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Behavioural profiles: individual consistency in male mating behaviour under varying sex ratios

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Variation in sex ratio can affect mating behaviour, with more intense competition predicted at biased sex ratios. In species with alternative mating behaviours, sex ratio variation can induce switches between behaviour types and this, together with the consistency with which behaviours are expressed, may also affect the intensity of sexual selection. All these factors can be combined to elucidate individual mating behaviour profiles. The establishment of individual behavioural profiles for male mating behaviour in one species, the guppy, *Poecilia reticulata*, is the focus of this study; specifically, we ask whether individual male mating behaviour profiles show that males have consistent reproductive behaviour across contexts where the advantages of using alternative mating tactics differ. The frequency of both sneak mating and display behaviours varied between sex ratios. Male display and sneak frequency were highly repeatable and males maintained consistent rankings of behaviour under equal, male- and female-biased sex ratios. We conclude, therefore, that male guppies have individual mating behaviour profiles. The use of behavioural profiles fills a gap in the existing literature by allowing behaviours that are functionally related but not correlated, such as alternative mating behaviours, to be treated as an integrated unit.

Keywords: behavioural profiles; behavioural syndromes; consistency; constraints; guppy; male mating behaviour; mating tactics; personality; *Poecilia reticulata*; repeatability; sex ratio

Variation in the operational sex ratio (OSR), defined as the number of sexually active males divided by the total number of sexually active adults of both sexes (Emlen & Oring 1977, reviewed in Kvarnemo & Ahnesjö 1996), is known to affect mating behaviour (Andersson 1994; Kvarnemo & Ahnesjö 1996; Mills & Reynolds 2003). When one sex becomes a limiting resource for the other, members of the available sex will be compelled to modify their behaviour by engaging in increased competition for access to mates of the limiting sex and will therefore be under greater sexual selection (Emlen & Oring 1977). In species in which males compete for females, and where females exercise mate choice, this form of sexual selection acts on males. As the OSR deviates from equality, more intense mating competition is predicted (Kvarnemo & Ahnesjö 1996) such that at male-biased OSRs competing males will be under strong selective pressures (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996).

An additional consideration in some species is the existence of alternative mating behaviours (Andersson 1994; Andersson & Iwasa 1996; Gross 1996; Andersson & Simmons 2006). Coercive mating tactics and forced copulation, for example, are sexual selection mechanisms that are likely to be favoured when competitors show superior mate attraction capabilities (Andersson 1994; Clutton-Brock & Parker 1995; Andersson & Iwasa 1996). In the context of OSR, at female-biased sex ratios there is more opportunity for courtship and more choice over where to direct this courtship. At male-biased sex ratios, increased competition from other males influences mating decisions (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996; Jirotkul 1999). For example, a male-biased OSR induces a switch from courting to sneak tactics in the garter snake, *Thamnophis sirtalis parietalis* (Shine et al. 2003), while in the grey mouse lemur, *Microcebus murinus*, males

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engage in more mate searching and less mate guarding as the OSR becomes progressively male biased (Eberle & Kappeler 2004). Among fish many species show alternative mating behaviours (reviewed in Taborsky 1994; Henson & Warner 1997) that could potentially be affected by changes in the OSR. The European bitterling, *Rhodeus sericeus*, for example, exchanges territoriality and courtship to compete for matings in groups at male-biased OSRs (Mills & Reynolds 2003) and in the two-spotted goby, *Gobiusculus flavescens*, male–male competition is replaced by female–female competition as the sex ratio moves from male biased to female biased over the season (Forsgren et al. 2004).

The strength of selection is also affected by the consistency with which a trait is expressed (Boake 1989; Wagner 1998). Repeatability assesses how consistent or stereotyped individuals are in their mating behaviour (Lessells & Boag 1987; Boake 1989; Falconer & Mackay 1996). Several studies have examined the repeatability of mating behaviour. Female mate preferences are repeatable in the field cricket, *Gryllus integer* (Wagner et al. 1995), the grasshopper, *Chorthippus biguttulus* (Reinhold et al. 2002) and the guppy, *Poecilia reticulata* (Godin & Dugatkin 1995; Brooks 1996; Kodric-Brown & Nicoletto 1997, 2001). Other examples are reviewed in Bakker (1999) and Jennions & Petrie (1997). Repeatability of male mating behaviour has received less attention. Agonistic hisses have been shown to be repeatable in male Madagascan hissing cockroaches, *Gromphadorhina portentosa* (Clark & Moore 1995), and repeatabilities in the characters of the male courtship song in *Drosophila montana* and *Drosophila littoralis* have been illustrated (Aspi & Hoikkala 1993).

The guppy, *P. reticulata*, is a small, live-bearing fish that exists in dynamic schools in the rivers of Trinidad's Northern Range. Male guppies have two alternative mating behaviours, courting (sigmoid displays) or sneaking (gonopodial thrusts), and all males can use either behaviour at any time (Liley 1966; Farr 1989). Guppies have been studied extensively and many factors have been shown to influence the use of these alternative behaviours (see Houde 1997 for a review). Adult sex ratio varies in these populations (Pettersson et al. 2004); so males are likely to be adapted to accommodate this. Sex ratio has already been shown to affect male mating behaviour (Farr 1976; Jirotkul 1999). Farr (1976) found that males increased the frequency of displays in the presence of competitors. However, he only examined female-biased and equal sex ratios. Jirotkul (1999) investigated a range of OSRs and showed that the frequency of displays decreases at male-biased OSRs and sneak mating was most frequent at equal OSRs (Jirotkul 1999); while another study that examined both male- and female-biased sex ratios found no differences in either aspect of male behaviour (Head & Brooks 2006).

Surprisingly, despite the widespread attention received by the guppy mating system, to date no studies have assessed the consistency of individual male mating behaviour. Here, we aim to address this omission. Furthermore, combining the three aspects of sexual selection outlined above: variation in male mating behaviour with OSR, the existence of alternative mating behaviours that allow a choice between behaviours used in different circumstances, and the consistency or repeatability of male mating behaviour will allow males to be characterized in terms of individual mating behaviour 'profiles'. Specifically, through the establishment of these behavioural profiles, we investigate whether males have consistent reproductive behaviour across contexts where the advantages of using alternative mating tactics differ. Individuals frequently show limited behavioural plasticity and differ consistently in their response to environmental stimuli (Sih et al. 2004; Dingemanse & Réale 2005). This consistency has been used to form the framework for personality traits (e.g. Budaev 1997; Budaev & Zhuikov 1998; van Oers et al. 2004) and behavioural syndromes (Sih et al. 2004; reviewed in Dingemanse & Réale 2005). Unlike these concepts, behavioural profiles do not require correlations across situations and so allow behaviours that are functionally related, but not necessarily correlated, to be treated as an integral unit.

This study tests the hypothesis that male guppies have consistent patterns of mating behaviour that can be characterized as behaviour profiles. In line with OSR theory (Emlen & Oring 1977; Kvarnemo & Ahnesjö 1996), we expect sneak matings to predominate in male-biased OSRs and courtship behaviour to predominate in the female ones. However, importantly, we also predict that individual rankings in behaviour will be maintained both within and amongst sex ratio conditions. No a priori assumptions are made about correlations between behaviour types, that is, a high (or medium/low) level of display activity will not necessarily be correlated with a high (or medium/low) level of sneak activity.

METHODS

We collected fish from a 20-m stretch of the Arima River in Trinidad's Northern Range (from 10°41.5062′N, 061°17.5150′W to 10°41.3949′N, 061°17.4215′W obtained with a Garmin eTrex GPS, Garmin (Europe) Ltd., Southampton, U.K.) using a seine net. Fish were transported over a few hundred metres to their destination in covered buckets. They were allowed to acclimate in tanks for several days before experimentation, during which we measured the total length (TL) under light anaesthesia (MS222) to match the size of experimental males as closely as possible (TL: 21–24 mm). All fish recovered from being anaesthetized within a few minutes. We identified 39 experimental males by colour drawings of their individually unique colour patterns and housed these in two tanks. All other fish (67 females and 68 males) were placed in a stock tank. Observations were carried out in six experimental tanks (32 × 20 cm and 17 cm high) filled with 8 litre of river water treated with a water conditioner and an antifungal solution. Each tank had an air supply and a river gravel substratum. The fish were kept at an ambient temperature (around 22–25°C) and light regime (approximately 12:12 h light:dark cycle) and were fed on flaked fish food at least once per day.

Each evening we selected stock fish at random and added them to the six experimental tanks. The following morning, 1 h after being fed, we randomly selected experimental