

Sexual size dimorphism and assortative mating in Carolina Wrens

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ABSTRACT. Sexual size dimorphism (SSD) may be due to sexual and natural selection, but identifying specific mechanisms that generate such dimorphism in a species is difficult. I examined SSD in Carolina Wrens (*Thryothorus ludovicianus*) by examining (1) the degree of SSD in the population and between pairs using five morphometrics, (2) assortative mating patterns based on size and age, and (3) relationships between size and longevity. Analysis revealed that males were significantly larger than females in all body measurements. For example, mass, bill, and wing measurements yielded a canonical variable that permitted separation of the sexes and linear classification functions correctly determined the sex of 95% (238/250) of all wrens measured. No evidence was found to suggest that SSD was related to resource partitioning. However, assortative mating trends based on morphometrics (e.g., wing length), positive associations between longevity and morphometrics (e.g., wing length in females and body size in males), and intense male-male contests for territorial resources year-round provide evidence that sexual selection may contribute to SSD in Carolina Wrens.

SINOPSIS. Dimorfismo sexual en tamaño y diversidad en el apareamiento en *Thryothorus ludovicianus*

El dimorfismo sexual en tamaño, puede ser el efecto de la selección sexual o natural, pero la identificación de los mecanismos particulares que generan el mismo son difíciles de establecer. Estudié el dimorfismo sexual en el reyezuelo *Thryothorus ludovicianus* examinando (1) el grado de dimorfismo sexual en tamaño (DST), (2) el patrón de la selección de parejas, basado en el tamaño y la edad de los individuos y (3) la relación entre tamaño y longevidad. El análisis reveló que los machos son significativamente morfométricamente más grandes que las hembras. Por ejemplo, la masa corporal, y el tamaño del pico y del ala rindieron una variable que permitió la separación de los sexos y una función de clasificación lineal que además permitió determinar correctamente el sexo del 95% (238/250) de todos los reyezuelos medidos. No se encontró evidencia que sugiera que el DST este relacionado a la repartición en el uso de recursos. Sin embargo, la tendencia a la selección de parejas, basada en morfometría (ejemplo, largo del ala), asociación positiva entre la longevidad y la morfometría (ejemplo, largo del ala en las hembras y tamaño del cuerpo en los machos), y la intensa competencia entre machos por territorios con buenos recursos, (a través del año), proveen evidencia para indicar que la selección sexual pudiera contribuir al DST en el ave estudiada.

Key words: assortative mating, Carolina Wren, sexual dimorphism, sexual selection, *Thryothorus*

Although sexual size dimorphism (SSD) is common in birds, there is considerable interspecific variation and the mechanisms and factors contributing to the variation are complex and remain equivocal (Hedrick and Temeles 1989, Andersson 1994, Owens and Hartley 1998, Badyaev and Martin 2000, Blondel et al. 2002, González-Solís 2004). The causation and maintenance of SSD in birds are typically explained by sex- and environment-related hypotheses (Webster 1997, Blondel et al. 2002). The sex-related hypotheses involve sexual selection and propose that SSD results from intrasexual contests (typically between males) where large size

offers a selective advantage or one sex (typically female) prefers large mates (Searcy 1979, Price 1984a, Andersson 1994). Environment-related hypotheses involve natural selection, with SSD resulting from males and females adapting differently to ecological factors (Selander 1966, Shine 1989). For example, intersexual food competition or different food requirements can lead to a divergence in morphology and foraging behavior between the sexes (Temeles et al. 2000, González-Solís 2004, Radford and du Plessis 2004).

Identifying the specific selective pressures that cause and maintain SSD in a population is difficult (Price 1984b, Hedrick and Temeles 1989, González-Solís 2004), but important initial steps include measuring the degree and variation of SSD, as well as acquiring a detailed knowledge

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of the life history of a species (Price 1984a, Jehl and Murray 1986, Magrath et al. 2003, Radford and du Plessis 2004). Additionally, examining mating or pairing patterns may provide evidence of the selective mechanisms at work (Jehl and Murray 1986). For instance, assortative mating may indicate that mate choice is occurring (Marzluff and Balda 1988, Sandercock 1998, Delestrade 2001, Forero et al. 2001). Also, examining associations among phenotypic traits and measures of fitness (e.g., lifespan) can help explain SSD patterns (Price 1984a, Marzluff and Balda 1988).

The Carolina Wren (*Thryothorus ludovicianus*) is a small, monochromatic passerine that inhabits wooded areas through much of the eastern United States and parts of Central America. Its life history is similar to those of tropical passerines, with territories and pair bonds maintained year-round and infrequent mate switching (Haggerty and Morton 1995, Haggerty et al. 2001, Hyman 2002, 2005, Gorrell et al. 2005). Both parents contribute to raising young and multiple broods can be raised in a season (Haggerty and Morton 1995). In addition, Carolina Wrens are genetically, as well as socially, monogamous (Haggerty et al. 2001). Although intersexual differences in morphometrics have been noted in Carolina Wrens (Haggerty and Morton 1995, Pyle 1997), sample sizes were small. Within-pair dimorphism has not been reported, and no correlates with SSD have been studied. The objectives of my study were to examine SSD in Carolina Wrens by (1) measuring the degree of SSD in a population and within pairs using morphometrics, (2) examining assortative mating patterns based on size and age, and (3) examining potential associations among morphological traits and lifespan.

METHODS

My study was conducted from 1988 to 2004 in a 43-ha mixed hardwood forest on the Tennessee Valley Authority Reservation in Muscle Shoals, Colbert County, Alabama (34°49'N, 87°38'W). The overstory and understory are dominated by Hackberry (*Celtis laevigata*) and Chinese privet (*Ligustrum sinense*), respectively.

Individuals were captured with mist nets and marked with a U.S.G.S. band and a unique combination of colored leg bands. For each captured

wren, I determined (1) body mass (± 0.25 g) using a spring scale (Pesola, Baar, Switzerland), (2) wing chord (± 0.1 mm; distance from bend of unflattened wing to the tip of longest primary), (3) bill length (± 0.1 mm; distance from anterior nares to tip), (4) tail length (± 0.1 mm; distance from tail base to tip of longest rectrix), and (5) tarsus length (± 0.1 mm; distance from intertarsal joint to distal end of tarsometatarsus). For intrapair comparisons, a sixth variable, body size, was estimated based on wing, tarsus, bill, tail, and mass measurements using principal component analysis (Rising and Somers 1989). Eigenvectors of principle component one (PC1) showed positive loadings (wing = 0.53, tarsus = 0.51, bill = 0.41, and mass = 0.53), and PC1 explained 61% of the variance in body size.

I performed all measurements, and the mean number of individuals measured per year was 17.3 (SD = 4.05, range = 2–40). Because no significant associations between year and any measurements were found (ANOVA, $P > 0.05$), individuals from all years were pooled. Carolina Wrens typically molt between July and October (Haggerty and Morton 1995), and plumage is often worn before that period and fresh afterward. Therefore, I only compared 67 mated pairs measured during the same period (14 pairs from July to October, 8 from November to March, and 45 from April to June). Age is a possible confounding variable when comparing mated pairs, so paired t -tests were used to examine first and second measurements on 31 individuals subsequently captured and measured in different years. Because I found no significant relationships between age and any of the measurements (paired t -tests, $P > 0.05$), individuals of all ages were pooled.

Individuals were sexed by the presence or absence of a cloacal protuberance or brood patch and by behavior (only males sing and only females incubate; Haggerty and Morton 1995). Sex determination analysis was conducted only on individuals whose sex was known. Intrapair measurement comparisons were conducted only on individuals known to have paired during a breeding season. Observations at nests were used to identify mated pairs. Although some pairs and individuals were observed in multiple years, unique pairs were used only once in all analyses. Carolina Wrens are site tenacious (Haggerty and Morton 1995, pers. obs.), so individuals that disappeared were assumed to be dead. Lifespan

estimates were based on the number of breeding seasons an individual remained on the study area.

Two-tailed *t*-tests were used for comparisons of males and females, and paired *t*-tests for comparisons of mated pairs. Stepwise discriminant analysis was used to select the variables that best discriminated between the sexes, and these variables were then used in canonical discriminant analysis to derive a linear combination of variables that best summarized between-sex variation. Minimization of Wilks' λ was the criterion used for variable selection in the stepwise procedure, and the significance level of 0.15 was used for entering variables. Classificatory discriminant analysis was used to compute linear discriminant functions for classifying individuals to a particular sex. The classification criterion was based on within-group covariance matrices. A cross-validation procedure was used to assess the effectiveness of the discriminant functions. This procedure classifies each observation in the data set using a discriminant function computed from other observations in the data set, but excluding the observation being classified (SAS Institute 1999). Pearson's product-moment correlations were used to explore two sets of relationships: assortative mating by age and morphometrics, and associations among age and morphometrics. SAS version 8.1 (SAS Institute 1999) and JMP version 5.1.2 (JMP 2004) were used for all statistical tests and statistical significance was set at $P \leq 0.05$.

RESULTS

Sexual size dimorphism. Male Carolina Wrens were significantly larger than females in all body measurements, with some overlap (Table 1). Wing chord and mass differed most between the sexes, and bill and tail lengths least (Table 1).

Wing chord ($F_{1,210} = 353.0$, $P < 0.0001$), mass ($F_{1,207} = 59.6$, $P < 0.0001$), and bill length ($F_{1,207} = 3.2$, $P < 0.0001$) were identified by stepwise discriminatory analysis as having the best discriminatory power. When used in canonical discriminant analysis, these variables yielded a canonical variable that significantly discriminated between male (1.43 ± 0.18 95% CI) and female (-1.73 ± 0.17 95% CI) group means (Wilks' $\lambda = 0.27$, eigenvalue = 2.7, $F = 219.4$, $P < 0.0001$) and accounted for 73% of the variance between the sexes. Classificatory analysis also indicated that wing, mass, and bill measurements were good predictor variables for determining sex. Together, these three variables produced two linear classification functions that correctly classified 95% (127/133) of the individuals using cross-validation methods ($D_{\text{male}} = \text{wing} \times 27.28 + \text{mass} \times 11.75 + \text{bill} \times 2.24 - 1068.00$; $D_{\text{female}} = \text{wing} \times 25.60 + \text{mass} \times 10.16 + \text{bill} \times 21.33 - 929.15$).

SSD within pairs. For 42 mated pairs, 98% (41) of the males were larger than their mates. The difference in size between mated pairs was due to differences in all morphometrics (Table 2). The greatest difference between mated pairs was mass (Table 2). Males averaged 11% heavier, and only three females (5.3%) were heavier than their mates. All males had longer wing chords than their partners, averaging 6% longer. Males also had tails 6% longer than those of their mates, but 18% (8/44) of the females had longer tails than their partners (Table 2). Structures that differed least between pairs were bill and tarsus lengths. Although male bills averaged 5% longer than those of their mates, there was considerable overlap and 22% (14/64) of the females had longer bills than their partners. Mean tarsus length of females was 4% shorter than that of their mates, but 15% (10/65) had tarsi longer than those of their partners.

Table 1. Morphometrics of male and female Carolina Wrens from all years and seasons, 1988–2004.

Variable	Male				Female				<i>t</i>	<i>P</i>
	<i>N</i>	Mean \pm SD	Range	C.V.	<i>N</i>	Mean \pm SD	Range	C.V.		
Wing chord (mm)	141	59.1 \pm 1.5	55.0–63.0	2.6	131	55.3 \pm 1.3	52.0–58.4	2.4	21.3	< 0.0001
Tarsus (mm)	141	22.3 \pm 0.7	19.5–23.8	3.1	134	21.4 \pm 0.7	18.5–23.6	3.4	10.7	< 0.0001
Mass (g)	134	21.2 \pm 1.3	18.5–27.0	6.3	118	18.7 \pm 5.1	16.2–21.5	5.1	16.5	< 0.0001
Bill (mm)	142	12.3 \pm 0.6	11.0–14.0	5.0	132	11.7 \pm 0.6	10.1–13.6	5.4	8.3	< 0.0001
Tail (mm)	121	49.8 \pm 2.6	39.6–56.3	5.3	103	46.9 \pm 2.6	38.6–53.3	5.5	8.4	< 0.0001

Table 2. Degree of sexual dimorphism in morphometrics of mated pairs of Carolina Wrens.

Variable	<i>N</i>	Mean difference	SE	Paired <i>t</i>	<i>P</i>	Dimorphism index
Wing chord (mm)	64	3.8	0.22	17.1	0.0001	0.94
Tarsus (mm)	65	0.86	0.12	6.9	0.0001	0.96
Mass (g)	57	2.2	0.23	9.9	0.0001	0.89
Bill (mm)	64	0.67	0.11	6.0	0.0001	0.95
Tail (mm)	44	3.1	0.46	6.7	0.0001	0.94
Size ^a	42	-2.7	0.18	15.2	0.0001	—

^aBody size was estimated based on wing, tarsus, bill, tail, and mass measurements using principal component analysis. See the Methods section for additional details.

Assortative mating. I found no assortative mating by age ($r = -0.1$, $P = 0.24$, $N = 127$ pairs). Among pairs, 40% (51) consisted of individuals that were new to the study area and assumed to be 1-yr old, and the other 60% included at least one individual that had been paired previously. Wing chord length showed a significant assortative association between mated pairs ($r = 0.29$, $P = 0.05$, $N = 44$). Mass, bill length, tarsus length, tail length, and overall size showed no assortative relationships between partners ($P \geq 0.16$).

Morphometric relationships with lifespan. The lifespans of males (mean = 1.75 ± 1.19 [SD] yr; $N = 148$) and females (mean = 1.40 ± 0.87 yr; $N = 152$) did not differ ($t = -1.75$, $P = 0.08$). However, there were significant positive associations between lifespan and both tail length ($r = 0.22$, $P = 0.01$, $N = 118$) and body size ($r = 0.20$, $P = 0.04$, $N = 113$) for males, and between lifespan and both wing length ($r = 0.24$, $P = 0.006$, $N = 122$) and tarsus length ($r = 0.31$, $P = 0.001$, $N = 126$) for females.

DISCUSSION

My results clearly indicate male-biased size dimorphism in Carolina Wrens and concur with studies of two similar-sized tropical congeners, the Spot-breasted Wren (*T. maculipectus*; Winker et al. 1996) and the Rufous-and-white Wren (*T. rufalbus*; Mennill and Vehrencamp 2005). Like Carolina Wrens, males in these species are significantly larger than females and the degree of dimorphism is similar in all three species. Also, like the Spot-breasted Wren (Winker et al. 1996), size overlap between male and female Carolina Wrens was minimal, as indicated by the low multivariate misclassifi-

cation value (5%) using similar measurements (e.g., wing chord and mass). Similarities in SSD among these related species suggest a phylogenetic component to SSD in Carolina Wrens and similar selective regimes (Andersson 1994). My results also indicate that multivariate analyses using morphometrics should prove useful in determining the sex of Carolina Wrens.

Owens and Hartley (1998) indicated that species, like Carolina Wrens, that are socially and genetically monogamous, and show little sexual difference in parental care, are less sexually dimorphic than species with more intense sexual selection such as polygamous species or species where individuals engage in mixed reproductive strategies (e.g., see Magrath et al. 2003). The degree of SSD in Carolina Wrens is less than in polygamous species, and my results suggest possible causations and directions for future work. For example, male and female Carolina Wrens share territories year-round (Haggerty and Morton 1995), and size dimorphism may reduce intersexual competition for food (Selander 1966, Hedrick and Temeles 1989, Blondel et al. 2002), especially in winter when food may be limiting (Haggerty and Morton 1995). However, overlap between paired wrens in bill length and the lack of disassortative mating for bill length do not support the resource-partitioning hypothesis (Shine 1989, Temeles et al. 2000, Radford and du Plessis 2004). Resource partitioning may still occur, however, if larger males socially dominate females and force them into different foraging microhabitats (Peters and Grubb 1983). Although I have not observed males dominating females, and pairs often forage close together and on the same substrates (Haggerty and Morton 1995), specific foraging studies of mated pairs during the nonbreeding (e.g., Peters and Grubb 1983) and breeding

seasons (e.g., Przybylo 1995) are needed before the resource-partitioning hypothesis can be rejected.

Although I have no evidence that intersexual competition is responsible for SSD in Carolina Wrens, there is evidence for sexual selection. First, I found evidence of possible mate choice. For example, although the mass and wing chords of male and female Carolina Wrens overlap (Table 1), no females had longer wing chords than their mates. In addition, only one female was larger than her mate and few females (4%) were heavier. Also, males and females with longer wing chords tended to pair with each other more often than expected by chance, and there were assortative trends for tail length and overall body size as well.

Even in monogamous species, variation in mate quality is expected and sexual selection should occur (Andersson 1994). Mutual mate choice is theoretically adaptive and predicted to occur in both sexes of species with shared parental care (Johnstone et al. 1996, MacDougall and Montgomerie 2003). My lifespan data reveal variation in quality, and the positive correlation between lifespan and both tail length and body size in males, and between lifespan and wing length in females may help explain the assortative mating pattern observed. One explanation may be that longer wings, and possibly longer tails and larger body size, are signals of individual quality, and individuals of high quality tend to mate with other such individuals (Helfenstein et al. 2004). Interestingly, during courtship and agonistic encounters in Carolina Wrens, the tail is often fanned and wings drooped (Haggerty and Morton 1995), suggesting a possible use for signaling. Although assortative mating by tarsus length (Boag and Grant 1978, Delestrade 2001, Helfenstein et al. 2004), bill dimensions (Boag and Grant 1978, Coulter 1986, Stern and Jarvis 1991, Wagner 1999, Forero et al. 2001), and mass (Chardine and Morris 1989, Wagner 1999, Forero et al. 2001) have been noted in other species; this is, to my knowledge, the first report of significant assortative mating based on wing chord length.

Pairs in some species also assort by age (Marzluff and Balda 1988, González-Solís 2004), but this was not the case in my study. Carolina Wrens pair during their first year and 1-yr-old individuals often pair (40%), but many males and females (60%) that lost mates formed

pair bonds with individuals of varying ages, including 1-yr olds. This suggests that age and experience may not be important criteria for mate selection in Carolina Wrens (Reid 1988) and that the costs of waiting or searching (e.g., remain unpaired, delayed breeding, and loss of territorial resources) for an individual of a certain age may be outweighed by the benefits of mating quickly with individuals of any age or experience. This may be especially true for Carolina Wrens because they are relatively short-lived and sedentary, and may have limited breeding opportunities and mate choices.

Sexual selection is theoretically more intense in males than in females (Trivers 1972), and evidence for this in Carolina Wrens is provided by sexual dimorphism in the song system and defense behaviors (Haggerty and Morton 1995, Nealen and Perkel 2000, Hyman 2002, 2005). Because larger size is an important trait of dominant birds, and male wrens vigorously defend their territories, sexual selection for larger size in male wrens seems plausible (Searcy 1979, Andersson 1994, Webster 1997). The positive relationship between male size and longevity in my study does suggest that size may help males maintain territories for longer periods. All males in my study had territories and were paired and, therefore, a comparison of the size of mated and unmated males was not possible. This fact, in combination with the lack of extrapair mating in my study population (Haggerty et al. 2001), suggests little variance in mating success among males and that mate selection may be based on immediate reproductive or survival benefits (e.g., territorial resources) rather than benefiting indirectly through improving the genetic quality of their offspring (Dunn et al. 2001).

In summary, there is male-biased size dimorphism in Carolina Wrens. If larger male size advertises quality and influences mate choice, then intersexual selection may help maintain SSD. In addition, because competition among males for territories occurs year-round and male size was positively related with longevity (i.e., time on territory), intrasexual selection might also contribute to SSD in Carolina Wrens.

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