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How pre- and postcopulatory sexual selection influence male mating decisions in a promiscuous species

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When females mate multiply, male reproductive success depends on both pre- and postcopulatory processes, including female choice and sperm competition. However, these processes can favour different mating tactics in males. Here we used the Trinidadian guppy, *Poecilia reticulata*, system to understand how this conflict is resolved. We asked whether knowledge of recent female mating history leads males to adjust their mating effort with respect to the time devoted to mating activity, and the frequency and the sequence of mating tactics employed. To do this we quantified male mating behaviour in three competitive scenarios: (1) Single, when a focal male arrives near a single female and remains alone with her; (2) First, when a focal male is joined by a rival male; and (3) Second, when a focal male arrives after a rival male. We hypothesized that males adjust their behaviour based on arrival order. If female sequential mate choice is the main process shaping male mating behaviours (favouring First males in guppies), males should avoid competition and invest most when Single. Alternatively, if last-male sperm precedence is the major driver of decision making, males should invest more in mating attempts in the Second scenario. Greatest investment when First implies an intermediate strategy. We found that order of arrival influenced mating decisions with most mating activity during the First rather than the Single and Second scenarios. This result suggests that both pre- and postcopulatory processes influence mating investment, and that individual males make contingent decisions to maximize both mating and fertilization success.

When females mate with multiple males within the same breeding season, often referred to as polyandry, males gain more mating opportunities but, at the same time, face the challenge of cryptic female choice (Eberhard, 1996) and sperm competition (Parker, 1970; 1998). This means that both precopulatory and postcopulatory processes influence the evolution of male sexual traits.

There is considerable interest in the contribution of secondary sexual traits to male reproductive success both during and after mating, and how they are influenced by pre- versus postcopulatory processes (reviewed by Evans & Garcia-Gonzalez, 2016). However, the relative influence of these two selective forces on male mating sexual traits continues to be debated (Buzatto, Roberts, & Simmons, 2015; Collet, Richardson, Worley, & Pizzari, 2012; Devigili, Evans, Di Nisio, & Pilastro, 2015; Pischedda & Rice, 2012; Pélissié, Jarne, Sarda, & David, 2014; Turnell & Shaw, 2015). Recent studies have focused on physical and sperm traits (e.g. body and sperm length, respectively; Evans & Garcia-Gonzalez, 2016), but few have considered mating behaviours (Buzatto et al., 2015; Devigili et al., 2015; Turnell & Shaw, 2015).

As with other male sexual traits, mating behaviours are subject to both pre- and postcopulatory sexual selection pressures (Andersson & Simmons, 2006), and are correlated with male reproductive success (Buzatto et al., 2015; Devigili et al., 2015; Fisher, Rodríguez-Muñoz, & Tregenza, 2016; Pélissié et al., 2014; Turnell & Shaw, 2015). Unlike most physical traits however,

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behaviours can be adjusted with respect to the social context. For instance, mating behaviours can promote both mating and fertilization success by stimulating or circumventing female mate choice (e.g. courtship displays and unsolicited mating attempts, respectively; Gross, 1984; Andersson, 1994), and by avoiding or overcoming mating competition (e.g. mate guarding and sneaking, respectively; Andersson, 1994; Neff & Svensson, 2013).

Male order of arrival at or near a female can greatly affect male reproductive success, at both the pre- and postcopulatory levels (Evans & Garcia-Gonzalez, 2016; Pischedda & Rice, 2012; Pélissié et al., 2014). For instance, when females choose sequentially (Jennions & Petrie, 1997; Real, 1990) a male's mating success will vary if he is the first or last to arrive near a female, depending on whether females are less or more discriminating (choosy) towards a first than a second male. Similarly, when sperm competition occurs, male fertilization success can only be maximized if he mates first or last, depending on whether there is first- or last-male sperm precedence (Birkhead & Hunter, 1990; Dosen & Montgomerie, 2004; Plath & Bierbach, 2011; Wedell, Gage, & Parker, 2002). Female mating history can thus play a crucial role in determining which mating behaviours a male should adopt.

In natural conditions males may have little opportunity to evaluate female mating history (Parker, Ball, Stockley, & Gage, 1997), raising the question of how males cope with this uncertainty. Considering this, we hypothesized that, if mating order has no effect on male mating decisions, a male should approach and invest in mating attempts whenever near a female. In contrast, a male could adjust his behaviour based on whether he arrives before or after a rival male.

Males face a particularly challenging decision when pre- and postcopulatory processes favour different mating orders. This arises, for example, when females are less choosy towards the first male they encounter, but where sperm precedence favours a male that mates afterwards. According to the trade-up hypothesis, females benefit from being less choosy with a first male, particularly when males are scarce, because they can ensure the fertilization of all their eggs (Halliday, 1983; Jennions & Petrie, 2000). Females may then become progressively choosier, and mate with any higher-quality males they subsequently encounter to enhance the genetic quality of their brood. This hypothesis has been supported in species of birds (e.g. Gabor & Halliday, 1997), mammals (e.g. Klemme, Eccard, & Ylönen, 2006), insects (e.g. Bateman, Gilson, & Ferguson, 2001), fishes (e.g. guppies, *Poecilia reticulata*: Pitcher, Neff, Rodd, & Rowe, 2003) and reptiles (e.g. Laloi, Eizaguirre, Fédérici, & Massot, 2011).

Here, we asked whether males adjust their mating decisions over a short timescale based on the order in which they encounter a female. We further examined whether female mate choice or sperm precedence has the strongest influence on this decision making. To answer these questions, we studied the mating behaviours of male Trinidadian guppies in mixed-sex groups. In these tests we mimicked the situation in the wild by allowing free interactions between individuals. First, we determined whether a focal male approached a female before or after another male (approach decision), and, second, whether his investment in mating behaviours depended on order of arrival (behavioural adjustment; Fig. 1). The Trinidadian guppy is a freshwater livebearing fish. In this species, the precopulatory process of female mate choice should favour the first male to approach since females are less discriminatory towards him than towards subsequent males (Houde, 1997; Liley, 1966; Pitcher et al., 2003). However, sperm competition (postcopulatory process) favours the last male to mate since mixed-paternity broods (Becher & Magurran, 2004) are predominantly sired by these males (Evans & Magurran, 2001; Pitcher et al., 2003).

Male guppies perform two mating tactics: consensual courtship displays and unsolicited mating attempts (Magurran, 2005). Courtship displays result in the greatest paternity success (Evans & Magurran, 2001). Unsolicited mating attempts, on the other hand, do not require female cooperation (Houde, 1988; Magurran, 2005) and typically result in the transfer of only modest amounts of sperm (Pilastro & Bisazza, 1999). This mating tactic is more frequent when other males are present (Magurran, 2005; Magellan, Pettersson, & Magurran, 2005).

We hypothesized that, if males are able to evaluate female mating history based on their own assessment of male–male competition, they will adjust their mating behaviour based on whether they are with a female alone (Single), or they approach before (First) or after (Second) a rival male (Fig. 1). In more detail, if female mate choice gives the most advantage to males, they should avoid competition during mating, and invest more in following and trying to mate when they are alone with a female (Single), particularly using the mating tactic that allows them to transfer more sperm (courtship display). In this case, we expected male guppies to approach females with no rival male following them, to court more and repeatedly, and to spend more time with a female when Single. On the other hand, if sperm precedence gives the most advantage to males, they should invest more when there is competition, particularly in the mating tactic that transfers less sperm, but may help secure last-male sperm precedence (unsolicited attempt). In this case, we predicted that male guppies should approach females with at least one rival male following them, perform more unsolicited mating attempts and spend more time with a female when Second. However, if both pre- and postcopulatory processes are important, males should invest more when First, again due to potential advantages in terms of female choice, and, simultaneously, to secure sperm precedence. Fig. 1 summarizes these scenarios.

Alternatively, if information available to males during the current encounter conveys little fitness benefit to them, then order of arrival should not influence their behaviour towards the female. Here we expected no difference in mating behaviour if a male is the only, the first or the second to approach a female (Fig. 1).

METHODS

Experimental Set-up

We used descendants from wild guppies from the Lower Tacarigua River, in Trinidad. Following other studies with guppies (e.g. Deacon, Ramnarine, & Magurran, 2011), observations were carried out in two mesocosm tanks (100 × 56 cm and 30 cm deep). Behavioural observations in mesocosms have the advantage of allowing individuals to behave and interact more freely (Devigili et al., 2015). Each mesocosm contained gravel, an aerating system and two thermostat heaters. The range of temperatures (24.1–25.7 °C) was similar to that found in the wild (Reeve et al., 2014).

Inside each mesocosm we placed one mixed-sex group of fish: four males and three females. Wild females are only receptive either as virgins or in the few days immediately following parturition (Liley, 1966; Liley & Wishlow, 1974); thus male guppies are expected to typically encounter nonreceptive females in the wild. Therefore, to better simulate natural situations, all females used in our experiments came from a stock tank and were thus likely to be nonvirgin and nonreceptive.

Two groups of three females were haphazardly chosen (standard length mean ± SE: 2.09 ± 0.45 mm) from the same stock tank and allocated to each of the two mesocosms in the afternoon on the day before the observations. This allowed females to acclimate to