The mix matters: behavioural types and group dynamics in water striders

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Summary

The effect of an individual's behavioral type (e.g., its boldness or aggressiveness) on fitness likely depends on the environmental context. In many species, an important component of an individual's environment is its social environment — the mix of individuals in its social group. Accordingly, much of game theory assumes that the mix of behavioral types (BTs) in a social group influences individual fitness and group dynamics. Few experimental studies, however, have directly investigated how the group's mix of BTs influences individual and group outcomes. Here we manipulated social group composition in the water strider Aquarius remigis and evaluated the effects of our manipulation on individual behavior and various group outcomes (overall group activity, aggression, mating success). We formed 12 groups that differed substantially in average male BT (activity and aggression level), each with a low variance in BT. That is, one group had only the most active and aggressive males, a second group was made up of the next most active and aggressive males, and on down to a group of all very inactive and unaggressive males. All groups also had females. We found that, on average, groups made up of more active-aggressive males continued to be more active than other groups, but that contrary to predictions, these groups did not tend to enjoy higher mating success. Instead, a major factor affecting group mating activity was the presence of hyper-aggressive males. Hyper-aggressive males drove females out of the group and thereby decreased the group's overall mating activity. We discuss these findings in terms of their importance to the study of behavioral plasticity in social groups and the potential role of keystone individuals in determining group dynamics.

Keywords: behavioral syndromes, game theory, aggressive behavior, mating behavior, mating success, male-female conflict, keystone individuals.

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Introduction

In recent years, there has been a surge of interest in individual variation in behavioural types, sometimes referred to as 'animal personalities' or 'behavioural syndromes' (Gosling, 2001; Sih et al., 2004a, b). The idea is that individuals might often vary in behavioural tendencies that carry over across a range of situations. For example, some individuals might be more active, aggressive or bold than others in various contexts, such as feeding, antipredator, contests, mating and/or dispersal (Huntingford, 1976; Verbeek et al., 1996; Koolhaas et al., 1999). A growing body of evidence suggests that an individual's behavioural type (BT) can affect its fitness (Reale & Festa Bianchet, 2003; Dingemanse et al., 2004). In particular, in a variable environment, it appears that selection favoring a particular BT in one environment can spillover to cause inappropriate behaviour in other environments. For example, selection favoring a high activity type in the absence of predation can carry over to cause inappropriately high activity in the presence of predators (Sih et al., 2003). The key is that the effect of a BT on fitness is environmentdependent (Sih et al., 2003; Dingemanse et al., 2004).

The fitness of a BT, however, likely depends on not just the external environment, but also on the mix of BTs — or the social composition of the group. In essence, the group's social composition is also an important part of an individual's environment. This notion, that the mix of BTs influences the fitness of each BT, is a central tenet of game theory (Maynard Smith, 1982). For example, in the simple hawk-dove model, the fitness of both hawks and doves should depend on their relative frequency. Despite the importance of this premise, few experimental studies have manipulated a group's mix of BTs to examine effects on individual fitness or group dynamics (Erhard et al., 1997; Lange & Leimar, 2004). This mismatch between theory and empirical study probably derives at least in part from the fact that until relatively recently, few studies have focused on BTs. For example, few workers have attempted to identify individual hawks and doves in study populations to then test whether the relative frequency of these BT's affects fitness.

In theory, the group's social composition could affect numerous individual and group outcomes. Game theory focuses on one key individual outcome — individual fitness. Another individual outcome is behaviour per se. The actual behaviour expressed by different BTs could depend on the mix of BTs. Continuing with the hawk-dove metaphor, some hawks might reduce their aggressiveness when surrounded by other hawks, and some doves might increase their aggressiveness when surrounded by other doves. With regard to group outcomes, one obvious idea is that the mix of BTs should influence the average behaviour expressed by the group. A group of hawks should engage in more aggression than a group of doves. More interestingly, the mix of BTs could influence other aspects of group behaviour and success. For example, the frequency of bold-aggressive individuals could influence overall mating activity, the group's impact on prey, and/or survival with predators.

The simplest game models looked at interactions between two or three BTs (e.g., hawks, doves and perhaps eavesdroppers (Maynard Smith, 1982; Johnstone, 2001)). In many perhaps most systems, however, groups might be made up of a continuous range of BTs. In that case, we can characterize a group by its mean and variance in BTs. Some groups are, on average, more aggressive or active than others, and some groups have more among-individual variation in BTs than others.

Our previous work showed that males of a semi-aquatic insect, the stream water strider, *Aquarius remigis* (hereafter, referred to as striders) exhibit BTs; i.e., that some males are consistently more active or aggressive than others (Sih, unpubl. data). Here, we experimentally manipulated the social group's average male activity-aggression BT and examined effects on the group's behaviour (male activity-aggression level, female response to males) and mating activity (proportion of time spent mating).

The system

Water striders (family Gerridae) are common, abundant bugs that skate across the surfaces of standing or flowing water throughout much of the world. Numerous studies have been done on their ecology and behaviour (Spence, 1981; Rubenstein, 1989; Fairbairn, 1993; Blanckenhorn, 1994; Rowe et al., 1994; Sih & Krupa, 1995; Sih et al., 2002; Vermette & Fairbairn, 2002). In general, gerrids are diurnal, opportunistic predators that feed primarily on arthropods trapped on the water's surface. Our focal species, *A. remigis*, is commonly found in small streams often with alternating small pools and riffles.

A. remigis' life cycle varies with latitude (Blanckenhorn & Fairbairn, 1995). In central California, striders reach adulthood in late spring-summer,

but probably due to high densities and food limitation, do not mate until the following late winter-spring. During the mating season, solitary males spend much of their time actively skating over the water, apparently searching for females and interacting with other males. Males typically alternate between resting near the banks and cruising on the open water. While active, males approach and jump on other adult striders — both males and females. Males usually immediately jump back off other males, but engage females in mating struggles (see below). Males vary considerably in activity. Many are moderately active, while others are less active. Some inactive males are in poor condition, but others appear to be inactive as a 'sit-and-wait' mating strategy. On average, more active males tend to encounter more females and thus mate more frequently (Sih et al., 2002).

Males also vary in aggressiveness. Although most males jump quickly on and off other males, some males attack and chase other males more aggressively. Aggressive males are usually also relatively active; however, males can be active without being very aggressive. Still, on average, male activity and aggressiveness tend to be positively correlated (Sih et al., 2002). A few males are 'hyper-aggressive'. These males spend much of their time chasing after, and often struggling with *any* adult strider that they encounter. Since in most pools, most of the active animals are other males, hyperaggressive males spend an inordinate amount of time struggling with and apparently attempting to mate with other males.

Solitary females are usually inactive along the banks (Wilcox, 1984; Krupa et al., 1990). When females move out on the open water, they are immediately harassed by males that attempt to mount without courtship. Females heavily resist male mating attempts (Lauer, 1996; Lauer et al., 1996; Weigensberg & Fairbairn, 1996). In most cases, females escape from males; but males sometimes position themselves correctly, and immediately begin copulating. Pairs typically stay in copula, with the male on the female's back for several hours (Clark, 1988; Sih et al., 1990). The tendency for females to be inactive and to disperse from pools likely represents female avoidance of male harassment (Wilcox, 1984; Krupa et al., 1990; Haskins et al., 1997).

Methods

We used a 2-stage experimental design to study BTs and group social composition in water striders. In stage 1, we assayed the BT (activity and aggressiveness) of a large number of individual male water striders. To do this, animals were observed in 4 large groups of randomly chosen males and females. Each group had the same average BT and a relatively high within-group variance in BTs. Using the BT assessments from stage 1, in stage 2, we experimentally created 12 smaller groups that differed in average BT (activity and aggressiveness), each with a low within-group variance in BT. That is, we created a group made up entirely of the most active and aggressive males, followed by a group of the next most active and aggressive males, and so on down to a group made up of the males that were the least active and aggressive. In stage 2, we quantified effects of the group's social composition on various outcomes.

We tested the following a priori hypotheses on how the group's mix of BTs might influence the group's behaviour and mating activity. First, we expected groups consisting of all higher activity-aggression males to continue to be more active and aggressive than groups made up of less active-aggressive males. That is, we expected males to generally retain their BT regardless of the social background. With regard to mating activity, since higher male activity is generally associated with higher mating activity (Sih et al., 2002), we expected groups made up of all higher activity-aggression males to engage in more mating than groups made up of lower activity-aggression males. Alternatively, groups made up of very high activity-aggression males might engage in so much male-male aggression that they show reduced mating activity for both very low and very high activity-aggression groups, but higher mating activity for groups made up of males that exhibit intermediate levels of activity and aggression.

Experiments were run in 4 semi-natural streams each consisting of 5 plastic pools (each 1.5 m diameter, filled to a depth of 40 cm with well water) connected by riffles (1.3 m long, 30 cm wide). The surface flow patterns in the pools resembled those in nature. Streams were located outdoors at the Institute of Ecology at UC/Davis under a structure with open sides (about 5 m high) that protected the streams from rain and direct sun. Water striders thrive in these streams. Social interactions and levels of mating activity in these pools resemble those in nature. Females use riffles and styrofoam blocks (attached to the sides of the pools) as refuge from male harassment, and both sexes readily use riffles to move among pools. Females oviposit on styrofoam blocks or on the sides of the tanks. Eggs hatch and juveniles can grow to adulthood with no assistance from us.

Animals were collected from a stream in the UC/Davis Cold Canyon Natural Reserve. Some individuals had wings; however, in this population, they cannot fly during the mating season. Each individual was given a unique mark on the dorsum with colored paint markers.

For stage 1, the day after striders were marked, groups of 25 males and 25 females were randomly chosen and introduced into each stream. Striders began mating within the first hour. On each of 7 days, we performed spot checks every hour from 900-1800 to record each individual male and female's habitat use (pool vs. riffle), microhabitat use (edge, center, on styrofoam, on the sides of pools), movement if on the water (moving or not), feeding status (feeding or not), and mating status (mating or not, and if mating, the partner's identity). These spot checks assayed each individual's mean activity (defined as either in the center or along the edge and moving), feeding rate, mating frequency (number of matings/day), mean mating duration, and mating success (product of mating frequency and mating duration) in each social condition. If pairs were observed at 1800 hr, additional observations were done at sunset (around 2100), and at midnight to check for mating.

On each day, we also conducted one 8 min continuous observation in each pool mapping locations of all individuals on the water, and recording movements and interactions. Interactions included struggles (extended physical contacts typically including somersaults, rolls, etc.), chases (extended interactions with little or no contact, but with one individual moving rapidly behind the other), jumps (mounting attempts with no extended struggle) and touches (with no attempt to mount). Based on these observations, each male's aggression level was scored from 0 to 3 (3 = highest aggression level). Males that initiated no interactions despite being near other water striders received a score of zero. Males that frequently chased and jumped on most nearby striders, including frequent struggles with both females and other males received a score = 3. Individuals who frequently chased or jumped on nearby striders, and struggled with females, but not with males received a score = 2. Males who only occasionally chased or jumped on nearby striders, and sometimes only touched a nearby strider received a score of 1. Half-point scores (0.5, 1.5, 2.5) were given to males who fell between these main categories. A score of 3 represents hyper-aggressiveness (see the description in the System section).

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After 7 days (roughly 60 observations per individual), we calculated activity (proportion of time spent active) and aggression scores for individual males when they were not mating. Out of the 100 original males, 23 died or disappeared during stage 1. Out of the remaining 77, only 59 had sufficient data on aggression and activity while solitary to assess their BT. Because activity and aggression scores were significantly positively correlated, we combined them into a principal component score (PCact, PC1 explained 70.4% of the variance in behaviour) which was our measure of the individual's BT. PCact influenced mating success. As expected, more active-aggressive males enjoyed higher mating success (r = 0.64, N = 59, p < 0.001).

We split males into 12 'bins' ranked by PCact scores and randomly chose 4 males from each bin, and paired them with 3 randomly chosen females to create experimental groups for stage 2 of the experiment. This sex ratio and density is commonly seen in patches of water strider habitat in natural pools (Krupa & Sih, 1993). Our 12 experimental groups differed in mean male BT (PCact), but each group had relatively little variance in male BT. For stage 2, we observed our groups of 4 males and 3 females for 3 days (using the methods described above) in separate groups using screening at the bottom of each riffle to create 12 separate units each with a pool and a downstream riffle. Two of the pools had male deaths, and were excluded from further analyses. On day 1, striders did relatively little mating; apparently, they were still adjusting to their local conditions. By day 3, three pools had missing males, and three other pools had more than 90% of the females mating, and thus little data on the behaviour of single males. Our analyses thus focused on behaviour and mating activity on day 2 in the 10 pools that had all 4 males.

All proportions were arcsine square root transformed before doing parametric analyses. We used linear regressions to test the hypotheses that groups made up of higher activity-aggression males (based on PCact in stage 1) have higher activity or aggression, and higher mating activity in stage 2. To examine the alternative hypothesis that groups with intermediate activityaggression males have higher mating activity, we ran a polynomial regression, looking for a positive linear term and a negative squared term. We tested for effects of hyper-aggressive males on mating activity, above and beyond effects of male activity per se, by running a multiple regression. This analysis suggested that hyper-aggressive males do in fact affect mating activity of the group. To determine if this effect on mating activity occurred as a result of female response to the presence of hyper-aggressive males, we used a t-test to compare habitat use (of pool or riffle) of females in groups with and without hyper-aggressive males. Finally, we used a linear regression to test the effect of female riffle use on mating activity of the group. We used one-tailed tests whenever we had a priori hypotheses (see the above list of hypotheses).

Results

As expected, groups made up of males that were more active in stage 1 tended to be more active in stage 2 (mean PCact for each group from stage 1 vs mean activity for the group in stage 2: r = 0.82, p = 0.001, N = 10 for all analyses; Figure 1a). Groups with higher mean PCact also showed a tendency to be more aggressive and to mate more in stage 2; however, these effects were not quite statistically significant (for aggression: r = 0.49, p = 0.075; for mating: r = 0.51, p = 0.065; Figures 1b and 1c). A polynomial regression showed a non-linear relationship between the group's average PCact and its mating activity (linear term, r = 0.39, p = 0.087; squared term, r = -0.56, p = 0.033). The group made up of all very low activity-aggression males had unusually low mating activity. Except for that one group, there was no apparent linear relationship between the group's average PCact and mating activity.

Instead, to understand a group's mating activity, it was necessary to account for the existence of hyper-aggressive males. Hyper-aggressive males emerged in 5 of the 10 pools. A multiple regression showed that the proportion of time that hyper-aggressive males were present and single (males are not aggressive when they are paired) was negatively related to group mating activity (partial r = -0.66, p = 0.017). After accounting for the effect of hyper-aggressive males, overall mating activity was positively related to male activity per se (partial r = 0.53, p = 0.036). Hyper-aggressive males apparently reduced the group's mating activity in part by drastically reducing female activity in the pools (r = -0.82, p = 0.002). During the entire experiment not a single female was observed active in pools with a hyperaggressive male. Instead, the presence of a hyper-aggressive male drove females out of pools entirely, into riffles (t-test comparing female use of riffles in groups with versus without hyper-aggressive males: t = 3.24, p < 0.01; Figure 2) where females rarely mate (r = -0.65, p = 0.02; Figure 3). Hyper-aggressive males emerged in 4 out of the 5 highest ranked (PCact)

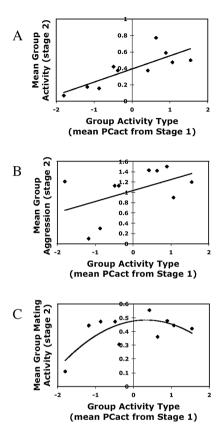


Figure 1. Group outcomes (A, activity; B, aggression; C, mating) of N = 10 groups in stage 2 of the social composition experiment. Plots show group outcomes as a function of group activity type as described by mean PCact in stage 1. Raw data are plotted. A: Mean group PCact score in stage 1 was positively correlated with group activity in stage 2 (p = 0.001). B: Groups with higher mean PCact scores tended to be more aggressive in stage 2 (p = 0.075). C: Mating activity in stage 2 was best explained by a polynomial relationship with PCact with a non-significant linear term (p = 0.087), and a significant negative squared term (p = 0.033).

groups, but also in the pool that had the lowest PCact rank. The group made up of the lowest activity-aggression males thus had particularly low mating activity because it consisted of males that are generally inactive and thus not searching for females, along with one hyper-aggressive male who drove females out of the pool.

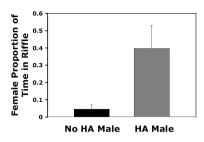


Figure 2. Females' habitat use in groups with (N = 5 groups) and without (N = 5 groups) a hyper-aggressive (HA) male. Females spent a larger proportion of their time (\pm standard error) in riffles when their social group included a HA male.

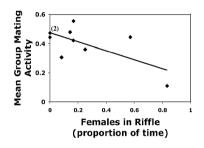


Figure 3. The effect of the proportion of time that females spent in riffles on mean group mating activity (N = 10 groups). Group mating activity decreased when females spent more time in the riffle (p = 0.02).

Discussion

The main results from our study are that: (1) BTs exist and are largely maintained even when individuals are placed in new social groups (activity in the two stages was highly correlated); (2) however, some individuals change their behaviour substantially when placed in a new social group (e.g., one very low PCact individual became hyper-aggressive when placed in a group with other low PCact males); (3) the group composition of BTs affects group outcomes; and (4) keystone 'hyper-aggressive' males can have a major effect on social and mating dynamics. Below, we discuss the significance of these points in a bit more detail.

One basic outcome of our study is the fact that individual males tended to exhibit a BT. Activity and aggressiveness from stage 1 carried over to stage 2 (i.e., across two different social conditions). The existence of BTs opens up new ways of thinking about behavioral plasticity in a game context. Most game theory models assume either that individuals have a pure BT (e.g., pure hawk or pure dove), or no BT (i.e., all individuals follow the same optimal probabilistic or condition-dependent ESS). In the former case, individuals exhibit no plasticity, while in the simplest form of the latter, they exhibit unlimited, optimal plasticity. In contrast, studies on BTs suggest that many real animals show some, but limited (less than optimal) plasticity (Sih et al., 2003). Relatively few studies, however, have looked at BTs in a game context. Some work on producers and scroungers suggests that individuals are so plastic that the frequency of producing and scrounging in the group is fixed regardless of the experimental mix of 'types' (Mottley & Giraldeau, 2000). Other studies showed that BTs are generally maintained (e.g., aggressive individuals stay relatively aggressive) regardless of the group's social composition (van Erp-van der Kooij et al., 2003; this study).

Even if most individuals retain a BT, some might substantially alter their behaviour depending on social circumstances. For example, some hawks might reduce their aggressiveness when surrounded by other hawks, and some doves might increase their aggressiveness when surrounded by other doves. We indeed found that when we created a group made up of all very low activity-aggression males, one of these males became hyper-aggressive (i.e., drastically increased its activity and aggressiveness). We did not have a large enough sample of hyper-aggressive males to do analyses on correlates of hyper-aggressiveness (e.g., size, other morphological characters, or previous experience). Clearly, more study is needed to better understand how and why BTs vary in their behavioural response to the group's social composition.

Hyper-aggressive males had a strong effect on the behaviour and mating success of other individuals in the social group. They continually harassed females (and other males). As a result, when hyper-aggressive males were present, females were totally inactive, and spent much of their time in the riffle where they rarely mate. Hyper-aggressive males thus caused a reduction in the group's overall mating activity. On a larger scale (e.g., in a natural stream, or in our artificial streams with partitions removed), females that are chased into riffles usually disperse into other pools. Hyper-aggressive males would then affect not just interactions within a given pool (and adjoining riffle), but also the social composition (density, sex ratio, mix of BTs) within their own and other pools.

Hyper-aggressive water strider males are an example of what we call keystone individuals — individuals that have a particularly large effect on other individuals in the group and on the group's overall social dynamics. An obvious example is the dominant (often, aggressive) individual (e.g., the alpha male or female) that acquires a disproportionate share of resources, affects the physiology of others, and/or shapes interactions within the group (Barrette & Vandal, 1986; Hand, 1986; Liley & Kroon, 1995). In some cases, keystone individuals that establish dominance of one group over another can enhance the across-group dominance of the individuals in their entire group (e.g., the coat-tail effect; Wiley, 1990; Cristol, 1995). In other cases, keystone individuals can serve as conflict mediators, or facilitators (Aureli & De Waal, 2000). When keystone individuals leave, the entire group's dynamics can be significantly altered. For example, Sapolsky & Share (2004) observed that after aggressive male baboons died (due to their tendency to feed at a garbage dump where they contracted bovine tuberculosis from eating infected meat), the entire 'culture' of a group changed (to be more affiliative, and less stressful) in ways that have persisted for a decade or more. While keystone individuals and their effects have been emphasized in systems that have sophisticated sociality --- where investigators historically focus on individual variation and BTs (e.g., in primates), they have not received as much attention in 'less sophisticated' social groups. More theoretical and empirical work on the existence and impacts of keystone individuals on groups should prove rewarding.

Finally, note that our study only scratched the surface on possible experiments to examine effects of the mix of BTs on individual and group outcomes. In our view, the next obvious step is to manipulate the mean and variance of the group's BTs (i.e., the relative frequency of more versus less aggressive individuals) to examine effects on a range of individual (e.g., individual behaviour and fitness) and group (e.g., overall mating activity, aggression rates, survival) outcomes.

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