



## Intrasexual competition and courtship in female and male Japanese medaka, *Oryzias latipes*: effects of operational sex ratio and density

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Most studies of intrasexual mating competition have focused only on males, and have typically shown an increase in aggression and a decrease in courtship rate with increasing operational sex ratio (OSR), the ratio of ready-to-mate males to females. We manipulated the number of males (1, 2 or 4) and females (2, 4, 8 or 16) in a factorial design to investigate mating competition and courtship rate in Japanese medaka, a species with conventional sex roles, over a broad range of OSRs (0.0625 to 2), and in relation to the density of both sexes. As predicted, the rates of intrasexual interactions by both males and females increased with the number of competitors and decreased with the number of potential mates, whereas the rates of courtship decreased with the number of competitors and increased with the number of mates. At OSRs between 0.35 and 2, males engaged in more intrasexual interactions and courtship behaviour than females. However, females became the more competitive sex at OSRs less than 0.35, and engaged in more courtship than males at OSRs greater than 2, rather than at an OSR of 1, as predicted by conventional mating system theory. Our results indicate that OSR can predict the considerable within-sex variability in reproductive behaviour of both males and females, regardless of which sex is more competitive.

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Conventional sex roles occur when males are the more competitive sex (Vincent et al. 1994; Forsgren et al. 2004), which often leads to greater choosiness in females than in males. Because males typically have a higher potential rate of reproduction than females (Clutton-Brock & Parker 1992), the operational sex ratio (OSR), the ratio of males to females in a population that are ready to mate (Emlen & Oring 1977), is often biased in favour of males. The OSR can be used to predict the intensity of intrasexual competition for mates and mating system structure (Emlen & Oring 1977). Perhaps the most powerful test of OSR theory (e.g. Kvarnemo & Ahnesjö 1996) has been its ability to predict the occurrence of species with conventional versus 'reversed' sex roles (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992).

Sex roles were initially thought to be fixed traits, linked to the reproductive behaviour and physiology of a species (Forsgren et al. 2004). More recent research, however, indicates that sex roles are more flexible and can be determined by changes in the abundance of food (Gwynne & Simmons 1990) or nest sites (Almada et al. 1995), water temperature (Kvarnemo 1996), odour cues in the environment (Moore et al. 2001), and the seasonal availability of mates (Forsgren et al. 2004). This more dynamic view suggests that

while the average sex role of a species can be predicted by potential rate of reproduction and OSR, we might expect individual males and females to both compete for and choose mates depending on local conditions (Gowaty & Hubbell 2005).

OSR theory can also predict the patterns of behaviour in both sexes regardless of which is more competitive (Kvarnemo & Ahnesjö 1996; Grant & Foam 2002). When the OSR is less than 1, males are predicted to court the relatively abundant females and engage in little aggression (Jirotkul 1999; Grant et al. 2000). As the OSR increases, the relative abundance of females decreases, so the rate of male aggression and propensity to court females (sensu Forsgren et al. 2004) will increase (Enders 1993; Kvarnemo & Ahnesjö 1996). However, the observed rate of male courtship often decreases with increasing OSR, because of a lower encounter rate with females and a trade-off between the time spent competing with other males and the time spent courting females (Jirotkul 1999; Grant et al. 2000). At extremely high values of OSR, however, resource defence theory predicts that aggression will no longer be effective because of the costs of chasing multiple intruders, so males will switch from interference to exploitation competition (Brown 1964; Grant 1993). Hence, there is an apparent contradiction in the OSR literature that predicts either a monotonic increase in aggression with increasing OSR (Kvarnemo & Ahnesjö 1996), or a dome-shaped relationship (Emlen & Oring 1977; Grant et al. 2000).

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Because males are typically the more competitive sex, female competition and courtship behaviour have not received a great deal of attention (Clutton-Brock 2007). Opposite to the patterns in males, female intrasexual competition is predicted to decrease with increasing OSR and has been verified in sand gobies, *Pomatoschistus minutus* (Kvarnemo et al. 1995), Japanese medaka (Grant & Foam 2002), European lobsters, *Homarus gammarus* (Debusse et al. 1999) and two-spotted gobies, *Gobiusculus flavescens* (Forsgren et al. 2004). To date, these are the only studies to examine simultaneously the aggressive and courtship behaviour of both males and females in response to changes in OSR (also see de Jong et al. 2009).

Because OSR is inherently affected by the densities of both males and females (Emlen & Oring 1977; Kvarnemo et al. 1995; Smith 2007; de Jong et al. 2009), it will be virtually impossible to distinguish between the effects of OSR independently of the density of either males or females in observational field studies. Even in experimental studies it has been difficult to distinguish between these two effects because OSR is typically manipulated by changing the number of males while holding female number constant (e.g. Grant et al. 2000; Mills & Reynolds 2003), or by changing the number of females while holding male number constant (e.g. Souroukis & Cade 1993; Grant et al. 1995). Only a handful of studies have attempted to disentangle the effects of OSR and density using a factorial design to manipulate either the number of both males and females (e.g. Alonso-Pimentel & Papaj 1996; Fairbairn & Wilby 2001; Smith 2007), or OSR and total density (Spence & Smith 2005; de Jong et al. 2009). In the former design, an effect of OSR independent of male or female density is indicated by a significant interaction between the main effects (see Fairbairn & Wilby 2001), whereas OSR is a main effect in the latter design. However, even the results of such experiments have been mixed. Mating system dynamics are primarily affected by the density of males or females, rather than OSR per se, in some studies (Verrell 1982; Alonso-Pimentel & Papaj 1996; Smith 2007), whereas other studies suggest that both OSR and density of a particular sex can be important (Sih & Krupa 1995; Fairbairn & Wilby 2001). Using the latter design, mating system structure is influenced more by OSR than by total density in two-spotted gobies (de Jong et al. 2009), whereas both OSR and total density affect male reproductive behaviour in zebrafish, *Danio rerio* (Spence & Smith 2005). Interestingly, even when OSR per se has no significant effect on reproductive behaviour, the effects of male or female density are typically consistent with the predictions of OSR theory. For instance, male–male interactions increase with increasing male density (Spence & Smith 2005; Smith 2007) and decrease with increasing female density (Sih & Krupa 1995).

Previous work on the Japanese medaka indicates that males are more aggressive than females at OSRs between 0.66 and 3 (Grant & Foam 2002). Male intrasexual aggression initially increases with increasing OSR, peaks at an OSR of 2, and then decreases. Because there has been little work on female competitive behaviour, this study will focus primarily on female behaviour. Hence, we manipulated male and female density in a factorial design to create a broad range of OSRs (0.0625 to 2), allowing us to test for the independent effects of male density, female density and OSR. Specifically, we tested the predictions that: (1) male–male interactions initially increase with increasing male density; (2) male courtship rate initially decreases with increasing male density because of a trade-off between the time spent competing versus courting; (3) female–female interactions and courtship rates follow the same patterns as those of males, and initially increase and decrease, respectively, with increasing female density; and (4) rates of intrasexual interactions in males and females either increase or decrease, respectively, or exhibit a dome-shaped relationship with increasing OSR.

## METHODS

### Experimental Subjects

Japanese medaka are small (standard length = 2.5–3.5 cm) freshwater fish native to the streams and rice paddies of eastern Asia (Howard et al. 1998). During the mating season, female medaka can spawn daily, producing 10–50 eggs. The sticky egg masses remain attached to the female for a few hours until they become attached to vegetation as the female swims by (Howard et al. 1998). Males can spawn with up to 20 females per day (Weir & Grant, in press).

All 150 fish used in this study were purchased from a biological supply company and were kept at a male:female sex ratio of 2:3 in two mixed-sex stock tanks measuring 91.5 × 46 × 38 cm (L × W × H). Fish were fed a mixture of previously frozen brine shrimp and commercial flake food once per day. The fish were kept under a 13:11 h light:dark cycle, with lights on at 0900 hours. Fish were held for approximately 1 month in the stock tanks before experimentation to ensure that the females' egg-laying cycle had commenced, which was readily confirmed by observing egg masses on the female's ventral surface within 1 h of lights on. We assumed that all fish had previous breeding experience by the time experiments began. All experiments were conducted from mid-June to mid-September 2007.

### Experimental Design

Four experimental tanks, measuring 60 × 30 × 30 cm (L × W × H), were covered with dark, opaque plastic wrap on three sides to prevent interactions between fish in adjacent tanks. The fourth side was left uncovered for filming purposes. Experimental tanks were also equipped with an airstone and gravel to a depth of 2 cm. Each trial lasted 7 days and was divided into two parts: training (days 1–4) and filming (days 5–7). Female fish (in groups of 2, 4, 8 and 16) were placed in the experimental tanks on day 0.

Females were then given 4 days for acclimation and training. Training consisted of placing males into the experimental tanks each morning at 0930 hours. The OSR during the training period was always 0.5 (e.g. 4 males:8 females), except for the group size of 16, which received only four males, to limit the total number of fish in the experimental tanks. This minor exception had no apparent effect, as the data for female groups of 16 were consistent with the trends noted among the other group sizes (see below).

After training, female groups were exposed to one, two and four males in a repeated measures design, creating a range of OSRs from 0.0625 to 2. Ten replicates of each female group size were completed, so that the average female was used 3.3 times during the experiment. However, female groups were drawn randomly from the stock tank, so that the probability of reusing the same group of females was extremely low. Sixteen males were placed into a holding tank for use in the experiments each week. Each day, the required number of males was removed randomly from the holding tanks for use in the trials. Males remained in the experimental tanks for 1 h or until all females had spawned, whichever came first; afterwards, the males were removed and returned to the holding tank, separated from the stock tanks. On average, each of the 16 males was used 1.75 times during the week, and each male was used 4.7 times over the course of the 10 replicates. The probability of reusing the same group of males was very low, and the probability of reusing the same group of males with the same group of females was even lower. Hence, we think the animal care benefits of using fewer experimental animals more than offset the slight chance or reusing a group of fish.

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