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Sperm competition risk and mate choice in male Trinidadian guppies, *Poecilia reticulata*

Sarah B. Jeswiet [a,1], Stacey S.Y. Lee-Jenkins [a,1], Indar W. Ramnarine [b,2], Jean-Guy J. Godin [a,*]

[a] *Department of Biology, Carleton University*
[b] *Department of Life Sciences, University of the West Indies*

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Sperm competition theory predicts that males should be sensitive to socio-sexual cues that provide information about the risk of sperm competition at any mating and correspondingly adjust their mating tactics in a manner that maximizes their reproductive success. Here, we investigated male mating preferences in response to socio-sexual cues as predictors of sperm competition risk (SCR) in the Trinidadian guppy, *Poecilia reticulata*, as a model study species. In a natural Trinidadian population, we observed that free-ranging females were most commonly pursued sexually by only one male at a time, which presumably represents a SCR associated with that female from the vantage of a nearby male observer. We tested whether wild-caught male guppies would modify their initial mating preference for either of two stimulus females presented by experimentally increasing the male's apparent SCR. This was done by allowing focal males to observe a rival male either placed near (but not physically interacting nor copulating with) or sexually interacting with their initially preferred female. In the absence of any apparent increase in SCR, the preference of focal males for either of the two stimulus females presented remained consistent. However, males significantly reduced their preference for their initially preferred female after having observed her either sexually interact with or merely in the vicinity of a rival male. Our results indicate that male guppies are sensitive to perceived SCR and adjust their mate choice behaviour in an apparently adaptive manner, as predicted by sperm competition theory.

In species with conventional sex roles, females are typically the choosier sex and show mate choice (Andersson 1994). Although male mate choice has been observed in diverse taxa (e.g. Andersson 1994; Bonduriansky 2001; Wedell et al. 2002; Clutton-Brock 2007), our understanding of its evolution is limited compared with our understanding of female mate choice. Males are expected to be discriminating and to express mate choice whenever (1) they experience a cost to mating that subsequently reduces their chances of fertilizing other females in the short term, (2) there are multiple females to choose from and (3) females vary in quality (Andersson 1994; Simmons 2001; Wedell et al. 2002; Clutton-Brock 2007). Because high-quality females may attract more male sexual attention, they may be more likely to be multiply mated (e.g. Herdman et al. 2004) and consequently be associated with higher sperm competition risk (Wedell et al. 2002). Sperm competition risk (SCR) is the probability that a focal male's sperm will compete against the sperm from other males for a given set of ova (Parker et al. 1997; Simmons 2001). Because sperm production is costly and potentially limited (Dewsbury 1982; Nakatsuru & Kramer 1982) and owing to sperm competition within a multiply mated female, a male could potentially achieve greater reproductive success by rejecting females that have previously mated and mate preferentially with unmated females (Simmons 2001). Selection should thus favour males that are able to accurately assess the SCR associated with any given mating opportunity and choose mates in a manner that maximizes their reproductive success (Wedell et al. 2002).

Males can potentially gain information about their immediate SCR using various cues depending on the species. One type of potential cue is social information (Danchin et al. 2004), such as a female seen interacting sexually with another male. In fact, several studies have shown that males adjust their mating preference after viewing their initially preferred female with one or more rival males (Schwagmeyer & Parker 1990; White & Galef 1999; Dosen & Montgomerie 2004; Wong & McCarthy 2009; Ziege et al. 2009), as would be predicted by sperm competition theory (Parker 1970; Simmons 2001). In some species, full interaction between a female and a rival male is required to serve as a reliable cue of SCR (White & Galef 1999; Dosen & Montgomerie 2004), whereas only the presence

* Correspondence: J.-G. J. Godin, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada.
E-mail address: jgodin@carleton.ca (J.-G.J. Godin).
[1] S. B. Jeswiet and S. S. Y. Lee-Jenkins are at the Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada.
[2] I. W. Ramnarine is at the Department of Life Sciences, The University of the West Indies, St Augustine, Trinidad and Tobago.

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of a rival male near the initially preferred female is sufficient to indicate a risk of sperm competition in other species (Wong & McCarthy 2009). Notwithstanding these and other studies (e.g. Smith et al. 2003), additional research is required for a more comprehensive understanding of the prevalence of use and importance of social-cue predictors of SCR on flexible male mating tactics.

Here, we investigated male mating preferences in response to socio-sexual cues as predictors of SCR using the Trinidadian guppy, *Poecilia reticulata*, as a model study species. The guppy is an internally fertilizing poeciliid fish that shows a non-resource-based, promiscuous mating system (Houde 1997). In nature, males typically encounter females concurrently within shoals (Houde 1997) and spend most of their time sexually pursuing females (Magurran & Seghers 1994). Males can achieve matings using two alternative tactics (Houde 1997), namely, cooperative mating using courtship behaviour (sigmoid displays) or coerced copulation (sneak gonopodial thrusting). In natural populations, most adult females have multiply sired broods (Kelly et al. 1999; Neff et al. 2008). Therefore, male guppies experience high sperm competition risk in the wild. As a consequence and as expected from sexual selection theory (Parker 1970; Simmons 2001), they are choosy in their mate choice (Herdman et al. 2004) and are sensitive to information associated with female mating status and sexual receptivity (Guevara-Fiore et al. 2009, 2010). To our knowledge, there is only one study to date (Dosen & Montgomerie 2004), using laboratory-born guppies descended from a Venezuelan population, that has reported evidence that male guppies are able to use social information predicting SCR in making mate choice decisions. However, because these investigators may have used more rival males to simulate an elevated risk of sperm competition than would occur in nature, it remains unknown whether the number of males that simultaneously pursue a female in the wild is able to influence a male guppy's mate choice.

In the current study, we tested whether wild-caught male guppies would modify their initial mating preference for either of two stimulus females by experimentally increasing the male's apparent SCR. This was done by allowing focal males to observe either (1) a rival male placed near (but not physically interacting nor copulating with) their initially preferred female or (2) a rival male sexually interacting (pursuing, courting and potentially copulating) with their initially preferred female. In the absence of a nearby rival male (i.e. absence of apparent local SCR), we expected that focal males would be consistent in their mating preferences between two consecutive preference tests. However, based on sperm competition theory (Parker 1970; Simmons 2001), we predicted that focal males would modify their initial mating preference in the face of apparent SCR and prefer to associate with the female that was not recently observed in the presence of, or sexually interacting with, a rival male. We further predicted that the magnitude of any SCR-mediated shift in mating preference would be greater in the second experimental treatment above (copulation by rival male possible), which we assumed would represent a more elevated SCR than in the first treatment (copulation by rival male not possible). In addition, we carried out field observations in Trinidad to ascertain how many male guppies concurrently pursue individual females in nature, and we used this information to experimentally simulate increases in SCR in our laboratory mate choice trials.

METHODS

Study Population

The current study was conducted on wild guppies from the Quaré River, Trinidad, West Indies (10°41′25″N, 61°11′51″W). This population has a female-biased sex ratio (Godin 1995), adult females vary widely in body size and fecundity (Kelly et al. 1999; Herdman et al. 2004), and most (60–100%) adult females have broods that are multiply sired, with the number of sires per brood ranging from one to nine (Kelly et al. 1999; Neff et al. 2008). Therefore, males in this population experience high levels of SCR.

Field Observations

We conducted visual focal observations (Martin & Bateson 1986) of free-ranging females in the Quaré River to determine the number of males simultaneously sexually pursuing individual females. At each of eight locations (small pools) along two sections (280 m and 210 m in length, respectively) of the river 1.2 km apart, we delineated an 'arena' ($\sim$1 m^2 quadrat) using natural landmarks on the substratum and observed focal female guppies as they entered the arena. A focal female was continuously observed once she entered the arena and the number of males in pursuit was recorded until she exited the arena or was lost from sight. Observations were made between 0830 and 1500 hours over 5 days between 4 May and 1 June 2009. Since the observed fish were not marked individually, no more than 10 females were observed in any one pool on the same day to minimize the likelihood of repeatedly observing the same females.

Laboratory Experiment

Subjects and holding conditions

All experimental fish were collected haphazardly by hand seining from the Quaré River in May 2009 and used in the experiment described below within 2 weeks of collection. The fish were held in 150-litre mixed-sex aquaria filled with filtered aged tap water (24–26 °C) at the University of the West Indies, St Augustine, Trinidad and fed ad libitum twice daily with commercial flake food until used in the experiment. Males from one holding aquarium were always tested with unfamiliar females taken from a different holding aquarium. The guppies were returned to the Quaré River at the end of the study.

Experimental apparatus

The experimental apparatus consisted of a test aquarium (40 × 20 × 25 cm; L × W × H), flanked by a clear Plexiglas container (15 × 20 × 22 cm) at either end (Fig. 1). Vertical lines drawn on the front and back walls of the test aquarium demarcated a 10 cm wide male-mating preference zone near each of the end compartments. The two end compartments held the stimulus fish (female alone or female and a rival male, depending on the treatment). Each compartment could be either divided in half by a clear Plexiglas

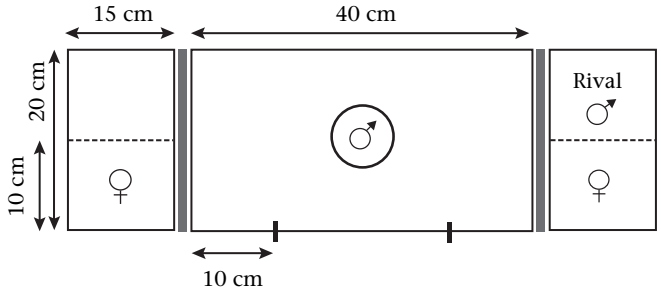

Figure 1. Schematic top view of the experimental apparatus. The central aquarium held the focal male and each of the two end compartments held a stimulus female and, depending on the treatment, a rival male or no male. The circle represents a removable clear Plexiglas tube, in which the focal male could be temporarily placed. Dashed lines represent removable clear Plexiglas partitions that allowed the end compartments to be either open or divided in half; shaded lines denote removable opaque screens; 'tick' marks on one side of the central aquarium denote the limits of the 10 cm wide preference zones.