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SHORT COMMUNICATIONS

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PASSERINES ARE SEXUALLY DIMORPHIC IN SHAPE AS WELL AS SIZE

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Abstract. Passerine birds are commonly the subjects of studies of sexual size dimorphism. Yet, save for secondary sexual characters, passerine sexual dimorphism is commonly treated as a mere size difference without regard to its shape distribution. Using principal components analysis (PCA) to generate estimates of relative size and reduced major axis (RMA) regression to test for isometry, I analyzed 19 skeletal measurements from 31 socially monogamous passerines of 15 genera. Dimorphism does not scale isometrically within the skeleton. Most sexual size dimorphism resides in the pectoral girdle and wing in the Savannah Sparrow (*Passerculus sandwichensis*), in the wood-warbler genus *Dendroica*, in the wood-warbler family (Parulidae), and in a selection of six passerine families. These results suggest that comparisons that include both sexes but that rely on a single measurement in order to “correct for body size” (commonly the tarsus) are unlikely to be reliable.

Key words: isometry, mass, passerine birds, sexual selection, sexual size dimorphism, skeleton, tarsus.

Las Aves Paserinas son Sexualmente Dimórficas en Forma así como en Tamaño

Resumen. Las aves paserinas son sujetos comunes en estudios acerca del dimorfismo sexual en el tamaño. Sin embargo, con excepción de los caracteres sexuales secundarios, el dimorfismo sexual de las aves paserinas comúnmente se considera sólo como una mera diferencia en tamaño, sin tener en cuenta la forma. Usando análisis de componentes principales para generar estimados del tamaño relativo, y análisis de regresión de eje principal reducido para evaluar la isometría, analicé 19 medidas del esqueleto para 31 especies de aves paserinas socialmente monógamas pertenecientes a 15 géneros. El dimorfismo no varía siguiendo una escala isométrica dentro del esqueleto. La mayor parte del dimorfismo sexual en tamaño reside en la cintura pectoral y en las alas en *Passerculus sandwichensis*, en el género

Dendroica, en la familia Parulidae y en una selección de seis familias de aves paserinas. Estos resultados sugieren que es poco probable que las comparaciones que incluyen a ambos sexos pero que se basan en una sola medida para “corregir por el tamaño corporal” (comúnmente el tarso) sean confiables.

In studies of sexual size dimorphism, common study organisms include passerine birds, an order in which dimorphism is widespread but usually modest. Among 92 species for which masses by sex are given by Dunning (1984; minimum five individuals per sex), males exceed females on average by 9.9%. After excluding blackbirds, which are commonly polygynous, that figure drops to 6.0% ($n = 79$), a reasonable estimate for socially monogamous passerines. The prevailing view is that sexual selection related to mating behavior generates sexual size dimorphism in birds (Dunn et al. 2001, Székely et al. 2004), although competing theories include fecundity selection (Andersson 1994) and ecological niche selection (Gonzalez-Solis 2004) as causes.

Some sexual size dimorphism is clearly manifested in secondary sexual features such as wattles, elongated tails, fighting spurs, and vocal apparatus. Otherwise, however, sexual size dimorphism is commonly conceptualized as a general difference in mass or size, with little attention granted to how this dimorphism is distributed within the body. The common assumption is one of isometric scaling. The legitimacy of this assumption has been questioned (Brown 1996, Tubaro and Bertelli 2003), but it continues in the current setting where the general somatic distribution of passerine sexual size dimorphism remains unrecognized.

Here, using passerine skeletal features, I show that sexual size dimorphism is not distributed equally among body regions; size differences between males and females reside disproportionately in the midbody (chest and wings). Accordingly, selection does not appear to be acting to merely generate a size differential between the sexes. Instead, different selection pressures experienced by males and females appear also to be generating differences in shapes. In addition, I show that reliance upon an assumption of isometric sexual size dimorphism distribution in studies of body condition, ecomorphology, and sexual size dimorphism is likely to lead to false or distorted conclusions.

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METHODS

I included 31 socially monogamous passerine species (six families) from central Ontario breeding communities (Appendix) in my study. Several analyses relied upon a data subset of 12 *Dendroica* wood-warbler (Parulidae) species. For each sex of each species, I used five randomly selected skeletons from the Royal Ontario Museum (ROM) collection. Most specimens were adults from eastern Canada or the northeastern United States. A small number of samples (10.3%) included autumn hatching-year individuals, but a comparison of age groups using the Black-throated Blue Warbler (*Dendroica caerulescens*) and Red-eyed Vireo (*Vireo olivaceus*), species for which I had samples of five adult and five fall immature individuals each, demonstrated that the effect of age on size was small (<0.8%).

I selected 19 linear skeletal traits (Robins and Schnell 1971). Five were beak and skull measures (anterior: skull length, skull width, culmen length, mandible length, and mandible width), eight were chest and wing measures (midbody: coracoid length, scapula length, sternum length, sternum depth, keel length, humerus length, ulna length, and carpometacarpus length), and six were pelvic girdle and leg measures (posterior: synsacrum length, synsacrum width, femur length, tibiotarsus length, tarsometatarsus [i.e., tarsus] length, and hallux length; data file at <http://web2.uwindsor.ca/biology/pitcher/Pitcher%20lab/7F6A7F00-9F67-49C1-8E60-69680BF77D0B.html>). I calculated sexual size dimorphism for each trait ($\log[\text{male measurement}/\text{female measurement}]$; Greenwood [2003]), and made comparisons within *Dendroica* (weighting each of 12 species equally), within wood-warblers (weighting each of eight genera equally), and within passerines (weighting each of six families equally).

To obtain a measure of overall size for each sex of each species, I subjected the bone matrix to principal components analysis (PCA; [Lipkovich and Smith 2001]). To avoid phylogenetic effects, I confined this analysis to one genus only (*Dendroica*; 24 body forms: two sexes of 12 species). Because apparent differences in sexual size dimorphism among the three body regions warranted further testing, I first removed from the matrix two

traits for testing the relationship between particular metrics and overall body size: tarsometatarsus (hereafter tarsus) length (a leg metric commonly used in the field as a measure of body size) and carpometacarpus length (distal wing bone) as a comparative, alternative (but not field-friendly) metric from the midbody. I used Reduced Major Axis (RMA) regression analysis (Bohonak 2002) to test for isometry and strength of relationship. Interpreting the first component (PC1) values from the PCA as a reflection of absolute size (Rising and Somers 1989), I tested those PC1 values against standardized tarsus and carpometacarpus values. Having demonstrated that sexual size dimorphism is not isometric in *Dendroica*, I then made additional comparisons using tarsus (the commonly used field metric) and keel length (the trait exhibiting the greatest sexual size dimorphism).

RESULTS

In all taxa (12 species in *Dendroica*, eight genera in Parulidae, six passerine families), males were larger than females. Sexual size dimorphism appeared to not be isometric, however, as sexual size dimorphism is relatively large in midbody traits when compared to anterior and posterior traits (Fig. 1).

Using the 12-species *Dendroica* dataset, more than 99% of variation among the 24 body forms was captured by PC1. In all cases, values were positive, indicating that PC1 captured differences in absolute size and that almost all of the difference among the 24 body forms was in size rather than shape. In all cases, male PC1 values exceeded those of conspecific females, indicating that males were without exception structurally larger than females.

Analyses of RMA regression indicated that body shape was not isometric. When standardized PC1 values, used as a measure of size, were regressed against standardized tarsus values, the calculated slopes were not different from unity (males: $b = 1.06$, bootstrap CI: 0.53–1.59; $r^2 = 0.49$, bootstrap CI: 0.10–0.80; females: $b = 1.28$, bootstrap CI: 0.56–2.01; $r^2 = 0.35$,

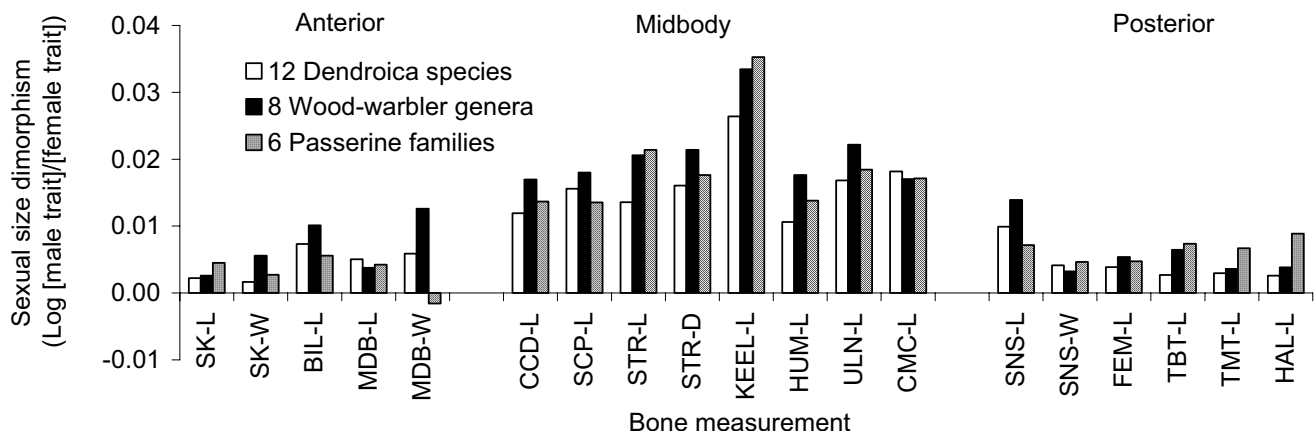


FIGURE 1. The degrees to which males exceed females in size for different bone measurements ($n = 19$), arranged by body region (anterior [head]: $n = 5$, midbody [chest and wing]: $n = 8$, posterior [pelvis and leg]: $n = 6$) for 12 species of *Dendroica* Wood-warblers, eight genera of Wood-warblers (Parulidae) weighted equally, and six passerine families weighted equally (Vireonidae, Paridae, Regulidae, Turdidae, Parulidae, and Emberizidae). Skeletal abbreviations: L = length, W = width, D = depth, SK = skull, BIL = bill, MDB = mandible, CCD = coracoid, SCP = scapula, STR = sternum, HUM = humerus, ULN = ulna, CMC = carpometacarpus, SNS = synsacrum, FEM = femur, TBT = tibiotarsus, TMT = tarsometatarsus (i.e., tarsus), HAL = hallux.

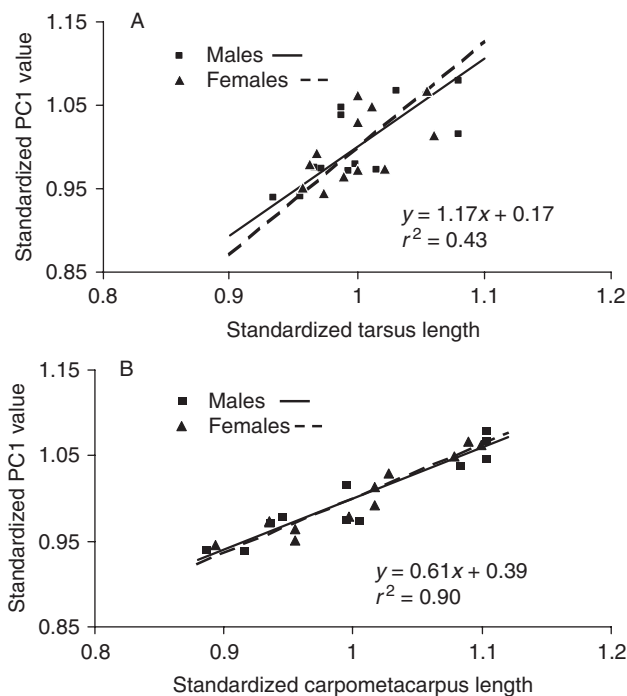


FIGURE 2. Reduced major axis regression of the standardized first principal component (PC1) values of a principal components analysis (PCA) of 17 bone measurements of both sexes of 12 *Dendroica* species as a measure of overall size, versus the standardized (A) tarsus and (B) carpometacarpus lengths, which were not part of the PCA. In both (A) and (B), the two regression lines do not differ from one another. However, the carpometacarpus analysis slope is different from unity, whereas the tarsus analysis slope is not. Because the male and female regression lines in each case do not differ from one another, one equation with its corresponding r^2 value is given in each case, using both male and female data.

bootstrap CI: 0.05–0.77; Fig. 2A). When standardized PC1 values were regressed against standardized carpometacarpus values, however, the calculated slopes were different from unity (males: $b = 0.60$, bootstrap CI: 0.46–0.74; $r^2 = 0.89$, bootstrap CI: 0.80–0.98; females: $b = 0.64$, bootstrap CI: 0.50–0.79; $r^2 = 0.90$, bootstrap CI: 0.78–0.97; Fig. 2B). While these results do not indicate that the two sexes exhibit different patterns of relative size, they do indicate different relationships between particular metrics (such as carpometacarpus and tarsus lengths) and overall body size. Accordingly, although both tarsus and carpometacarpus can predict overall body size in either sex, the carpometacarpus does so more effectively (based on high r^2 values) and indicates allometry, while the tarsus is less effective and indicates isometry.

The apparent differences in shape between sexes were not demonstrated using RMA regression. This is likely because the overwhelming difference between males and females is size, as demonstrated by PCA, with the consequence that the apparent modest differences in shape between males and females were not detectable. However, given the regression evidence for allometry among body parts and the apparent differences using Greenwood's measure of sexual size dimorphism, what other

confirmation is there of the apparent male and female differences in shape? A common means of estimating overall size or of correcting for size is to divide by tarsus length, yet applying this practice to these data demonstrates not only the difference in relative shape between the sexes but also the futility of relying on one measure to achieve these purposes. Among 12 *Dendroica* species, the keel:tarsus ratio for males ($\bar{X} = 0.79$) differs from that for females ($\bar{X} = 0.74$; Wilcoxon signed-rank test $T = 0$, $P < 0.001$). Male and female ratios similarly differ for eight genera within Parulidae (male $\bar{X} = 0.74$; female $\bar{X} = 0.69$; Wilcoxon signed-rank test $T = 0$, $P = 0.008$) and for six passerine families (male $\bar{X} = 0.81$; female $\bar{X} = 0.76$; Wilcoxon signed-rank test $T = 0$, $P = 0.03$).

Rising (2001) provided mean male and female tarsus and keel measurements for 45 Savannah Sparrow (*Emberizidae*: *Passerculus sandwichensis*) populations. The tarsus measurements ranged from 193 to 223 mm for females and from 198 to 228 mm for males. For each tarsus length represented in both male and female datasets (14 measurements ranging from 198 to 223 mm), I compared mean male and female keel lengths, finding the male keel ($\bar{X} = 198.5$ mm) to be significantly larger than the female keel ($\bar{X} = 185.9$ mm) for given tarsus lengths ($t_{26} = 5.1$, $P < 0.001$). Only four keel lengths were represented in both male and female datasets, indicating much less intersexual overlap in that metric.

DISCUSSION

Studies considering sexual size dimorphism or other sexual differences in birds connected to size generally refer to the larger size of males without consideration of the shape distribution of that dimorphism (Selander 1972, Kissner et al. 2003, Serrano-Meneses and Szekely 2006), with the explicit or implicit assumption being that general size is the trait under selection. Here, when separate regions of passerine skeletal anatomy are considered, intersexual structural differences are significantly larger in the midbody than in the anterior or posterior. Selection that operates differentially on males and females generates changes not merely in overall size, but differentially among body regions. The widespread prevalence of this pattern is evidence of its biological significance, but it is also of practical significance whenever studies comparing size features of individuals of both sexes are undertaken.

There are a number of alternative selection pressures that might result in a larger wing-chest complex in males. Among them are selection in males for stronger flight, larger size with minimal aerodynamic costs, and greater vocalization facilitation, or in females for incubation facilitation.

From a practitioner's point of view, differences in male and female shape should be borne in mind when comparisons among individuals include both sexes, such as is common in studies of body condition. This is so whether the measurement is used to document size differences between the sexes or where it is used to "correct" for size differences. Unfortunately, in the usual case where subject animals are not destroyed, the number of possible alternative size measurements is necessarily reduced.

Based on an analysis of three passerine species (the Red-winged Blackbird *Agelaius phoeniceus*, Red Crossbill *Loxia curvirostra*, and Harris's Sparrow *Zonotrichia querula*), Freeman and Jackson (1990) argued that univariate metrics are inadequate for estimating avian body size, but suggested that tarsus length or mass are the preferable choices if a single metric is to be relied upon. Most commonly, researchers do rely on tarsus length and body mass, sometimes using tarsus as the sole index of size

(Badyaev et al. 2003), but more often by using it as a scaling factor, either by dividing mass by it (Moreno 1989) or by analyzing residuals from a linear regression of body mass against tarsus (Ringsby et al. 1998). However, among measures frequently employed in assessing bird size, Rising and Somers (1989) concluded that mass is inherently unreliable, as it varies with time of day, season, reproductive state, and condition. My data support Freeman and Jackson (1990) in that single metrics are inadequate, but do not support their preference for tarsus among single metric choices. Wing chord length is preferred by banding stations but is not particularly dependable because age and wear in feathers reduce confidence in delineating size differences (Francis and Wood 1989).

Warnings have been presented elsewhere against reliance either on ratios between different body part lengths (Ranta et al. 1994) or on residuals of mass-length regressions (Green 2001) in the analysis of dimorphism. An even more fundamental problem is illustrated by the empirical results reported here. No single measurement can correct for body size differences between the sexes because it cannot account for shape differences. Further, even if the shape differences were to be disregarded as insignificant, tarsus length is relatively poor at capturing absolute size, at least in the average passerine; the mean amount by which male tarsi exceed female tarsi in the 31-species sample here is less than 1%. Accordingly, if reliance is made upon tarsus length, male-female size differences are likely to be underestimated. Conversely, if reliance instead were to be placed upon keel length, the error would be in the opposite direction, leading to an overstatement of overall size dimorphism.

It is important to recognize that the extent to which conspecific males and females are not the same shape necessarily impairs size comparisons between them. In order to minimize the impairment, and assuming study animals cannot be destroyed, dependable results are more likely when reliance is upon linear measurements of several body parts, especially if they scale volumetrically (Piersma 1984), and particularly if they can be analyzed in a multivariate fashion using PCA (Brotons and Broggi 2003).

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APPENDIX. Thirty-one species of socially monogamous passerines from six families used to generate a dataset of 19 linear skeletal traits for analysis of male and female shape differences, based on specimens from the Royal Ontario Museum, Toronto.

Family	Species
Vireonidae	Red-eyed Vireo (<i>Vireo olivaceus</i>)
	Philadelphia Vireo (<i>V. philadelphicus</i>)
	Blue-headed Vireo (<i>V. solitarius</i>)
Turdidae	American Robin (<i>Turdus migratorius</i>)
	Wood Thrush (<i>Hylocichla mustelina</i>)
	Swainson's Thrush (<i>Catharus ustulatus</i>)
Paridae	Black-capped Chickadee (<i>Poecile atricapilla</i>)
Regulidae	Ruby-crowned Kinglet (<i>Regulus calendula</i>)
	Golden-crowned Kinglet (<i>R. satrapa</i>)
Parulidae	Nashville Warbler (<i>Vermivora ruficapilla</i>)
	Golden-winged Warbler (<i>V. chrysoptera</i>)
	Northern Parula (<i>Parula americana</i>)
	Yellow Warbler (<i>Dendroica petechia</i>)
	Chestnut-sided Warbler (<i>D. pensylvanica</i>)
	Cape May Warbler (<i>D. tigrina</i>)
	Magnolia Warbler (<i>D. magnolia</i>)
	Black-throated Blue Warbler (<i>D. caerulescens</i>)
	Black-throated Green Warbler (<i>D. virens</i>)
	Blackburnian Warbler (<i>D. fusca</i>)
	Yellow-rumped Warbler (<i>D. coronata</i>)
	Pine Warbler (<i>D. pinus</i>)
	Palm Warbler (<i>D. palmarum</i>)
	Bay-breasted Warbler (<i>D. castanea</i>)
	Blackpoll Warbler (<i>D. striata</i>)
	American Redstart (<i>Setophaga ruticilla</i>)
Emberizidae	Black-and-white Warbler (<i>Mniotilta varia</i>)
	Mourning Warbler (<i>Oporornis philadelphia</i>)
	Common Yellowthroat (<i>Geothlypis trichas</i>)
	Canada Warbler (<i>Wilsonia canadensis</i>)
	Wilson's Warbler (<i>W. pusilla</i>)
Emberizidae	Dark-eyed Junco (<i>Junco hyemalis</i>)