

Sexually size dimorphic brains and song complexity in passerine birds

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Neural correlates of bird song involve the volume of particular song nuclei in the brain that govern song development, production, perception, and learning. Intra- and interspecific variation in the volume of these song nuclei are associated with overall brain size, suggesting that the integration of complex songs into the brain requires general neural augmentation. In a comparative study of passerine birds based on generalized least square models, we tested this hypothesis by exploring the interspecific relationship between overall brain size and repertoire size. We found no significant association between song complexity of males and brain size adjusted for body size. However, species in which males produced complex songs tended to have sex differences in overall brain size. This pattern became stronger when we controlled statistically for female song complexity by using sex differences in song complexity. In species with large differences in song complexity, females evolved smaller brains than did males. Our results suggest no role for the evolution of extended neural space, as reflected by total brain size, owing to song complexity. However, factors associated with sexual selection mirrored by sex differences in song complexity were related to sexual dimorphism in overall brain size. *Key words:* bird song, brain size, comparative analysis, generalized least square models, repertoire size, sexual selection. [*Behav Ecol*]

Bird song is one of the few models in which behavior has been successfully linked to anatomically defined brain structures (for reviews, see Garamszegi and Eens, 2004; Marler and Doupe, 2000; Nottebohm, 1993; Wild, 1997). Neurobiological studies revealed that neural space is required for storing large repertoires, because a considerable amount of neurons and greater synaptic and dendritic development in specialized areas of the brain, such as HVC and RA, are required for the auditory and motor government of sound production.

The relationship between brain space and song complexity raises important questions about song and brain evolution (DeVoogd and Székely, 1998). Bird song is a sexually selected trait, as in many songbird species females prefer males that sing more complex songs (Catchpole and Slater, 1995; Gil and Gahr, 2002; Searcy and Yasukawa, 1996). Female preference for complex songs will have consequences for the evolution of song nuclei in the brain, because sexual selection by females requires several behavioral and neural coadaptations. Hence, neural structures in the brain that are associated with song should be the potential targets of sexual selection. Female mate choice based on song complexity should thus result in higher mating success of males with larger song nuclei, if males with more complex songs have a larger HVC or RA. However, this prediction remains to be justified (Airey et al., 2000a). If song is to signal aspects of male heritable quality, song and the associated nuclei in the brain should be heritable. Airey et al. (2000b) provided evidence that the volume of different song structures shows highly positive phenotypic and genetic correlations and significant heritabilities.

The role of sexual selection in song and brain evolution can be revealed in an interspecific context. If driven by female preference and if evolutionary changes in song enhance neural adaptation in the brain, the complexity of song should

be positively related to the size of brain structures among species. Accordingly, phylogenetic analyses have revealed a positive interspecific relationship between the volume of HVC and repertoire size (DeVoogd et al., 1993; Székely et al., 1996).

To the best of our knowledge, all previous comparative studies have focused on specific brain nuclei (such as HVC or RA). On the other hand, several studies in vertebrates (most importantly mammals and birds) testing for ecological and behavioral correlates of encephalization tend to use total brain size as a focus of study, even if selection may act on individual brain structures (see Barton, 1998; Bennett and Harvey, 1985; Garamszegi et al., 2002; Gittleman, 1994; Iwaniuk and Arnold, 2004; Lefebvre et al., 1997; Madden, 2001; Reader and Laland, 2002; Winkler et al., 2004). Therefore, it may also be expected that constraints arising from female preference for complex songs will affect the size of the entire brain on an evolutionary time scale. A quantitative-genetic analysis using natural intraspecific variation in brain weight and telencephalic volume revealed significant heritabilities for these traits, suggesting that they can also be potential targets of sexual selection (Airey et al., 2000b). Repertoire size can be predicted by variance in the sizes of several brain nuclei, which show significant covariation not only with each other but also with the size of the telencephalon or overall brain size (Airey et al., 2000b; Airey and DeVoogd, 2000; MacDougall-Shackleton et al., 1998; Nottebohm et al., 1981). In addition, interspecific studies also revealed that a larger telencephalon is needed to accommodate a larger HVC (DeVoogd et al., 1993; Székely et al., 1996). These relationships may suggest that although functionally the volumetric significance of the song system is probably small, it is impossible to have larger song nuclei without increasing the overall size of the brain on an evolutionary scale. Thus, the maintenance of complex songs requires the maintenance of an elaborate neural song system, but this in turn may be linked to augmented anatomy and function of other neural systems. The causal mechanism that

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generates a relationship between large brain space and song complexity is unknown (Gil and Gahr, 2002). However, the potential integration of male song into the brain as a whole, requiring general neural augmentation, suggests that there may be substantial costs associated with complex songs. If this is the case, such neural costs may guarantee the reliability of acoustic signals of male quality. Hence, according to the handicap signaling theory (Zahavi and Zahavi, 1997), only individuals in prime condition will be able to bear the costs of the maintenance of both large repertoires and large brains. Alternatively, elaborate male song may have at least partly evolved as an honest indicator of some aspects of overall brain capacity (Airey et al., 2000b). If any of these mechanisms applies to birds, female preference for elaborate songs may result in a positive relationship between overall brain size and song complexity among species.

One aim of our comparative study of songbirds, as a first attempt in the literature, was to determine the phylogenetic correlation between relative brain mass of males and repertoire size. We used song type and syllable repertoire size with the assumption that these species-specific estimates of song complexity reflect the importance of the complex mechanisms involved in song development, production, perception, and learning (Brenowitz and Kroodsmas, 1996; Catchpole and Slater, 1995; Gil and Gahr, 2002; Kroodsmas, 1982). We also assumed that these particular aspects of song are related to female preference (Catchpole and Slater, 1995; Searcy and Yasukawa, 1996). A link between overall brain capacities and song complexity owing to female preferences for reliable signals of male quality would require that males of species evolving complex songs should have larger brains for their body size than do species with simple songs. If regions other than HVC are evolutionarily related to the complexity of songs, and these relationships have volumetric significance, repertoire size should also explain some of the residual variance in brain volumes of males after statistically controlling for effects of HVC size. Therefore, we predicted that overall brain size of males will be positively correlated with measures of song complexity among species.

Songbirds exhibit some of the most extreme sex differences in the brain of all vertebrates (Gahr, 1994). Although natural selection theory predicts that the increase in brain size owing to behavioral adaptation to ecological constraints should be similar in the two sexes, behavioral differences during mating and reproduction may favor sexually size dimorphic brains (Jacobs, 1996). Therefore, sexual selection acting on bird song and the associated neural tissue in males may cause asymmetric selection pressures on the brain of the two sexes. For example, a previous comparative study revealed that intersexual differences in song are associated interspecifically, with intersexual differences in the size of specific song nuclei (MacDougall-Shackleton and Ball, 1999). Because there is a potential for sexual selection to mediate a relationship between extravagant song displays and brain size in males, the same selective factors may set up different evolutionary constraints for female brains. Given the relationship between the intensity of sexual selection and male song at the interspecific level (Read and Weary, 1992), differences in song complexity of males among species may be associated with several sex-dependent behaviors and their corresponding neural government. Such associations involving asymmetric selection pressures on the brains of the two sexes may drive an interspecific association between male song and brain size dimorphism.

The second aim of the present study was to assess the extent of interspecific variation in sexual dimorphism in brain size that is related to differences in song complexity among species. We predicted that species in which males have high song com-

plexity should have larger sex differences in brain size relative to body size than do species in which males produce less complex songs. However, in some species females may also sing complex songs (Langmore, 1998), which should be controlled statistically in our comparative analyses, because such complexity may affect the evolution of brain size in females. Hence the relationship between brain size dimorphism and song should be robust if comparisons are based on sex differences in song complexity that may reflect behavioral differences between sexes more closely than does male song complexity per se.

METHODS

The size of the brain was obtained from postmortem examinations of dead birds brought to a taxidermist (J.E.) between 26 June 1994–8 January 2003 in Christiansfeld, Denmark. In the present study, we used brain mass and body mass of 584 individual dead adult birds of known sex belonging to 39 species. Brain and body masses were weighed to the nearest mg on a precision balance, blindly with respect to the hypothesis under test. Because birds were frozen when received until examination, we assume that any effects of storage on measurements should only cause noise in the data set, and there is no reason to expect sex differences in such effects. To test this assumption, by combining information on males and females for each species, we calculated mean body and brain sizes and checked whether our measurements were significantly repeatable with respect to those reported in the literature (see Armstrong and Bergeron, 1985; Crile and Quiring, 1940; Mlikovsky, 1990; Portmann, 1947). For both traits we found large and highly significant repeatabilities ($\log_{10}(\text{body mass})$: $F_{33,91} = 276.152$, $p < .001$, $R = .990$; $\log_{10}(\text{brain mass})$: $F_{33,91} = 67.596$, $p < .001$, $R = .961$). Hence, potential differences in measurements among studies should not cause bias, and information from different sources is comparable.

We controlled for allometric effects by using residuals from the phylogenetically corrected linear regression of \log_{10} -transformed brain size on \log_{10} -transformed body size for each sex (see below). These residuals were used in the subsequent analyses as estimates of sex-specific relative brain sizes. An anonymous referee suggested avoiding the use of residuals, because they make an implicit assumption that independent variables are orthogonal (Freckleton, 2002). However, when we estimated the interspecific associations between variables of interest holding body size constant by calculating the phylogenetically corrected partial correlation coefficients, the results and conclusions were identical to findings based on residuals. For simplicity, only analyses relying on residuals from phylogenetically adjusted linear regressions are presented here.

Variance in relative brain size after adjusting for differences in body size among species was larger than was the variance within species, as required for comparative analysis (females: $F_{38,203} = 9.919$, $p < .001$; males: $F_{38,380} = 13.769$, $p < .001$). By using data for species for which we had at least two measurements, we found significant repeatabilities for sex-specific relative brain sizes (females: $R = .666$; males: $R = .656$). A two-way ANOVA revealed significant effects for species and for sex by species interaction on relative brain size (species: $F_{38,38} = 20.748$, $p < .001$; sex: $F_{1,1} = 1.876$, $p = .171$; species \times sex: $F_{38,38} = 1.504$, $p = .030$). These results indicate that intrasexual variation in these traits within species is negligible compared to variation among species, and that sex-specific relative brain sizes are species-specific attributes that can justifiably be represented by a single measurement (when we repeated our analyses with species for which we have at least two data points for both females and males, the

results were similar). Therefore, we used mean relative brain size for adult females and males separately.

Sampling date might influence size estimates of brain size, as it has repeatedly been demonstrated that song nuclei show annual fluctuations (Brenowitz et al., 1991; Leitner et al., 2001; Nottebohm et al., 1986; Ritters et al., 2002; Tramontin and Brenowitz, 2000). Body mass may also show seasonal variation in temperate birds. We tested whether date of sampling differed among species, but there was no significant difference in median sampling date in our sample (Kruskal-Wallis ANOVA: $p > .817$). Therefore, we assumed that the subsequent analyses would not be confounded by sampling date.

We expressed absolute brain size dimorphism as the \log_{10} -transformed ratio of absolute female and male brain size (thus without controlling for body size effects at this stage). We did not calculate brain size dimorphism based on sex-specific relative brain sizes, because these variables are residuals from the relevant regression lines causing them to scale with the independent variable used (sex-specific body size). Therefore, combining residuals from two regression lines may introduce bias. Absolute brain size dimorphism measured as $\log_{10}(\text{absolute female brain size}/\text{absolute male brain size})$ was normally distributed with a mean of -0.017 ($SE = 0.010$). Because the numerator and the denominator of the absolute brain size ratio scale similarly, absolute brain size dimorphism larger than zero indicates that females have relatively larger brains than do males; values smaller than zero reflects the opposite trend. The mean absolute brain size dimorphism of 39 species was smaller than the expectation of zero ($t_{38} = -1.715$, $p_{\text{one-tailed}} = .048$), implying that there are more species in which males have larger brains than do females. However, because of allometric effects, absolute brain size dimorphism may result from absolute body size dimorphism. Thus the \log_{10} -transformed ratio of absolute female and male brain size should be corrected for the similar ratio in body size. This correction was based on the phylogenetically independent regression of $\log_{10}(\text{absolute female brain size}/\text{absolute male brain size})$ on $\log_{10}(\text{absolute female body size}/\text{absolute male body size})$. Note that absolute brain and body size dimorphism were not residuals by definition, allowing them to be combined in a single regression. Residuals from this regression were subsequently termed relative brain size dimorphism and used in the subsequent analyses. Positive values for relative brain size dimorphism thus indicate that females have relatively larger brains when allometric effects were held constant. Data for the volume of the HVC of males were from DeVoogd et al. (1993), and these were \log_{10} -transformed. Absolute HVC volume was positively correlated with our overall brain size measurement for males ($r = .565$, $p = .006$, $N = 22$), and this effect was taken into account. We calculated relative HVC volume based on the phylogenetic regression of absolute HVC volume on relative male brain size.

To characterize song complexity of males in different species, we used reported song type and syllable repertoire size from the literature. Song type repertoire size is the number of particular song types within the entire repertoire of a male, and syllable repertoire size is the number of particular syllable types within single songs (Read and Weary, 1992). Syllables are usually the simplest figures that appear on spectrograms separated by noticeable time intervals, and they are the smallest recognizable elements on the sonogram, probably playing a functionally important role (Horn and Falls, 1996). Analyses of reliability of these traits showed that song type repertoire size is highly repeatable within species ($R > .900$), and that syllable repertoire size is predictable by alternative measures of short-term song complexity (Garamszegi and Møller, 2004; Garamszegi et al., 2003).

Table 1

Estimates of female song complexity relative to male song complexity, as calculated by the ratio between male and female song complexity based on quantitative information from the literature, and as assessed from handbook descriptions

Species	Based on literature data	Scores based on handbooks	Reference
<i>Agelaius phoeniceus</i>	40.37	1	Beletsky, 1983a,b; Weatherhead et al., 1993
<i>Cistothorus palustris</i>	0	0	Brenowitz et al., 1994
<i>Erethacus rubecula</i>	78.8	2	Hoelzel, 1986
<i>Sturnus vulgaris</i>	47.63	2	Pavlova et al., 2002
<i>Thryothorus ludovicianus</i>	0	0	MacDougall-Shackleton and Ball, 1999
<i>Zonotrichia albicollis</i>	100	2	DeVoogd et al., 1995
<i>Zonotrichia leucophrys</i>	100	2	Baptista et al., 1993

We intended to calculate sexual differences in song complexity in each species based on comparable and quantitative measures of sex-specific song complexity. However, song in female passerines has not been well studied quantitatively, and thus such calculations are impossible using literature data. As an alternative, to estimate song complexity of females, we used information on female song from handbooks (Cramp and Perrins, 1985–1994; Poole et al., 1993–2002; von Blotzheim, 1985–1997), which usually contain short descriptions for female song. Without any knowledge about the brain data, we classified song complexity of females relative to males according to the following criteria. Relative song complexity of females was scored as follows: zero, if females do not produce songs; one, if females were observed to sing but their repertoire size is smaller than that of males; and two, if females sing as complex songs as do males and the sexes have comparable repertoires. These weights were significantly repeatable among sources and observers (among sources: $F_{63,128} = 3.057$; $p < .001$; $R = .505$; among observers: $F_{10,43} = 9.346$, $p < .001$, $R = .676$). Therefore, we used the averages of our weights for relative female song complexity obtained from handbooks. We assumed that precise values for absolute complexity of males did not bias our assessment of relative song complexity of females using the three-point scale. The nonsignificant association between male song complexity and our scores for relative female song complexity supported our assumption of independence (song type repertoire size: $r = .214$, $p = .265$; $N = 29$; syllable repertoire size: $r = .081$, $p = .651$; $N = 34$). To test for the reliability of our estimation of female relative song complexity, we collected available quantitative information about relative female song complexity from the literature (Table 1). We found studies for seven species that simultaneously estimated song complexity of the two sexes by relying on the same measures. By using these quantitative estimates, we calculated the ratio between female and male song complexity, which is analogous to our assessment of relative female song complexity using the three-point scale. Without showing these data, we also asked an ornithologist colleague to score relative female song complexity in the same species based on handbook information. There was a significant positive correlation between the two estimates of female absolute song complexity (Kendall $\tau = 0.858$; $p = .015$; $N = 7$). These correlations

provide evidence that our definition of relative song complexity of females has a biological basis. Any level of arbitrariness in the information provided in handbooks would only cause noise in our analyses and hence render any detected relationships conservative. We note that such noise may increase type I errors in the data independent of the hypothesis at hand, but not consistent bias. To estimate absolute song complexity of females, we applied the following formula: male absolute song complexity \times (score for female song complexity/2), in which song type and syllable repertoire size were used as measures of absolute male song complexity. Difference in song complexity between sexes was simply the difference between absolute estimates of song complexity in the two sexes based on song type or syllable repertoire size. Hence, song complexity differences can be derived by the following formula: male absolute song complexity \times [1-(score for female song complexity/2)], in which the parenthetical expression reflects relative song complexity of males in percentage. Therefore, sexual differences in song complexity can be regarded as the weighted song complexity of males that is controlled for female song complexity based on our handbook estimations. We avoided using scores for relative song complexity of females to test our prediction posed in the Introduction, because this prediction is specifically related to differences in song complexity. Relative song complexity of females may be the same in two species (e.g., *Corvus monedula* and *Ficedula hypoleuca*), but this may involve substantially different deviations from male song complexity. In theory, we suspect that these absolute deviations are important determinants of brain size dimorphism. Absolute song complexity of males was \log_{10} -transformed, whereas intersexual difference in song complexity was $\log_{10}(+1)$ -transformed and used in the comparative analysis.

Large song and syllable repertoires may be associated with a polygynous mating system and migratory habit (Read and Weary, 1992). Therefore, these confounding factors should be controlled in a comparative study. Species were classified as having either (1) no polygyny (a score of zero), (2) irregular polygyny (species with less than 5% of males attracting more than one female were given a score of one), or (3) regular polygyny (species with more than 5% of males attracting more than one female were given a score of two). Migratory behavior was scored on a three-point scale as (1) resident (a score of zero), (2) partial migrant (species having resident and migratory populations; a score of one), or (3) migrant (a score of two). Information on migration and polygyny originated from handbooks and field guides (Cramp and Perrins, 1985–1994; Heinzel et al., 1997; National Geographic, 2000; Poole et al., 1993–2002). Confounding variables were treated as continuous variables in the comparative analyses. This treatment was applied because of the constraints of the chosen phylogenetic program (see below), which accepts continuous variables only. The use of migration and polygyny on a continuous scale implies the assumption that intermediate states are biologically meaningful and comparable. Similar approaches have been widely used in comparative biology (see Bennett and Owens, 2002). The entire database is given in Table 2.

Phylogenetic information for our comparative analyses originated from a number of sources using molecular techniques. We constructed a composite phylogenetic hypothesis at the family level mainly based on information in Sibley and Ahlquist (1990) derived from extensive studies of DNA–DNA hybridization. This phylogeny for higher taxa was supplemented with information from Arnaiz-Villena (1998; *Carduelidae*), Blondel et al. (1996; *Sylviidae*), Cibois and Pasquet (1999; *Corvidae*), and Grapputo et al. (2001; *Emberizidae*) to resolve relationships in taxa with many species.

We applied branch lengths from the tapestry tree of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families the distance between different genera was set to 3.4 ΔT_{50H} units; between species within genera, to 1.1 ΔT_{50H} units (Bennett and Owens, 2002; Sibley and Ahlquist, 1990). The phylogeny is given in Figure 1. Recent studies indicated that the phylogeny of Sibley and Ahlquist (1990) may be incorrect for some taxa (Barker et al., 2002; Sheldon and Gill, 1996). However, when we reconstructed our composite phylogeny based on Barker et al. (2002) and used equal branch lengths, the conclusions of this article did not change.

We applied the general method of comparative analysis for continuous variables based on generalized least squares (GLS) models using the statistical software Continuous (Pagel, 1997, 1999a). The GLS model characterizes evolutionary changes along each branch of a phylogenetic tree through the variance components of traits (Pagel, 1997). Hypotheses are tested with likelihood ratio statistics. This compares the log-likelihood of the model corresponding to a null hypothesis (H_0) over the model for an alternative hypothesis (H_1), where the likelihood ratio = $-2 \log_e[H_0/H_1]$. The likelihood ratio statistic is asymptotically distributed as a chi-squared variate with degrees of freedom equal to the difference in the number of parameters between the two models. First, we assessed the contribution of scaling parameters sequentially by estimating the maximum likelihood values of the branch length scaling parameters κ , and the phylogeny scaling factor λ (recent simulations showed that the estimation of δ , overall path length scaling factor is biased (Freckleton et al., 2002); thus we avoided estimating this parameter). The κ parameter by differentially stretching long and short branches would yield a punctuational mode of trait evolution at $\kappa = 0$, whereas $\kappa \geq 1$ indicates the importance of long branches in trait evolution (gradualism). Values of $\lambda < 1$ would correspond to traits being less similar among species than expected from their phylogenetic relationship, whereas $\lambda = 1$ suggests the reverse. Any of these potential effects present in the data can be detected by comparing the log-likelihood of a H_0 model containing default (= 1) values for the scaling parameters with the log-likelihood of an alternative H_1 model in which one parameter is permitted to take its maximum likelihood value. If a significant effect was found ($p < .05$), the estimated values were used in the final model; otherwise default settings were used. Second, by using the appropriate scaling parameters, the correlation between pairs of traits was tested by log-likelihood ratio statistics comparing model H_0 that fits the data, forcing the correlation to be zero with the alternative H_1 model and permitting correlated evolution of the two characters. Third, by using the best model fitting the data, we estimated the phylogenetic correlation between traits. We assumed that the evolution of traits followed standard constant-variance random walk evolutionary model, and thus we used the corresponding settings in Continuous (model A). The appropriate scaling parameters and the log-likelihood ratio statistics testing for correlated trait evolution are presented. When we controlled for potentially confounding factors, we entered these variables together with the variables of interest in the same model, and calculated the partial phylogenetic correlation for the relationship in question. Sex-specific brain size was statistically controlled for sex-specific body size, whereas absolute brain size dimorphism was controlled for absolute body size dimorphism. These allometric effects were controlled statistically by calculating the phylogenetically corrected regression of the dependent variable on the independent variable (using Continuous). Based on this relationship, residuals were calculated for the raw species data (see also Purvis and Rambaut, 1995). The phylogenetic method implemented in the program Continuous

Table 2

Male body mass, male brain size, female body mass, female brain size, sample size for males, sample size for females, the volume of the HVC, song type repertoire size of males, syllable repertoire size of males, score for relative song complexity of females, sexual difference in repertoire size, sexual difference in syllable repertoire size, migration, and polygyny in bird species used in this study

Species	Mbod	Mbr	Fbod	Fbr	Nm	Nf	HVC	MSTR	MSR	FSC	DSTR	DSR	M	PG	Ref
<i>Alauda arvensis</i>	40.61	0.966	38	0.91	1	5			15	1		7.5	2	0	a
<i>Carduelis chloris</i>	26.34	0.888	27.29	0.857	11	34	1.082	22	3	1	11	1.5	2	2	a,b
<i>Carduelis flammea</i>	10.97	0.55	12.71	0.527	1	1		16		0.5	12		3	0	c
<i>Carduelis spinus</i>	12.32	0.607	11.36	0.523	4	6			15	1		7.5	3	0	a
<i>Certhia familiaris</i>	8.8	0.45	10.4	0.57	1	1	0.640	1	5	0.5	0.75	3.75	1	1	a
<i>Cinclus cinclus</i>	72	0.92	58.03	1.44	2	1			12	2		0	1	1	a
<i>Corvus monedula</i>	232.47	4.883	165.26	4.41	6	3	1.200			0			2	1	
<i>Emberiza calandra</i>	57.8	1.138	53.31	1.149	1	2		2	20	0	2	20	2	2	a
<i>Emberiza citrinella</i>	28.72	0.785	28.2	0.781	12	26		2	3	0	2	3	2	1	a,b
<i>Emberiza schoeniclus</i>	20.8	0.645	20.1	0.75	2	2	0.836	20	3	0	20	3	2	1	a
<i>Erithacus rubecula</i>	18.27	0.629	17.19	0.713	3	9	1.551	1000	4	2	0	0	2	0	a
<i>Ficedula hypoleuca</i>	12.71	0.443	14.52	0.51	1	3		1000	9	0	1000	9	3	2	a,b
<i>Fringilla coelebs</i>	24.28	0.761	23.61	0.743	17	39	0.737	3	9	0.5	2.25	6.75	2	0	a,d
<i>Garrulus glandarius</i>	171.45	3.999	161.18	3.864	17	17	1.266			0			1	1	
<i>Hippolais icterina</i>	13.09	0.518	14.63	0.483	3	3			1.5	0		1.5	3	0	a
<i>Hirundo rustica</i>	16.06	0.584	17.09	0.538	6	6	0.841	1000	19.8	0	1000	19.8	3	0	c,e,f
<i>Motacilla alba</i>	20.96	0.569	18.95	0.53	2	9			9	0		9	2	0	a
<i>Parus caeruleus</i>	10.99	0.596	10.79	0.64	3	10	0.756	5	2	1.5	1.25	0.5	1	1	a,b
<i>Parus major</i>	17.75	0.88	17.32	0.793	7	15	0.830	3	2.4	0.5	2.25	1.8	1	1	a,b
<i>Passer domesticus</i>	28.51	0.886	28.35	0.892	10	33		1	1	0	1	1	1	2	g-i
<i>Passer hispaniolensis</i>	29.1	0.95	30.5	0.89	1	1		1	1	0	1	1	2	0	g-i
<i>Passer montanus</i>	22.24	0.77	22.99	0.779	6	9		1	6	0	1	6	1	0	a
<i>Phoenicurus phoenicurus</i>	13.34	0.454	15.82	0.35	1	7		200	18	0.5	150	13.5	3	2	a,b
<i>Phylloscopus collybita</i>	8.99	0.292	7.3	0.32	3	2	0.534	1	2	0.5	0.75	1.5	3	2	a
<i>Pica pica</i>	229.22	5.640	200.70	5.036	15	13	1.454			0			1	1	
<i>Prunella modularis</i>	20.25	0.69	21.52	0.623	6	10	1.017	4	12	1	2	6	1	2	a
<i>Regulus regulus</i>	5.89	0.38	5.46	0.343	6	11		1	6	0.5	0.75	4.5	2	0	a
<i>Sayornis phoebe</i>	18.1	0.793	17.5	0.75	1	1		2	2	1	1	1	2	0	a
<i>Serinus canaria</i>	17.1	0.848	15.3	0.564	1	1	1.111	316	10	1	158.1	5	1	0	j
<i>Sturnella loyca</i>	64.7	2.175	60.65	1.905	2	2		8		0	8		1		b
<i>Sturnus vulgaris</i>	80.85	1.837	75.5	1.72	3	7	1.170	39.9	15	1	19.95	7.5	2	1	a,k
<i>Sylvia atricapilla</i>	18.57	0.628	18.68	0.594	3	10	0.768	1000	25	1	500	12.5	2	0	aj
<i>Sylvia borin</i>	18.38	0.657	19.24	0.52	2	6	1.241	1000	20	0.5	750	15	3	1	aj
<i>Sylvia communis</i>	13.61	0.518	15.17	0.54	4	5			15	0		15	3	1	a
<i>Sylvia curruca</i>	11.51	0.482	13.61	0.47	3	5			8	0		8	3	0	a
<i>Troglodytes troglodytes</i>	9.79	0.52	8.65	0.445	2	7	0.680	6.5	47	0.5	4.875	35.25	2	2	a
<i>Turdus iliacus</i>	68.15	1.354	62.26	1.076	1	1		76	10.4	0	76	10.4	2	0	l-n
<i>Turdus merula</i>	95.82	1.773	101.87	1.765	22	34	1.527	32	6	0.5	24	4.5	2	0	a
<i>Turdus philomelos</i>	69.45	1.542	70.38	1.429	14	19		171	9	0	171	9	2	0	a

Mbod indicates male body mass (in grams); Mbr, male brain size (in grams); Fbod, female body mass (in grams); Fbr, female brain size (in grams); Nm, sample size for males; Nf, sample size for females; HVC, the volume of the HVC (in mm³); MSTR, song type repertoire size of males; MSR, syllable repertoire size of males; FSC, score for relative song complexity of females; DSTR, sexual difference in repertoire size; DSR, sexual difference in syllable repertoire size; M, migration; and PG, polygyny. The sources for male repertoire sizes are given in a separate column (Ref). ^aRead and Weary, 1992; ^bMacDougall-Shackleton, 1997; ^cMøller et al., 2000; ^dRiebel and Slater, 1999; ^eGaleotti et al., 1997; ^fGaleotti et al., 2001; ^gCramp and Perrins, 1985–1994; ^hBlotzheim, 1985–1997; ⁱPoole et al., 1993–2002; ^jDeVoogd et al., 1993; ^kEens, 1997; ^lLampe and Espmark, 1987; ^mH.M. Lampe, personal communication; ⁿEspmark et al., 1989.

does not allow insight on the phylogenetically transformed data (Pagel, 1999b). For illustrative purposes we present figures based on the raw species data, on which we superimpose the phylogenetically corrected regression lines.

RESULTS

Relying on GLS models, there was no significant evidence for relative brain size being related to song complexity in males (song type repertoire size: $\kappa = 1.000$, $\lambda = 1.000$, phylogenetic correlation = 0.080, LR = 0.094, df = 1, $p = .664$, $N = 29$, Figure 2A; syllable repertoire size: $\kappa = 1.000$, $\lambda = 1.000$, phylogenetic correlation = -0.090, LR = 0.137, df = 1, $p = .601$, $N = 34$; Figure 3A). This pattern remained unchanged when we controlled for potentially confounding factors of polygyny and migratory habits (partial phylogenetic correla-

tions, song type repertoire size: $r = -.043$, $p = .833$; syllable repertoire size: $r = -.158$, $p = .353$).

When we included HVC volume in the analysis, we found significant and positive interspecific associations between relative HVC volume and song type repertoire size, but the relative size of the rest of the brain did not explain any of the remaining residual variance in song complexity (partial phylogenetic correlations, HVC and song type repertoire size: $r = .596$, $p = .005$, $N = 16$; relative brain size of males and song type repertoire size: $r = .121$, $p = .649$, $N = 16$; HVC and syllable repertoire size: $r = -.102$, $p = .703$, $N = 16$; relative brain size of males and syllable repertoire size: $r = .414$, $p = .073$, $N = 16$).

Relative brain size dimorphism was negatively but not significantly associated with absolute measures of male song complexity (song type repertoire size: $\kappa = 1.000$, $\lambda = 0.000$,

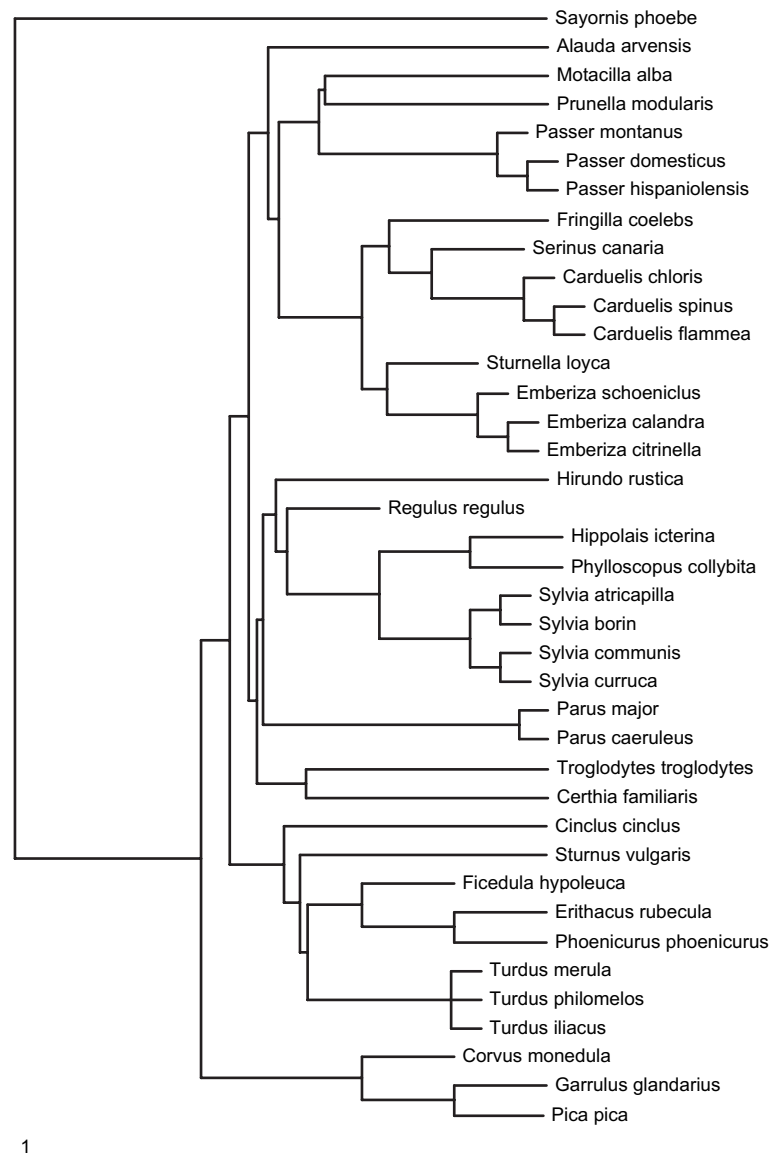


Figure 1
Phylogeny of birds used for the phylogenetic analysis of relative brain size in association with song complexity. The scale is given at the bottom left based on $\Delta T_{50}H$ units.

phylogenetic correlation = -0.260 , $LR = 1.013$, $df = 1$, $p = .155$, $N = 29$, Figure 2B; syllable repertoire size: $\kappa = 0.489$, $\lambda = 0.000$, phylogenetic correlation = -0.205 , $LR = 0.729$, $df = 1$, $p = .227$, $N = 34$; Figure 3B). Similar, but more robust patterns for both song type and syllable repertoire size emerged when we used sexual differences in song complexity (song type repertoire size: $\kappa = 1.000$, $\lambda = 0.000$, phylogenetic correlation = -0.367 , $LR = 2.100$, $df = 1$, $p = .040$, $N = 29$, Figure 2C; syllable repertoire size: $\kappa = 0.524$, $\lambda = 0.000$, phylogenetic correlation = -0.489 , $LR = 4.644$, $df = 1$, $p = .002$, $N = 34$; Figure 3C). After controlling for migration and polygyny, we obtained similar results (partial phylogenetic correlations, song type repertoire size: $r = -.376$, $p = .025$; syllable repertoire size: $r = -.478$, $p = .001$).

We tested whether the observed negative phylogenetic association between relative brain size dimorphism and song complexity differences between sexes was mediated by an evolutionary decrease in relative brain size of females or by an evolutionary increase in relative brain size of males relative to

that of females. To control for covariation between relative size of the brain of the two sexes, we introduced brain sizes of the sexes adjusted for body size in the same model and tested for their effects on sexual differences in song complexity. Holding allometric effects constant, we found that male brain size was positively, and female brain size was negatively related to song complexity differences, with females showing more robust effects (partial phylogenetic correlations, female relative brain size and differences in song type repertoire size: $r = -.588$, $p < .001$; male relative brain size and differences in song type repertoire size: $r = .307$, $p = .071$; Figure 2D; female relative brain size and differences in syllable repertoire size: $r = -.593$, $p < .001$; male relative brain size and differences in syllable repertoire size: $r = .351$, $p = .021$; Figure 3D).

DISCUSSION

Our results partially supported our predictions. We predicted that song complexity was positively related to relative brain

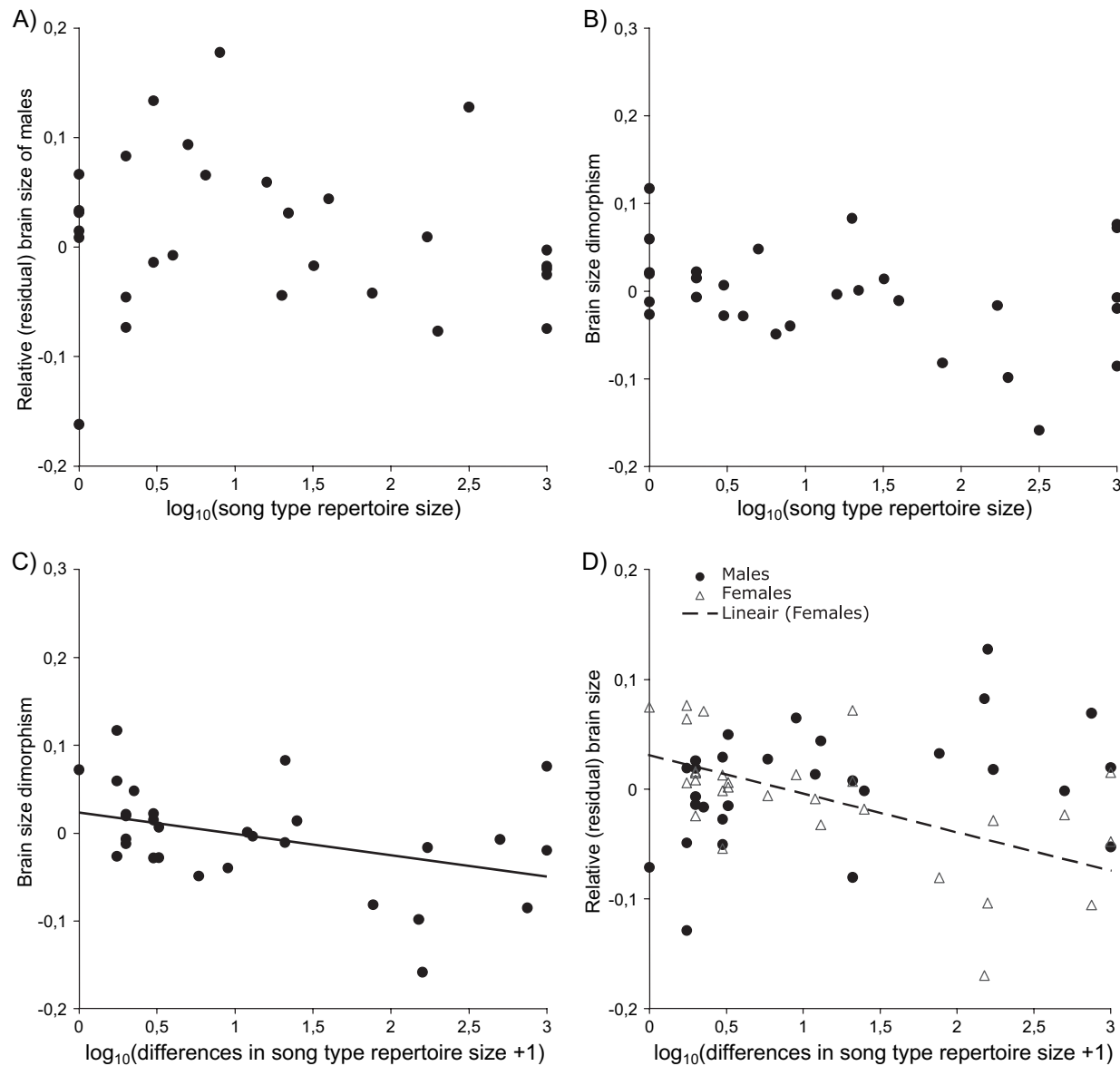


Figure 2

Song type repertoire size in relation to relative brain size and brain size dimorphism based on raw species data of birds. Positive values of brain size dimorphism indicate that females have relatively larger brains than do males. Regression lines are given if the regressions are significant (for phylogenetic associations, see text). (A) Absolute song type repertoire size and brain size in males adjusted for body size: $r = -.160$, $p = .407$, $N = 29$. (B) Song type repertoire size of males and brain size dimorphism: $r = -.287$, $p = .132$, $N = 29$. (C) Sexual differences in song type repertoire size and brain size dimorphism: $r = -.401$, $p = .031$, $N = 29$. (D) Sexual differences in song type repertoire size and brain size of the two sexes adjusted for body size when covariation between brain sizes of the two sexes was controlled statistically in a multiple regression: $F_{2,28} = 7.993$, $p = .002$; slope for females = -9.974 (SE = 2.605), $p < .001$; slope for males = 5.120 (SE = 2.841), $p = .083$.

size of males among species, but we failed to detect such an association. Even after controlling for potentially confounding factors, the phylogenetic correlation between male brain size and repertoire size was very close to zero. Only variation in relative HVC volume explained variance in song complexity estimated by song type repertoire size, as previously found by DeVogd et al. (1993). According to our results, if brain regions outside the HVC coevolve with song complexity, their concerted evolution does not lead to enlargement of overall brain size. Hence, males of species with larger repertoires do not need to maintain larger brains than do males of species with small song complexity. Although sample size was limited in the present study, we assume that our negative findings with overall brain size are of biological relevance, because even in

a very small sample we were able to reproduce the observations of DeVogd et al. (1993) with respect to HVC size and songs and HVC and overall brain size, respectively. Therefore, we suggest that there is no direct evolutionary link between brain enlargement and song complexity in male birds, and that selection for complex songs may not have led to the evolution of volumetrically extended overall brain size. The major determinants of species-specific brain size should be sought among factors associated with ecology, life history, diet, parental care, behavioral flexibility, diurnal activity, habitat, and foraging technique (Barton, 1998; Bennett and Harvey, 1985; Clutton-Brock and Harvey, 1980; Garamszegi et al., 2002; Jerison, 1973; Lefebvre et al., 1997; Pagel and Harvey, 1988).

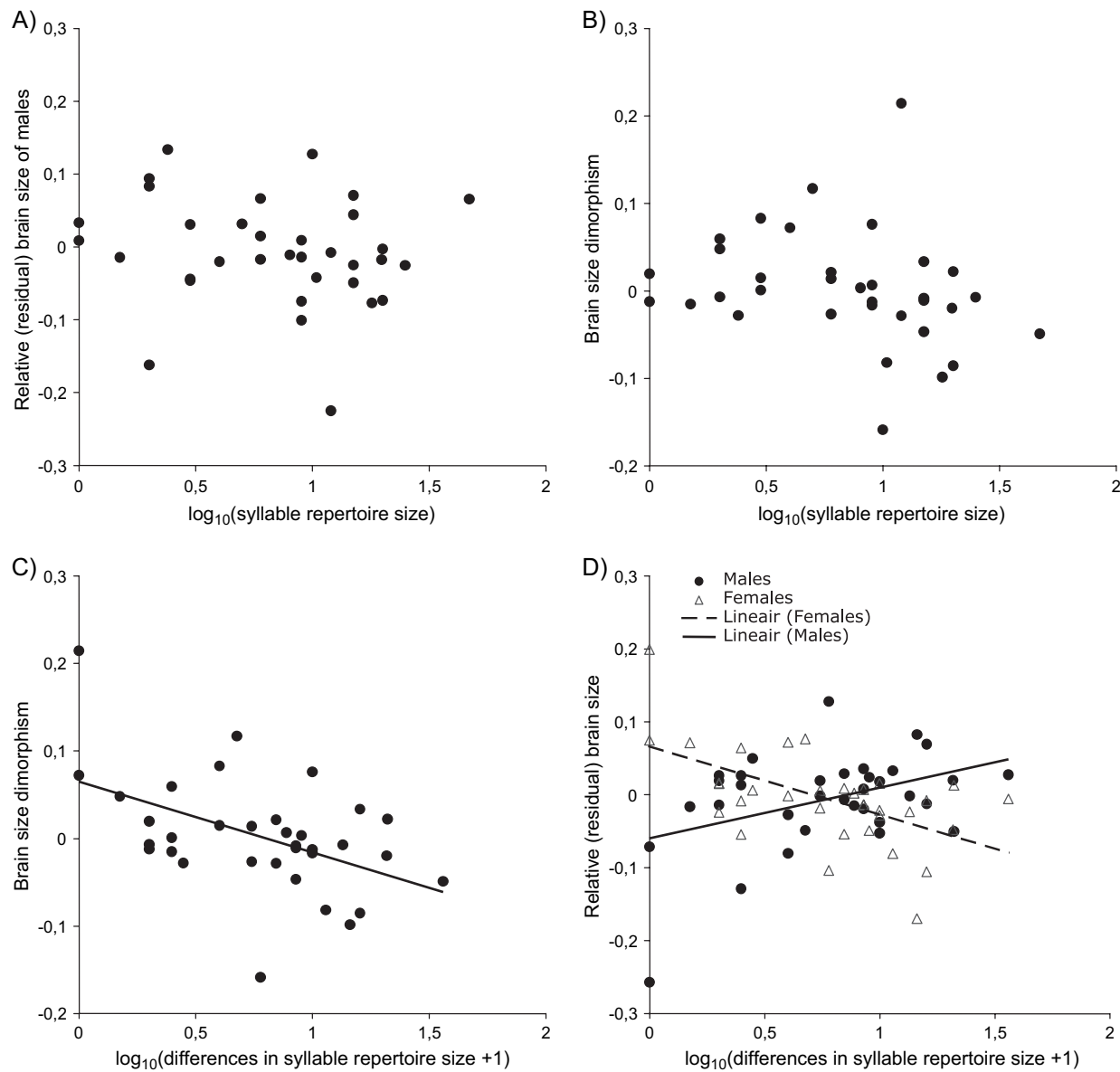


Figure 3

Syllable repertoire size in relation to relative brain size and brain size dimorphism based on raw species data of birds (for phylogenetic associations, see text). Positive values of brain size dimorphism are for species in which females have relatively larger brains than males. Regression lines are given if regressions are significant. (A) Syllable repertoire size and relative brain size of males adjusted for body size: $r = -.158$, $p = .373$, $N = 34$. (B) Syllable repertoire size of males and brain size dimorphism: $r = -.251$, $p = .152$, $N = 34$. (C) Sexual differences in syllable repertoire size and brain size dimorphism: $r = -.480$, $p = .004$, $N = 34$. (D) Sexual differences in syllable repertoire size and brain size of the two sexes adjusted for body size when covariation between brain sizes of the two sexes was controlled statistically in a multiple regression: $F_{2,33} = 8.328$, $p = .001$; slope for females = -3.738 (SE = 0.916), $p < .001$; slope for males = 1.872 (SE = 0.887), $p = .043$.

On the other hand, we found that intersexual difference in brain size tended to relate to song complexity in males interspecifically. In addition, when we controlled for female singing behavior by directly assessing sexual differences in song complexity, the relationships appeared to be robust and significant. These results are in accordance with our second set of predictions.

Large intra- and interspecific variation in temporal organization and complexity of bird song of males can be attributed to factors associated with male-male competition and female choice (Catchpole and Slater, 1995; Read and Weary, 1992). Hence song complexity of males might cover an entire suite of sexually different, reproduction-related behaviors subject to

sexual selection. This association led us to hypothesize an evolutionary link between brain size dimorphism and male song complexity, which we found. However, when females compete, they may also sing for broadly the same reasons as males, at least in few species: to defend territories or mates against other females and to attract mates (Langmore, 1998). Such factors may have confounding effects, but at present, it is difficult to assess female song complexity quantitatively for the majority of species. Here, we applied a rough but unbiased and biologically relevant approach to estimate song type and syllable repertoire size in females. When we controlled for female song performance by calculating sexual differences in song complexity, the association with brain size dimorphism

was even more pronounced in the expected direction. Alternatively, when we controlled for female song complexity by removing confounding species in which females sing as complex songs as do males (*Cinclus cinclus* and *Eriothacus rubecula*), the relationship becomes significant for absolute male song complexity. Therefore, we suspect that with the two variables we captured similar biological phenomena. Hence song complexity of males, or more precisely sexual differences in song complexity, might cover an entire suite of sexually different, reproduction-related behaviors subject to sexual selection. These measures may reflect the degree of a difference in many behaviors such as territory or mate defense and in several courtship behaviors. If these behavioral differences have different neural representation in males and females, then the corresponding brain regions should show sex-specific evolutionary patterns, even if there is no direct association between overall brain size and songs. As differences in song complexity might be associated with complex behavioral differences, it could also be associated with intersexual differences in overall brain capacities determining these behavioral patterns. For example, sexual selection acting differently on female and male behavior may cause variation in brain capacity. The same selection pressures may shape song production as well, both in males and females. These evolutionary constraints may thus produce a positive relationship between differences in song complexity and sexual dimorphism in brain size without requiring a direct causal link between song and overall brain size. Hence, the repertoire size of males and, more importantly, the differences in repertoire size between sexes, reflecting the impact of sexual selection on behavior, may be differentially related to the evolution of brain size in males and females. We suggest that the relationship between sexual dimorphism in relative brain size and song performance reflects a role for complex, sex-specific behavioral adaptations during reproduction leading to sexually asymmetric evolution of brain size.

Our detailed analysis with brain sizes of the two sexes adjusted for body mass revealed that females have relatively smaller brains than do males with increasing differences in song complexity between sexes, whereas males have relatively larger brains than do females. These patterns may indicate that selection pressures favoring more complex songs in males increased brain size of males relative to that of females. On the other hand, the evolution toward similarity in song structure of the two sexes as reflected by small or no differences in song complexity was accompanied by brain enlargement in females. Based on the correlative nature of our findings, it is difficult to make a judgment about the causal mechanism and to disentangle the role of the two sexes in mediating such interspecific patterns. In addition, the small sample size that was available for the present study calls for cautious interpretations.

There is some evidence suggesting that brain size evolution may be different in the two sexes. Gittleman (1994) found sex differences in patterns of overall brain size in carnivorous mammals associated with maternal investment. In bowerbirds Madden (2001) demonstrated a positive relationship between bower complexity, as a measure of a sexually selected character, and relative brain size. Although this relationship was stronger for males than for females, the relationship appeared to be present in both sexes. We found among passerine birds that intersexual variation in brain size may be explained by differences in sexual behavior reflected by absolute song complexity of males or sex differences in song complexity, although there is no direct relationship between songs and overall brain size. This may arise from selection on song differing between the sexes, for example, owing to territory defense or mate attraction affecting the evolution of

sexually dimorphic, complex behavior and the associated neural tissue. Brain capacity in relation to sex-specific behavior may thus be asymmetrically shaped by sexual selection.

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