

# The role of female dominance hierarchies in the mating behaviour of mosquitofish

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**While studies of sexual selection focus primarily on female choice and male–male competition, males should also exert mate choice in order to maximize their reproductive success. We examined male mate choice in mosquitofish, *Gambusia holbrooki*, with respect to female size and female dominance. We found that the number of mating attempts made by a male was predicted by the dominance rank of females in a group, with dominant females attracting more mating attempts than subordinates. The number of mating attempts made by males was independent of the female size. The observed bias in the number of mating attempts towards dominant females may be driven either by straightforward male mate choice, since dominance and female fecundity are often closely related, or via the dominant females mediating male mating behaviour by restricting their access to subordinate females.**

**Keywords:** mate choice; fitness; dominance; hierarchy; fecundity

## 1. INTRODUCTION

While studies of mate selection have historically focused on female choice, there are many scenarios where males may also benefit from being choosy with respect to their mates [1]. Theory predicts that male mate choice should be most likely to occur where females vary in quality and where males have either to make a sizeable investment in reproduction or where the encounter rate with potential mates is high [2]. Where there is a large variation in characteristics that correlate with female fecundity, males may potentially benefit by biasing their reproductive effort according to their appraisal of these characteristics [3,4]. In many species, female fecundity is positively correlated with size, and males exhibit preferences for larger females [5–7].

Males may also benefit from selecting females on the basis of social rank. Female dominance hierarchies are found in species representing a wide range of taxa [8–11]. The fitness benefits of occupying higher ranks in a dominance hierarchy are often considerable, both for males [12] and for females. For example, dominant females benefit from increased foraging efficiency and can displace subordinates from feeding

patches [13] or steal their food [14]. Additionally, stress experienced by subordinates can impair reproductive function [15]. Overall, dominant females may provide offspring better and produce larger and healthier broods than subordinates [16], potentially making them more attractive as mates.

The mosquitofish, *Gambusia holbrooki*, is a livebearing Poeciliid with a promiscuous mating system. Adult males are typically smaller than adult females and do not court, but rely on coercion. Both sexes are organized into dominance hierarchies [17] where the dominant individual is often the largest. In this species, the hierarchies are often ‘monarchistic’ in nature, with a single individual dominating a small group of relatively equal subordinates [17]. While prior studies have investigated male preference for larger females [18], it is not known whether and how this relates to a female’s position in the dominance hierarchy. While dominance often covaries with size and growth, this is by no means always the case [19,20]; hence it is insufficient to take size as a proxy for dominance. If male mosquitofish gain fitness benefits from mating with dominant females, then they may be expected to be choosy in this respect. Alternatively, females may mediate male mating preferences through their behaviour, particularly through dominant females restricting male access to subordinate females. Here, we examine whether male mosquitofish allocate their mating efforts according to female dominance rank, in the absence of major size differences.

## 2. MATERIAL AND METHODS

We collected mosquitofish during late 2009 from Manley Dam, Australia (33°46′35.45″ S, 151°14′50.38″ E). Captured mosquitofish were held in 180 l vats at the University of Sydney at 23.1 ± 1°C with 12:12 h light regime. The fish were stocked at high densities (approx. 200 fish with an even sex ratio per 180 l vat) to prevent the possible development of familiarity preferences [21]. Each female used in the experiment was given a unique individual identification marker using elastomer (NorthWest Marine Technology, Washington, USA) at least one week prior to beginning experiments.

Two experimental tanks measuring 40 × 19.5 × 23 cm (l × w × d) were filled with aged, conditioned water to a depth of 17 cm. Both tanks had aquarium gravel added to a depth of 1 cm with two artificial plants to provide refuge for the fish and an airstone to circulate the water. Each tank was lit from above and enclosed within a black plastic shelter to minimize external disturbance.

For each experimental replicate, five adult females measuring 29.22 ± 1.52 mm (mean ± s.d.), range 26–33.4 mm, were placed in the tank and left for a period of 20–24 h, following which we conducted a 20 min observational period. During this period, we recorded agonistic interactions between females; individuals chase their subordinates and are chased by those dominant to them, hence rank is simple to determine [22]. Following this, a single male measuring 19.54 ± 0.85 mm (mean ± s.d.) was placed in the tank and allowed to acclimate for 20 min. This was followed by a further 20 min observation period where the number of mating attempts the male made towards each female was recorded. As with other Poeciliid fishes, a mating attempt is clear and unambiguous, which involves the male rotating his intromittent organ (the gonopodium) towards the female’s genital pore. We conducted 12 replicates, each time with new individuals.

### (a) Data analysis

The data were analysed using a linear multiple regression technique, with the number of mating attempts made by each male towards each of the five females as the outcome and both female size and female dominance as predictors. We used a Durbin–Watson procedure to determine residual independence in the model, assessed collinearity by examining tolerance and the variance inflation factor and tested assumptions of homoscedasticity and normality of distribution using residual plots and probability–probability plots, respectively [23].

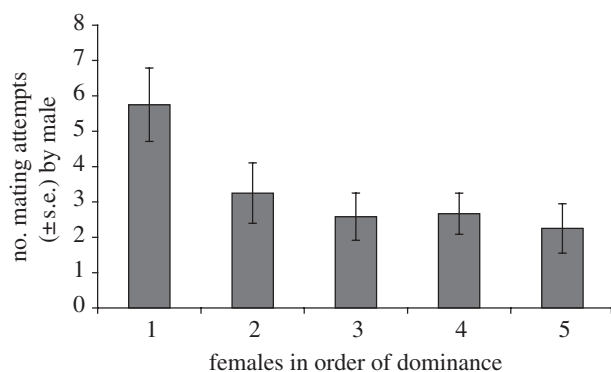


Figure 1. Mean mating attempts directed towards each female according to the female's dominance rank.

### 3. RESULTS

The model successfully predicted the number of matings attempted by the male mosquitofish (regression:  $r = 0.413$ ,  $F_{2,57} = 5.88$ ,  $p = 0.005$ ). Of the two predictor variables, female rank (standardized  $\beta = -0.37$ ,  $t = 3.02$ ,  $p = 0.004$ ; figure 1), but not the female size (standardized  $\beta = 0.15$ ,  $t = 1.22$ ,  $p = 0.23$ ), was a significant predictor of the number of mating attempts made by the male—higher ranked females attracted more mating attempts from the males than the lower ranked females. All regression analysis assumptions were met.

### 4. DISCUSSION

Male mosquitofish allocate their mating attempts according to the female's position in the dominance hierarchy, but the experiments failed to detect an effect of the female size. This bias in male mating effort may be driven by their preference for dominant females, or as a result of the aggressive interactions between females increasing their probability of encountering dominant females, or an interaction of these two. Male preference for dominant females has previously been documented in animals with particular social systems, especially in hierarchical social mammals [24–26] and where sex roles are reversed [27]. To our knowledge, this is the first demonstration of male preference for dominant females in a promiscuous mating system with regular (non-reversed) sex roles.

Why should males choose to mate with dominant females? Dominant animals may be better provisioned [13,28], and more fecund than subordinates [29], hence mating with a dominant female may confer a direct fitness benefit to a male since the quantity and quality of food the female consumes affects her reproductive success. Food availability and offspring number are positively correlated in egg-laying fish [30], while in livebearers, like *G. holbrooki*, females may reabsorb oocytes [31] or produce smaller offspring when food is scarce [32]. Furthermore, dominant females can sometimes directly suppress reproduction in subordinates through chemical means [33], including in *Gambusia* [34].

Despite the coercive nature of the mosquitofish mating system, females are not passive participants. For example, the fact that males showed a strong preference for the dominant female but appeared to show

little discrimination between the other ranks may be indicative of the monarchic nature of mosquitofish hierarchies and the agonistic and chemical suppression of subordinates by the most dominant fish [17,34]. Furthermore, the structure of the female dominance hierarchy and the aggression between its members are likely to feed back to affect male behaviour. The behaviour of dominant females probably affects the encounter rate of males with potential mates, since dominant individuals aggressively drive-off their subordinates and thus occupy a greater proportion of available space.

In many species, size may be a proxy for dominance. Here, female size did not play a part in male choice, although given a wider size range, males may choose larger females, on the basis of size-related fecundity [35,36], or, in light of current findings, on the basis of dominance-related fecundity.

Even where females vary in quality, male choosiness should only occur when there is a high male investment in courtship or mating, or when there is a low cost to choosiness [2,37]. In most other cases, males might be best served to take any mating opportunity. For most of their breeding season in Australia, mosquitofish live at extremely high densities, allowing males a high encounter rate with their mates and, importantly, imposing low costs for choosiness. Under these circumstances, males may potentially maximize fitness by being selective. However, if all males were to target dominant females, the payoff for selecting dominant females would drop and a less choosy male strategy could be favoured. Intriguingly, therefore, male strategy may be dependent on female density, switching from choosiness to an indiscriminate strategy when the ratio of females to males drops below some threshold value.

All experiments were approved in advance by the University of Sydney Animal Ethics Committee.

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