

Song Frequency Does Not Reflect Differences in Body Size among Males in Two Oscine Species

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Abstract

Large animals, having large vocal organs, produce low sound frequencies more efficiently. Accordingly, the frequency of vocalizations is often negatively related to body size across species, and also among individuals of many species, including several non-oscine birds (non-songbirds). Little is known about whether song frequency reveals information about body size within oscine species, which are characterized by song learning and large repertoires. We asked whether song frequency is related to body size in two oscines that differ in repertoire size: the dark-eyed junco (*Junco hyemalis*) and the serin (*Serinus serinus*). We also asked whether the extent to which receivers sample repertoires might influence the reliability of their assessment of body size. We found that none of the frequency traits of song that we investigated was related to male body size, nor did more extensive sampling of repertoires lead to any relationship between frequency and body size. Possible reasons for these results are the small range of variation in size within species, or the elaborate vocal physiology of oscines that gives them great control over a wide frequency range. We discuss these results as they relate to female preferences for high-frequency song that have been previously reported for oscine species.

Introduction

Differences in body size among conspecific animals are often important determinants of competitive ability or genetic quality (Andersson 1994). Therefore, both in competitive interactions and also in the context of mate choice, it should be valuable to evaluate the body size of conspecifics. In many species, the frequency of vocalizations reveals information on body size or mass (e.g. insects: Brown et al. 1996; fish: Ladich 1998; Amorim & Hawkins 2005; de Jong et al. 2007; anurans: reviewed in Searcy & Nowicki 2005; reptiles: Hibbitts et al. 2007; mammals: Pfefferle & Fischer 2006; but see also review in Searcy & Nowicki 2005; non-oscine birds: Guillotin

& Jouventin 1980; Appleby & Redpath 1997; Barbaud et al. 2000; Miyasaki & Waas 2003; Madsen et al. 2004; Hardouin et al. 2007; Mager et al. 2007), despite the fact that individuals may, to some extent, vary the frequency of their vocalizations. The likely explanation is that, all else being equal, larger vocal organs and vocal tracts produce and radiate lower-frequency sounds more efficiently than smaller ones (Bradbury & Vehrencamp 1998). This has consequences for the behavioural ecology and evolution of acoustic signals. For example, females often prefer lower-frequency vocalizations (e.g. insects: Brown et al. 1996; anurans: Howard & Young 1998; mammals: Collins 2000; non-oscine birds: Beani & Dessì-Fulgheri 1995; Miyasaki & Waas 2003; Madsen

et al. 2007), which has been interpreted as a way of choosing bigger males that are either more competitive or of higher quality (Davies & Halliday 1978; Ladich 1998; Seddon et al. 2004).

Regarding oscine song, the negative relationship between frequency and body size usually stands among species (e.g. Bergmann 1976; Bowman 1979; Wallschläger 1980; Ryan & Brenowitz 1985; Badyaev & Leaf 1997; but see also Cardoso & Mota 2007), but it is unclear if such a relationship exists within species, because differences in size among conspecifics are generally small, and so are the predicted differences in frequency. Studies within species are few and with mixed results. Schubert (1976) found that larger bullfinches (*Pyrrhula pyrrhula*) sing lower-frequency songs. However, the bullfinches studied were from different subspecies that differed considerably in size. Shy (1983) and Hanford & Loughheed (1991) recorded summer tanagers (*Piranga rubra*) and rufous-collared sparrows (*Zonotrichia capensis*) in populations across the species ranges, and found that song frequency does not match population differences in body size. Galeotti et al. (1997) found that the peak frequency of a particular component of barn swallow (*Hirundo rustica*) song, the rattle, does correlate negatively with body mass. Logue et al. (2007) reported that, in black-bellied wrens (*Thryothorus fasciatoventris*), body size does not appear to be related to song frequency after controlling for differences in size between males and females. Finally, Irwin et al. (2008) found that, despite their smaller body size, northern populations of the greenish warbler (*Phylloscopus trochiloides*) sing lower minimum frequencies, presumably because those populations experience stronger sexual selection. Thus, there is little evidence on whether bird receivers can use song to obtain information on the size of conspecifics within their population.

Female oscine preferences for song frequency seem to differ from what is commonly found in other taxa. In three out of four oscine species tested so far, females respond more strongly to high- rather than low-frequency songs (blackbird, *Turdus merula*: Dabelsteen & Pedersen 1993; white-throated sparrow, *Zonotrichia albicollis*: S.B. Meek, L. Ratcliffe & R. Weisman, unpubl. data, in Ratcliffe & Otter 1996; serin, *Serinus serinus*: Cardoso et al. 2007; see also Pasteau et al. 2007 for the opposite result with the domestic canary, *Serinus canaria*). Also, male chestnut-sided warblers (*Dendroica pensylvanica*) that sing high-frequency songs gain more extra-pair paternity, suggesting that females prefer these males (Byers 2007). These female oscine preferences are at odds

with the usual pattern of low frequency indicating male quality. To understand these preferences, we need to know more about how the frequency of oscine songs relates to differences in conspecific body size within populations.

More than in other taxa, oscines have a remarkable control of the frequencies in their vocalizations. For example, in several species, the left side of the syrinx specializes in producing low frequency sounds while the right side produces high frequencies (Suthers 1997; Suthers et al. 2004). Also, the pure-tone quality typical of many songbirds is due to active filtering of harmonics by the vocal cavity, which greatly alters the distribution of sound energy across the frequency range during the course of singing (Nowicki 1987; Ride et al. 2006). These and other aspects of oscine vocal physiology allow birds to learn and sing a great variety of syllables, which often differ in frequency, and this may obscure a possible relationship with body size. Therefore, to test for a relationship between song frequency and body size in oscines, the potentially confounding effect of diversity within repertoires should be taken into account.

Here, we test for a relationship between song frequency and body size in two oscine species – the dark-eyed junco and the serin – taking advantage of differences in their repertoire size and song organization. Most songs of dark-eyed juncos consist of a single repeated syllable and males have repertoires of about two to seven song types (Williams & MacRoberts 1977; Newman et al. 2008). Males usually sing the same song type for long periods before changing to another, so that a receiver needs time to sample the complete repertoire (listening to approx. 350 songs, Newman et al. 2008, or approx. 2 h of singing, Williams & MacRoberts 1977). The serin, in contrast, has no song types, but has a repertoire of approx. 50 different syllable types that are for the most part sung without immediate repetition, and a song of average duration (3 s) typically contains about half the syllable repertoire (Mota & Cardoso 2001). Thus, a passing serin receiver samples more than 20 different syllables listening to a single average length song, which is a much more extensive sampling of syllable types than is possible for a junco receiver. Therefore, if repertoire sampling makes the assessment of body size more reliable, we would predict serin song to be a particularly good indicator of size. We ask whether frequency characteristics of song in these species reveal the body size of the singer, and whether repertoire sampling improves the reliability of this information: i.e. how reliable is the information that a passing junco receiver obtains

by listening only to a single syllable type from each male, compared to a junco receiver that listens to a few syllable types from each male, compared to a serin receiver that listens to many.

Methods

We recorded male dark-eyed juncos (subspecies *Junco h. thurberii*) in two populations in San Diego County, California, USA, from Feb. to July 2006 using an Audio-Technica AT835b directional Microphone (Audio-Technica, Tokyo, Japan) and an M-Audio Microtrack 24/96 solid-state recorder (M-Audio, a subsidiary of Avid Technology, Irwindale, CA, USA). We recorded male serins in a population near Coimbra, Portugal, during the breeding seasons of 2002 through 2007 using a Sennheiser MKH70 directional microphone (Sennheiser, Wedermark-Wennenbostel, Germany) and either tape or solid-state recorders (Marantz CP430 tape recorder, Marantz PMD670 and PMD660 solid-state recorders; Marantz, Kanagawa, Japan). All males were adults and singing full song. Details of the study sites are given in Yeh & Price (2004) and Newman et al. (2008) for juncos and Mota & Cardoso (2001) for serins. Males were captured with mist nets, colour banded, and measured in the same breeding season as the recordings. In the rare cases when the same male was measured more than once, we averaged the measurements taken on multiple captures. For the junco, we measured tarsus length, skull breadth, length of skull plus beak, wing chord length and tail length. For the serin, we measured tarsus length, beak height, wing chord length and tail length. As a measure of size for each species, we used the score of the principal component (PC) that best represents body size, from an unrotated PC analysis (PCA) on the correlation matrix of the untransformed morphological measurements. We used the PC instead of any single metric measurement, because it has the advantages of being a more comprehensive measure of size, and being less susceptible to possible inaccuracies in measuring single traits. We also weighted males of both species to the nearest decigram. Sample sizes were 83 male juncos (measurement of tarsus length missing for one) and 41 male serins (measurement of mass missing for one).

Song measurements were made with the software Avisoft SASLAB (Avisoft Bioacoustics, Berlin, Germany) on sound files with a sampling frequency of 22 050 or 24 000 Hz (Fast Fourier Transform size 512, which corresponds to a resolution of 43 or 47 Hz respectively). Peak frequency (i.e. the frequency with the highest sound amplitude) was

taken from amplitude spectra with a lower cut-off filter at 2 kHz to eliminate low-frequency background noise, which was sometimes louder than the song's peak frequency. Minimum and maximum frequencies were measured reading cursor values over the spectrograms at the lowest and highest frequencies visible (no cut-off filters used). We used this method because softer song components at the border of the frequency envelope can be recognized visually, even in the presence of background noise, although they would not be included using an automated method of measurement. These measurements are exemplified in Fig. 1. Weak harmonics were sometimes present that surpass the maximum frequency of regular syllables with no harmonics, especially in serin song (e.g. at approx. 2 s in Fig. 1), and those were not considered for measuring maximum frequency. Recording conditions (e.g. distance, vegetation) may alter the relative amplitude of sound across frequencies (e.g. higher frequencies attenuate more and are more scattered by vegetation), but this variation is random regarding a relationship with body size or mass. Most junco song types consist of the repetition of a single syllable type (e.g. Fig. 1), but a few contain two or more syllable types repeated one at a time (Newman et al. 2008). Here we focus on the individual syllable types, and in recordings that have more than one, we treat each separately. For the juncos, we chose up to five songs ($\bar{x} = 4.45$) per recording per syllable type, and separately measured each syllable in the songs except for the few first and last 10% syllables, which were sometimes sung more softly and hence could be difficult to measure. We averaged measurements across all syllables of the same type and then, in the case of syllable types recorded more than once from the same male, across the recordings of the same syllable type and male. For the serin, we chose a good-quality recording from each male, and a song longer than 3 s was measured (average duration of measured songs is $4.33 \text{ s} \pm 1.29 \text{ SD}$, $n = 41$). Each measurement was made over the entire song (Fig. 1), mimicking the situation in which a receiver integrates across its several different syllables. Note that for minimum frequency this equates to taking the lowest value of all syllables, which is convenient because the lowest frequency a bird can sing might be the trait that is more dependent on the body size.

For the junco, we first tested for a relationship between the frequency traits and body size or mass, in a situation intended to correspond to a receiver that listens to only one syllable type from each male. We randomly chose one syllable type from each

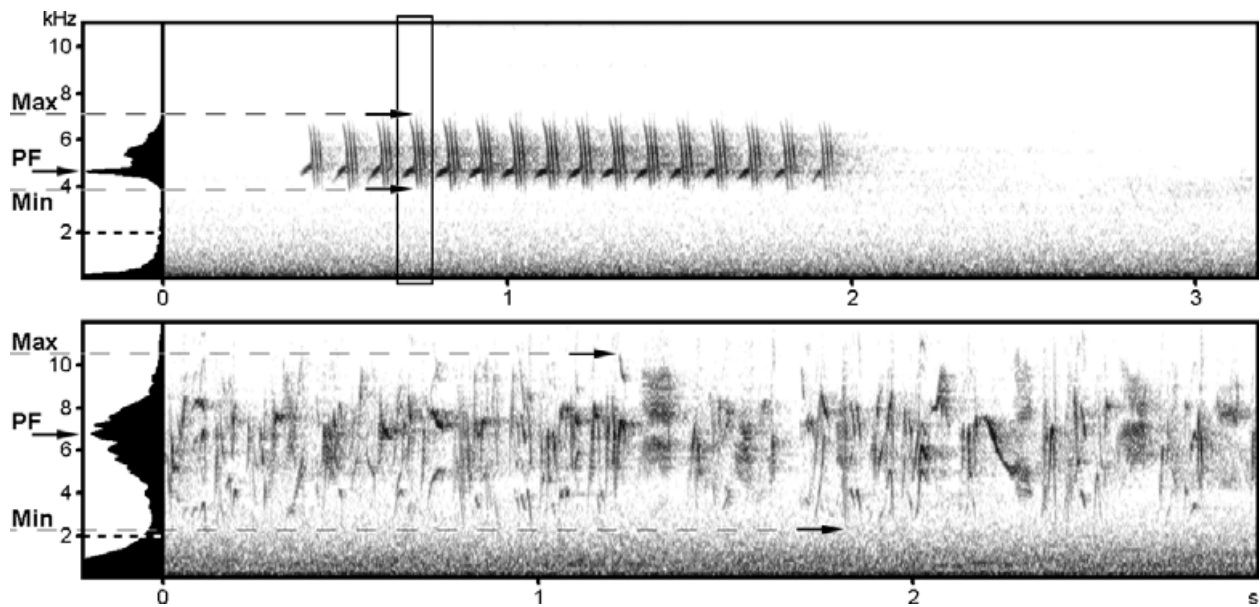


Fig. 1: Spectrograms of a junco song (top panel) and part of a serin song (bottom panel), exemplifying the frequency measurements. Arrows indicate maximum frequency (Max) and minimum frequency (Min), which are measured on the spectrograms, and peak frequency (PF), which is measured on the mean spectra (left panels). In juncos, measurements were made on a syllable-by-syllable basis, and the figure illustrates measures on the fourth syllable. In serins, measurements were made across the entire song, which is longer than shown here. Bold hatched lines in the mean spectra indicate the location of the high-pass filter used for measuring the peak frequency.

male and calculated the Pearson correlations between frequency traits and body size or mass. To provide a reliable estimate of this correlation, we repeated the random choice of one syllable type for all males 1000 times and each time calculated the correlation coefficient. We reported the average correlation coefficient, and its 95% confidence interval. We then conducted tests that correspond to a situation where the receiver listens to two syllable types from each male (and then three, four and five) and averages across those or, alternatively, takes the lowest frequency value (because body size should constrain the lowest frequencies the most). The procedure was as above, except that we randomly chose two syllable types (or three, four or five) from each male, and either averaged across those syllable types or took the lowest value before computing the correlation coefficients. Sample sizes decrease as we increase the number of different syllable types, because the number of males for which we recorded enough different types is progressively smaller. We stopped the analyses at five syllable types because the sample size became small (the number of recorded males with six different syllable types was only nine). For the serin, we ran simple Pearson correlations between the frequency traits and body size or mass, because each frequency measurement

already encompasses a large number of different syllables.

In our sample of junco recordings, there are 59 syllable types that are shared by two or more males, totalling 72 males. On this subset of data, we tested for a relationship between the frequency traits and body size or mass using univariate ANOVAs, where a frequency trait is the dependent variable, body size or mass is the independent variable, and syllable type is controlled for as a random factor. This tests if receivers can obtain information on body size by comparing the same syllable type as sung by different males. We did not perform a similar analysis for the serin, because its different syllables are always sung in very compact sequences within songs and therefore must be evaluated together by receivers. A two-tailed 0.05 criterion of significance was used throughout.

Results

Descriptive statistics for the morphological and frequency measurements are given in Table 1. The coefficients of variation of the morphological measurements were similar in juncos and serins, and similar to what is commonly found for these species (Cramp & Perrins 1994; Nolan et al. 2002). From the

Table 1: Descriptive statistics of morphological measurements, and of frequency traits for male dark-eyed juncos and serins

	Dark-eyed juncos			Serins		
	n	$\bar{x} \pm SD$	Coefficient of variation (%)	n	$\bar{x} \pm SD$	Coefficient of variation (%)
Morphological measurements						
Tarsus length (mm)	82	19.95 \pm 0.75	3.77	41	15.86 \pm 0.60	3.79
Skull breadth (mm)	83	16.14 \pm 0.49	3.01			
Length of skull plus beak (mm)	83	29.42 \pm 5.87	1.99			
Beak height (mm)				41	5.79 \pm 0.08	5.87
Wing chord length (mm)	83	76.74 \pm 2.36	3.07	41	71.24 \pm 1.93	2.71
Tail length (mm)	83	68.16 \pm 2.20	3.22	41	48.37 \pm 2.05	4.23
Mass (grams)	83	17.31 \pm 0.84	4.86	40	11.02 \pm 0.65	5.90
Song frequency traits (kHz)						
Peak frequency	83 ^a	4.97 \pm 0.28	5.63	41	6.59 \pm 0.61	9.24
Minimum frequency	83 ^a	3.50 \pm 0.42	11.85	41	2.26 \pm 0.30	13.45
Maximum frequency	83 ^a	6.49 \pm 0.50	7.67	41	10.68 \pm 0.56	5.25

^aData points are averages of the different song types of each male dark-eyed junco.

values in Table 1, the peak frequency was approximately midway between the minimum and maximum frequencies for both species (on average at 0.49 of the frequency range for the junco, and 0.52 for the serin). Using the values in Table 1 and Wallschlager's (1980) equation relating peak frequency of song to body mass among oscine species [frequency (kHz) = 7.204 * mass (g)^{-0.24}], junco and serin peak frequencies were higher than predicted for their mass by 1.34 and 2.54 kHz respectively.

The PCA for morphological measurements revealed two PCs with eigenvalues >1 for the junco, and one PC for the serin (trait loadings and eigenvalues in Table 2). The first PC for the juncos was characterized by high loadings (>0.8) of the three skeletal measurements, and we used it as a measure of body size. The second PC reflected variation in

wing and tail length. Results relating song frequency to this second PC (not shown) were identical to the ones obtained with body size. The first PC for the serin was the only one with eigenvalue >1 and was characterized by high loadings (>0.5) of all measurements. We used it as the measure of body size for the serins.

In dark-eyed juncos, none of the song frequency traits was significantly related to size or mass (Table 3). Correlation coefficients were close to zero, and no trend towards a negative relationship with frequency emerged with increased sampling of the repertoire (Table 3). As we recorded male juncos in two populations, we also ran this analysis for each population separately obtaining similar results (not shown). Similarly, song frequency and morphological measurements were not related in serins (Table 4).

When comparing only syllable types that were shared among male juncos, none of the frequency traits was related to body mass (all $F_{109,1} < 0.86$, all $p > 0.35$). Contrary to expected, maximum frequency tended to be positively related to body size ($F_{109,1} = 4.15$, $p = 0.04$, not significant if correcting for multiple comparisons). Peak and minimum frequency were not related to body size (both $F_{109,1} < 0.55$, both $p > 0.46$).

Discussion

None of the frequency traits in dark-eyed junco or serin songs was related to body size, and there was no tendency for more extensive repertoire sampling to improve the signal content of frequency regarding

Table 2: Trait loadings on the size principal components (PC) with eigenvalues larger than one (i.e. correlation coefficients of trait measurements with PC scores), from two PC analyses (PCA) on metric measurements of dark-eyed juncos and serins

	Dark-eyed juncos		Serins
	First PC	Second PC	First PC
Tarsus length	0.86	-0.05	0.56
Skull breadth	0.84	-0.22	
Length of skull plus beak	0.88	-0.07	
Beak height			0.60
Wing chord length	0.09	0.91	0.79
Tail length	0.24	0.88	0.80
Eigenvalue	2.28 (46%)	1.67 (33%)	1.95 (48%)

Table 3: Average correlations (*r*) and significance values (*p*) of song frequency traits with size and mass of male dark-eyed juncos, and 95% confidence intervals of the average correlation coefficients ($r_{\pm 0.95}$)

	n	Peak frequency	Minimum frequency	Maximum frequency	Peak frequency	Minimum frequency	Maximum frequency
1 syllable type sampled per male							
Size	82	r^a (p^b) = -0.04 (0.73)	-0.02 (0.88)	-0.01 (0.92)			
		$r_{\pm 0.95}$ = -0.25, 0.18	-0.23, 0.20	-0.23, 0.21			
Mass	83	-0.02 (0.89)	0.05 (0.63)	0.07 (0.55)			
		-0.23, 0.20	-0.16, 0.27	-0.15, 0.20			
2 syllable types sampled per male and averaged							
					... or minimum value taken		
Size	72	-0.05 (0.68)	0.01 (0.92)	0.00 (0.98)	-0.06 (0.59)	0.02 (0.90)	-0.02 (0.89)
		-0.28, 0.18	-0.22, 0.24	-0.23, 0.23	-0.29, 0.17	-0.22, 0.25	-0.25, 0.22
Mass	73	-0.02 (0.84)	0.08 (0.50)	0.03 (0.80)	-0.02 (0.87)	0.04 (0.75)	-0.01 (0.95)
		-0.25, 0.21	-0.15, 0.30	-0.20, 0.26	-0.25, 0.21	-0.19, 0.27	-0.24, 0.22
3 syllable types sampled per male and averaged							
					... or minimum value taken		
Size	57	-0.07 (0.63)	0.04 (0.77)	0.03 (0.81)	-0.07 (0.60)	-0.06 (0.65)	-0.07 (0.59)
		-0.32, 0.20	-0.22, 0.30	-0.23, 0.29	-0.33, 0.19	-0.32, 0.20	-0.33, 0.19
Mass	58	-0.03 (0.78)	0.10 (0.45)	0.06 (0.64)	-0.05 (0.70)	-0.11 (0.42)	0.01 (0.95)
		-0.29, 0.22	-0.16, 0.35	-0.20, 0.32	-0.31, 0.21	-0.36, 0.15	-0.25, 0.27
4 syllable types sampled per male and averaged							
					... or minimum value taken		
Size	42	-0.05 (0.74)	0.04 (0.82)	0.10 (0.55)	0.04 (0.80)	-0.10 (0.54)	-0.07 (0.66)
		-0.35, 0.26	-0.27, 0.34	-0.22, 0.39	-0.27, 0.34	-0.39, 0.21	-0.37, 0.24
Mass	42	0.07 (0.68)	0.03 (0.87)	0.23 (0.14)	0.07 (0.64)	-0.29 (0.07)	0.08 (0.59)
		-0.25, 0.36	-0.30, 0.31	-0.09, 0.49	-0.24, 0.37	-0.54, 0.02	-0.22, 0.38
5 syllable types sampled per male and averaged							
					... or minimum value taken		
Size	23	0.08 (0.72)	0.07 (0.75)	0.00 (1.00)	-0.09 (0.69)	-0.10 (0.67)	-0.15 (0.48)
		-0.34, 0.48	-0.35, 0.47	-0.41, 0.41	-0.48, 0.34	-0.49, 0.33	-0.53, 0.28
Mass	23	0.15 (0.48)	0.15 (0.50)	0.14 (0.53)	0.13 (0.54)	-0.22 (0.31)	0.12 (0.60)
		-0.28, 0.53	-0.25, 0.55	-0.29, 0.52	-0.29, 0.52	-0.58, 0.21	-0.31, 0.50

^aPearson regression coefficient averaged over 1000 random sampling of syllable types within the repertoire of each male.

^bSignificance value for the average regression coefficient.

body size. Comparing the frequency of shared syllable types of male juncos also did not reveal any negative relationship with body size. Overall, we found no obvious way for junco or serin receivers to assess the body size of singing males from the frequency of their songs.

A likely explanation is that differences in size among conspecifics are too small to influence song frequency appreciably. For example, a decrease of 1 SD in mass in juncos and serins (Table 1) would predict an increase in the frequency of only 44 and 60 Hz respectively, using Wallschläger's (1980) equation for oscine song. At the predicted frequencies, this corresponds to 1.20 and 1.47 Webers (frequency shift * 100/base frequency), which are only about two to three times the auditory limens typically reported for birds (e.g. Kuhn et al. 1980; Dent et al. 2000). Similar small values are reached using Fletcher's (2004) theoretical equation for optimal scaling of frequency to body size in vertebrates (frequency = $B * \text{mass}^{-0.4}$, where *B* is a constant that we calibrated for each species): 100 Hz and 2 Webers

for the junco, and 162 Hz and 2.46 Webers for the serin. Considering these small predicted changes in frequency, it is surprising that associations of frequency with body size were reported so often in a variety of taxa, including non-oscine birds. Note that coefficients of variation of body size in the non-oscine studies are similar to the ones of serins and juncos (e.g. Barbaud et al. 2000; Mager et al. 2007), and as the relationship of frequency and size is inversely exponential, similar coefficients of variation predict even smaller differences in absolute frequency for larger animals.

It could be that the diversity of syllable types that makes up the repertoires of individual birds (with each syllable type having its different frequency properties) obscures a possible relationship between the frequency and body size or mass. If the lack of a relationship were due to syllable diversity, we might expect that averaging across the repertoire, or taking the lowest frequency value, would factor out the idiosyncrasies of each syllable type, and would show a relationship between frequency and body size. This

Table 4: Correlations (*r*) and significance values (*p*) of song frequency traits with size and mass of male serins, and 95% confidence intervals of the correlation coefficients ($r_{\pm 0.95}$)

	n	Peak frequency	Minimum frequency	Maximum frequency
Size	41	<i>r</i> (<i>p</i>) = -0.01 (0.93) $r_{\pm 0.95}$ = -0.32, 0.29	0.13 (0.42) -0.19, 0.42	0.07 (0.67) -0.25, 0.37
Mass	40	0.18 (0.26) -0.14, 0.47	-0.20 (0.22) -0.48, 0.12	-0.15 (0.35) -0.44, 0.17

was not the case, even in the quite extreme situation of the serin where songs normally contain more than 20 different syllable types. Therefore, syllable diversity alone does not seem to account for the lack of relationship between frequency and body size in these two species.

Unique aspects of the oscine vocal physiology may interfere with a possible relationship between body size or mass and frequency. As mentioned in the introduction, oscines are able to use a wide range of frequencies. Fundamental frequency is controlled mostly by the contraction of specialized syringeal muscles, and each side of the syrinx can specialize in producing low- or high-frequency sounds (Suthers 1997). This contrasts with the more limited scope for frequency modulation in non-oscine birds, where frequency seems to be determined by variation in air sac pressure (Beckers et al. 2003). The ability of oscine birds to control frequency over a wide range of frequencies may, to a certain extent, make the frequency of song depend more on the learned template than on the birds' vocal limitations.

In junco and serin songs, the peak frequency is near the midpoint of their respective frequency ranges, while in some oscine species the peak frequency is located at about the lower one-fourth of the frequency range, where it is thought that syringeal membranes and muscles are relatively relaxed and, therefore, it should be easier to sing (Lambrechts 1996). Also, juncos and serins sing at considerably higher frequencies than is typical for an oscine of their body size. The clearest prediction relating frequency to body size concerns minimum frequency, because that is the most difficult to alter given the size of the vocal organ (Bradbury & Vehrencamp 1998). Since these two species do not emphasize their lower frequencies, body size may not be the most important limiting factor for the frequency profile of their songs. This could help explaining the different result obtained for bullfinches, where a negative correlation exists between song frequency and body size (Schubert 1976). Unlike juncos and serins, bullfinches seem to emphasize

their lower frequencies: peak frequency is at the lower part of their frequency range and is approx. 1 kHz lower than expected for their mass (personal observations, based on average male mass in Cramp & Perrins 1994; the song recording in Perrins 1998; and the equation of Wallschläger 1980). In addition, the bullfinches studied were from different subspecies that differ considerably in size.

The lack of a relationship between frequency and body size aids in understanding the female preference for high-frequency song that is found in serins and other oscine species (Dabelsteen & Pedersen 1993; Ratcliffe & Otter 1996; Cardoso et al. 2007). A putative explanation for these preferences was that higher frequency signals smaller size, which may confer greater flight agility and thus be a preferred trait in some species (e.g. Grønstøl 1996; Blomqvist et al. 1997). We can now exclude this possibility for the serin. An explanation that remains viable is that singing at high frequencies is costly, for example because it requires coping with greater muscle contraction (Suthers et al. 1999). Accordingly, in some species, males sing less consistently at high than low frequencies (Lambrechts 1997; Christie et al. 2004). The lack of a relationship between frequency and body size also implies that preferences for body size (either small or large) need not lead to preferences for song frequency. For example, in the dark-eyed junco, large size (measured as wing length) confers a mating advantage to males (McGlothlin et al. 2005) but, based on our results, this does not imply that females should prefer low-frequency song. Instead, this can result from direct visual assessment of size or other behavioural correlates of body size.

We cannot exclude the possibility that information on body size exists in frequency traits other than the ones we measured. For example, in mammals, the frequency of vocalizations is generally a poor predictor of body size (reviewed in Searcy & Nowicki 2005; but see e.g. Pfefferle & Fischer 2006), while formant dispersion depends on the size of the vocal tract and, therefore, is more closely related to

body size (e.g. Fitch 1997; Sanvito et al. 2007). Formants are peaks of amplitude of certain frequencies due to the resonant properties of the vocal tract, and are independent of the frequency at the sound source (Bradbury & Vehrencamp 1998). For some non-passerines, the size and shape of the vocal tract is known to influence formant profiles (Suthers 1994), and differences in formant dispersion are known to be perceptible (Fitch & Kelley 2000). Therefore, formants may convey information on body size in birds. The negative correlation between barn swallow rattles and body mass (Galeotti et al. 1997) may be one such case, because those rattles are composed by broadband, non-harmonic clicks and, therefore, their peak frequency should depend on formant location rather than periodicity at the sound source. In fact, sexually dimorphic elongation of the trachea is common in birds (mostly non-oscines), and is thought to have evolved to allow males to vocalize as if they were larger (Fitch 1999). However, unlike the swallow rattles, the songs of juncos and serins are mostly tonal, having few broadband harsh sounds against which formants can be perceived or measured. Also, tonal purity in oscines is attained by actively modifying the shape of the vocal tract so that the fundamental frequency is emphasized while the others are filtered (Nowicki 1987; Riede et al. 2006), and so the resonant properties of the vocal tract change continuously during singing. For these reasons, communication of body size by formant dispersion in junco or serin song is very unlikely. It is, however, a mechanism that deserves investigation in species with less tonal, harsher sounding songs, or in other type of vocalizations (e.g. threat vocalizations are commonly harsh sounding, Morton 1977).

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Literature Cited

- Amorim, M. C. P. & Hawkings, A. D. 2005: Ontogeny of acoustic and feeding behaviour in the Grey Gurnard, *Eutrigla gurnardus*. *Ethology* **111**, 255–269.
- Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton.
- Appleby, B. M. & Redpath, S. M. 1997: Indicators of male quality in the hoots of Tawny Owls (*Strix aluco*). *J. Raptor Res.* **31**, 65–70.
- Badyaev, A. V. & Leaf, E. S. 1997: Habitat associations of song characteristics in *Phylloscopus* and *Hippolais* warblers. *Auk* **114**, 40–46.
- Barbaud, C., Mariani, A. & Jouventin, P. 2000: Variation in call properties of the snow petrel, *Pagodroma nivea*, in relation to sex and body size. *Aust. J. Zool.* **48**, 421–430.
- Beani, L. & Dessì-Fulgheri, F. 1995: Mate choice in the grey partridge, *Perdix perdix*: role of physical and behavioural male traits. *Anim. Behav.* **49**, 347–356.
- Beckers, G. J. L., Suthers, R. A. & ten Cate, C. 2003: Mechanisms of frequency and amplitude modulation in ring dove song. *J. Exp. Biol.* **206**, 1833–1843.
- Bergmann, H. H. 1976: Konstitutionsbedingte Merkmale in Gesängen und Rufen europäischer Grasmücken (Gattung *Sylvia*). *Z. Tierpsychol.* **42**, 315–329.
- Blomqvist, D., Johansson, O. C., Unger, U., Larsson, M. & Flodin, L. A. 1997: Male aerial display and reversed sexual size dimorphism in the dunlin. *Anim. Behav.* **54**, 1291–1299.
- Bowman, R. I. 1979: Adaptive morphology of song dialects in Darwin's finches. *J. Ornithol.* **12**, 353–389.
- Bradbury, J. W. & Vehrencamp, S. L. 1998: Principles of Animal Communication. Sinauer Associates, Sunderland.
- Brown, W. D., Wideman, J., Andrade, M. C. B., Mason, A. C. & Gwynne, D. T. 1996: Female choice for an indicator of male size in the song of the black-horned tree cricket *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution* **50**, 2400–2411.
- Byers, B. E. 2007: Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behav. Ecol.* **18**, 130–136.
- Cardoso, G. C. & Mota, P. G. 2007: Song diversification and complexity in canaries and seedeaters (*Serinus* spp.) *Biol. J. Linn. Soc.* **92**, 183–194.
- Cardoso, G. C., Mota, P. G. & Depraz, V. 2007: Female and male serins (*Serinus serinus*) respond differently to derived song traits. *Behav. Ecol. Sociobiol.* **61**, 1425–1436.
- Christie, P. J., Mennill, D. J. & Ratcliffe, L. M. 2004: Pitch shifts and song structure indicate male quality in

- the dawn chorus of black-capped chickadees. *Behav. Ecol. Sociobiol.* **55**, 341–348.
- Collins, S. A. 2000: Men's voices and women's choices. *Anim. Behav.* **60**, 773–780.
- Cramp, S. & Perrins, C. M. 1994: The birds of the Western Palearctic, Vol. VIII. Oxford Univ. Press, Oxford.
- Dabelsteen, T. & Pedersen, S. B. 1993: Song-based discrimination and behaviour assessment by female blackbirds, *Turdus merula*. *Anim. Behav.* **45**, 759–771.
- Davies, N. B. & Halliday, T. R. 1978: Deep croaks and fighting assessment in toads *Bufo bufo*. *Nature* **274**, 683–685.
- Dent, M. L., Dooling, R. J. & Pierce, A. S. 2000: Frequency discrimination in budgerigars (*Melopsittacus undulatus*): effects of tone duration and tonal context. *J. Acoust. Soc. Am.* **107**, 2657–2664.
- Fitch, W. T. 1997: Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *J. Acoust. Soc. Am.* **102**, 1213–1222.
- Fitch, W. T. 1999: Acoustic exaggeration of size in birds via tracheal elongation: comparative and theoretical analyses. *J. Zool.* **248**, 31–48.
- Fitch, W. T. & Kelley, J. P. 2000: Perception of vocal tract resonances by whooping cranes *Grus americana*. *Ethology* **106**, 559–574.
- Fletcher, N. H. 2004: A simple frequency-scaling rule for animal communication. *J. Acoust. Soc. Am.* **115**, 2334–2338.
- Galeotti, P., Saino, N., Sacchi, R. & Møller, A. P. 1997: Song correlates with social context, testosterone and body condition in male barn swallows. *Anim. Behav.* **53**, 678–700.
- Grønstøl, G. B. 1996: Aerobic components in the song-flight display of male lapwings *Vanellus vanellus* as cues in female choice. *Ardea* **84**, 45–55.
- Guillot, M. & Jouventin, P. 1980: Le pétrel des neiges à Pointe Géologie. *Le Gerfaut* **70**, 51–72.
- Hanford, P. & Loughheed, S. 1991: Variation in duration and frequency characters in the song of the rufous-collared sparrow, *Zonotrichia capensis*, with respect to habitat, trill dialects and body size. *Condor* **93**, 644–658.
- Hardouin, L. A., Reby, D., Bavoux, C., Burnelau, G. & Bretagnolle, V. 2007: Communication of male quality in owl hoots. *Am. Nat.* **169**, 552–562.
- Hibbitts, T. J., Whiting, M. J. & Stuart-Fox, D. M. 2007: Shouting the odds: vocalization signals status in a lizard. *Behav. Ecol. Sociobiol.* **61**, 1169–1176.
- Howard, R. D. & Young, J. R. 1998: Individual variation in male vocal traits and female mating preferences in *Bufo americanus*. *Anim. Behav.* **55**, 1165–1179.
- Irwin, D. E., Thimman, M. P. & Irwin, J. H. 2008: Call divergence is correlated with geographic and genetic distance in greenish warblers (*Phylloscopus rochiloides*): a strong role for stochasticity in signal evolution? *J. Evol. Biol.* **21**, 435–448.
- de Jong, K., Bouton, N. & Slabbekoorn, H. 2007: Azorean rock-pool blennies produce size-dependent calls in a courtship context. *Anim. Behav.* **74**, 1285–1292.
- Kuhn, A., Leppelsack, H.-J. & Schwartzkopff, J. 1980: Measurement of frequency discrimination in the Starling (*Sturnus vulgaris*) by conditioning of heart rate. *Naturwissenschaften* **67**, 102.
- Ladich, F. 1998: Sound characteristics and outcome of contests in male croaking gouramis (Teleostei). *Ethology* **104**, 517–529.
- Lambrechts, M. M. 1996: Organisation of birdsong and constraints on performance. In: *Ecology and Evolution of Acoustic Communication in Birds* (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, pp. 305–319.
- Lambrechts, M. M. 1997: Song frequency plasticity and composition of phrase versions in great tits *Parus major*. *Ardea* **85**, 99–109.
- Logue, D. M., Droessler, E. E., Roscoe, D. W., Vokey, J. R., Rendall, D. & Kunimoto, R. M. 2007: Sexually antithetical song structure in a duet singing wren. *Behaviour* **144**, 331–350.
- Madsen, V., Balsby, T. S. J., Dabelsteen, T. & Osorno, J. L. 2004: Bimodal signalling of a sexually selected trait: gular pouch drumming in the magnificent frigatebird. *Condor* **106**, 156–160.
- Madsen, V., Dabelsteen, T., Osorio, D. & Osorno, J. L. 2007: Morphology and ornamentation in male magnificent frigatebirds: variation with age class and mating status. *Am. Nat.* **169**, S93–S111.
- Mager, J. N. III, Walcott, C. & Piper, W. H. 2007: Male common loons, *Gavia immer*, communicate body mass and condition through dominant frequencies of territorial yodels. *Anim. Behav.* **73**, 683–690.
- McGlothlin, J. W., Parker, P. G., Nolan, V. Jr & Ketterson, E. D. 2005: Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution* **59**, 658–671.
- Miyasaki, M. & Waas, J. R. 2003: Acoustic properties of male advertisement and their impact on female responsiveness in little penguins *Eudyptula minor*. *J. Avian Biol.* **43**, 229–232.
- Morton, E. S. 1977: On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Am. Nat.* **111**, 855–869.
- Mota, P. G. & Cardoso, G. C. 2001: Song organisation and patterns of variation in the serin (*Serinus serinus*). *Acta Ethol.* **3**, 141–150.
- Newman, M. M., Yeh, P. J. & Price, T. D. 2008: Song variation in a recently founded population of the Dark-eyed Junco (*Junco hyemalis*). *Ethology* **114**, 164–173.
- Nolan, V. Jr, Ketterson, E. D., Cristol, D. A., Rogers, C. M., Clotfelter, E. D., Titus, R. C., Schoech, S. J. &

- Snajdr, E. 2002: Dark-eyed Junco (*Junco hyemalis*). In: The Birds of North America, No. 716 (Poole, A. & Gill, F., eds). The Birds of North America, Inc., Philadelphia, PA, pp. 1—44.
- Nowicki, S. 1987: Vocal tract resonances in oscine bird sound production: evidence from birdsongs in a helium atmosphere. *Nature* **325**, 53—55.
- Pasteau, M., Nagle, L. & Kreutzer, M. 2007: Influences of learning and predispositions on frequency level preferences on female canaries (*Serinus canaria*). *Behaviour* **144**, 1103—1118.
- Perrins, C. M. (ed.) 1998. The Complete Birds of the Western Palearctic – CD-ROM. Oxford Univ. Press, Oxford.
- Pfefferle, D. & Fischer, J. 2006: Sounds and size: identification of acoustic variables that reflect body size in hamadryas baboons, *Papio hamadryas*. *Anim. Behav.* **72**, 43—51.
- Ratcliffe, L. & Otter, K. 1996: Sex differences in song recognition. In: Ecology and Evolution of Acoustic Communication in Birds (Kroodsma, D. E. & Miller, E. H., eds). Cornell Univ. Press, Ithaca, pp. 339—355.
- Riede, T., Suthers, R. A., Fletcher, N. H. & Blevins, W. E. 2006: Songbirds tune their vocal tract to the fundamental frequency of their song. *Proc. Natl Acad. Sci. U.S.A.* **103**, 5543—5548.
- Ryan, M. J. & Brenowitz, E. A. 1985: The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* **126**, 87—100.
- Sanvito, S., Galimberti, F. & Miller, E. H. 2007: Vocal signalling of male southern elephant seals is honest but imprecise. *Anim. Behav.* **73**, 287—299.
- Schubert, M. 1976: Über die variabilität von lockrufen des gimpels, *Pyrrhula pyrrhula*. *Ardea* **64**, 61—71.
- Searcy, W. A. & Nowicki, S. 2005: The Evolution of Animal Communication. Princeton Univ. Press, Princeton.
- Seddon, N., Amos, W., Mulder, R. A. & Tobias, J. A. 2004: Male heterozygosity predicts territory size, song structure and reproductive success in a cooperatively breeding bird. *Proc. R. Soc. Lond., B, Biol. Sci.* **271**, 1823—1829.
- Shy, E. 1983: The relation of geographical variation in song to habitat characteristics and body size in North American tanagers (Thraupinae: *Piranga*). *Behav. Ecol. Sociobiol.* **12**, 71—76.
- Suthers, R. A. 1994: Variable asymmetry and resonance in the avian vocal tract: a structural basis for individually distinct vocalizations. *J. Comp. Physiol.* **175**, 457—466.
- Suthers, R. A. 1997: Peripheral control and lateralization of birdsong. *J. Neurobiol.* **33**, 632—652.
- Suthers, R. A., Goller, F. & Pytte, C. 1999: The neuromuscular control of bird song. *Philos. Trans. R. Soc. Lond., B, Biol. Sci.* **354**, 927—939.
- Suthers, R. A., Vallet, E., Tanvez, A. & Kreutzer, M. 2004: Bilateral song production in domestic canaries. *J. Neurobiol.* **60**, 381—393.
- Wallschläger, D. 1980: Correlation of song frequency and body weight in passerine birds. *Experientia* **36**, 412.
- Williams, L. & MacRoberts, M. H. 1977: Individual variation in the songs of dark-eyed juncos. *Condor* **79**, 106—112.
- Yeh, P. J. & Price, T. D. 2004: Adaptive phenotypic plasticity and the successful colonization of a novel environment. *Am. Nat.* **164**, 531—542.