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Early social experience significantly affects sexual behaviour in male guppies

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Studying the mechanisms by which immature males learn courtship behaviour is essential to our understanding of the evolution of different mating strategies, yet generally this has been neglected. Here I demonstrate an effect of early social experience on the sexual behaviour of male guppies, *Poecilia reticulata*. I tested whether the social rearing environment (visual access to females only, males only or both males and females) affects males' sexual performance, including the time and frequency of courtship displays and forced copulation attempt frequency. I conducted trials in which focal male guppies were allowed to interact with a female. Males that experienced early social interactions with mature males performed significantly longer courtship displays than males that grew up without observing other males. This result suggests that young males learn to court efficiently by observing other males courting. Males raised with females performed more forced copulation attempts, possibly because males might need to physically interact with females in order to learn to strategically alternate courtship displays and forced copulation attempts. Early social interactions may play a stronger role in the structure of the mating system in guppies than previously recognized, and might contribute to the differences in sexual behaviour observed between different populations of guppies.

Males are under strong selection to use a variety of strategies to encourage females to mate. Consequently, learning to perform both courtship and alternative mating strategies efficiently is fundamental to male mating success. Most arthropods, fish, amphibians and reptiles show innate species-specific sexual behaviours, so that normal courtship is expressed even when animals are raised in isolation (Burghardt 1973). Other animals, such as some birds, require exposure to conspecifics during a sensitive period to imprint signals used in their species, and show few subsequent modifications (Irwin & Price 1999). However, the acquisition of sexual behaviours can also be flexible. Learning, the change of behaviour caused by the integration of new information (Pearce 1997), allows animals to adjust their behaviour to current conditions (Galef & Laland 2005). For example, males may learn to court by individual experience (i.e. practice), by observing and interacting with conspecifics (i.e. social learning) or both (Freeberg 2000; Pfaus et al. 2001).

'Social experience' refers to the interactions an individual has with conspecifics (Freeberg 2000). Early experience with conspecific females can affect the efficacy of sexual behaviour in males of many taxa (fruit flies: Polejack & Tidon 2007; geckos: Sakata et al. 2002; sheep: Orihuela & Aguirre 2011). For instance, naïve isolated male quail, *Coturnix japonica,* usually fail to complete copulation at their first encounter with a female, but males previously exposed to females when they are young achieve successful copulations as well as sexually experienced males (Cornil & Ball 2010). Females strongly influence the development of courtship in males by reinforcing preferred sexual behaviours. For example, in brown-headed cowbirds, *Molothrus ater* (Miller et al. 2008), nonvocal stimulation (i.e. body movements and social interactions) by females allows males to recognize the elements in their songs that are more preferred by females; as a result, after experience with females, males increase their vocal improvisation during courtship (Miller et al. 2008). In other systems, experience with mature males is necessary as a source for learning courtship (Freeberg 2000). This is the case for most songbirds, in which immature males learn elements of songs from experienced males and this learning allows them to display courtship that is preferred by females (Payne & Payne 1993; Beecher et al. 1996; White et al. 2002).

Most studies of effect of social experience on male courtship development consider only acoustic signals in birds (Freeberg 2000; Galef & Laland 2005). This bias prevents us from recognizing how widespread social learning of courtship is among other animals. Additionally, one is restricted in the predictions that can be made regarding the presence or absence of social learning, and when present, what form of learning could be expressed based on the ecology, life history and social dynamics of a particular group of animals. Here, I used the guppy, *Poecilia reticulata*, to investigate how visual cues involved in early social experience affect the development of male sexual behaviour.

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Guppies are an ideal system for studying the effects of social experience. Complex social learning processes are known in different contexts, such as foraging, predation, migration and mating preferences (e.g. local/stimulus enhancement, social facilitation, observational conditioning; Dugatkin & Godin 1993; Brosnan et al. 2003; Kelley et al. 2003; Reader et al. 2003; Makowicz et al. 2010). Guppies are livebearers with a promiscuous mating system and strong sexual dimorphism (Houde 1997). Males devote most of their time to trying to inseminate females (Magurran & Seghers 1994). They can mate with a female's consent using courtship displays or by forcing copulations, and individual males usually do both (Liley 1966). Females prefer higher intensity courtship displays and attempt to avoid harassment by males (Houde 1997). Although there is a genetic basis for the ratio of consensual copulation attempts to forced copulation attempts (Evans 2010), different environmental and ecological factors determine how male guppies balance these two mating tactics (Farr 1976; Endler 1987; Rodd & Sokolowski 1995; Evans & Magurran 1999). The social context males experience also influences male sexual behaviour, particularly because females can store sperm from several males (Houde 1997), so high sperm competition is expected. Previous studies suggest that males increase their sexual activity in the presence of male competitors (Farr & Herrnkind 1974; Farr 1976; Evans & Magurran 1999; Magellan et al. 2005). However, these results contradict each other regarding which mating tactic (courtship or forced copulation attempt) is increased during high intrasexual competition. Farr (1976) and Farr & Herrnkind (1974) showed that when males interact with females only, the frequency of courtship displays is lower than when males interact with females and competitors. They interpreted this increase of courtship as a way for males to attract females when other males compete for the females' attention. Other results show that males reared in male-biased tanks perform fewer courtship displays and more forced copulation attempts in comparison with males reared in female-biased groups (Evans & Magurran 1999; Magellan et al. 2005).

Here I tested whether social rearing environment (visual access to females only, males only or both males and females) affects males' sexual behaviour. I hypothesized that immature males would develop their courtship displays more efficiently if allowed to observe the behaviour of mature males. Namely, the quality of the courtship display would be affected by having visual access to the courtship of adult males during development. I first predicted that young males without visual access to mature males during their development would perform less efficient courtship displays (e.g. shorter displays) at maturity than males that were able to observe mature males. I also predicted that number of courtship displays would be lower in the male treatment compared with the female and the mixed treatments, because such a pattern has been observed in males reared in male-biased groups (Evans & Magurran 1999). I also hypothesized that females would be able to modulate the sexual behaviour of immature males by approaching and interacting with the males that perform more courtship displays. I then predicted that young males housed with females would perform fewer forced copulation attempts than males in the other treatments, because females are attracted to higher frequencies of courtship displays (Houde 1997) and because males reared in female-biased groups tend to perform fewer forced copulation attempts than males reared in male-biased groups (Evans & Magurran 1999).

METHODS

Population and Fish Maintenance

I used third-generation wild-type guppies that were descendants of a population from a remote population in Alligator Creek, Bowling Green Bay National Park, Queensland (Queensland permit number WITK07655010), and that had been kept in John Endler's laboratory at Deakin University since September 2009. Alligator Creek guppies resemble, in coloration and mating preferences, guppies from low to medium predation sites in Trinidad (J. Endler, unpublished data) and were probably introduced in this remote site during the 1910s mosquito control programmes in Queensland. Stock male and female guppies were housed together in large aerated aquaria (90×60 cm and 30 cm high; ca. 200 individuals per tank) furnished with natural river gravel and they were maintained at 24 ± 1 °C under a 12:12 h light:dark photoperiod. Fish were fed twice a day ad libitum with live brine shrimp nauplii (*Artemia salina*), commercial flakes and home-made liver paste. All experimental tanks had clean gravel at the bottom and were filled with water taken from the stock aquaria, which ensured that the fish experienced the same conditions they were raised in during the trials. I obtained standard length measures by gently placing a fish against the glass of the aquarium using a soft net and measuring it with electric callipers against the glass; no anaesthetic was necessary and no signs of distress were observed as a result of this procedure. Stimulus fish were sexually mature and randomly selected from the population. At the end of all the trials, experimental fish were returned to the breeding stock tanks.

Experimental Design

In order to test whether early social experience affects male sexual displays, I tested males that were raised under three different social treatments. First, I isolated females from the population to collect their fry. After birth, young siblings were housed together with no contact with other fish until sexual identification was possible (ca. 4 weeks). At this time males begin the development of the gonopodium, a modified fin used to transfer sperm, although neither males nor females are sexually mature (Evans et al. 2002). From each litter (27 families in total), the first three brothers that showed signs of gonopodial growth were allocated to one of three treatments.

(1) Male treatment: focal males develop observing only adult males. In the absence of females, mature males court each other (Field & Waite 2004), so focal males in this treatment were exposed to high rates of courtship displays.

(2) Female treatment: focal males develop observing only adult females. Females do not perform courtship displays, so focal males were raised without visual access to courtship displays.

(3) Mixed treatment: focal males develop observing both male and female adults. Focal males in this treatment observed high rates of courtship displays (Farr & Herrnkind 1974; Magurran & Seghers 1994).

All treatments had three replicates (tank size 90×60 cm and 35 cm high, nine tanks in total) with nine small chambers (9×16 cm and 12 cm high) inside them. Each small chamber contained one focal immature male. Twenty stimulus fish were placed in the main tank and could swim freely around all small chambers (Fig. 1). The small chambers were covered on two sides to prevent focal males from seeing each other, and the two remaining sides were transparent, allowing males to see the stimulus fish when they were in the vicinity. I used three different batches of stimulus fish, replacing each batch of 20 fish every 2 weeks, for a total of 6 weeks of treatment (i.e. 60 stimulus fish in total per replicate tank). No data were collected during the treatment period. However, focal males in all treatments performed courtship displays during their development (P. Guevara-Fiore, personal observation), and only focal males in the male and mixed treatment were able to observe courtship displays from adult males (Magurran & Seghers 1994; Field & Waite 2004). At the end of the