



Female aggression towards same-sex rivals depends on context in a tropical songbird

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ABSTRACT

Agonistic conflict is ubiquitous throughout taxa, although the intensity of aggression observed is often highly variable across contexts. For socially monogamous species, a coordinated effort by both pair members can improve the chances of successfully warding off challengers and reinforce pair bonds. However, the intensity of aggression exerted by any one pair member may vary with respect to contextual factors, including the intensity of their mate's aggression. Thus, experimentally exploring how individuals respond to potential rivals via multiple assays with varying social contexts can advance our basic understanding of how aggression varies in socially monogamous systems. We used simulated territorial intrusion and mirror image simulation assays to explore this issue in white-shouldered fairywrens (*Malurus alboscapulatus moretoni*) of Papua New Guinea. While males tended to be more responsive than females during simulated territorial intrusions, females were more aggressive towards their mirrored reflection than males. Further, individual females that were most aggressive in mirror image simulations were the least aggressive during simulated territorial intrusions, whereas males were inconsistent. These results suggest that female behavioral phenotypes appear to be flexible, relative to context. We discuss how multiple commonly used measurements of aggression might in fact measure different types of responses.

1. Introduction

Behavioral flexibility allows animals to respond to abrupt changes in social and/or ecological environment (Piersma and Drent, 2003; West-Eberhard, 2003; Ghalambor et al., 2010). Even the most commonly studied behaviors that are repeatable across context and time (e.g., “personality” traits; Sih et al., 2004; Sgoifo et al., 2005), are often context dependent (Frost et al., 2007; Chenar and Duckworth, 2021). For example, there exists tremendous variation among individuals, populations, and species in the intensity of territorial aggression. Yet, conflict is a risky and energetically expensive endeavor, and thus an individual's ability to appropriately match aggression intensity to context is likely to have important fitness consequences (Parker, 1974; Maynard Smith and Harper, 1988; Duque-Wilckens et al., 2019). For this reason, a better understanding of context-dependent flexibility in aggressive behavior represents an important goal among behavioral ecology researchers.

Both female and male animals throughout taxa engage in agonistic encounters, but the intensity of aggression is expected to differ between sexes due to sex-specific variation in selection pressures (Archer, 1988; Arnott and Elwood, 2009; Elias et al., 2010). Differences between sexes in fighting costs, encounter rates with rivals, and/or perceived resource value may contribute to overall differences in behavioral tactics during same-sex encounters. For example, male *Phidippus clarus* jumping spiders frequently encounter other male rivals, and thus selection has favored the evolution of ritualized displays that preemptively settle contests without overt aggression (Elias et al., 2010). On the other hand, contests in females of the same species are more likely to end in injury or even death, as the intensity of aggression seen is dictated by perceived value of the resource rather than resource holding potential per se (Elias et al., 2010). Among socially monogamous species, both females and males are thought to mutually benefit from holding a common territorial space, as territory loss is likely to have negative fitness consequences for both sexes. Indeed, joint territorial defense may play a key role in the

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evolution of social monogamy (Roberts and DunBar, 2000; Whiteman and Côté, 2004; Ralls et al., 2007; Quinard and Cézilly, 2012; Hirsch and Komdeur, 2017). Nevertheless, the degree to which sexes exhibit differential intensity of territorial aggression in varying contexts, and why such differences may occur, remains unclear. Studying the aggressive behavior of both sexes in different contexts may provide important insights into the adaptive significance of aggression as well as the evolutionary forces underlying sex differences in territoriality that may be overlooked when only a single sex is studied in isolation (Arnott and Elwood, 2009). Two pivotal factors that may influence the intensity of individual aggression are (1) whether the mate is present during territorial defense and, if so, (2) the intensity of the mate's response. Thus, for species with mutual territory defense, any one individual's response may be impacted by their mate's behavior, thus impacting our interpretation of individual aggression. For example, Schuppe et al. (2016) found that, in mated pairs of downy woodpeckers (*Picoides pubescens*), the first individual to respond to a simulated threat, regardless of sex, altered their aggressive intensity upon arrival of their mate and that both sexes coordinate effectively against high-threat intruders (see also Miles and Fuxjager, 2019). These and other studies show that the relationship between context and individual behavioral choices is complex between sexes, further highlighting the need to better understand the factors that might contribute to individual variation and sex-specific differences in territorial aggression.

Among the most common behavioral assays ethologists use to estimate aggression in wild animals are simulated territorial intrusions. These tests are commonplace throughout studies of vertebrate (e.g., Goymann et al., 2019; Moore et al., 2020) and invertebrate taxa (e.g., Iyengar et al., 2013) due to their relative simplicity, general cost effectiveness, and their usefulness as a proxy of how territory residents respond to experimental intruders under relatively natural conditions. These playback experiments are commonly used to discern how various experimental stimuli of differing modalities (e.g., visual and/or acoustic) may elicit differential territorial behaviors. For example, researchers may explore how variation in visual stimuli influence territoriality via the use of either a caged, live conspecific decoy or that of a static mount (either artificial or a dead, stuffed conspecific). While the static mount decoy may easily be standardizable, it does not interact with focal individuals and such a lack of interaction may insufficiently mimic natural social competition (Scriba and Goymann, 2008). This, in turn, would not elicit a full neurogenomic response of the resident individuals as would be seen in contests with physical contact (Scriba and Goymann, 2008; Calisi and Bentley, 2009; Goymann, 2009; Oliveira et al., 2016). However, although a caged, live decoy may interact with the focal individual, the disparity between the behavioral phenotype of the decoy per se and focal individuals may yield distinct outcomes (Scriba and Goymann, 2008). That is to say, if caged individuals are "higher quality" than focal individuals, the free-living individual may respond fundamentally differently than a "lower quality" individual.

To mitigate these limitations, an alternate approach may involve the use of mirror image stimulation assays, or those that temporarily place individuals in a captive environment and expose them to their own mirrored reflection (Gallup Jr, 1968). During mirror assays, an individual's reaction to their own reflection is interpreted as how they may perceive a conspecific, assuming they are unable to self-recognize (as is the case in most bird species; Medina et al., 2011; Kraft et al., 2017; Leitão et al., 2019, but see Prior et al., 2008). This approach presents a dynamic stimulus for individuals to respond to rather than static mounts conventionally used during simulated intrusions. Unlike interactions that may take place in the wild and/or during simulated territorial intrusions (e.g., if the visual stimuli is a caged individual), the perceived rival that tested experience during mirror assays with does not operate independently. That is, the mirrored reflections are not capable of initiating any given behavior, and as such, the pace at which individuals escalate or deescalate aggression is set by the focal individual. Further, the perceived rival is of equal "quality" to the tested individual.

Together, these factors may eliminate some of the confounds posed by simulated intrusions, whether the decoys presented are taxidermic mounts or live caged intruders (Scriba and Goymann, 2008). However, alongside these beneficial attributes, mirror tests are not without several caveats. For example, temporary captivity may evoke a stress response in wild animals that may influence their overall behavioral and physiological profile (e.g., Dickens et al., 2009). Moreover, males and females may respond to exposure to captivity differentially (Beiko et al., 2004), which may preclude reliably determining sex-specific differences in aggression. Finally, although mirror studies have previously shown elicit similar levels of aggression as would be seen with live opponents in zebrafish (Teles et al., 2013), they do not elicit the same hormonal (Oliveira et al., 2005) nor transcriptomic changes (Oliveira et al., 2016) that would be seen in response to live opponents. This is likely due in part to the fact that mirror assays inherently stalemate and a self-assessment of outcome (either winning or losing) is required to elicit these changes (Oliveira et al., 2016).

In sum, both simulated territorial intrusions and mirror assays yield different, but important insights into the evolution of variable behavioral phenotypes between sexes. Together, these tests complement one another by mitigating and/or circumventing the limitations imposed by each test individually. Using both techniques on the same individuals may provide an opportunity to assess sex differences in aggression across different contexts. For example, in socially monogamous species with joint territory defense, such an approach may answer how individuals flexibly respond to simulated rivals that are perceived as differing degrees of a threat to the individual. Thus, using both techniques on the same individuals has the opportunity to provide a more holistic understanding of sex-specific differences in territorial aggression. Use of both assays may also mitigate some of the limitations imposed by each test individually. However, to our knowledge, there is limited research using wild animals and coupling these two assay techniques (but see Hirschenhauser et al., 2008).

Here, we applied both simulated territorial intrusion and mirror image stimulation assay techniques back-to-back on the same individuals to experimentally test how females and males respond to simulated rivals in differing contexts. We studied the white-shouldered fairywren (*Malurus alboscapulatus moretoni*), a tropical passerine that defends territories in mated pairs year-round (Enbody et al., 2019). Enbody et al. (2018) and Jones et al. (2021) previously used simulated territorial intrusions to test how males and females respond as a territorial pair to stimuli of either of a mount and song playback of intruding pair (i.e., male and female mounts and song playback) or solo female mount intruders. The authors found that both sexes responded with equal intensity to the mount and song playbacks, but females and males always respond together in both studies, limiting an understanding of how both sexes may respond independently of their mate. The current study builds on this earlier foundational work by conducting both mirror and simulated intrusion assays on the same individuals, allowing us to directly assess how the same individuals adjusted their response to a perceived threat in varying contexts. For example, because mirror assays isolate the mated pair from one another, our approach allows us to explore individual behavior in the absence of a mate. Alternatively, it may be that males and females differentially respond to stimuli of varying perceived threats. Because each technique may vary the "level" of threat perceived by focal individual (i.e., static versus dynamic stimuli), we may be able to parse apart differences between males and females on what the "trigger point" is for them to behave aggressively. That is to say, what females perceive as a sufficient threat warranting aggression may vary from what males perceive. This outcome would be consistent with the idea that individuals exhibit behavioral flexibility based upon social and/or ecological contexts, which may aid in mitigating the risks associated with agonism.

2. Methods

2.1. Study species and general field methods

White-shouldered fairywrens are tropical songbirds endemic to New Guinea. Females vary across geographically-separated subspecies in degree of plumage ornamentation (but not within populations), while males uniformly exhibit iridescent black body plumage with white scapular patches across their range (Enbody et al., 2019). In this study, we investigate a subspecies (*M. a. moretoni*) where both males and females are ornamented, and where female coloration is derived (Driskell et al., 2011; Johnson et al., 2013; Karubian, 2013; ED Enbody unpubl. data) and is likely driven by changes in social selection pressure (Jones et al., 2021). We studied a population of *M. a. moretoni* in Podagha Village (9.692°S, 149.895°E), Milne Bay Province, Papua New Guinea from June–July 2019 at the beginning of the local dry season.

All behavior assays were conducted on individuals who had not been caught before, thus minimizing the effect of handling on observed aggression scores. Adults were captured via mist-nets for banding, standard morphometric measurements, and were aged via skull ossification. Like many bird species in the tropics (Stutchbury and Morton, 2001), white-shouldered fairywrens breed asynchronously (Enbody et al., 2019). Through routine observation of each group for two weeks, we confirmed all individuals involved in this study were paired adult males and females defending territories. We estimated breeding status as either “breeding” or non-breeding by the presence/absence of an active brood patch or juveniles on territory, although previous work in this population found it was not related to aggression during these assays these assays (see Jones et al., 2022).

Both assay types occurred back-to-back, such that simulated territorial intrusions always occurred immediately prior to capture, and mirror image stimulation assays occurred >15 min of being handled for every individual. While randomizing the order in which individuals received each assay type would be preferable, we opted for this approach as this was a previously untested population of songbirds, and thus were not accustomed to being handled. That is, we wanted to mitigate our presence biasing the simulated intrusion results on these otherwise naïve individuals, as we found that focal birds behaved markedly different upon repeated visits after their initial capture.

2.2. Simulated territorial intrusions

We conducted simulated territorial intrusions to determine individual behavior in both sexes of the focal pair of free flying fairywrens. Male and female fairywrens respond to intruders and defend territories jointly in this species and we have found that individuals separated from each other will focus on finding their mate instead of responding to audio playback. We used pre-recorded *M. a. moretoni* female songs paired alongside a female 3-D cardstock mount (adapted from a generic wren design by Johan Scherft (<http://www.johanschferft.com>) and painted to resemble our species; Supplemental Fig. S1) to elicit aggressive responses following methods previously used in this species (Enbody et al., 2018). Mounts and songs were chosen at random prior to each trial (out of a pool of four mount and five song exemplars). We located both members of the focal pair and set up our exemplars in the estimated center of a pair’s territory, retreated to a distance >30 m, and played an audio recording of a female song for 5 min, followed by 2 min of silence. We recorded behaviors throughout the playback period, including the latency to respond (how long it took for an individual to approach the mount), individual distance to the focal mount, flybys (within 2 m of the mount), and individual songs. To estimate individual distance from our exemplars, we set up our mount and audio playback in such a way that there was always a perch to land on within 1, 5, 10, and 15 m from the exemplar. Doing so also allowed us to limit the effect of variation among territories in habitat structure as much as possible.

Although the inclusion of a male song (i.e., an audio duet) would

present a different threat to males within this study, previous work on a nearby population of fairywrens found that males and females respond with equal intensity during female-only simulated intrusion stimuli (Jones et al., 2021), a similar pattern found to audio duet stimuli found by Enbody et al. (2018). We have found that exposure to mounts alone is not sufficient to elicit a behavioral response from our focal individuals, and thus the use of song is required. Finally, we chose a female-only stimulus to address female signal function explicitly in a separate study beyond the scope of the current manuscript (Jones et al., 2022). As such, the resulting assays assess a female responding to a same-sex rival whereas males experienced distinct stimuli across the two assays (i.e., an intruding solo female during simulated territorial intrusions, but a solo male rival during mirror image stimulation. In other words, our experiment does not test the same behavioral response in males as it does in females; for this reason, we focused our main predictions of behavioral flexibility in females, although we do discuss male response in the discussion.

Female song exemplars ($n = 5$) were recorded from a geographically distinct population of fairywrens during previous field seasons using a Marantz PMD 661 Mk II (96 kHz sampling rate, 24-bit depth; D&M Professional, Itasca, IL) with a Sennheiser ME66 shotgun microphone and K6 power module (Sennheiser Electronic Corporation, Old Lyme, CT). We used Audacity (v2.2.2, Audacity Team, 2018) to filter out noise below 500 Hz and to standardize amplitude. Each exemplar consisted of a single female song repeated at 10 s intervals for 5 min total. Playbacks were broadcast using a Samsung Galaxy S9 (Samsung Group, Seoul, South Korea) over Bluetooth via an Ultimate Ears Roll 2 speaker (Irvine, CA).

2.3. Mirror image stimulation

We exposed both sexes to mirror image stimulation (Gallup Jr, 1968), a behavioral technique that has been used in several taxa to estimate aggression to conspecifics, including fish (Rowland, 1999; Balzarini et al., 2014), mammals (Svendsen and Armitage, 1973; Mazzamuto et al., 2019), and birds (Branch et al., 2015; Leitão et al., 2019), including the species of the current study (Jones et al., 2022). Our trials occurred either from 0600 to 1100 or 1530 to 1730 local time (GMT +10) while avoiding rain and intense heat; each behavioral assay occurred in a shaded location within the territory of the focal bird to minimize stress-induced behavioral changes. Fairywrens were temporarily placed within a cage on the grassland floor measuring 60 cm (length) x 40 cm (width) x 40 cm (height), one side of which held a mirror that was initially hidden by a wooden cover. Inside the cage, we provided three perches at the same height but at varying distances relative to the mirror (Fig. 1A; see also Fig. 1C in Jones et al., 2022 for diagram illustration) to determine the focal individual’s distance from the mirror as “close”, “neutral”, or “far” from the mirror (Fig. 1B). We covered the cage with a white cloth on all but one side to (1) reduce the likelihood of external stimuli influencing individual behavior and (2) reduce the number of potential ‘exits’ that might distract the bird from the mirror. Each trial consisted of a 5 min acclimation period to the cage followed by ~7 min exposure to their mirror reflection (Jones et al., 2022). Throughout the acclimation phase, individuals attempted to find an exit and never “settled down,” although they also did not fly around the cage erratically. During pilot work for this project, we found that ~5 min was a sufficient period to facilitate a switch in behavior between attempting to escape the cage (which makes up the entirety of the acclimation phase) and instead focusing on the mirrored reflection.

During both phases (acclimation and exposure), we recorded the distance of the focal individual to the mirror (above) as well as any aggressive responses, including attacking the mirror (i.e., flying at the mirror, jumping from the base of the mirror, and pecks), threatening displays and soft-song rate (no birds sang at full volume whilst in the cage). Here, we only present post-exposure responses (with one exception, below), as no aggressive behaviors were observed during the period

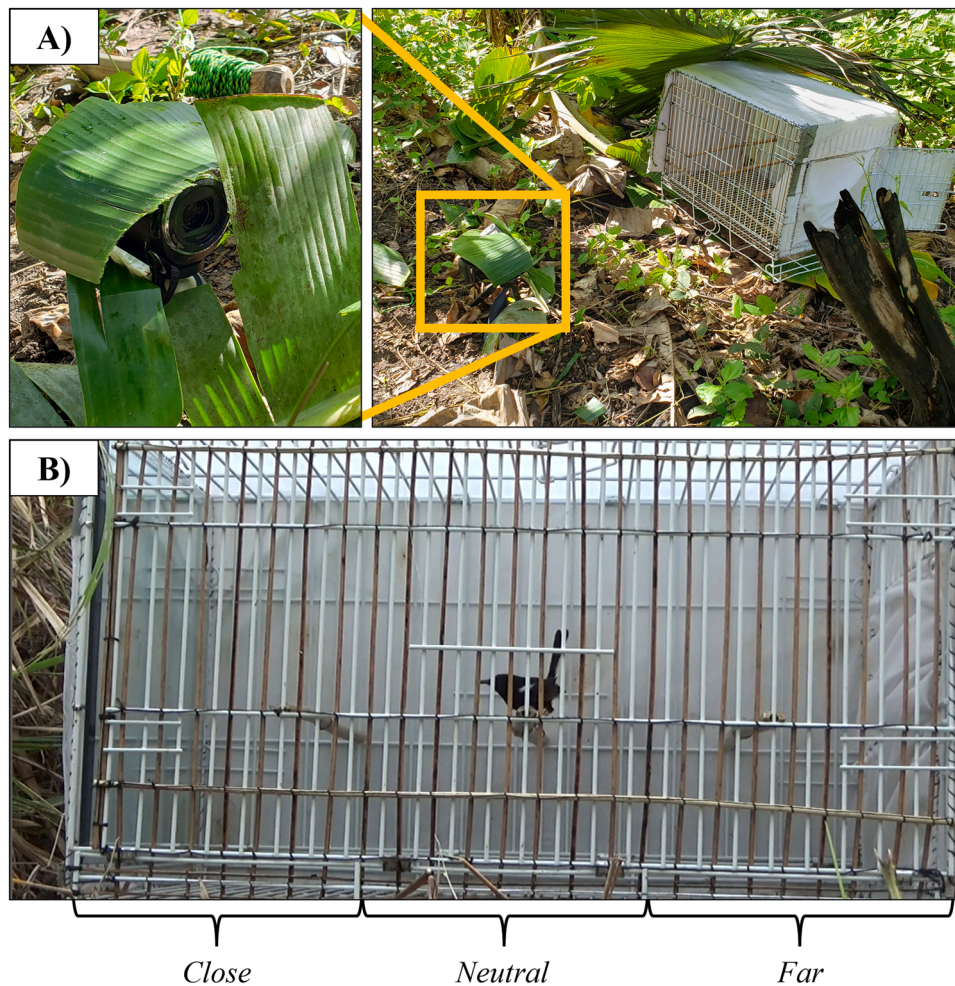


Fig. 1. Experimental design of mirror image stimulation. (A) Focal individuals were placed in a cage (clothed on all sides except one) on the ground and were video recorded with camera that was at least partially camouflaged with available flora on the target's territory. (B) We recorded the time an individual spent at three distinct distance classes relative to the mirror with "close" being assumed a more aggressive response and "far" as the least aggressive response.

when the mirror was covered. However, as it is unclear if there are sex differences in how they respond to being subjected to captivity per se, differences in aggression perceived may reflect sexually dimorphic stress responses to captivity. To that end, we recorded overall movement throughout the cage and interpreted it as a non-aggressive behavior that may be indicative of underlying stress. We define movement as any transition from one spatial zone (close, neutral or far) to another within the cage; while individuals can and do move within these classes, we found that, in general, birds that appear to be disinterested in the mirror reflection move from zone to zone quite frequently.

We recorded each trial with a GoPro Hero CHDHA-301 (San Mateo, CA) or Sony HDR-CX405 Handycam (Tokyo, Japan) that were partially camouflaged with local vegetation to reduce the risk of object neophobia.

2.4. Statistical analysis

We conducted a principal component analysis (PCA) to explore how free-flying individuals respond to mock intruders during simulated territorial intrusions. We included the following behaviors for this PCA: latency to respond (in sec), flyby rate, proportion of time within 5 m of the mount, average distance from the mount, and song rate. We normalized each response variable by $\log(x + 1)$ transformation followed by centering and scaling prior to running the PCA (following Filardi and Smith, 2008).

We compared sex responses on the top two PCs (hereafter: STI-PC,

Table 1

Loading scores for the principal component analysis exploring how (1) female and male fairywrens responded to mirror image stimulation, after exposure to the mirror, and (2) how free-flying individuals responded to simulated territory intrusion.

	Mirror-PC1	STI-PC1	STI-PC2
Eigenvalue	1.308	1.495	1.09
Proportion of Variance	0.570	0.447	0.238
Aggression (strikes + pecks + displays + soft songs)	0.545		
Proportion of time spent close	0.677		
Proportion of time spent far	-0.494		
Latency		-0.367	0.322
Attack rate		0.324	0.585
Proportion of time spent close within 5 m		0.584	-0.173
Average distance		-0.604	0.217
Song rate		0.223	0.691

Table 1) using linear mixed effects models using the lme4 package in R (Bates et al., 2015; R Core Team, 2021). We included sex as the only fixed effect, with the pair's numerical ID as a random intercept in our models, as well as exemplar mount ID (n = 4 mounts) and female song stimulus ID (n = 5) to reduce the effect of pseudoreplication (Kroodtsma et al., 2001). Covariates, including pair breeding stage (i.e., breeding versus non-breeding) and time of day of the behavior assay, did not have an effect in any model and thus were removed. Residuals of the full

model did not violate assumptions of normality nor homoscedasticity. The significance of each model was evaluated using a type II ANOVA the car package in R (Fox and Weisberg, 2011).

As some behavioral responses during mirror assays were infrequent among individuals (e.g., displays), we enumerated the total amount of aggressive behaviors as one variable after the mirror was exposed to the individual following the statistical methods of Leitão et al. (2019) and Jones et al. (2022): strikes, pecks, soft songs, and displays. Although vocal behaviors are important in white-shouldered fairywren territorial intrusion contexts (Jones et al., 2021), both sexes rarely sang while in cage and not frequently enough for statistical analysis as a stand-alone variable. Thus, as soft songs are seen as a signal of aggressive intent in other species (e.g., Templeton et al., 2012), we included it in our 'total aggression' variable. We conducted a second PCA on these behavioral responses to mirror assays, generating only one PC (hereafter, Mirror-PC1) with an eigenvalue >1.0 that includes the total aggression score as well as the proportion of time spent spatially close to and far away from the mirror after the mirror was exposed (Table 1; Leitão et al., 2019). Finally, to explore a non-aggressive behavior that varied in response to captivity and to determine if there were sex differences in stress related to temporary captivity, we compared male and female total movements (as a rate with respect to trial length) for with captivity to determine we compared overall movement between males and females during the acclimation phase as well as mirror exposure phase of the experiment. For each test, we compared sexes using a Welch's t-test.

Finally, we explored if the level of aggression expressed during simulated intrusion was consistent with that during an individual's mirror trial, separated by sex, via Pearson's correlation. We computed the correlations between Mirror-PC1 and the two STI-PCs separately. Spearman's rank-sum correlation yielded biologically identical results and thus are not presented here.

2.5. Ethical note

Our study was carried out in strict accordance with the guidelines established by the Tulane University Institutional Animal Care and Use Committee (#0395R2) as well as in adherence to research permits from the Conservation and Environment Protection Authority of Papua New Guinea (#99902100765). All birds were captured, processed, exposed to a mirror assay, and then released onto their home territory in under one hour. Mist-nets were continuously monitored, and birds were removed immediately upon hitting the net. All individuals involved in removal of birds from mist-nets had been trained in the appropriate way to handle birds. Repeated visits of focal pairs after exposure to the assays outlined in the current manuscript found that our treatments had no adverse effects on their welfare.

3. Results

3.1. Simulated territorial intrusions

We conducted 43 simulated territorial intrusions (STI). The first two STI-PCs account for 68.5 % of the variation (Table 1). Higher scores for STI-PC1 indicate a more aggressive response, in that the individual spent a greater proportion of time near the mount, responded quicker, and attacked more frequently during the assay. STI-PC2 loads in a similar manner, with higher scores being associated with individuals who attacked the mount more often and sing in response to stimuli (Table 1).

There was no difference between sexes in STI-PC1 ($F = 1.34$, $df = 1, 74$, $p = 0.25$, Fig. 2A). However, mean male STI-PC2 scores were higher than those of females, indicative of males that attacked and counter-sang more frequently in response to stimuli response on this component ($F = 4.49$, $df = 1, 74$, $p = 0.04$, Fig. 2B).

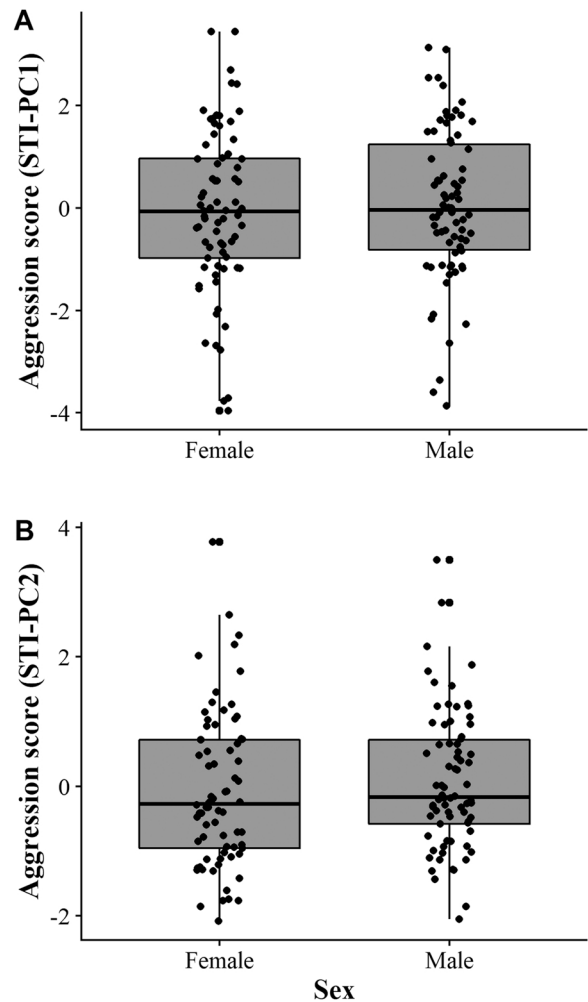


Fig. 2. Sex-specific differences in behavioral response while responding to simulated territorial threats as a coordinated duo. (A) Although there is no statistically significant difference between sexes in STI-PC1, (B) male STI-PC2 scores are higher than females, such that males attack and counter-sing in response to exemplar more frequently than females. Middle line represents mean, bottom and top hinges represent 25 and 75th percent, respectively, and the whiskers are 1.5x beyond the interquartile range.

3.2. Mirror image stimulation

We exposed 44 females and 26 males to one mirror image assay each. Mirror-PC1 accounted for 59.7 % of the behavioral variation during mirror trials (Table 1). Higher scores of Mirror-PC1 were associated with individuals who performed more aggressive behaviors (i.e., pecks, strikes, soft songs, and/or displays) and spent more time close to the mirror relative to far away.

Mean female Mirror-PC1 scores were higher than those of males, indicating a higher degree of aggression in response to their own reflection than males to their own ($t = 2.60$, $df = 49.02$, $p = 0.01$; Fig. 3). There was no significant difference between sexes in overall movement behaviors prior to exposure to their mirrored reflection ($t = 1.35$, $df = 61.39$, $p = 0.18$; Supplemental Fig S2A). However, after exposure, there is a near-significant trend ($t = 1.84$, $df = 67$, $p = 0.07$; Supplemental Fig S2B) that females (mean movement score: 54.45) traverse the cage less than males do (mean score: 80.12); this may be explained by female aggressive scores being higher than males, and thus they are more likely to be near the mirror per se.

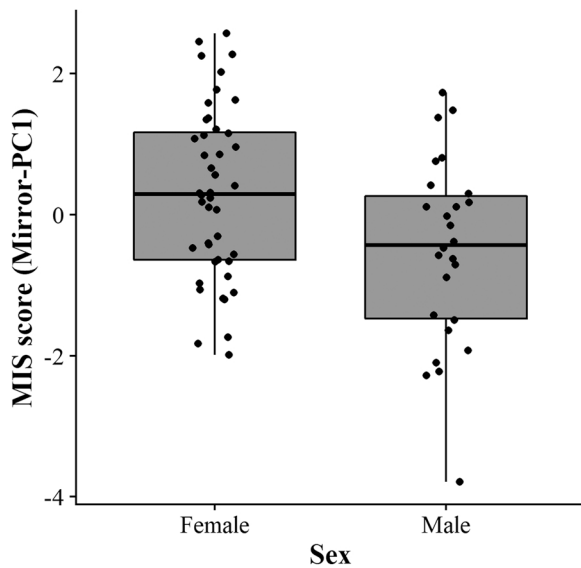


Fig. 3. Sex-specific differences in aggression during MIS assays. In contrast to STI results, females are more aggressive than males during MIS assays (i.e., higher Mirror-PC1 scores) that mimic a simulated same-sex threat during which individuals are isolated from their social mate. Middle line represents mean, bottom and top hinges represent 25 and 75th percent, respectively, and the whiskers are 1.5x beyond the interquartile range.

3.3. Congruency of individual level response to different behavioral assays

Among females exposed to both assays, we found a significantly negative relationship between Mirror-PC1 and STI-PC1 ($r = -0.33$, $n = 44$, $p = 0.03$; Fig. 4); females that attacked the mirror more frequently (i.e., higher Mirror-PC1 scores) tend to spend less time near the exemplars of the simulated territorial intrusion as well as attacked it less frequently. In contrast, there was no relationship between Mirror-PC1 and STI-PC1 in males ($r = -0.29$, $n = 23$, $p = 0.20$). We did not find a significant relationship between female Mirror-PC1 scores and STI-PC2 scores ($r = -0.09$, $n = 44$, $p = 0.56$), but did find a positive, but non-statistically significant, trend in males ($r = 0.56$, $n = 23$,

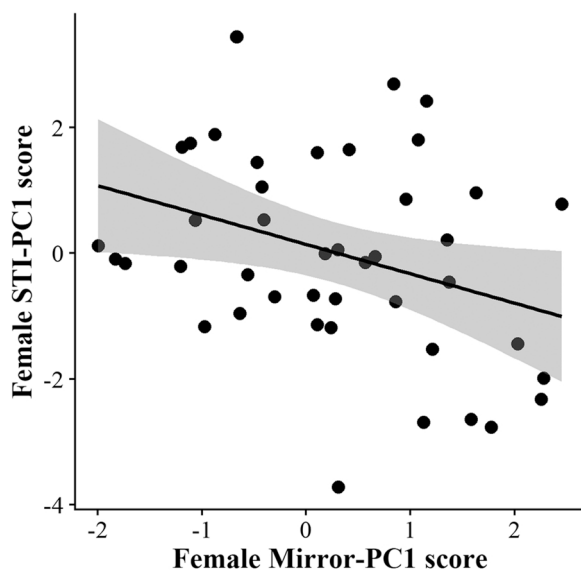


Fig. 4. Correlation between individual responses to both behavioral assay types in female fairywrens. Females with the highest Mirror-PC1 scores (i.e., more aggressive when isolated from their mate) are the least aggressive during paired STIs (lower mirror STI-PC1 scores).

$p = 0.07$), such that males with higher STI-PC2 scores (defined by increased song and attack rates) also tended to be relatively aggressive during mirror assays.

4. Discussion

When studying aggression under natural conditions in the field on species with joint territory defense, it is often not possible to isolate the behavior of one member of the pair from potential impacts by the behavior of the mate. One member of the pair may modulate aggression depending on the response of its mate, but this possibility remains poorly explored by simulated territorial intrusion assays which present a static stimulus to free-flying pairs. Moreover, it may be that the threshold in the relative degree of threat perceived to warrant an intense aggressive response differs between sexes, such that one sex may behave aggressively only when perceived rivals are more dynamic. As a consequence, our understanding about how each member of the pair will individually behave when responding to rivals remains limited (but see Miles and Fuxjager, 2019). To address this knowledge gap, we explored how female and male white-shouldered fairywrens respond to perceived rivals using two back-to-back behavioral assays: simulated territory intrusion (where individuals responded together to a static mount and playback stimulus) and mirror image stimulation (where individuals are isolated from their mate and respond to a dynamic stimulus). We found that males tend to be more responsive during simulated territorial intrusions, but this may be driven by the fact that males tend to sing more frequently than females in general (pers. obs.). In other words, it may be that male aggression scores, as we have defined it via PCA, is confounded by their general increased frequency of singing relative to females. However, females were more aggressive than males during mirror assays, and the females that were most aggressive during mirror image stimulation were the same females that were the least aggressive during simulated territorial intrusions. We did not find a reciprocal pattern in males, instead finding no predictable pattern if males with a given aggression score would consistency respond with more, or less, aggression between behavioral assays. that they were inconsistent. Finally, we did not find evidence that there are differences in how female and male white-shouldered fairywrens responded to captivity, as we found that sexes did not differ in non-aggressive movement behaviors observed during the acclimation phase. Taken together, these results suggest that females appear to have the capacity to recognize variation in the level of threat perceived, and thus flexibly adjust their relative commitment in aggressive conflict based on context.

Our two assays (simulated territorial intrusion and mirror image stimulation) yield contexts that are not “apples to apples” and they differ more than just the presence / absence of their mate. For this reason, interpreting observed behaviors during any aggression assay is limited to its own given context, but we believe that our joint approach may provide a more integrated perspective of individual and joint territorial aggression. Both simulated territorial intrusions and mirror image stimulations ostensibly measure a component of individual aggression (relative to context). While simulated territorial intrusions are undoubtedly useful tests of territorial aggression (Goymann et al., 2019; Moore et al., 2020), we would argue the individual aggressive intensity is difficult to discern for species with mutual defense, as individual responses are not truly independent and an individual’s territorial response in a pair context may differ from if it were responding alone. Moreover, simulated territorial intrusions commonly involve a mount (whether taxidermic or not) that do not respond to the focal individuals in real time (i.e., are static in nature). Assays that are designed to be more responsive/dynamic to the focal individual may result in a more aggressive response than a mount and/or song by itself (e.g., Yang et al., 2018).

In contrast, mirror image tests provide an opportunity to isolate individuals from their mates, to test how they respond to a same-sex rival of equivalent visual quality (i.e., honest visual signals via size and/or

coloration), and dynamic nature of these assays means the pace to which individuals (de)escalate is dictated by the focal individual. This is useful in that it controls for external environmental and social stimuli, yielding a biologically relevant sex-specific difference in aggression that may have previously been missed using simulated territorial intrusions alone in this species (e.g., Enbody et al., 2018; Boersma et al., 2020; Jones et al., 2021). However, these assays also potentially mimic a scenario where a focal individual is off-territory and responding to a conspecific rather than defending their own territory per se (Leitão et al., 2019). This distinction makes determining motivation of the tested individual difficult to discern, as the focal bird has a greater cost associated with aggressive encounters due to owner/intruder asymmetry (i.e., prior ownership/familiarity of a territory increases motivation; Bradbury and Vehrencamp, 1998). Caged assays also introduces other, novel stressors and sexes may differentially respond to these stressors (Beiko et al., 2004). In the current study, however, we did not find that sexes appear to differentially respond to the stress of temporary captivity. Moreover, both sexes responded strongly to their reflections in this study and the behaviors observed in this study are similar to those seen in natural interactions among conspecifics (see also Leitão et al., 2019). Taken together, while we acknowledge that there are multiple differences between these assays that may potentially influence behavior, we propose that this combination of tests provides a broader perspective on behavioral differences between the sexes in different contexts.

Selection should favor the capacity for phenotypes to be flexible to match acute environmental variation with an appropriate behavioral, morphological, and/or physiological phenotypic shift (Piersma and Drent, 2003; Sinha 2005; Kelly and Wilson 2020). In this study, we find evidence that female fairywrens appear to have this capacity for behavioral flexibility, and we posit that variation in social environment (i.e., presence or absence of the mate) and/or the level of threat perceived may play a key role. Even among socially monogamous species, females typically invest more into reproductive output than do males (Fitzpatrick et al., 1995), and this greater investment may consequently promote various flexible responses in different competitive scenarios (reviewed in Stockley and Campbell, 2013). The energy to ward off rivals may limit the physiological resources available to invest in reproduction (Fitzpatrick et al., 1995; Young and Bennett, 2013). As a consequence, overt female aggression tends to be less common than that of males, with aggression being reserved only for defense of particularly high valued resources required for reproductive success (Fedy and Stutchbury, 2005; Elias et al., 2010; Huchard and Cowlshaw, 2011; Tubert et al., 2012; Wu et al., 2019; Leese and Blatt, 2021). If our mount stimuli (during simulated territorial intrusions) are not sufficient of a threat to warrant an intense response, a strategic decrease in female aggression may be expected. Female fairywrens are more aggressive towards a simulated female rival perceived via her mirrored reflection than they are during simulated territorial intrusions. If we assume a certain threshold of aggressive intensity is required a win during a territorial contest, one possibility is that females recognize that the static nature of the simulated territorial intrusion is not as high of a threat as the rival she perceives in the mirror that is visually equal quality to her. The presence of her mate during simulated territorial intrusions, but not caged mirror assays, may further support this.

Males are, on average, less aggressive than are females when exposed to their own mirrored reflection. This stands in contrast to what one may have expected, as males are responding to a same-sex rival during mirror image stimulations, but a solo female intruder during simulated territorial intrusions. A perceived male rival should elicit a heightened aggressive response from focal males, as the perceived rival in the mirror would be a more direct threat than a solitary female. It may be that males favor the longevity and strength of the partnership rather than meeting additional females as a strategy to reduce the frequency of intrasexual competition for mates, thus enhancing pair coordination (Ens et al., 1996) by perceiving both sexes as an equal threat to territory (Guo et al., 2020). Alternatively, females may be more aggressive than

males during mirror exposure because females experience a female intruder during the simulated territorial intrusion and then again a short-time later during mirror assays; because our wrens do not typically sing during mirror trials, it is possible the focal individual perceived the rival in the mirror to be the same one experienced during the simulated intrusion, and the repeated exposure may lead to a more intense response. That said, Jones et al. (2022) found that repeated exposure to mirror assays lead to a decrease in aggression. Nevertheless, as male rival stimuli varied between trial types in a way that was not consistent with females, we are hesitant to draw definitive conclusions based on the male context in the current study, but the possibility of this avenue as the subject of future research is exciting.

The use of multiple behavioral assays on the same individual over the course of a single experiment is commonplace in studies of behavioral syndromes, which focus on suites of correlated behaviors/physiological traits across time and contexts (e.g., Sih et al., 2004a,b; Sih and Bell, 2008; MacKay and Haskell, 2015; see also animal personality: Sgoifo et al., 2005; Frost et al., 2007; Duckworth, 2010). That said, we believe a combination of simulated territorial intrusions and mirror image stimulations on the same individuals potentially sheds a new light on exploring sex-specific differences in territorial aggression. Here, we find that while male behaviors appear inconsistent throughout assays, individual females vary in the intensity of aggression observed across social and/or ecological context. Moreover, that males have higher aggressive scores than females in one context (during simulated intrusions) whereas females are higher in another (mirror assays) suggests that determining which sex is most active in aggressive conflict and/or territory defense is nuanced and potentially context-dependent. Comparing variation in observed aggressive behavior in a manner such as ours has the potential to be relevant beyond territorial aggression for socially monogamous species. For example, maintaining territories is important in many group living, cooperatively breeding species (Taborsky, 1984; Putland and Goldizen, 1998; Schradin, 2004; Arnott and Elwood, 2009; Gübel et al., 2021; Humphries et al., 2021), but the intensity of selection via intrasexual competition that either males or females (or both) face in these systems are different than those experienced in non-cooperatively breeding systems (Rubenstein and Lovette, 2009). Use of multiple behavioral assays on the same individuals in differing contexts is likely to provide a more nuanced understanding of when and how individuals modify aggressive response in these systems, as well as reveal if pre-existing documented patterns of aggression are consistent with respect to variation in these contexts.

CRediT authorship contribution statement

Jones, JA: Conceptualization, Methodology, Investigation, Formal analysis, Funding acquisition, Writing – original draft preparation and editing. Boersma, J: Methodology, investigation, writing – review and editing. Karubian, J: Conceptualization, supervision, funding acquisition, writing - review and editing.

Declaration of Competing Interest

We do not have any conflicts of interest to disclose.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.beproc.2022.104735](https://doi.org/10.1016/j.beproc.2022.104735).

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