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Population-dependent conflict between individual sociability and aggressiveness

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In some species, populations with the highest average aggressiveness also have the lowest sociability, suggesting a conflict between the expression of these behaviours. While this negative relationship has been found between populations, whether the same relationship can be found within a population, where the most aggressive individuals are also the least social ones, has not been tested in vertebrates. In the present study, we found a negative correlation between aggressiveness and sociability in only one of two populations of juvenile threespine sticklebacks, *Gasterosteus aculeatus*, reared in a common environment. Nevertheless, highly aggressive individuals that were also highly social were absent in both populations. Our results suggest that specific constraints or selection pressures resulted in the absence of this behaviour combination in both populations. Our findings also suggest that population-specific selection pressures may have resulted in the negative correlation present in only one population, although an effect of genetic drift or population-specific maternal effects are also possible. Our results do not support the hypothesis that this correlation was due to genetic constraints.

Sociability and aggressiveness are two social behaviours that can have a tremendous positive or negative impact on fitness, depending on the ecological context (Dochtermann, Jenkins, Swartz, & Hargett, 2012; Goodson, 2013; Huntingford, Tamilselvan, & Jenjan, 2012; Krause & Ruxton, 2002). Among-population differences in these behaviours are observed in several animals, including lizards, birds, insects and mammals (Baird & Sloan, 2003; Beck, Kuningas, Esteban, & Foote, 2012; Chapman, Thain, Coughlin, & Hughes, 2011; Madden, 2006). The existence of a negative relationship between the average aggressiveness of a population and the average sociability of its members, measured as grouping tendency (Goodson, 2013), has been shown in guppies (Magurran & Seghers, 1991). This negative correlation has been suggested to represent a conflict between the expressions of these two behaviours, which were thus proposed to be fundamentally incompatible, and resulted in the prediction that ecological conditions selecting for high sociality in a population would lead to a reduction in average aggressiveness (Magurran & Seghers, 1991).

While such a negative relationship has been found between populations (using the average of each behaviour for each population), whether the same relationship exists within populations, where the most aggressive individuals are also the least social ones, has not been tested in vertebrates. In the spider *Anelosimus studiosus*, Pruitt et al. (2010) found a negative relationship between average sociability and average boldness among 18 populations. They also found the same relationship within these populations, with the least social individuals of a given population also being the boldest. However, it is unknown whether there is a similar negative relationship between sociability and aggressiveness within populations of vertebrates. This lack of information is significant, because identifying conditions under which a negative correlation between sociability and aggressiveness occurs would further our understanding of the evolution of social behaviour and allow us to predict the settings in which it should occur.

The correlation between two behaviours among individuals of a population (often termed behavioural syndrome) has been hypothesized to result either from a constraint, such as a common underlying cause controlling both behaviours (genetic or hormonal pleiotropy or genetic linkage: Aubin-Horth, Deschenes, & Cloutier, 2012; Baugh, van Oers, Naguib, & Hau, 2013; Edeline, Bardonnet, Bolliet, Dufour, & Elie, 2005; van Oers, de Jong, Drent, & van Noordwijk, 2004), from correlational selection on the two behaviours, or from physiological allocation trade-offs (Bell, 2005; Herczeg, Gonda, & Merila, 2009; Sih, Bell, & Johnson, 2004). It has been predicted that if this correlation between two behaviours is driven by a constraint, it should be hard to break (Sih et al., 2004).

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However, correlations between behaviours such as aggressiveness and boldness, or activity and boldness, are found in some but not all populations of a given species and, furthermore, their presence depends on ecological conditions (Bell, 2005; Brydges, Colegrave, Heathcote, & Braithwaite, 2008; Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011; Dingemanse et al., 2007), thus not supporting the constraint hypothesis for these behaviours (Dingemanse & Réale, 2005; Sih et al., 2004). If there is a conflict for an individual between being highly aggressive and being highly social, as proposed by Magurran and Seghers (1991), then, based on population averages, we would predict a negative correlation between sociability and aggressiveness at the individual level. Furthermore, if this correlation results from a constraint (genetic or hormonal pleiotropy, genetic linkage), then it would be predicted to occur in all populations studied.

To address these questions, we aimed to measure individual levels of aggressiveness and sociability in juvenile threespine stickleback, *Gasterosteus aculeatus*, from two populations that differed in ecological conditions and in several behaviours (Lacasse & Aubin-Horth, 2012). We used a common rearing environment to focus on behavioural divergence resulting from genetic differences between the two populations, rather than resulting from a differential encounter rate with predators or other environmental effects, which can affect behaviour in sticklebacks (Bell & Sih, 2007). Juvenile sticklebacks can exhibit sociability and are also aggressive towards a conspecific intruder (Bakker & Feuth-De Bruijn, 1988; Lacasse & Aubin-Horth, 2012; Wark, Greenwood, Taylor, Yoshida, & Peichel, 2011; Wright & Huntingford, 1993) without the confound of behavioural changes associated with reproduction. These characteristics make them highly amenable to test the prediction that (1) individual levels of sociability and aggressiveness are negatively correlated and that (2) this correlation occurs in all populations.

METHODS

Populations Studied

We studied two freshwater populations of threespine sticklebacks from neighbouring lakes in Québec, Canada, situated 3 km apart. The two lakes (Témiscouata: 47°48′29″N, 68°52′2″W; Rond: 47°44′31″N, 68°50′5″W) are globally similar (ecosystem, weather, latitude) but differ in some respects. Lake Rond has a higher altitude (Rond: 226 m, Témiscouata: 149 m), is smaller (Rond: 1.3 km^2, Témiscouata: 67 km^2) and has a shallower maximum depth (Rond: 25 m, Témiscouata: 74 m). Lake Rond has only one other known fish species in addition to threespine sticklebacks, *Pimephales promelas*, a nonpredatory cyprinid. Brook trout, *Salvelinus fontinalis*, were also released in the lake in 1983 (Québec Minister of Natural Resources and Wildlife, 2006), although their actual numbers or presence is unknown. In contrast, Lake Témiscouata contains about 20 fish species, including common predators of sticklebacks, such as salmonids (*Coregonus clupeaformis*, *Salvelinus fontinalis*) and perch, *Perca flavescens* (Reimchen, 1994). Bird predation at the two lakes was unknown, but we assumed it was similar at both lakes because of their close proximity. Insect predation was also unknown for both lakes. We hypothesized that the lower number of predatory fish species in Lake Rond potentially resulted in a lower probability of piscine predation there than in Lake Témiscouata. In support of this hypothesis, we previously found that predator defence morphology of sticklebacks (lower number of lateral bony plates, shorter dorsal and pelvic spines, absence of a pelvic girdle in 61% of the population) was significantly lower in Lake Rond than in Lake Témiscouata (Lacasse & Aubin-Horth, 2012). Furthermore, we also found that juveniles from Lake Rond were significantly more aggressive on average than juveniles from Lake Témiscouata but that they did not differ in average sociability (Lacasse & Aubin-Horth, 2012).

Sampling

Adult threespine sticklebacks were collected from Lake Témiscouata ($N = 14$) and Lake Rond ($N = 14$) during the reproductive period in June 2010 to perform crosses (for details, see Lacasse & Aubin-Horth, 2012). Fertilized eggs were transported to the Laboratoire régional des sciences aquatiques (LARSA) at Université Laval, Québec, Canada. Broods were split in several rearing tanks at equal density. Juveniles were raised in common environment at 18 °C on a 12:12 h light:dark cycle (characteristic of summer conditions). Fish were fed frozen bloodworms and *Artemia*, representing 4% of their biomass, twice daily. Behavioural testing began at 5 months when fish were still immature (138–177 days old, 8 November–14 December 2010). We tested 56 fish per population.

Experimental Design

The individual observation tanks had a volume of 45 litres ($61 \times 25 \times 10$ cm), and water temperature and light regime were kept the same as in the group tanks. The individual observation tanks contained artificial vegetation and a refuge. A single focal fish was placed in the individual observation tank. We tested the two behaviours over a 3-day period. In total, there were seven series of 3 days (8 fish per population tested per series, total of 16 fish per series). All tests were done at the same time of day (0800 hours). Social behaviour was tested on the first day, while aggression towards a stimulus fish from the same population was quantified on the third day. Focal individuals were checked daily for signs of stress or disease. Each behavioural test was filmed with a digital camera (JVC model GZ-MS120) mounted in front of the observation tank. All individuals reacted to the test stimulus. Each fish was used only once.

Behavioural Assays

Sociability

We quantified sociability as the tendency of fish to join a group of conspecifics (Goodson, 2013) (also referred to as 'schooling' and 'shoaling'). To measure the level of sociability, we used an assay based on a group of model sticklebacks (Wark et al., 2011). A motorized mobile was constructed on which five artificial flexible fish, similar in size and coloration to juvenile sticklebacks, were hung using invisible thread. The artificial group was immersed 10 cm under the water surface, 10 cm from the bottom, in an 80-litre tank. The focal fish was then placed in the tank. Following an acclimatization period of 15 min (following Wark et al., 2011), a rotating motor connected to the mobile was turned on to move the fish group in a circle around the tank for 15 min and the focal fish's behaviour in the tank was filmed from above the tank. We quantified sociability as time spent swimming within one body length of the group in the same direction. After the test, each fish was placed in a new observation tank in which it remained throughout the rest of the behavioural experiment.

Aggressiveness towards an intruder

We measured aggressiveness of focal fish based on their reaction towards a conspecific intruder (Huntingford, 1976). After the focal fish spent 3 days in the new individual observation tank, we placed a fish of the same population in a 1-litre transparent glass container inside the observation tank and quantified the resulting interactions for 5 min. The glass container was placed in the tank the day before the test to control for the potential effect of