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2 **CONTRASTING PATTERNS OF SELECTION ON THE SIZE AND COLORATION OF A**
3 **FEMALE PLUMAGE ORNAMENT IN COMMON YELLOWTHROATS**

4
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26 **Abstract**

28 Females often possess ornaments that appear smaller and duller than homologous traits in males.
30 These ornaments may arise as nonfunctional byproducts of sexual selection in males and cause
32 negative viability or fecundity selection in females in proportion to the cost of their production
34 and maintenance. Alternatively, female ornaments may function as signals of quality that are
36 maintained by sexual or social selection. In a four-year study of 83 female common
yellowthroats (*Geothlypis trichas*) and their 222 young, we found strong viability and fecundity
selection on the yellow bib, a carotenoid-based plumage ornament that is a target of sexual
selection in males. Females with larger bibs were older, larger, and more fecund than females
with smaller bibs. However, bib size positively covaried with bib total brightness and carotenoid
chroma, aspects of bib coloration that were under negative viability and fecundity selection.
Females with more colorful bibs laid fewer eggs in their first clutch, were more likely to suffer
total brood loss due to predation, and were less likely to return to the study area. Selection
against bib coloration limits the value of bib size as a quality indicator in females and may
constrain the elaboration of bib attributes in males.

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Key words: sexual dimorphism, epigamic signaling, good genes, condition-dependence

48 **Introduction**

50 The ecology and evolution of elaborate ornamentation in males has been the subject of extensive
research for over 40 years (Andersson, 1994; Andersson & Simmons, 2006). Early controversies
surrounding the plausibility of indicator (handicap) mechanisms of sexual selection have given
52 way to a plethora of studies exploring how males signal phenotypic and/or genetic quality to
potential mates (Roberts *et al.*, 2004; Nowicki & Searcy, 2005; Dowling & Simmons, 2009). By
54 contrast, the occurrence of elaborate ornamentation in females has received much less attention
despite the taxonomic breadth of its occurrence (Amundsen, 2000a; Amundsen & Pärn, 2006;
56 Clutton-Brock, 2009) and recent theoretical work pointing to the possibility of mutual mate
choice and a role for epigamic signaling in both sexes (Johnstone *et al.*, 1996; Kokko &
58 Johnstone, 2002; Chenoweth *et al.*, 2006).

In part, this lack of empirical study reflects the influence of early work by Lande (1980) who
60 pointed out that female ornaments may arise simply as a correlated response to selection for
elaborate displays in males (see Amundsen, 2000a; Kraaijeveld *et al.*, 2007). According to the
62 genetic correlation hypothesis, female ornamentation is nonfunctional and neutral at best; at
worst, bright or elaborate ornaments in females may experience negative viability or fecundity
64 selection in proportion to the cost of their production and maintenance. In this latter scenario,
the sexually antagonistic selection that ensues may be fully or partially resolved through the
66 evolution of sexual dimorphism (Bonduriansky & Chenoweth, 2009; Cox & Calsbeek, 2009).
Across species, then, variation in the degree of female ornamentation is expected to reflect the
68 extent of sexual selection in favor of ornamentation in males, natural selection against the
expression of ornamentation in females, or some combination of the two (Lande, 1980; Martin &
70 Badyaev, 1996; Dunn *et al.*, 2001; Badyaev & Hill, 2003; Owens, 2006).

Evidence for sexually antagonistic selection on ornamentation is surprisingly rare
72 (Kraaijeveld *et al.*, 2007), even in birds where the expression of bright or colorful plumages in
females might be expected to increase the incidence of whole brood loss due to predation
74 (Haskell, 1996; Martin & Badyaev, 1996) or come at a substantial physiological or
immunological cost. Price & Burley (1994) found that the expression of a sexually selected trait
76 in female zebra finches (*Taeniopygia guttata*) was correlated with lower female fecundity, but
similar evidence from populations in the field is lacking. In a survey of 33 studies, only five
78 showed a negative association between female ornamentation and fecundity (Nordeide *et al.*,
2013).

80 By contrast, female ornamentation is often *positively* correlated with indices of individual
quality, pointing to a potential role for female ornaments in sexual or social signaling (reviewed
82 in Amundsen & Pärn, 2006; Nordeide *et al.*, 2013; Tobias *et al.*, 2013). Female plumage
ornaments vary with age and condition (Johnsen *et al.*, 1996; Dreiss & Roulin, 2010); parasite
84 load, immune function, and physiological stress (Roulin *et al.*, 2001b, 2008; Hill, 2002; Kelly *et al.*,
2012); parental effort (Siefferman & Hill, 2005); annual fecundity (Jawor *et al.*, 2004);
86 offspring quality (Remeš & Matysioková, 2013); and lifetime reproductive success (Roulin *et al.*,
2010; Potti *et al.*, 2013). Further, experimental manipulation of female nutritional state and
88 reproductive effort has been shown to affect both carotenoid-based and structurally-based
plumage ornaments (Siefferman & Hill, 2005; Doutrelant *et al.*, 2007, 2012). In aviary trials,
90 males prefer more elaborate females in some species (Hill, 1993; Amundsen *et al.*, 1997), and
female ornamentation has been linked to intrasexual competition for territories, mates, and other
92 limiting resources (reviewed in Kraaijeveld *et al.*, 2007; Tobias *et al.*, 2013).

Although the non-adaptive (genetic correlation) and adaptive (direct selection) hypotheses
94 make contrasting predictions about the relationship between female ornamentation and fitness,
the two hypotheses need not be mutually exclusive. In the case of multi-component signals,
96 different elements of a single ornament in females may experience net positive or negative
selection depending on the costs and benefits specific to each trait. For example, fecundity or
98 viability selection against the size of a female ornament may occur independently of sexual
selection in favor of its conspicuousness, leading to the evolution of small but colorful
100 ornaments. While complex, multi-component displays have received substantial attention in
males (e.g., Badyaev *et al.*, 2001), relatively few studies have considered the strength and
102 direction of selection on multiple ornaments or ornament components in females (but see Jawor
et al., 2004; Siefferman & Hill, 2005; Doutrelant *et al.*, 2007; Roulin *et al.*, 2010; Remeš &
104 Matysioková, 2013).

We explored sexual, viability, and fecundity selection on a carotenoid-based plumage
106 ornament in female common yellowthroats (*Geothlypis trichas*). Male and female common
yellowthroats possess a UV-yellow bib (throat and breast) pigmented solely by the carotenoid
108 lutein (McGraw *et al.*, 2003). In New York, USA, bib size and reflectance are associated with
the health, oxidative stress, and survivorship of males, especially among inexperienced (young)
110 birds new to the study area (Dunn *et al.*, 2010; Freeman-Gallant *et al.*, 2010, 2011). Females
prefer large-bibbed males in the aviary (Dunn *et al.*, 2008) and male bib attributes are under
112 strong sexual selection in the field (Freeman-Gallant *et al.*, 2010; Taff *et al.*, 2012, 2013).

However, selection on bib traits has not previously been studied in females, where bibs appear
114 much less conspicuous.

116 **Methods**

118 We studied common yellowthroats nesting along riparian and power line corridors in
Saratoga County, New York, USA from 2005 to 2008. See Freeman-Gallant *et al.* (2010) for
detailed descriptions of the study sites and field techniques. Briefly, we captured adults in mist
120 nets soon after their arrival and fitted each individual with a unique combination of 1-3 colored
leg bands. At the time of banding, we measured wing length (to nearest 0.5 mm) and
122 tarsometatarsus length (to nearest 0.1 mm) and collected a small sample of blood (< 30 μ L) from
the brachial vein for use in paternity analysis.

124 Females generally arrived on territory one week after males (mean 7.2 days \pm 5.6 SD; N = 52
females from 2005-2006) and in most cases, began building nests within 2-3 days of settling. In
126 2005, the breeding history of females was unknown, but starting in 2006, females new to the
study sites could be distinguished from females with prior breeding experience. Common
128 yellowthroats show strong breeding philopatry, and most returning females settled within 1-2
territories of their previous location. Females new to the area (inexperienced females) were
130 therefore likely to be yearlings in their first breeding season. We directed our sampling effort to
newly arriving females and recaptured returning birds opportunistically. In total, 83 different
132 females nested in our study areas, 12 of which were recaptured in subsequent years. To avoid
pseudoreplication, we restricted our analyses to the first observation of each female but used
134 information from recaptured birds to test for age-related changes in ornament size and coloration.
Two additional females that nested in areas peripheral to our study sites are included in analyses
136 of female ornamentation but not reproductive success.

Nests were censused every other day (2005-2006) or daily (2007-2008) to determine the clutch
138 size, hatching success, and fate of each brood (fledged or not). Predation is common in this

population; 43 of 78 first clutches (55.1%) were lost to predation during the incubation or nestling
140 stages. Females produced 1-3 replacement clutches (up to 12 eggs in one season) due to repeated
brood loss. After fledging a successful first brood, 15 of 35 females (42.9%) produced a second
142 clutch, and one female produced three broods in a single season. We use the size of the first
clutch and presence/absence of a second brood as estimates of female fecundity.

144 The 83 females in our study area produced a total of 222 young that survived to be banded
and sampled on day 5 (day of hatching = day 1). We assigned each offspring to its genetic
146 parents using a suite of 3-4 microsatellite loci. Details of microsatellite protocols and paternity
analyses can be found in Freeman-Gallant *et al.* (2010). The paternity of all 222 young is
148 known, including parentage for 46 extra-pair young produced by 17 females. We used a male's
extra-pair status (sired extra-pair young or not) and age (breeding experience) as indices of male
150 quality since both are strong predictors of male reproductive success (Freeman-Gallant *et al.*,
2010).

152 **Ornamentation**

To estimate the size of the bib, females were held against a background grid of known
154 dimensions and filmed with a Sony DCR-H120 digital video camera. Two still images showing
the bib were captured from the video and imported into ImageJ (<http://rsb.info.nih.gov/ij>). We
156 used the Threshold plugin to assist in delimiting the bib (Hue 20-50; Saturation 100-255) and
obtained one estimate of bib area (to nearest 0.1 mm²) for each of the two images, which were
158 averaged. Estimates of bib area were highly repeatable across the two images (intra-class
correlation coefficient, $r = 0.94$, $n = 85$ unique females and 12 recaptures in subsequent years).

160 At the time of banding, we collected four feathers from the center of each female's bib and
stored them in a 1.5 mL microfuge tube. The reflectance properties of the feathers were later

162 characterized in the laboratory using an Ocean Optics 2000 UV-vis spectrometer. The four
feathers were overlapped and secured against a matte black background and their reflectance
164 relative to a WS-1 white standard measured between 320-700 nm. Four separate readings were
performed for each bird (with the probe removed between each reading) and the results averaged
166 (for details, see Freeman-Gallant *et al.*, 2010).

Following Peters *et al.* (2004a, 2007), we calculated ultraviolet saturation as the proportion of
168 total reflectance across 320-700 nm that could be attributed to reflectance in the UV (320-400
nm) and carotenoid chroma (C_{car}) as $(R_{700nm} - R_{450nm})/R_{700nm}$. We calculated ultraviolet brightness
170 and yellow brightness as average reflectance between 320-400 nm and 550-625 nm, respectively.
Because UV brightness and yellow brightness were highly correlated with each other (Pearson
172 correlation: $r = 0.76$, $n = 94$, $P < 0.0001$) and with total reflectance across 320-700 nm (Pearson
correlation: $r > 0.89$, $n = 94$, $P < 0.0001$), we present results pertaining only to total reflectance
174 to simplify the analysis.

Data analysis

176 We searched for relationships between bib attributes and components of female fitness using
a two-stage approach. First, we characterized the overall relationship between each bib trait and
178 female fitness (apparent survival and aspects of fecundity) using a series of univariate analyses.
These analyses do not distinguish between selection on the focal trait and correlated traits—
180 rather, they reveal the overall presence or absence of selection on each trait (*sensu* Lande &
Arnold, 1983). Second, we used a set of nested, multivariate models to more thoroughly
182 characterize fitness relationships by taking inter-trait correlations into account. We began by
regressing the initial clutch size of females on body size (wing length, tarsus length), timing of
184 breeding (arrival date), and ornamentation (bib size, total brightness, carotenoid chroma, and

ultraviolet saturation). We then used logistic regression to examine nest predation in relation to
186 initial clutch size and the other seven variables in the first model. Lastly, we used logistic
regression to examine the probability of producing a second clutch in relation to prior nest
188 predation (yes/no) and the other eight variables mentioned above. Viability selection on females
was estimated with logistic regression of apparent survival (returned to the study site the next
190 year or not) on female size, timing of breeding, ornamentation, and initial clutch size. We used
backwards step-wise regression to eliminate variables with little explanatory power but present
192 results for both full and reduced models.

We took a similar approach when characterizing the relationship between female
194 ornamentation and male quality. We used univariate analysis of bib traits and indices of male
quality (male breeding experience and extra-pair success) to test for overall patterns of sexual
196 selection and multivariate models that included all four bib traits, body size, and timing of
breeding to account for inter-trait correlations.

198 Because the size and reflectance of bib attributes showed significant differences across years,
we adjusted raw data according to population means each year. To facilitate the comparison of
200 effect sizes, we further standardized values to have a mean of zero and unit variance. Since
including year as a random effect had little qualitative or quantitative impact on the identity or
202 relative importance of significant variables in any model, we present results from simplified
analyses (lacking year as a covariate). Sample sizes vary where incomplete information forced
204 the exclusion of some females

206

208 **Results**

Natural selection on female bib traits

210 In univariate analysis, female bib size was positively related to fecundity but not to
 survivorship. Females with larger bibs had larger initial clutch sizes (Pearson's correlation, $r =$
 212 0.25 , $n = 77$, $P = 0.028$) and were more likely to produce a second brood (logistic regression, χ^2
 $= 4.2$, $n = 77$, $P = 0.04$) than females with smaller bibs. There was no association between bib
 214 size and apparent survival (logistic regression, $\chi^2 = 0.32$, $n = 72$, $P = 0.57$).

No aspect of bib coloration was positively associated with female fecundity or survivorship in
 216 univariate analysis. Instead, bib total brightness tended to be negatively correlated with a
 female's initial clutch size (Pearson's correlation, $r = -0.20$, $n = 78$, $P = 0.075$) and positively
 218 correlated with the occurrence of nest predation (logistic regression, $\chi^2 = 3.0$, $n = 78$, $P = 0.08$).
 No other bib component was significantly correlated with initial clutch size (Pearson's
 220 correlation, $P > 0.13$), occurrence of nest predation (logistic regression, $\chi^2 < 1.0$, $P > 0.33$),
 probability of producing a second clutch (logistic regression, $\chi^2 < 1.1$, $P > 0.28$), or apparent
 222 survivorship (logistic regression, $\chi^2 < 0.19$, $P > 0.66$).

Because bib total brightness ($r = 0.30$, $n = 84$, $P = 0.006$), carotenoid chroma ($r = 0.26$, $n =$
 224 83 , $P = 0.02$), and UV saturation ($r = 0.24$, $n = 83$, $P = 0.03$) increased with bib size, we used a
 series of multiple regressions to more fully describe fecundity and viability selection acting on
 226 female bib traits.

In a multiple regression of all four bib components, body size (wing length, tarsus length),
 228 and timing of breeding (arrival date) on initial clutch size, initial clutch size increased with
 increasing bib size, body size (tarsus length), and earlier breeding but declined with increasing
 230 bib brightness and carotenoid chroma (full model: $R^2 = 0.40$, $n = 71$, $P < 0.0001$; Table 1).

232

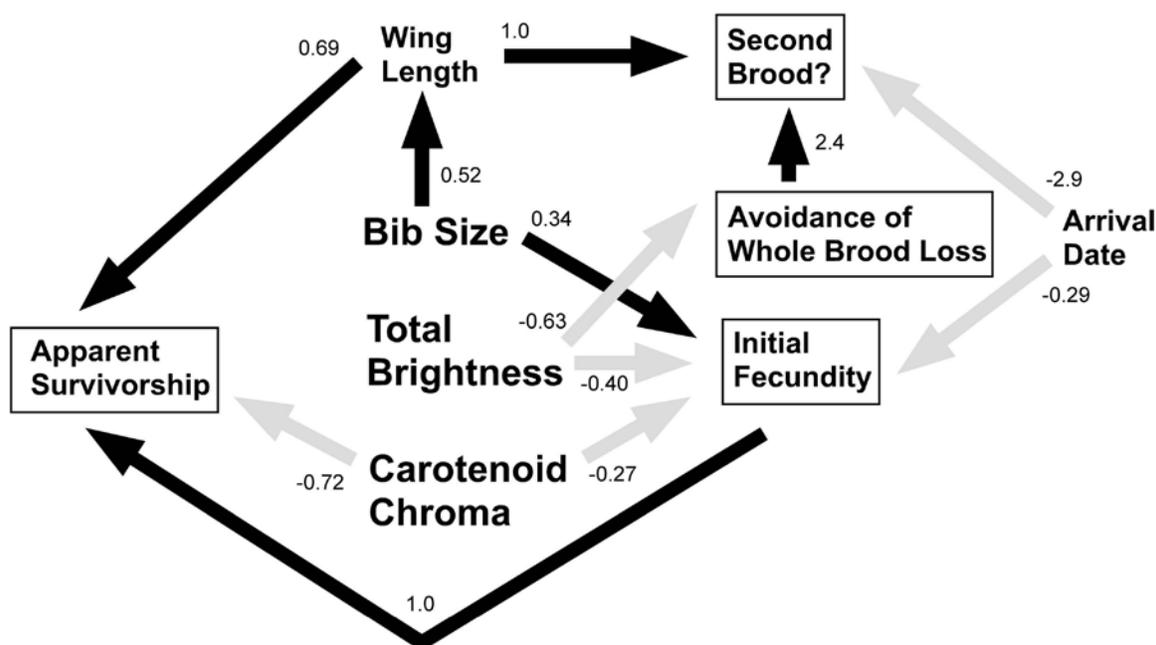
Table 1 Effect of bib traits, body size, and timing of breeding on components of female fecundity and survivorship. F- and χ^2 statistics are for multiple linear or logistic regressions. Effects in bold were included in reduced models constructed through backwards step-wise regression. Effect sizes for the reduced model are shown in Figure 1.

	Components of Female Fecundity									Apparent Survivorship		
	Initial Clutch Size			Avoidance of Predation? (absence of whole brood loss)			Second Clutch?			Return?		
	Effect	F	P	Effect	χ^2	P	Effect	χ^2	P	Effect	χ^2	P
Overall Model	$R^2 = 0.40, P < 0.0001$			$R^2 = 0.16, P = 0.05$			$R^2 = 0.66, P < 0.0001$			$R^2 = 0.36, P = 0.0002$		
Bib Size	0.40	10.9	0.002	0.08	0.0	0.83	-0.08	0.0	0.94	-0.35	0.5	0.49
Bib Total Brightness	-0.27	4.0	0.05	-1.12	5.8	0.02	1.56	1.4	0.24	0.52	1.2	0.28
Bib Carotenoid Chroma	-0.33	9.4	0.003	-0.63	2.8	0.09	1.74	2.8	0.09	-0.96	4.1	0.04
Bib UV Saturation	-0.20	2.2	0.14	-0.01	0.0	0.98	0.65	0.5	0.47	-0.91	3.2	0.07
Tarsus Length	0.35	12.8	0.001	0.36	1.2	0.27	-0.32	0.3	0.61	0.10	0.1	0.82
Wing Length	-0.10	0.7	0.39	0.63	3.2	0.07	0.77	1.3	0.26	1.18	6.0	0.01
Arrival Date	-0.33	8.9	0.004	-0.37	1.1	0.29	-3.53	4.9	0.03	-----		
Initial Clutch Size	-----			-0.39	1.0	0.31	1.01	1.0	0.32	1.49	6.4	0.01
Avoidance of Predation?	-----			-----			4.08	6.0	0.01	-----		

234

Backwards step-wise regression converged on these traits in the final model (reduced model: R^2
 236 = 0.37, $n = 71$, $P < 0.0001$; all predictors: $P \leq 0.01$, see Fig. 1 for effect sizes). Brighter bibs
 were also associated with increased risk of predation, which, along with timing of breeding, was
 238 strongly related to the probability of producing a second clutch (Table 1 for full models; Fig. 1).

In a multiple logistic regression of bib traits, body size, and clutch size on apparent survival,
 240 female return rates increased with wing length and initial clutch size but declined with increasing
 carotenoid chroma and tended to decline with increasing UV saturation (full model: $R^2 = 0.36$, n
 242 = 71, $P = 0.0002$; Table 1). Backward step-wise regression converged on these traits in the final
 model (reduced model: $R^2 = 0.24$, $n = 67$, $P < 0.0004$; see Fig. 1 for effect sizes).



244

246 **Figure 1** Relationship between female bib attributes and components of fecundity and viability based on multiple
 248 linear and logistic regressions. Effect sizes are from reduced models identified by backwards stepwise regression
 250 (Table 1) and pertain to data standardized to a mean of zero with unit variance. Dark arrows show positive
 relationships; shaded arrows show negative relationships. For purposes of clarity, significant, positive correlations
 between bib size, brightness and carotenoid chroma are not shown, along with a significant, positive relationship
 between tarsus length and initial fecundity (initial clutch size).

252 Because of the importance of body size and timing of breeding to initial fecundity and
 apparent survivorship, we examined the relationship between bib attributes and these other
 254 aspects of a female's phenotype to determine if bib traits might experience indirect selection
 (through their correlation with body size and timing of breeding). Of the four bib traits, only bib
 256 size was related to wing length (multiple regression; $F_{1,78} = 21.5$, $P < 0.0001$; Fig. 1). No bib
 traits predicted female arrival date or tarsus length in separate multiple regressions ($P > 0.11$).

258 Experienced females had larger bibs, on average, than inexperienced females (ANOVA with
 female identity coded as a random effect, $F_{1,60} = 10.4$, $P = 0.01$) owing to increases in ornament
 260 size with age (paired-t test, $t_{10} = 2.4$, $P = 0.037$). Although experienced females also had longer
 wings than inexperienced females ($F_{1,60} = 8.3$, $P = 0.02$), they did not have larger initial clutch

262 sizes ($F_{1,54} = 3.2, P = 0.17$). Correlations between bib traits and female fecundity are thus
 unlikely to be attributed to age-related changes in ornament expression and reproductive success.
 264 Indeed, in multivariate analyses, bib traits continued to be related to initial clutch size (bib size:
 partial $\beta = 0.31, P = 0.037$; C_{car} : partial $\beta = -0.24, P = 0.06$), probability of whole brood loss due
 266 to predation (bib total brightness: partial $\beta = 1.3, P = 0.04$) and apparent survivorship (C_{car} :
 partial $\beta = -1.2, P = 0.06$; bib size: partial $\beta = -1.8, P = 0.05$) even after restricting the analysis to
 268 the 46 females known to be inexperienced (cf. Table 1, Fig. 1).

Sexual selection on female bib traits

270 All 83 females in our study area had equivalent pairing success (one social mate), but sexual
 selection on female ornaments could also have occurred through variation in male quality
 272 (Amundsen, 2000b). Evidence pointing to a relationship between male quality and female bib
 traits is weak or inconsistent, however.

274 In univariate analysis, the probability that females paired with an experienced (older) male
 tended to increase with increasing carotenoid chroma ($\chi^2 = 3.4, n = 64, P = 0.066$), and females
 276 with larger bibs were more likely to be paired to males who sired young outside the pairbond
 (logistic regression: bib size, $\chi^2 = 4.4, n = 77, P = 0.036$), but other bib components were not
 278 significantly related to these indices of male quality ($P > 0.10$). In multivariate analyses
 including all bib traits, body size (tarsus and wing lengths), and timing of breeding, females with
 280 brighter and more chromatic (C_{car}) bibs were more likely to pair with experienced males ($\chi^2 >$
 $3.9, n = 57, P < 0.05$) while females with larger bibs were more likely to pair with successful
 282 extra-pair sires ($\chi^2 = 4.3, n = 69, P = 0.034$).

The expression of bib traits is strongly condition-dependent among young, inexperienced
 284 males in our population, (Freeman-Gallant *et al.*, 2010), yet there is no evidence for assortative

286 mating by bib attributes among females paired to inexperienced males (Pearson's correlations; n
 = 30, $P > 0.13$). Among females paired to experienced males, females with smaller, less UV
 saturated bibs tended to be paired to males with larger bibs (Pearson's correlations; $r \approx -0.30$, $n =$
 288 33-34, $P < 0.08$).

Females with larger, brighter, and more saturated bibs did not arrive and pair earlier in the
 290 season than females with less elaborate bibs (Pearson's $r < 0.11$, $n = 79-80$, $P > 0.34$). Thus, any
 fitness benefits accruing to females through rapid pair formation and early breeding do not
 292 pertain in our population.

Sexual dichromatism

294 In each of three years (2006-2008), inexperienced females had bibs that were smaller
 (ANOVA, $F_{1,101} = 96.2$, $P < 0.0001$) less bright (ANOVA, $F_{1,100} = 46.6$, $P < 0.0001$), and less
 296 saturated (ANOVA, $F_{1,99} > 20.7$, $P < 0.0001$) than inexperienced males, although the extent of
 dichromatism varied across years for some bib components (ANOVA, interaction between sex
 298 and year; $C_{\text{car}}: F_{2,99} = 3.7$, $P = 0.029$; bib size: $F_{2,101} = 4.9$, $P = 0.009$; Table 2). Sexual
 dimorphism was not analyzed in 2005 because the breeding history (age) of most adults was
 300 unknown, and bib size increased with increasing breeding experience in both sexes (see above,
 Freeman-Gallant *et al.*, 2010). Small sample sizes of experienced females prevented comparison
 302 of ornamentation among older adults.

Discussion

304 In contrast to strong sexual selection favoring more colorful bibs in male common
 yellowthroats (Freeman-Gallant *et al.*, 2010; Taff *et al.*, 2012), we detected viability and
 306 fecundity selection against brighter and more saturated bibs in females. Females with brighter
 bibs laid fewer eggs in first clutches and were more likely to suffer whole brood loss due to

308 predation. Bib carotenoid chroma was also associated with lower initial fecundity and reduced
 310 female survivorship. In general, if males and females share genes for ornamental traits and each
 312 sex has different fitness optima for the traits, then this difference could generate sexually
 314 antagonistic selection on the phenotype and intra-locus conflict at the genetic level (Bedhomme
 & Chippindale, 2007). Over time, such selection is expected to enhance the degree of sexual
 dimorphism (Bonduriansky & Chenoweth, 2009; Cox & Calsbeek, 2009). Indeed, compared to
 males, female bibs are less bright and show reduced UV saturation and carotenoid chroma.

316 **Table 2** Bib size and coloration for inexperienced adults in 2006, 2007, and 2008. Males had larger, brighter, and
 more saturated bibs, although the extent of sexual dichromatism varied across years. Data are presented as mean \pm
 SE (n).

	2006		2007		2008	
	Females	Males	Females	Males	Females	Males
Bib Size (mm ²)	259.0 \pm 29.9 (25)	600.3 \pm 41.7 (14)	262.6 \pm 22.5 (18)	533.4 \pm 36.5 (17)	325.5 \pm 36.2 (14)	470.5 \pm 18.1 (19)
Carotenoid Chroma	0.84 \pm 0.02 (24)	0.97 \pm 0.02 (13)	0.85 \pm 0.02 (18)	0.89 \pm 0.01 (17)	0.71 \pm 0.03 (14)	0.76 \pm 0.01 (19)
UV Saturation	-0.03 \pm 0.02 (24)	0.07 \pm 0.1 (13)	0.02 \pm 0.01 (18)	0.09 \pm 0.01 (17)	0.09 \pm 0.01 (14)	0.14 \pm 0.00 (19)
Total Brightness	11.9 \pm 0.1 (25)	16.2 \pm 0.8 (13)	13.3 \pm 0.7 (18)	17.5 \pm 0.6 (17)	19.3 \pm 1.3 (14)	24.3 \pm 0.5 (19)

318 Selection against bright coloration in females has long been considered an important source of
 320 sexual dichromatism in birds. Wallace (1889), for example, argued that since bright coloration
 at the nest may increase the risk of predation on eggs and young, females (more so than males)
 322 should experience selection against exaggerated plumages because females often spend more
 time incubating and tending offspring. Wallace's logic has been supported by experimental work
 324 using artificial nests (Haskell, 1996) and also by phylogenetic analyses relating interspecific
 variation in female plumage brightness to the risk of predation (Martin & Badyaev, 1996).
 326 Surprisingly, however, our study appears to be the first intraspecific study to demonstrate an

association between female plumage brightness and nest predation, although it is not clear
328 whether the lack of empirical data can be traced to publication bias against negative results or
simply to lack of study. Indeed, it seems intuitively obvious that bright colors at the nest should
330 attract visually oriented predators, and such costs are commonly invoked in the literature (see,
for example, Burns 1998).

332 Common yellowthroats typically nest on or near the ground (elevation < 0.5 m), and a
female's ventral (bib) coloration is not exposed during the incubation of eggs or young. We
334 therefore suspect that it is the conspicuousness of females as they approach or leave the nest that
influences the likelihood of predation. Such activity occurs regularly during both the egg and
336 nestling stages—at our study sites, females feed nestlings 2-3 times per hour (Mitchell et al.,
2003) and the average length of incubation bouts is ~60 minutes (range: 30 min – 90 min; C.C.
338 Taff, unpublished data) during the day. Adults also respond aggressively to predators, and it is
possible that female coloration is associated with nest defense (see Da Silva *et al.*, 2013).
340 Disentangling the relative and potentially synergistic contributions of female behavior and
coloration will require an experimental approach, and the results may depend on the visual
342 sensitivity of specific predators and the importance of other cues to nest detection (odor, sound).

Less intuitive are the negative relationships in common yellowthroats between carotenoid
344 chroma (C_{car}) and a female's initial clutch size and over-winter survival. In part, these negative
relationships may arise from investment in feather coloration at the expense of other
346 physiological processes. Importantly, C_{car} measures the degree to which blue-green wavelengths
are subtracted by the presence of lutein in what would otherwise be a UV-white feather. All else
348 being equal, increasing C_{car} should be correlated with increasing carotenoid deposition
(Andersson & Prager, 2006; also see Shawkey *et al.*, 2006). If carotenoids are limiting for

350 females (due, for example, to yolk production; Blount *et al.*, 2000), then there may be tradeoffs
between feather coloration and other uses for carotenoids, such as immunocompetence and
352 reducing oxidative stress (von Schantz *et al.*, 1999; Faivre *et al.*, 2003; Peters *et al.*, 2004b;
Dowling & Simmons 2009), both of which have been linked to fecundity and survivorship in
354 birds (for example, Hausmann *et al.*, 2005; Bize *et al.*, 2008; Freeman-Gallant *et al.*, 2011).
More saturated plumage may also make females more conspicuous to predators throughout the
356 annual cycle, contributing to their lower return rates (Götmark *et al.*, 1997).

Regardless of the mechanism of selection, the fitness costs incurred by colorful females may
358 constrain the evolution of bib attributes in males. Although males with larger, more colorful bibs
experience greater social and extra-pair mating success than males with less conspicuous bibs
360 (Freeman-Gallant *et al.*, 2010; Taff *et al.*, 2013), selection against bib attributes in females will
indirectly oppose the exaggeration of male traits to the extent that homologous traits (in the two
362 sexes) are genetically correlated (Badyaev & Martin, 2000; McGlothlin *et al.*, 2005). Although
we have no data pertaining to genetic covariance between traits expressed in males and females,
364 genetic correlations are likely to be high, as found in several other birds (Møller, 1993; Roulin *et al.*,
2001a; Potti & Canal, 2011).

366 **Bib Size**

In contrast to bib coloration, bib size experienced positive fecundity selection and, through its
368 strong association with wing length and initial clutch size, increased with increasing survivorship
(Fig. 1). Overall, then, selection favored larger but duller bibs, and bib size alone could
370 potentially act as a signal of female quality and breeding experience (age) that functions in
intrasexual competition for limiting resources, male choice for more experienced and fecund
372 females, or both (Amundsen & Pärn, 2006; Clutton-Brock, 2009; Tobias *et al.*, 2013).

Evidence for male choice in common yellowthroats is weak. Females with larger bibs were
374 more likely to be paired to males that ultimately sired extra-pair young, but they did not pair
earlier in the season or with males that were older or more elaborately ornamented. From a
376 male's perspective, the value of bib size as an indicator of fecundity is limited by its positive
correlation with coloration. For example, a 1 SD increase in bib size is associated with an
378 increase in initial clutch size of 1/3 egg when bib coloration is held constant in multivariate
analysis, but only 1/5 egg in univariate analysis (representing ~5% increase in fecundity for the
380 typical, four-egg clutch). Although variance in female fecundity contributes to variance in the
number of young that males sire (I_s), variance in social mating success (i.e., acquiring a mate or
382 not) is even more important, accounting for >40% of I_s (Freeman-Gallant *et al.*, 2010). It seems
unlikely that males should risk zero within-pair fertilization success by rejecting a smaller-
384 bibbed female in hope of pairing with a more fecund, larger-bibbed female.

A role for bib signaling in social competition for resources seems more likely. For example,
386 territorial interactions among female streak-backed orioles (*Icterus pustulatus*) during the
breeding season are mediated by plumage ornamentation (Murphy *et al.*, 2009a), and bill color
388 among female American goldfinches (*Spinus tristis*) signals dominance in competition for food
(Murphy *et al.*, 2009b). In common yellowthroats, such social selection is more likely to occur
390 during pair formation early in the breeding season, when we have observed females engaging in
agonistic interactions, than during the winter months when interactions among conspecifics are
392 rare (Guzy & Ritchison, 1997). Although badges of dominance in birds are often melanin-based
(Senar, 2006), several studies have implicated carotenoid-based ornaments in intrasexual
394 competition and aggressiveness (e.g., Pryke *et al.*, 2001; Murphy *et al.*, 2009a,b; Midamegbe *et*

396 *al.*, 2011). As with bib size in common yellowthroats, badges of dominance are often age-, size-,
or condition-dependent (Senar, 2006).

Importantly, the fact that bib size contains information on female quality does not necessarily
398 mean that the signal is “received” (or functional) in any context, since correlations between
ornament expression and measures of quality can arise as a non-functional byproduct of selection
400 on males (Amundsen, 2000b; Amundsen & Pärn, 2006). Indeed, if the genetic and physiological
architecture underlying ornamentation in males and females is the same, it should not be
402 surprising that the bib is associated with age (breeding experience), size, and indices of quality in
females, since similar relationships occur in males (cf. Freeman-Gallant *et al.*, 2010; Taff *et al.*
404 2012). It will take experimental manipulation of female plumage in the field to determine if or
when the bib functions as a signal of quality in our population.

406

408 **Summary**

The occurrence of female ornamentation has attracted increasing attention, mostly in the
410 context of sexually antagonistic selection and the evolution of sexual dimorphism (Cox &
Calsbeek, 2009; van Doorn, 2009) but also with the goal of understanding the behavioral and
412 functional ecology of sexual signaling (Amundsen & Pärn, 2006; Kraaijeveld *et al.*, 2007;
Clutton-Brock, 2009; Tobias *et al.*, 2013). The fact that different components of a single
414 plumage ornament (size, coloration) are under positive and negative selection in female common
yellowthroats suggests that both perspectives will be necessary to understand the origin and
416 maintenance of exaggerated phenotypes. While some ornament components may convey
information on female fecundity or competitiveness, other components may engender fitness

418 costs that contribute to sexually antagonistic selection. Further work on the costs and benefits of
female ornamentation is clearly warranted in this and other species.

420
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REFERENCES

- 428 Amundsen T., Forsgren, E. & Hansen, L. T. T. 1997. On the function of female ornaments: male
bluethroats prefer colourful females. *Proc. R. Soc. Lond. B* **264**: 1579-1586.
- 430 Amundsen, T. 2000a. Why are female birds ornamented? *Trends Ecol. Evol.* **15**: 149-155.
- Amundsen, T. 2000b. Female ornamentation, mate choice and sexual selection. Reply. *Trends*
432 *Ecol. Evol.* **15**: 471-472.
- Amundsen, T. & Pärn, H. 2006. Female coloration: review of functional and nonfunctional
434 hypotheses. In *Bird coloration, volume 2: Function and evolution* (eds. G. E. Hill & K. J.
McGraw), pp. 280-345. Cambridge, Massachusetts: Harvard University Press.
- 436 Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.
- Andersson, M. & Simmons, L. 2006. Sexual selection and mate choice. *Trends Ecol. Evol.* **21**:
438 s296-302.

- Andersson, S. & Prager, M. 2006. Quantifying Colors. In *Bird coloration volume 1: Mechanisms and measurements* (eds. G. E. Hill & K. J. McGraw), pp. 41-89, Massachusetts: Harvard University Press.
- 440
- 442 Badyaev, A. V. & Marin, T. E. 2000. Sexual dimorphism in relation to current selection in the house finch. *Evolution* **54**: 987-997.
- 444 Badyaev, A. V., Hill, G. E., Dunn, P. O. & Glen, J. C. 2001. Plumage color as a composite trait: developmental and functional integration of sexual ornamentation. *Am. Nat.* **158**: 221-
- 446 235.
- Badyaev, A. V. & Hill, G. E. 2003. Avian sexual dichromatism in relation to phylogeny and
- 448 ecology. *Ann. Rev. Ecol. Syst.* **34**: 27-49.
- Bedhomme, S. & Chippindale, A. K. 2007. Irreconcilable differences: when sexual dimorphism fails to
- 450 resolve sexual conflict. In *Sex, size and gender roles* (eds. D. J. Fairbairn, W. U. Blanckenhorn & T. Székely), pp. 185-194. Oxford: Oxford University Press.
- 452 Bize, P., Devevey, G., Monaghan, P., Doligez, B. & Christe, P. 2008. Fecundity and survival in relation to resistance to oxidative stress in a free-living bird. *Ecology* **89**: 2584-2593.
- 454 Blount, J. D., Houston, D. C. & Møller, A. P. 2000. Why egg yolk is yellow. *Trends Ecol. Evol.* **15**: 47-49.
- 456 Bonduriansky, R. & Chenoweth, S. F. 2009. Intralocus sexual conflict. *Trends Ecol. Evol.* **24**: 280-288.
- Burns, K. J. 1998. A phylogenetic perspective on the evolution of sexual dichromatism in tanagers
- 458 (Thraupidae): the role of female versus male plumage. *Evolution* **52**: 1219-1224.
- Chenoweth, F. F., Doughty, P. & Kokko, H. 2006. Can non-directional male mating preferences
- 460 facilitate honest female ornamentation? *Ecol. Letters* **9**: 179-184.
- Cox, R. M. & Calsbeek, R. 2009. Sexually antagonistic selection, sexual dimorphism, and the resolution

- 462 of intralocus sexual conflict. *Am. Nat.* **173**: 176-187.
- Clutton-Brock, T. 2009. Sexual selection in females. *Anim. Behav.* **77**: 3-11.
- 464 Da Silva, A., van den Brink, V., Emaresi, G., Luzio, E., Bize, P., Dreiss, A. N. & Roulin, A. 2013.
Melanin-based color polymorphism signals aggressive personality in nest and territory defense in
466 the tawny owl (*Strix aluco*). *Behav. Ecol. Sociobiol.* **67**: 1041-1052.
- Doutrelant, C., Grégoire, A., Grnac, N., Gomez, D., Lambrechts, M. M. & Perret, P. 2007. Female
468 coloration indicates female reproductive capacity in blue tits. *J. Evol. Biol.* **21**: 226-233.
- Doutrelant, C., Grégoire, A., Midamegbe, A., Lambrechts, M. & Perret P. 2012. Female plumage
470 coloration is sensitive to the cost of reproduction. An experiment in blue tits. *J. Anim. Ecol.* **81**:
87-96.
- 472 Dowling, D.K. & Simmons, L.W. 2009. Reactive oxygen species as universal constraints in life-
history evolution. *Proc. R. Soc. Lond. B* **276**: 1737-1745.
- 474 Dreiss, A. N. & Roulin, A. 2010. Age-related change in melanin-based coloration of barn owls
(*Tyto alba*): females that become more female-like and males that become more male-
476 like perform better. *Biol. J. Linn. Soc.* **101**: 689-704.
- Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. 2001. Mating systems, sperm competition, and the
478 evolution of sexual dimorphism in birds. *Evolution* **55**: 161-175.
- Dunn, P. O., Whittingham, L. A., Freeman-Gallant, C. R. & DeCoste, J. 2008. Geographic variation in
480 the function of ornaments in the common yellowthroat. *J. Avian Biol.* **39**: 66-72.
- Dunn, P. O., Garvin, J. C., Whittingham, L. A., Freeman-Gallant, C. R., & Hasselquist, D. 2010.
482 Carotenoid and melanin-based ornaments signal similar aspects of male quality in two
populations of the common yellowthroat. *Funct. Ecol.* **24**: 149-158.
- 484 Faivre, B., Gregoire, A., Préault, M. Cézilly, F. & Sorci, G. 2003. Immune activation rapidly mirrored in

a secondary sexual trait. *Science* **300**: 103.

- 486 Freeman-Gallant, C. R., Taff, C. C., Morin, D. F., Dunn, P. O., Whittingham, L. A. & Tsang, S. M.
2010. Sexual selection, multiple male ornaments, and age- and condition-dependent signaling in
488 the common yellowthroat. *Evolution* **64**: 1007-1017.
- Freeman-Gallant, C.R., Amidon, J., Berdy, B., Wein, S., Taff, C.C., & Hausmann, M.F. 2011.
490 Oxidative damage to DNA related to survivorship and carotenoid-based sexual ornamentation in
the common yellowthroat. *Biology Letters* **7**: 429-432.
- 492 Götmark, F., Post, P., Olsson, J. & Himmelmann, D. 1997. Natural selection and sexual dimorphism:
sex-biased sparrowhawk predation favours crypsis in female chaffinches. *Oikos* **80**: 540-548.
- 494 Guzy, M. J. & Ritchison, G. 1999. Common Yellowthroat (*Geothlypis trichas*), *The Birds of North
America Online* (Poole, A. Ed.). Ithaca, New York: Cornell Lab of Ornithology.
- 496 Haskell, D. G. 1996. Do bright colors at nests incur a cost due to predation? *Evol. Ecol.* **10**: 285-288.
- Hausmann, M. F., Winkler, D. W., Huntington, C. E., Vleck, D., Sanneman, C. E., Hanley, D. & Vleck,
498 C. M. 2005 Cell-mediated immunosenescence in birds. *Oecologia* **145**: 270-275.
- Hill, G. E. 1993. Male mate choice and the evolution of female plumage coloration in the house finch.
500 *Evolution* **47**: 1515-1525.
- Hill, G. E. 2002. *Red bird in a brown bag: the function and evolution of colorful plumage in the house
502 finch*. New York: Oxford University Press.
- Jawor, J. M., Gray, N., Beall, S. M. & Breitwisch, R. 2004. Multiple ornaments correlate with aspects of
504 condition and behaviour in female northern cardinals, *Cardinalis cardinalis*. *Anim. Behav.* **67**:
875-882.
- 506 Johnsen, T. S., Hengeveld, J. D., Blank, J. L., Yasukawa, K. & Nolan, V. 1996. Epaulet brightness and
condition in female red-winged blackbirds. *Auk* **113**: 356-362.

- 508 Johnstone, R. A., Reynolds, J. D. & Deutsch, J. C. 1996. Mutual mate choice and sex differences in
choosiness. *Evolution* **50**: 1382-1391.
- 510 Kelly, R. J., Murphy, T. G., Tarvin, K. A. & Burness, G. 2012. Carotenoid-based ornaments of female
and male American goldfinches (*Spinus tristis*) show sex-specific correlations with immune
512 function and metabolic rate. *Physiol. Biochem. Zool.* **85**: 348-363.
- Kokko, H. & Johnstone, R. A. 2002. Why is mutual mate choice not the norm? Operational sex ratios,
514 sex roles and the evolution of sexually dimorphic and monomorphic signaling. *Phil. Trans. R.
Soc. Lond. B* **357**: 319-330.
- 516 Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Komdeur, J. 2007. The evolution of mutual ornamentation.
Anim. Behav. **74**: 657-677.
- 518 Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*
34: 292-305.
- 520 Lande, R. & Arnold, S. J. 1983. The measurement of selection on correlated characters.
Evolution **36**: 1210-1226.
- 522 Martin, T. E. & Badyaev, A. V. 1996. Sexual dichromatism in birds: importance of nest predation and
nest location for females versus males. *Evolution* **50**: 2454-2460.
- 524 McGraw, K. J., Beebee, M. D., Hill, G. E. & Parker, R. S. 2003. Lutein-based plumage
coloration in songbirds is a consequence of selective pigment incorporation into feathers.
526 *Comp. Biochem. Physiol. B* **135**: 689-696.
- McGlothlin, J. W., Parker, P. G., Nolan, V. & Ketterson, E. D. 2005. Correlational selection leads to
528 genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution*
59: 658-671.
- 530 Midamegbe, A., Grégoire, A., Perret, P. & Doutrelant, C. 2011. Female-female aggressiveness is

influence by female coloration in blue tits. *Anim. Behav.* **82**: 245-253.

- 532 Mitchell, D. P., Dunn, P. O., Whittingham, L. A. & Freeman-Gallant, C. R. 2006. Attractive males
provide less parental care in two populations of the common yellowthroat. *Anim. Behav.* **73**: 165-
534 170.
- Møller, A. P. 1993. Sexual selection in the barn swallow *Hirundo rustica* III. Female tail ornaments.
536 *Evolution* **47**: 417-431.
- Murphy, T.G., Hernández-Muciño, D., Osorio-Beristain, M., Montgomerie, R. & Omland, K.E. 2009a.
538 Carotenoid-based status signaling by females in the tropical streak-backed oriole. *Behav. Ecol.*
20: 1000-1006.
- 540 Murphy, T.G., Rosenthal, M. F., Montgomerie, R. & Tarvin, K. A. 2009b. Female American
goldfinches use carotenoid-based bill coloration to signal status. *Behav. Ecol.* **20**: 1348-1355.
- 542 Nordeide, J. T., Kekäläinen, J., Janhunen, M. & Kortet, R. 2013. Female ornaments revisited – are they
correlated with offspring quality? *J. Anim. Ecol.* **82**: 26-38.
- 544 Nowicki, S. & Searcy, W. A. 2005. Song and mate choice in birds: how the development of
behavior helps us understand function. *Auk* **122**: 1-14.
- 546 Owens, I. P. F. 2006. Ecological explanations for interspecific variability in coloration. In *Bird*
coloration, volume 2: Function and evolution (eds. G. E. Hill & K. J. McGraw), pp. 380-416.
548 Cambridge, Massachusetts: Harvard University Press.
- Peters, A., Delhey, K., Denk, A. G. & Kempenaers, B. 2004a. Trade-offs between immune
550 investment and sexual signaling in male mallards. *Am. Nat.*, **164**: 51-59.
- Peters, A., Denk, A. G., Delhey, K. & Kempenaers, B. 2004b. Carotenoid-based bill colour as an
552 indicator of immunocompetence and sperm performance in male mallards. *J. Evol. Biol.*
17: 1111-1120.

- 554 Peters, A., Delhey, K., Johnsen, A. & Kempenaers, B. 2007. The condition-dependent
development of carotenoid-based and structural plumage in nestling blue tits: males and
556 females differ. *Am. Nat.* **169**: S122-S136.
- Potti, J. & Canal, D. 2011. Heritability and genetic correlation between the sexes in a songbird
558 sexual ornament. *Heredity* **106**: 945-954.
- Potti, J., Canal, D. & Serrano, D. 2013. Lifetime fitness and age-related female ornament
560 signaling: evidence for survival and fecundity selection in the pied flycatcher. *J. Evol.
Biol.* doi: 10.1111/jeb.12145
- 562 Price, D. K. & Burley, N. T. 1994. Constraints on the evolution of attractive traits: selection in male and
female zebra finches. *Am. Nat.* **144**: 908-934.
- 564 Pryke, S. R., Lawes, M. J. & Andersson, S. 2001. Agonistic carotenoid signaling in male red-collared
widowbirds: aggression related to the colour signal of both the territory owner and model
566 intruder. *Anim. Behav.* **62**: 695-704.
- Remeš, V. & Matysioková, B. 2013. More ornamented females produce higher-quality offspring in a
568 socially monogamous bird: an experimental study in the great tit (*Parus major*). *Front. Zool.* **10**:
14.
- 570 Roberts, M. L., Buchanan, K. L. & Evans, M. R. 2004. Testing the immunocompetence handicap
hypothesis: a review of the evidence. *Anim. Behav.* **68**: 227-239.
- 572 Roulin, A., Dijkstra, C., Riols, C. & Ducrest, A. L. 2001a. Female- and male-specific signals of quality
in the barn owl. *J. Evol. Biol.* **14**: 255-266.
- 574 Roulin, A., Riols, C., Dijkstra, C. & Ducrest, A. L. 2001b. Female plumage spottiness signals parasite
resistance in the barn owl (*Tyto alba*). *Behav. Ecol.* **12**: 103-110.
- 576 Roulin, A., Almasi, B., Rossi-Pedruzzi, A., Ducrest, A., Wakamatsus, K., Miksik, I., Blount, J. D.,

- Jenni-Eiermann, S. & Jenni, L. 2008. Corticosterone mediates the condition-dependent
578 component of melanin-based coloration. *Anim. Behav.* **75**: 1351-1358.
- Roulin, A., Altwegg, R., Jensen, H., Steinsland, I. & Schaub, M. 2010. Sex-dependent selection on an
580 autosomal melanic female ornament promotes the evolution of sex ratio bias. *Ecol. Letters* **13**:
616-626.
- 582 Senar, J.C. 2006. Color displays as intrasexual signals of aggression and dominance. In *Bird coloration*,
volume 2: Function and evolution (eds. G. E. Hill & K. J. McGraw), pp.87-136. Cambridge,
584 Massachusetts: Harvard University Press.
- Shawkey, M. D., Hill, G. E., McGraw, K. J., Hood W. R. & Huggins, K. 2006. An experimental
586 test of the contributions and condition dependence of microstructure and carotenoids in
yellow plumage coloration. *Proc. R. Soc. Lond. B* **273**: 2985-2991.
- 588 Siefferman, L. & Hill, G. E. 2005. Evidence for sexual selection on structural plumage coloration in
female eastern bluebirds (*Sialia sialis*) *Evolution* **59**: 1819-1828.
- 590 Taff, C.C., Steinberger, D., Clark, C., Belinsky, K., Sacks, H., Freeman-Gallant, C.R., Dunn, P.O. &
Whittingham, L.A. 2012. Multimodal sexual selection in a warbler: plumage and song are related
592 to different fitness components. *Anim. Behav.* **84**: 813-821.
- Taff, C.C., Freeman-Gallant, C.R., Dunn, P.O., & Whittingham, L. A. 2013. Spatial distribution of nests
594 constrains the strength of sexual selection in a warbler. *J. Evol Biol.* doi: 10.1111/jeb.12141.
- Tobias, J. A., Montgomerie, R. & Lyon, B. E. 2012. The evolution of female ornaments and weaponry:
596 social selection, sexual selection and ecological competition. *Phil. Trans. R. Soc. B.* **367**: 2274-
2293.
- 598 van Doorn, G. S. 2009. Intralocus sexual conflict *Ann. N.Y. Acad. Sci.* **1168**: 52-71.
- von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D. & Wittzell, H. 1999. Good genes, oxidative

600 stress and condition-dependent sexual signals. *Proc. Roy. Soc. Lond. B* **266**: 1-12.

Wallace, A. R. 1889. *Darwinism: an Exposition of the Theory of Natural Selection with Some of its*

602 *Applications*. London: Macmillan.