van Oers, & Van Noordwijk, 2002; Montiglio, Garant, Pelletier, & Reale, 2012) or sociability (Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Pruitt & Riechert, 2011).

For ecology and evolution, a large part of the interest in behavioural syndromes comes from the fact that an individual's behavioural type can have important effects on components of fitness relative to natural selection (e.g. on the individual's feeding or growth rate, competitive ability or survival in the face of danger; Pruitt & Ferrari, 2011; Pruitt, Stachowicz, & Sih, 2012; Smith & Blumstein, 2008). To date, however, surprisingly few studies have measured sexual selection on behavioural type (Schuett, Tregenza, & Dall, 2010). While it is clear that being active can help males encounter more females and that being aggressive and winning fights can help males compete for access to females, and thus enhance mating success, few studies have tracked numerous males over time and quantified both consistent individual differences in male activity and aggressiveness and how variation in these behavioural types explains variation in mating success (Han & Brooks, 2013; Jennings, Hayden, & Gammell, 2013; Schuett et al., 2010).

Studies of natural selection on behavioural type have provided the key insight that effects of behavioural type on fitness are context dependent (Dingemanse & Reale, 2005; Quinn, Patrick, Bouwhuis, Wilkin, & Sheldon, 2009; Smith & Blumstein, 2008). Bold, aggressive individuals often do well in low-risk environments (e.g. outcompete shy, unaggressive individuals), but might suffer injury, parasitism or enhanced mortality risk in higher-risk environments (Kortet, Hedrick, & Vainikka, 2010; Sih et al., 2003). With regard to context-dependent sexual selection, numerous studies have examined how social conditions (e.g. sex ratio or density)

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influence mating dynamics ( Leftwich, Edward, Alphey, Gage, & Chapman, 2012; Weir, Grant, & Hutchings, 2011) and sexual selection on morphological traits (Arnqvist, 1992; Sih, Lauer, & Krupa, 2002). However, few studies have examined how variation in social context influences sexual selection on behavioural types via social selection on behaviour and mating success (McGlothlin, Moore, Wolf, & Brodie, 2010; Wolf, Brodie, & Moore, 1999).

A particularly interesting aspect of an individual's social context can be the mix of behavioural types in the social group. A central premise of evolutionary game theory is that the relative success of different behavioural types (e.g. aggressive hawks versus docile doves) should depend on the mix of behavioural types in the group (i.e. that the fitness of different behavioural types should be frequency dependent; Maynard Smith, 1982). Despite 40 years of game theory assuming that 'the mix matters', few studies have manipulated the group's behavioural type to quantify effects on mating dynamics and sexual selection. Among the exceptions are recent studies on stream water striders, *Aquarius remigis*, that have experimentally manipulated the group's average aggressiveness, or relative frequency of more versus less aggressive individuals (Eldakar, Dlugos, Wilcox, & Wilson, 2009; Eldakar, Wilson, Dlugos, & Pepper, 2010; Sih & Watters, 2005). These studies found that both the group's average mating activity and the relative mating success of different behavioural types depended on the mix of behavioural types in the social group.

In water striders, a key behavioural type that has major effects on the rest of the social group is the 'hyperaggressive male' (Eldakar et al., 2009; Eldakar et al., 2010; Sih & Watters, 2005). Hyperaggressive males are so aggressive that they disrupt the group's overall social dynamics, drive many, if not most, other individuals (male and female) into hiding and thus substantially reduce average mating activity (Sih & Watters, 2005). That is, the presence of a hyperaggressive male is a key aspect of the social environment that can have large impacts on sexual selection and mating dynamics. Sih and Watters (2005) referred to hyperaggressive males as 'keystone individuals' (modelled after the keystone species concept in community ecology; Paine, 1966), individuals that have a disproportionately large effect on the overall group's social dynamics and thus on individual and group outcomes.

As described in more detail below, we define hyperaggressive males by their indiscriminate tendency to attempt to mate forcibly not just with single females, but also with single males and pairs. Because attempts to mate with other males are obviously futile and attempts to separate pairs to take over the female are rarely successful, hyperaggressiveness appears to be an example of poor social skill, where social skill is defined as the ability and tendency to show adaptive adjustments in social behaviour (Sih & Bell, 2008). Others have used the term social competence for basically the same concept (Taborsky & Oliveira, 2012). However, to test this hypothesis, it is vital to know whether hyperaggressive behaviour is actually maladaptive (i.e. whether it reduces mating success). While we often hear anecdotes about indiscriminate males that attempt to mate with the wrong species or sex, or with inanimate objects, few studies have quantified variation among males in this tendency, or the effects of variation in social skill on mating success (but see Patricelli & Krakauer, 2010; Patricelli, Uy, Walsh, & Borgia, 2002).

Given that an individual's behavioural type and social environment might affect its mating success, how do these two variables interact? In our system, given that hyperaggressive males have large impacts on average mating activity, does an individual male's behavioural type affect its ability to mate successfully despite the presence of a hyperaggressive male?

Here, we experimentally created replicate groups with different social compositions (different average behavioural types) and tracked the behaviour and mating success of more than 100 male stream water striders, *Aquarius remigis*, through more than 500 matings. We thus quantified the relative importance of individual differences in male behavioural type and social skill and the males' social environment to examine variation in male mating success. We also examined how behavioural type influences a male's ability to mate in the presence of a hyperaggressive male. That is, we examined sexual selection on behavioural type and how it is mediated by the social context.

## *Study System*

Water striders are semiaquatic insects that feed on organic matter trapped on the water surface. In central California, their breeding season lasts from late February to early June depending on the weather. Their mating system consists of reluctant females and eager males. Males coerce copulations without courtship by jumping on and struggling with females to commence mating. Once mated, females carry passive males on their backs in copula for 30 min to 12 h, with an average of 3–6 h (Sih, Krupa, & Travers, 1990; Sih et al., 2002). Extended copulation duration increases the proportion of eggs fertilized by a male (Campbell & Fairbairn, 2001).

Multiple mating has costs for females, including the energy costs from carrying a mating male, and increased predation risk from reduced mobility during copulation (Fairbairn, 1993; Watson, Arnqvist, & Stallmann, 1998). Paired females, however, experience less male harassment than single females and are thus able to feed in relative peace. Overall, to avoid males, single females spend much of their time hiding in refuges at the edge of streams where food is scarce, only entering the centre of pools when hungry, where they are immediately harassed by males attempting to mate (Krupa & Sih, 1993; Rowe, Krupa, & Sih, 1996; Wilcox, 1984). Pairs still experience some mild harassment, as males are indiscriminate in initiating copulation attempts with other water striders. Most males, however, immediately dismount other males or pairs that they have mounted (i.e. most males can apparently quickly distinguish between single females, males and pairs upon contact, and only engage in extended struggles with single females).

Some males, however, engage in extended struggles with other males and pairs ('hyperaggressive males'), apparently attempting to mate with single males or break up pairs, presumably to mate with the female, which is rarely successful (Sih & Watters, 2005). A few males (<5%) maintain hyperaggressive behaviour daily for several days (5–7 days). About 10–20% of males show hyperaggressive behaviour occasionally, typically for a few hours or days (i.e. about 10–20% of the males show hyperaggressive behaviour 10–20% of the time). Chang and Sih (2013) found that at least one male in about 40% of the groups showed hyperaggressive behaviour during a 5-day period, but groups with four to six males almost never had more than one hyperaggressive male at any given time.

The primary male behaviours that tend to result in higher encounter rates with single females are activity and aggressiveness. Activity is defined as movement and use of the centre microhabitat, where available single females are easier to spot (as opposed to when females are unavailable, out of the water or otherwise in refuge). General aggressiveness is defined in terms of the tendency to chase and jump on other water striders. Animals can be aggressive without being hyperaggressive, but aggressive individuals are more likely than others to become hyperaggressive. Previous studies found that, as expected, more active or aggressive males tend to have higher individual mating success as long as they are not hyperaggressive (Sih et al., 2002). Previous papers, however, have not quantified sexual selection on 'hyperaggressiveness' as