Animal Behaviour 83 (2012) 1153–1161

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Signal value of male courtship effort in a fish with paternal care

Topi K. Lehtonen*

Section of Ecology, Department of Biology, University of Turku, Turku, Finland

ARTICLE INFO

Article history:
Received 14 November 2011
Initial acceptance 20 December 2011
Final acceptance 9 January 2012
Available online 9 March 2012
MS. number: 11-00915

Keywords:
courtship behaviour
mate preference
Pomatoschistus minutus
repeatability
sand goby
sexual selection
sexual signalling
signal reliability

Male courtship behaviour is known to correlate with body condition and other aspects of male phenotypic or genetic quality. Females often prefer males that express the most intense or elaborate displays, although recent findings indicate that this should not always be the case; males may be strategic in their courtship displays, signal dishonestly or deplete their energy reserves with intense courting. To study reliability of courtship effort as a mate choice signal, I assessed multiple aspects of male courtship using wild-caught sand gobies, *Pomatoschistus minutus*, in a controlled laboratory setting. I found consistent and repeatable between-male differences in courtship. However, females did not show a significant preference for males that courted intensively. Furthermore, other assessed male traits with a previously demonstrated role in sexual selection were not correlated with courtship effort. This indicates that courtship displays did not reliably signal male quality. The results also suggest that even when courtship has potential to convey useful information, females may have to trade between courtship and other cues they use in mate choice. Hence, to gain a more complete understanding of the selection regime acting on male courtship behaviour, and female preference for it, one should simultaneously investigate multiple factors that can affect female mating behaviour.

Intense courtship displays commonly increase male reproductive success (Andersson 1994; Kokko et al. 2003). In many species, females are known to prefer males expressing the most intense or elaborate displays, while male courtship effort, in turn, may correlate with a male's phenotypic or genetic quality (Andersson 1994; Kokko et al. 2003). For example, in a bird of prey, the northern harrier, *Circus cyaneus*, males in good condition exhibit more vigorous aerial displays and attain larger harems than males in poorer condition (Simmons 1988). Similarly, acoustic courtship vocalizations indicate male (genetic) quality in, for example, the fruit fly *Drosophila montana* (Hoikkala et al. 1998) and tree frog *Hyla versicolor* (Welch et al. 1998). In general, courtship behaviour is likely to be costly in terms of energy expenditure (Kotiaho et al. 1998; Judge & Brooks 2001) or predation risk (Lima & Dill 1990; Magnhagen 1991; Hoefler et al. 2008), and given that individuals differ in their ability to pay these costs, courtship effort is often assumed to be condition dependent (see Zahavi 1977; Grafen 1990; Johnstone 1995; Cotton et al. 2004).

Recent findings, however, indicate that courtship displays may not always reliably signal good condition or high quality of the male. For example, males may signal dishonestly when survival prospects are grim (i.e. as a terminal effort, see Kokko 1997, 1998; Polak & Starmer 1998; Candolin 1999; Kelly & Alonzo 2010), or when given an opportunity to escape social pressures that would otherwise enforce signal honesty (Wong et al. 2007). Moreover, the relationship between male courtship effort and body condition is not always positive, especially if intensively courting males deplete their energy reserves, which may have a negative impact on, for example, their parental quality (von Hippel 2000; Svensson et al. 2004). To regulate the costs of sexual signalling, males may also strategically adjust their courtship effort. For instance in the fiddler crab *Uca mjobergi*, males preferentially court larger females under both natural and experimental conditions (Reading & Backwell 2007). Indeed, various sources of within-individual variation in courtship effort may lower reliability and repeatability of courtship behaviour (Bell et al. 2009). Furthermore, courtship effort may sometimes be negatively correlated with other male traits that indicate mate quality or are otherwise attractive (Reynolds 1993; Cotar et al. 2008), resulting in a loose, or even nonexistent, relationship between courtship effort and male attractiveness or 'quality'. Finally, even when courtship honestly signals male vigour, females may be better off mating with males exhibiting only medium levels of courtship intensity, especially if vigorous males are also the most aggressive. For example in bowerbirds, *Ptilonorhynchus violaceus*, females sometimes flee when male courtship intensity gets too high (Patricelli et al. 2002).

* Correspondence: T. K. Lehtonen, Section of Ecology, Department of Biology, 20014 University of Turku, Turku, Finland.
E-mail address: topi.lehtonen@utu.fi.

0003-3472/$38.00 © 2012 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2012.01.040

Clearly then, there is no simple and general answer to the question of whether or not females should be attracted to vigorously courting males. Therefore, research efforts should focus on establishing when and why females should (or should not) prefer intense male courtship. To progress towards this goal, several aspects affecting reliability of the courtship signal should be simultaneously assessed within a single study system. To date, however, there has been a general lack of studies taking such a comprehensive approach. The aim of the current study was to redress this gap. This was achieved through a series of complementary laboratory-based assessments, using, as the model system, the sand goby, *Pomatoschistus minutus*, an increasingly popular fish species in sexual selection studies (Amundsen 2003). First, by testing a large number of males repeatedly within a short time frame, I examined whether males differ consistently in their courtship activity. Second, I explored whether males adjust their courtship effort according to female identity (sensu Wong & Svensson 2009; Lehtonen et al. 2011). This was assessed by allowing focal males to court not only the same females repeatedly but also different females in succession. Third, I examined the relationship between male courtship effort and other male attributes that are known to be relevant in the context of sexual selection, such as body size (Andersson 1994), nest appearance (Hoi et al. 1994; Östlund-Nilsson 2001; Olsson et al. 2009; or male attributes correlated with nest appearance, see Lehtonen & Wong 2009), and body condition (Hamilton & Zuk 1982; Milinski & Bakker 1990; Rowe & Houle 1996; Tomkins et al. 2004). Fourth, I inspected whether courtship intensity has the potential to signal benefits to the female, in terms of survival of the female's eggs, tended by the male, or the male's egg-tending rate (Pampoulie et al. 2004; Lindström et al. 2006). Finally, I tested whether sand goby females choose males based on their courtship effort.

METHODS

Model System

The sand goby is a small, widely distributed littoral fish (Baltic Sea: Jansson et al. 1985; Zander 1990; Sundell 1994; European side of Atlantic: Fonds 1973; Hesthagen 1977; Mediterranean Sea: Bouchereau & Guelorget 1997), which occupies a range of habitats (Zander 1990; Forsgren et al. 1996; Bouchereau & Guelorget 1997; Lehtonen & Lindström 2004). The species is an excellent model for studies of sexual selection and, in particular, courtship behaviour. First, its small size, ease of captive breeding and capacity to display natural behaviours in captivity make it ideal for laboratory studies. Second, the species is sexually dimorphic with males engaging in elaborate courtship displays, which have the potential to convey useful information about male quality. Specifically, after a male has established a nest under a suitable object, such as a mussel shell or flat rock (Lehtonen & Lindström 2004), it relies on conspicuous, potentially taxing displays (Svensson et al. 2004) to attract passing females for mating. The courtship displays involve erect fins, body shakes, 'displacement fanning' and movements leading towards and into the nest (Saaristo et al. 2009; T. K. Lehtonen, personal observations). A male successful in mate attraction cares for the eggs deposited in his nest. Some males manage to complete multiple breeding cycles during their single, prolonged breeding season (Healey 1971; Fonds 1973; Kvarnemo 1997), resulting in potential trade-offs between investment in current and future parental care and sexual signalling effort.

Study Site and Animal Care

The study was conducted at the Tvärminne Zoological Station (University of Helsinki), southern Finland (59°50.7′N, 23°15.0′E), during the sand goby breeding season (May–July) in 2005. Sand gobies were caught in shallow sand bottom areas near the station using a hand-trawl and dip nets. During a short (approximately 30 min) transport to the station, fish were kept in insulated 50 litre plastic tubs (coolers), filled with water to a depth of 30 cm. At the station, fish were separated by sex and distributed among several stock aquaria (ca. 100 litres), each of which contained on average 25 individuals. These stock tanks, as well as aquaria used for the experiments, were housed under natural light and supplied with a continuous through-flow of sea water, ensuring natural water conditions. Fish in stock tanks were fed twice a day ad libitum with frozen chironomid larvae, and occasionally with live *Neomysis integer* shrimps. All fish were measured (total length) and males were also weighed immediately prior to experimentation. Only males that had exhibited a high breeding motivation, as revealed by the construction of a nest, were used in the experiment. Females used as stimuli were ripe with eggs (as determined by their distended bellies) and were ready to spawn (see e.g. Lehtonen & Lindström 2008). To measure body lipid content, 63 focal males were killed (see below for details). The rest of the fish were either used for other, unrelated research, or released back to their natural habitat after the experiment.

All animal experimentation in this study was conducted under permit 'HY 84–2003' from the animal experimentation committee of the University of Helsinki.

Experimental Design

Tanks used for the experiment

Before the onset of the experiment, male sand gobies were introduced into individual compartments (measuring 20 × 25 cm) containing a halved clay flowerpot (diameter: 6 cm) as a nest (Fig. 1a). The entrance of the nest was positioned to face a small (6.5 × 25 cm), adjoining female compartment (Fig. 1a), separated by a transparent Plexiglas divider with holes for water exchange between the compartments. Sea water was pumped into the male compartments and flowed out via the female compartment. The bottom of the tanks

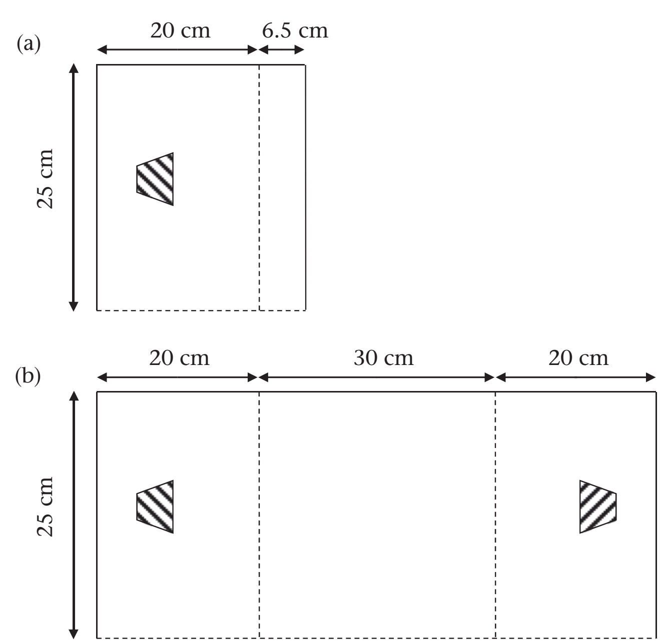

Figure 1. Tank design for (a) courtship measurements and (b) assessment of female preferences. Solid lines indicate opaque walls and dashed lines transparent walls. The hatched object indicates an artificial nest site (diameter: 6 cm).