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Female receptivity affects subsequent mating effort and mate choice in male guppies

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High mating effort leads to choosiness because each mating event reduces future reproductive potential. Many studies have shown that males adjust their sexual behaviour relative to female fecundity and encounter rate. However, little is known about the effects of a male's past mating experiences. We used guppies, *Poecilia reticulata*, to investigate how males change their sexual behaviour after experiencing high or low mating success. Each male was tested with two differently sized unreceptive females before and after encountering either four indiscriminate receptive virgin females or four nonreceptive pregnant females. Males that experienced high mating success with receptive females decreased their courtship displays but increased the frequency of sneaky behaviour, whereas low mating success males previously repetitively rejected by nonreceptive females showed an increase in courtship and a decrease in sneaky copulation attempts. Mating history also influenced male choosiness, with successful males showing stronger preferences for larger females than unsuccessful males. This overall adjustment in behaviour may be attributed to a reduction of resources, such as energy and gametes, as well as prior social interaction with receptive and nonreceptive females. Males that adjust their effort and choosiness based on their recent mating history and their own condition could optimize reproductive trade-offs.

Optimal reproductive investment in mating effort is observed in males even when they only provide females with sperm (Bonduriansky, 2001; Dewsbury, 1982). Male reproductive behaviour is not solely determined by parental investment (Trivers, 1972), traits used in reproduction such as gametes and ornaments are costly, and males spend time and energy finding and courting females or competing to gain access to them (Dewsbury, 1982). Males tune their courtship intensity based on predation risk (Fuller & Berglund, 1996; Godin, 1995; Kelly & Godin, 2001; Koga, Backwell, Jennions, & Christy, 1998; Tuttle, Taft, & Ryan, 1982) and mating effort is reduced when resources are low, as when males experience a drop in body condition due to low food intake or high parasite load (Houde & Torio, 1992; Hunt et al., 2004; Kolluru & Grether, 2005; Kolluru, Grether, Dunlop, & South, 2009; Kotiaho, 2000). When environmental factors increase the cost of mating, males adjust their effort accordingly, as in bird acoustic signal modification during urban noise (Patricelli & Blickley, 2006; Rios-Chelen, Lee, & Patricelli, 2015; Slabbekoorn, 2013) or reduced courtship in fish when swimming is costlier (Head, Wong, & Brooks, 2010; Magellan & Magurran, 2006; Wong & Jennions, 2003). Because there is a two-way interaction in courtship, males also pay attention to female responses (Guevara-Fiore, Stapley, Krause, Ramnarine, & Watt, 2010; Guevara-Fiore, Stapley, & Watt, 2010; Kahn, Dolstra, Jennions, & Backwell, 2013). For example, using a robotic female, Patricelli, Coleman, and Borgia (2006) showed that male satin bowerbirds, *Ptilonorhynchus violaceus*, decrease their courtship intensity in response to female startling during the display, in comparison to the control treatment without a startling response.

Possibly the most significant determinant of a male's mating effort is his own mating success (Bonduriansky, 2001; Dewsbury, 1982; Edward & Chapman, 2011; Kokko & Mappes, 2005), because the use of resources such as gametes in previous copulations limit a male's mating rate. This is why males that have recently mated are less likely to mate again (Baxter, Barnett, & Dukas, 2015; Guevara-Fiore, Svensson, & Endler, 2012; Hettyey, Vagi, Hevizi, & Torok, 2009; Marie-Orleach, Janicke, & Scharer, 2013; Mellan, Warren, Buckholt, & Mathews, 2014; Pilastro & Bisazza, 1999). However, although mating history is crucial to understand the balance between benefits and costs in each mating

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event, previous studies addressing male strategic change of mating effort have not tested for the effects of prior mating success directly, but instead have mainly focused on testing males after experiencing different kinds of females or different social environments (e.g. Cattelan, Evans, Pilastro, & Gasparini, 2016; Devigili, Doldan-Martelli, & Pilastro, 2015; Jordan & Brooks, 2012; Kahn et al., 2013; Svensson, Lehtonen, & Wong, 2010). Moreover, those experiments focused on understanding mating effort, but little is known about how mating experience affects mate choice in males. Here we evaluated how experiencing receptive or unreceptive females, and therefore high or low mating success, simultaneously affects mating effort and mate choice in male guppies (*Poecilia reticulata*). Because males invest energy and gametes in each copulation, we predicted that males would decrease their effort after a higher copulation rate with receptive females in comparison to males that interacted with nonreceptive females.

It is now well demonstrated that male mate choice can be as sophisticated as female mate choice (Bonduriansky, 2001; Edward & Chapman, 2011), yet, we still do not know how mating effort and mate choice interact as a consequence of a male's recent mating history. We recorded the change in the amount of courtship and sneaky attempts directed to a pair of females of different sizes, as well as their preference for the larger female, before and after male guppies experienced high or low mating success. Males experiencing high mating success interacted and mated with receptive indiscriminative virgin females for 4 days, whereas males experiencing low mating success interacted with pregnant nonreceptive females during the same period. Virgin female guppies are always receptive in their initial encounters with males (Liley & Wishlow, 1974), whereas pregnant females only mate by means of forced copulations; this insemination tactic is extremely infrequent compared to consented copulations (Houde, 1997; Liley, 1966).

We designed an experiment to test how an increase or a decrease in prior mating success could simultaneously affect male mating effort and mate choice. This is a central question for understanding male mate choice evolution (Bonduriansky, 2001; Edward & Chapman, 2011), and particularly male guppy sexual behaviour (Cattelan et al., 2016; Devigili, Kelley, Pilastro, & Evans, 2013; Guevara-Fiore, Stapley, Krause et al., 2010; Guevara-Fiore, Stapley, & Watt, 2010; Head et al., 2010; Jordan & Brooks, 2010, 2012; Kolluru & Grether, 2005; Miller & Brooks, 2005; Pilastro & Bisazza, 1999; Rahman, Kelley, & Evans, 2013). Because males housed with receptive females in our study were likely to use resources (like energy and gametes) to court and mate, and to receive biased positive responses from those females, in comparison to males housed with nonreceptive females, we predicted that males that experienced high mating success would decrease their mating effort and increase their choosiness in comparison to males that had low mating success.

METHODS

Population and Fish Maintenance

Guppies inseminate females either by performing a courting sigmoid display and subsequently inseminating the female with her cooperation, or by means of sneaky behaviour without previously courting her (Liley, 1966). Although each male uses both tactics, as these are not fixed alternative reproductive strategies, the proportion of courtship to forced attempts can be influenced by different environmental factors (Auld, Jeswiet, & Godin, 2015; Endler, 1987; Farr & Herrnkind, 1974; Godin, 1995; Jirotkul, 1999; Miller & Brooks, 2005; Rodd & Sokolowski, 1995). Male guppies increase their mating effort when they encounter receptive females (Guevara-Fiore, Stapley, Krause et al., 2010; Guevara-Fiore, Stapley, & Watt, 2010) and decrease their mating effort with sperm depletion (Pilastro & Bisazza, 1999). Males prefer conspecific (Magurran & Ramnarine, 2004), novel (Kelley, Graves, & Magurran, 1999), virgin (Guevara-Fiore, Skinner, & Watt, 2009) and larger females (Herdman, Kelly, & Godin, 2004), taking into account their risk of sperm competition (Auld & Godin, 2015; Evans & Magurran, 1999; Jeswiet, Lee-Jenkins, & Godin, 2012).

We used second-generation wild-type guppies that were descendants of a population from Alligator Creek in Bowling Green Bay National Park 30 km south of Townsville, Queensland, where they were introduced at least 80 years ago (Queensland permit WITK07655010). Fish were raised under laboratory conditions at 24 ± 1 °C under a 12:12 h light:dark photoperiod and fed twice per day ad libitum with live brine shrimp naupilii (*Artemia salina*) and commercial flakes. All experimental tanks had clean gravel at the bottom and were filled with water taken from the stock aquaria, which assured that the fish experienced the same conditions that they were raised in during the trials. We obtained the standard length of the fish (SL; i.e. excluding the caudal fin, presented here as mean ± SD) by anaesthetizing them with tricaine methanosulfate (MS-222, 150 mg/litre) before taking photographs using a digital camera (Canon E 300 D). When moved back to normal water, sedated fish recovered and swam normally within a few seconds. We used the programme Image-J version 1.40 g (ImageJ, National Institutes of Health, Bethesda, MD, U.S.A., http://rsbweb.nih.gov/ij/) to measure the SL of the fish from their photographs. Trials carried out in this experiment consisted of the observation of fish behaviour and no signs of distress were observed as a result of this procedure. This study complies with all the relevant federal and state laws of Australia, follows the ASAB/ABS Guidelines for the use of animals in research and all experimental procedures were carried out according to the guidelines of Deakin University (ethics approval A21-2010).

Conditioning Females, Experimental Males and Stimulus Females

All fish were sexually mature adults. To create high or low mating success conditions, we raised ‘conditioning females’ to be either receptive virgins or pregnant nonreceptive females of similar age and of medium size (SL: receptive females: 22.96 ± 0.35 mm; nonreceptive: 22.99 ± 0.36 mm). Virgin female guppies are always receptive and highly indiscriminative during initial encounters with males (Houde, 1997; Liley & Wishlow, 1974), whereas pregnant females are unreceptive to males and will not mate consensually (Liley, 1966). For the conditioning females, we obtained virgins by isolating females from males at the first sign of maturity (i.e. presence of dark coloration in gonopore area, at 4–6 weeks old). Once mature (ca. 5–7 months old), these females were divided into two groups. One group of virgin females was housed without any other fish in 50×30 cm aquaria ($N = 16$ per tank) for 10 days, and at the end of the housing period, these females were receptive virgin females with no experience with males, and they were used in the high mating success treatment. The other group of virgin females was housed in identical conditions but they were with males ($N = 8$ females, $N = 8$ males per tank), and after 10 days, they were pregnant nonreceptive females used in the low mating success treatment.

Experimental males ($\mathrm{SL} = 16.88 \pm 0.92$) and pairs of females used in trials (i.e. stimulus females) were randomly selected from the population, but to avoid familiarity among fish, we selected them from different breeding tanks. Pairs of stimulus females were formed so that the difference in SL between the females was between 4 and 5 mm (SL large females 25.062 ± 0.388 mm; SL small females 20.859 ± 0.439 mm; $t_{27.596} = 27.755$, $P < 0.0001$), which is a standard size difference used to test male guppy mating