Impacts of mate quality on female intrasexual aggression in two sister *Malurus* fairywren species

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Lay summary
Research on elaborate animal coloration overwhelmingly focuses on how males dress to impress potential mates or how color wards off potential rivals. In reality, female animals do this too, but it is less clear how competitive behavior varies among females that are pair-bonded with the prettiest males. In two closely-related songbird species, we did not find evidence that behavior varies in this context, showcasing how coloration may not be the most important variable females consider.

Abstract:
While the impacts of male phenotypic quality on female mating decisions are well-studied, less is known about how male attributes may influence female aggressive behavior. To address this, we evaluated the degree to which females mated to more attractive males may behave more aggressively toward simulated female rivals, as might be predicted if intrasexual competition exists over access to mates. We studied two sister taxa of fairywren (Maluridae) with distinct life-history strategies: white-shouldered fairywrens (*Malurus alboscapulatus moretoni*) in Papua New Guinea, a species with year-round territoriality and female-limited plumage polymorphisms, and red-backed fairywrens (*M. melanocephalus melanocephalus*) in temperate Australia, a species with seasonal breeding and one in which females do not exhibit any plumage ornamentation. We characterized male quality by assessing the plumage coloration alongside three morphological characteristics that are known to be important in *Malurus* fairywrens: body mass, cloacal protuberance volume, and tail length. We quantified female aggression using mirror image stimulations, finding that female white-shouldered fairywrens were more aggressive on average than female red-backed fairywrens. There was a non-significant tendency for more aggressive white-shouldered fairywren females to have heavier mates with longer tails, but male phenotype did not predict female behavior in the red-backed fairywrens. Overall, our results are consistent with the idea that variation in mating system and life-history help shape female aggressive behaviors between divergent species. In socially monogamous species that form long, multiyear bonds with their mates, phenotypic quality may not be the best predictor of mate choice as has historically been emphasized.

Keywords: Australasia, female-female competition, female ornamentation, mirror image stimulation, New Guinea

Introduction:
Agonistic conflict among same-sex rivals is expected when highly valued resources, whether ecological or sexual in nature, are limited (West-Eberhard 1979; West-Eberhard 1983; Lyon and Montgomerie 2012; West-Eberhard 2014). Aggressive contests are often necessary to acquire these limiting resources, but they can also incur substantial costs, including the time and energy committed to the engagement as well as the inherent risk of injury (Maynard Smith and Price 1973; Parker 1974; Maynard Smith and Harper 1988; Arnott and Elwood 2009; Duque-Wilckens et al. 2019). Thus, the ability to accurately assess the costs-benefits ratio to engage in these activities is likely adaptive, providing individuals with the capacity to flexibly match aggression

intensity to context (Brown 1964; Emlen and Oring 1977; Grant 1993; Grant et al. 2000; Noël et al. 2005). For example, male striped plateau (*Sceloporus virgatus*) increase their energic investment during intrasexual agonistic encounters when the contested female had larger ornaments (Weiss and Dubin 2018); assuming aggression impacts overall mating success, males may be more willing to sacrifice the energetic demands and accept the risk of agnostic encounters in order to secure the direct and/or indirect benefits from their mate preference (Weiss and Dubin 2018).

The study of animal aggression has predominantly been explored, both theoretically and empirically, from the male perspective. Intrasexual competition among females on the other hand has historically been understudied, despite that it is likely to be common (Fedy and Stutchbury 2005; Hrdy 2013; Rosvall 2013; Hare and Simmons 2019; Lipshutz and Rosvall 2021). Indeed, recent studies have shown that females across taxa engage in social competition in order to acquire the resources ultimately responsible for increased fitness benefits (Langston et al. 1990; Slagsvold 1993; Slagsvold and Lifjeld 1996; Cunningham and Birkhead 1998; Langmore 1998; Rosvall 2008; Cain et al. 2011; Tobias et al. 2012; Guo et al. 2020; Fischer et al. 2023). There is now little doubt that female-female competitive interactions are adaptive in a variety of taxa (Clutton-Brock 2007; Stockley and Bro-Jørgensen 2011; Tobias et al. 2012; Cain and Ketterson 2013; Stockley and Campbell 2013; Cain and Rosvall 2014; Wu et al. 2019; Lipshutz and Rosvall 2021), but because selection maximizes reproductive success in each sex differently (Trivers 1972; Westneat and Sargent 1996; Kappeler et al. 2022), it remains unclear if the same ecological and social stimuli that often predict patterns of male aggression may equally apply to females. A comparison of closely related species that differ in the relative degree of social competition experienced among females may help elucidate the role that such variation in the competitive environment and/or overall life-history plays in shaping the intensity of female aggression.

Social selection, a subset of natural selection that includes social competition for both sexual and non-sexual resources (Crook 1972), is among the most commonly proposed mechanisms for competitive traits in females (West-Eberhard 1979; West-Eberhard 1983; Lyon and Montgomerie 2012; Tobias et al. 2012). This is due, in part, to the perception that female-female competition most often occurs over ecological resources that enhance and/or are necessary for reproductive success (e.g., food availability, habitat quality) rather than the quality of mates per se (Heinsohn et al. 2005; LeBas 2006; Stockley and Bro-Jørgensen 2011; Tobias et al. 2012; Stockley and Campbell 2013). For example, superb fairywren (*Malurus cyaneus*) females that hold territories in lower-quality, patchier habitat are more aggressive to simulated territorial intrusions by same-sex rivals (Cain and Langmore 2016), and female aggression in the Qinghai toad-headed agama (*Phrynocephalus vlangalii*) is most intense when food is a limited resource (Wu et al. 2019). However, sexual selection via intrasexual competition over access to mates acts on females in much the same way as it does in males (Hare and Simmons 2019) and is present in a variety of invertebrate (Bain and Govedich 2004; Lewis et al. 2004; Rillich et al. 2009) and vertebrate taxa (Rosenqvist 1990; Summers 1990; Sandell and Smith 1997; Bain and Govedich 2004; Lewis et al. 2004; Thomas et al. 2018). Therefore, while females are typically not limited in the number of potential mates available, female-female competition may nevertheless occur over access to higher quality male partners (Rosvall 2008; Rosvall 2011).

There is considerable variation among taxa in sex-specific strategies of investment in intrasexual competition, mate choice, and/or parental care (Janicke et al. 2016; Lindsay et al.

2019). For the majority of bird species (~90%) that experience some form of social monogamy (Cockburn 2006), mate choice per se is not the end point of the reproductive cycle (Royle et al. 2012). Instead, reproductive success is only achieved post-copulation and after parental care is provided for the majority of (altricial) bird species. Although it is often assumed that females preferentially mate with the most attractive males, if chick-rearing requires the combined efforts of both parents, whether or not a male is physically attractive may only be useful to a female if male phenotype signals their parental investment, either through territory defense or feeding offspring, if not both (Préault et al. 2005; Pagani-Núñez and Senar 2014). Thus, while male phenotypic quality may be important for initial pairing, females in species that form longer-lasting pair ponds must also weigh the potential genetic quality of offspring (Hasselquist et al. 1996; Mays and Hill 2004), the fighting capacity (Reudink et al. 2009), and/or parental care (Préault et al. 2005; Pagani-Núñez and Senar 2014) provided when choosing a mate. The relationship between male phenotypic quality and the intensity of female aggression observed post-pairing has seldomly been explored (Hare and Simmons 2019; Lyu et al. 2022). Yet, it is important to remedy this gap in research, as aggression among females that prevents intrasexual rivals from accessing their social mate has been shown to be an adaptive behavioral strategy in socially monogamous species (Gowaty and Wagner 1988; Slagsvold 1993; Cézilly et al. 2000; Guo et al. 2020).

Mating systems may be linked to variation in sex roles for parental care (Andersson 1994). While "sex-roles" are more likely to be a spectrum of behaviors rather than discrete, stereotypical categories of behaviors that belong to one sex versus another (Ah-King and Ahnesjö 2013; Hare and Simmons 2019), in this context we are referring to them as the relative contribution one sex makes towards rearing offspring relative to their mate. In this sense, we can explore the relative convergence / divergence between sexes as a proxy for the strength of selection acting on each sex independently. For example, the strength of sexual selection acting on males and females is predicted to be similar in tropical regions where sex role convergence in year-round territory defense and parental care is common (Kunkel 1974; Slater and Mann 2004; Stutchbury and Morton 2022). Tropical species often consist of both sexes expressing some form of mutual ornamentation (Karubian 2013; Dale et al. 2015), which may ultimately reflect how shared phenotypes function as signals in mate-choice and/or competitive contexts in both sexes (Kraaijeveld et al. 2007; Murphy et al. 2009). In contrast, species occupying temperate ecosystems are often dichromatic, such that males are stereotypically highly adorned and territorial, whereas females are often muted in plumage coloration and do not defend the territory as vigorously (Stutchbury and Morton 2022). With that being said, Fargevieille et al. (2023) recently described how females of temperate songbird species with greater paternal care tend to be slightly brighter and more chromatic, suggesting that differences in dichromatism between sexes is not are reliable indication of the strength of sexual selection per se. Nonetheless, we may expect the intensity of female-female competition experienced tropical regions to exceed that commonly experienced by their temperate congeners as resources are tightly contested alongside variation in mating systems between geographic regions. If and how such variation in mating systems influences whether or not females are willing to engage in aggressive contests to secure mates remains understudied. Addressing this research gap may provide additional insight into how mating system, and the resulting observed differences in the intensity of intrasexual competition among species, predicts patterns of competitive trait evolution in females.

We studied two sister species that vary distinctly in mating systems: (1) white-shouldered fairywrens (*Malurus alboscapulatus moretoni*), a tropical songbird endemic to New Guinea that defend territories year-round, are mutually ornamented (in all but one subspecies (Enbody et al. 2019)), and have convergent sex roles, and (2) red-backed fairywrens (*M. melanocephalus melanocephalus*) of subtropical-to-temperate Australia, a dichromatic species with seasonal territoriality and breeding (Fig. 1). Both species are socially monogamous, but differ markedly in overall sociality and reproductive strategy. For example, red-backed fairywrens are highly social, with nesting groups that consist of breeding pair and often (but not always) contain additional auxiliary (both kin and non-kin) helpers (Rowley and Russell 1997; Karubian 2002; Webster et al. 2008), whereas helpers are the exception rather than the norm in the subspecies of white-shouldered fairywrens of the current study (Enbody et al. 2019). White-shouldered fairywrens also have lower levels of extra-pair paternity (~33%) and have smaller scaled cloacal protuberance volumes on average (7.85 mL^3) than red-backed fairywrens (~56% and 16.94 mL^3, respectively (Brouwer et al. 2017; Enbody et al. 2019)); among *Malurus*, larger cloacal protuberance volumes is positively associated with testes size, sperm quality and overall rates of extra-pair paternity (Tuttle et al. 1996; Rowe and Pruett-Jones 2011; Rowe and Pruett-Jones 2013).

Based on these species differences in mating systems and life-history strategy, we predicted that female white-shouldered fairywrens would be more likely to experience intense selection pressure via intrasexual competition than female red-backed fairywrens, and thus display overall higher levels of aggression. We quantified variation in how individuals respond to same-sex intruders between species through the use of mirror image simulations: behavioral assays that put individuals up against their own mirrored reflection, mimicking an intrasexual challenge against a rival of equivalent visual quality (Gallup Jr 1968; Leitão et al. 2019; Jones, Boersma, Liu, et al. 2022). Next, if males are a highly valued resource in tropical New Guinea that females compete over access for (sensu Lyu et al. 2017), we predicted that aggression in white-shouldered fairywren females would be correlated to the phenotype of her mate, assuming that male phenotype honestly communicates his quality. However, ornamentation may also be negatively associated with parental care, such that males in some species (Mitchell et al. 2007), including red-backed fairywrens (Webster et al. 2008; Dowling and Webster 2017), that are more ornamented invest in extra-pair copulations rather than parental care. To that end, coupled with the fact that red-backed fairywrens are seasonal breeders and may possess auxiliary helpers at the nest(Mulder et al. 1994), we did not expect to find that female aggression was related to male plumage coloration in this species. To address our second objective, we correlated mirror assay aggression scores with their mate's plumage coloration and morphological phenotype. Finally, we tested if male phenotype was related to their own aggression scores in red-backed fairywrens, although we were unable to in white-shouldered fairywrens as to not interfere with a concurrent behavioral study (Jones, Boersma, and Karubian 2022; Jones, Boersma, Liu, et al. 2022).

Methods:

Study species and general field methods:

Both sister species are predominately grassland specialists, but differ significantly in mating system structure, overall life-history strategy, and if females are ornamented or not (Rowley and

Russell 1997). In New Guinea, white-shouldered fairywren plumage coloration remains consistent year-round in both sexes (Fig. 1). Male plumage coloration remains black-and-white throughout the island, but females vary allopatrically in plumage phenotype that tracks with subspecies (Rowley and Russell 1997; Enbody et al. 2019). The current study explored *M. alboscapulatus moretoni*, a subspecies where both sexes are nearly monochromatic, with this coloration having been derived from that of an unornamented phenotype (Enbody et al. 2019; Enbody et al. 2022). In contrast, male red-backed fairywrens in Australia seasonally molt between an ornamented plumage phenotype (i.e., eumelanin-based black body coloration and carotenoid-based red backs and shoulders) during the breeding season and a drab (phaeomelanin-based brown) phenotype that resembles that of females during the non-breeding season (Rowley and Russell 1997; Karubian 2002; Karubian 2008). Female plumage color typically does not vary, such that they remain unornamented year-round, although it is possible that variation in bill coloration may exist as it does in males (Karubian 2008).

We studied a population of white-shouldered fairywrens in Podagha Village, Milne Bay Province, Papua New Guinea (9.692ºS, 149.895ºE) from June-July 2019, and red-backed fairywrens in Samsonvale, Queensland, Australia (27.271ºS, 152.857ºE) from August-November 2019. We captured individuals with mist-nets for banding and feather collection. We focused on three standard body measurements that we suspected may be important differences between sexes and/or species: (1) mass (± 0.01 g): both species exhibit size dimorphism, such that males are slightly heavier than females (Rowley and Russell 1997); (2) Tail length (±0.01 mm): shorter tails are thought to be a signal of social dominance in *Malurus* (Swaddle et al. 2000; Karubian et al. 2009); (3) Scaled cloacal protuberance (CP) volume (0.01 mL^3; Tuttle et al. 1996; Rowe and Pruett-Jones 2011, 2013). We calculated scaled CP as the ratio of CP volume (calculated as: 3.14 * (CP height/2) * (CP width/2) * CP length) to body mass for males (Tuttle et al. 1996).

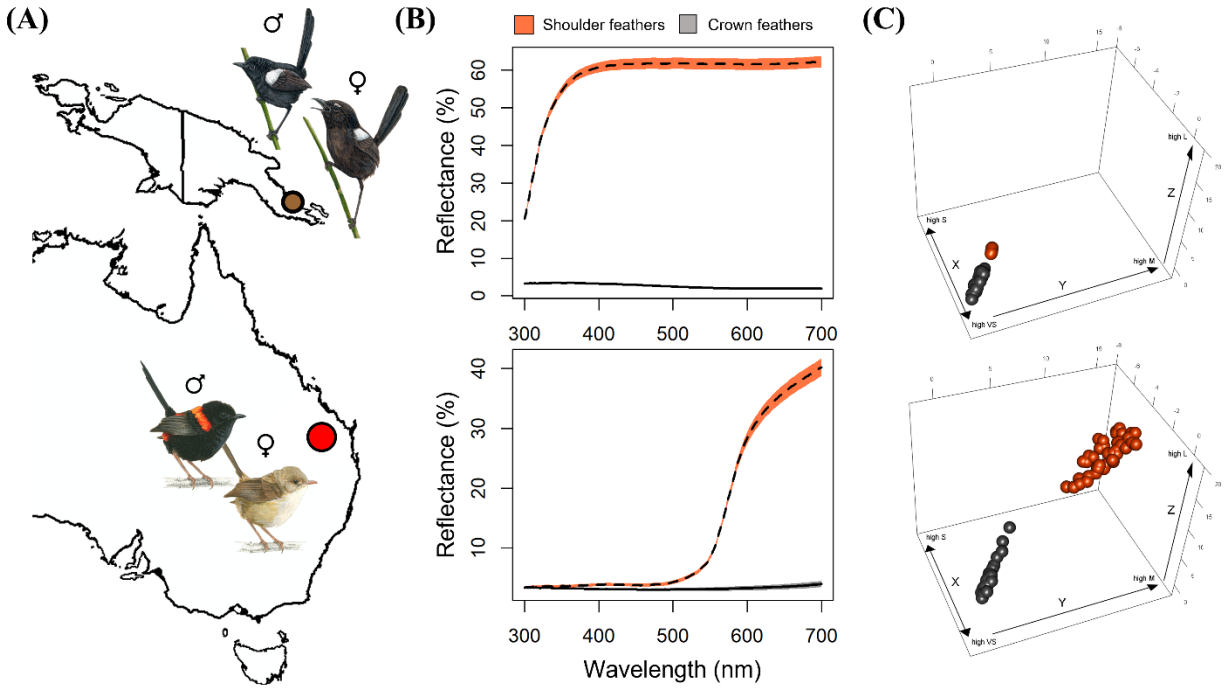

Figure 1. Visual illustration of (A) approximate sampling location and (B, C) male plumage coloration of white-shouldered fairywrens of New Guinea (top) and red-backed fairywrens of Australia (bottom). (B) Plumage reflectance spectra showing mean (± SD) amount of light reflected at a given wavelength of shoulder (orange, dashed lined) and crown (gray, solid line) feathers. (C) Variation in plumage coloration represented in avian tetrahedral colorspace *XYZ* coordinates, set to the same scale for species comparison purposes. Fairywren illustrations provided by Allison Johnson.

Mirror image stimulation:

We performed mirror image stimulation assays in both sexes of both fairywren species following the methods of Jones et al. (2022a,b). As most passerine species appear to be unable to self-recognize (Kraft et al. 2017, but see Prior et al. 2008), we interpreted aggressive behaviors as a response to a perceived same-sex rival of equivalent visual quality. We conducted our mirror assays from 0600-1100 or 1530-1730 local time (GMT +10) while avoiding rain and the intense midday heat. We held birds for ≥15 min post-capture, but prior to mirror assays, as this is when circulating corticosterone has likely reached its asymptotic peak and is unlikely to influence behavior beyond the scope of the current study (Cockrem and Silverin 2002). We temporarily placed fairywrens in a cage measuring 60 cm (length) x 40 cm (width) x 40 cm (height). One side of the cage consisted of a mirror that was initially hidden by a wooden cover, as well as three perches at the same height, but at uniform distance classes away from the mirror (defined as “close”, “neutral”, or “far” from the mirror; see Fig. 1C *in* Jones et al. 2022a). We covered the experimental cage on each side with a white cloth except the one exposed to the video recorder to (1) limit external stimuli influencing individual behavior and (2) reduce the number of potential exits that might distract the bird from the mirror. We placed the cage on the ground within the focal bird’s territory in a shaded location. We allowed focal individuals 5 min to acclimate to the cage prior to exposure to their mirrored reflection for ~7 min. In the current study, we report the behavioral responses post-mirror exposure, as this is the only period in which focal birds displayed aggressive behaviors (see also Jones et al. 2022a). We scored the relative proportion of time spent at each distance class relative to the mirror (e.g., close to the mirror is indicative as a more aggressive stance than far from the mirror) and calculated the total instances of aggression observed (i.e., physically striking the mirror, threatening displays, and soft songs). We video recorded the mirror assays using a partially camouflaged Sony HDR-CX405 Handycam (Tokyo, Japan).

Plumage coloration analysis:

In white-shouldered fairywrens, our *a priori* expectation was that achromatic coloration (i.e., brightness, or % reflected) and not chromatic variation, of the crown (melanin-based black feather coloration) and the shoulder (structurally-based white) feather regions were most likely to serve a signaling function. This assumption is based, in part, to the fact that crown feather coloration is the most variable black feather in this species (Jones unpubl. data). Nonetheless, because black plumage regions in male plumage are iridescent (whereas females are a matte black), we did explore the chromatic variation of these regions as well, although there is exceptionally little chromatic variation among males (Fig. 1B, C). For male red-backed fairywrens, our *a priori* expectation was that the chromatic variation of the red/orange shoulder

(carotenoid-based, Rowe & McGraw 2008) would be important to consider, as these carotenoid colors are targets of sexual selection (Karubian 2002; Karubian et al. 2008; Webster et al. 2008; Baldassarre and Webster 2013). For consistency, we also explored the black crown coloration in red-backed fairywrens.

We collected >6 feathers from each feather region from each male captured and stored them in a cool, dark environment until spectral analysis (detailed methods available in Jones et al. 2022a). We taped feathers on black cardstock (base reflectance: ~10%) in a manner that resembled the way feathers naturally lie on a bird. We then made three repeated measures of reflectance for each feather patch using a USB2000+ spectrometer (R400-7-UV-VIS probe, RPH-1 probe holder) with a PX-2 pulsed xenon light source using OceanView software (v.1.6.7; Ocean Optics, Dundin, FL, USA). The resulting reflectance spectra generated were calibrated relative to a white standard that reflects 100% of light evenly from 300-700nm (Ocean Optics WS-2). We took the mean of the three spectra readings and binned them into 5 nm increments to be used in a psychophysical model of avian vision (Vorobyev et al. 1998; Vorobyev and Osorio 1998), which explores color variation from the bird's visual perspective (as implemented by Delhey et al. (2015)).

Birds possess four types of single cones in their retinas that are sensitive to and detect variation in chromatic coloration (very short (VS), short (S), medium (M), and long (L) wavelengths) and one type of double cone responsible for achromatic (i.e., brightness) variation sensitivity (Cuthill 2006). White-shouldered and red-backed fairywrens are both V-type species (Ödeen et al. 2012) – species that possess ability to perceive UV wavelengths but with lower sensitivity than U-type species (Delhey et al. 2013; Ödeen & Håstad 2013)). Thus, we used the mean V-type peak sensitivity 416, 478, 542, 607 nm (Endler and Mielke 2005). We calculated signal-to-noise ratios for each cone type using formula 10 in Vorobyev et al. (1998), using the mean proportion of cones present in V-type birds from Hart (2001: VS = 0.381, S = 0.688, M = 1.136, L = 1.00), a Weber fraction of 0.1 for the L cone (Olsson et al. 2018), and an irradiance spectrum of standard daylight (D65; Vorobyev et al. 1998). This model of avian vision reduces variation among reflectance spectra to a set of three chromatic coordinates that define their position in avian tetrahedral colorspace: "*X*", "*Y*", and "*Z*." Here, the *X* axis represents the relative stimulation of the S cone relative to the VS cone, *Y* represents the relative stimulation of the M cone to both the VS and S cones, and *Z* represents the relative stimulation of the L cone to the VS, S, and M cones. Distances between points in tetrahedral colorspace are reported as Just Noticeable Differences (JNDs); values representing >1 are considered distinguishable.

We summarized *XYZ* coordinates with a separate principal components analysis (PCA) per plumage region per species using a covariance matrix (*sensu* Jones et al. 2022). All PCAs resulted in one component (hereafter: $PC1_{chroma}$) that explained >92% of the variation (Table 1). For melanin-based black crown coloration, both species had intermediate values for the *X* axis and larger, negative values for both *Y* and *Z*; spectra with larger, more negative Crown-$PC1_{chroma}$ values for this feather region provided low stimulation of the L cone relative to VS + S + M cones, low stimulation of the M cone relative to VS + S cones, and higher stimulation of the VS cone relative to the S cone. Positive Crown-$PC1_{chroma}$ values were those richer in shorter wavelengths (UV/blue) than in longer wavelengths (red). In white-shouldered fairywrens, higher Shoulder-$PC1_{chroma}$ values stimulated the same cones as crown coloration (as both colors are achromatic), although with a greater stimulation of VS than S cones. However, the eigenvalues for both crown and shoulder coloration in white-shouldered fairywrens were <1.0 despite

comprising a vast majority of the variation (>92%), suggesting that there is minimal chromatic variation in these plumage regions. For the carotenoid-based shoulder colors found in red-backed fairywrens, positive Shoulder-$PC1_{chroma}$ scores were feathers that provided higher stimulation of the L cone relative to VS + S + M cones and higher stimulation of the M cone relative to VS + S. Thus, individuals with larger values along this PC axis were individuals with richer red coloration and this axis explained little variation in the UV/blue region. We calculated overall brightness of both the crown and scapular feather patches by calculating the achromatic contrast between each plumage patch and an exceptionally dark spectrum by setting the double cone quantum catch value to 0.001 (Delhey et al. 2015).

	White-shouldered fairywren		Red-backed fairywren	
	Crown	Shoulder	Crown	Shoulder
Eigenvalue	0.470	0.014	2.950	13.51
Variation explained (%)	0.928	0.972	0.984	0.956
X	0.367	0.677	0.389	-0.005
Y	-0.638	-0.607	-0.633	0.727
Z	-0.677	-0.416	-0.669	0.687

Table 1. Loadings for principal components analysis of *XYZ* coloration ($PC1_{chroma}$) for male red-backed and white-shouldered fairywrens. Loadings are each feather patch per species for a single component which explains the majority of variation across patches.

Statistical analysis:

We performed all statistical analyses in R v.4.1.1 (R Core Team 2021). Following a previously established method for mirror image stimulations (Leitão et al. 2019; Jones, Boersma, Liu, et al. 2022), we aggregated mirror strikes, pecks, vocalizations, and displays in response to the female's mirrored reflection by summing them into one overall "Aggression" value, as the latter behaviors were infrequent on their own (Jones, Boersma, Liu, et al. 2022). Using these data alongside the proportion of time spent near versus far from the mirror, we explored species differences in female aggression via a Welch's t-test (as variance was unequal between species). Next, we generated a composite index of aggression in response to their mirrored image with separate PCAs for each species and sex individually (Leitão et al. 2019; Jones, Boersma, Liu, et al. 2022). Behavioral responses during mirror image stimulation assays resulted in a single component with an eigenvalue >1.0 to be retained for further analysis (sensu Leitão et al. 2019; Jones et al. 2022b; Table 2). All behavioral PCs loaded similarly, regardless of sex or species, such that individuals with higher $PC1_{MIS}$ loading scores were birds who responded more aggressively towards their mirror reflection, indicative of a greater proportion of time near the mirror rather than far away from it coupled with increased attack rate.

To explore the relationship between male phenotypic quality and female aggression, we ran a series of multiple regression analyses coupled with a finite sample corrected Akaike's information criterion (AICc) model selection procedure. For each model (i.e., species), individual female aggression scores were set as a dependent variable and our fixed effects were

seven (putative) indices of male condition (center and scaled tail length, mass, scaled CP volume, as well as chromatic and achromatic chroma of both the crown and scapular feather patches); only final models are presented in the main text (but see Supplemental Material for full AICc table). Finally, we ran a separate, but complementary statistical analysis using the same male morphological traits, condensed via PCA following the approach of Cain (2014). The results between statistical approaches were relatively consistent and we report these findings in the Supplemental Material.

For red-backed, but not white-shouldered fairywrens, we were able to obtain the mated male's mirror aggression assay scores alongside their plumage coloration. Therefore, we explored if a relationship exists between male phenotypic variation and their aggression profiles using both statistical analyses above. For all analyses of red-backed fairywrens, we only included males who had reached >50% of their nuptial molt (i.e., majority black-and-red), as males under this value (n =3) were significant outliers that skewed the dataset. While we acknowledge that females mated with unornamented, brown males are likely to differ from those mated with ornamented males (Karubian 2002; Karubian et al. 2008), our sample size of brown, unornamented males is insufficient to warrant inclusion here. White-shouldered fairywrens in our sampled subspecies do not vary based on coloration. We excluded one outlier female in each species, both of which were females that did not respond to their mirrored reflection and were >2 SD from the means.

	White-shouldered fairywren	Red-backed fairywren	
	Female	Female	Male
Eigenvalue	1.830	2.37	2.39
Variation explained (%)	0.609	0.791	0.798
Aggression (strikes + pecks + displays + songs)	0.493	0.531	0.542
Proportion of time spent close	0.657	0.621	0.618
Proportion of time spent far	-0.570	-0.577	-0.569

Table 2. Loading scores for the principal components analysis ($PC1_{MIS}$) exploring how fairywrens respond to mirror image stimulation. Presented are the single resulting component for female white-shouldered fairywrens and both red-backed fairywrens sexes.

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), Griffith University's Animal Ethics Committee (ENV/08/19/AEC), and in adherence to research permits from the Conservation and Environment Protection Authority of Papua New Guinea (#99902100765). All birds were captured, processed, exposed to mirror assays, and released in under one hour. We continuously monitored our mist-nets and removed birds immediately upon hitting the net. All individuals involved in removal of birds from mist-nets were trained in the appropriate technique to extract and safely handle birds.

Results:

Species comparison:

We conducted mirror assays on 26 female red-backed fairywrens and 44 white-shouldered fairywrens. On average, white-shouldered fairywren females were more aggressive than red-backed fairywren females, with a greater rate of aggressive behaviors observed per min ($t = 3.53$, $df = 64.40$, $p < 0.001$; Fig. 2) and proportion of time near the mirror ($t = 3.61$, $df = 45.32$, $p < 0.001$). Red-backed fairywrens were more likely to be positioned far from the mirror than white-shouldered fairywrens ($t = 3.68$, $df = 34.05$, $p < 0.001$).

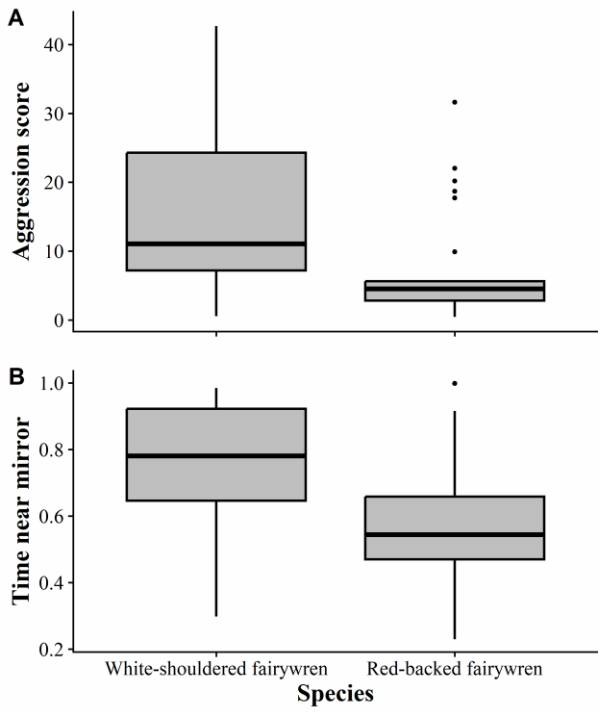

Figure 2. Responses of white-shouldered fairywrens and red-backed fairywrens to mirror image stimulation. (A) Aggression score represents the aggregation of mirror strikes, pecks, songs, and displays preformed throughout the mirror assay. On average, female white-shouldered fairywrens were significantly more aggressive towards their reflection than red-backed fairywrens, frequently attacking the mirror. (B) Time near mirror represents a proportion of time relative to the length of the trial, such that white-shouldered fairywrens spent a greater proportion of time near the mirror compared to red-backed fairywrens.

Female aggression with respect to male phenotypic quality:

Previous work in this population of white-shouldered fairywrens revealed that female aggression is unrelated to her own plumage coloration and body size (Jones, Boersma, Liu, et al. 2022), and thus we do not replicate those results here. We tested the relationship between male mate quality attributes on the aggression of 38 individual female white-shouldered fairywrens. The best fitting model predicting female white-shouldered fairywren aggression included male mass, tail length, and CP volume, although the overall model was not statistically significant (multiple $r^2 = 0.10$, $F_{3, 37} = 2.45$, $p = 0.08$; Fig. 3; Table 3; Table S1 for full model selection parameters). Within the best fitting model, females were most aggressive if their mate tended to be heavier (β est. = 0.62,

p = 0.10) and have a longer tail (β est. = 0.42, p = 0.06); despite appearing in the top model, CP volume was not significantly related to aggression (β est. = 0.04, p = 0.50). There were an additional five models < 2 ΔAICc (Table 3), all of which contained some combination of the above three characteristics and all in the same direction

	AICc	ΔAICc	Weight	adj. r^2	Model P
Mass + Tail length + CP Volume	143.02	0	0.238	0.098	0.08
Tail length + CP Volume	143.49	0.471	0.188	0.053	0.13
Mass + CP Volume	144.39	1.369	0.12	0.032	0.20
Mass + Tail length	144.82	1.801	0.097	0.083	0.07
CP Volume	144.92	1.902	0.092	-0.014	0.51
Mass	144.99	1.973	0.089	0.049	0.09

Table 3. Abbreviated model selection table exploring which male phenotypic variables best predict aggression in female white-shouldered fairywrens. Presented are the models < 2 ΔAICc from the best fitting model; see Table S1 for full model parameters.

In red-backed fairywrens, we first ran a series of Pearson's correlations and found that female aggression was not related to her own age (p = 0.34) nor any standard morphological measurement (e.g., mass, tarsus length, tail length; all p > 0.16). Including only pairwise observations, we compared female aggression to her mated male's phenotype for 18 female red-backed fairywrens. The best fitting model contained center and scaled CP volume as the sole predictor, but this model was not statistically significant (multiple r^2 = 0.09, $F_{1, 16}$ =1.65, p = 0.22; Fig. 3; Table S2 for full model selection parameters). There was one additional model < 2 ΔAICc containing male mass alongside CP volume, but neither parameter were significant predictors of aggression (both p > 0.19).

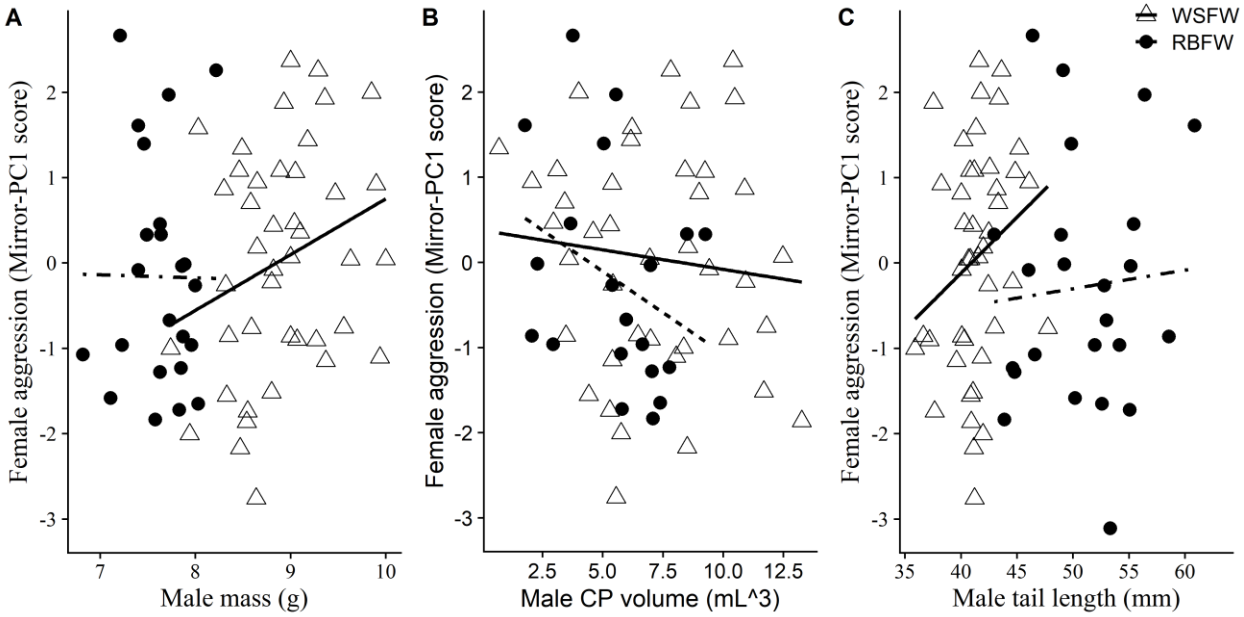

Figure 3. Relationship between female aggression and male (A) mass, (B) CP volume and (C) tail length in white-shouldered fairywrens (WSFW; triangle; solid line) and red-backed fairywrens (RBFW; circle, dotted line).

Male red-backed fairywren coloration and aggression:
In male red-backed fairywrens, we found the best fitting model predicting male aggression included the chroma coloration of the crown (black) and scapular (red) feather patches (multiple $r^2 = 0.36$, $F_{2, 21} = 5.94$, $p = 0.009$; Table S3 for full model selection parameters): males with greater UV/blue rich crowns (β est. = 0.57, $p = 0.04$), but overall less red scapular feathers (β est. = -0.41, $p = 0.002$), were most aggressive. There was one additional model < 2 ΔAICc, representing the full model including chromatic and achromatic variation of the crown and scapular, as well as mass, CP volume, and tail length ($r^2 = 0.65$, $F_{7,12} = 3.13$, $p = 0.03$; Table S3). While chroma of the crown and scapular feather patches remained significant predictors in this model, only CP volume emerged as a borderline significant variable such that males with smaller CP's tended to have higher aggression scores (β est. = -0.34, $p = 0.06$). No additional parameters were significant within the second model (all $p > 0.50$).

Discussion:
In the current study, we explored how females in two sister *Malurus* species with marked differences in mating system and overall life-history strategy vary in aggressive behaviors and whether or not females of these species who are mated with males in higher physical condition are more aggressive. Our results provide support for our prediction that white-shouldered fairywrens, a songbird species with female plumage ornamentation, endemic to tropical New Guinea that experiences intense year-round competition, would be more aggressive on average than their temperate sister species, red-backed fairywrens of Australia, a species lacking any female plumage ornamentation. Further, while we failed to support our predictions about a relationship between male coloration and female aggression in white-shouldered fairywrens, we were not expecting male mass nor tail length to emerge as partial (as they were not statistically significant) predictors of female aggression; the females who were most responsive to mirror stimulation were mated to males who tended to be heavier, but also had longer tails. On the other hand, in red-backed fairywrens we found that the best predictor of female aggression from our dataset was male CP volume, but critically, this variable was not statistically significant nor was there an apparent trend. These results suggest that there is not a relationship between female red-backed fairywren aggression and any metric of male condition, indicating that females may not compete among each other, and if they do, it may be over access to limited ecological resources instead of male quality.

Our results are consistent with the idea that intrasexual competition is elevated in female white-shouldered fairywrens. In particular, we found that female white-shouldered fairywrens are, on average, significantly more aggressive towards simulated female rivals than red-backed fairywrens, their sister species with clear sexual dichromatism and female preferences for male coloration (Baldassarre and Webster 2013). As is common in tropical ecosystems (Stutchbury and Morton 2022), the intensity of social competition white-shouldered fairywrens experience is likely high enough that it may require both sexes to coordinate in territory defense and/or

parental care in order to achieve any reproductive output at all. In tropical New Guinea, it may be that females perceive potential rivals as existential threats to their overall reproductive success, although it remains unclear at this point whether females are competing over access to territory versus mate quality per se. These results are also consistent with a similar study conducted between white-shouldered fairywren subspecies that differed in the extent to which females are ornamented. Specifically, Jones et al. (2021) argued that the presence of multiple morphological (e.g., female plumage coloration) and behavioral (e.g., aggression) traits often associated with competition in the ornamented *M. alboscapulatus moretoni* (the subspecies of the current study) is evidence of a correlated phenotypic shift in response to increased intensity of social selection pressure relative to an unornamented subspecies, *M. alboscapulatus lorentzi*.

One possible explanation for species differences in overall aggression involves the presence of auxiliary helpers. Red-backed fairywrens routinely (although not always) have auxiliary helpers that help feed nestlings (Mulder et al. 1994). It may be that such assistance liberates females, at least in-part, from the need to compete over males that would provide the best parental care. Alternatively, ornamented males appear to invest more in extra-pair copulations than in duller males (Webster et al. 2008; Dowling and Webster 2017), so it may also be likely that ornamentation plays little-to-no role in choice à la parental care for red-backed fairywrens. There is limited documentation of helpers at the nest in the *M. a. moretoni* subspecies of white-shouldered fairywrens (Enbody et al. 2019), and is overall much rarer relative to their Australian congeners (JAJ pers. obs.). The unornamented *M. a. lorentzi* subspecies, on the other hand, are highly social (Boersma et al. 2022), have similar group sizes (Enbody et al. 2019), and anecdotally behave in a similar manner to red-backed fairywrens. A behavioral comparison between red-backed fairywrens and *M. a. lorentzi* would be a potentially fruitful avenue of research, as these two species are share several life-history and mating system characteristics, despite the large latitudinal distance between species. Elucidating whether or not white-shouldered fairywrens overall provide more or less parental care than male red-backed fairywrens would also be enlightening.

Selection via female-female competition over male parental care may be indirectly related to the evolution of female ornamentation (Kokko and Johnstone 2002; Dale et al. 2015; Dunn et al. 2015; Lyu et al. 2017; Fargevieille et al. 2023). Female ornamentation in white-shouldered fairywrens (*M. a. moretoni*) is derived from an ancestral, brown phenotype that resembles red-backed fairywren females (Enbody et al. 2022). However, there is currently no evidence that plumage coloration is a signal used in female-female competitive interactions nor is color related to any other morphometric variables (e.g., mass; Jones et al. 2022b). While it appears that social competition is elevated in white-shouldered fairywrens, our experimental design does not permit us to disentangle whether females compete over access (higher quality) males versus access to any other ecological resources (i.e., territory control). After all, our white-shouldered fairywren models only trended towards statistical significance, which may suggest that male condition is only a secondary consideration for females (Cain 2014), or that male condition is simply that correlated with behavioral traits that females are actually interested in. Interestingly, we found the most aggressive females were those mated to males who were heavier, but had longer tails. This contrasts with prior fairywren studies that suggested shorter tails are associated with dominance in males and may be preferred by females (Swaddle et al. 2000; Karubian et al. 2009). Perhaps females mated to longer-tailed individuals have elevated aggression profiles to compensate if male territorial defense is effectively lacking (Langmore

1998). Alternatively, it may simply be the tails are not a signal that females pay attention to; Jones et al. (2021) found that male tail length did not vary across the two subspecies of white-shouldered fairywrens, despite large variation in the intensity of competitive pressure experienced, and subsequent aggression profiles, between populations. Nevertheless, as these data only tended towards statistical significance, we can only speculate about the possible relationship between male tail length and female aggression, if one exists at all.

In contrast to their New Guinean counterparts, male coloration is well-studied in red-backed fairywrens. Males in this species exhibit delayed plumage maturation, such that the majority of males are unornamented and appear identical (to humans, but not birds; Karubian et al. 2008) to females during their first breeding season (Webster et al. 2008; Karubian et al. 2011). Ornamented males are more aggressive towards (Karubian 2008) and have higher reproductive success than unornamented males (Webster et al. 2007; Webster et al. 2008). Yet, aggression itself is unlikely to deter rivals from copulating with their mates, but rather may function to secure territory resources and/or boundaries (Baldassarre et al. 2016). Finally, experimental research between red-backed fairywren subspecies have shown that females prefer redder dorsal plumage over orange coloration, with redder males siring significantly more extra-pair young (Baldassarre and Webster 2013). These studies provide compelling evidence that ornamentation in males is sexually selected, but through extra-pair copulations rather than females seeking more ornamented individuals for social partners. For example, Dowling and Webster (2017) found that while ornamented males sought more extra-pair paternity opportunities, unornamented males compensated by investing in physical and acoustic mate guarding in order to maximize reproductive success. Given these studies, it may not be surprising that we did not find a relationship between female aggression and her mate's plumage coloration; perhaps it is the case that females perceive male coloration as a reliable indicator of genetic benefits of their offspring (Hasselquist et al. 1996), as evidenced by the disproportionate amount of extra-pair copulations seen (Baldassarre and Webster 2013), but not necessary how viable those males would be as social partners. Overall, these results highlight the varying strategies employed by red-backed fairywrens of both sexes and signify the continued need for coloration studies of among-individual variation that goes beyond the "unornamented versus ornamented" dichotomy.

Using mirror image stimulation assays, we assessed aggression between two species of fairywrens that differ in mating strategy, life-history, and even geographical location in a manner that allows for reliable behavioral comparisons. The use of these assays allowed us to test how individuals would respond to a simulated same-sex rival of equivalent visual quality on as even a playing field as possible, as they remove external and social stimuli which may influence behavior. Moreover, focal individuals were tested while in isolation from their social mate, a consideration of particular noteworthiness for species which engage in joint territory defense like *Malurus*. Nevertheless, mirror assays are not without their own set of caveats worth considering, such as the stress involved with temporary captivity that may influence behavioral profiles (Dickens et al. 2009) and species- or sex-level differences in how well individuals respond to (temporary) captivity (Beiko et al. 2004). Despite that the level of aggression exerted by caged individuals may be comparable to that which would be to shown to live opponents (Teles et al. 2013), the very nature of mirror assays means that the tested individuals always stalemate, rather than decisively winning versus losing; a level of post-contest self-assessment of outcome is required to elicit changes in hormonal and/or transcriptomic pathways (Oliveira et al. 2005;

Oliveira et al. 2016). We also echo the sentiments of Cain (2014), in that this is a correlative study and we cannot exclude the possibility that females compete over resources that we were unable to quantify in the current study outside of male phenotype. For example, we cannot explore how male condition is correlated to territorial resources which may confound the results presented here. That said, the relationship between specific attributes of territory quality (e.g., local vegetation cover, insect abundance/diversity, etc.) and how this dictates territorial behavior and fitness is not well understood for either tropical or temperate regions (Stutchbury and Morton 2022). Furthermore, Stutchbury and Morton (2022) predict that territorially quality should be more predictive of reproductive success in temperate species rather than tropical ones, which may suggest that territory quality may not amount to much in the case of white-shouldered fairywren mate choice. Ultimately, we believe the value of mirror assays exceeds any of these potential limitations, as to be able to reliably compare behaviors between two markedly distinct species in this manner is novel, and we expect that it may be a useful technique for other species where multiple individuals normally participate in territory defense.

Recent evidence suggests that intrinsic quality of one's partner may not be as important as previously thought in socially monogamous systems (Ihle et al. 2015; Wang et al. 2017; Griffith 2019; Hurley et al. 2020). Rather, the quality of behavioral interactions between females and males (e.g., cooperativeness) in these species may be more important than phenotypic quality, particularly for tropical birds. Many Australasian birds follow this general life-history strategy, where long-term pairings, duetting (i.e., both sexes sing), mutual ornamentation, and allopreening are commonplace, suggesting that male and female collaboration around reproduction is just as, if not more important than individual quality (Griffith 2019; Ah-King 2022). That is not to say that condition-dependent sexual ornamentation is not useful in socially monogamous species, as such signals are important in initial mate choice decisions and females should view male signals as honest indicators of intrinsic quality (Griffith 2019). Sexual selection is more nuanced than one sex simply preferring a partner that is or is not more attractive. It is apparent that female animals are not by-standers in socially monogamous species, as it may have been presumed historically, but rather make calculated mating decisions based on a series of complex factors, which may, or may not include mate quality and/or the competitive environment that surrounds them. How intense intrasexual competition drives the evolution of competitive traits in females compared to males, what ultimately dictates commitment to an agnostic conflict, and/or what mediates the intensity of aggressive response seen during contests still remains an open question. We are excited to contribute to that discussion with our findings and encourage more multi-species, between-sex comparisons where applicable moving forward.

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Data accessibility:

Data used and R source code produced in this study have been made publicly available via Mendeley Data (DOI: 10.17632/mpfw9td2sw.1)

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