



Male mate-searching strategies and female cues: how do male guppies find receptive females?

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Locating potential mates is critical to mating. We studied males' association with females and mate-searching patterns in the guppy, *Poecilia reticulata*, a promiscuous live-bearer. In the field, we examined whether male guppies respond differently to a shoal of conspecific fish based on the members of the shoal. We found that more males were attracted to shoals that contained receptive females than to shoals of nonreceptive females or males. We also conducted laboratory experiments to investigate how males use olfactory cues of nonreceptive and receptive females to search for and associate with females. We gave males the option to associate with nonreceptive females when olfactory cues of receptive or nonreceptive females were present and absent, and when olfactory cues were presented alone. Males associated with females most strongly when both cues were presented simultaneously, but when cues were presented separately males' association with females differed with respect to the olfactory cues that were added. Males associated with females equally with visual and olfactory cues presented separately when the odour cues were from receptive females. However, when the odour cues were from nonreceptive females, males associated with females less with olfactory than visual cues. Searching activity increased when males had access only to olfactory cues. Taken together these results suggest that olfactory cues influence males' association with females and searching behaviour, and these changes in behaviour are likely to maximize a male's opportunity to encounter receptive females.

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Mate searching has broadly been observed in males rather than females (Andersson 1994). This disparity in searching effort between the sexes seems to be related to high multiple mating rates, and consequently high sperm competition, and a biased operational sex ratio rather than a difference in reproductive investment between the sexes (Kokko & Wong 2007). Finding potential mates is an essential component of a male's reproductive success. Males allocate a considerable amount of time searching for mates (Bonduriansky 2001) and by increasing mate-searching effort, males augment the probabilities of finding females and increase their mating opportunities (Real 1990). However, mate searching is costly not only in terms of time but also in terms of an increase in energy expenditure (Proctor 1992; Byers et al. 2005)

and it can increase male mortality as well (Gwynne 1987; Andrade 2003; Kasumovic et al. 2007; Kraus et al. 2008). For example, higher mate-searching activity by male wolf spiders, *Hygrolycosa rubrofasciata*, which increases their probability of finding females, also increases their risk of predation (Kotiaho et al. 1998). Variation in the costs of mate searching has been found to be an important selective agent in many systems. For instance, male searching effort varies with predation risk and males experiencing a higher risk of predation spend less time searching for females (DeRivera et al. 2003). Population density and sex ratio can also influence male mate-searching behaviour. This is the case for males of the fish ectoparasite *Argulus coregoni*, which stay in their host when there are females available, but when no females are present they tend to switch hosts (Bandilla et al. 2008). Indeed, at lower densities or when sex ratios are male biased, males are less likely to encounter females and alter their behaviour accordingly (Lawrence 1987; Carroll 1993; Mathews 2002; DeRivera et al. 2003; Bertin & Cezilly 2005; Kokko & Wong 2007).

In the face of the considerable costs of mate searching, males should prioritize their effort to find receptive females and avoid wasted effort on nonreceptive females (Real 1990). Discrimination between females then represents an important component of male

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fitness, and as a result many different discrimination mechanisms have evolved in males (Bonduriansky 2001). Most commonly, males use visual and/or odour cues to identify and find receptive females (Dunham 1978; Vane-Wright & Boppre 1993; Ayasse et al. 2001; Shine & Mason 2001; Diaz & Thiel 2004; Nahrung & Allen 2004; Aldridge et al. 2005; Head et al. 2005; Paxton 2005; Spiewok et al. 2006; Gaskett 2007; Toshova et al. 2007), but in some cases male searching involves integration of sensory mechanisms with highly developed memory (Wcislo 1992; Schwagmeyer 1995). Although animals use several cues during mate selection (Candolin 2003), some cues might play specific roles depending on the context in which they are used. For example, male garter snakes, *Thamnophis sirtalis parietalis*, differentiate females from males by means of dimorphic traits such as size, body temperature, muddiness and aggregation with conspecifics (Shine & Mason 2001). However, particular sensory modalities are used differently depending on the conditions in which females are found: when females are part of a mating ball males use principally odour cues to recognize them, but in a solitary context males rely mainly on visual cues (Shine & Mason 2001).

Despite the potential importance of accurate assessment of female receptivity to a male's reproductive success, there is little empirical evidence of male discrimination between receptive and nonreceptive females in natural conditions and how female cues influence male movement between groups of females. In the present study we examined male recognition of receptive females and the role of female olfactory cues in mate-searching strategies in the guppy, *Poecilia reticulata*, a small live-bearing fish with strong male-biased operational sex ratio (OSR) caused by asynchrony in female receptivity. Only virgin and postpartum females (i.e. females that have just given birth) are receptive to males (Liley 1966); pregnant females, in contrast, are nonreceptive and ignore males' continuous attempts to copulate (Liley 1966). Although considered a priori indiscriminate, males do exert mate choice: they prefer larger (Dosen & Montgomerie 2004; Herdman et al. 2004), unfamiliar (Kelley et al. 1999) and nonpregnant females (Ojanguren & Magurran 2004). As in other poeciliids (Brett & Grosse 1982; Sumner et al. 1994; Park & Propper 2002), male guppies are attracted to a female pheromone produced only by receptive females (Crow & Liley 1979; Guevara-Fiore et al. 2009). Males can achieve fertilization by solicited copulations after courting females or by forcing copulations (Liley 1966), and they allocate a significant proportion of their time to these mating activities (Magurran & Seghers 1994), but they also are known to search for females constantly (Houde 1997; Griffiths & Magurran 1998; Croft et al. 2003a, b). Whereas females are likely to school with familiar individuals and show site fidelity (Griffiths & Magurran 1998), male guppies tend to switch between shoals which results in high rates of shoal encounters (Croft et al. 2003b).

In this study we used both field and laboratory trials to test whether males discriminate between shoals of conspecifics based on sex and receptivity of the members within that shoal and how olfactory cues were used during the discrimination process. In the first experiment we tested whether males in the field were differentially attracted to shoals of fish that were composed of either males, nonreceptive or receptive females and we predicted that shoals of receptive females would attract the most males. In the second set of experiments, in the laboratory, we tested how olfactory cues from receptive and nonreceptive females influenced male movement and association behaviour in the presence of a shoal of size-matched nonreceptive females that was presented between three shoals of males (see below). We allowed males to associate with the female stimulus when olfactory cues and visual cues were presented alone or in combination. First, we predicted that males would spend longer periods associating with the female stimulus

when both odour and visual cues were presented together than when either was presented alone. However, we predicted that males would associate more with a female stimulus with receptive female odour present than with only visual cues, but that there would be no difference in association behaviour when the stimuli were a female with nonreceptive odour and a female without odour (i.e. visual cues only). Our second prediction was that males would be able to localize and move towards the shoal of females faster when males have complete information, that is, when both cues are present. Our third prediction was that male search activity should increase if males can smell females but no visual cues are available to them.

METHODS

Experimental Fish

Guppies in this study were from the Upper Aripo River (Grid Reference PS 931 817) in the Northern Range mountains of Trinidad. This is a low-predation locality where guppies coexist with the gape-limited cyprinodontid fish *Rivulus hartii* (Magurran 2005). Collections were made using a one-person seine net in May 2007. Fish were captured, and transported in groups of about 50 fish in covered 20-litre buckets to the laboratory at the University of the West Indies, St Augustine, Trinidad. Care was taken during handling to ensure that fish were not stressed. In the laboratory, fish were maintained on a 12:12 h light:dark regime at an ambient temperature (ca. 25 °C). Male and female guppies were housed together in large aerated aquaria (45 × 45 cm and 120 cm deep; ca. 150 individuals per tank) furnished with natural river gravel and were fed twice daily with commercial flake food. No fish died or showed no signs of stress throughout the study. After the experiment the fish remained in the laboratory as breeding stock. The study was approved by the University of the West Indies, Trinidad and Tobago.

During the study we individually isolated 60 females to record parturition; females were placed next to each other so that they had visual contact with other fish. Females were classified as nonreceptive when they were pregnant (15 ± 1 days after giving birth) or as receptive when females were postpartum, that is, selected during the first 3 days after giving birth. Female guppies store sperm and can use it several times to fertilize a new clutch of eggs (Liley 1966). Both receptive and nonreceptive females were isolated to control for possible differences between them caused by this procedure.

Field Experiment

To determine whether male guppies prefer to associate with shoals of receptive females we conducted an experiment in the Upper Aripo River in which we recorded the number of males in proximity to an enclosure containing different groups of fish. We grouped fish in four treatments: (1) no fish (control), (2) three males, (3) three nonreceptive females, and (4) three receptive females. Four different groups of fish were used as stimulus fish in the treatments (i.e. 12 males; mean ± SE standard length, SL = 18.05 ± 0.34 mm), 12 nonreceptive females (24.36 ± 0.26 mm) and 12 receptive females (24.28 ± 0.19 mm); nonreceptive females and receptive females presented in the same pool were matched by size (±2 mm). Fish were placed in a transparent and perforated plastic bottle (9 cm diameter, 11 cm high; perforations were ca. 2 mm diameter and were separated from each other ca. 1 cm evenly distributed around the bottle), which permitted the transmission of both visual and olfactory cues and this bottle was then placed into a pool within the river. A total of 14 pools were used and pools were chosen if they contained a shoal of guppies with at least 15 individuals and the water was no deeper than 13 cm.

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