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Environmental effects on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*

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In social species, the structure and patterning of social interactions have implications for the opportunities for sexual interactions. We used social network analysis to explore the effect of habitat structural complexity on the social and sexual behaviour of male Trinidadian guppies. We used replicated seminatural pools in which we quantified male social network structure and reproductive behaviour under simple and complex habitats. In addition, we compared two populations of guppies that differed in their evolutionary history of predation (one high, one low). The level of habitat complexity did not significantly affect social network structure. However, social networks differed significantly between populations, which we suggest is due to differences in predator experience. Males from the high-predation population had greater overall social network differentiation and fewer male–male associations than their low-risk counterparts. Contrary to our prediction that males would associate more frequently with relatively large (more fecund) females, we observed a negative correlation between female size and the strength of male–female associations. We also found no effect of population or habitat complexity on either harassment or sexual network structures. There was, however, a significant interaction between habitat structure and population on the expression of reproductive strategies, with high-predation males expressing fewer sigmoid displays in the complex habitat and the opposite trend in low-predation males. We suggest this pattern is driven by population differences in male–male competition. We discuss our results in the context of the evolution of social structure and male reproductive strategies.

Differences between males and females in sexual strategies are largely determined by differences in reproductive investment (Bateman 1948; Trivers 1972; Clutton-Brock & Parker 1995). Males have evolved a number of precopulatory behaviours that are used by females during mate choice, such as courtship displays and territory defence (Houde 1997; Hoglund & Sheldon 1998). However, male mating strategies have also evolved to subvert female choice. For example, males may parasitize another male's investment (Taborsky 1997) and/or coerce females to obtain matings (Gross 1996). The individual expression of mating tactics in many species is plastic, with males alternating between strategies to maximize reproductive potential (Godin 1995). The adoption of one reproductive strategy over another is often dependent upon multiple social and environmental stimuli (Magurran & Seghers 1994b; Endler 1995; Godin 1995; Kokko & Rankin 2006). For example, in guppies individual males employ two tactics interchangeably to attain a successful mating (Godin 1995). First, during courtship males adopt an 'S' shape, known as a sigmoid display, to display their bright colour patterns to females. Second, males may attempt unsolicited matings by thrusting their intromittent organ, the gonopodium, towards the female's genital pore without prior display. It has been shown that in high-predation localities males engage in gonopodial thrusts more than sigmoid displays (Luyten & Liley 1985; Godin 1995), which is likely to be caused by males exploiting the female's preoccupation with predator avoidance under high-risk conditions (Evans et al. 2002). By contrast, in low-predation localities males exhibit the opposite trend, engaging in significantly fewer gonopodial thrusts and more sigmoid displays that are longer in duration (Luyten & Liley 1985).

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In social species, the structure and patterning of social interactions, that is, who meets whom, will have implications for the opportunity for sexual interactions and thus male and female reproductive strategies. For example, increased social mixing and male–male interactions have the potential to increase competition for access to females and it has been shown that males adjust the frequency of their displays in response to competitors (Farr 1980; Houde 1988). Furthermore, the level of male–male competition has the potential both to facilitate and to hinder precopulatory female choice (reviewed in Wong & Candolin 2005). Previous work suggests that habitat complexity may play an important role in influencing patterns of social interactions. For example, Orpwood et al. (2008) compared the shoaling behaviour of European minnows, *Phoxinus phoxinus*, between simple and complex habitats in the presence of a predator. Minnows formed larger shoals in simple habitats when exposed to predators, supporting the hypothesis that individuals shoal as a sheltering mechanism, that is, the selfish herd principle (Hamilton 1971) and/or the dilution effect (reviewed in Krause & Ruxton 2002). Habitat complexity may also influence the frequency and outcome of behavioural interactions between individuals. For example, Hibler & Houde (2006) demonstrated that the structural complexity of the environment plays an important role in sexual interactions of guppies. In the presence of visual barriers, male interference competition and courtship displays decreased while female responsiveness increased. This was attributed to structural complexity increasing privacy, benefiting both males, via reduced competition, and females, via increased ability to assess males in the absence of interference by other males. The structural complexity of the environment can therefore influence both social and sexual interactions, as well as reproductive strategies employed by males in a population. Currently, however, we know very little about how the ecological environment influences the fine-scale population social structure (i.e. distribution of social association/interactions) and what implications this structure has for male reproductive strategies. The ecological environment also typically covaries with the physical environment, and therefore any attempt to understand their relative influence and interactive effects demands careful experimentation.

In this study, we used social network analysis to examine how habitat structural complexity, population differences and their interactive effects influence the population social structure (i.e. who meets whom, based on spatial proximity of individuals) and sexual interactions (courtship intensity and harassment; defined as sigmoid displays and combined scores of nips, chases and gonopodial thrust events, respectively) in guppies. We also examined the effect of habitat structural complexity on male reproductive strategies (the rate/min of sigmoid displays and gonopodial thrusts) allowing us to explore the relationship between the ecological environment, the social environment and male reproductive behaviour. Guppies have a promiscuous mating system (Houde 1997), categorized as female-based polygyny, in which males compete with one another for female mating access with no parental care contribution (Kodric-Brown 1985). In this mating system, females are sexually receptive for short periods (Liley & Wishlow 1974) and during this receptive phase females solicit copulations with multiple males via behavioural (Liley 1966), visual and chemical cues (Crow & Liley 1979; Guevara-Fiore et al. 2009), resulting in mixed-paternity broods (Neff et al. 2008). Previous work has shown that the structural complexity of the habitat can influence both the shoaling behaviour of fish (see Mikheev 2009 for a discussion) and reproductive strategies in male guppies (Hibler & Houde 2006).

In our approach, we compared the structure of social and sexual interaction networks and male reproductive behaviour under two environmental conditions: (1) a structurally simple habitat and (2) a structurally complex habitat. Furthermore, we examined these effects for two populations from the same river drainage that differ in their evolutionary history of predation risk. We hypothesized that the structural complexity of a habitat will have an effect on both social and sexual network structure, as well as male reproductive strategies. Previous studies have shown that visual obstructions can reduce predator detection abilities and increase risk sensitivity (Schooley et al. 1996; Whittingham et al. 2004; Devereux et al. 2006). By contrast, visual barriers may also present a 'safe haven' and reduce perceived risk (Candolin & Voigt 1998; Dzieweczynski & Rowland 2004). We therefore predicted that, in our structurally complex habitat, high-predation fish will move less freely within their environment, either because these structures present a refuge or because they limit the ability to detect risk. We therefore expected that social mixing, encounter frequencies and sexual interactions would be limited in this habitat type, with the opposite pattern expected in the simple habitat. Moreover, we predicted that low-predation individuals would have higher levels of social mixing and more evenly distributed sexual interactions regardless of habitat structural complexity. As our study was restricted to two populations, we lacked the replication needed to draw general conclusions regarding the effect of predation risk on social network structure or male reproductive behaviour. However, our approach did allow us to explore the potential for population differences in social network structure and male reproductive behaviour, and, importantly, to gain insights into how these traits respond to different levels of environmental structural complexity. To our knowledge, this is the first study to compare social network structure between different populations of conspecifics. Furthermore, as far as we are aware, this is also the first study to implement focal animal sampling for the construction of animal social networks. This approach is especially novel in the fact that, as well as association data, we could also extract data on behavioural interactions during these associations simultaneously, which would otherwise not be possible with the point sampling methods generally implemented in animal social network studies (Croft et al. 2008).

METHODS

Experiments were conducted in June 2007. We collected guppies from two sampling sites in the Aripo River, Northern Mountain Range of Trinidad: high predation (10°39′27N, 61°13′34W) and low predation (10°40′49N, 61°13′44W). Fish were collected using seine net (1×1 m, mesh size 3 mm) sweeps within single pools and transferred to covered 30-litre buckets containing 10 litres of river water (approximately 30–40 individuals per bucket). All of the pools in high- and low-predation localities were similar in their structural complexity. These pools were characteristically open bodies of water with few visual obstructions (such as vegetation and large rocks). They were selected to reduce the potential for confounding experiential effects owing to natural structural differences between populations. However, wild guppies were not restricted to the specific pools from which they were collected, and thus we were unable to control for an individual's previous experience of habitat structural complexity.

Adult guppies were transported to the University of the West Indies (within 45 min of capture) and, upon arrival, fish (125 individuals) were transferred immediately to an outdoor holding pool (diameter 244 cm, average water depth 20 cm) and allowed to acclimatize for 24 h. During the study 500 fish were collected (250 per population), of which 480 were used in trials. Although guppies are prolific and found in high densities in tributaries of the Northern Mountain Range, because of the large number of individuals used in