



# The evolutionary origin of variation in song length and frequency in the avian family Cettiidae

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Aspects of bird song have been shown to correlate with morphological and ecological features, including beak and body size, and habitat. Here we study evolution of song length and song frequency among 30 species belonging to the Cettiidae. Frequency is negatively correlated with body size, and song length increases with latitude. Although migration distance correlates with latitude, the association of song length with latitude is only present within the non-migratory species, implying the association is not a consequence of migration. We place these correlations in a historical framework to show that the body size-frequency association arose early in the group, but the latitude-song length association is more evolutionarily labile. We suggest that latitudinal correlates of song length may reflect increased importance of sexual selection by female choice.

In the oscine passerine birds (the ‘songbirds’), songs are acquired through learning (Catchpole and Slater 2008) and thus can potentially evolve rapidly through cultural evolution (Payne 1996). Despite this potential for rapid evolution, various cross-species morphological and ecological correlates of song imply that song evolution is constrained by a species’ ecology. In comparisons across selected species, song frequency is regularly negatively correlated with body size (Wallschläger 1980, Linhart and Fuchs 2015), as well as affected by habitat openness and ambient noise (Boncoraglio and Saino 2007, Luther and Baptista 2010). These correlations have been related to transmission efficiency (Morton 1975, Martens 1980, Ryan and Brenowitz 1985, Patricelli and Blickley 2006). A second correlate of songs is that complexity and/or length regularly increases with latitude (Irwin 2000, Singh and Price 2015, Kaluthota et al. 2016). This has been related to variation in the intensity of sexual selection on song, reduced costs of singing, as well as changes in the acoustic environment (Singh and Price 2015). Latitude is also correlated with migration propensity, which comes with an additional suite of hypotheses, related to breeding synchrony and need to pair quickly (Catchpole 1980, Spottiswoode and Møller 2004). Separating out these various alternatives has proven challenging (Singh and Price 2015).

The family Cettiidae (typical bush warblers *Cettia/Horornis* and their relatives) shows spectacular interspecific variation

in song (Bairlein et al. 2006, Kennerley and Pearson 2010). In this study, we evaluate species differences in song variables to ask how these traits are associated with latitude, migration and body size. We focused our study on two aspects of songs, i.e. song frequency and song length, which are most easily assessed. Correlations across species may arise deep in evolutionary time and persist through speciation events, or reflect more recent evolution due to divergence between related species. In birds, body size appears to be often quite conserved (Harmon et al. 2010, Price et al. 2014), whereas range size and range position are evolutionarily more labile traits (Price et al. 1997, Webb and Gaston 2000). We asked if this general pattern applies more specifically to the Cettiidae and whether this affects patterns of song evolution.

## Material and methods

### Study taxa and phylogeny

The Cettiidae (sensu Alström et al. 2006) contains 7 genera and 31–32 species (Alström et al. 2011, Dickinson and Christidis 2014, Gill and Donsker 2015). Alström et al. (2011) present the most recent classification, revised from former classifications based on non-monophyly of the genus *Cettia* and the demonstration that some genera or species that had not previously been considered closely related to

Cettiidae belonged in the clade. The different species are mainly distributed across southern and eastern Asia, plus several on Asian Pacific islands, one *Cettia* (*C. cetti*) in the Western Palearctic, and one, *Hemitesia neumanni*, restricted to east Africa (Bairlein et al. 2006, Kennerley and Pearson 2010). Many species inhabit bushes, bamboo or forest undergrowth in mountainous areas from mid to high elevations, while some extend their breeding range to above the tree limit (e.g. *Cettia brunnifrons*, *C. major*), and some (e.g. *Cettia cetti*) breed in marshy areas in the lowlands (Bairlein et al. 2006, Kennerley and Pearson 2010). Most species are residents or altitudinal/short-distance migrants, but *Urosphena squameiceps* and *Horornis canturians* migrate over relatively long distances (Bairlein et al. 2006, Kennerley and Pearson 2010). We included 30 species in this study. We built a time-dated phylogeny in BEAST 1.8.2 (Drummond et al. 2012) using the data in Alström et al. (2011) (described further in the Supplementary material Appendix 1 and 2 Fig. A1).

### Song measurement

Song recordings with good quality (rated on the website as A or B) were downloaded from xeno-canto.org. We measured 1–5 (mean 3.9) individuals and 2–14 (mean 6.0) song strophes for each species (Supplementary material Appendix 2 Table A1). Although males of some species have more than one song type, the recordings and songs we used in the study were randomly selected, and therefore should not introduce any bias. We generated spectrograms using Avisoft-SASLab 5.2 with the following settings: Flat-Top window, sample frequency = 22050 Hz, FFT = 256 points, overlap = 50%, frame size = 100%, frequency resolution = 86 Hz, time resolution = 5.805 ms. In the current study, notes were defined as the smallest continuous units on the spectrogram within a song. We measured the following variables for each song strophe: strophe duration, number of notes, duration of longest note, peak frequency, highest frequency, lowest frequency and frequency bandwidth (Supplementary material Appendix 2 Fig. A2). One species (*Abroscopus albogularis*) is known to have harmonics extending to the ultrasonic (Narins et al. 2004). Here, we ignored ultrasonic frequency, because no other species is known to sing in this range, and not all recordings available to us are likely to have been made with sufficiently sensitive equipment. We computed the species mean values (Supplementary material Appendix 2 Table A1) and used log-transformed values in subsequent analysis. Across species, the number of notes and song duration are highly correlated with each other, as are the three frequency parameters (Supplementary material Appendix 2 Table A2). Phylogenetic principal component analysis (Revell 2009) was conducted for both log-transformed song length parameters (i.e. number of notes and strophe duration), and song frequency parameters (i.e. peak frequency, highest frequency and lowest frequency) separately. The first principal components of these sets of traits were designated as proxies of song length and song frequency, and were subsequently used in the analysis (see Supplementary material Appendix 2 Table A3 and A4 for details of the principal component analysis).

### Predictor variables

We extracted information on morphology, migration status, and latitude from the literature, museum specimens and online databases. We obtained tarsus length and wing length from Kennerley and Pearson (2010) and Price et al. (2014), based as far as possible on male birds. In Kennerley and Pearson (2010), morphology of three species (two *Tessia* species and *Horornis seebohmii*) was recorded based on the sexes combined, which we consider to introduce only small error, as these species are generally monomorphic. Two male *Hemitesia neumanni* (FMNH 385162, FMNH 385165) were measured from specimens in the Field Museum of Natural History, Chicago. Tarsus length and wing length are highly correlated across species ( $r = 0.70$ ). Because the use of the first principal component from wing and tarsus gave similar conclusions to tarsus length alone, we present tarsus length throughout as it is the more intuitive measure than a principal component. We extracted breeding ranges from maps downloaded from BirdLife (BirdLife International and NatureServe 2015). Breeding latitudes of *Horornis diphone* and *H. canturians* were measured manually in Google Earth (<<http://earth.google.com>>) based on Kennerley and Pearson (2010) as the breeding ranges of these two species in BirdLife database are problematic. Using the *sp* package (Pebesma and Bivand 2005) in R 3.3.2 (R Core Team) we calculated the mid-point breeding latitude as the average of maximum and minimum breeding latitudes. The absolute values of latitude (in the units of degrees) were used in the subsequent analysis (that is, the eight species with southern mid-point latitudes had their position positivized). Migration status were obtained from Bairlein et al. (2006) and Kennerley and Pearson (2010) and classified into three categories: resident (score 0), altitudinal or short distance migrant, i.e. without geographically well-separated breeding and nonbreeding areas (score 1), and medium or long distance migrant with well-separated breeding and nonbreeding areas (score 2).

### Statistical analysis

We calculated phylogenetic independent contrasts (Felsenstein 1985), in APE (Paradis et al. 2004). We then calculated significance of correlations between variables using both phylogenetic independent contrasts and species mean values. As altitude and migration are correlated with each other and are both significantly correlated with song length, to understand which variable is the better predictor for song length we further compared regression models with different combinations of predictor variables based on AICc values. We also performed regression of song length on latitude within resident and migratory species separately to separate the effect of migration. We estimated Blomberg's  $K$  as an indicator the amount of phylogenetic signal, with  $K \ll 1$  indicating phylogenetic lability and  $K \gg 1$  implying phylogenetic conservatism ( $K = 1$  is consistent with Brownian motion; Blomberg et al. 2003), using the *Picante* package (Kembel et al. 2010). Significance of phylogenetic signal was tested by comparing the observed variance of the contrasts with the variance of contrasts computed from data permuted randomly across

the tips of the tree (Blomberg et al. 2003). We also tested alternative models of trait evolution (Brownian motion, Ornstein–Uhlenbeck, early burst) using the GEIGER package (Harmon et al. 2008). To visualize the history of co-evolution between traits we mapped absolute values of the contrasts on to the nodes on the Cettiidae phylogeny and identified places where large, correlated, trait changes occurred. All statistical analyses were carried out in R 3.3.2 (R Core Team).

## Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.r14ch>> (Wei et al. 2017).

## Results

### Song frequency

Species singing at higher frequencies have shorter tarsi (non-phylogenetic:  $r = -0.68$ ,  $p = 0.00$ , phylogenetic:  $r = -0.55$ ,  $p = 0.00$ , Table 1, Fig. 1A, Supplementary material Appendix 2 Table A5). Both song frequency and tarsus length show strong phylogenetic signal, with  $K$  values exceeding one (song frequency:  $K = 1.08$ , tarsus length:  $K = 1.24$ , Table 2). As implied by these large  $K$  values, associated evolutionary changes in tarsus length and song frequency arise deep in the phylogeny, e.g. between the *Abroscopus* clade and the clade comprising *Phyllergates/Tickellia/Horornis*, but some associated changes do appear among sister species, e.g. *Horornis seebohmi* and *Horornis canturians* (Fig. 2A, D).

### Song length

Species with longer songs that include more notes breed at higher latitudes (non-phylogenetic:  $r = 0.48$ ,  $p = 0.01$ , phylogenetic:  $r = 0.46$ ,  $p = 0.01$ , Table 1, Fig. 1B, D, Supplementary material Appendix 2 Table A5). Song length correlates with migration as well, but migration status and latitude are highly correlated with each other ( $r = 0.82$ , Supplementary material Appendix 2 Table A6). Statistically, it is difficult to separate migration status and latitude, but latitude has greater power in explaining song length (Table 1). When comparing regression models that include different combinations of predictor variables, the model including latitude and not migration was the best model in both non-phylogenetic analysis and phylogenetic analysis (Supplementary material Appendix 2 Table A7, A8). More convincingly, when we analyzed latitude separately within the non-migratory and migratory species, we found strong evidence for a role for latitude within the non-migratory

species (non-phylogenetic:  $r = 0.60$ ,  $p = 0.01$ , phylogenetic:  $r = 0.73$ ,  $p = 0.00$ , Fig. 1D) while the regression of song length in migratory species with latitude is not significant (non-phylogenetic:  $r = 0.02$ ,  $p = 0.96$ , phylogenetic:  $r = 0.08$ ,  $p = 0.80$ , Fig. 1D). Thus, latitude with residents is the strong predictor of song length. As *Horornis brunnescens* and *H. acanthizoides* have much longer songs we also run regressions with two species excluded, all significant results are unchanged if the outliers are removed. Song length and latitude show weak phylogenetic signal (song length:  $K = 0.60$ , latitude:  $K = 0.43$ , Table 2) and the association between them was generally formed recently in the evolutionary history (Fig. 2B, D), e.g. between sister species *Urosphena whiteheadi* and *U. squameiceps*, or between species and small clades like *Tesia olivea* and *T. superciliaris/everetti*.

## Discussion

In the Cettiidae, song frequency is negatively correlated with body size (i.e. tarsus length), and song length is positively correlated with latitude. These two correlations historically arose in different ways. The correlation between frequency and body size was generated earlier in the history of the group and has been conserved through subsequent speciation events. Latitude and song length are more evolutionarily labile, and any patterns deeper in the history of the group have been erased as a result of more recent evolution. Behavioural traits are often considered to be more labile than morphological traits (Blomberg et al. 2003). However, if the behavioural trait is determined by a morphological or ecological trait, it is these causal factors that drive evolutionary lability. In this case, evolutionary lability in latitudinal position has been associated with evolutionary lability in song length.

A negative correlation of song frequency and body size is widespread in birds (Wallschläger 1980, Ryan and Brenowitz 1985, Seddon 2005). Sounds travel further the greater the amplitude and the lower the frequency (Morton 1975, Kuttuff 2007). Although often considered a constraint, if a species transmits sound with optimal efficiency the amplitude/frequency ratio should be correlated with body size, because it is energetically inefficient to produce low frequency sounds when the vibrating structure is small (Ryan and Brenowitz 1985).

A latitudinal gradient in the length of songs has been noted both within and between species. Examples include the rufous-browed peppershrike *Cyclarhis gujanensis* (Tubaro and Segura 1995), the greenish warbler *Phylloscopus trochiloides* complex (Irwin 2000) and leaf warbler family Phylloscopidae (Tietze et al. 2015). Hypotheses for why songs should be longer at higher latitudes include some based on migration,

Table 1. Correlations of song frequency and song length with predictor variables. Correlation coefficient  $r$  and  $p$  value of regressions are shown. Results based on phylogenetic independent contrasts (PICs) are shown after the non-phylogenetic analysis. Significant results ( $p < 0.05$ ) are indicated in bold.

Song trait	Latitude		Migration		Tarsus	
	$r$ (p)	$r$ (p) PICs	$r$ (p)	$r$ (p) PICs	$r$ (p)	$r$ (p) PICs
Song frequency	0.02 (0.91)	0.00 (1.00)	-0.02 (0.90)	-0.13 (0.49)	<b>-0.68 (0.00)</b>	<b>-0.55 (0.00)</b>
Song length	<b>0.48 (0.01)</b>	<b>0.46 (0.01)</b>	<b>0.46 (0.01)</b>	<b>0.39 (0.03)</b>	-0.18 (0.48)	-0.24 (0.19)

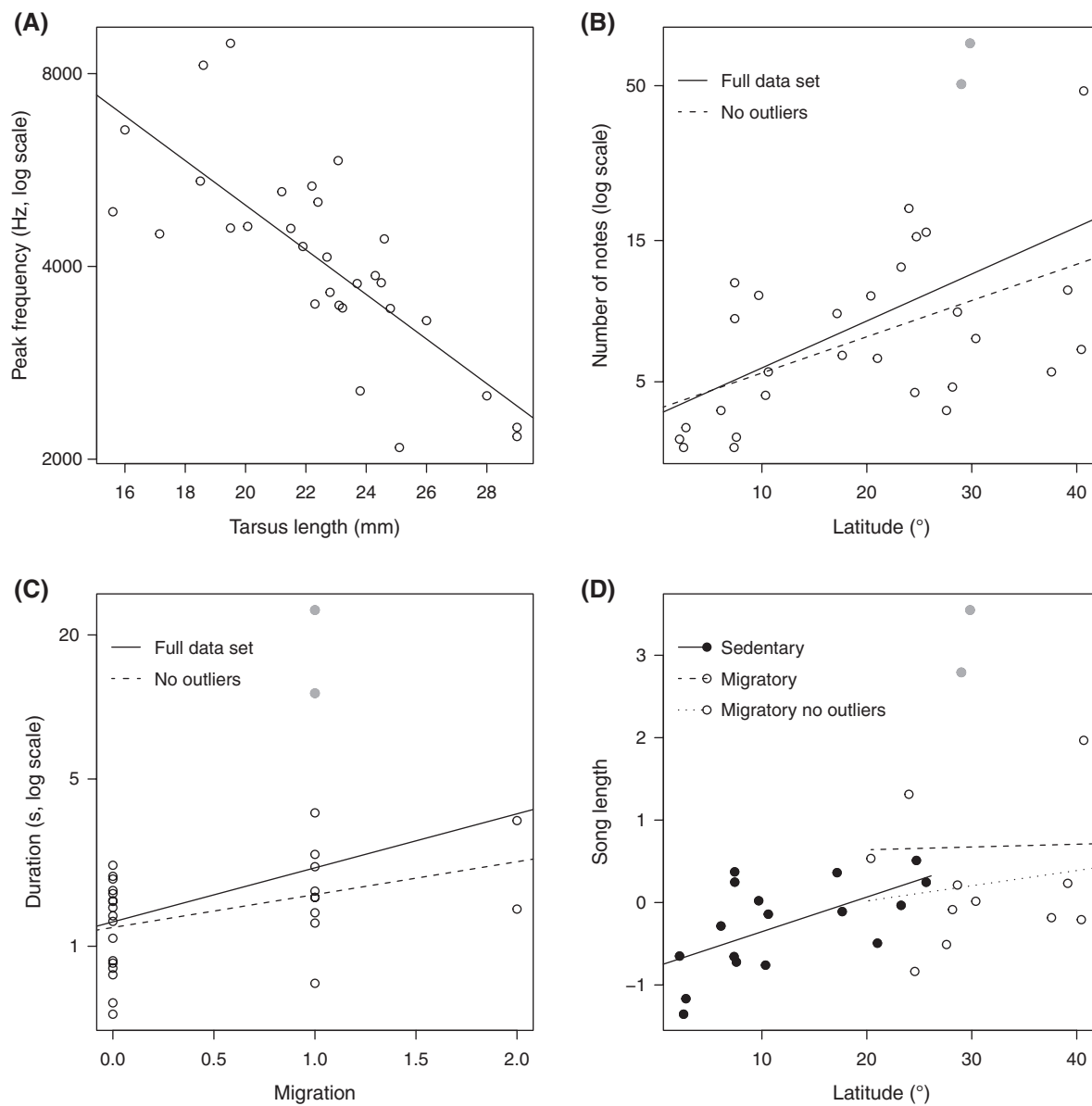


Figure 1. Selected bivariate plots of song variables on morphological and ecological variables: (A) peak frequency on body size, (B) number of notes on absolute values of latitude, (C) song duration on migration status, (D) song length on absolute values of latitude. Regressions of data from migratory and sedentary birds, and with or without two outlier species (*Horornis brunnescens* and *H. acanthizoides*) are shown in the same plot with different lines and circles. Outlier species were indicated with filled grey circles.

Table 2. Significance and strength of phylogenetic signal and best fitted evolutionary model for song variables and predictors. Blomberg's  $K$  with  $p$  value for each variable is shown.  $\Delta\text{AICc}$  values of the evolutionary models for each variable are shown. BM: Brownian motion, OU: Ornstein-Uhlenbeck, EB: early burst.  $K$  values greater than one and evolutionary models with the lowest  $\Delta\text{AICc}$  values are indicated in bold.

Trait	$K$ ( $p$ )	BM	OU	EB
Song trait				
Song frequency	<b>1.08 (0.00)</b>	<b>0.00</b>	2.16	2.48
Song length	0.64 (0.07)	2.44	<b>0.00</b>	4.92
Predictor				
Latitude	0.43 (0.37)	8.35	<b>0.00</b>	10.83
Migration	0.48 (0.19)	5.27	<b>0.00</b>	7.75
Tarsus	<b>1.24 (0.00)</b>	<b>0.00</b>	1.83	2.48

which is correlated with latitude, as well as some that apply equally to residents and migrants (Singh and Price 2015). In this study, latitudinal position, rather than migration is a stronger correlate of song length. Longer songs appear to be generally favored by females (Clayton and Pröve 1989, Kempnaers et al. 1997, Neubauer 1999), perhaps because song length is an indicator of male quality (Spencer et al. 2003). Songs may be subject to more intense inter-sexual selection in high latitudes because a lower population density increases the importance of songs for broadcasting to females rather than defending territories (Irwin 2000). Counterbalancing this, costs of singing may be reduced in temperate area if food is more plentiful there (Irwin 2000, Scordato 2017). Alternatively, more intense male competition in

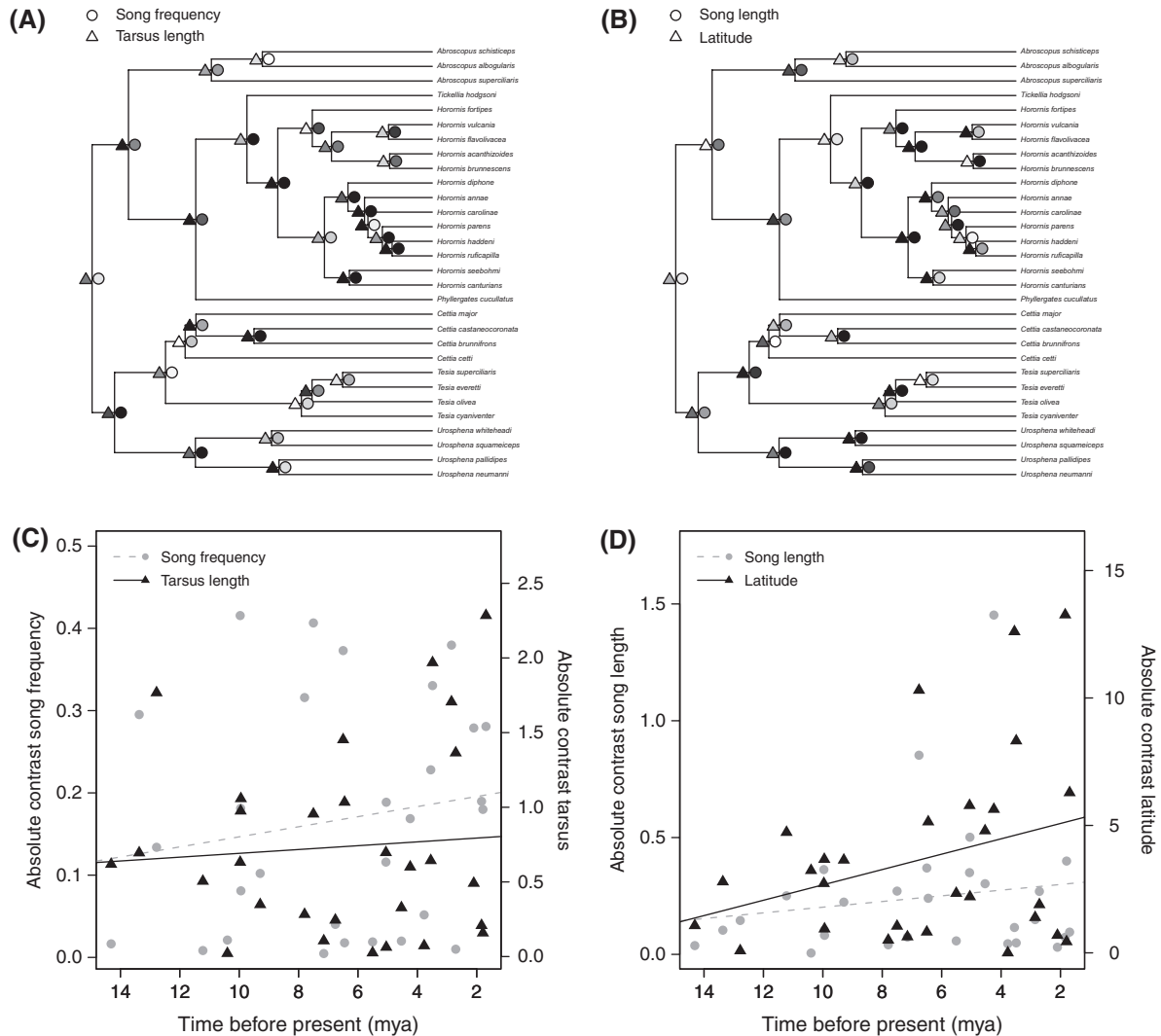


Figure 2. Phylogeny of the Cettiidae and bivariate plots of absolute values of contrast against time. Larger contrast values are indicated with a darker color on the nodes of phylogeny in (A) and (B). Regression lines of contrasts of song frequency and song length on time are indicated with dashed lines, and regression lines of contrasts of tarsus and latitude on time are indicated with solid lines in (C) and (D).

more populous tropical latitudes may promote short, simple, stereotyped songs (Catchpole 1983, Park and Park 2000), which may facilitate position learning and individual recognition in territorial behaviours (Catchpole 1980, 1982).

In summary, we have here shown that two features of songs are strongly determined by ecological factors, in ways that are consistent with previous studies in other groups. Because migration seems of lesser importance than latitude in affecting song length, we are able to narrow down causes of song length variation across species to a few hypotheses, which can be tested in future studies with data from experimental playbacks, field measurements of ecological conditions and manipulations of food abundance.

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Supplementary material (Appendix JAV-01366 at <[www.avianbiology.org/appendix/jav-01366](http://www.avianbiology.org/appendix/jav-01366)>). Appendix 1–2.