Male social dominance affects access to mates but not female mate choice in a livebearing fish

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Abstract

Male-male competition and female mate choice are often assumed to act in concert, with male social dominance serving as a reliable cue in female choice reflecting overall male quality. However, few studies have explicitly disentangled the effects of male competition and female mate choice, leaving gaps in our understanding of how these processes interact to shape male fitness. Here, we experimentally separated the effects of male-male competition and female mate choice in the pygmy halfbeak *Dermogenys colletei*, a small freshwater fish, to test whether i) male social dominance drives access to females in the presence and absence of direct male-male competition, and ii) females prefer socially dominant males. Our results show that dominant males monopolized access to females, spending more time courting females and engaging in more courtship behaviors. Additionally, female halfbeaks did not show a preference for dominant males, providing no evidence that females use male dominance when assessing males. Overall, these findings highlight that when male-male competition facilitates mate monopolization there may be less scope for pre-copulatory female mate choice.

Keywords: Intra-sexual competition, mate choice, social dominance, sexual selection, halfbeaks

1 Introduction

An individual's reproductive success is shaped by both competition among members of the same sex for mating opportunities (intra-sexual selection) and mate choice (inter-sexual selection) (Darwin, 1871; Kokko et al., 2012). In species with conventional sex roles, males typically exhibit greater variance in reproductive success than females (Janicke et al., 2016), and are therefore expected to increase their reproductive success primarily through male-male competition. In turn, the sex limited by their investment into offspring, typically females, commonly benefits from selecting high-quality mates (female mate choice). Intra- and inter-sexual selection are expected to generate directional selection for traits that are correlated with either success in competition or mate choice, leading to the evolution of exaggerated traits, such as weapons and larger body sizes used to resolve competitive interactions (Emlen, 2008; Hardy and Briffa, 2013; McCullough et al., 2016). However, there is ample scope for interactions between these mechanisms of sexual selection, with male-male competition and female mate choice potentially acting in concert, in opposing directions, or independently (Berglund et al., 1996; Wiley and Poston, 1996; Wong and Candolin, 2005). Yet, despite its potential to shape the strength and direction of sexual selection (Hunt et al., 2009), interactions between male-male competition and female mate choice remain poorly understood (Wong and Candolin, 2005; McCullough et al., 2016).

Male-male competition and female mate choice have traditionally been viewed as mutually reinforcing mechanisms of sexual selection (Berglund et al., 1996; Wiley and Poston, 1996; Wong and Candolin, 2005). Traits that provide males with a competitive advantage in male-male competition may also represent a reliable indicator of male quality (Berglund et al., 1996; Khazraıe and Campan, 1999). Females who select dominant males as mating partners may therefore gain either direct fitness benefits, such as access to better resources or protection, or indirect benefits, such as superior genetic traits for their offspring (Berglund et al., 1996; Wong and Candolin, 2005; Hunt et al., 2009). Female preference for dominant males has been recorded for a variety of species (reviewed in Wong and Candolin, 2005). Such female preference can be shaped by females gaining information about social dominance by observing interactions between males (Doutrelant and McGregor, 2000). Competitive interactions between males are a conspicuous form of social information, akin to other information available in the social environment that influences mate choice decisions (e.g., other individuals mating, Dugatkin, 1996, presence of rivals, Plath and Bierbach, 2011). The reproductive outcomes associated with female preference typically translate into higher fitness for dominant males (Bulger, 1993; Rus Hoelzel et al., 1999; Baxter et al., 2015; Montana et al., 2022). However, distinguishing whether reproductive benefits observed in dominant males arise from active female preference or male-imposed constraints remains challenging without experimental manipulation. Indeed, in many species, males that are more successful

during male-male competition can monopolize access to females, thereby constraining female choice by preventing interactions between females and subordinate males and reducing the overall pool of potential mates (Wong and Candolin, 2005).

Experimental studies examining the interaction between male-male competition and female mate choice have produced mixed results. In some cases, females prefer to associate with socially dominant males after assessing visual and olfactory cues associated with agonistic interactions between males, as shown in fighting fish (*Betta splendens*, Doutrelant and McGregor, 2000), red swamp crayfish (*Procambarus clarkii*, Aquiloni et al., 2008; Aquiloni and Gherardi, 2010), and black-capped chickadees (*Parus atricapillus*, Mennill et al., 2002). In contrast, other species show no effect of male-male competition on female preference, including the Pacific blue-eye fish (*Pseudomugil signifier*, Wong, 2004) and the jumping spider (*Thiania bhamoensis*, Chan et al., 2008). Some species even exhibit reversed patterns, where females prefer subordinate males after observing male social interactions, as observed in the Mexican livebearing fish (*Poecilia mexicana*, Bierbach et al., 2013) and Japanese quail (*Coturnix japonica*, Ophir and Galef Jr, 2003). These findings suggest that the influence of male-male competition on female mate choice is complex, context-dependent and species-specific, highlighting the need for further research to clarify how these mechanisms interact.

In this study, we investigate how male-male competition influences access to mates and female mate choice in the pygmy halfbeak *Dermogenys collettei*, a small, internally fertilizing, freshwater fish native to south-east Asia (Meisner, 2001; Greven et al., 2010). Halfbeaks live in loosely organized mixed-sex groups, where intra- and inter-sexual interactions are frequent (Greven et al., 2010; Devigili et al., 2021). Males compete with rival males for access to females, often directing behavioural threat displays to rivals and using and their elongated lower jaws (called beaks) as an armament during competitive interactions. Furthermore, males are vigorous courters (Devigili et al., 2021), and females can discriminate and choose males based on the amount of red fin coloration displayed (Reuland et al., 2020; McNeil et al., 2021). In highly competitive scenarios, dominant males exhibit superior ejaculate quality compared to subordinate males (Reuland et al., 2021), hinting at the potential benefits of female preference for dominant males. Here, we experimentally examine i) how male social dominance influences access to females in the presence or absence of direct physical interactions between males and ii) how the outcome of male-male competition influences female choice. We predicted that i) dominant males would monopolize access to mates, but only when they could physically interact with subordinate males, and ii) female preference would be based on male social dominance, with females preferring dominant over subordinate males.

2 Methods

2.1 Study populations and rearing conditions

Halfbeaks used in this study were sexually mature, wild-caught (Experiment 1) or lab-reared descendants of a wild-caught population (Experiment 2) from the Johor State of Malaysia (Johor River for Experiment 1 and Tebrau River for Experiment 2). The different sources of fish were a consequence of the availability of fish from a commercial exporter. Fish were reared in the laboratory using a standard set of husbandry practices. Fish were maintained on a 12:12 light:dark cycle at 26-27°C and fed daily a mixture of either ground flake food, freshly hatched Artemia, *Drosophila melanogaster*, or mosquito larvae (*Chaoborus crystallinus*). Aquaria contained ∼2 cm of gravel, were oxygenated, and contained live or artificial plants. Sexually mature fish were kept in mixed sex 160L aquaria in groups of 10-25 individuals. To generate lab-reared descendants of wild-caught fish, gravid females were placed in 7.5L tanks and monitored daily until they produced offspring (i.e., fry). Alternatively, fry were removed from stock tanks whenever they were observed. Fry were then separated from adults to prevent cannibalism and kept in 5-7.5L tanks with up to five other fry. The onset of sexual maturity was determined by observing a thickening of the male's andropodium, the modified set of five fin rays that males use to transfer sperm to female. At the onset of sexual maturity, females and males were separated into either mixed sex or sex-specific tanks (to maintain their mating status as 'unmated') and reared in 160L aquaria. Experiments were approved by the Animal Research Ethical Board (permit number 3967-2020).

2.2 Experimental overview

We performed two experiments to assess how male social dominance influences reproduction in halfbeaks. In Experiment 1, we tested the hypothesis that male-male social dominance influences access to mates by examining the link between male social dominance and courtship behaviours directed towards females in the presence or absence of direct physical interaction between males. In Experiment 2, we tested the hypothesis that male-male social dominance influences female mate preferences.

2.2.1 Experiment 1: Does male social status influence access to mates?

To assess the effect of male social dominance on access to mates, we placed two size-matched (by eye) males and two randomly selected females in an experimental tank (42 x 24.5 x 17.5 cm), which was divided differently depending on the experimental treatment described below. All tanks were filled to a depth of ∼12 cm and contained a ∼1cm layer of gravel. All experimental treatments began in the same way. First, each experimental tank was partitioned into two compartments using an opaque barrier. Both males were placed on one side of the barrier (24,5 x 24.5 x 17.5 cm), while both females were placed on the other side (30 x 24.5 x 17.5 cm). Within the male compartment, an additional opaque divider was

used to further separate the males, confining each male to an individual area (12 x 24.5 x 17.5 cm) with no visual access to one another at the start of the experiment. In contrast, the two females could interact freely with one another but had no visual access to either male. Fish were given a 30-minute habituation period after being placed in their respective areas of the experimental tank. Following habituation, the experiment proceeded in two phases: a male-male competition phase and a mate interaction phase.

Male-male competition phase

During the male-male competition part of the experiment, the opaque barrier separating the two males was lifted and the males were allowed to interact for 30 minutes. A total of 74 males were used, forming 37 dyads. Male-male competitive interactions are common in halfbeaks, with a range of agonistic behaviours used during contests with rivals. Contests typically start with both males swimming parallel to each other and *gill flaring*, a behaviour which consists of repeatedly opening and closing their gills usually with their beak open. During these standoffs, males also *head shake* by jerking their bodies in an S pattern. Contests can include biting and chasing (Devigili et al., 2021; Reuland et al., 2021). Occasionally, males interlock their beaks together, a behaviour knowm as *beak wrestling* (Greven et al., 2010). Following a rival's aggressive display, an individual may be displaced, turning quickly and swimming away, increasing the distance between himself and its aggressor (Reuland et al., 2021). Male dominance within each dyad was scored during this interaction period by recording displacement behaviours, where one male (the aggressor) approaches the other or performs an agonistic behaviour (e.g., gill flares, head shakes, bites, chasing), making the targeted male distance himself from the aggressor male. These displacement behaviours were used to create a dominance index, calculated as:

$$D_{Index} = 1 - \frac{\text{(Displacements by an aggressor male)}}{\text{Total number of displacements in the dyad}} \tag{1}$$

Dominance index values range from 0 to 1, with 0 meaning a male was completely subordinate (i.e., males were only displaced by rival males) and 1 completely dominant (i.e., males only displaced rival males, Reuland et al., 2021). Following Reuland et al. (2021), males were classified as socially dominant in their dyad if they had a dominance score > 0.7 (i.e., males displaced their rival in $> 70\%$ of interactions). Dominant males had an average $\pm$ SE dominance index score of 0.96 ± 0.04, while the dominance index score of subordinate males was 0.05 ± 0.04. Importantly, the opaque barrier partitioning the males from females was left in place throughout the male-male competition part of the experiment to prevent females from directly observing male-male interactions.

Mate interaction phase

Following the male-male competition phase of the experiment, the opaque barrier separating males and

females was lifted. In n=13 trials, both the dominant and subdominant males (26 males in total) were allowed to freely interact with both females and one another for 30 minutes (henceforth called *mate interactions with male-male competition* trials). In n=24 trials, only one of the two males was allowed to interact with the two females, while the other male was placed behind a transparent partition (henceforth called *mate interactions without male-male competition* trials). The partition prevented the focal males from physically interacting with the males confined by the transparent partition (i.e. the stimuli males) during the mate interaction part of the experiment. However, the transparent partition allowed the passage of visual signal, and by drilling several holes into the partition, we allowed the exchange of chemical cues between males and females. Thus, in the *mate interaction* trials either *with* or *without male-male competition*, the number of fish visually present remained constant, ensuring a consistent adult sex ratio across trials, while the potential for male-male competitive interactions to affect access to mates varied. In the *mate interactions without male-male competition* trials, males were randomly assigned to either the focal or stimuli male role (i.e., males were assigned blind to their social dominance scores from the previous part of the experiment). As a result, the sample size was n=14 dominant males and n=10 subordinate males acting as focal males (and conversely n=10 dominant males and n=14 subordinate males as stimuli males).

In *mate interactions with* and *without male-male competition*, we recorded the total amount of courtship behaviours males directed towards either female. Courtship behaviours include *circling*, where the male swims in a semi-circular pattern around the female, *swimming under*, where the male positions himself under the female with his head located below the female's genital pore, and *mating*, where the male males rapidly (∼40-80 ms) twists his body in an attempt to use his andropodium to transfer sperm to the females' genital pore (Greven et al., 2010). Males frequently attempt to swim under females, with some attempts being successful and others being considered unsuccessful when females swim away as males attempt to swim under. We treated the total number of *swimming under attempts* as a measure of male sexual interest. Other courtship behaviours present in the male's repertoire (e.g., *nipping*, where males rapidly open and close their beaks while swimming under the female, and *checking* where males use their beak to make physical contact with the female) were difficult to observe in our experimental setup and were therefore not considered. We recorded the total number of courtship behaviours (circling, swimming under attempts and mating attempts, henceforth called total courtship count) and the total amount of time males spent swimming under each female.

All assays were recorded by the use of GoPro 10 and videos were analysed with the use of the software BORIS (version 8.24.1; Friard and Gamba, 2016).

Quantifying phenotypic traits

As both male and female phenotypes could influence social dominance and mate choice in halfbeaks

(Reuland et al., 2020; Ogden et al., 2020; Reuland et al., 2021; McNeil et al., 2021), we quantified relevant phenotypic traits of all fish used in the experiment. We placed the fish inside an aquarium (27 x 17,5 x 15,5 cm), filled with conditioned water, with the aquarium itself positioned inside a photography chamber under standardized light conditions and fitted with a scale. Fish were positioned against the side of the aquarium with help from a plastic sheet with a groove deep enough to hold them in place for the pictures and not cause them any physical harm. The fish were only held in this position for a few seconds while the pictures were taken. The photos were taken with a Canon EOS 800D camera and were used to measure body length (mm), measured from the anterior side of the eye to the caudal peduncle (Fernlund Isaksson et al., 2022), beak length (mm) and total area of red colouration on the anal, dorsal and caudal fin (mm^2) using the polygon selection tool in ImageJ (version 1.54; Schneider et al., 2012). For stimuli females, the females' ventral side was photographed by placing females (for $<$ 1minute) in a clear plastic photography container (75 x 50 x 25 mm) filled with water from their own tank. The container was placed on top of a plexiglass sheet held in place above the same Canon camera that was used to take pictures from the side of the fish. From these pictures, female body length (mm) and gravid spot area (mm^2) was measured using ImageJ.

2.2.2 Experiment 2: Does male social status influence female mate preferences and mating behaviour?

Male social dominance and female preferences

To assess if male social dominance influences female mate preferences, we performed mate choice assays in dichotomous choice tanks (45 x 25 x 20 cm), consisting of one main chamber (45 x 15 x 20 cm) and three smaller stimulus chambers (each 15 x 10 x 20 cm). All chambers were separated by removable transparent and opaque dividers, allowing for changes in chamber configurations throughout the experiment. A focal virgin female was placed in the main chamber. While virgin females are commonly assumed to be less choosy than mated females (Jennions and Petrie, 2000; Kokko and Mappes, 2005), a recent meta-analysis found no evidence that mating status influences choosiness in females (Richardson and Zuk, 2023). However, because experience with members of the opposite sex and exposure to courtship behaviours can influence female mating behaviours (Coleman et al., 2004; Dukas, 2005; Bailey and Zuk, 2008), we used virgin females that had visual access to 70 L tanks housing 10 males and 10 females for 11-12 days before entering the experiment. Two males were placed randomly in either the right or left stimuli chambers of the dichotomous choice tanks. Males were photographed 3-4 days before entering the experimental tank (as described in section 2.2.1). All fish were given one hour to habituate in the experimental chambers, during which time opaque barriers were in place to prevent the fish from visually interacting with one another.

Following the habituation period, the opaque barriers were lifted and females were allowed to freely explore the experimental chamber and visually interact with both stimuli males for one hour. This experimental step ensured that females were familiar with the experimental set up with the aim of reducing potential stress responses in females prior to subsequent experimental steps. The opaque barriers separating the stimulus males were then removed, allowing the males to freely interact with each other for one hour, allowing female the opportunity to observe male-male interactions. During male-male interactions, we recorded the number of times a male displaced the other male and calculated the dominance index score for each male (as above). We also recorded the number of agonistic behaviours displayed (see *mate competition phase* section above) to assess the overall aggression of males. After one hour of interactions, males were guided back to the stimuli chambers and the opaque barriers between the stimuli chambers were re-erected. We then assessed female preference for one hour, during which time they could move freely in the main chamber. The duration of time a female spent within 5 cm in front of each stimulus male's chamber (termed the *association zone*; total dimension: 15 x 5 cm), was recorded. The time females spend in such association zones is commonly used as a measure of mating preference that is predictive of female preference during mating interactions in many species (Bischoff et al., 1985; White et al., 2003; Walling et al., 2010) and was previously used for halfbeaks (Reuland et al., 2020; McNeil et al., 2021).

In total, 64 dichotomous mate choice trial were conducted. Five trials were excluded from the final analysis due to low levels of female activity. Additionally, 13 dyads were omitted as, in each dyad, one male did not displace their rival in $> 70\%$ of interactions. leading to an unclear dominance hierarchy (scores between 0.52 and 0.69). This reduced the final sample size for analysis to $n = 46$. All tanks were recorded from above using a Point Grey Grasshopper 3 4.1 megapixel camera (Teledyne FLIR LLC, Wilsonville, United States) with Fujinon CF25HA-1 lens (Fujifilm, Minato, Japan). Recorded videos were scored using BORIS (version 8.24.1; Friard and Gamba, 2016).

2.3 Statistical analysis

Statistical analyses were carried out using R version 4.3.1 (Team, 2023). Linear and generalized linear mixed effects models (LMMs and GLMMs) were performed using the *lme4* (Bates et al., 2015) and *glmmTMB* (Brooks et al., 2017) packages.

2.3.1 Experiment 1: Does male social status influence access to mates?

To examine whether male access to females was influenced by male dominance status, female body size or gravid spot size, LMMs and GLMMs were used. Two metrics reflecting male mating behaviours (duration of swimming under and total courtship count) were included as response variables. The duration of

swimming under the female was log-transformed to obtain a normal distribution and assessed using LMMs, while courtship behaviors were assessed using GLMMs fitted with a negative binomial distribution to account for overdispersion in the data. The male identity was incorporated as a random effect in each model to consider potential variability between males. Two-way interactions were initially included in all models, but were excluded from the final models as they were non-significant.

Combined models including an interaction between male dominance status and trial type (i.e. mate interactions with or without male-male competition) were initially fitted to additionally test whether dominance effects differed between experimental settings. However, due to non-significant interactions (*P-value* = 0.28 and 0.38, see results Table 1) and to reduce the risk of Type II error due to sample size limitations and model complexity, we subsequently ran separate models for each trial type (see Table **??** for details). This approach provides an additional understanding of the context-specific effects of male dominance on mating behavior while still accounting for the effect of female morphological traits.

2.3.2 Experiment 2: Does male social status influence female mate preferences and mating behaviour?

To assess whether females showed a preference for one of the two males, we first calculated the strength of preference (SOP) for the preferred males as follows:

$$SOP = \frac{\text{Time in preferred male's association zone - Time in non-preferred male's association}}{\text{Time in both association zones}} \quad (2)$$

This provides a SOP range from 0 to 1. A value close to 0 indicates little preference between the two males, while a value closer to 1 indicates a strong preference for one male over the other. To determine whether females significantly preferred one male over the other, we conducted a one-tailed Wilcoxon signed-rank test comparing SOP scores to a median of 0. This non-parametric test was chosen over a one-sample t-test because SOP scores were not normally distributed (Shapiro-Wilk test, $p < 0.05$). This tested whether the observed preferences were significantly greater than would be expected by chance (i.e., SOP > 0).

To examine whether female halfbeaks display a sexual preference for males based on male social dominance, SOP was then calculated for the male in the left stimuli chamber (i.e., an arbitrary male) as follows:

$$SOP = \frac{\text{Time in left association zone - Time in right association}}{\text{Time in both association zones}} \quad (3)$$

A SOP closer to - 1 indicates a preference towards the right male, while a SOP closer to 1 indicates a preference towards the left male. A SOP of 0 indicated an unbiased mating preference. To assess

morphological differences between the left and right stimulus males, we compared their body length, beak length, and total area of red coloration. This was done by subtracting the right male's measurements from those of the left male. SOP for the left male scores were used as the response variable in a single LMM. The difference between body length, beak length, and red area of the two stimulus males were included as fixed factors, along with male dominance. We included tank identity as a random factor to accounted for potential variation among the experimental tanks.

3 Results

3.1 Experiment 1: Male social dominance influences access to mates

3.1.1 Combined models

Dominant males swam under females on average 2.1 times longer than subordinate males (Dominants: 97.94±28.01 s, Subordinates: 45.97±15.10 s; mean±SE) (LMM; Table 1, a, Figure 1) and directed 2.0 times more total courtship behaviors towards females (Dominants: 23.08±3.73 behaviors; Subordinates: 11.77±2.23 behaviors) (GLMM; Table 1, b, Figure 1). However, dominance effects did not significantly differ between trial types (i.e. *mate interactions with* versus *without male-male competition* trials, 1). Additionally, the duration of time males spent swimming under females and the total courtship counts did not significantly differ based on female body size or the size of the gravid spot (LMM; Table 1, a, b).

3.1.2 Separate models

Mate interactions with male-male competition trials

When dominant and subordinate males were both presented with females, dominant males swam under females significantly longer than subordinate males (LMM; Table **??**) and directed significantly more total courtship behaviors (GLMM; Table **??**, b, Figure 1). The duration of time males spent swimming under females and the total courtship counts did not significantly differ based on female body size or the size of the gravid spot (LMM; Table **??**, a, b).

Mate interactions without male-male competition trials

When only one of the two males was allowed to interact with females, there was no difference between dominant and subdominant males in the amount of time males spent swimming under females (LMM; Table **??**, c) or directing total courtship behaviors towards females (GLMM; Table **??**, d). However, males spent overall more time swimming under large females than smaller females (LMM; Table **??**, c, d).

Table 1: Effect of male social dominance and female traits on male access to females

Response variable	N	Predictors	Estimates	SE	*z*	*P-values*
Combined models						
		Dominance (Dominant)	1.40	0.67	2.10	**0.04(*)**
		Female body size	0.53	0.55	0.96	0.34
(a) *Swimming under (s)*	*100*	Gravid spot size	0.07	0.09	0.73	0.47
		Trial type (No competition)	1.04	0.71	1.45	0.15
		Dominance x trial type	-0.85	0.97	-0.88	0.38
		Dominance (Dominant)	1.16	0.50	2.31	**0.02(*)**
		Female body size	-0.20	0.38	-0.54	0.59
(b) *Total courtship counts*	*100*	Gravid spot size	0.05	0.06	0.96	0.34
		Trial type (No competition)	1.04	0.53	1.96	0.05
		Dominance x trial type	-0.50	0.72	-0.69	0.49
Separate models						
Mate interactions with male-male competition						
		Dominance (Dominant)	1.40	0.68	2.06	**0.05(*)**
(c) *Swimming under (s)*	*52*	Female body size	-0.38	0.65	-0.59	0.56
		Gravid spot size	0.02	0.08	0.21	0.84
		Dominance (Dominant)	1.15	0.47	2.45	**0.01(*)**
(d) *Total courtship counts*	*52*	Female body size	-0.31	0.47	-0.67	0.50
		Gravid spot size	0.01	0.06	0.20	0.84
Mate interactions without male-male competition						
		Dominance (Dominant)	0.43	0.65	0.68	0.51
(e) *Swimming under (s)*	*48*	Female body size	1.90	0.89	2.14	**0.04(*)**
		Gravid spot size	0.38	0.23	1.70	0.11
		Dominance (Dominant)	0.62	0.54	1.20	0.25
(f) *Total courtship counts*	*48*	Female body size	-0.03	0.60	-0.05	0.96
		Gravid spot size	0.18	0.11	1.67	0.09

We tested the effect of male social dominance and female traits on the time each male spent swimming under each female (a, b, c) and on all discrete courtship behaviors (b, d, f) using linear mixed effects models (LMMs) and generalized linear mixed effects models (GLMMs), in 13 *mate interactions with male-male competition* trials (a, b, c, d) and in 12 *mate interactions without male-male competition* trials (a, b, e, f). In the combined models, was additionally tested the interaction between dominance and trial type (with vs without male-male competition) (a, b). The total number of pairs assessed (N) is presented, along with the standard error (SE), test statistic (z) and *P-value* for each effect. Significant *P-values* are shown in bold.

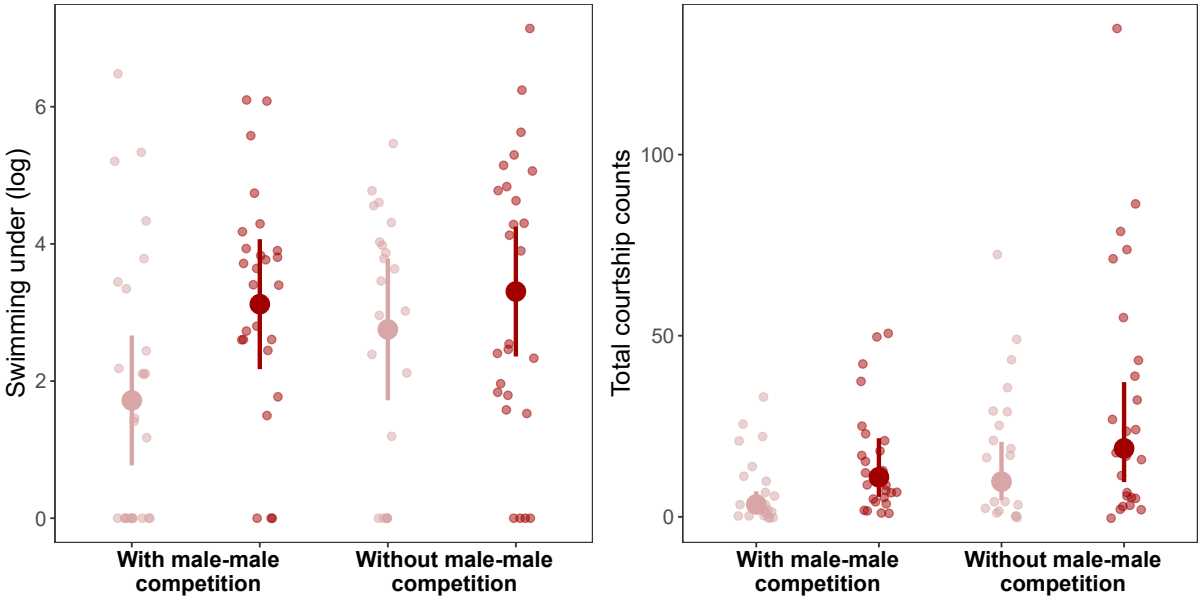

Fig. 1: Duration of time (seconds, log-transformed) that each male spent swimming under each female (a) and courtship behaviors (i.e. circling, swimming under attempts and mating attempts) performed by each male towards each female during the 30-minute observation period. Subordinate males are shown in light red; dominant males in dark red. Grey points represent raw observations, and colored dots show model-predicted means ± 95% confidence intervals.

3.2 Experiment 2: Male social dominance does not influence female mate choice

Females showed a significant preference for one of the two males presented in the dichotomous choice experiment ($V = 1081$, *P-value* < 0.0001). However, female strength of preference (SOP) was not influenced by male dominance status nor any of the morphological traits (i.e., body length, beak length, red colouration) considered in our analyses (Table 2,a). Thus, female halfbeaks appear to exhibit an unbiased mating preference, particularly with respect to male social dominance.

Table 2: Effect of male social dominance and male traits on female mate preference and choice

Response variable	N	Predictors	Estimates	SE	z	*P-values*
Female mate preference						
$SOP_{left\ male}$	*46*	Dominance (Dominant)	0.08	0.17	0.47	0.64
		Male body length	0.03	0.05	0.59	0.56
		Male beak length	-0.02	0.11	-0.21	0.83
		Male red coloration	-0.10	0.15	-0.64	0.52

We tested the effect of male social dominance and morphological differences between stimulus males on the strength of preference for the left male scores (an arbitrary male) using a linear mixed effects model (LMM) in dichotomous mate choice trials. The total number of trials (N) is presented, along with the standard error (SE), test statistic (z and *P-value* for each effect. Significant *P-values* are shown in bold.

4 Discussion

In this study, we experimentally examined if male social dominance provides fitness benefits through male-male competition, female mate choice, or a combination of these factors in the pygmy halfbeak. We first show that socially dominant males gain more reproductive access to females. Specifically, dominant males courted females more than socially subordinate mates. Moreover, by experimentally assessing female mate choice based on male social dominance, our findings also suggest that the greater reproductive access to females enjoyed by dominant males is not driven by female preference for these males. Instead, females showed no preference for males based on social dominance. Together, our integrated series of experiments demonstrate that male-male competition, not female mate choice, shapes male fitness in pygmy halfbeaks.

Social dominance offers a well-known route to securing fitness in a wide range of species (e.g. in fish, Deaton, 2008; Paull et al., 2010; Weir et al., 2004; in birds, Nelson-Flower and Ridley, 2015; in mammals, Rus Hoelzel et al., 1999; Ortega et al., 2003). In halfbeaks, dominant males monopolize reproductive access to females and spend more time courting females than subordinate males. Since courtship effort is often positively correlated with male fitness (e.g., Shamble et al., 2009; Stoltz et al., 2009; Alonso et al., 2010), dominant male halfbeaks may increase their reproductive potential at the expense of subordinate males. The reproductive potential of socially subordinate male halfbeaks may be further impaired by the physiological costs associated with male-male competition. Specifically, Reuland et al. (2021) found that high levels of male-male competition led to impaired ejaculate quality in subordinate males. Such costs of social subordination are common in animals, with subordinate males often having higher levels of stress hormones (e.g., Fox et al., 1997; Creel, 2001; Milewski et al., 2022), lower levels of sex hormones (e.g., androgens, Oliveira et al., 2002; Nelson, 2005), and reduced investment in testicular tissue (e.g., Fitzpatrick et al., 2006). However, maintaining social dominance can be costly, potentially leading to trade-offs with other sexually selected or life history traits. (Fitzpatrick et al., 2012; Parker et al., 2013; Lüpold et al., 2014; Simmons and Emlen, 2006). Although our experimental time frame was too short to reveal the potential costs of social dominance, this remains an interesting avenue for future investigation. It is also interesting to note there was no longer an effect of social dominance on male mating behaviors in trials without male-male competition when we ran separate models for each trial type. This suggests that persistent physical interactions may be required for socially dominant male halfbeaks to maintain their reproductive advantage, potentially generating selection on agonistic male behaviours.

We found no evidence that male social dominance influences pre-copulatory female mate choice in halfbeaks, contradicting the general assumption that traits involved in male-male competition serve as

honest signals for female choice (Berglund et al., 1996). This finding also contrasts with the abundant empirical evidence that females often prefer dominant males as mates (Cox and Le Boeuf, 1977; Candolin, 1999; Kunc et al., 2006; Aquiloni et al., 2008; Aquiloni and Gherardi, 2010; Loranger and Bertram, 2016). While female halfbeaks showed a clear preference for one male over the other in the dichotomous choice experiment, male social dominance did not predict female preference. This suggests that female halfbeaks may be indifferent to social dominance even after having the opportunity to eavesdrop on male-male interactions. One possible explanation is that male-male competition only influences female preferences when it provides net fitness gains (Wong and Candolin, 2005). If dominance is not directly correlated to offspring viability, female halfbeaks may not gain useful information that will impact their fitness prospects from observing male bouts. For example, in the Pacific blue-eye fish *Pseudomugil signifier*, hatching success of eggs guarded by dominant or subordinate males did not differ, and females consequently showed no preference for winners or losers when privy to male competition (Wong, 2004). Similarly, in the sand goby *Pomatoschistus minutus*, females did not prefer dominant males but instead preferred good fathers (Forsgren, 1997). These results suggest that alternative traits may therefore be more important in signaling genetic quality or male investment in activities (e.g. defence of spawning sites) that translate into actual fitness gains to females. The potential links between social dominance and aspects of male quality that could offer females direct or indirect benefits in halfbeaks remain poorly understood and require further investigations.

An alternative explanation for our observed lack of female preference for dominant males could be that females are not under selection to discriminate based on male social dominance because male-male competition effectively eliminates subordinate males as potential suitors. This possibility was clearly evident from our experiment that allowed male-male competition during male-female interactions. By displacing subordinate males, dominant males may "pre-select" potential mates, resulting in females being predominantly courted by dominant males, and eliminating the need for females to exhibit an active preference for male social status (Wong and Candolin, 2005). Halfbeaks live in large mix sexed shoals where male-male agonistic behaviours are common (Devigili et al., 2021), suggesting that male-male social interactions mediate access to mates in wild halfbeak populations. This raises the possibility that strong male-male competition could relax selection on pre-copulatory female mate choice.

In conclusion, we provide robust evidence that male-male competition, not female mate choice, explains the reproductive advantage of socially dominant males in the pygmy halfbeak. Although females are often assumed to use the outcome of male-male competition to select high-quality mates (Berglund et al., 1996; Wiley and Poston, 1996; Wong and Candolin, 2005), our study challenges this assumption, since female halfbeaks showed no particular preference for males they observed winning intra-sexual

contests. To prioritize tractability, our experimental design focused on the minimum number of males necessary to generate a dominance hierarchy: two males. However, in the wild halfbeaks live in shoals of 6 to 120 individuals (Devigili et al., 2021), where dominant males may face greater challenges in monopolizing mates as group size increases (Newton-Fisher et al., 2010; Lardy et al., 2012), potentially limiting the role of social dominance in securing male fitness (Reeve et al., 1998; Clutton-Brock, 1998). Future research should assess how male-male competition influences male fitness in more dynamic and ecologically relevant social conditions.

References

Alonso, J. C., M. Magaña, C. Palacín, and C. A. Martín. 2010. Correlates of male mating success in great bustard leks: the effects of age, weight, and display effort. Behavioral Ecology and Sociobiology 64:1589–1600. Publisher: Springer.

Aquiloni, L., M. Buřič, and F. Gherardi. 2008. Crayfish females eavesdrop on fighting males before choosing the dominant mate. Current Biology 18:R462–R463. Publisher: Elsevier.

Aquiloni, L., and F. Gherardi. 2010. Crayfish females eavesdrop on fighting males and use smell and sight to recognize the identity of the winner. Animal Behaviour 79:265–269. Publisher: Elsevier.

Bailey, N. W., and M. Zuk. 2008. Acoustic experience shapes female mate choice in field crickets. Proceedings of the Royal Society B: Biological Sciences 275:2645–2650. Publisher: The Royal Society London.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48.

Baxter, C. M., R. Barnett, and R. Dukas. 2015. Aggression, mate guarding and fitness in male fruit flies. Animal Behaviour 109:235–241. Publisher: Elsevier.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biological Journal of the Linnean Society 58:385–399. Publisher: Oxford University Press.

Bierbach, D., V. Sassmannshausen, B. Streit, L. Arias-Rodriguez, and M. Plath. 2013. Females prefer males with superior fighting abilities but avoid sexually harassing winners when eavesdropping on male fights. Behavioral Ecology and Sociobiology 67:675–683. Publisher: Springer.

Bischoff, R. J., J. L. Gould, and D. I. Rubenstein. 1985. Tail size and female choice in the guppy (Poecilia reticulata). Behavioral Ecology and Sociobiology 17:253–255. Publisher: Springer.

Brooks, M. E., K. Kristensen, K. J. v. Benthem, A. Magnusson, C. W. Berg, A. Nielsen, H. J. Skaug, M. Mächler, and B. M. Bolker. 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9:378–400.

Bulger, J. B. 1993. Dominance rank and access to estrous females in male savanna baboons. Behaviour pages 67–103. Publisher: JSTOR.

Candolin, U. 1999. Male–male competition facilitates female choice in sticklebacks. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:785–789. Publisher: The Royal Society.

Chan, J. P., P. R. Lau, A. J. Tham, and D. Li. 2008. The effects of male–male contests and female eavesdropping on female mate choice and male mating success in the jumping spider, Thiania bhamoensis (Araneae: Salticidae). Behavioral Ecology and Sociobiology 62:639–646. Publisher: Springer.

Clutton-Brock, T. H. 1998. Reproductive skew, concessions and limited control. Trends in Ecology & Evolution 13:288–292. Publisher: Elsevier.

Coleman, S. W., G. L. Patricelli, and G. Borgia. 2004. Variable female preferences drive complex male displays. Nature 428:742–745. Publisher: Nature Publishing Group UK London.

Cox, C. R., and B. J. Le Boeuf. 1977. Female incitation of male competition: a mechanism in sexual selection. The American Naturalist 111:317–335. Publisher: University of Chicago Press.

Creel, S. 2001. Social dominance and stress hormones. Trends in ecology & evolution 16:491–497. Publisher: Elsevier.

Darwin, C. 1871. The Descent of Man, and Selection in Relation to Sex, vol. 1. Murray, London.

Deaton, R. 2008. Use of microsatellite paternity analysis to determine male mating success in the western mosquitofish, Gambusia affinis. Behaviour pages 795–814. Publisher: JSTOR.

Devigili, A., E. Fernlund Isaksson, N. Puniamoorthy, and J. L. Fitzpatrick. 2021. Behavioral Variation in the Pygmy Halfbeak Dermogenys collettei: Comparing Shoals With Contrasting Ecologies. Frontiers in Ecology and Evolution 9. Publisher: Frontiers.

Doutrelant, C., and P. McGregor. 2000. Eavesdropping and mate choice in female fighting fish. Behaviour 137:1655–1668. Publisher: Brill.

Dugatkin, L. 1996. Copying and mate choice. In "Social Learning in Animals: The Roots of Culture"(CM Heyes and BG Galef, Eds.) Publisher: Academic Press, San Diego.

Dukas, R. 2005. Learning affects mate choice in female fruit flies. Behavioral Ecology 16:800–804. Publisher: Oxford University Press.

Emlen, D. J. 2008. The evolution of animal weapons. Annual review of ecology, evolution, and systematics 39:387–413. Publisher: Annual Reviews.

Fernlund Isaksson, E., C. Reuland, A. F. Kahrl, A. Devigili, and J. L. Fitzpatrick. 2022. Resource-dependent investment in male sexual traits in a viviparous fish. Behavioral Ecology 33:954–966.

Fitzpatrick, J., J. Desjardins, K. Stiver, R. Montgomerie, and S. Balshine. 2006. Male reproductive suppression in the cooperatively breeding fish Neolamprologus pulcher. Behavioral Ecology 17:25–33. Publisher: Oxford University Press.

Fitzpatrick, J. L., L. W. Simmons, and J. P. Evans. 2012. Complex patterns of multivariate selection on the ejaculate of a broadcast spawning marine invertebrate: multivariate selection on the ejaculate. Evolution 66:2451–2460.

Forsgren, E. 1997. Female sand gobies prefer good fathers over dominant males. Proceedings of the Royal Society of London. Series B: Biological Sciences 264:1283–1286. Publisher: The Royal Society.

Fox, H. E., S. A. White, M. H. Kao, and R. D. Fernald. 1997. Stress and dominance in a social fish. Journal of Neuroscience 17:6463–6469. Publisher: Soc Neuroscience.

Friard, O., and M. Gamba. 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7:1325–1330.

Greven, H., M. Uribe, and H. Grier. 2010. What do we know about reproduction of internally fertilizing halfbeaks (Zenarchopteridae). Viviparous fishes II. Homestead (FL): New Life Publications pages 121–142.

Hardy, I. C., and M. Briffa. 2013. Animal contests. Cambridge University Press.

Hunt, J., C. J. Breuker, J. A. Sadowski, and A. J. Moore. 2009. Male–male competition, female mate choice and their interaction: determining total sexual selection. Journal of Evolutionary Biology 22:13–26. _eprint: https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1420-9101.2008.01633.x.

Janicke, T., I. K. Häderer, M. J. Lajeunesse, and N. Anthes. 2016. Darwinian sex roles confirmed across the animal kingdom. Science advances 2:e1500983. Publisher: American Association for the Advancement of Science.

Jennions, M. D., and M. Petrie. 2000. Why do females mate multiply? A review of the genetic benefits. Biological Reviews 75:21–64.

Khazraıe, K., and M. Campan. 1999. The role of prior agonistic experience in dominance relationships in male crickets Gryllus bimaculatus (Orthoptera: Gryllidae). Behavioural Processes 44:341–348. Publisher: Elsevier.

Kokko, H., H. Klug, and M. D. Jennions. 2012. Unifying cornerstones of sexual selection: operational sex ratio, Bateman gradient and the scope for competitive investment. Ecology Letters 15:1340–1351.

Kokko, H., and J. Mappes. 2005. Sexual selection when fertilizations is not guarenteed. Evolution 59:1876–1885.

Kunc, H. P., V. Amrhein, and M. Naguib. 2006. Vocal interactions in nightingales, Luscinia megarhynchos: more aggressive males have higher pairing success. Animal Behaviour 72:25–30. Publisher: Elsevier.

Lardy, S., A. Cohas, E. Desouhant, M. Tafani, and D. Allainé. 2012. Paternity and dominance loss in male breeders: the cost of helpers in a cooperatively breeding mammal. PLoS One 7:e29508. Publisher: Public Library of Science San Francisco, USA.

Loranger, M. J., and S. M. Bertram. 2016. The effect of male dominance on female choice in a field cricket (Gryllus assimilis). Animal Behaviour 114:45–52. Publisher: Elsevier.

Lüpold, S., J. L. Tomkins, L. W. Simmons, and J. L. Fitzpatrick. 2014. Female monopolization mediates the relationship between pre-and postcopulatory sexual traits. Nature communications 5:3184. Publisher: Nature Publishing Group UK London.

McCullough, E. L., C. W. Miller, and D. J. Emlen. 2016. Why sexually selected weapons are not ornaments. Trends in Ecology & Evolution 31:742–751. Publisher: Elsevier.

McNeil, R. M., A. Devigili, N. Kolm, and J. L. Fitzpatrick. 2021. Does brain size affect mate choice? An experimental examination in pygmy halfbeaks. Behavioral Ecology 32:1103–1113.

Meisner, A. D. 2001. Phylogenetic systematics of the viviparous halfbeak genera Dermogenys and Nomorhamphus (Teleostei: Hemiramphidae: Zenarchopterinae). Zoological Journal of the Linnean Society 133:199–283. Publisher: Oxford University Press.

Mennill, D. J., L. M. Ratcliffe, and P. T. Boag. 2002. Female eavesdropping on male song contests in songbirds. Science 296:873–873. Publisher: American Association for the Advancement of Science.

Milewski, T., W. Lee, F. Champagne, and J. Curley. 2022. Behavioural and physiological plasticity in social hierarchies. Philosophical Transactions of the Royal Society B 377:20200443. Publisher: The Royal Society.

Montana, L., W. J. King, G. Coulson, D. Garant, and M. Festa-Bianchet. 2022. Large eastern grey kangaroo males are dominant but do not monopolize matings. Behavioral Ecology and Sociobiology 76:78. Publisher: Springer.

Nelson, R. J. 2005. An introduction to behavioral endocrinology. Sinauer Associates.

Nelson-Flower, M. J., and A. R. Ridley. 2015. Male-male competition is not costly to dominant males in a cooperatively breeding bird. Behavioral ecology and sociobiology 69:1997–2004. Publisher: Springer.

Newton-Fisher, N. E., M. E. Thompson, V. Reynolds, C. Boesch, and L. Vigilant. 2010. Paternity and social rank in wild chimpanzees (Pan troglodytes) from the Budongo Forest, Uganda. American Journal of Physical Anthropology 142:417–428. Publisher: Wiley Online Library.

Ogden, H. J. P., R. A. de Boer, A. Devigili, C. Reuland, A. F. Kahrl, and J. L. Fitzpatrick. 2020. Male mate choice for large gravid spots in a livebearing fish. Behavioral Ecology 31:63–72.

Oliveira, R. F., K. Hirschenhauser, L. A. Carneiro, and A. V. Canario. 2002. Social modulation of androgen levels in male teleost fish. Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology 132:203–215. Publisher: Elsevier.

Ophir, A. G., and B. G. Galef Jr. 2003. Female Japanese quail that 'eavesdrop'on fighting males prefer losers to winners. Animal Behaviour 66:399–407. Publisher: Elsevier.

Ortega, J., J. E. Maldonado, G. S. Wilkinson, H. T. Arita, and R. C. Fleischer. 2003. Male dominance, paternity, and relatedness in the Jamaican fruit-eating bat (Artibeus jamaicensis). Molecular Ecology

12:2409–2415. Publisher: Wiley Online Library.

Parker, G. A., C. M. Lessells, and L. W. Simmons. 2013. Sperm competition games: a general model for precopulatory male–male competition. Evolution 67:95–109. Publisher: Blackwell Publishing Inc Malden, USA.

Paull, G. C., A. L. Filby, H. G. Giddins, T. S. Coe, P. B. Hamilton, and C. R. Tyler. 2010. Dominance hierarchies in zebrafish (Danio rerio) and their relationship with reproductive success. Zebrafish 7:109–117. Publisher: Mary Ann Liebert, Inc. 140 Huguenot Street, 3rd Floor New Rochelle, NY 10801 USA.

Plath, M., and D. Bierbach. 2011. Sex and the public: social eavesdropping, sperm competition risk, and male mate choice. Communicative & integrative biology 4:276–280. Publisher: Taylor & Francis.

Reeve, H. K., S. T. Emlen, and L. Keller. 1998. Reproductive sharing in animal societies: reproductive incentives or incomplete control by dominant breeders? Behavioral Ecology 9:267–278. Publisher: Oxford University Press.

Reuland, C., B. M. Culbert, A. Devigili, A. F. Kahrl, and J. L. Fitzpatrick. 2020. Contrasting female mate preferences for red coloration in a fish. Current Zoology 66:425–433.

Reuland, C., B. M. Culbert, E. Fernlund Isaksson, A. F. Kahrl, A. Devigili, and J. L. Fitzpatrick. 2021. Male–male behavioral interactions drive social-dominance-mediated differences in ejaculate traits. Behavioral Ecology 32:168–177.

Richardson, J., and M. Zuk. 2023. Unlike a virgin: a meta-analytical review of female mating status in studies of female mate choice. Behavioral Ecology 34:165–182.

Rus Hoelzel, A., B. J. Le Boeuf, J. Reiter, and C. Campagna. 1999. Alpha-male paternity in elephant seals. Behavioral Ecology and Sociobiology 46:298–306. Publisher: Springer.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nature methods 9:671–675. Publisher: Nature Publishing Group.

Shamble, P. S., D. J. Wilgers, K. A. Swoboda, and E. A. Hebets. 2009. Courtship effort is a better predictor of mating success than ornamentation for male wolf spiders. Behavioral Ecology 20:1242–1251. Publisher: Oxford University Press.

Simmons, L. W., and D. J. Emlen. 2006. Evolutionary trade-off between weapons and testes. Proceedings of the National Academy of Sciences 103:16346–16351. Publisher: Proceedings of the National Academy of Sciences.

Stoltz, J., D. Elias, and M. Andrade. 2009. Male courtship effort determines female response to competing rivals in redback spiders. Animal Behaviour 77:79–85. Publisher: Elsevier.

Team, R. C. 2023. R: A Language and Environment for Statistical Computing.

Walling, C. A., N. J. Royle, J. Lindström, and N. B. Metcalfe. 2010. Do female association preferences predict the likelihood of reproduction? Behavioral Ecology and Sociobiology 64:541–548. Publisher:

Springer.

Weir, L. K., J. A. Hutchings, I. A. Fleming, and S. Einum. 2004. Dominance relationships and behavioural correlates of individual spawning success in farmed and wild male Atlantic salmon, Salmo salar. Journal of Animal Ecology 73. Publisher: Citeseer.

White, E. M., J. C. Partridge, and S. C. Church. 2003. Ultraviolet dermal reflexion and mate choice in the guppy, Poecilia reticulata. Animal Behaviour 65:693–700. Publisher: Elsevier.

Wiley, R. H., and J. Poston. 1996. Perspective: indirect mate choice, competition for mates, and coevolution of the sexes. Evolution 50:1371–1381. Publisher: Wiley Online Library.

Wong, B. B. 2004. Superior fighters make mediocre fathers in the Pacific blue-eye fish. Animal Behaviour 67:583–590. Publisher: Elsevier.

Wong, B. B., and U. Candolin. 2005. How is female mate choice affected by male competition? Biological Reviews 80:559–571. Publisher: Cambridge University Press.