

*Evolutionary Ecology Research*, 2006, **8**: 75–90

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## Avian song complexity is associated with high field metabolic rate

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### ABSTRACT

**Question:** Is the production of bird song costly? Analyses of oxygen consumption during singing provided conflicting results.

**Data studied:** Data on 28 passerine species with quantitative information on song complexity and field metabolic rate, which reflects energy requirements of wild birds. The phylogenetic relationship data came from molecular sources.

**Search method:** Generalized least squares models to control for phylogenetic associations. First, we adjusted field metabolic rate to body size, and calculated the phylogenetic correlation between relative field metabolic rate and measures of song complexity. Second, we compared song complexity of birds inhabiting arid and mesic environments.

**Conclusion:** A measure of short-term song complexity, relative syllable repertoire size, is positively and significantly related to relative field metabolic rate. Species from arid habitats have less complex songs than species from mesic habitats.

*Keywords:* bird song, cost, energetics, field metabolic rate, repertoire size, song complexity.

### INTRODUCTION

Energy is behind all life, and it is crucial in determining adaptations to different environments, reproductive success, survival and, ultimately, inclusive fitness in all organisms (Garland and Carter, 1994; Williams and Vezina, 2001; McNab, 2002). Energetic needs may constrain reproduction through limited availability of resources, through negative effects on future reproduction or through interactions with other metabolically demanding life-history traits (e.g. Drent and Daan, 1980; Meijer *et al.*, 1989; Tinbergen and Dietz, 1994; Moreno *et al.*, 1995, 2001). Accordingly, several studies in different taxa reported a relationship between metabolic rate and reproduction (for a review, see McNab 2002). However, the boundaries for energy expenditure associated with reproduction are still difficult to draw. For example, the general extent of the variation in reproductive success that energy or metabolism can explain remains obscure. Some

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studies show very strong relationships, some studies show moderate effects, while others demonstrate that the highest fitness corresponds to intermediate metabolic levels (Tatner and Bryant, 1993; Williams and Vezina, 2001; McNab, 2002). In addition, the component of the reproduction that is vitally constrained by energy requirements is still unclear in many cases (McNab, 2002). For example, little is known about the role of sexual selection in mediating a link between metabolism and reproduction, although sexual selection plays an important role in the evolution of reproductive mechanisms. The main pattern that we intend to explain here is the interspecific variation in the complexity of bird song in association with field metabolic rate.

Complex songs provide males with an advantage in sexual selection in many passerine birds, because females prefer males with such songs (Searcy and Yasukawa, 1996). Signals given in social contexts where senders and receivers have different evolutionary interests, as in sexual selection, must be stabilized by costs or constraints on senders that guarantee signal reliability (Zahavi, 1975; Grafen, 1990). If the cost imposed by the production of complex songs varies among males, the potential exists for song to reveal the ability of the singer to cope with these costs, and thus advertise the signaller's phenotypic or genetic quality. Individual variation in the expression of these signals will therefore depend on the condition of the male.

Is singing costly? This challenging question has triggered researchers to investigate the energy budget underlying sound production in birds (Vehrencamp *et al.*, 1989; Eberhardt, 1994; Chappell *et al.*, 1995; McCarty, 1996; Oberweger and Goller, 2001; Ward *et al.*, 2003, 2004). Most authors agree that singing is a costly activity, because it involves complex muscular contractions that need energy, and it competes with other types of behaviour that require time (e.g. foraging). However, studies determining the metabolic cost of generating vocalizations in birds disagree on the size of increase in energy consumption due to singing (Eberhardt, 1994; Gaunt *et al.*, 1996; Oberweger and Goller, 2001; Ward *et al.*, 2003, 2004). Furthermore, the energetic background for song content and song complexity remains controversial, because available data have provided negative evidence. In a comparative analysis of passerine birds, Read and Weary (1992) did not find a correlation between absolute and relative resting metabolic rate and avian song complexity described by versatility, syllable and song repertoire size. Oberweger and Goller (2001) showed that the increase in metabolic rate during singing was no greater in a species that produces very complex songs than in two other species.

However, the possibility that inbred lines of caged birds sing differently to those in the wild might be at odds with available results on the metabolic cost of song production (Gil and Gahr, 2002). Additionally, methodological problems, differences in experimental design between studies and the inclusion of a mixture of passerine and non-passerine taxa without controlling for phylogeny also suggest that, based on available comparative data, it might be premature to eliminate the possibility that interspecific differences in song complexity may be linked to differences in energy expenditure. To investigate evolutionary mechanisms mediated by energetic constraints that act on the complexity of bird songs, more comprehensive investigations are needed, using standardized data on metabolism and song complexity recorded under field conditions.

The rate at which a wild animal uses resources in its environment is determined primarily by its metabolic energy requirements (Nagy, 1987; Nagy *et al.*, 1999). Field metabolic rate (FMR) is the total energy cost that a wild animal pays during its daily activity in natural conditions. Field metabolic rate offers an integrated measure of metabolism over a protracted period as it includes all components of the energy budget, from basal maintenance functions, as

expressed by the basal metabolic rate, to thermoregulation and activity. Energy metabolism in the field is measured routinely by means of the doubly labelled water technique (Speakman, 1997). There has been widespread application of the doubly labelled water technique to measure field metabolic rate in wild animals, and a substantial number of diverse vertebrate groups has now been studied (Nagy, 1987). A large body of FMR data for different terrestrial vertebrates has now been published, permitting comparative investigations. These inter-specific comparisons of field metabolic rate have revealed taxon-dependent allometric effects, and associations with different environmental factors (Nagy, 1987; Nagy *et al.*, 1999; Tieleman and Williams, 2000).

If the production of complex songs in birds is constrained by energetic costs, it may have metabolic consequences. If the production of complex songs involves intense muscular activity or requires neural machinery with significant energy consumption, there would be selection for increased metabolic visceral capacity to sustain the high energy expenditure involved in complex song. This increased capacity would, in turn, result in an increase in field metabolic rate (Daan *et al.*, 1990). If energetic requirements constrain song evolution, field metabolic rate should be positively associated with song complexity across different avian species. This relationship can be mediated by female preference for costly signals reflecting individual quality, and sexual selection may thus favour an increase in field metabolic rate. However, an opposite causal mechanism between metabolism and song may be at work if species occupying habitats that are rich in net resources are those that are able to invest more in trait expression. Under these schemes, a positive association between song complexity and field metabolic rate would indicate a role for energetic constraints in the evolution of bird song.

On the other hand, the assimilation capacity model (Koteja, 2000) predicts a positive association between field metabolic rate and song complexity without any direct causal link between the two. According to this model, field metabolic rate could be linked to the capacity for high short-term exertion, or to the maintenance of complex behaviours through its association with increased capacity of visceral organs. Hence, selection for enhanced parental care, for example, would concurrently drive selection for increased field metabolic rate in endotherms (Koteja, 1991). If song reflects the contribution made by males to brood provisioning in species with intense parental care (Read and Weary, 1992), this could drive an apparent relationship between song complexity and field metabolic rate across avian species.

No correlation between field metabolic rate and song would be expected if the former does not respond directly to intense but short bursts of activities like song. This may be because field metabolic rate could only be correlated intraspecifically with allocation to very costly and/or time-consuming activities like flight (Carlson and Moreno, 1992) or diving (Wilson and Culik, 1993). A lack of covariation between field metabolic rate and song complexity could also result if energetic requirements do not constrain complex song production.

Based on these predictions, the aim of the present study was to re-analyse the relationship between avian song complexity and metabolism. In our comparative approach, based on a literature search, we used field metabolic rate and other variables to describe song complexity for 29 passerine species. Here, we have avoided using basal metabolic rate because its biological meaning remains unclear (Koteja, 1991; Ricklefs *et al.*, 1996). The absence of a direct association between basal metabolic rate and field metabolic rate in birds (Ricklefs *et al.*, 1996) suggests that the two measures are in part structurally independent. Only field metabolic rate refers to the energy budget of animals in their natural environment. First, we

assessed whether passerine bird species that have evolved complex songs had a higher field metabolic rate while controlling for relationships due to common descent, body size and other potentially confounding factors, such as inter-seasonal variation and migration habits. Second, we examined whether an energetically constrained ecological factor affected song complexity by comparing birds differing in the aridity of their breeding environment. We predicted that metabolic adaptation to arid environments should limit the energy available for costly song traits.

## MATERIALS AND METHODS

From the literature we obtained information on the field metabolic rate of passerines, expressed in  $\text{kJ} \cdot \text{day}^{-1}$  and determined by the doubly labelled water method (Speakman, 1997). If more than one estimate was available for a species, we used the mean in the analyses. For experimental studies, only data for control treatments were considered. Regardless of the time of the year, we found significant repeatability of field metabolic rate within species for which multiple data were published in independent papers or particular studies ( $R = 0.63$ ,  $F_{28,58} = 7.552$ ,  $P < 0.0001$ ). Consequently, to obtain a larger sample size, we included all available data irrespective of season. However, we also performed the analyses excluding data for wintering birds to control for any potential effect of inter-seasonal variation.

To adjust for body size in the subsequent analyses, we used body mass data as presented in the original source. Depending on the taxonomic level, there are several allometric equations available that permit body size adjustment (Nagy, 1987; Weathers and Sullivan, 1989; Tatner and Bryant, 1993). In this study, taking the allometric equation calculated for our data into account [linear regression on  $\log_{10}$ -transformed data,  $r^2 = 0.780$ ,  $F_{1,27} = 95.801$ ,  $P < 0.0001$ ; slope (standard error) = 0.646 (0.066)], we divided field metabolic rate by mass elevated to 0.65. However, when we used alternative exponents (0.75, 0.87) or multiple regression to control for body size effects, the results and conclusions were very similar.

We primarily obtained information about song complexity from the literature. We intended to use song repertoire size as the measure of long-term song complexity, and syllable repertoire size to reflect short-term song complexity, since previous comparative studies have demonstrated that these estimates are subject to sexual selection (Read and Weary, 1992; MacDougall-Shackleton, 1997). However, reported song data were limited: we found information on song repertoire size and syllable repertoire size for 19 and 18 species, respectively. We were conscious that a test of our predictions using these variables was likely to suffer from insufficient statistical power.

Hence, to increase sample size we used our measure for short-term syllable repertoire size (see also Garamszegi *et al.*, 2003). Without knowledge of the FMR data, we analysed sonagrams for male advertisement territorial songs (mean  $\pm$  standard error =  $2.311 \pm 0.123$  songs; range = 1–5 per species) presented in handbooks (Cramp and Perrins, 1985–1994; Poole *et al.*, 1993–2002). Syllables were defined as continuous figures separated by detectable time intervals in the spectrograms. The availability of sonagrams for different species may vary due to differences in study intensity, resulting in potential biases. To control for this confounding effect, we calculated the average syllable repertoire size/length of the analysed songs. The repeatability of song complexity calculated among different observers who independently estimated song complexity for a subset of birds was high ( $R = 0.98$ ,  $F_{10,22} = 159.9$ ,  $P < 0.0001$ ). The within-species repeatability of our measurement for relative syllable repertoire size was also high (for a larger data set:  $R = 0.76$ ,  $F_{93,139} = 9.866$ ,  $P < 0.0001$ ). We

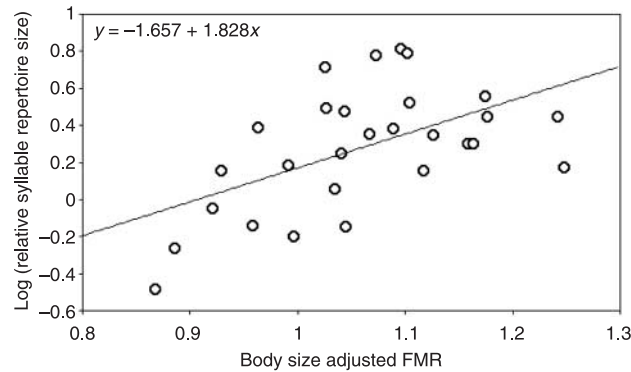
examined the reliability of our estimate by testing the prediction that a positive relationship should exist between variables designated to reflect similar measures of song complexity. Our relative syllable repertoire size measurement was significantly positively correlated with syllable repertoire size as reported by Read and Weary (1992) (Pearson's  $r = 0.517$ ,  $N = 17$ ,  $P = 0.034$ ). In addition, we found a significant positive correlation between relative syllable repertoire size and the relative volume of the nucleus HVC in the brain (Pearson's  $r = 0.410$ ,  $N = 23$ ,  $P = 0.037$  [data from DeVoogd *et al.* (1993) and Székely *et al.* (1996)]). The size of the HVC relative to the rest of the forebrain is the main neural correlate of song complexity (Garamszegi and Eens, 2004). Therefore, in addition to song data from the literature (Read and Weary, 1992; Galeotti *et al.*, 1997; MacDougall-Shackleton, 1997; Møller *et al.*, 2000; Garamszegi *et al.*, 2002), we used our relative syllable repertoire size assessment, based on the assumption that this is an appropriate and reliable estimate of short-term song complexity that can be measured with high repeatability. A song repertoire size scored as infinity by Read and Weary (1992) was assigned an arbitrary value of 1000. The data were  $\log_{10}$ -transformed.

We controlled statistically for migratory habit, because it was related to repertoire size (Read and Weary, 1992). However, migration may also affect energy metabolism, creating a potentially confounding effect. We obtained information on migration from handbooks (Cramp and Perrins, 1985–1994; Poole *et al.*, 1993–2002). Species performing complete migration with no overlap between breeding and wintering range were given a score of 3, birds with partial migration were given a score of 2, and resident species received a score of 1. These scores represented increasing levels of migration. The complete data set is given in Appendices 1 and 2.

We applied the general method of comparative analysis for continuous variables based on generalized least squares models using the statistical software Continuous (Pagel, 1999). We assessed the contribution of the branch length scaling parameter  $\kappa$  and the phylogeny scaling factor  $\lambda$  by estimating their maximum likelihood values. Since no significant deviations ( $P > 0.05$ ) were found, the default ( $= 1$ ) settings were used in the final models. We tested for the correlation between pairs of traits using log-likelihood ratio statistics comparing the likelihood of model  $H_0$  fitted to the data while forcing the correlation between traits to be zero to the likelihood of an alternative model  $H_1$ , in which correlated evolution of the two characters is permitted. We present phylogenetic correlations, as estimated by model  $H_1$ , and the associated log-likelihood ratio test. The phylogeny we used in the comparative analysis is given in Appendix 3.

## RESULTS

Using raw species data there was a significant positive relationship between body size corrected field metabolic rate and our assessment of relative syllable repertoire size ( $r^2 = 0.299$ ,  $F_{1,26} = 11.068$ ,  $P = 0.003$ ; Fig. 1). Similar but non-significant patterns emerged when we used data for song complexity from the literature (song type repertoire size:  $r^2 = 0.161$ ,  $F_{1,16} = 3.081$ ,  $P = 0.098$ , slope  $\pm$  standard error =  $7.149 \pm 4.073$ ; syllable repertoire size:  $r^2 = 0.132$ ,  $F_{1,15} = 3.081$ ,  $P = 0.151$ , slope  $\pm$  standard error =  $2.335 \pm 1.544$ ; statistical power = 0.395 and 0.326 respectively). When we applied a generalized least squares approach to control for phylogeny, we found similar results (phylogenetic correlations: relative syllable repertoire size,  $r = 0.416$ ,  $\chi^2 = 2.664$ , d.f. = 1,  $P = 0.021$ ; song type repertoire size,  $r = 0.225$ ,  $\chi^2 = 0.467$ , d.f. = 1,  $P = 0.333$ ; syllable repertoire size,  $r = 0.115$ ,  $\chi^2 = 0.113$ , d.f. = 1,  $P = 0.634$ ). Due to the low power of tests relying on literature data for song



**Fig. 1.** Relationship between song complexity assessed by relative syllable repertoire size (number of unique syllables within songs/song length) of passerine birds and body size adjusted field metabolic rate [FMR in  $\log_{10}(\text{kJ} \cdot \text{day}^{-1} \cdot \text{g}^{-0.65})$ ]. Line and equation are from linear regression based on raw species data.

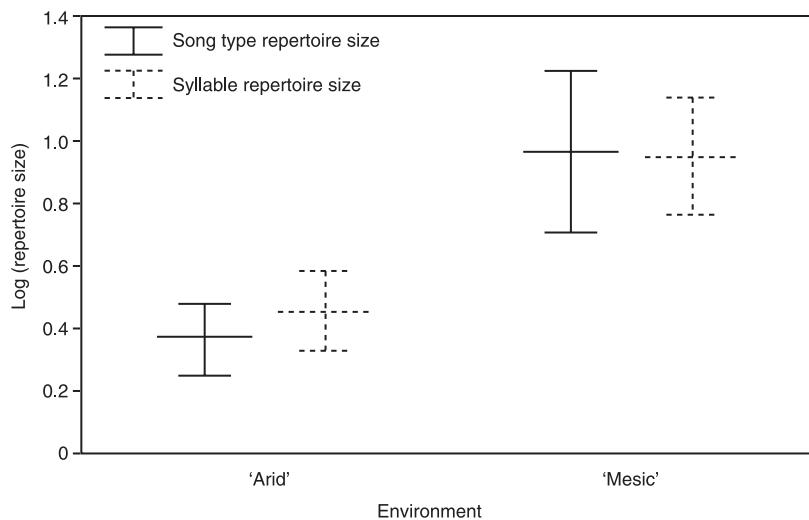
complexity, we continued our analysis with our measure of relative syllable repertoire size.

When we excluded data for wintering birds, the significant, positive relationship between relative syllable repertoire size and body size adjusted field metabolic rate remained (raw species data:  $r^2 = 0.314$ ,  $F_{1,19} = 8.715$ ,  $P = 0.008$ ; phylogenetic correlation:  $r = 0.446$ ,  $\chi^2 = 2.324$ , d.f. = 1,  $P = 0.031$ ). Consistent with Read and Weary (1992), we found a positive relationship between relative syllable repertoire size and migration (phylogenetic correlation:  $r = 0.325$ ,  $\chi^2 = 1.565$ , d.f. = 1,  $P = 0.077$ ), and between metabolic rate and migration (phylogenetic correlation:  $r = 0.416$ ,  $\chi^2 = 2.754$ , d.f. = 1,  $P = 0.019$ ). When we introduced migration, field metabolic rate and relative syllable repertoire size into the same generalized least squares model, and calculated partial phylogenetic correlation coefficients, we found that the covariance between field metabolic rate and relative syllable repertoire size was little affected by migration (partial correlation:  $r = 0.327$ ,  $P = 0.095$ ).

Adaptation to arid environments, where primary productivity is low, can change energy expenditure, as birds from arid habitats have a reduced field metabolic rate (Tieleman and Williams, 2000). In our data, we found three species inhabiting relatively arid areas (*Auriparus flaviceps* Sundevall, *Lanius excubitor* Linnaeus and *Turdoides squamiceps* Cretzschmar). When we compared body size adjusted field metabolic rate and song complexity of these species with those of others, we found that habitat type was associated with both field metabolic rate and relative syllable repertoire size (Mann-Whitney  $U$ -tests: field metabolic rate,  $\text{Mean}_{\text{arid species}} = 0.891$ ,  $\text{Mean}_{\text{mesic species}} = 1.077$ ,  $Z = -2.793$ ,  $P = 0.005$ ; relative syllable repertoire size,  $\text{Mean}_{\text{arid species}} = 0.547$ ,  $\text{Mean}_{\text{mesic species}} = 2.210$ ,  $Z = -2.563$ ,  $P = 0.010$ ). Excluding species inhabiting arid environments, the previously found significant positive relationship between relative syllable repertoire size and field metabolic rate weakened (raw species data:  $r^2 = 0.088$ ,  $F_{1,23} = 2.212$ ,  $P = 0.151$ ; phylogenetic correlation:  $r = 0.188$ ,  $\chi^2 = 0.449$ , d.f. = 1,  $P = 0.343$ ). Using song type and syllable repertoire size data in pairwise comparisons of closely related passerines differing in relative dryness of their habitat (Table 1), a significant environmental effect on song complexity also emerged (paired  $t$ -tests: song type repertoire size,  $t_{11} = 2.408$ ,  $P = 0.034$ ; syllable repertoire size,  $t_{10} = 2.389$ ,  $P = 0.038$ ; Fig. 2).

**Table 1.** Song type repertoire size (STR) and syllable repertoire size (SYR) in pairs of closely related passerine species differing in the aridity of their habitat

'Arid' species	STR	SYR	'Mesic' species	STR	SYR
<i>Anthus campestris</i>	1	3	<i>Prunella modularis</i>	4	12
<i>Cardinalis cardinalis</i>	9	1	<i>Pheucticus ludovicianus</i>	19	10
<i>Carpodacus mexicanus</i>	4	1.3	<i>Carduelis chloris</i>	22	3
<i>Catharus minimus</i>	3		<i>Catharus guttatus</i>	13	4
<i>Catherpes mexicanus</i>	3	3	<i>Troglodytes troglodytes</i>	21	47
<i>Cisticola juncidis</i>	1	2	<i>Acrocephalus palustris</i>	1000	90
<i>Emberiza hortulana</i>	2.5	3	<i>Emberiza citrinella</i>	2	3
<i>Passerculus sandwichensis</i>	1	5	<i>Zonotrichia albicollis</i>	1	4
<i>Passerina amoena</i>	1	9	<i>Passerina cyanea</i>	1	9
<i>Pipilo fuscus</i>	6	1	<i>Pipilo erythrophthalmus</i>	7	1
<i>Spizella pallida</i>	1	1	<i>Spizella pusilla</i>	1	2
<i>Sturnella neglecta</i>	8	8	<i>Sturnella magna</i>	70	5

**Fig. 2.** A pair-wise comparison of song complexity estimated by song type repertoire size and syllable repertoire size of species inhabiting environments with different aridity (mean  $\pm$  standard error).

## DISCUSSION

We found that field metabolic rate, which represents the energy requirements of wild birds, was positively related to measures of song complexity. This relationship was only significant for relative syllable repertoire size, probably because of the low sample sizes for song type and syllable repertoire size. However, based on the repeatability analyses, and the significant relationship between our estimate for short time song complexity and that of Read and Weary (1992), we assume that relative syllable repertoire size estimated from handbooks is a reliable surrogate of short time song complexity. In addition, this measure was also related to migration and immune function (Garamszegi *et al.*, 2003; present study), which are well-known

correlates of song complexity (Read and Weary, 1992; Møller *et al.*, 2000). The association between field metabolic rate and relative syllable repertoire size was independent of seasonal trends and was little affected by migratory habits.

The positive covariation of song complexity with daily metabolic balance suggests that sexual selection for energetically costly song traits advertising male quality could be linked to metabolic capacities that determine field metabolic rate. Species inhabiting niches of inferior quality were found to have a reduced field metabolic rate and less complex songs, which could indicate that in energetically marginal species environmental attributes constrain the evolution of song traits that are costly to produce. Since song complexity appeared to be involved in this process, it supports the hypothesis that song content represents specific energetic costs, which is inconsistent with previous findings (for a review, see Gil and Gahr, 2002). Alternatively, independent selection for metabolic equipment associated with high parental effort in species with intense paternal care (Koteja, 2000), and for complex songs that signal paternal quality, may generate a positive relationship between field metabolic rate and song complexity without any causal linkage. Migration may play a similar mediator role, as it seems to have little effect on the relationship in focus. However, as the correlation between relative syllable repertoire size and field metabolic rate when migration was controlled was still greater than 0.3, we suggest that the mediator role of migration should be minor. To unravel both possible evolutionary pathways, associations among metabolic machinery, parental care, migration and song complexity need to be studied in a comparative context. This task exceeds the aims of the present paper, as we are constrained by limited data availability. Our findings at least permit us to speculate about the possible repercussions of energetic constraints on song complexity for sexual selection.

If complex songs are costly to produce, it may be because of increased energy consumption by the brain. Neural costs have been assumed to be associated with bird song, since song production involves considerable neurons and greater synaptic and dendritic development in the nucleus HVC and other specialized auditory areas in the brain (Marler and Doupe, 2000; Garamszegi and Eens, 2004). The central nervous system is known to consume a significant amount of energy, as species with large brains have increased basal metabolic rate, emphasizing the energetic costs associated with the maintenance of neural structures (Martin, 1981; Bennett and Harvey, 1985). Annual cycles in the size of parts of the brain related to singing covary with singing activity (Alvarez-Buylla and Kirn, 1997; Tramontin and Brenowitz, 2000), and interspecific differences in the size of song related nuclei (such as HVC and RA) have been associated with interspecific variation in song complexity (DeVoogd *et al.*, 1993; Székely *et al.*, 1996). Such relationships imply that structures associated with song complexity may be costly to maintain.

Another possible constraint accounting for a large proportion of energy demands of elaborate singing may act at the muscular level. There are two main muscular systems (syringeal and respiratory muscles) that regulate vocalization, and the harmonic contraction of these muscles provides the mechanical basis for sound generation (Suthers *et al.*, 1999). Birds performing variable and complex vocalizations would therefore be expected to maintain a finely organized muscular system that controls the specific breathing activity and structural changes of the syrinx. A more variable song would hence require more energy to provide fuel for perfect functioning.

The potential cost associated with complex song production in birds would have important theoretical implications for signal evolution, because of the predicted close match between signal design and cost type (Vehrencamp, 2000). Animal handicap signals could evolve as long as the signal entails some cost to the signaller (Zahavi, 1975; Grafen, 1990). On the



other hand, index signals are stabilized by physical and developmental constraints that invariably force the signal to provide reliable information independent of production costs (Maynard-Smith, 1991; Maynard-Smith and Harper, 1995). Repertoire size, a traditional measure of song complexity, is considered to be an index signal (Vehrencamp, 2000). However, in the European starling *Sturnus vulgaris* Linnaeus and in the pied flycatcher *Ficedula hypoleuca* Linnaeus, repertoire size is related to body condition (Lampe and Espmark, 1994; Mountjoy and Lemon, 1996). These results, in combination with our findings, suggest that the maintenance of song complexity involves costs, raising the possibility that song complexity should be treated as a condition-dependent handicap signal.

Here we have demonstrated that song complexity is positively related to metabolism across species, and that this can be mediated by adaptation to environmental factors that constrain energy expenditure. We have discussed the possibility that this link may reflect that the signal function of complex songs is stabilized by costs or constraints on senders. However, our approach has some limitations. Compared with laboratory experiments in which the energy expenditure of singing can be measured under controlled conditions, we were only able to test this relationship in an indirect way by using information from the literature. We must therefore assume that any heterogeneity in the data in relation to differences in field metabolic rate gave rise to random noise. At present, the limited availability of data also renders the findings and consequences conservative. Hence, we view our results as the first indication that avian song complexity may be associated with energetic costs, but further experimental research is needed to decide on the position of this vocal trait in our signal categorization.

Although the analyses presented above were limited in terms of sample size and taxonomic coverage, our findings may have theoretical implications for the study of the evolution of sexual traits. Models of sexual selection generally assume that sexual characters are condition-dependent, which guarantees signal reliability (Zahavi, 1975; Grafen, 1990). If the production or maintenance of such traits requires significant amounts of energy, the elaboration of these signals may be expected to affect, on a phylogenetic scale, other aspects of reproductive physiology that also require energy. For example, acoustic displays are energetically costly in the sage grouse *Centrocercus urophasianus* Bonaparte (Vehrencamp *et al.*, 1989), but vocalization in other taxa, such as amphibians, fishes and insects, seems to be energetically constrained as well (Prestwich, 1994; Grafe, 1996; Grafe and Thein, 2001; Amorim *et al.*, 2002). Therefore, females preferring males calling at high rates also selects for the metabolic machinery that provides energy for such displays. This selection force in diverse animal groups should result in interspecific associations between the expression of acoustic traits and variables reflecting energy expenditure, similar to the patterns we found in passerines. If such relationships exist, it could be predicted that environmental constraints that affect energy metabolism also have consequences for trait elaboration. Such roles would indicate a close link between species adaptation and sexual selection that is mediated by energy metabolism. Future interspecific studies in other vertebrates may help us to understand the generality of this potential relationship.

#### ACKNOWLEDGEMENTS

We thank D. Gil and M. Max for scoring sonagrams. D. Gil and C. Spottiswoode provided useful comments and suggestions.

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## APPENDIX 1

Different subsets of data of mean field metabolic rate (FMR,  $\text{kJ} \cdot \text{day}^{-1}$ ) and body mass (g)

Species	Total		Winter excluded		Reference for FMR
	FMR	Body mass	FMR	Body mass	
<i>Auriparus flaviceps</i>	28.2	6.5	22.8	6.3	Webster and Weathers (1988, 2000)
<i>Cinclus cinclus</i>	220.6	62.6	218.3	62.8	Bryant and Tatner (1988), Brown and Bryant (1996)
<i>Delichon urbica</i>	83.5	18.7	83.5	18.7	Hails and Bryant (1979), Bryant and Westerterp (1980, 1984)
<i>Erithacus rubecula</i>	71.3	18.7	71.3	18.7	Tatner and Bryant (1986, 1993), Godfrey and Bryant (2000)
<i>Ficedula albicollis</i>	75.2	14.3	75.2	14.3	Moreno <i>et al.</i> (1991), Pärt <i>et al.</i> (1992)
<i>Ficedula hypoleuca</i>	63.4	12.5	63.4	12.5	Moreno and Sanz (1994), Moreno <i>et al.</i> (1995, 1997, 2001)
<i>Hirundo rustica</i>	98.7	18.3	98.7	18.3	Westerterp and Bryant (1984), Cuervo <i>et al.</i> (1996)
<i>Junco hyemalis</i>	76.6	19.6	82.7	21.4	Weathers and Sullivan (1993)
<i>Junco phaeonotus</i>	71.5	19.5	71.5	19.5	Weathers and Sullivan (1993)
<i>Lanius excubitor</i>	112.1	61.8	112.1	61.8	Degen <i>et al.</i> (1992)
<i>Mimus polyglottos</i>	121.0	46.9	121.0	46.9	Utter (1971)
<i>Muscicapa striata</i>	52.0	14.4			Bryant (1997)
<i>Oenanthe oenanthe</i>	90.5	27.1	90.5	27.1	Moreno (1989), Tatner (1990)
<i>Parus ater</i>	47.4	9.5			Moreno <i>et al.</i> (1988)
<i>Parus caeruleus</i>	64.1	11.5	64.1	11.5	Tatner and Bryant (1993)
<i>Parus cinctus</i>	51.4	12.8			Carlson <i>et al.</i> (1993)
<i>Parus cristatus</i>	40.6	11.1			Moreno <i>et al.</i> (1988)
<i>Parus major</i>	93.4	17.7	93.4	17.7	Daan <i>et al.</i> (1990), Nagy <i>et al.</i> (1999), Sanz <i>et al.</i> (2000), Sanz and Tinbergen (1999), Tinbergen and Dietz (1994)
<i>Parus montanus</i>	44.2	11.4			Carlson <i>et al.</i> (1993), Moreno <i>et al.</i> (1988)
<i>Passerculus sandwichensis</i>	79.7	19.3	79.7	19.3	Williams and Nagy (1984), Williams (1987) Williams and Nagy (1985)
<i>Progne subis</i>	163.2	50.9	163.2	50.9	Utter and LeFebvre (1973)
<i>Prunella modularis</i>	86.0	21.2			Bryant (1997)
<i>Pyrrhula pyrrhula</i>	88.0	25.1			Bryant (1997)
<i>Riparia riparia</i>	91.9	12.9	91.9	12.9	Westerterp and Bryant (1984)
<i>Sialia mexicana</i>	95.0	27.4	95.0	27.4	Mock (1991)
<i>Sturnus vulgaris</i>	251.2	80.1	251.2	80.1	Ricklefs and Williams (1984), Westerterp and Drent (1985)
<i>Tachycineta bicolor</i>	126.7	20.7	126.7	20.7	Williams (1988)
<i>Troglodytes aedon</i>	58.2	10.5	58.2	10.5	Dykstra and Karasov (1993)
<i>Turdoides squamiceps</i>	119.1	72.3	114.4	68.1	Anava <i>et al.</i> (2000)

## APPENDIX 2

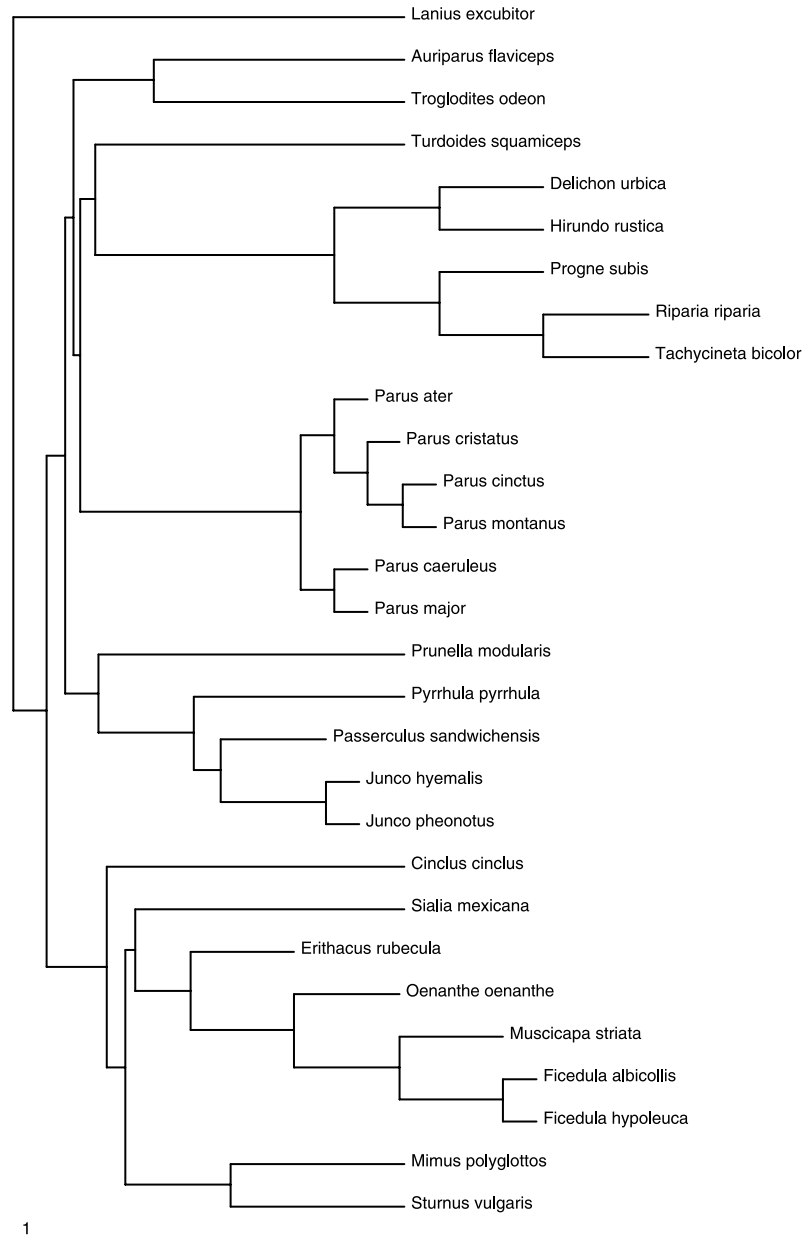
Mean song type repertoire size, syllable repertoire size, relative syllable repertoire size and migration in birds

Species	Repertoire size			Migration
	Song type	Syllable	Relative syllable	
<i>Auriparus flaviceps</i>			0.90	1
<i>Cinclus cinclus</i>			2.82	2
<i>Delichon urbica</i>			6.50	1
<i>Erithacus rubecula</i>	1000	4	3.11	2
<i>Ficedula albicollis</i>	1000	8.40	2.24	3
<i>Ficedula hypoleuca</i>	1000	9	2.43	3
<i>Hirundo rustica</i>	1000		3.60	3
<i>Junco hyemalis</i>	5	1	0.71	2
<i>Junco phaeonotus</i>	2			1
<i>Lanius excubitor</i>			0.55	2
<i>Mimus polyglottos</i>	190	20	0.63	1
<i>Muscicapa striata</i>			2.44	3
<i>Oenanthe oenanthe</i>		18	5.16	3
<i>Parus ater</i>	14	2	1.78	1
<i>Parus caeruleus</i>	5	2	1.43	1
<i>Parus cinctus</i>	1		1.53	1
<i>Parus cristatus</i>	1	2	1.43	1
<i>Parus major</i>	3	2	2.00	1
<i>Parus montanus</i>	1	1	0.72	1
<i>Passerculus sandwichensis</i>	1	5	2.25	3
<i>Progne subis</i>	1	10	3.33*	3
<i>Prunella modularis</i>	4	12	6.00	2
<i>Pyrrhula pyrrhula</i>			1.14	2
<i>Riparia riparia</i>			2.80	3
<i>Sialia mexicana</i>			3.00	2
<i>Sturnus vulgaris</i>	49	15	2.00	3
<i>Tachycineta bicolor</i>			1.50	3
<i>Troglodytes aedon</i>	1000	6	6.20	3
<i>Turdoides squamiceps</i>			0.33	1

\* Estimated from Read and Weary (1992).

## APPENDIX 3

Phylogeny of passerine birds used for the comparative analysis of song complexity and field metabolic rate (the scale is given in the bottom left)



The phylogenetic hypothesis was based on a composite phylogeny reported by Sibley and Ahlquist (1990), combined with information from other sources for Emberizidae (Arnaiz-Villena *et al.*, 1998), Paridae (Sheldon *et al.*, 1992) and Hirundinidae (Sheldon and Winkler, 1993). 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  $3.4 \Delta T_{50}H$  units, and between species within genera to  $1.1 \Delta T_{50}H$  units (see also Bennett and Owens, 2002).