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Raisa Lück

University of Southern Maine

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A female audience increases frequency of showy agonistic displays in male Siamese fighting fish

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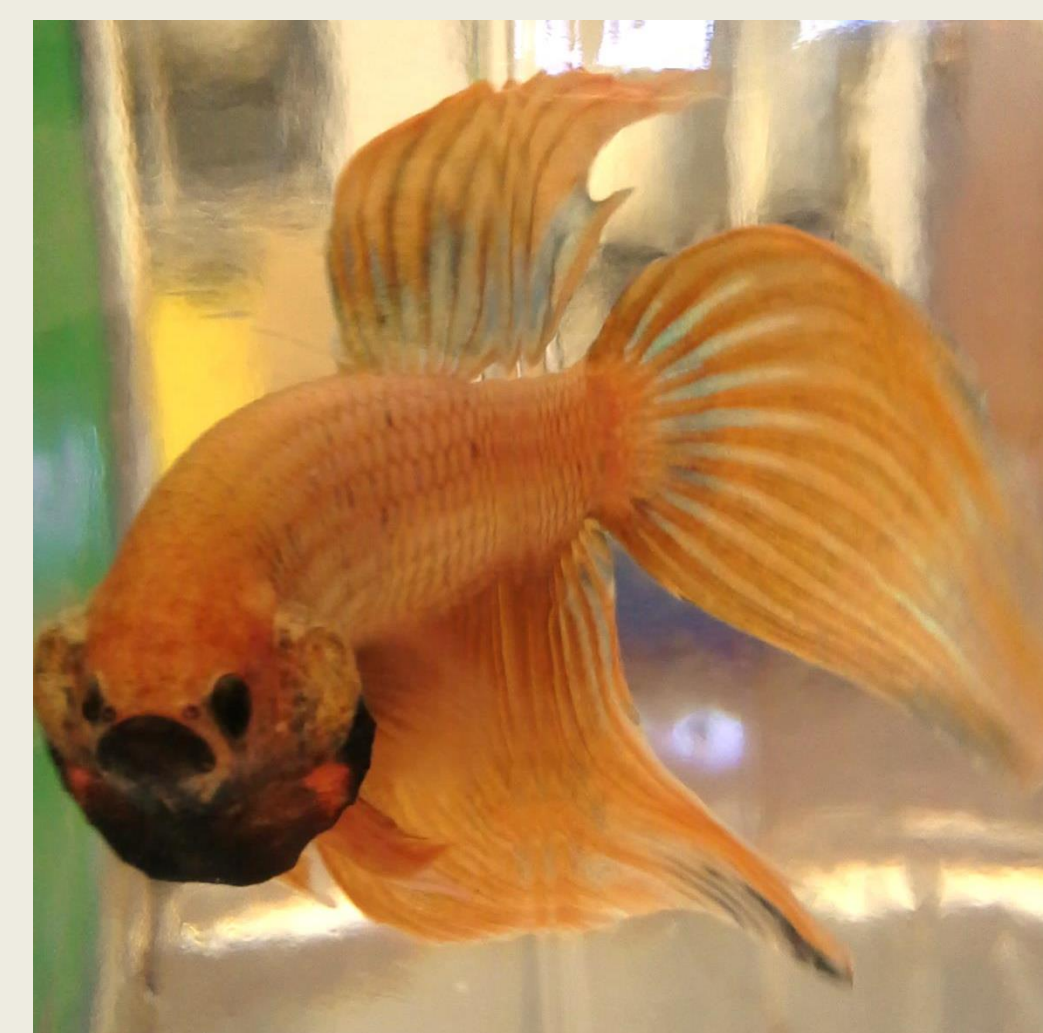
Department of Biology, University of Southern Maine, Portland, ME 04104

ABSTRACT

The audience effect refers to a situation where individuals alter displays in the presence of bystanders. By changing display choice, displayers can optimize their effectiveness against both the opponent and audience. Many displays – territorial, aggressive, warning, and threatening – fall into the broad category of agonistic behavior. Male Siamese fighting fish (*Betta splendens*) are known for being territorial, and they use the same set of stereotypical displays repeatedly from one male to the next. I observed effects of a female audience on male *Betta* displays to determine if males use certain displays more frequently than others when a female is present versus absent. I predicted that, in order to court a female audience and still defend his territory, males increase the frequency of showy displays, whereas males use aggressive displays more frequently when no audience is present. To test my predictions, I continuously recorded the frequency of each display type between males in the presence and absence of females. Males significantly increased the proportion of showy displays used with a female audience present as well as substantially decreased aggressive displays, suggesting that males alter display frequencies in the presence of an audience. The presence of a female audience strongly influences display choice in males, suggesting a trade-off between courting a female and defending a territory.

INTRODUCTION

Agonistic displays are displays directly involved in conflict between two or more individuals. Researchers have observed some form of agonistic behavior in fish, birds, mammals, insects, and amphibians (Dzieweczynski et al. 2012). While individuals perform agonistic displays, other individuals nearby may not be involved in displaying, i.e., audiences, and their presence may change display choice because displayers sense the presence of these individuals (Matos & McGregor, 2002). Displayers must choose displays that maximize their effectiveness against both the opponent and audience, resulting in a trade-off between defending themselves against the opponent and conveying information to the audience (Matos & McGregor, 2002).



Male *Betta* flaring his fins with his operculum extended

Male Siamese fighting fish (*Betta splendens*) have easily identifiable agonistic displays that make them ideal candidates for testing the audience effect in a lab setting (Matos & McGregor, 2002). Male *Bettas* are notably territorial and display shortly after they encounter another male; if a female were present during these displays, then a male may attempt to court her while still asserting his territorial claim (Matos & McGregor, 2002). My objective was to determine if a female audience changes the type and frequency of displays in males.

PREDICTIONS

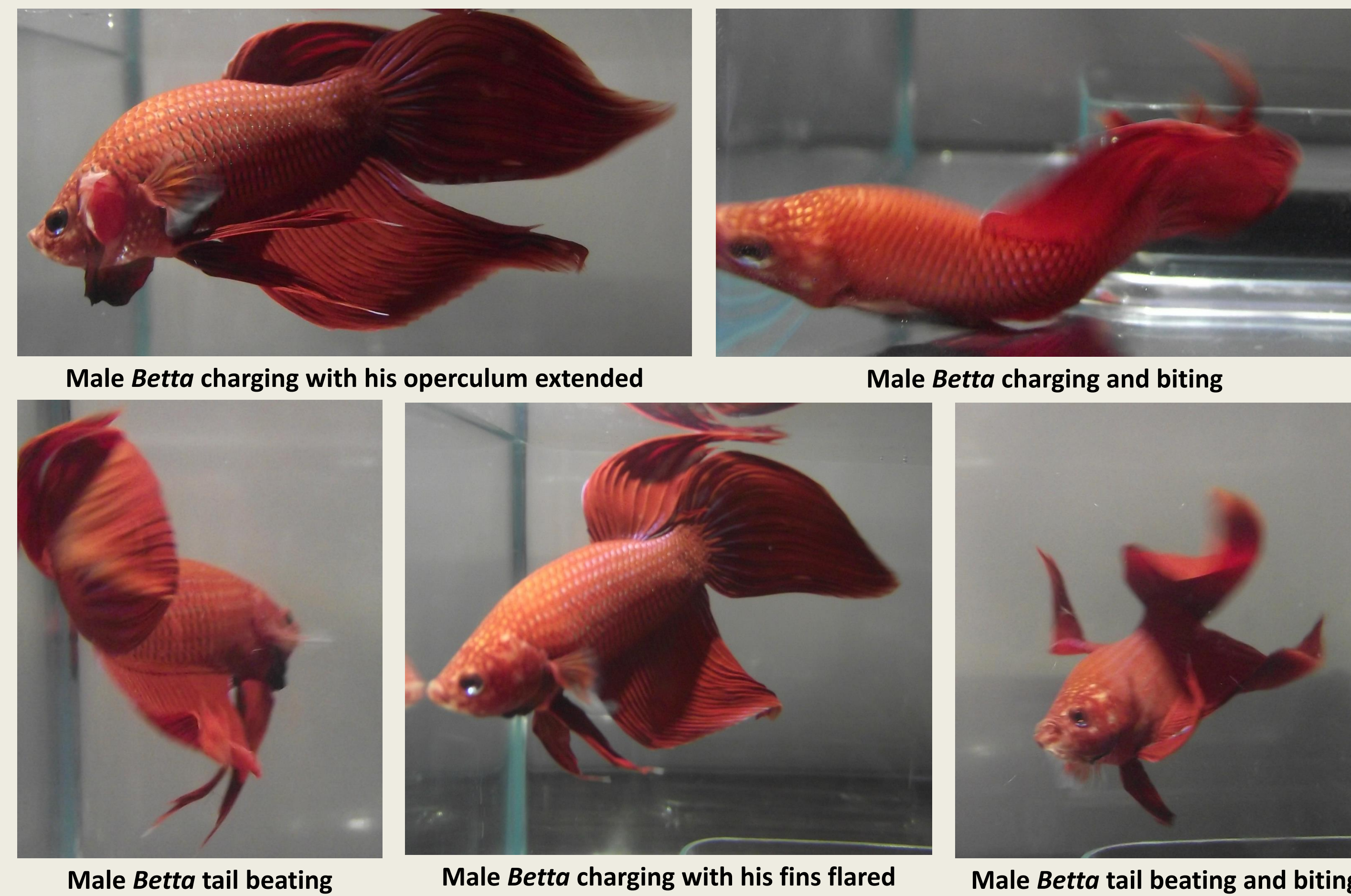
- When a female audience is present, males use showy displays more frequently to court the female.
- When no female is present, males increase the frequency of aggressive displays to more effectively defend their territory.

METHODS AND MATERIALS

I conducted the study in Room 160 Science at the University of Southern Maine with a total of 8 males and 3 females. I kept males in separate 3.8 l tanks at room temperature where they were visually separated from each other by screens. I tested each focal male with every other male once with a female audience and once without an audience for a total of 14 tests per male.

For my tests, I randomly selected two males (control test) or two males and a female (experimental test), and I set their tanks side-by-side. I continuously recorded frequency of focal male displays for 10 min, once males began to display to each other. Displays included tail beats, operculum extensions, flares, bites, charges, and retreats. I did not test the same male more than twice in one testing session.

I calculated mean display frequencies for each male during control and experimental tests. I then performed a repeated measures, two-tailed t test to compare mean cumulative frequencies, measured as percent of total displays, of each display type (showy, aggressive, and submissive) to test for the audience effect. I used JMP software with a significance level of $P < 0.05$.



Male *Betta* charging with his operculum extended

Male *Betta* charging and biting

Male *Betta* tail beating

Male *Betta* charging with his fins flared

Male *Betta* tail beating and biting

RESULTS

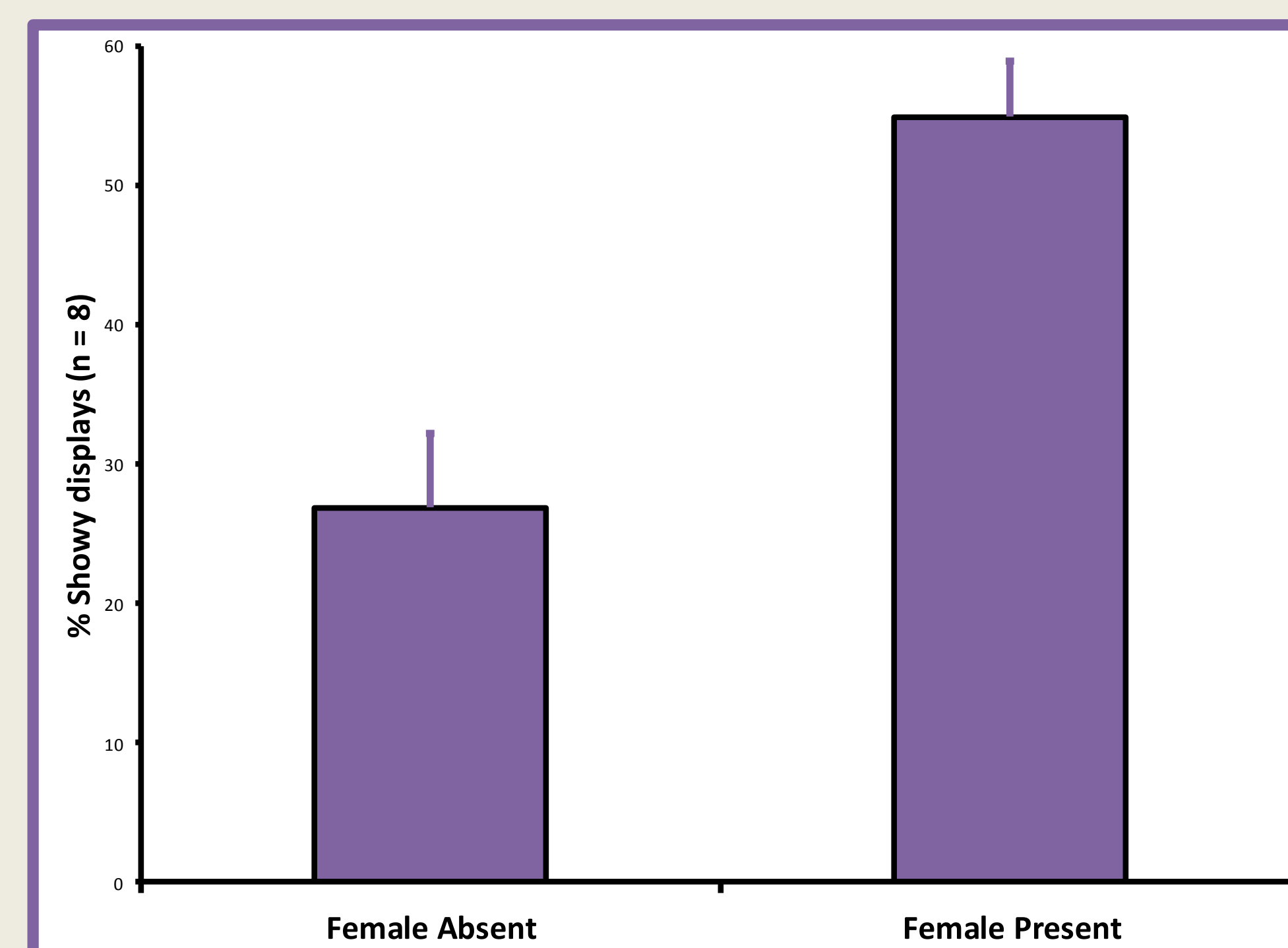


Fig. 1 Mean (+ SD) percentage of showy displays for both treatments. Males significantly increased their mean frequency of showy displays in the presence of a female ($t = -23.39$, $DF = 7$, $P < 0.0001$). Percentage of showy displays nearly doubled in the presence of a female.

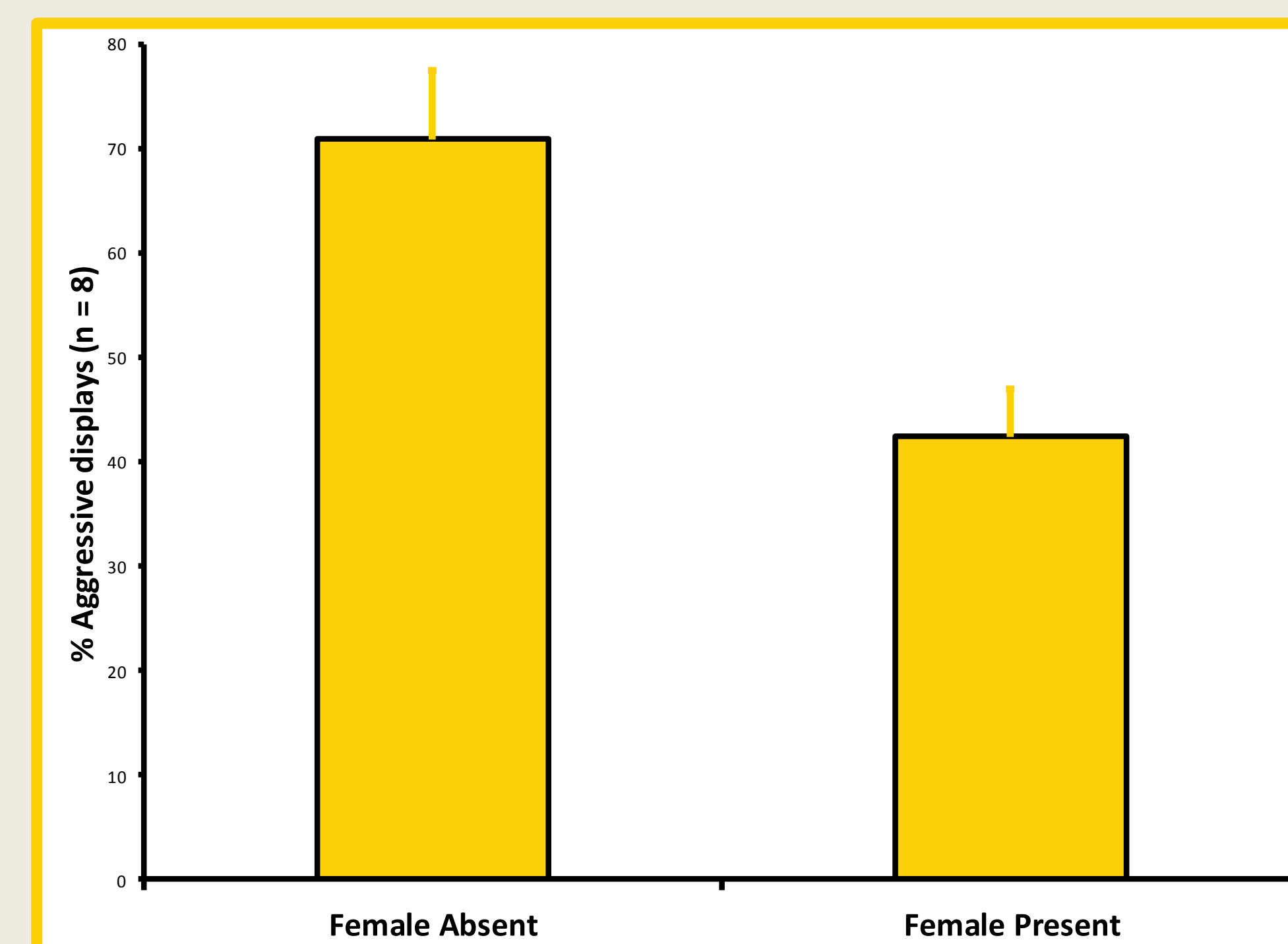


Fig. 2 Mean (+ SD) of aggressive displays for both experiment types. Males significantly increased mean frequency of aggressive displays in the absence of a female ($t = 22.80$, $DF = 7$, $P < 0.0001$). Aggressive displays increased by forty percent in the absence of a female.

DISPLAY GUIDE

Showy	Aggressive	Submissive
Tail beats Fin flares	Operculum extensions Attempted bites Charges	Retreats

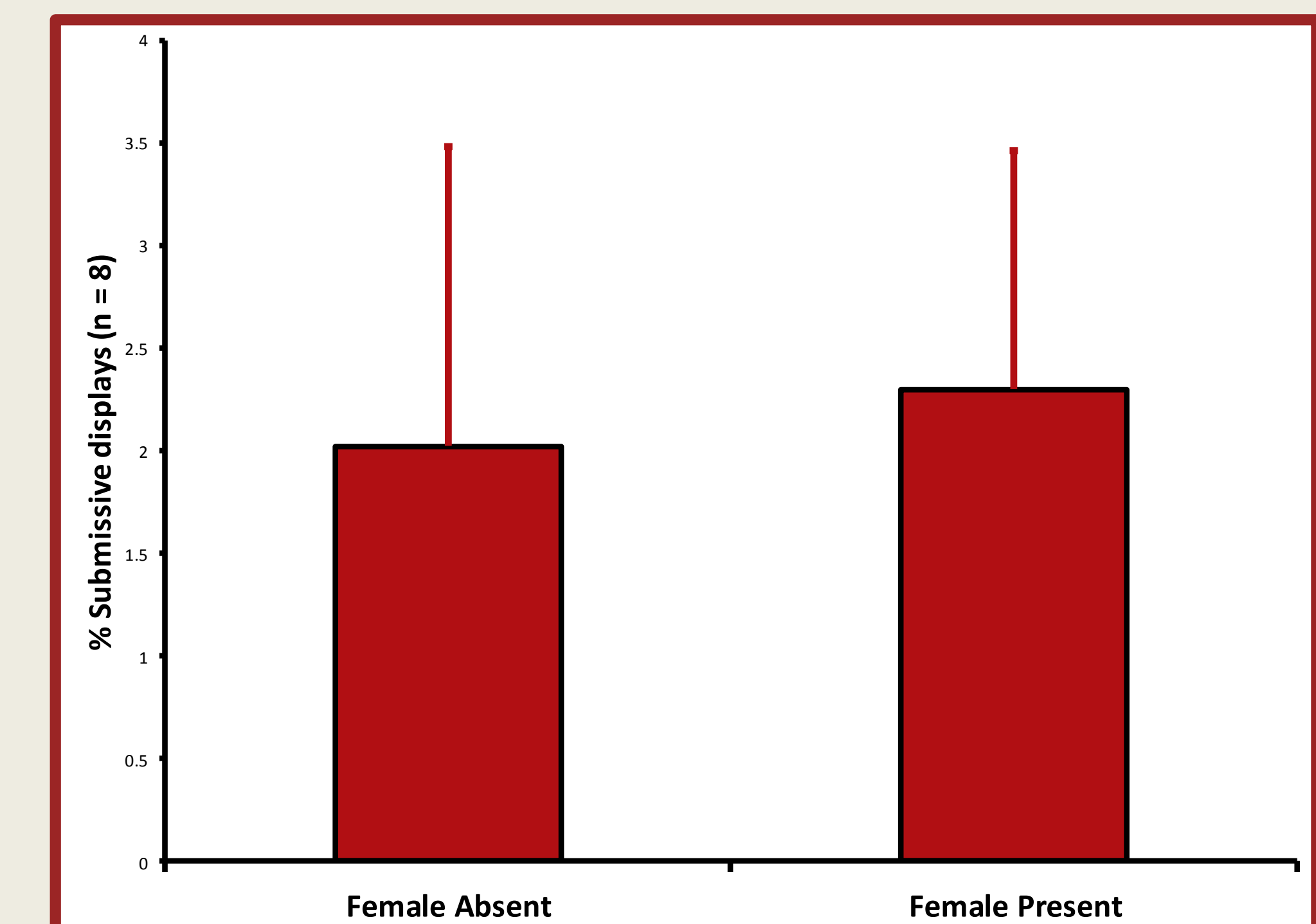


Fig. 3 Mean (+ SD) percentage of submissive displays for both treatments. Mean frequency of submissive displays did not differ when a female was present versus absent ($t = -0.93$, $DF = 7$, $P = 0.3831$).

CONCLUSIONS

Males respond to a female audience by increasing the frequency of showy displays and decreasing the frequency of aggressive displays. By increasing showy displays, males may attempt to court the female amidst their territorial displays (Matos & McGregor, 2002). Furthermore, males have a limited number of displays to choose from; if they increase one type of display, it inevitably results in a decrease of the other. Males may decrease displays of aggression in the presence of a female to avoid driving her away; females may prefer males that display less aggression, particularly biting, to avoid injury (Doutrelant & McGregor, 2000; Matos & McGregor, 2002). Submissive displays remained unchanged across treatments, most likely because any acts of submission would be unfavorable during courting and territory defense (Dzieweczynski et al. 2012; Matos & McGregor, 2002).

My results are similar to other studies observing male *Betta* displays and the audience effect (Matos & McGregor, 2002). Tail beating indicates male stamina, and females use tail beating to assess a male's overall condition (Matos & McGregor, 2002). By increasing showy displays such as tail beating that require high inputs of energy, males may increase their reproductive success in the wild, where they are likely to encounter a female audience (Matos & McGregor, 2002). However, using high energy displays and giving more attention to the audience than the opponent leaves displaying males at a disadvantage against opponents, and they may be less effective at defending their territory (Matos & McGregor, 2002).

Even though display frequencies changed markedly in the presence of a female audience, nearly 50% of all displays were aggressive. Operculum extensions, classified as an aggressive display in this experiment, also can be considered a showy display because males flare the operculum at females as well as males (Matos & McGregor, 2002). By not differentiating which fish was the recipient of each operculum extension, I was unable to include operculum extensions as a showy display. Further research paying careful attention to operculum extensions in males would be beneficial, in which operculum extensions directed at females were separated from those directed at males.

My results support the prevalence of the audience effect on displaying male *Bettas*. Males are aware of audiences and respond accordingly by choosing displays that allow them to interact with both the opponent and audience.

ACKNOWLEDGEMENTS

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