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BROOD SEX RATIOS ARE RELATED TO MALE SIZE BUT NOT TO ATTRACTIVENESS IN COMMON YELLOWTHROATS (*GEOTHYLPIS TRICHAS*)

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ABSTRACT.—When the reproductive value of sons differs from that of daughters, selection will favor broods biased toward the sex that can provide greater fitness benefits. In species where female choice is based on male ornamentation, females mated to highly ornamented males may experience a reproductive advantage by skewing the brood sex ratio toward sons. In the Common Yellowthroat (*Geothlypis trichas*), males with larger black facial masks are more likely to gain a social mate and sire extrapair young and, as a result, have increased seasonal reproductive success. Females mated to larger-masked males could benefit if they produced more sons. Given that larger-masked males are preferred as extrapair sires, females may also benefit by producing more extrapair sons. We tested these hypotheses during a five-year study of Common Yellowthroats in Wisconsin. Contrary to our predictions, females did not produce more sons when mated to males with larger masks, and extrapair young were not more likely to be male. However, sons were more likely to be sired by males with longer tarsi, which suggests that females may respond to male body size rather than to male ornament size. *Received 13 October 2005, accepted 25 January 2006.*

Key words: brood sex ratio, Common Yellowthroat, extrapair mating, *Geothlypis trichas*, male ornaments, paternity, sexual selection.

El Cociente de Sexos en las Nidadas Está Relacionado con el Tamaño de los Machos pero no con el Atractivo en *Geothlypis trichas*

RESUMEN.—Cuando el valor reproductivo de los hijos difiere del de las hijas, la selección favorecerá las nidadas sesgadas hacia el sexo que puede brindar mayor adecuación biológica. En las especies en las que la elección de las hembras se basa en la ornamentación de los machos, las hembras que se aparean con machos con muchas ornamentaciones pueden obtener una ventaja reproductiva sesgando el cociente de sexos de la nidada hacia los hijos. En *Geothlypis trichas*, los machos con antifaces negros más grandes tienen una mayor probabilidad de conseguir una pareja social y engendrar juveniles extra pareja y, como resultado, incrementar su éxito reproductivo estacional. Las hembras que se aparean con machos con antifaces más grandes podrían beneficiarse si ellos produjesen más hijos. Dado que los machos con antifaces más grandes son los preferidos como progenitores extra pareja, las hembras pueden también beneficiarse produciendo más hijos extra pareja. Evaluamos estas hipótesis en un estudio sobre *G. trichas* durante cinco años en Wisconsin. Contrariamente a nuestras predicciones, las hembras no produjeron más hijos cuando se aparearon con machos con antifaces más grandes, y los juveniles extra pareja no presentaron mayor probabilidad de ser machos. Sin embargo, los hijos tuvieron una probabilidad mayor de ser engendrados por machos con tarsos mayores, lo que sugiere que las hembras podrían responder al tamaño del cuerpo de los machos, más que al tamaño de la ornamentación de éstos.

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SEX ALLOCATION THEORY predicts that individuals should vary the sex ratio of their offspring when the reproductive value of sons differs from that of daughters (Trivers and Willard 1973, Charnov 1982). Several factors may influence the relative benefits of producing sons and daughters, including the relative variance in reproductive success of the sexes (Trivers and Willard 1973). For example, in polygynous species, males typically have greater variance in reproductive success than females and, as a consequence, a successful son has the potential to produce many more offspring and provide greater fitness benefits than a successful daughter. Until recently, the variance in reproductive success was assumed to be similar for males and females in monogamous species; however, it is now clear that extrapair fertilizations are common, and this can sometimes allow successful males to produce many more offspring than females (Whittingham and Dunn 2005). Thus, even in monogamous species, some females may achieve greater fitness benefits by producing sons, if the latter are successful at gaining extrapair matings. Alternatively, if sons are not successful, it may be better for females to produce more daughters or an even sex ratio.

In some species, the high variance in male reproductive success may be attributable to female mating preferences for males with more exaggerated ornamental traits. In this case, we might expect females mated to males with preferred traits to produce relatively more sons, because those sons will inherit the exaggerated ornament and, subsequently, gain more mates. Although males in many species of birds have elaborate ornamental traits, there are few species in which (1) a male ornamental trait that confers an extrapair mating advantage has been identified (Griffith et al. 2002), (2) females produce male-biased broods when mated to more attractive males (Ellegren et al. 1996, Sheldon et al. 1999, Griffith et al. 2003), and (3) the sex of young has been examined in relation to traits of both within-pair and extrapair sires (Sheldon and Ellegren 1996, Kempenaers et al. 1997). The Common Yellowthroat (*Geothlypis trichas*) provides a rare opportunity to test the hypothesis that females adjust the sex of their young in relation to a male ornamental trait.

The Common Yellowthroat is a small, sexually dimorphic passerine that is socially monogamous; however, 46% of broods contain extrapair

young (Thusius et al. 2001), which contributes to high variance in male reproductive success (Whittingham and Dunn 2005). Males have a black facial mask and bright yellow bib (throat and chest) that is absent (mask) or subdued (bib) in females. Males with larger black masks were more likely to have prior breeding experience, and they were also more likely to attract a social mate and sire extrapair young than males with smaller black masks (Thusius et al. 2001). In a paired comparison, extrapair sires had larger masks than the males they cuckolded (Thusius et al. 2001). Thus, males with larger masks have greater reproductive success, and females could benefit by producing more sons when mated to these males. Furthermore, mate-choice experiments in an aviary indicate that females have a strong preference for males with larger masks (Tarof et al. 2005). There may also be a weaker preference for males with larger bibs (Tarof et al. 2005) but, to date, bib size is not related to mating success in our population (P. O. Dunn unpubl. data). On the basis of these previous studies, we predicted that (1) males with larger masks would sire more sons than daughters and (2) extrapair young would be male more often than female.

METHODS

We analyzed the sex ratios of broods sampled in 2002, 2003, and 2004 and in a previous study done in 1998 and 1999 (Peterson et al. 2001, Thusius et al. 2001). Field work was conducted at the University of Wisconsin-Milwaukee Field Station in Saukville, Wisconsin (43°23'N, 88°01'W). The study area consists of 5.4 ha of bog and sedge marsh wetlands. The Common Yellowthroat is a migratory warbler distributed widely across North America (Guzy and Ritchison 1999). They nest at the base of tufts of grass or shrubs in wetland habitats. Nests were located by close observation of male and female behavior during nest building and incubation. Clutch size ranges from two to five eggs. Only females incubate the clutch, but both sexes feed the nestlings, which fledge eight days after hatching.

Adults were captured in mist nets and banded with a federal band and a unique combination of three colored leg bands. For each adult and nestling (four days old), tarsus length and body mass were measured. A blood sample was

taken from the brachial vein of each individual and stored in lysis buffer at 4°C for molecular analyses of paternity and sex. Unhatched eggs were collected and stored at -20°C.

Mask and bib size were measured from still video images using the image-analysis program IMAGEJ, version 1.28 (National Institutes of Health; details in Thusius et al. 2001). Briefly, heads and bibs of males were recorded on videotape in front of a grid of 1-cm gray and white squares. We captured two still images of each side of the mask (four images total) and two images of the bib. Mask and bib size were estimated by tracing the outline of each ornament using IMAGEJ. We defined mask size (mm²) as the sum of the mean area for each side of the head.

Hue, saturation and brightness of the bib were analyzed using PHOTOSHOP ELEMENTS, version 2.0 (Adobe, San Jose, California; details in Tarof et al. 2005). Briefly, images were standardized for color and brightness using a gray square included in each image, and the gray point tool was set so that the red, green, and blue channels (RGB) were set to 72, 86, and 110, respectively, on a scale of 0 to 255 (see Massaro et al. [2003] for similar techniques). The eyedropper tool (set to average 5 × 5 pixels) was then placed over three equidistant points along the midline of the chin, neck, and breast. Hue (0 = red, 60 = yellow, 120 = green), saturation (%), and brightness (%) at each of these nine points were recorded and averaged. We entered these three variables into a principal component analysis (PCA) to yield a single bib-color score (first principal component [PC1]) that was used in analyses.

PATERNITY ANALYSIS

Parentage of nestlings was determined using four highly variable microsatellite loci: *Dpu01* and *Dpu16* (Dawson et al. 1997), and *Dca24* and *Dca28* (Webster et al. 2001). For *Dpu01* (respective amounts for *Dpu16*, *Dca24*, *Dca28* in parentheses), we used 50–100 ng of genomic DNA, 0.5 pmol of both the fluorescently labeled forward primer and reverse primer (0.1, 0.5, 1.0), 10 mM Tris-HCL (pH 8.3), 2.5 mM MgCl₂ (3.75, 1.5, 2.5), 0.8 mM dNTP, and 0.1 U *Taq* in a 10-μL reaction. The thermal cycling program included an initial denaturing at 94°C for 3 min (3, 3, 2) followed by 30 cycles of: 94°C for 30 s (30, 60, 60), 52°C (57, 44, 48) for 30 s (30, 60, 60),

72°C for 30 s (30, 45, 45), and concluded with a final extension of 72°C for 5 min. Polymerase chain reaction (PCR) products were run on a 6% polyacrylamide gel on an ABI 373 automated sequencer with a fluorescently labeled size standard in each lane (Genescan 500). GENESCAN ANALYSIS and GENOTYPER 2.0 software (PE Biosystems, Foster City, California) were used to determine allele sizes for each individual. All individuals were genotyped at all four loci.

The number of alleles at each of the four loci ranged from 15 to 33, and observed heterozygosity ranged from 0.85 to 0.95 (Peterson et al. 2001). For each locus, we calculated allele frequency (P_i) and probability of paternal exclusion (P_{ei}), which is the probability that a randomly chosen male in the population will not possess that allele for any particular offspring, given that the mother's allele is known (Jaimieson 1994). The probability of paternal exclusion for all four loci (P_{ei}) was 0.999.

All broods contained at least two young. All young possessed their mother's allele at all four loci. Young were considered within-pair if they matched their putative father at all four loci. Young that mismatched the paternal allele at one or more loci were considered extrapair young. For young that mismatched their putative sire at only one locus (14 of 93 extrapair young), we calculated the probability of chance inclusion with the putative sire (Jeffreys et al. 1992) at the other three (matching) loci. Offspring with a high probability of chance inclusion ($P > 0.05$) with the putative father were considered extrapair young (Johnsen et al. 2000). Fourteen young mismatched their putative father at one locus, and in all cases the probability of chance inclusion was high (>0.05 ; mean ± SE = 0.38 ± 0.04; range: 0.06–0.69). These offspring were considered extrapair. Extrapair sires were assigned when they matched an extrapair young at all four loci. In all cases, there was only one male in our sample that completely matched the genotype of each extrapair young.

SEX DETERMINATION

Common Yellowthroat nestlings are sexually monomorphic, so we determined the sex of young using primers that amplify an intron of the CHD1 gene on the avian sex chromosomes (Griffiths et al. 1998). Each PCR contained

50–100 ng of genomic DNA, 0.5 pmol of each primer (P2 and P8), 10 mM Tris-HCL (pH 8.3), 1.5 mM MgCl₂, 0.8 mM dNTP, and 0.1 U *Taq* in a 10- μ L total reaction volume. The thermal program for amplification included an initial 2-min denaturation at 94°C, followed by 29 cycles of 94°C for 30 s, 47°C for 45 s, and 72°C for 45 s, and one final cycle of 48°C for 1 min and 72°C for 5 min. The PCR products were run on a 2% NuSieve 3:1 agarose gel stained with ethidium bromide to visualize the amplified products. Males were identified by one band, and females by two bands (Griffiths et al. 1998). The accuracy of this sexing technique for Common Yellowthroats was verified initially with adults of known sex (five males and five females).

STATISTICAL ANALYSIS

We examined the sex of each nestling in relation to several predictor variables of male and female quality and the paternity of the nestling. We used the sex of each nestling as the response variable, but each nestling is not an independent observation, because within a brood they all share the same mother. To account for this variation between mothers and their broods, we used a generalized linear mixed model (GLMM; GENSTAT 7.0, Numerical Algorithms Group, Oxford, United Kingdom) to examine the sex of individual offspring in relation to traits of the sire. This provides a more powerful and less biased method of analysis than conventional generalized linear models that do not consider fully the clustered nature of sex-ratio data (see Krackow and Tkadlec [2001] for discussion, and Dowling and Mulder [2006] for a similar analysis). Nestling sex was the response variable, with a binomial error and logit link function, and the dispersion parameter was fixed at 1. Nest identity (a unique code for each brood) was nested within female identity (unique for each female) and included in the model as a random effect. Predictor variables included sire mask size, bib size, bib color (PC1), and tarsus length, as well as body mass and tarsus length of the female, and whether the nestling was extrapair or within-pair. Female condition was estimated by the effect of body mass in the GLMM, which controls for tarsus length (a measure of overall size). Significance of these variables was assessed using the Wald statistic,

which has a chi-square distribution. Of the 138 broods analyzed, we included data from eight females that bred with different males in different years and four females that bred with the same male in different years. The GLMM included the identity of each female, so data from these multiple nests were treated as one pooled sample for each female.

RESULTS

Over all five years, we determined the sex of 486 young (embryos and nestlings) from 138 broods of 112 breeding pairs, of which 26 (23%) were double brooded. The sex ratio (proportion of males) was 0.50 in 1998 ($n = 13$ pairs), 0.49 in 1999 ($n = 19$), 0.47 in 2002 ($n = 23$), 0.51 in 2003 ($n = 31$), and 0.45 in 2004 ($n = 26$). Extrapair young accounted for 93 of 486 offspring (19%) and were present in 60 of 138 broods (43%). We were unable to determine the sex of 35 unhatched eggs; thus, we sampled 93% (486 of 521) of all eggs.

We used a GLMM to examine the sex of individual offspring in relation to the sire's traits, the mother's condition, and the paternity of the nestling (within-pair or extrapair). Contrary to our prediction, the sex of nestlings was not related to the mask size of sires, nor was nestling sex related to bib size or color of the sire (Table 1). However, males with longer tarsus length were significantly more likely to sire sons than daughters (Table 1 and Fig. 1). Nestling sex was not related to the condition of the female

TABLE 1. Nestling sex in relation to traits of the sire, female, and paternity (extrapair or within-pair). Shown are fixed effects from a GLMM. Significance was assessed with the Wald statistic (W). Positive effects indicate more males in the brood, and negative effects indicate more females. Brood identity and female identity were random effects in the model.

Predictor variable	Effect	SE	W	P
Sire tarsus	0.591	0.257	5.31	0.02
Sire mask size	0.001	0.005	0.03	0.86
Sire bib size	0.001	0.001	0.56	0.46
Sire bib color (PC1)	-0.001	0.131	0.00	0.99
Paternity			0.37	0.67
Female mass	0.131	0.180	0.53	0.47
Female tarsus	-0.182	0.333	0.30	0.59

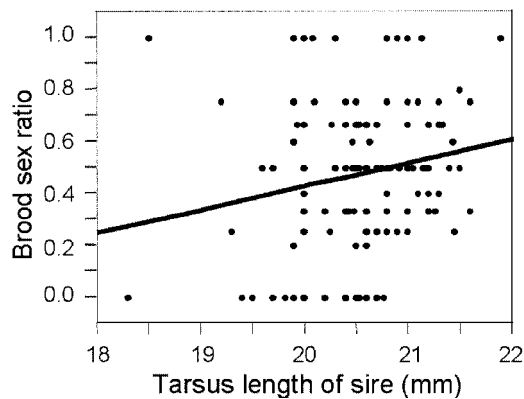


FIG. 1. Brood sex ratio (percentage of males) in relation to tarsus length (mm) of sires ($n = 130$ broods). Broods can contain all within-pair young, all extrapair young, or a mixture of both types of young. Tarsus length was averaged when there was more than one sire in a nest. Line is from a linear regression and is presented for descriptive purposes only (slope = 0.09). Inferential analysis was performed using a GLMM with the sex of each nestling as the response variable (see Table 1).

(mass corrected for tarsus and capture date; Table 1). As found previously (Thusius et al. 2001), extrapair males had larger black facial masks than the males they cuckolded (paired $t = 2.97$, $df = 48$, $P = 0.005$); however, contrary to our prediction, extrapair young were not more likely to be sons (48%, 45 of 93) than within-pair young (47%, 186 of 393; Table 1). There were no significant interactions between variables in the GLMM, and results were qualitatively similar when year was added to the model.

Because sex ratio was associated with male tarsus length in the GLMM, we performed several linear regressions to determine whether male tarsus length was associated with other aspects of male quality. Male tarsus length was not related to the following variables: male body mass ($r^2 = 0.02$, $P = 0.14$, $n = 100$), mask size ($r^2 < 0.01$, $P = 0.39$, $n = 102$), bib size ($r^2 < 0.01$, $P = 0.44$, $n = 69$), bib color (PC1) ($r^2 < 0.01$, $P = 0.66$, $n = 69$), or arrival date ($r^2 < 0.01$, $P = 0.41$, $n = 94$). There was also no relationship between tarsus length and whether a male was cuckolded (yes–no; logistic regression: $\chi^2 = 0.15$, $df = 1$, $P = 0.70$) or whether he survived to the next breeding season (yes–no; logistic regression: $\chi^2 = 0.86$, $df = 1$, $P = 0.77$).

DISCUSSION

Although male Common Yellowthroats with larger masks have a reproductive advantage, we did not find that brood sex ratio was adjusted to the mask size of sires. Further analyses showed that nestling sex was also not related to other male plumage ornaments or paternity of the nestling. However, males with longer tarsi sired more sons, which suggests that larger sons may have a fitness advantage. These results add to a growing number of studies that have examined nestling sex in relation to male ornaments or morphology.

Few other studies have examined nestling sex in relation to male plumage traits that are related to male mating success. The forehead patch size of male Collared Flycatchers (*Ficedula albicollis*), a signal of male quality (Gustafsson et al. 1995, Pärt and Qvarnström 1997), was related positively to the proportion of sons per brood in a Swedish population (Ellegren et al. 1996) but not in a Hungarian population (Rosivall et al. 2004). In Blue Tits (*Cyanistes caeruleus*), females preferred males with brighter ultraviolet crown color (Andersson et al. 1998, Hunt et al. 1998) and produced broods with more male offspring when paired with these males (Sheldon et al. 1999, Griffith et al. 2003), though this relationship varied among years (Griffith et al. 2003). Similarly, female Barn Swallows (*Hirundo rustica*) preferred males with longer outer tail feathers (Saino et al. 1997), and sex ratios were biased toward males when females mated with preferred males in one study (Saino et al. 2002) but not another (Saino et al. 1999). Thus, under some conditions, the sex of young may be biased toward sons when females are mated to more ornamented males; however, the relationship appears to differ between seasons and populations (Rosivall et al. 2004). In contrast, brood sex ratios were not biased in relation to male plumage characteristics in House Sparrows (*Passer domesticus*), even across multiple years (Westneat et al. 2002).

Given that the benefit of adjusting the sex ratio of offspring is maximized reproductive success, we would expect females to adjust the sex of extrapair offspring to favor sons, if sons inherit the trait that increases extrapair mating success. In the case of Blue Tits, nestlings sired by extrapair males were more likely to be male in one population (Kempnaers et al. 1997)

but not in another (Leech et al. 2001). There was also a tendency for extrapair young to be male in Red-capped Robins (*Petroica goodenovii*; Dowling and Mulder 2006). In contrast, studies of several other species have reported no bias in brood sex ratio, regardless of whether they compared the proportion of male offspring between broods that contained extrapair young and those that did not (Westerdahl et al. 1997, Whittingham and Dunn 2001, Ramsay et al. 2003) or the number of sons that were actually within-pair and extrapair young (Sheldon and Ellegren 1996, Saino et al. 1999). In Common Yellowthroats, there was no relationship between paternity and the sex of young, despite a sample of extrapair young that was more than twice as large as that of a previous study that found an effect (Dowling and Mulder 2006).

We found that broods contained more males when females were mated to larger males (i.e., those with longer tarsi), which is similar to results of other studies. In the Great Tit (*Parus major*) and the Varied Tit (*Sittiparus varius*), tarsus length of the putative sire was correlated positively with the proportion of males in broods and with the male's ability to gain a nest site (Kölliker et al. 1999; Yamaguchi et al. 2001, 2004). Thus, if tarsus length is heritable, as it is in other species of birds (e.g., Riddington and Gosler 1995, Merilä 1997, Merilä and Fry 1998), sons of larger males are likely to gain a reproductive advantage and, consequently, females would benefit by producing sons sired by larger males. In our population of Common Yellowthroats, males with longer tarsi did not have an obvious fitness advantage. However, the benefit of being larger may occur earlier in life, during the period between fledging and establishing a breeding territory. Indeed, nestling size (tarsus length) is related positively to survival and recruitment of young in other bird species (e.g., Ringsby et al. 1998, Horak 2003).

There are a number of possible reasons why brood sex ratios were not adjusted in response to male traits or paternity. Sex ratio adjustment may be constrained by the chromosomal mechanism of sex determination in birds (Krackow 1995, West and Sheldon 2002). However, there is evidence that sex ratio adjustment can occur through pre-ovulatory follicle selection in birds (Komdeur et al. 2002, Pike 2005) and in response to experimental manipulation of male characteristics or breeding environment (Sheldon et al. 1999,

Komdeur et al. 2002). An important point, which is often overlooked, is that we may not see an adjustment of brood sex ratio if the trait does not affect the relative reproductive value of sons and daughters. Although larger masks provide a mating advantage to male Common Yellowthroats, we may not see an adjustment in brood sex ratio if the trait also has a positive influence on female reproductive success. For example, the benefit to females of producing sons when mated to males with sexually selected traits could be offset if daughters have better survival prospects than sons (Saino et al. 1999, Grindstaff et al. 2001). The survival and reproductive success of daughters of males with large masks remain unknown for Common Yellowthroats. However, in this species and others in which there is no bias in nestling sex in relation to a male trait (Westerdahl et al. 1997, Westneat et al. 2002), it may be useful to consider whether male traits confer a fitness benefit for both sons and daughters.

In the Common Yellowthroat, males with larger masks experience a reproductive advantage that would theoretically enhance the reproductive value of sons if mask size is heritable. Contrary to our predictions, there was no evidence that females produced more sons when mated to males with larger masks, either as social or extrapair mates. However, females were more likely to produce sons when mated to larger males. While the importance of larger male size is not clear, larger males may be more likely to recruit into the breeding population or could incur a reproductive advantage through dominance in male-male interactions. Further research is needed to identify the benefit females might realize from producing more sons when mated to larger males.

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