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Strategic male signalling effort in a desert-dwelling fish

Bob B. M. Wong · P. Andreas Svensson

Abstract Males often use elaborate courtship displays to attract females for mating. Much attention, in this regard, has been focused on trying to understand the causes and consequences of signal variation among males. Far less, by contrast, is known about within-individual variation in signal expression and, in particular, the extent to which males may be able to strategically adjust their signalling output to try to maximise their reproductive returns. Here, we experimentally investigated male courtship effort in a fish, the Australian desert goby, *Chlamydogobius eremius*. When offered a simultaneous choice between a large and a small female, male gobies spent significantly more time associating with, and courting, the former, probably because larger females are also more fecund. Male signalling patterns were also investigated under a sequential choice scenario, with females presented one at a time. When first offered a female, male courtship was not affected by female size. However, males adjusted their courtship effort towards a second female depending on the size of the female encountered previously. In particular, males that were first offered a large female significantly reduced their courtship effort when presented with a subsequent, smaller, female. Our findings suggest that males may be able to respond adaptively to differences in female quality, and strategically adjust their signalling effort accordingly.

Keywords Male mate choice · Previous female effect · Sequential mate choice · Sexual selection · Signal honesty

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Introduction

Males often use elaborate ornaments and/or showy courtship displays to attract females for mating (Andersson 1994). The extent to which such traits are expressed can have a direct bearing on male reproductive opportunities, and is important in explaining differential male mating success (Wong and Candolin 2005). In many taxa, females often prefer individuals that exhibit the most exaggerated signals (Kokko et al. 2003). A central tenet in sexual selection theory is that choosy females use these signals to assess the quality of potential mates (Maynard Smith and Harper 2003). However, in order for such signals to be reliable, theory suggest that they must also be costly to produce and/or maintain so that only the 'best' males can afford the high cost of bearing the most spectacular ornaments and/or displays (Zahavi 1975, 1977; Grafen 1990; Walther and Clayton 2004).

Recent evidence, however, suggests that the condition dependence of sexual signalling is not always guaranteed (Badyaev and Duckworth 2003; Hunt et al. 2004), and that the extent to which signals are displayed can often exhibit remarkable variation, not only between, but also within, individuals (e.g. Candolin 2000a; Wong et al. 2007). Such plasticity can arise due to life-history tradeoffs between present and future signalling effort (Candolin 2000a, b; Polak and Starmer 1998), with the allocation of finite resources into current sexual advertisement being contingent upon future reproductive opportunities and/or survival (Kokko 1997). Investment by males into sexual advertisement may also occur in competition with other components of reproductive investment (e.g. parental care), and this, too, can have an important bearing on the extent to which signals are expressed (Qvarnström 1997; Kokko 1998; Griffith and Sheldon 2001). Despite this, phenotypic plastic-

ity in signal expression remains a largely neglected and understudied component of variation in sexual displays. This is surprising because, like the variation that can occur among individuals, an understanding of within-individual variation in signal expression is important for what it may reveal about the costs associated with, and the evolutionary potential of, sexual selection (Griffith and Sheldon 2001).

Few studies have explicitly considered male mate choice as a potential source of within-individual variation in male sexual displays. This is true despite the fact that males are known to respond adaptively to both the costs and benefits of being choosy, and are capable of allocating their mating effort accordingly across a wide range of contexts (Engqvist and Sauer 2001; Wong and Jennions 2003; Byrne and Rice 2006). For instance, in many taxa, male courtship can often be energetically taxing to perform (Kotiaho et al. 1998; Judge and Brooks 2001), sperm can be costly to produce (Dewsbury 1982; Galvani and Johnstone 1998) and male mating attempts can sometimes result in serious injuries or even death (Stuart-Fox and Whiting 2005; Kasumovic et al. 2007; Woods et al. 2007). Given that females may often vary considerably in reproductive value (Côte and Hunte 1989; Katvala and Kaitala 2001), males should try to maximise their reproductive returns by signalling strategically in response to differences in perceived female quality and direct greater courtship effort towards more 'attractive' suitors (Reading and Backwell 2007). Here, we experimentally investigate male mate choice and within-individual variation in male courtship effort in the Australian desert goby, *Chlamydogobius eremius*.

The Australian desert goby is a remarkable freshwater fish endemic to the Lake Eyre Basin of Central Australia. This small (<6 cm), colourful species is locally abundant throughout its range where it inhabits both permanent and temporary bodies of water, from spring-fed pools to ephemeral desert streams (Allen et al. 2002). Males establish nests under rock crevices in shallow water and attract passing females using elaborate courtship displays involving the blackening and raising of the male's dorsal and anal fins. These vigorous fin flaring displays may, in addition, be accompanied by occasional jerky body movements. If a male is successful in his efforts, the female will follow him to the nest where she will deposit her eggs. After spawning, males assume exclusive care of the developing brood. Several aspects of the natural history of desert gobies make them ideal subjects for investigating individual variation in male signalling effort. First, male courtship displays are highly conspicuous, vigorous and easy to quantify. Second, males are likely to benefit from being choosy, with larger females capable of producing a larger clutch (Glover 1973). In addition, as in other gobies, paternal care is likely to be energetically taxing (Reynolds

and Jones 1999), with the demands of care compounded by the extreme environment in which the species occurs (Thompson and Withers 2002). Male investment in reproduction is, for these reasons, likely to be quite substantial. Accordingly, the aim of this study is to test whether male gobies are capable of allocating their courtship effort strategically. In particular, we ask the following: (1) do males, when given the opportunity, preferentially court larger females, and (2) do they adjust their signalling output depending on the quality of females encountered previously?

Methods

Collecting and housing

Desert gobies were collected from the Neales River in South Australia and transported back to the laboratory where they were housed in separate-sex aquaria kept at a temperature of 24–26°C on a 12-h light:dark cycle. Tanks were filled to a depth of 15 cm with water maintained at a salinity of 5‰ to mimic field conditions (using Coralife Scientific Marine Grade Salt, ESU Inc., USA). Salt levels were monitored weekly with a Hanna H198130 conductivity meter and, if necessary, adjusted to achieve the desired concentration by the addition of either salt or filtered tap water. Sexually mature males—identified by their nuptial colouration—were kept in individual aquaria measuring (length × width) 30×20 cm. Each male was provided with his own nest in the form of a 9-cm-long PVC pipe (3 cm diameter) positioned horizontally in the middle of the aquarium on top of a fine layer of gravel. Each pipe was capped at one end with the opening facing the front of the tank. The pipe was anchored in place by securing it onto a piece of ceramic tile that was buried into the substrate. Adult females were kept together in several large holding tanks (length×width=60×45 cm) with a gravel substrate, rocks and plastic plants for cover. All fish were fed daily on a diet of commercially prepared pellets and frozen *Artemia*.

We conducted two separate experiments to investigate male signalling effort (Fig. 1). In experiment 1, we tested male ($N=16$) association time and courtship effort when presented simultaneously with two females in a dichotomous choice design (Fig. 1a). This was achieved by introducing a large and a small stimulus female into individual compartments inside a small aquarium positioned at the front of the male's tank. The mean total length (±SD) of large and small females was 48.2±3.8 and 38.2± 1.3 cm, respectively. The two females were separated using an opaque plastic partition to prevent any contact with one another. The male, however, was able to see and interact with both females. Before the commencement of the trial, a
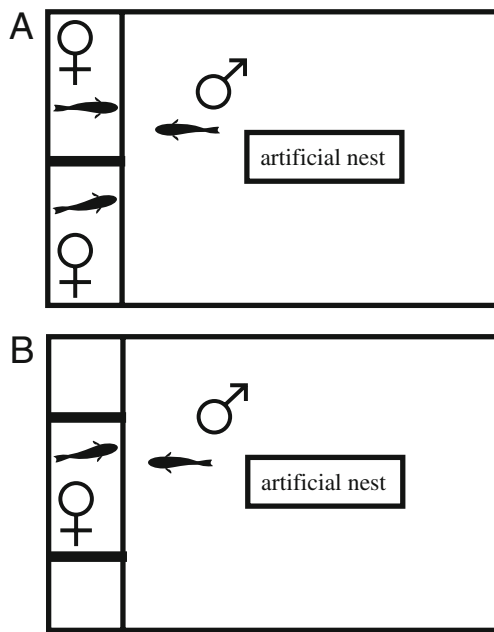
Fig. 1 Experimental set up for the **a** simultaneous and **b** sequential choice experiments

sheet of black plastic was inserted between the male and female tanks to prevent visual contact. After a 5-min acclimation period, the sheet was removed. We then quantified male courtship effort directed towards each of the two stimulus females. This was achieved by conducting spot samples every 10 s over a 10-min period. During each spot sample, we noted whether the male was associating with a particular female and, if so, which one. A male was recorded as associating with a particular female if he was within 5 cm of her compartment, with his body oriented unambiguously towards her (Wong and Jennions 2003). We also recorded whether the male was engaged in courtship behaviour (i.e. fin displays) towards the female. At the end of the trial, we tallied the total number of times the male was associating with, and courting, each female as a measure of his mate choice and signalling effort.

In experiment 2, we quantified male signalling effort when large and small females were presented in a sequential manner ($N=16$). Such a design was chosen to more closely reflect patterns of mate encounters in nature, since the opportunity for a simultaneous comparison of potential mates is often limited (Wong et al. 2004). Here, we were interested in investigating male signalling effort when females were encountered one at a time (Fig. 1b), and whether males adjusted their signalling output depending on the size of the female encountered previously ("previous female effect" *sensu* Wong et al. 2004). The experimental procedure was similar to that of the previous experiment.

Before the trial, individuals were visually isolated from one another using an opaque sheet and allowed to acclimate for 5 min. We then removed the sheet and recorded, during 10-s spot samples taken over a 10-min period, the number of times the male was observed associating with, and courting, a stimulus female. After this, we reinserted the sheet between the male and female compartments, removed the first stimulus female and replaced her with another. Ten minutes after the first female presentation, we repeated the acclimation and sampling procedure using the second stimulus female. We randomly assigned half of the males to be presented with a large female first followed by a small female, while the remainder were presented with females in the reverse order. From this, we were able to compare the amount of time males spent associating with, and courting, large and small females. In this experiment, the mean total length ($\pm$SD) of large and small females was 49.7$\pm$3.0 and 39.0$\pm$1.5 cm, respectively.

Statistical analyses

Both experiments were analysed using mixed models. In experiment 1 (simultaneous presentation), female size was entered as a fixed factor, and male ID as a random factor. In experiment 2 (sequential presentation), both female size and presentation order were entered as fixed factors to allow analysis of the interaction between female size and presentation order. Male ID was entered as a random factor. Time spent associating and number of courtship displays were arcsine square-root transformed prior to analysis, whenever this improved the normality of the residual errors (Crawley 2002). Models were fitted using maximum likelihood (ML), and likelihood ratio (G^2) tests were used to calculate P values of interaction terms (Quinn and Keough 2002). Estimates are presented as mean$\pm$1 SE.

Results

When presented with a simultaneous choice between a large and a small female, male desert gobies spent significantly more time associating with the larger female ($t_{15}=2.27$, $P=0.039$; Fig. 2a). Males also performed more courtship displays towards the large female ($t_{15}=4.01$, $P=0.001$; Fig. 2b).

In the sequential preference trials, we found a significant interaction between female size and presentation order on male association time ($G^2=9.0$, $P=0.003$) and courtship displays ($G^2=8.9$, $P=0.003$). During the first female presentation, there was no difference in response between males that had been offered a large female versus those that had been given a small female (association time: $F_{1, 14}=$
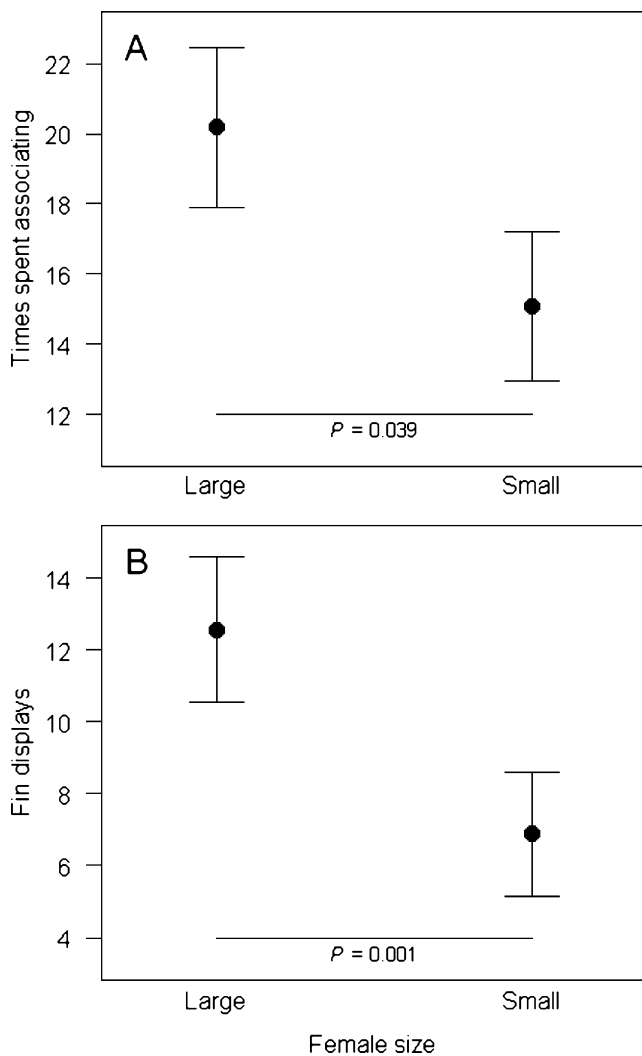
Fig. 2 Mean ± SE time spent **a** associating with, and **b** courting, large and small females during simultaneous choice trials

Discussion

Male desert gobies appeared to strategically allocate their courtship effort in response to variation in female quality. In our first experiment, when presented with a simultaneous choice between two females differing in body size, we found that male gobies preferentially spent more time courting the larger female. Since female body size is correlated positively with fecundity in desert gobies (Glover 1973), males are expected to benefit by mating with larger females (Candolin and Wong 2008). Courtship, in this regard, is an important signal in mate attraction, with female gobies preferring vigorously courting males (e.g. Forsgren 1997; Takahashi and Kohda 2004). Hence, it would befit a male to invest greater effort into courting a
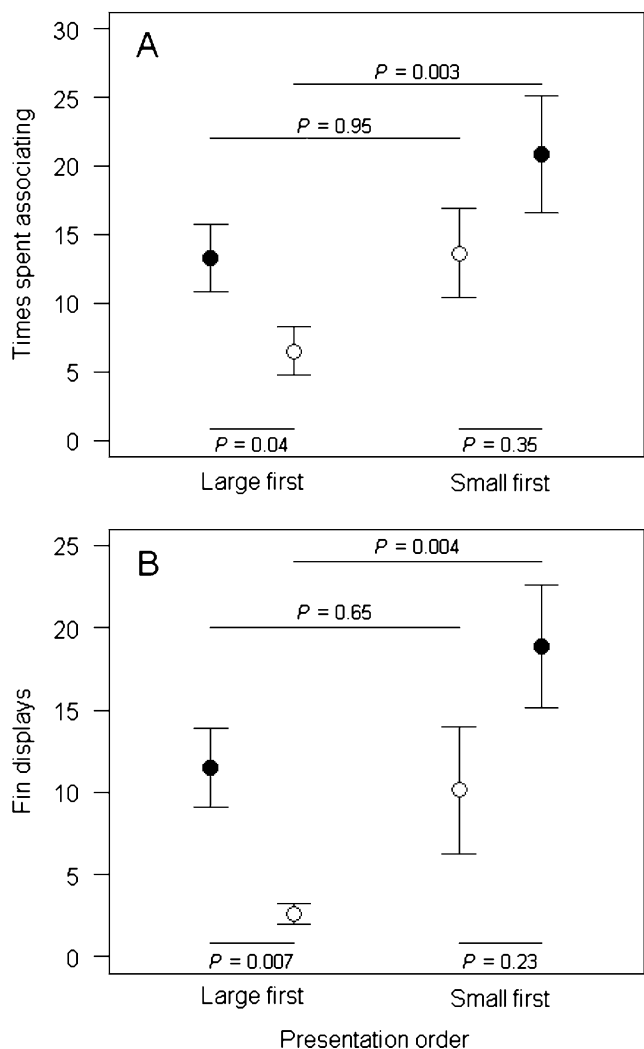

Fig. 3 Mean ± SE time spent **a** associating with, and **b** courting, large (*filled symbols*) and small (*open symbols*) females during sequential choice trials

0.004, P=0.95; courtship: $F_{1, 14}$=0.22, P=0.65, Fig. 3). However, during the second female presentation, males offered a large female spent more time associating with and courting that female compared to those with a small female (association time: $F_{1, 14}$=5.89, P=0.003; courtship: $F_{1, 14}$=12.07, P=0.004, Fig. 3). Males, in this regard, were adjusting their behaviours in the second presentation depending on their experiences during the first. Specifically, males that were initially offered a large female reduced their association time (t_7=2.52, P=0.04; Fig. 3a) and courtship displays (t_7=3.78, P=0.007; Fig. 3b) upon presentation of the subsequent smaller female, whereas those that had been offered females in the reverse order (i.e. small first, large second) did not significantly change their response (association time: t_7=0.99, P=0.35, Fig. 3a; courtship displays: t_7=1.31, P=0.23, Fig. 3b).

larger female in order to increase his chances of securing her as a mate.

In nature, however, the opportunity for a simultaneous comparison of potential mates can often be limited (Sæther et al. 2001; Forbes et al. 1996). Male desert gobies defend and guard nests under rock crevices and must therefore rely on females to visit their territories. Under such a scenario, males may seldom encounter more than one mate-searching female at a time. Our second experiment was designed to explore male signalling effort under a more natural situation in which females were encountered in a sequential manner. Here, when males were first presented with a female, they courted females regardless of their size. This result is concordant with those reported in sticklebacks, *Gasterosteus aculeatus* (Rowland 1982), salamanders, *Desmognathus santeelah* (Verrell 1995) and fiddler crabs, *Uca mjobergi* (Reading and Backwell 2007). Together, these studies underscore the possibility that even though larger females may represent better reproductive value, males should not necessarily forego the opportunity to attract a 'less preferred' female. Here, the context of potential mate encounters is important, and any courtship effort invested into the present female may also depend on the perceived probability of encountering additional, higher quality females in the future (Wong et al. 2004).

Our results suggest that the quality of the previous female (and hence the order of female presentation) can also be important. Males that initially courted a large female subsequently spent less time courting the smaller female. This decrease is unlikely to be caused by male exhaustion or differences in female behaviours, because males that first encountered a small female did not significantly change their courtship intensity when subsequently offered a larger female.

So why should responsiveness to potential mates be affected by the order of encounter? Studies of sequential female choice have shown that mate-searching females are sensitive to the local distribution of male quality (Bakker and Milinski 1991; Bateman et al. 2001; Pitcher et al. 2003), and have the capacity to adjust their reproductive decisions depending on the attractiveness of the male encountered previously ("previous male effect", *sensu* Bakker and Milinski 1991). Since females increase their reproductive success by maximising the quality of their mating partners (Bateman 1948), it makes sense for females to respond in this way to avoid ending up with a low quality mate in a population of high quality suitors (Milinski 2001). But what about males?

Because males are expected to maximise their reproductive success by increasing their number of mating opportunities (Bateman 1948), previous encounters with potential mates are predicted to have less of an effect on males than on females (Wong et al. 2004). In the Pacific blue eye fish,

Pseudomugil signifer, the size of the female encountered previously had no effect on the amount of effort invested by males into subsequent courtship attempts (Wong et al. 2004). Similarly, in crickets, *Gryllus bimaculatus*, males that had merely courted (but not mated) with previous females did not adjust their courtship investment when exposed to subsequent females of different size (Bateman and Fleming 2006). Male crickets, however, became far more discerning if they had mated previously, suggesting that costly reproductive investment can have an important bearing on male behavioural decisions. In gobies, a significant investment of male reproductive effort goes into paternal care. Males, for example, tend to their clutch by removing waste and debris, and actively fan the brood to direct oxygenated water over the developing embryos (Lindström 1998; Lissåker and Kvarnemo 2006; Skolbekken and Utne-Palm 2001). Evidence from other gobies has shown that low oxygen levels (Reynolds and Jones 1999; Lissåker et al. 2003) and higher water temperatures (Skolbekken and Utne-Palm 2001) can increase the burden of care for egg-tending males. Desert gobies, in this regard, inhabit an extreme environment characterised by high temperatures, variable salinity and low oxygen conditions (Thomson and Withers 2002). As a result, it may be especially important for males to be able to fine tune their courtship effort according to the local distribution of female quality to try to maximise their reproductive returns. Our findings, in this regard, are comparable to those reported recently in a fiddler crab, *U. mjobergi*, where high mating investment—through prolonged mate guarding—resulted in similar strategic adjustment of male courtship displays (Reading and Backwell 2007).

In conclusion, male choice can be an important source of variation in the expression of sexual displays in desert gobies, with males adjusting their courtship effort in response to differences in female quality. The implication that this may have for female fitness is unknown. However, if sexual signals are important indicators of male quality, and if females prefer intensively courting males, variation in male signal expression can potentially undermine signal reliability (Wong and Candolin 2005). Accordingly, it is important to try to understand the causes and consequences of signal variation within males. Like the variation that can occur among individuals, plasticity in the expression of sexual signals has the potential to influence the power of selection (Griffith and Sheldon 2001) and, as a result, warrants greater empirical attention.

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