



Do operational sex ratio and density affect mating behaviour? An experiment on the two-spotted goby

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Males generally compete for females through courtship and aggression (conventional sex roles). However, sex roles are reversed in some species and can even vary between populations or over time within a single species. The operational sex ratio (OSR), the sex ratio of ready-to-mate individuals, is a central factor proposed to explain the strength and direction of mating competition. Density can both act as a cue for OSR and have its own effects on competition. In the two-spotted goby, *Gobiusculus flavescens*, a seasonal switch in sex roles coincides with a change in OSR from male to female biased and a decrease in male density. This dynamic system provides an ideal opportunity to test the effects of OSR and density on competitive behaviour experimentally. In an aquarium experiment, we created two different sex ratios at two different densities and observed courtship and agonistic behaviour in both sexes. We changed sex ratio to equality after 4 days of treatment, to test for a lag in the behavioural response. Contrary to our predictions, males courted more after prolonged exposure to a female-biased sex ratio, although we also found a tendency for a positive effect of male density on male courtship frequency. We did not find any other effects of treatment on either male or female behaviour. Furthermore, we did not find evidence for a lag in the response to a change in density or sex ratio. We conclude that OSR and density did not affect individual frequencies of behaviour in the expected direction.

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Sexual selection drives the evolution of many striking traits and can conflict with natural selection (Darwin 1871). One of the driving forces behind sexual selection is the competition for mating opportunities (Darwin 1871; Andersson 1994). Mating competition is generally stronger in one sex than in the other, leading to fixed sex roles. These can be either conventional, where males compete for females, or reversed, where females compete for males (Trivers 1972; Andersson 1994). In some species, mating competition varies over time or between populations and dynamic sex roles have been found (insects: Gwynne 1984, 1985; fishes: Forsgren et al. 2004; Shibata & Kohda 2006). Such systems provide unique opportunities to study the factors affecting the strength of mating competition in both sexes.

It is generally agreed that selection pressures promoting competition are similar for both sexes. Mating competition arises if the availability of the opposite sex limits the production of offspring (Emlen & Oring 1977; Clutton-Brock & Vincent 1991). The level of competition in each sex should therefore depend on the ratio of ready-to-mate males to ready-to-mate females, known as the operational sex ratio (OSR; Emlen 1976; Emlen & Oring 1977). The OSR is modified by two principal factors: first, the adult sex ratio (ASR) or, more precisely, the sex ratio of qualified-to-mate individuals in a population (Ahnesjö et al. 2001) and second, the sex difference in potential reproductive rate (PRR; Clutton-Brock & Vincent 1991), defined as the maximum number of offspring that an average parent can produce per unit time if access to mates was not limited (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992). The higher the PRR, the sooner an individual is ready to mate again. The ASR and PRR in their turn could be influenced by differences in parental investment (Trivers 1972) and costs of reproduction (Kokko & Monaghan 2001), although a difference in relative costs of reproduction between the sexes could also affect competition directly (Trivers 1972; Emlen & Oring 1977; Kokko & Monaghan 2001).

Same-sex and opposite-sex densities are inherently correlated with OSR and may thus be used as a cue to changes in OSR, and

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hence which behaviour to adopt. On the other hand, same-sex density could also affect behaviour directly, for example by increasing the level of competition simply by increasing the encounter rate of competitors, while opposite-sex density could, for example, lead to the aggregation of potential mates, affecting the opportunity for monopolization (Kokko & Rankin 2006). It is therefore interesting to distinguish between the effects of OSR and density of each of the sexes on mating behaviour. Teasing apart these effects can be difficult, but can be achieved statistically as an interaction effect of OSR and total density.

The OSR correctly predicts existing sex roles in several species (e.g. Vincent et al. 1994; Thomas & Manica 2005; Sogabe & Yanagisawa 2007). Furthermore, field studies have revealed that OSR correlates well with changes in the strength and direction of mating competition and associated behaviours within species in a wide range of taxa, such as birds (Colwell & Oring 1988), fish (Vincent et al. 1994; Borg et al. 2002; Forsgren et al. 2004) and rodents (Schwagmeyer & Brown 1983; but see Davis & Murie 1985; Michener & McLean 1996). While these field studies clearly show a link between OSR and competitive behaviour, causality is often easier to demonstrate in laboratory manipulations, especially when there are confounding factors that may affect behaviour and covary with OSR, such as food availability (Kim & Choe 2003; Kolluru et al. 2007), time of season (Goldman et al. 2004), temperature (Denoël et al. 2005; Silva et al. 2007) and density of same-sex or opposite-sex individuals (Spence & Smith 2005; Smith 2007).

Until now, surprisingly few laboratory studies have investigated the effect of OSR on competitive behaviour while controlling for confounding factors, and the results are inconsistent (e.g. Kvarnemo et al. 1995; Grant et al. 2000; Spence & Smith 2005; Head et al. 2008). A potential explanation for the variation in these results may be that different species react differently to a change in the OSR. For example, males can resort to more sneaking and less courtship in highly competitive situations, as shown in, for example, the garter snake, *Thamnophis sirtalis parietalis* (Shine et al. 2003) and the Amur bitterling, *Rhodeus sericeus* (Mills & Reynolds 2003). A combination of field and laboratory studies in a range of species would thus be needed to assess whether these are differences between species or between situations.

Most empirical work on mating competition has focused on the more competitive sex (but see Kvarnemo et al. 1995), justifiably, because the behavioural changes in the dominant sex can be expected to be more obvious and easier to test. However, OSR theory explains the behaviour of both sexes by the same processes and changes in sex roles may depend on an interaction between the behavioural changes in both sexes. Additionally, the behaviour of one sex could be strongly related to the behaviour of the other sex. Hence, there is a need for studies that analyse behavioural responses simultaneously in the two sexes.

What cues animals use to assess OSR is not known, nor whether there is a time lag in the behavioural response to a change in the OSR. In the field, local OSR may fluctuate on an hourly basis, while the overall population OSR may be fixed or change more slowly, rendering it advantageous to delay the response to a sudden change in OSR or to adopt Bayesian updating (McNamara & Houston 1980; Stephens & Krebs 1986). Such a lag could make it harder to find effects of experimental treatments, especially when the treatment time is short or when OSR changes during treatment. Such a change in OSR could, for instance, occur if free interaction between the sexes results in mating, removing one or both mated individuals from the pool of ready-to-mate individuals.

Two-spotted gobies, *Gobiusculus flavescens*, are an excellent model system for the study of factors controlling the strength of mating competition. Unlike in most species, sex roles are not fixed. Instead, they switch from conventional to reversed during

a breeding season, coinciding with, although slightly lagging behind, a change in OSR from male to female biased, caused by a dramatic decrease in male density (Forsgren et al. 2004). This suggests an unusual flexibility in the behavioural patterns of both sexes, possibly caused by changes in OSR or male density. Furthermore, both males and females have ornaments, indicating that sexual selection is acting on both sexes (e.g. Amundsen & Forsgren 2001; Svensson et al. 2009). In this study we experimentally tested the effects of OSR and density on competitive behaviour (courtship and aggression) in both sexes and over several days. A previous field study found that males showed more courtship and agonistic behaviour in a high male density, male-biased situation, while females showed more courtship and agonistic behaviour in a low male density, female-biased situation (Forsgren et al. 2004). Therefore, depending on which of the cues they react to, we expected males to compete more in either high male density or male-biased treatments or both, and females to compete more in low male density or female-biased treatments or both. Additionally, we tested for a lag in the behavioural response to a subsequent change in sex ratio. To our knowledge, this is the first study to explore the effects of OSR on competitive behaviour in a laboratory setting in a species where a change in behaviour with OSR has been found in the field.

METHODS

Model Species

The two-spotted goby is a small marine fish, common along the coast of Europe from northwest Spain to northern Norway. It typically lives only a year. During its breeding season (May–July in our study area) it inhabits shallow waters along rocky shores, where nonbreeding individuals often form semipelagic foraging shoals (Miller 1986; Svensson et al. 2000). Breeding males defend a nest in empty blue mussel, *Mytilus edulis*, shells, in crevices, or in brown algae (*Saccharina latissima* and *Laminaria digitata*). Females visit males to spawn, and the male provides all parental care, defending the nest and cleaning and aerating the eggs until they hatch (Skolbekken & Utne-Palm 2001). Males care for clutches of up to six different females simultaneously (Mobley et al. 2009). Females generally lay all eggs of one clutch in the same nest (Skolbekken & Utne-Palm 2001). Both males and females have ornaments, which they emphasize in courtship. Males have coloured fins and an iridescent blue pattern on their body, whereas females develop bright orange bellies during egg development (Amundsen & Forsgren 2001; Svensson et al. 2006).

Experimental Design

Our experiment ran from May until July 2006 at the The Sven Lovén Centre for Marine Sciences at Kristineberg, situated on the west coast of Sweden (58.15°N, 11.27°E). Treatments were designed to investigate OSR and density effects on mating behaviour. We created two different sex ratios at two different densities, resulting in four treatments: 8:4, 4:2, 4:8 and 2:4 males:females adult sex ratio (Table 1). Treatments lasted for 4 days. After 4 days, we exposed two males and two females from each treatment to an equal sex ratio treatment (2:2) for another day, to test for a potential lag in the response to the social environment, that is, whether the response to the previous treatment was preserved.

Fish Collection and Husbandry

All fish were caught by snorkellers with hand-held dip nets around islands up to 3 km from the research station. We stored the

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