

1 **Assessing the relationship between female aggression and male phenotype in two sister**
2 ***Malurus* fairywren species**

3
4
5 John Anthony Jones^{1*}, William E Feeney^{2,3}, Darryl N Jones³, Doka Nason⁴, Serena Ketaloya⁴,
6 and Jordan Karubian¹.

7
8 1- Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, LA
9 USA

10 2- Doñana Biological Station (CSIC), Sevilla, Spain

11 3- Centre for Planetary Health and Food Security, Griffith University, Brisbane, QLD, Australia

12 4- Porotona Village, Alotau, Milne Bay Province, Papua New Guinea

13
14 ***Corresponding author:**

15 Email: johnajones91@gmail.com

16 Phone: +1 910-255-4000

17

18

19 **Acknowledgments:**

20 In Papua New Guinea, our research would not have been possible without the logistical and in-
21 field support from D. Nason and S. Ketaloya as well as the hospitality offered to us by the
22 residents of Podagha Village (Milne Bay Province). We thank the Milne Bay provincial
23 government for permits and permissions, and the National Research Institute for their assistance
24 in acquiring country-level research permits (#99902100765) and visas. For Australia, we thank
25 M. Webster for logistical support and Southeast Queensland Water for access to our field site.
26 We respectfully acknowledge the Aboriginal peoples and Torres Strait Islander peoples as the
27 Traditional Owners and Custodians of the land on which our research took place and pay our
28 respects to the Elders both past and present.

29 Our study was funded by the National Science Foundation (IOS-1354133) awarded to
30 JK, an Australian Department of Education and Training Endeavour Research Leadership
31 fellowship (JAJ), the American Ornithological Society (JAJ), the American Philosophical
32 Society (JAJ), the Department of Ecology and Evolutionary Biology of Tulane University (JAJ),
33 Birds Queensland (WEF) and a Hermon Slade Project Grant (HS15/1) (WEF). Funders have had
34 no influence on the content of the current manuscript nor do they require approval of the final
35 manuscript to be published.

36

37 **Data accessibility:**

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

40

41 **Abstract:**

42 In a large and ever-growing number of animal species, it is now appreciated that females use
43 colors as a visual signal in a range of social interactions, including both courtship and territorial
44 aggression. Yet, it remains unclear whether female color phenotypes and/or aggressive behaviors
45 are correlated with any attributes of their mate's phenotype. For example, we might expect
46 species in which males contribute more to parental care or territorial defense to have more
47 colorful or aggressive females. On the other hand, within species, we might expect those females
48 mated to higher quality males to be more colorful or aggressive than those mated to lower quality
49 males. To begin to address these possibilities, we conducted a preliminary study in two sister
50 taxa of fairywren (Maluridae) with distinct life-history strategies and plumage dichromatism:
51 white-shouldered fairywrens (*Malurus alboscapulatus moretoni*) in tropical Papua New Guinea,
52 a species in which both males and females have ornamented plumage and jointly defend
53 territories year-round, and red-backed fairywrens (*M. melanocephalus melanocephalus*) in
54 temperate Australia, a sexually dichromatic species with ornamented males and unornamented
55 females. At the between species level, we predicted white-shouldered fairywren females would
56 be more aggressive in same-sex interactions than red-backed fairywrens, as both white-
57 shouldered males contribute to year-round territorial defense, whereas territories break-down
58 during non-breeding in red-backed fairywrens. Further, we predicted that, within species,
59 females mated to males of higher quality would be more aggressive in simulated same-sex
60 encounters. Between species, female white-shouldered fairywrens were more aggressive on
61 average than female red-backed fairywrens as predicted. Within both species, indices of male
62 quality were not related to female aggression (although there was a non-significant tendency for
63 more aggressive female white-shouldered fairywren to have heavier mates with longer tails).
64 These results point to a need for additional research exploring relationships between life history,
65 female plumage, and female aggressive behaviors in a wider range of species.

66

67 *Keywords:* Aggression, fairywren, female ornamentation, mirror image simulation, New Guinea,
68 social competition

69

70 **Introduction:**

71 Social selection theory posits that competition over any critical resource, whether sexual or non-
72 sexual in nature, should lead to the evolution of competitive traits (e.g., aggression, ornaments,
73 armaments, etc.) that aid in resource acquisition (Crook 1972; West-Eberhard 1979; Lyon and
74 Montgomerie 2012; Tobias et al. 2012). Though the study of competitive interactions has been
75 well explored both theoretically and empirically from the male perspective, female animals also
76 compete aggressively for access to limited resources crucial to survival and reproduction
77 (Langston et al. 1990; Slagsvold and Lifjeld 1996; Fedy and Stutchbury 2005; Rosvall 2008).
78 Despite centuries of academic neglect, there is now little doubt that female-female competitive
79 interactions are adaptive and indirect selection pressures in a variety of taxa (Clutton-Brock
80 2007; Stockley and Bro-Jørgensen 2011; Tobias et al. 2012; Cain and Ketterson 2013; Stockley
81 and Campbell 2013; Cain and Rosvall 2014; Lipshutz and Rosvall 2021; Fischer et al. 2023).
82 Indeed, social selection is often invoked as an explanation for the evolution of competitive
83 phenotypes in females, as the most aggressive females are those who are more likely to acquire

84 resources necessary for breeding (Yasukawa and Searcy 1982; Jawor et al. 2006; Pryke 2007;
85 Rosvall 2008), ultimately achieving greater reproductive success (Slagsvold and Lifjeld 1996;
86 Rosvall 2011; Cain and Ketterson 2012).

87 Because selection maximizes reproductive success in each sex differently (Trivers 1972;
88 Westneat and Sargent 1996; Kappeler et al. 2022), it remains unclear if the same ecological and
89 social stimuli that commonly predict patterns of male aggression equally apply to females.
90 Would we expect to find the most aggressive females to be mated to the highest quality males?
91 Females are typically not limited by the number of potential mates available, and as such, a
92 common perception is such that females-female competition most often occurs over ecological
93 resources that enhance and/or are necessary for reproductive success (e.g., food availability,
94 oviposition sites, etc.) rather than mates per se (Heinsohn et al. 2005; Stockley and Bro-
95 Jørgensen 2011; Tobias et al. 2012; Stockley and Campbell 2013). Nevertheless, while males
96 often compete for access to the greatest number of potential mates, females may compete for
97 access to the highest quality mates that provide the best parental care, indirect (genetic) benefits,
98 and/or access to highly preferred nesting locations (Rosvall 2011). For example, intrasexual
99 aggression among female sharknose gobies (*Elacatinus evelinae*) is most intense over larger
100 males, as this phenotype is typically associated with elevated paternal care (Whiteman and Côté
101 2003). However, intrasexual female competition over the highest quality mates is not universal;
102 aggression among female dark-eyed juncos (*Junco hyemalis*) is most intense over nonsexual
103 resources (nest site quality), with male quality as a secondary consideration (Cain 2014). Given
104 this overall paucity and diversity of findings on degree of within species female competition,
105 such as whether female aggression or other traits accurately predict quality of their mates, further
106 explorations would help to advance our understanding of female signal evolution.

107 On a similar note, a comparison of closely related species that differ in the relative degree
108 of female social competition may help elucidate the role that such variation in the competitive
109 environment and/or overall life-history plays in shaping the intensity of female aggression.
110 Variation in the breeding season length, mating system, and food resources all have a large role
111 in influence the direction of territorial aggression among songbirds (Stutchbury and Morton
112 2023) including females. The strength of social selection acting on males and females is
113 predicted to be similar in tropical regions where sex role convergence in year-round territory
114 defense and parental care is common (Kunkel 1974; Slater and Mann 2004; Stutchbury and
115 Morton 2023) versus that of temperate regions, where territory defense typically occurs only in
116 the spring and summer (Fedy and Stutchbury 2005; Catchpole and Slater 2008). Tropical species
117 often consist of both sexes expressing some form of mutual ornamentation (Karubian 2013; Dale
118 et al. 2015), potentially reflecting how shared phenotypes function as signals in mate-choice
119 and/or competitive contexts in both sexes (Kraaijeveld et al. 2007; Murphy et al. 2009). In
120 contrast, species occupying temperate ecosystems are commonly dichromatic, with males
121 stereotypically highly adorned and territorial, whereas females are often muted in plumage
122 coloration and do not defend the territory as vigorously (Stutchbury and Morton 2023). These
123 observations are consistent with the idea that female-female competition experienced in tropical
124 regions may exceed that commonly experienced by their temperate congeners, but there are
125 limited examples of comparative behavioral studies between closely related, recently diverged
126 species. Moreover, few behavioral assays reliably compare aggression between geographically
127 isolated species while controlling for the influence of the social environment.

128 In this descriptive study, we studied two sister species that vary distinctly in overall life
129 history strategy and sexual dichromatism: (1) white-shouldered fairywrens (*Malurus*
130 *alboscapulatus moretoni*), a tropical songbird endemic to New Guinea that defend territories
131 year-round, are mutually ornamented (in all but one subspecies (Enbody et al. 2019)), and have
132 convergent sex roles, and (2) red-backed fairywrens (*M. melanocephalus melanocephalus*) of
133 subtropical-to-temperate Australia, a dichromatic species with seasonal territoriality and
134 breeding (Fig. 1). Both species are socially monogamous, but differ markedly in overall sociality
135 and reproductive strategy. Red-backed fairywrens are highly social, with nesting groups that
136 consist of breeding pair and often (though not always) contain additional auxiliary (both kin and
137 non-kin) helpers (Rowley and Russell 1997; Karubian 2002; Webster et al. 2008), whereas
138 helpers are the exception, rather than the norm, in the subspecies of white-shouldered fairywrens
139 of the current study (Enbody et al. 2019). White-shouldered fairywrens also have lower levels of
140 extra-pair paternity (~33%) and have smaller scaled cloacal protuberance volumes on average
141 (7.85 mL^3) than red-backed fairywrens (~56% and 16.94 mL^3 , respectively (Brouwer et al. 2017;
142 Enbody et al. 2019)); among *Malurus*, larger cloacal protuberance volumes is positively
143 associated with testes size, sperm quality and overall rates of extra-pair paternity (Tuttle et al.
144 1996; Rowe and Pruett-Jones 2011; Rowe and Pruett-Jones 2013). Finally, male red-backed, but
145 not white-shouldered fairywrens, exhibit delayed plumage maturation, such that the majority of
146 males are unornamented and appear identical to females (to humans, but not birds; Karubian et
147 al. 2008) during their first breeding season (Webster et al. 2008; Karubian et al. 2011). There is
148 evidence that male coloration is sexually selected in red-backed fairywrens, as experimental
149 research between red-backed fairywren subspecies have shown that females prefer redder dorsal
150 plumage over orange coloration, with redder males siring significantly more extra-pair young
151 (Baldassarre and Webster 2013).

152 Based on these species differences in mating systems and life-history strategy, we
153 predicted that female white-shouldered fairywrens would be more likely to experience intense
154 selection pressure via intrasexual competition than female red-backed fairywrens, and thus
155 display overall higher levels of aggression. Both within and between species, we quantified
156 variation in how individuals respond to same-sex intruders through the use of mirror image
157 simulations behavioral assays that put individuals up against their own mirrored reflection,
158 mimicking an intrasexual challenge against a rival of equivalent visual quality (Gallup Jr 1968;
159 Leitão et al. 2019; Jones, Boersma, Liu, et al. 2022). A strength of this behavioral approach is
160 that it allows for reliable and relatively standardized comparisons between two species of
161 fairywrens that differ in mating strategy, life-history, and even geographical location. Moreover,
162 these assays isolate focal individuals from their social mate, a consideration of particular
163 noteworthiness for species which engage in joint territory defense like *Malurus* (Jones, Boersma,
164 and Karubian 2022). We additionally conducted an exploratory analysis on if more (or less)
165 aggressive females are partnered with males of higher phenotypic quality by correlating
166 aggression scores with male plumage coloration and body condition indices. We predicted that,
167 if females compete over access to the most attractive males, the most aggressive females will be
168 partnered with males of higher phenotypic quality. This preliminary assessment of how female
169 aggression may relate to between species variation in life history and dichromatism, and within
170 species variation in mate quality, is intended to promote and guide further research rather than a
171 definitive test of these predictions per se.

172 **Methods:**

173 *Study species and general field methods:*

174 Both sister species are predominately grassland specialists, but differ significantly in mating
175 system structure, overall life-history strategy, and if females are ornamented or not (Rowley and
176 Russell 1997). In New Guinea, white-shouldered fairywren plumage coloration remains
177 consistent year-round in both sexes (Fig. 1). Male plumage coloration is consistently black-and-
178 white throughout the island, but females vary allopatrically in plumage phenotype that tracks
179 with subspecies (Rowley and Russell 1997; Enbody et al. 2019). The current study is of *Malurus*
180 *alboscapulatus moretoni*, a subspecies where both sexes are mutually ornamented, with such
181 female coloration having been derived from that of an unornamented phenotype that resembles
182 their sister species (Enbody et al. 2019; Enbody et al. 2022). In contrast, male red-backed
183 fairywrens in Australia seasonally molt between an ornamented plumage phenotype (i.e.,
184 eumelanin-based black body coloration and carotenoid-based red backs and shoulders) during
185 the breeding season and a drab (phaeomelanin-based brown) phenotype that resembles that of
186 females during the non-breeding season (Rowley and Russell 1997; Karubian 2002; Karubian
187 2008). Female plumage color typically does not vary, such that they remain unornamented year-
188 round, although it is possible that variation in bill coloration may exist as it does in males
189 (Karubian 2008).

190 We studied a population of white-shouldered fairywrens in Podagha Village, Milne Bay
191 Province, Papua New Guinea (9.692°S, 149.895°E) from June-July 2019, and red-backed
192 fairywrens in Samsonvale, Queensland, Australia (27.271°S, 152.857°E) from August-
193 November 2019. We captured individuals with mist-nets for banding and feather collection. To
194 explore for evidence that female coloration is related to male phenotype, we focused on three
195 standard body measurements that we suspected may be important differences between sexes
196 and/or species: (1) mass (± 0.01 g): both species exhibit size dimorphism, such that males are
197 slightly heavier than females (Rowley and Russell 1997); (2) Tail length (± 0.01 mm): shorter
198 tails are thought to be a signal of social dominance in *Malurus* (Swaddle et al. 2000; Karubian et
199 al. 2009); (3) Scaled cloacal protuberance (CP) volume (0.01 mL^3 ; Tuttle et al. 1996; Rowe and
200 Pruett-Jones 2011, 2013). We calculated scaled CP as the ratio of CP volume (calculated as: 3.14
201 $\times (\text{CP height}/2) \times (\text{CP width}/2) \times \text{CP length}$) to body mass for males (Tuttle et al. 1996).

202

203 *Mirror image stimulation:*

204 We performed mirror image stimulation assays in both sexes of both fairywren species following
205 the methods of Jones et al. (2022a,b). As most passerine species appear to be unable to self-
206 recognize (Kraft et al. 2017, but see Prior et al. 2008), we interpreted aggressive behaviors as a
207 response to a perceived same-sex rival of equivalent visual quality. We conducted our mirror
208 assays from 0600-1100 or 1530-1730 local time (GMT +10) while avoiding rain and the intense
209 midday heat. We held birds for ≥ 15 min post-capture, but prior to mirror assays, as this is when
210 circulating corticosterone has likely reached its asymptotic peak and is unlikely to influence
211 behavior beyond the scope of the current study (Cockrem and Silverin 2002). We temporarily
212 placed fairywrens in a cage measuring 60 cm (length) x 40 cm (width) x 40 cm (height). One
213 side of the cage consisted of a mirror that was initially hidden by a wooden cover, as well as
214 three perches at the same height, but at uniform distance classes away from the mirror (defined

215 as “close”, “neutral”, or “far” from the mirror; see Fig. 1C *in* Jones et al. 2022a). We covered the
216 experimental cage on each side with a white cloth except the one exposed to the video recorder
217 to (1) limit external stimuli influencing individual behavior and (2) reduce the number of
218 potential exits that might distract the bird from the mirror. We placed the cage on the ground
219 within the focal bird’s territory in a shaded location. We allowed focal individuals 5 min to
220 acclimate to the cage prior to exposure to their mirrored reflection for ~7 min. In the current
221 study, we report the behavioral responses post-mirror exposure, as this is the only period in
222 which focal birds displayed aggressive behaviors (see also Jones et al. 2022a). We scored the
223 relative proportion of time spent at each distance class relative to the mirror (e.g., close to the
224 mirror is indicative as a more aggressive stance than far from the mirror) and calculated the total
225 instances of aggression observed (i.e., physically striking the mirror, threatening displays, and
226 soft songs). We video recorded the mirror assays using a partially camouflaged Sony HDR-
227 CX405 Handycam (Tokyo, Japan).

228

229 *Plumage coloration analysis:*

230 In white-shouldered fairywrens, our *a priori* expectation was that achromatic coloration (i.e.,
231 brightness, or percent of light reflected) and not chromatic variation, of the crown (melanin-
232 based black feather coloration) and the shoulder (structurally-based white) feather regions were
233 most likely to serve a signaling function. This assumption is based, in part, to the fact that crown
234 feather coloration is the most variable black feather in this species (Jones unpubl. data).
235 Nonetheless, because black plumage regions in male plumage are iridescent (whereas females
236 are a matte black), we did explore the chromatic variation of these regions as well, although there
237 is exceptionally little chromatic variation among males (Fig. 1). For male red-backed fairywrens,
238 our *a priori* expectation was that the chromatic variation of the red/orange shoulder (carotenoid-
239 based, Rowe & McGraw 2008) would be important to consider, as these carotenoid colors are
240 targets of sexual selection (Karubian 2002; Karubian et al. 2008; Webster et al. 2008;
241 Baldassarre and Webster 2013). For consistency, we also explored the black crown coloration in
242 red-backed fairywrens.

243 We collected ≥ 6 feathers from each feather region from each male captured and stored
244 them in a cool, dark environment until spectral analysis (detailed methods available in Jones et
245 al. 2022a). We taped feathers on black cardstock (base reflectance: ~10%) in a manner that
246 resembled the way feathers naturally lie on a bird. We then made three repeated measures of
247 reflectance for each feather patch using a USB2000+ spectrometer (R400-7-UV-VIS probe,
248 RPH-1 probe holder) with a PX-2 pulsed xenon light source using OceanView software (v.1.6.7;
249 Ocean Optics, Dundin, FL, USA). The resulting reflectance spectra generated were calibrated
250 relative to a white standard that reflects 100% of light evenly from 300-700nm (Ocean Optics
251 WS-2). We took the mean of the three spectra readings and binned them into 5 nm increments to
252 be used in a psychophysical model of avian vision (Vorobyev et al. 1998; Vorobyev and Osorio
253 1998), which explores color variation from the bird’s visual perspective (as implemented by
254 Delhey et al. (2015)).

255 Birds possess four types of single cones in their retinas that are sensitive to and detect
256 variation in chromatic coloration (very short (VS), short (S), medium (M), and long (L)
257 wavelengths) and one type of double cone responsible for achromatic (i.e., brightness) variation
258 sensitivity (Cuthill 2006). White-shouldered and red-backed fairywrens are both V-type species

259 (Ödeen et al. 2012) – species that possess ability to perceive UV wavelengths but with lower
260 sensitivity than U-type species (Delhey et al. 2013; Ödeen & Håstad 2013)). Thus, we used the
261 mean V-type peak sensitivity 416, 478, 542, 607 nm (Endler and Mielke 2005). We calculated
262 signal-to-noise ratios for each cone type using formula 10 in Vorobyev et al. (1998), using the
263 mean proportion of cones present in V-type birds from Hart (2001: VS = 0.381, S = 0.688, M =
264 1.136, L = 1.00), a Weber fraction of 0.1 for the L cone (Olsson et al. 2018), and an irradiance
265 spectrum of standard daylight (D65; Vorobyev et al. 1998). This model of avian vision reduces
266 variation among reflectance spectra to a set of three chromatic coordinates that define their
267 position in avian tetrahedral colorspace: “X”, “Y”, and “Z.” Here, the X axis represents the
268 relative stimulation of the S cone relative to the VS cone, Y represents the relative stimulation of
269 the M cone to both the VS and S cones, and Z represents the relative stimulation of the L cone to
270 the VS, S, and M cones. Distances between points in tetrahedral colorspace are reported as Just
271 Noticeable Differences (JNDs); values representing >1 are considered distinguishable.

272 We summarized XYZ coordinates with a separate principal components analysis (PCA)
273 per plumage region per species using a covariance matrix (*sensu* Jones et al. 2022). All PCAs
274 resulted in one component (hereafter: PC1_{chroma}) that explained >92% of the variation (Table 1).
275 For melanin-based black crown coloration, both species had intermediate values for the X axis
276 and larger, negative values for both Y and Z; spectra with larger, more negative Crown-PC1_{chroma}
277 values for this feather region provided low stimulation of the L cone relative to VS + S + M
278 cones, low stimulation of the M cone relative to VS + S cones, and higher stimulation of the VS
279 cone relative to the S cone. Positive Crown-PC1_{chroma} values were those richer in shorter
280 wavelengths (UV/blue) than in longer wavelengths (red). In white-shouldered fairywrens, higher
281 Shoulder-PC1_{chroma} values stimulated the same cones as crown coloration (as both colors are
282 achromatic), although with a greater stimulation of VS than S cones. However, the eigenvalues
283 for both crown and shoulder coloration in white-shouldered fairywrens were <1.0 despite
284 comprising a vast majority of the variation (>92%), suggesting that there is minimal chromatic
285 variation in these plumage regions. For the carotenoid-based shoulder colors found in red-backed
286 fairywrens, positive Shoulder-PC1_{chroma} scores were feathers that provided higher stimulation of
287 the L cone relative to VS + S + M cones and higher stimulation of the M cone relative to VS + S.
288 Thus, individuals with larger values along this PC axis were individuals with richer red
289 coloration and this axis explained little variation in the UV/blue region. We calculated overall
290 brightness of both the crown and scapular feather patches by calculating the achromatic contrast
291 between each plumage patch and an exceptionally dark spectrum by setting the double cone
292 quantum catch value to 0.001 (Delhey et al. 2015).

293

294 *Statistical analysis:*

295 We performed all statistical analyses in R v.4.1.1 (R Core Team 2021). Following a previously
296 established method for mirror image stimulations (Leitão et al. 2019; Jones, Boersma, Liu, et al.
297 2022), we aggregated mirror strikes, pecks, vocalizations, and displays in response to the focal
298 individual’s mirrored reflection by summing them into one overall “Aggression” value, as the
299 latter behaviors were infrequent on their own (Jones, Boersma, Liu, et al. 2022). Using these data
300 alongside the proportion of time spent near versus far from the mirror, we explored species
301 differences in female aggression via a Welch’s t-test (as variance was unequal between species).
302 Next, we generated a composite index of aggression in response to their mirrored image with

303 separate PCAs for each species and sex individually (Leitão et al. 2019; Jones, Boersma, Liu, et
304 al. 2022). Behavioral responses during mirror image stimulation assays resulted in a single
305 component with an eigenvalue >1.0 to be retained for further analysis (sensu Leitão et al. 2019;
306 Jones et al. 2022b; Table 2). All behavioral PCs loaded similarly, regardless of sex or species,
307 such that individuals with higher PC1_{MIS} loading scores were birds who responded more
308 aggressively towards their mirror reflection, indicative of a greater proportion of time near the
309 mirror rather than far away from it coupled with increased attack rate.

310 To explore the relationship between male phenotypic quality and female aggression, we
311 ran a series of multiple regression analyses coupled with a finite sample corrected Akaike's
312 information criterion (AICc) model selection procedure. For each model (i.e., species),
313 individual female aggression scores were set as a dependent variable and our fixed effects were
314 seven (putative) indices of male condition (center and scaled tail length, mass, scaled CP
315 volume, as well as chromatic and achromatic chroma of both the crown and scapular feather
316 patches); only final models are presented in the main text (but see Supplemental Material for full
317 AICc table). Finally, we ran a separate, complementary statistical analysis using the same male
318 morphological traits, condensed via PCA (following the approach of Cain (2014)). The results
319 between statistical approaches were consistent and we present these findings in the Supplemental
320 Material.

321

322 *Ethical note:*

323 Our study was carried out in strict accordance with the guidelines established by the Tulane
324 University Institutional Animal Care and Use Committee (#0395R2), Griffith University's
325 Animal Ethics Committee (ENV/08/19/AEC), and in adherence to research permits from the
326 Conservation and Environment Protection Authority of Papua New Guinea (#99902100765). All
327 birds were captured, processed, exposed to mirror assays, and released in under one hour. We
328 continuously monitored our mist-nets and removed birds immediately upon hitting the net. All
329 individuals involved in removal of birds from mist-nets were trained in the appropriate technique
330 to extract and safely handle birds.

331

332 **Results:**

333 *Species comparison:*

334 We conducted mirror assays on 26 female red-backed fairywrens and 44 white-shouldered
335 fairywrens. On average, white-shouldered fairywren females were more aggressive than red-
336 backed fairywren females, determined as a greater rate of aggressive behaviors observed per min
337 ($t = 3.53$, $df = 64.40$, $p < 0.001$; Fig. 2) and proportion of time near the mirror ($t = 3.61$, $df =$
338 45.32 , $p < 0.001$). Red-backed fairywrens were more likely to be positioned far from the mirror
339 than white-shouldered fairywrens ($t = 3.68$, $df = 34.05$, $p < 0.001$).

340

341 *Female aggression with respect to male phenotypic quality:*

342 Previous work in this population of white-shouldered fairywrens revealed that female aggression
343 is unrelated to her own plumage coloration and body size (Jones, Boersma, Liu, et al. 2022). We

344 tested the relationship between male mate quality attributes on the aggression of 38 individual
345 female white-shouldered fairywrens. The best fitting model predicting female white-shouldered
346 fairywren aggression included male mass, tail length, and CP volume, although the overall model
347 was not statistically significant (multiple $r^2 = 0.10$, $F_{3, 37} = 2.45$, $p = 0.08$; Fig. 3; Table 3; Table
348 S1 for full model selection parameters). Within the best fitting model, females were most
349 aggressive if their mate tended (non-significantly) to be heavier (β est. = 0.62, $p = 0.10$) and have
350 a longer tail (β est. = 0.42, $p = 0.06$); despite appearing in the top model, CP volume was not
351 significantly related to aggression (β est. = 0.04, $p = 0.50$). There were an additional five models
352 $< 2 \Delta AICc$ (Table 3), all of which contained some combination of the above three characteristics
353 and all in the same direction

354 In red-backed fairywrens, we first ran a series of Pearson's correlations and found that
355 female aggression was not related to her own age ($p = 0.34$) nor any standard morphological
356 measurement (e.g., mass, tarsus length, tail length; all $p > 0.16$). Including only pairwise
357 observations, we compared female aggression to her mated male's phenotype for 18 female red-
358 backed fairywrens. The best fitting model contained center and scaled CP volume as the sole
359 predictor, but this model was not statistically significant (multiple $r^2 = 0.09$, $F_{1, 16} = 1.65$, $p =$
360 0.22 ; Fig. 3; Table S2 for full model selection parameters). There was one additional model < 2
361 $\Delta AICc$ containing male mass alongside CP volume, but neither parameter were significant
362 predictors of aggression (both $p > 0.19$).

363

364 **Discussion:**

365 We explored how females in two sister *Malurus* species with marked differences in mating
366 system and overall life-history strategy vary in aggressive behaviors and whether or not females
367 of these species who are mated with males in higher physical condition are more aggressive.
368 First, we found support for our prediction that white-shouldered fairywrens, a tropical songbird
369 species endemic to New Guinea that experiences intense year-round competition, would be more
370 aggressive on average than their temperate sister species, red-backed fairywrens of Australia.
371 Second, we failed to find a relationship between male coloration and female aggression in white-
372 shouldered fairywrens. However, that male mass and tail length emerged in our analysis as
373 potential (as they were marginally non-significant) predictors of female aggression is interesting
374 and warrants further study; the females who were most responsive to mirror stimulation were
375 mated to males who tended to be heavier, but also had longer tails. Nonetheless, as these results
376 were not statistically significant, we failed to find evidence for a signaling function for these
377 phenotypic traits and any other possibilities are at best speculative for now. In red-backed
378 fairywrens we found that the best predictor of female aggression from our dataset was male CP
379 volume, but critically, this relationship was not statistically significant nor was there an apparent
380 trend. These results suggest that there is not a relationship between female red-backed fairywren
381 aggression and any metric of male condition we measured, which may indicate that females do
382 not compete for access to more attractive males in this species.

383 Though we cannot say with certainty what resource females compete over, our results
384 suggest that, for both species, it is likely not for males of the highest phenotypic quality. A
385 common assumption is that females preferentially mate with the most attractive male, though an
386 appreciation for how females actively compete for such males has only occurred recently
387 (reviewed in Rosvall 2011, Hare and Simmon 2019). For example, female topi (*Damaliscus*

388 *lunatus*) use cranial horns to attack rival females over access to preferred males (Bro-Jørgensen
389 2002). However, recent evidence suggests that intrinsic quality of one's partner may not be as
390 important for partnering decisions as previously thought, at least within socially monogamous
391 systems (Ihle et al. 2015; Wang et al. 2017; Griffith 2019; Hurley et al. 2020). Rather, the quality
392 of behavioral interactions between females and males (e.g., cooperativeness) in these species
393 may be more important than phenotypic quality, particularly for tropical birds. Perhaps chick-
394 rearing in the tropics requires the combined efforts of both parents, and as such, whether or not a
395 male is physically attractive may only be useful to a female if male phenotype honestly signals
396 parental investment (Préault et al. 2005; Pagani-Núñez and Senar 2014). In this sense, while
397 male phenotypic quality may be important for initial pairing for some species (Griffith 2019),
398 females in species that form longer-lasting pair bonds must also weigh the potential genetic
399 quality of offspring (Hasselquist et al. 1996; Mays and Hill 2004), the fighting capacity (Reudink
400 et al. 2009), and/or parental care (Préault et al. 2005; Pagani-Núñez and Senar 2014) provided
401 when choosing a mate. This is consistent with our results, in that female intrasexual aggression
402 was not related to any attribute of the mated male phenotype in either socially monogamous
403 species. With that said, that male phenotype trended towards statistical significance in white-
404 shouldered fairywrens may be noteworthy and warranting further study. It is possible that male
405 phenotype is a secondary consideration for female as is in dark-eyed juncos (Cain 2014),
406 though it also possible that the highest quality males disproportionately control the highest
407 quality territory sites that females compete over.

408 In line with our expectation that the intensity of female-female aggression experienced in
409 tropical regions would exceed that of temperate congeners, we found that female white-
410 shouldered fairywrens are, on average, significantly more aggressive towards intrasexual rivals
411 than red-backed fairywrens, their sister species with clear sexual dichromatism and female
412 preferences for male coloration (Baldassarre and Webster 2013). In New Guinea, it may be that
413 females perceive potential rivals as existential threats to their overall reproductive success,
414 driving the behavioral patterns we observed. The strength of selection acting on males and
415 females is predicted to be similar between sexes in tropical regions (Kunkel 1974; Slater and
416 Mann 2004). Thus, the relative contribution one sex makes towards rearing offspring relative to
417 their mate is likely to converge in socially monogamous tropical songbirds that pair and defend
418 territories year-round (Stutchbury and Morton 2023). In this sense, how (dis)similar males and
419 females are may act as a proxy for the strength or type of social selection acting on each sex
420 independently. Several comparative studies have suggested that the female ornamentation is
421 greatest closer to the equator (Karubian 2013; Dale et al. 2015), which likely reflect how shared
422 phenotypes function as signals in mate-choice and/or competitive contexts in both sexes
423 (Kraaijeveld et al. 2007; Murphy et al. 2009). In contrast, species that live in temperate
424 ecosystems are often dichromatic, such that males are stereotypically highly adorned and
425 territorial, whereas females are often muted in plumage coloration and do not defend the territory
426 as vigorously (Stutchbury and Morton 2023). With that being said, Fargevieille et al. (2023)
427 recently described how females of temperate songbird species with greater paternal care tend to
428 be slightly brighter and more chromatic, suggesting that differences in dichromatism per se may
429 not be a reliable indication of the strength of social selection.

430 An interesting distinction between our two focal species is the presence of auxiliary
431 helpers. Most fairywren species are thought to breed cooperatively, with groups comprised of a
432 breeding male and female alongside kin and non-kin group members that all contribute in chick

433 raising (Rowley and Russell 1997). Red-backed fairywrens are no exception, as they routinely
434 (though not always) have auxiliary helpers that help feed nestlings (Mulder et al. 1994). It may
435 be that such assistance liberates females, at least in-part, from the need to compete over males
436 that would provide the best parental care. Alternatively, as ornamented males appear to invest
437 more in extra-pair copulations than in duller males (Webster et al. 2008; Dowling and Webster
438 2017), it may also be likely that ornamentation plays little-to-no role in choice à la parental care
439 for red-backed fairywrens. In stark contrast, there is limited documentation (or anecdotal
440 observation; JAJ pers. obs.) of helpers at the nest in the *M. a. moretoni* subspecies of white-
441 shouldered fairywrens (Enbody et al. 2019), and helping behavior appears overall much rarer,
442 relative to their Australian sister species. Interestingly, the unornamented subspecies of white-
443 shouldered fairywren, *M. a. lorentzi*, is highly social (Boersma et al. 2022), live in large groups
444 (Enbody et al. 2019), and anecdotally behave in a similar manner to red-backed fairywrens (i.e.,
445 similar social grouping and helper behavior). Furthermore, the unornamented female phenotype
446 of *M. a. lorentzi* closely resembles that of female red-backed fairywrens and is thought to be the
447 ancestral phenotype for the other, more ornamented white-shouldered fairywren subspecies
448 (Enbody et al. 2022). A behavioral comparison between red-backed fairywrens and *M. a. lorentzi*
449 would likely be a fruitful avenue of research, as these two species share several life-history
450 and mating system characteristics, despite the latitudinal distance between species.

451 In this preliminary study, we indirectly assessed the degree to which females within and
452 between species compete over access to males of differing phenotypic quality as well as tested if
453 commonly assumed behavioral differences between tropical and temperate birds were likely to
454 be found in two sister species of fairywren. We failed to find support for our predictions that the
455 most aggressive females would be mated to males of higher phenotypic quality, as measured by
456 body size and plumage coloration, suggesting that female-female competition in these two
457 species is likely over ecological resources when it occurs. We found that female white-
458 shouldered fairywrens are on average more aggressive towards simulated same-sex rivals than
459 females in their sister species, red-backed fairywrens, consistent with the idea that tropical birds
460 experience an elevated competitive environment. This study raises as many questions as it
461 answers about associations between female aggression and male phenotype (or quality), but it
462 represents an important step in addressing these key questions. Together with the demonstration
463 of the utility of mirror trials for studies of this sort that we have provided, we hope this work will
464 spur further research into this current knowledge gap.

465

466 **References:**

467 Ah-King M. 2022. A female turn in bird research. In: The female turn: How evolutionary science
468 shifted perceptions about females. Singapore: Palgrave Macmillan. p. 127–167.

469 Baldassarre DT, Webster M. 2013. Experimental evidence that extra-pair mating drives
470 asymmetrical introgression of a sexual trait. Proc R Soc. 280:1–7. doi:10.1098/rspb.2013.2175.
471 <http://rspb.royalsocietypublishing.org/content/280/1771/20132175.short>.

472 Beiko J, Lander R, Hampson E, Boon F, Cain DP. 2004. Contribution of sex differences in the
473 acute stress response to sex differences in water maze performance in the rat. Behav Brain Res.
474 151(1–2):239–253. doi:10.1016/j.bbr.2003.08.019.

475 Boersma J, Jones JA, Enbody ED, Welklin JF, Ketaloya S, Nason D, Karubian J, Schwabl H.
476 2022. Hormones and behavior male white-shouldered fairywrens (*Malurus alboscapulatus*)
477 elevate androgens greater when courting females than during territorial challenges. *Horm Behav.*
478 142:105158. doi:10.1016/j.yhbeh.2022.105158. <https://doi.org/10.1016/j.yhbeh.2022.105158>.

479 Bro-Jørgensen J. 2002. Overt female mate competition and preference for central males in a
480 lekking antelope. *Proc Natl Acad Sci.* 99(14):9290–9293. doi:10.1073/pnas.142125899.

481 Brouwer L, van de Pol M, Aranzamendi NH, Bain G, Baldassarre DT, Brooker LC, Brooker
482 MG, Colombelli-Négrel D, Enbody E, Gielow K, et al. 2017. Multiple hypotheses explain
483 variation in extra-pair paternity at different levels in a single bird family. *Mol Ecol.*
484 26(23):6717–6729. doi:10.1111/mec.14385.

485 Cain KE. 2014. Mates of competitive females: The relationships between female aggression,
486 mate quality, and parental care. *Adv Zool.* 2014:319567. doi:10.1155/2014/319567.

487 Cain KE, Ketterson ED. 2012. Competitive females are successful females; phenotype,
488 mechanism and selection in a common songbird. *Behav Ecol Sociobiol.* 66(2):241–252.
489 doi:10.1007/s00265-011-1272-5. [accessed 2013 Oct 1].
490 [http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3278083&tool=pmcentrez&renderty](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3278083&tool=pmcentrez&rendertype=abstract)
491 [pe=abstract](http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3278083&tool=pmcentrez&rendertype=abstract).

492 Cain KE, Ketterson ED. 2013. Costs and benefits of competitive traits in females: aggression,
493 maternal care and reproductive success. *PLoS One.* 8(10). doi:10.1371/journal.pone.0077816.

494 Cain KE, Rosvall KA. 2014. Next steps for understanding the selective relevance of female-
495 female competition. *Front Ecol Evol.* 2:32. doi:10.3389/fevo.2014.00032.

496 Catchpole CK, Slater PJB. 2008. *Bird song: Biological themes and variations.* Second Edi.
497 Cambridge, UK: Cambridge University Press. www.cambridge.org/9780521872423.

498 Clutton-Brock TH. 2007. Sexual selection in males and females. *Science (80-).* 318:1882–1885.
499 doi:10.1126/science.1133311.

500 Cockrem JF, Silverin B. 2002. Variation within and between birds in corticosterone responses of
501 great tits (*Parus major*). *Gen Comp Endocrinol.* 125:197–206. doi:10.1006/gcen.2001.7750.

502 Crook JH. 1972. Sexual selection, dimorphism, and social organization in the primates. In:
503 Campbell BG, editor. *Sexual Selection and the Descent of Man.* Chicago, IL: Aldine. p. 213–
504 281.

505 Cuthill IC. 2006. Color perception. In: Hill GE, McGraw. KJ, editors. *Bird Coloration I:
506 Mechanisms and Measurements.* Cambridge, MA: Harvard University Press. p. 3–40.

507 Dale J, Dey C, Delhey K, Kempenaers B, Valcu M. 2015. The effects of life-history and social
508 selection on male and female plumage coloration. *Nature.* 527(7578):367–370.
509 doi:10.1038/nature15509. <http://dx.doi.org/10.1038/nature15509>.

510 Delhey K, Delhey V, Kempenaers B, Peters A. 2015. A practical framework to analyze variation
511 in animal colors using visual models. *Behav Ecol.* 26(2):367–375. doi:10.1093/beheco/aru198.

512 Delhey K, Hall M, Kingma SA, Peters A. 2013. Increased conspicuousness can explain the

513 match between visual sensitivities and blue plumage colours in fairy-wrens. *Proc R Soc B*.
514 280(1750):20121771. doi:10.1098/rspb.2012.1771.

515 Dickens MJ, Earle KA, Romero LM. 2009. Initial transference of wild birds to captivity alters
516 stress physiology. *Gen Comp Endocrinol*. 160(1):76–83. doi:10.1016/j.ygcen.2008.10.023.
517 <http://dx.doi.org/10.1016/j.ygcen.2008.10.023>.

518 Dowling J, Webster MS. 2017. Working with what you've got: unattractive males show greater
519 mate-guarding effort in a duetting songbird. *Biol Lett*. 13(1):20160682.
520 doi:10.1098/rsbl.2016.0682.

521 Enbody ED, Boersma J, Jones JA, Chatfield MWH, Ketaloya S, Nason D, Baldassarre DT,
522 Hazlehurst J, Gowen O, Schwabl H, et al. 2019. Social organisation and breeding biology of the
523 white-shouldered fairywren (*Malurus alboscapulatus*). *Emu*. 119(3):274–285.
524 doi:10.1080/01584197.2019.1595663. <https://doi.org/10.1080/01584197.2019.1595663>.

525 Enbody ED, Sin SYW, Boersma J, Edwards S V., Ketaloya S, Schwabl H, Webster MS,
526 Karubian J. 2022. The evolutionary history and mechanistic basis of female ornamentation in a
527 tropical songbird. *Evolution (N Y)*. 76(8):1720–1736. doi:10.1111/evo.14545.

528 Endler JA, Mielke PW. 2005. Comparing entire colour patterns as birds see them. *Biol J Linn*
529 *Soc*. 86(4):405–431. doi:10.1111/j.1095-8312.2005.00540.x.
530 <http://doi.wiley.com/10.1111/j.1095-8312.2005.00540.x>.

531 Fedy BC, Stutchbury BJM. 2005. Territory defence in tropical birds: Are females as aggressive
532 as males? *Behav Ecol Sociobiol*. 58(4):414–422. doi:10.1007/s00265-005-0928-4.

533 Fischer S, Duffield C, Davidson AJ, Bolton R, Hurst JL, Stockley P. 2023. Fitness costs of
534 female competition linked to resource defense and relatedness of competitors. *Am Nat*. 201:256–
535 268. doi:10.1086/722513.

536 Gallup Jr GG. 1968. Mirror-image stimulation. *Psychol Bull*. 70(6):782–793.
537 doi:10.1037/h0026777. <http://psycnet.apa.org/psycinfo/1969-06577-001>.

538 Griffith SC. 2019. Cooperation and coordination in socially monogamous birds: Moving away
539 from a focus on sexual conflict. *Front Ecol Evol*. 7:1–15. doi:10.3389/fevo.2019.00455.

540 Hart NS. 2001. The visual ecology of avian photoreceptors. *Prog Retin Eye Res*. 20:675–703.
541 doi:10.1016/S1350-9462(01)00009-X.

542 Hasselquist D, Bensch S, von Schantz T. 1996. Correlation between male song repertoire, extra-
543 pair paternity and offspring survival in the great reed warbler. *Nature*. 3181(6579):229–232.
544 doi:10.1038/381229a0. www.nature.com.

545 Heinsohn R, Legge S, Endler JA. 2005. Evolution: Extreme reversed sexual dichromatism in a
546 bird without sex role reversal. *Science (80-)*. 309(5734):617–619. doi:10.1126/science.1112774.
547 <http://www.sciencemag.org/cgi/content/abstract/309/5734/617>.

548 Hurley LL, Rowe M, Griffith SC. 2020. Reproductive coordination breeds success: The
549 importance of the partnership in avian sperm biology. *Behav Ecol Sociobiol*. 74:3.
550 doi:10.1007/s00265-019-2782-9.

551 Ihle M, Kempnaers B, Forstmeier W. 2015. Fitness benefits of mate choice for compatibility in
552 a socially monogamous species. *PLoS Biol.* 13(9):1–21. doi:10.1371/journal.pbio.1002248.

553 Jawor JM, Young R, Ketterson ED. 2006. Females competing to reproduce: Dominance matters
554 but testosterone may not. *Horm Behav.* 49(3):362–368. doi:10.1016/j.yhbeh.2005.08.009.

555 Jones JA, Boersma J, Karubian J. 2022. Female aggression towards same-sex rivals depends on
556 context in a tropical songbird. *Behav Processes.* 202:104735. doi:10.1016/j.beproc.2022.104735.
557 <https://doi.org/10.1016/j.beproc.2022.104735>.

558 Jones JA, Boersma J, Liu J, Nason D, Ketaloya S, Karubian J. 2022. Female ornamentation does
559 not predict aggression in a tropical songbird. *Behav Ecol Sociobiol.* 76:57. doi:10.1007/s00265-
560 022-03165-x.

561 Kappeler PM, Benhaiem S, Fichtel C, Fromhage L, Höner OP, Jennions MD, Kaiser S, Krüger
562 O, Schneider JM, Tuni C, et al. 2022. Sex roles and sex ratios in animals. *Biol Rev.* 6.
563 doi:10.1111/brv.12915.

564 Karubian J. 2002. Costs and benefits of variable breeding plumage in the red-backed fairy-wren.
565 *Evolution (N Y).* 56(8):1673–1682. doi:10.1554/0014-
566 3820(2002)056[1673:CABOVB]2.0.CO;2.

567 Karubian J. 2008. Changes in breeding status are associated with rapid bill darkening in male
568 red-backed fairy-wrens *Malurus melanocephalus*. *J Avian Biol.* 39(1):81–86.
569 doi:10.1111/j.0908-8857.2008.04161.x.

570 Karubian J. 2013. Female ornamentation in *Malurus* fairy-wrens: A hidden evolutionary gem for
571 understanding female perspectives on social and sexual selection. *Emu.* 113(3):248–258.
572 doi:10.1071/MU12093.

573 Karubian J, Lindsay WR, Schwabl H, Webster MS. 2011. Bill coloration, a flexible signal in a
574 tropical passerine bird, is regulated by social environment and androgens. *Anim Behav.*
575 81(4):795–800. doi:10.1016/j.anbehav.2011.01.012.
576 <http://dx.doi.org/10.1016/j.anbehav.2011.01.012>.

577 Karubian J, Sillett TS, Webster MS. 2008. The effects of delayed plumage maturation on
578 aggression and survival in male red-backed fairy-wrens. *Behav Ecol.* 19(3):508–516.
579 doi:10.1093/beheco/arm159.

580 Karubian J, Swaddle JP, Varian-Ramos CW, Webster MS. 2009. The relative importance of
581 male tail length and nuptial plumage on social dominance and mate choice in the red-backed
582 fairy-wren *Malurus melanocephalus*: Evidence for the multiple receiver hypothesis. *J Avian*
583 *Biol.* 40(5):559–568. doi:10.1111/j.1600-048X.2009.04572.x.

584 Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007. The evolution of mutual ornamentation.
585 *Anim Behav.* 74(4):657–677. doi:10.1016/j.anbehav.2006.12.027.

586 Kraft FL, Forštová T, Utku Urhan A, Exnerová A, Brodin A. 2017. No evidence for self-
587 recognition in a small passerine, the great tit (*Parus major*) judged from the mark/mirror test.
588 *Anim Cogn.* 20(6):1049–1057. doi:10.1007/s10071-017-1121-7.

589 Kunkel P. 1974. Mating systems of tropical birds: The effects of weakness or absence of external

590 reproduction□timing factors, with special reference to prolonged pair bonds. *Z Tierpsychol.*
591 34(3):265–307. doi:10.1111/j.1439-0310.1974.tb01802.x.

592 Langston NE, Freeman S, Rohwer SA, Gori D. 1990. The evolution of female body size in red-
593 winged blackbirds: The effects of timing of breeding, social competition, and reproductive
594 energetics. *Evolution (N Y)*. 44(7):1764–1779. doi:10.1111/j.1558-5646.1990.tb05247.x.

595 Leitão A V., Hall ML, Delhey K, Mulder RA. 2019. Female and male plumage colour signals
596 aggression in a dichromatic tropical songbird. *Anim Behav.* 150:285–301.
597 doi:10.1016/j.anbehav.2019.01.025.
598 <https://linkinghub.elsevier.com/retrieve/pii/S0003347219300375>.

599 Lipshutz SE, Rosvall KA. 2021. Nesting strategy shapes territorial aggression but not
600 testosterone: A comparative approach in female and male birds. *Horm Behav.* 133:104995.
601 doi:10.1016/j.yhbeh.2021.104995. <https://doi.org/10.1016/j.yhbeh.2021.104995>.

602 Lyon BE, Montgomerie R. 2012. Sexual selection is a form of social selection. *Philos Trans R*
603 *Soc B.* 367(1600):2266–2273. doi:10.1098/rstb.2012.0012.

604 Mays HL, Hill GE. 2004. Choosing mates: Good genes versus genes that are a good fit. *Trends*
605 *Ecol Evol.* 19(10):554–559. doi:10.1016/j.tree.2004.07.018.

606 Mulder RA, Dunn PO, Cockburn A, Lazenby-Cohen KA, Howell MJ. 1994. Helpers liberate
607 female fairy-wrens from constraints on extra-pair mate choice. *Proc R Soc B.* 255(1344):223–
608 229. doi:10.1098/rspb.1994.0032.

609 Murphy TG, Hernández-Muciño D, Osorio-Beristain M, Montgomerie R, Omland KE. 2009.
610 Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav Ecol.*
611 20(5):1000–1006. doi:10.1093/beheco/arp089.

612 Ödeen A, Håstad O. 2013. The phylogenetic distribution of ultraviolet sensitivity in birds. *BMC*
613 *Evol Biol.* 13:36. doi:10.1186/1471-2148-13-36.

614 Ödeen A, Pruett-Jones S, Driskell AC, Armenta JK, Håstad O. 2012. Multiple shifts between
615 violet and ultraviolet vision in a family of passerine birds with associated changes in plumage
616 coloration. *Proc R Soc B.* 279(1732):1269–1276. doi:10.1098/rspb.2011.1777.

617 Oliveira RF, Carneiro LA, Canário A V. 2005. No hormonal response in tied fights. *Nature.*
618 437:207–208. doi:10.1038/437207a.

619 Oliveira RF, Simes JM, Teles MC, Oliveira CR, Becker JD, Lopes JS. 2016. Assessment of fight
620 outcome is needed to activate socially driven transcriptional changes in the zebrafish brain. *Proc*
621 *Natl Acad Sci.* 113(5):E654–E661. doi:10.1073/pnas.1514292113.

622 Olsson P, Lind O, Kelber A. 2018. Chromatic and achromatic vision: parameter choice and
623 limitations for reliable model predictions. *Behav Ecol.* 29(2):273–282.
624 doi:10.1093/beheco/ax133.
625 http://fdslive.oup.com/www.oup.com/pdf/production_in_progress.pdf.

626 Pagani-Núñez E, Senar JC. 2014. Are colorful males of great tits *Parus major* better parents?
627 Parental investment is a matter of quality. *Acta Oecologica.* 55:23–28.
628 doi:10.1016/j.actao.2013.11.001. <http://dx.doi.org/10.1016/j.actao.2013.11.001>.

629 Pr  ault M, Chastel O, C  zilly F, Faivre B. 2005. Male bill colour and age are associated with
630 parental abilities and breeding performance in blackbirds. *Behav Ecol Sociobiol.* 58(5):497–505.
631 doi:10.1007/s00265-005-0937-3.

632 Prior H, Schwarz A, G  nt  rk  n O. 2008. Mirror-induced behavior in the magpie (*Pica pica*):
633 Evidence of self-recognition. *Plos Biol.* 6(8):e202. doi:10.1371/journal.Citation.

634 Pryke SR. 2007. Fiery red heads: Female dominance among head color morphs in the Gouldian
635 finch. *Behav Ecol.* 18(3):621–627. doi:10.1093/beheco/arm020.

636 Reudink MW, Studds CE, Marra PP, Kurt Kyser T, Ratcliffe LM. 2009. Plumage brightness
637 predicts non-breeding season territory quality in a long-distance migratory songbird, the
638 American redstart *Setophaga ruticilla*. *J Avian Biol.* 40(1):34–41. doi:10.1111/j.1600-
639 048X.2008.04377.x.

640 Rosvall KA. 2008. Sexual selection on aggressiveness in females: Evidence from an
641 experimental test with tree swallows. *Anim Behav.* 75(5):1603–1610.
642 doi:10.1016/j.anbehav.2007.09.038.

643 Rosvall KA. 2011. Intrasexual competition in females: Evidence for sexual selection? *Behav*
644 *Ecol.* 22(6):1131–1140. doi:10.1093/beheco/arr106.

645 Rowe M, McGraw KJ. 2008. Carotenoids in the seminal fluid of wild birds: Interspecific
646 variation in fairy-wrens. *Condor.* 110(4):694–700. doi:10.1525/cond.2008.8604.

647 Rowe M, Pruett-Jones S. 2011. Sperm competition selects for sperm quantity and quality in the
648 Australian Maluridae. *PLoS One.* 6(1):e15720. doi:10.1371/journal.pone.0015720.

649 Rowe M, Pruett-Jones S. 2013. Extra-pair paternity, sperm competition and their evolutionary
650 consequences in the Maluridae. *Emu.* 113(3):218–231. doi:10.1071/MU12084.

651 Rowley I, Russell E. 1997. Bird families of the world: Fairy-wrens and Grasswrens. Oxford,
652 United Kingdom: Oxford University Press.

653 Slagsvold T, Lifjeld JT. 1996. Polygyny in birds: The role of competition between females for
654 male parental care. *Am Nat.* 143(1):59–94. doi:10.1086/285596.

655 Slater PJB, Mann NI. 2004. Why do the females of many bird species sing in the tropics? *J*
656 *Avian Biol.* 35:289–294. doi:10.1111/j.0908-8857.2004.03392.x.

657 Stockley P, Bro-J  rgensen J. 2011. Female competition and its evolutionary consequences in
658 mammals. *Biol Rev.* 86(2):341–366. doi:10.1111/j.1469-185X.2010.00149.x.

659 Stockley P, Campbell A. 2013. Female competition and aggression: Interdisciplinary
660 perspectives. *Philos Trans R Soc B.* 368:20130073. doi:10.1098/rstb.2013.0073.

661 Stutchbury BJM, Morton ES. 2023. Behavioral ecology of tropical birds. 2nd editio. Academic
662 Press.

663 Swaddle JP, Karubian J, Pruett-Jones S. 2000. A novel evolutionary pattern of reversed sexual
664 dimorphism in fairy wrens: Implications for sexual selection. *Behav Ecol.* 11(3):345–349.
665 doi:10.1093/beheco/11.3.345.

666 Team RC. 2021. R: A language and environment for statistical computing. R Foundation for
667 Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

668 Teles MC, Dahlbom SJ, Winberg S, Oliveira RF. 2013. Social modulation of brain monoamine
669 levels in zebrafish. *Behav Brain Res.* 253:17–24. doi:10.1016/j.bbr.2013.07.012.
670 <http://dx.doi.org/10.1016/j.bbr.2013.07.012>.

671 Tobias JA, Montgomerie R, Lyon BE. 2012. The evolution of female ornaments and weaponry:
672 Social selection, sexual selection and ecological competition. *Philos Trans R Soc B.*
673 367(1600):2274–2293. doi:10.1098/rstb.2011.0280.

674 Trivers RL. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent*
675 *of Man*. Chicago, IL: Aldine Publishing Compnay. p. 136–179.

676 Tuttle EM, Pruett-Jones S, Webster MS. 1996. Cloacal protuberances and extreme sperm
677 production in Australian fairy-wrens. *Proc R Soc B Biol Sci.* 263(1375):1359–1364.
678 doi:10.1098/rspb.1996.0199.

679 Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proc R Soc*
680 *B.* 265:351–358. doi:10.1098/rspb.1998.0302.

681 Vorobyev M, Osorio D, Bennett AT, Marshall NJ, Cuthill IC. 1998. Tetrachromacy, oil droplets
682 and bird plumage colours. *J Comp Physiol A.* 183:621–633. doi:10.1007/s003590050286.

683 Wang D, Forstmeier W, Kempenaers B. 2017. No mutual mate choice for quality in zebra
684 finches: Time to question a widely held assumption. *Evolution (N Y).* 71(11):2661–2676.
685 doi:10.1111/evo.13341.

686 Webster MS, Varian CW, Karubian J. 2008. Plumage color and reproduction in the red-backed
687 fairy-wren: Why be a dull breeder? *Behav Ecol.* 19(3):517–524. doi:10.1093/beheco/arn015.

688 West-Eberhard MJ. 1979. Sexual selection, social competition, and evolution. *Proc Am Philos*
689 *Soc.* 123(4):222–234.

690 Westneat DF, Sargent RC. 1996. Sex and parenting: The effects of sexual conflict and parentage
691 on parental strategies. *Trends Ecol Evol.* 11(2):87–91. doi:10.1016/0169-5347(96)81049-4.
692 [http://www.sciencedirect.com/science/article/B6VJ1-3WJG1XR-](http://www.sciencedirect.com/science/article/B6VJ1-3WJG1XR-6G/2/521cf5f6aa7339906ef1800b9581b44d)
693 [6G/2/521cf5f6aa7339906ef1800b9581b44d](http://www.sciencedirect.com/science/article/B6VJ1-3WJG1XR-6G/2/521cf5f6aa7339906ef1800b9581b44d).

694 Whiteman EA, Côté IM. 2003. Social monogamy in the cleaning goby *Elacatinus evelynae*:
695 Ecological constraints or net benefit? *Anim Behav.* 66(2):281–291. doi:10.1006/anbe.2003.2200.

696 Yasukawa K, Searcy WA. 1982. Aggression in female red-winged blackbirds: A strategy to
697 ensure male parental investment. *Behav Ecol Sociobiol.* 11(1):13–17. doi:10.1007/BF00297660.

698

699

700 **Tables:**

701

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

	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
<i>X</i>	0.367	0.677	0.389	-0.005
<i>Y</i>	-0.638	-0.607	-0.633	0.727
<i>Z</i>	-0.677	-0.416	-0.669	0.687

705

706 **Table 2.** Loading scores for the principal components analysis ($PC1_{\text{MIS}}$) exploring how
 707 fairywrens respond to mirror image stimulation.

	White-shouldered fairywren	Red-backed fairywren
Eigenvalue	1.96	2.36
Variance (%)	0.653	0.788
Aggression (strikes + pecks + displays)	0.495	0.525
Proportion of time spent close	0.645	0.625
Proportion of time spent far	-0.582	-0.577

708

709 **Table 3.** Abbreviated model selection table exploring which male phenotypic variables best
 710 predict aggression in female white-shouldered fairywrens. Presented are the models $< 2 \Delta AICc$
 711 from the best fitting model; see Table S1 for full model parameters.

	AICc	$\Delta AICc$	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

712

713 **Figure legends:**

714

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

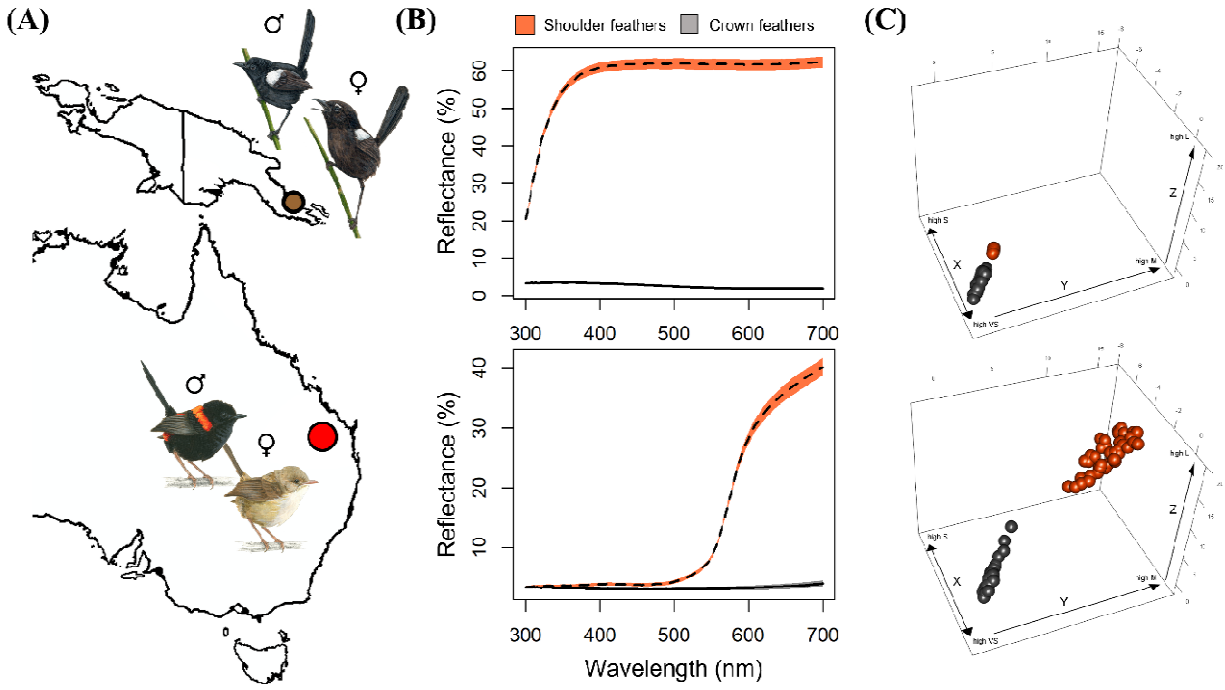
722

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

730

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

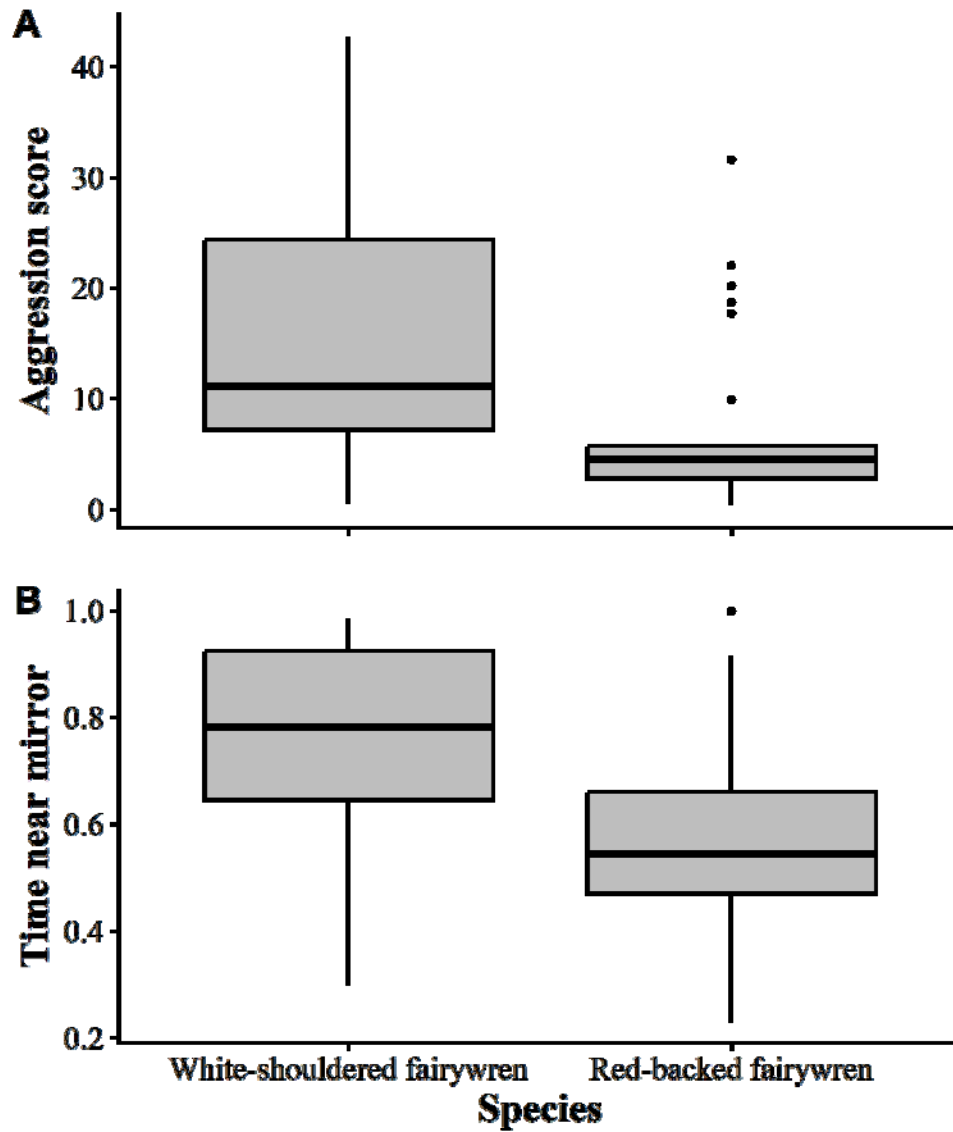
734



735

736 Fig 1

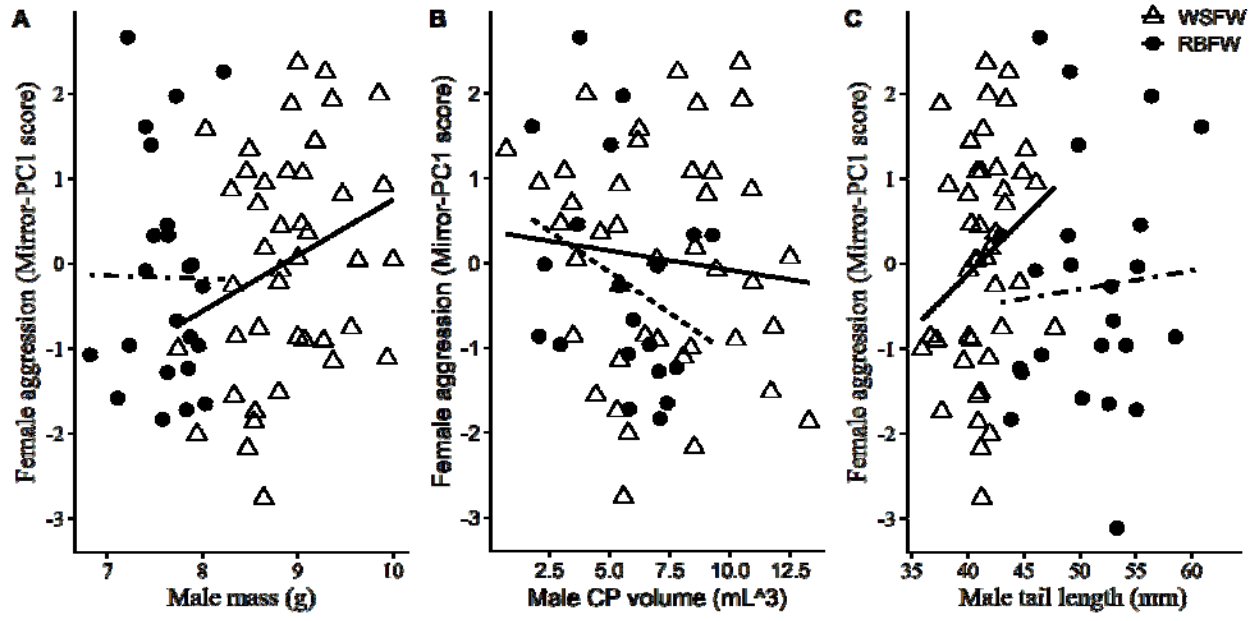
737



738

739 Fig 2

740



741

742 Fig 3