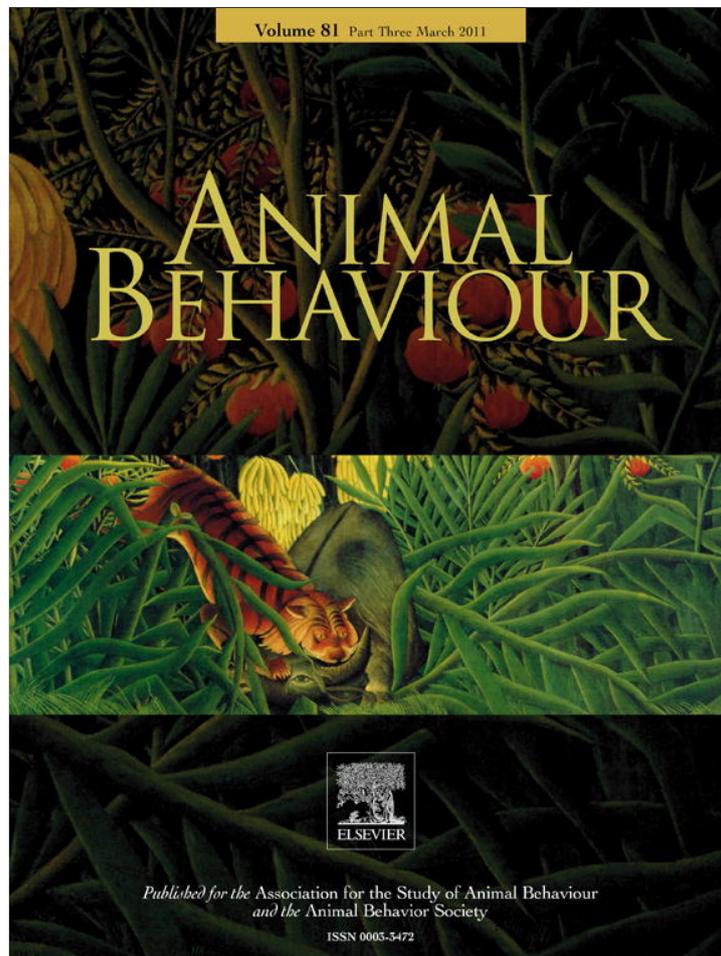


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Relationship between brood sex ratio and male ornaments depends on male age in a warbler

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Sex allocation theory predicts that females should bias the sex ratio of their offspring in response to differences in the reproductive value of sons and daughters. For example, paternal traits (ornaments) that are associated with male quality and reproductive success may result in male-biased sex ratios when inheritance of these traits is more beneficial to sons than to daughters. However, the information content of male ornaments, as well as the ornaments themselves, may change with male experience. If females are responsive to changes in the information content of signals, the result may be context-specific patterns of sex allocation. In a 3-year study of 50 common yellowthroat, *Geothlypis trichas*, females and their 287 young, we found that biased sex ratios were associated with male ornamentation, but that these deviations were not consistent across male experience classes. Females produced clutches with male-biased sex ratios when they were mated to young males with elaborate ornaments, but not when they were mated to older males. Male-biased broods were also associated with differences in offspring quality, as measured by average nestling mass. At our field site in New York, U.S.A., ornaments are generally more indicative of viability and condition among young, inexperienced males than among older males. We suggest that the relationship between male traits and the relative value of sons and daughters may change across male experience classes. Such changes may obscure patterns of adaptive sex-ratio bias and contribute to mixed results in the sex allocation literature.

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When the reproductive value of sons and daughters differs, females are expected to gain a fitness advantage by biasing the sex ratio of their offspring towards the more valuable sex (Trivers & Willard 1973; Charnov 1982). For example, in many species, the variance in reproductive success is greater for males than for females. Therefore, a high-quality son is likely to have greater fitness than a high-quality daughter, while the opposite is true for sons and daughters of low quality (Trivers & Willard 1973).

In species with biparental care, such as birds, the reproductive value of sons can vary as a consequence of differences in the quality of the female and male, their parental care and their territory (reviewed by Hasselquist & Kempenaers 2002). Indeed, there is evidence that the sex ratio of broods is related to time of season or resource

abundance (Andersson et al. 2003; Badyaev et al. 2005), body condition of the female (Nager et al. 1999; Whittingham & Dunn 2000; Dowling & Mulder 2006; Abroe et al. 2007), or the condition (Oddie & Reim 2002; Rathburn & Montgomerie 2005), parental care (Westerdahl et al. 2000) or attractiveness (Ellegren et al. 1996; Griffith et al. 2003) of males. However, similar studies often find no evidence for sex-ratio adjustment (Westerdahl et al. 1997; Saino et al. 1999; Radford & Blakey 2000; Rosivall et al. 2004; Rutstein et al. 2005; Cockburn & Double 2008), and few studies provide evidence that sex-biased broods actually result in increased fitness (but see Badyaev et al. 2002). Some authors have argued that sex-ratio adjustment is rare in birds based on mixed results and small effect sizes (Ewen et al. 2004; Cassey et al. 2006).

Some of the apparent contradictions in the literature may arise from the application of general theoretical models to complex and varied life histories (Komdeur & Pen 2002). If females respond to current conditions, then inconsistent or conflicting results may reflect changing costs and benefits of allocating sex, rather than evidence against sex-ratio adjustment (Pike & Petrie 2003; Thuman et al. 2003). For example, females may adjust the sex ratio of a brood in response to a male's sexual signals (ornaments), because they indicate direct benefits, such as greater parental provisioning,

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which will increase the survival of sons, or indirect benefits, such as good genes for attractiveness that will be inherited by sons (Hasselquist & Kempenaers 2002; Fawcett et al. 2007). Increasing evidence suggests that the information content of sexual signals can vary across years, populations or age classes (Candolin 2000; Badyaev & Duckworth 2003; Freeman-Gallant et al. 2010). Females may respond to changes in the information content of these signals such that they only adjust brood sex ratios in contexts where they have access to reliable information about the relative value of sons versus daughters. However, there is mixed evidence that brood sex ratios are adjusted to the ornamental traits of mates (Ellegren et al. 1996; Sheldon et al. 1999; Pike & Petrie 2005; Abroe et al. 2007; Dolan et al. 2009).

One potential reason for these differences among studies is that they often do not account for young sired by extrapair males. Older studies, which often did not assign sires to all offspring, analysed brood sex ratios in relation to the ornaments of social mates, rather than the actual sire, which may have been an extrapair mate. If sons benefit primarily by inheriting attractive ornaments from their genetic fathers (indirect benefits), then we would expect sex ratios to be adjusted to the ornaments of true sires, whether they are within-pair or extrapair. However, it is unclear whether females are able to bias the sex of individual offspring (i.e. bias the sex of extrapair young, EPY, without biasing the sex of within-pair young, WPY, in the same brood), and theoretical models suggest that the costs and constraints of biasing the sex of particular offspring will result in weak selection when it is based simply on male attractiveness (Fawcett et al. 2007). Indeed, only four of 18 studies of birds have found a bias towards more sons in broods sired by extrapair males, which are presumably more attractive (Du & Lu 2010). Thus, it may be easier for females to bias the brood sex ratio in relation to the ornaments of her social mate, who may actually have sired a substantial portion of the brood. The ornaments of social mates may also indicate direct benefits to the female and her sons, such as territory quality and the ability of the male to provide parental care, which may influence the later development of ornaments in sons.

We studied sex-ratio adjustment in the common yellowthroat, *Geothlypis trichas*, a socially monogamous, migratory wood warbler with sexually dimorphic plumage ornaments and high variance in male reproductive success (Whittingham & Dunn 2005; Freeman-Gallant et al. 2010). Males possess a black, melanin-based facial mask and a UV-yellow carotenoid-based bib; the mask is absent and the bib is subdued in females. Both ornaments are targets of sexual selection in New York, U.S.A. (Dunn et al. 2008; Freeman-Gallant et al. 2010). In aviary trials at our field site, we found that mask size mediated male dominance interactions, while bib attributes predicted female preference for males (Dunn et al. 2008). However, the condition-dependence of some bib attributes, particularly colour, changed with male breeding experience (age), and sexual selection paralleled these changes (Freeman-Gallant et al. 2010). If females benefit from producing more ornamented sons, then we predicted that (1) females would adjust the sex ratio of their broods in relation to bib attributes that are correlated with male mating success, (2) sex-ratio adjustments would be most pronounced at times when male ornaments conveyed information about aspects of male quality, such as body condition and (3) male traits associated with sex-ratio biases would also be associated with offspring quality.

METHODS

General Field Methods and Study Sites

We studied common yellowthroats breeding at two field sites in Saratoga County, New York (43°10'24.6"N, 73°53'19.7"W) from 2005 through 2007. Upon arrival on the breeding grounds in early May,

birds were continuously monitored until the end of the breeding season (early August). All adult birds were individually marked with a U. S. Fish and Wildlife Service band and a unique combination of one to three coloured plastic leg bands for visual identification with binoculars. Both field sites are composed of a linear array of territories surrounded by unsuitable habitat on all sides. Adults were classified as either inexperienced, if they were breeding for the first time within our study sites, or experienced, if they were present in the previous year. Banded males returning to our sites always established territories within 150 m of their previous year's location; therefore, unbanded males settling in our site were most likely true yearlings, rather than older males moving in from other areas. Thus, experience class probably represents male age. All adult males were captured in mist nets during each breeding season; females were captured during their first breeding season, but only rarely in subsequent seasons. Nestlings were sampled on day 5 after hatching. For paternity analysis, we collected a small blood sample (<30 µl) from the brachial vein of adults and nestlings as described in Freeman-Gallant et al. (2010). Morphological measurements for adults and nestlings were also taken at this time. All handling methods were approved by the Skidmore College Animal Care and Use Committee (protocol no. 69).

For adult males, we determined the size of the mask and the size and spectral characteristics of the bib in each year. To measure the area of the mask and bib we videotaped each male against a standardized grid with a Sony DCR-H120 digital camera. Using ImageJ software (<http://rsb.info.nih.gov/ij>), we scaled each image to the grid and measured total area of the ornament. When we captured males, we also collected a sample of four feathers from the centre of the bib. Using these feathers, four separate spectral readings were taken in the laboratory using an Ocean Optics 2000 UV–vis spectrometer. We defined ultraviolet brightness and yellow brightness as average reflectance (R) between 320–400 nm and 550–625 nm, respectively. Following Peters et al. (2004, 2007) we calculated carotenoid chroma (hereafter C_{car}) as $(R_{700nm} - R_{450})/R_{700nm}$. For a more detailed discussion of our choice of colour metrics and methodology see Freeman-Gallant et al. (2010).

Paternity for each nestling was assigned using a suite of three to four microsatellite markers (for details see Freeman-Gallant et al. 2010). We assigned paternity by comparing the multilocus genotype of each nestling with those of its putative parents. In all cases offspring matched their mothers, but 49 of 287 young possessed alleles that could not be attributed to their putative father. These young were classified as extrapair young (EPY), and in each case only a single male could account for all of the paternally derived alleles. Thus, the paternity of all 287 nestlings was known. Following Kahn et al. (1998), we determined the sex of each nestling using a PCR procedure that amplifies an intron in the chromohelicase DNA binding gene that differs in length between the W and Z sex chromosomes. Both sexes showed a band at 236 ± 11 base pairs (bp), and females showed an additional band at 281 ± 10 bp.

Statistical Analysis

Sex ratio data were analysed using generalized linear mixed models (GLMMs) in SAS software version 9.1 for Windows (SAS Institute Inc., Cary, NC, U.S.A.). Because each nest shares a common mother and environment, individual offspring are not truly independent (Krackow & Tkadlec 2001). GLMMs account for this nonindependence by testing the significance of fixed effects only after controlling for variation among random effects (Krackow & Tkadlec 2001). We used GLMMs with a binomial distribution, logit link function and a dispersion parameter fixed at 1; significance was assessed by F tests. In our models, we fitted nestling sex (male = 1, female = 0) as the response variable, female identity (unique for each

female) as the random subject effect, and brood identity, nested within female identity, as an additional random effect. Brood identity is necessary because 22 females produced multiple broods either within a year or by breeding in multiple years.

We analysed the sex of individual nestlings with two approaches. First, we ran our models with the morphological and ornamental measures of the putative sire of each nestling included as predictors. Second, we ran the same models but with all predictors representing the true genetic sire. In both cases we included a categorical predictor to indicate whether the nestling was sired by within-pair or extrapair males. This method allows for comparison with previous studies regardless of whether they had information on true genetic sires or not. Additionally, although recent studies have generally followed the second approach when possible, it is not clear that it will always be superior and a comparison of the two may be informative for several reasons. First, few authors have found evidence for sex-ratio biases among extrapair young (e.g. Abroe et al. 2007; Cockburn & Double 2008), and it is unclear whether females possess the fine control needed to bias individual offspring sex (i.e. bias the sex of EPY without biasing the sex of WPY in the same brood). Second, it is difficult to predict the relative importance of genetic and environmental inheritance in determining offspring reproductive value. For example, one study found that territorial male condition predicted offspring sex ratio despite the fact that a large percentage of nestlings were not genetically related to the putative sire (Rathburn & Montgomerie 2005; but see Cockburn & Double 2008). Feeding rates and territory quality may be important for nestling condition (Hasselquist & Kempenaers 2002) and even sexual ornamentation in birds can be heavily influenced by parental or environmental factors that are often ignored in studies of sexual selection (Griffith et al. 1999).

In each approach, we began by testing the effects of a number of predictor variables in a model that included both inexperienced and experienced males. Predictor variables represented information about the brood (clutch size, presence of partial mortality), female size (tarsus length), and characteristics of the sire of each nestling, including size (male tarsus length, male mass), male experience class (inexperienced or experienced), ornaments (mask size, bib size, bib yellow brightness, bib UV brightness, bib C_{car}) and paternity (within versus extrapair). Because females were only captured in their first breeding season, we could not include female mass as a predictor in our models. All male traits were corrected for differences between years and then standardized to have a mean of zero and unit variance. Clutch size and female tarsus length were also standardized to have means of zero and unit variance so that all effect sizes in our models would be comparable. Information content of signals and patterns of sexual selection in this population change with experience class (Freeman-Gallant et al. 2010); therefore, we also included two-way interactions between male experience and each predictor. After finding several significant and near significant interactions between predictor variables and male experience, we proceeded to analyse each experience class in a separate model.

To analyse offspring quality we performed multiple linear regressions in JMP software version 8.01 (SAS Institute Inc.) with nestling mass as the response variable. Exploratory analyses revealed no sex differences in nestling mass at time of sampling or in the effect of predictor variables on nestling mass. Therefore, we averaged the mass of all offspring in each nest and analysed each complete nest as a single data point to avoid pseudoreplication. In birds, mass during the early growth period has been associated with likelihood of survival and recruitment to the adult breeding pool (Tinbergen & Boerlijst 1990; Magrath 1991; Naef-Daenzer et al. 2001) and may influence reproductive success as an adult (Lindström 1999). Potential predictor variables in our models included female tarsus length and the same putative sire traits used in the GLMMs above (mass,

tarsus length, UV brightness, yellow brightness, C_{car} , bib size, mask size). Experience classes were analysed separately because of the observed differences in the patterns of sex-ratio bias.

In analyses of brood sex ratio and offspring quality we began with a full model and dropped nonsignificant terms, starting with the least significant two-way interactions (where applicable) and followed by the least significant fixed effects. We checked our models by adding previously dropped terms one at a time to confirm their nonsignificant effects. For 15 broods, male experience class was unknown, and because our final models discriminated by experience, these broods were only included in summary statistics that included all males. To illustrate relationships between colour variables and sex ratio, we used a prediction formula built from the intercept and fixed effect sizes from our final model. Sample sizes varied between models where incomplete data forced the exclusion of some observations. All other summary statistics were performed in R software version 2.8 (R Core Development Team 2008).

RESULTS

Over the 3 years of this study, a total of 328 eggs were laid among 86 broods. We determined the sex of 287 of these offspring (88%). Of the 41 offspring for which sex was not identified, 2 had insufficient DNA samples, 30 did not hatch, and 9 hatched but died before sampling. Overall, 150 of 287 offspring were male (52%). We tested overall sex ratio for departure from 1:1 using optimally weighted estimators to account for the nonindependence of brood mates; we found no significant departure from an even sex ratio ($Z = 1.05$, $P = 0.29$) (test described in Neuhäuser 2004).

Even when overall sex ratio is 1:1, the variance in sex ratios between nests may be greater than expected (under the assumption of random sex allocation) when some females overproduce sons while others overproduce daughters. Therefore, greater than expected variance between nests may indicate adaptive sex-ratio adjustment, although negative results do not preclude the possibility of adjustment (Krackow et al. 2002; Ewen et al. 2003). Following Ewen et al. (2003), we tested for departure from the expected binomial distribution by randomly redistributing nestlings among nests and calculating deviance in a generalized linear model through 100 000 iterations; deviance was significantly larger than expected given the binomial expectation ($P = 0.022$) and remained significant when only a single randomly chosen nest was included for each female ($P = 0.043$). Of the 86 broods sampled, 58 (67%) contained entirely within-pair young, 5 (6%) contained entirely extrapair young and 23 (27%) contained a mix of within-pair and extrapair young. Overall, 49 of the 287 offspring sexed (17%) were extrapair young.

Analysis of Nestling Sex

The results of our models based on the traits of putative versus true genetic sires were qualitatively similar in most respects. Both approaches converged on the same final set of predictors and the direction of effect sizes matched in all cases. We present the results from the analysis including traits of the putative sire here but note where the results differed slightly.

Nestling sex was related to male traits among inexperienced, but not experienced, males. We analysed nestling sex separately for each experience class because there were interactions between male experience and female tarsus length, male mass, male tarsus length, bib yellow brightness and C_{car} (Table 1; GLMM including males of both experience classes; $N = 227$ nestlings from 71 broods). Among inexperienced males, nestlings were more likely to be male when produced by parents with longer tarsi and when their sires possessed bibs with greater UV brightness and C_{car} values. When this model was run with the traits of true genetic sires, the effect of C_{car} became

Table 1
Sex of nestling common yellowthroats in relation to parental and nest characteristics for all males ($N = 227$ young from 71 broods, $df = 1,147$)

Predictor	Effect size	SE	F	P
Clutch size	-0.34	0.19	3.13	0.079
Partial mortality	1.07	0.47	5.21	0.024*
♀ Tarsus	3.71	1.41	6.95	0.009*
♂ Mass	-2.60	1.07	5.91	0.016*
♂ Tarsus	4.38	1.35	10.59	0.001*
♂ Experience	0.88	0.45	3.76	0.055
Yellow brightness	-4.49	1.67	7.22	0.008*
UV brightness	3.49	1.69	4.25	0.041*
Carotenoid chroma (C_{car})	2.96	1.35	4.79	0.030*
Experience*♀ Tarsus	-1.85	0.72	6.50	0.012*
Experience*♂ Mass	1.59	0.63	6.35	0.013*
Experience*♂ Tarsus	-2.45	0.71	11.77	0.001*
Experience*Yellow brightness	2.33	0.90	6.75	0.010*
Experience*UV brightness	-1.72	0.93	3.38	0.068
Experience* C_{car}	-1.55	0.73	4.48	0.036*

Shown is the final reduced GLMM including male experience class (inexperienced and experienced). Partial mortality was entered as a two-level factor; all other predictors were continuous. Negative and positive effect sizes indicate increased likelihood of daughters and sons, respectively. * $P < 0.05$.

marginally nonsignificant ($P = 0.068$). On the other hand, daughters were more likely to be produced by heavier males with greater yellow brightness (Table 2; GLMM for inexperienced males; $N = 93$ nestlings from 27 broods). Among experienced males, no variable that we measured was a significant predictor of offspring sex in the final model ($P > 0.1$); we present a model including the variables that remained in the inexperienced male model to facilitate comparison (Table 2; GLMM for experienced males; $N = 134$ nestlings from 44 broods). Type of sire (extrapair versus within-pair), mask size and bib size were not significantly related to nestling sex in any model that we examined. Despite differences in the patterns of sex-ratio biases between experience classes, a univariate analysis showed no significant difference between the overall sex ratio of offspring produced by experienced and inexperienced sires.

We included data from both completely and incompletely sampled broods in our models. Although some authors have excluded broods with partial mortality, complete broods do not represent a better estimate of primary sex ratio than incomplete

Table 2
Sex of nestling common yellowthroats in relation to parental characteristics for inexperienced males ($N = 93$ young from 27 broods, $df = 1,61$) and experienced males ($N = 134$ young from 44 broods, $df = 1,87$)

Predictor	Effect size	SE	F	P
Inexperienced males				
Intercept	-1.15	0.46	–	–
Female tarsus	1.80	0.67	7.15	0.010*
Partial mortality	1.95	1.08	3.26	0.076
Male mass	-1.38	0.55	6.31	0.015*
Male tarsus	2.07	0.69	8.97	0.004*
Yellow brightness	-2.22	0.80	7.65	0.008*
UV brightness	1.91	0.79	5.86	0.019*
Carotenoid chroma	1.61	0.69	5.45	0.023*
Experienced males				
Intercept	0.07	0.30	–	–
Female tarsus	-0.05	0.30	0.04	0.850
Partial mortality	0.81	0.57	2.06	0.155
Male mass	0.46	0.41	1.24	0.269
Male tarsus	-0.39	0.27	1.98	0.163
Yellow brightness	0.14	0.43	0.11	0.742
UV brightness	0.12	0.52	0.05	0.822
Carotenoid chroma	-0.05	0.37	0.02	0.896

Partial mortality was entered as a two-level factor; all other predictors were continuous. Negative and positive effect sizes indicate increased likelihood of daughters and sons, respectively. * $P < 0.05$.

broods, and both should be included when analysing sex ratio (Fiala 1980; Krackow & Neuhauser 2008). However, disparities in sex ratio between complete and incomplete broods may still arise through correlations between sex ratio and offspring mortality (Krackow & Neuhauser 2008); therefore, we included partial mortality as a predictor in our models. In the GLMM including males of both classes, there was a significant sex-ratio bias between complete broods and those with partial mortality, with completely sampled nests having a lower proportion of males (Table 1). This effect remained in the separate model for inexperienced males, but was nonsignificant (Table 2). Among experienced males, this result became marginally significant when the traits of true genetic sires were used ($P = 0.047$).

Offspring Quality and Parental Traits

Parental traits were related to average brood mass for both experienced (multiple regression: $r^2 = 0.12$, $N = 41$, $P = 0.028$) and inexperienced (multiple regression: $r^2 = 0.64$, $N = 24$, $P = 0.009$) males (Table 3). Among experienced males, only yellow brightness of the bib was related to average brood mass, with brighter males producing heavier offspring (Table 3). Among inexperienced males, both parental morphology and ornamentation were related to average brood mass. In this case, heavier broods were produced both by mothers with long tarsi and by heavy fathers. Additionally, two measures of paternal bib coloration (C_{car} and UV brightness) were associated with heavier offspring, while one measure (yellow brightness) was associated with lighter offspring (Table 3). In general, the ornamental traits associated with more sons were also associated with the production of higher-quality offspring and greater male reproductive success (Table 4).

DISCUSSION

The ability of female birds to adaptively bias their brood sex ratio remains controversial, primarily due to a large number of studies reporting the lack of bias even when the female would benefit from producing more sons, as in the case when young are sired by males possessing a strongly sexually selected trait. However, previous studies have generally not considered whether the information content of male sexual signals varies with male breeding experience. At our study site in New York, common yellowthroat females produced higher-quality, male-biased broods in relation to male plumage ornamentation, but only when mated to inexperienced males. Specifically, nestlings were more likely to be male, and to be heavier, when females were mated to inexperienced males that had bibs with higher C_{car} and UV brightness. These plumage attributes

Table 3
Mean body mass of nestling common yellowthroats in relation to parental characteristics

Predictor	Effect size	SE	T	P
Inexperienced males				
Female tarsus	0.83	0.24	0.38	0.004*
Male mass	0.61	0.27	2.27	0.037*
Yellow brightness	-0.89	0.35	-2.52	0.023*
UV brightness	1.13	0.45	2.53	0.022*
Carotenoid chroma	1.16	0.31	3.77	0.002*
Bib size	0.55	0.30	1.88	0.078
Mask size	-0.57	0.31	-1.84	0.085
Experienced males				
Yellow brightness	0.39	0.17	2.29	0.028*

Shown are the reduced multiple regression models for inexperienced ($r^2 = 0.64$, $N = 24$ broods, $P < 0.01$) and experienced ($r^2 = 0.12$, $N = 41$ broods, $P < 0.03$) males. Positive and negative effect sizes correspond to greater and lesser average nestling mass respectively. * $P < 0.05$.

Table 4

Summary of sex-ratio bias, offspring quality and reproductive success in relation to paternal ornamentation for inexperienced male common yellowthroats (+ and – represent significant relationships; 0 represents nonsignificant relationships)

Predictor	Proportion sons*	Nestling mass†	Reproductive success‡
Yellow brightness	–	–	0
UV brightness	+	+	+
Carotenoid chroma	+	+	+
Bib size	0	0	+
Mask size	0	0	0

* GLMM of offspring sex ratio (Table 2).

† Multiple linear regression on average nestling mass (Table 3).

‡ Logistic regression on social mating success (Table 5 in Freeman-Gallant et al. 2010).

are also a reliable signal of male condition and positively influence male fertilization success in this population, but only for inexperienced males (Freeman-Gallant et al. 2010). Thus, bib UV brightness and C_{car} are sexually selected male traits that signal male quality and are related to both offspring quality and the production of more males. Since these relationships are limited to inexperienced males, only the subset of females mated to these males will realize the benefits of producing more sons. If variation in the information content of sexual signals in relation to breeding experience is a common phenomenon, then it is not surprising that few studies have found the predicted bias in brood sex ratio in relation to sexually selected male ornamentation.

In general, females are predicted to bias the sex ratio of their brood whenever the reproductive value of sons and daughters differs. However, differences in reproductive value may be generated in several ways, and the distinctions between these scenarios have often been unclear in the literature. In the original Trivers & Willard (1973) paper, reproductive value differed between males and females according to parental body condition or resource availability. Because males in many species have greater variance in reproductive success, females should produce more sons when: (1) mated to males in good condition, as long as paternal condition is heritable (either genetically or via parental effects), or (2) when females are in good condition (Trivers & Willard 1973). In the first scenario, females may assess male condition directly, but assessment may also be mediated by condition-dependent signals. Burley (1981, 1986) extended this model by suggesting that females might also adjust offspring sex ratio in response to the attractiveness of male ornaments, regardless of body condition. In this case, inheritance of elaborate ornaments per se determines the reproductive value of offspring, and ornaments may or may not be correlated with male condition (Fawcett et al. 2007). Finally, recent evidence also suggests that offspring reproductive value can differ in relation to sex when sexually antagonistic selection results in negative correlations between parental and opposite-sex offspring fitness (Calsbeek & Bonneaud 2008; Connallon & Jakubowski 2009).

Under each of these hypotheses, a different factor generates disparity in son and daughter reproductive value; yet, in many systems, the direction of sex-ratio bias will be the same. For example, higher-quality males may be in better condition, have more attractive signals and produce high-quality sons (but not daughters) because of sexually antagonistic selection. In this case, all three hypotheses result in more sons from females mated to high-quality males and more daughters from females mated to low-quality males. However, when the information content of signals changes over a male's lifetime, females may be more or less responsive to male ornaments depending on male age or breeding experience and on whether differences in offspring reproductive value are generated primarily by inheritance of paternal ornamentation or paternal condition. Recent studies suggest that there are often consistent changes in the

condition-dependence of sexually selected male signals across years or contexts (Candolin 2000; Badyaev & Duckworth 2003; Peters et al. 2006). For example, among young blue tits, *Cyanistes caeruleus*, testosterone level and UV ornamentation are positively correlated and bright males achieve high reproductive success through increased within-pair paternity; however, among older blue tits, testosterone and UV ornamentation are negatively correlated and individuals with elaborate crowns achieve greater reproductive success due to increased extrapair paternity (Delhey et al. 2003; Peters et al. 2006). Brood sex-ratio bias may also change in relation to age class and crown UV brightness in blue tits; in one study, females produced more sons when mated with younger, UV bright males and produced more daughters when mated with older, UV bright males (Delhey et al. 2007; but see Griffith et al. 2003).

In common yellowthroats, males that successfully attract a social mate and produce extrapair young generally have larger masks and larger, more colourful bibs (Freeman-Gallant et al. 2010). To some extent, this sexual selection for increased ornamentation reflects the mating advantage realized by older, more experienced males, but even among young, inexperienced males, bib attributes are positively condition dependent and under strong selection with respect to social mating success. Several of these same attributes, however, are either negatively condition dependent or uninformative among older birds, and the strength and direction of sexual selection changes accordingly (Freeman-Gallant et al. 2010). As in blue tits, we found that patterns of sex-ratio bias in common yellowthroats parallel these experience-related changes in sexual selection, with the production of higher-quality offspring and more sons occurring when females are mated to males with the most informative plumage signals.

Among inexperienced males, individuals with greater UV brightness and C_{car} and larger bibs achieved greater reproductive success (Freeman-Gallant et al. 2010). In this experience class, UV brightness and bib size are correlated with male condition and survival prospects, respectively (Freeman-Gallant et al. 2010). Increasing C_{car} , although not correlated with any known measure of male quality, represents a greater deposition of carotenoids into the bib feathers (Peters et al. 2004, 2007). Because carotenoids are thought to be important for other biological functions (McGraw 2006), C_{car} may indicate another aspect of male quality, such as resistance to oxidative stress (Alonso-Alvarez et al. 2007). In accordance with these patterns of sexual selection and signal information content, females mated to inexperienced males that had greater UV brightness and C_{car} scores (but not large bibs) produced more and heavier sons. Holding all other variables constant, our final model predicted an increase of 29% and 31% in the probability of producing sons when C_{car} and UV brightness increased by one standard deviation, respectively. On the other hand, an increase of one standard deviation in yellow brightness was predicted to result in a 46% increase in the probability of producing daughters. Yellow brightness was not related to condition and was not a target of sexual selection in this experience class, so it is unclear why it should be correlated with biased sex ratios. These patterns were present regardless of whether we included the traits of the social or true genetic sire as predictors in our model. If females lack sufficient control to bias sex on an individual offspring level, it may be most beneficial to bias brood sex ratios based on the attributes of the social male. In this population 94% of nests contain at least some young sired by the social mate. Therefore, females biasing their brood sex ratio based on the traits of the social male may increase their fitness through both direct benefits for all of the offspring in their brood and indirect genetic benefits for those sired by the social male.

In contrast, no ornament or ornament component predicted brood sex ratios among females mated to experienced males, even though some bib traits were related to male morphology, offspring quality and the likelihood of siring extrapair young in this experience class. If male breeding experience reflects male quality, females may

be more likely to produce sons when paired to older males (Hasselquist & Kempenaers 2002) regardless of their ornamentation; however, in our population the overall sex ratio of nestlings did not differ between experienced and inexperienced sires. Also, note that experienced and inexperienced males did not differ in average C_{car} and UV brightness of their bibs (Freeman-Gallant et al. 2010), which were the main correlates of producing more sons among females mated to inexperienced males. If sex-ratio biases were driven only by inheritance of genes that confer greater ornamentation, we would expect biases in relation to C_{car} and UV brightness to continue across age classes. The patterns that we observed suggest that changes in the information content of sexual signals may be at least as important as the expression of signals per se in generating differences in offspring reproductive value. Because our results were similar when considering the traits of putative versus genetic sires, it is difficult to disentangle the relative influence of genetic and environmental heritability on these patterns. However, regardless of the overall effect of male experience, females appear to follow different sex allocation rules when mated to males in different experience classes.

Sex allocation rules also appear to vary to some extent geographically in common yellowthroats. In New York, we found that biased brood sex ratios were associated with both male ornamentation and parental body mass and tarsus length. Similarly, in Wisconsin, females produce broods with more sons when mated to males with longer tarsi (Abroe et al. 2007). However, in contrast to this study, females in Wisconsin did not produce more sons when mated to males with larger facial masks (Abroe et al. 2007), despite strong selection on mask size in Wisconsin (Thusius et al. 2001). If females are making facultative changes to their brood sex ratio, then these geographical differences may be related to (1) the relative benefits of producing larger or more ornamented sons and (2) the ability of females to adjust sex ratio to produce high-quality sons. For example, heritabilities and environmental conditions can differ geographically (Charmantier & Garant 2005), limiting the ability of females to produce sons with larger or more colourful ornaments (note, for example, the low estimate of additive genetic variation for carotenoid coloration in the yellow breast colour of tits studied by Hadfield & Owens 2006).

Sex allocation theory predicts that females will adjust the sex ratio of their broods in relation to male traits that provide information about the relative value of sons and daughters and that these adjustments will increase maternal fitness. As predicted, we found that common yellowthroats in New York bias the sex ratio of their offspring in response to parental traits and that these same traits were related to offspring quality. However, the deviations in both sex ratio and offspring quality were not consistent across experience classes, and tended to parallel changes in the information content of sexual signals. We suggest that the relationship between male traits and the relative value of sons and daughters may change across years, locations or age classes and that similar patterns may be observed across taxa (see also Candolin 2000; Badyaev & Duckworth 2003; Peters et al. 2006). Such patterns may obscure adaptive sex-ratio bias and contribute to mixed results in the literature.

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