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

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Abstract

Females often possess ornaments that appear smaller and duller than homologous traits in males. These ornaments may arise as nonfunctional byproducts of sexual selection in males and cause negative viability or fecundity selection in females in proportion to the cost of their production and maintenance. Alternatively, female ornaments may function as signals of quality that are 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.

Introduction

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 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 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; 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 & Johnstone, 2002; Chenoweth *et al.*, 2006).

In part, this lack of empirical study reflects the influence of early work by Lande (1980) who 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 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 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 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 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 & 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 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, 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 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 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 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 & Matysioková, 2013).

We explored sexual, viability, and fecundity selection on a carotenoid-based plumage 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 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) 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 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 much less conspicuous.

Methods

  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

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

tarsometatarsus length (to nearest 0.1 mm) and collected a small sample of blood (< 30 μL) from

the brachial vein for use in paternity analysis.

  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

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

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

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

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

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

of female ornamentation but not reproductive success.

  Nests were censused every other day (2005-2006) or daily (2007-2008) to determine the clutch

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 mm^2) 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}-$R_{450 nm}$)/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

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).

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.

232

	Components of Female Fecundity									Apparent Survivorship		
	Initial Clutch Size			Avoidance of Predation? (absence of whole brood loss)			Second Clutch?			Return?		
Overall Model	$R^2 = 0.40, P < 0.0001$			$R^2 = 0.16, P = 0.05$			$R^2 = 0.66, P < 0.0001$			$R^2 = 0.36, P = 0.0002$		
	Effect	F	P	Effect	χ^2	P	Effect	χ^2	P	Effect	χ^2	P
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: $R^2 = 0.37$, $n = 71$, $P < 0.0001$; 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 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, 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: $R^2 = 0.36$, $n = 71$, $P = 0.0002$; 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
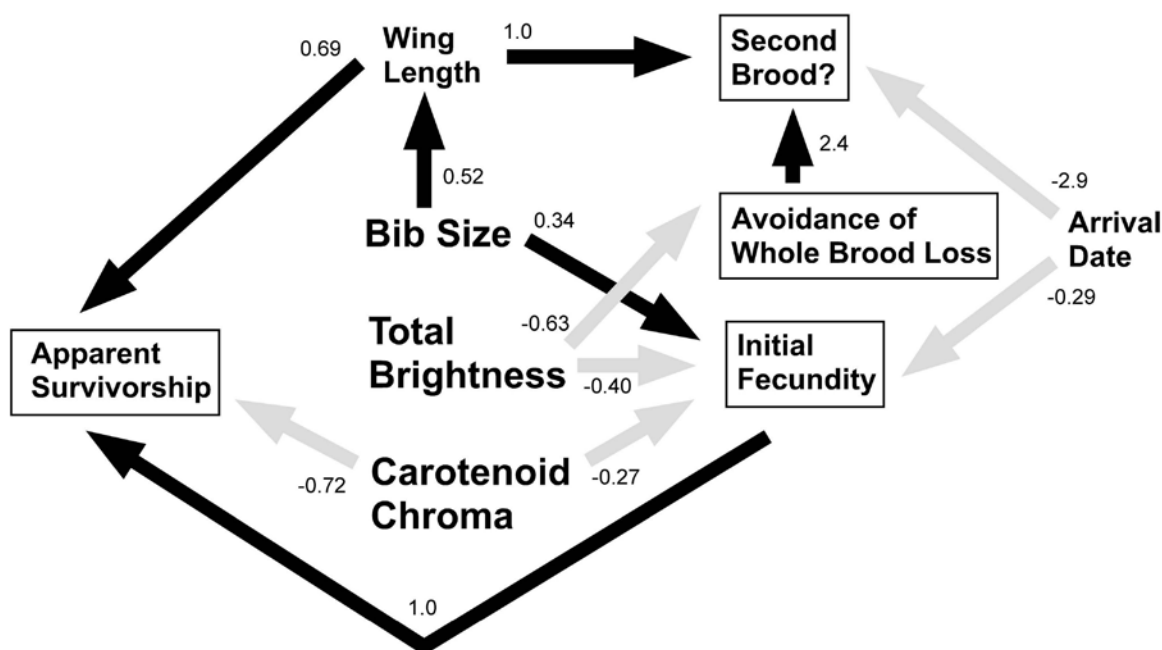
Figure 1 Relationship between female bib attributes and components of fecundity and viability based on multiple linear and logistic regressions. Effect sizes are from reduced models identified by backwards stepwise regression (Table 1) and pertain to data standardized to a mean of zero with unit variance. 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).

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

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

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 ($P > 0.11$).

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

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

mating by bib attributes among females paired to inexperienced males (Pearson's correlations; n

286 = 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_{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

        female survivorship. In general, if males and females share genes for ornamental traits and each

310   sex has different fitness optima for the traits, then this difference could generate sexually

        antagonistic selection on the phenotype and intra-locus conflict at the genetic level (Bedhomme

312   & Chippindale, 2007). Over time, such selection is expected to enhance the degree of sexual

        dimorphism (Bonduriansky & Chenoweth, 2009; Cox & Calsbeek, 2009). Indeed, compared to

314   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 ± SE (n).

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

al., 2011). As with bib size in common yellowthroats, badges of dominance are often age-, size-,

396   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 <u>any</u> 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 <u>and</u> 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.

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