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The Evolution of Song in the *Phylloscopus* Leaf Warblers (Aves: Sylviidae): A Tale of Sexual Selection, Habitat Adaptation, and Morphological Constraints

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*Un oiseau chante d'autant mieux qu'il chante dans son arbre généalogique**
Jean Cocteau (French poet and playwright, 1889–1963)

I. INTRODUCTION

Differences in song are often the most reliable criteria by which closely related bird species can be differentiated. For instance, only by carefully listening to the song of leaf warblers could the 18th century naturalist Gilbert White identify the chiffchaff, the willow and the wood warblers as different species (*Phylloscopus collybita, P. sybilatrix*, and *P. trochilus*) (White, 1789). Observations such as these have been interpreted as suggestive of speciation events being tightly linked to the evolution of bird song, a signal of great importance in sexual selection processes (Price, 2007).

*It is from its genealogical tree that the bird sings at its best

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Bird song presents some peculiarities that add an additional layer of complexity to the study of its evolution, by comparison with a standard morphological trait. In several avian groups, notably so in the oscine Passeriformes, songs are passed on down the generations by cultural transmission, often between neighbors (Lachlan and Slater, 2003; Nordby et al., 1999), or, more rarely, from father to son (Grant and Grant, 1996; Mann and Slater, 1995). This type of cultural evolution may, in principle, lead to a higher mutation rate than traits with a higher genetic component (Lynch and Baker, 1993; Slater et al., 1980). However, behavioral mechanisms may select for conformity and thus reduce mutation rates considerably (Baker and Gammon, 2008; Lachlan et al., 2004). In addition, not all aspects of song are culturally transmitted. Even in oscines, genetically transmitted sensory templates, singing styles and predispositions for certain sounds, filter and direct vocal learning to a large extent (Leitner and Catchpole, 2007; Mundinger, 1995).

Despite a remarkably high copying fidelity, colonization events by birds with poorly developed songs (Thielcke, 1983) and impoverished cultural transmission in small and fragmented populations (Laiolo and Tella, 2005) can lead to the establishment of diverging vocal traditions. Furthermore, mathematical models have shown that song learning can greatly facilitate the development of genetic isolation, thus fostering allopatric speciation rates (Lachlan and Servedio, 2004). Interestingly, a counterintuitive prediction of this model is that the probability of speciation is higher when the cultural mutation rate is low (Lachlan and Servedio, 2004).

Most comparative studies in a variety of avian groups, ranging from herons to several subfamilies of Passeriformes, have found that song encodes significant amounts of phylogenetic signal, and thus closely related species share certain features of the song due to common ancestry (Mann et al., 2009; McCracken and Sheldon, 1997; Päckert et al., 2003; Price and Lanyon, 2002; Seddon, 2005; ten Cate, 2004; van Buskirk, 1997). However, a general pattern that arises from these studies is that, despite phylogenetic similarity, song characteristics are not enough to reconstruct a reliable phylogeny, and that bird song is a labile trait. Several hypotheses, both adaptive and nonadaptive, have been proposed to account for this evolutionary lability of bird song. These are summarized in the following subsections.

A. Morphological Constraints

Song in birds is produced by a specialized organ, the syrinx, but is also shaped by other physical characteristics such as body size, or beak shape (Suthers, 2004). Since these traits can be subject to natural selection in relationship to food habits or other selective pressures, song characteristics may be hijacked by these particular selection regimes. For example, body

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size has been shown to be a limiting factor in the frequencies that can be produced. The negative relationship between body size and song frequency can be largely explained by large-bodied species not being able to produce high-pitched sounds (Ryan and Brenowitz, 1985; Tubaro and Mahler, 1998; Wallschläger, 1980). More specifically, selection for particular beak shapes due to trophic adaptation can cause correlated changes in song characteristics. For instance, selection for strong, deep beaks in Darwin finches (*Geospiza* spp.) has resulted in correlated changes in song: rapid trills of a wide frequency range are simply incompatible with deep beaks (Podos, 2001). Several recent studies suggest that this type of relationship between beak and song characteristics may be widespread and may explain a substantial part of variation in song between species (Badyaev et al., 2008; Ballentine, 2006; Palacios and Tubaro, 2000; Podos, 1997; Seddon, 2005).

B. Functional Selective Pressures

Experiments and observational evidence show that bird song has two basic functions: territorial defense and mate attraction (Catchpole and Slater, 2008; Eriksson and Wallin, 1986; Krebs et al., 1978; McDonald, 1989; Mountjoy and Lemon, 1991). Thus, it is to be expected that the evolution of several song characteristics may be related to variation in the strength of sexual selection (Catchpole, 1980; Kroodsma, 1977; Read and Weary, 1990, 1992). However, studies present conflicting evidence about the strength and the direction of this relationship (Garamszegi and Møller, 2004; Price and Lanyon, 2002; Shutler and Weatherhead, 1990). A possibility is that the different modes of sexual selection (male–male competition and female choice) may select for different song characteristics (Collins et al., 2009; Slater, 1981). Read and Weary (1992), in the largest comparative study so far, show that large repertoires are associated with a relatively long migration distance, which they considered to be a proxy of the strength of sexual selection. Similarly, in the different morphs of the ring species *Phylloscopus trochiloides*, evolutionary transitions toward higher latitudes correlate with increases in song complexity (Irwin, 2000; Irwin et al., 2001).

C. Adaptation to Acoustic Properties of the Habitat

Habitats differ in their acoustic properties, thus filtering particular temporal and frequency characteristics of song (e.g., Martens, 1980; Morton, 1975; Ryan and Brenowitz, 1985; Wiley, 1991). Song is typically loud and directed at rather distant birds, and thus we expect selection for song characteristics that transmit well in the particular habitat where the bird lives (Brumm and Naguib, 2009). A recent meta-analysis does, indeed,

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show that the songs of species living in closed habitats have lower frequencies and narrower frequency ranges than those of species living in open habitats (Boncoraglio and Saino, 2007).

D. Character Displacement

Although most species sing species-specific song patterns, differences between some species may sometimes be rather minor, given high phylogenetic loads in many song characters (e.g., Päckert et al., 2003; Seddon, 2005; ten Cate, 2004; van Buskirk, 1997). Thus, selection against heterospecific matings is expected to reinforce acoustic differences between species. Such a mechanism would lead to higher differences between species-specific songs in sympatric closely related species. For instance, a comparative study in the antbirds (Thamnophilidae, suboscine Passeriformes) showed evidence for character displacement of both temporal and pitch characteristics in sympatric species (Seddon, 2005).

The *Phylloscopus* warblers are a large genus of insectivorous warblers, encompassing 56 species, which inhabit forested areas mostly in Eurasia, as well as some regions in Africa (del Hoyo et al., 2006). Most species are migratory, and winter south of their breeding ranges either in India, Asia, or Africa. The highest local diversity is found in the Himalayas, an area which is considered the center of speciation for most *Phylloscopus* species (Price, 1991; Price et al., 1997). The relationship between distribution ranges and latitude follows Rappoport's rule (i.e., larger ranges in higher latitudes) and has been explained as a result of differential ability of taxa to colonize Northern habitats in the last 2 million years following glaciations (Price et al., 1997). Changes in species-specific midlatitudes show high evolutionary lability (Price et al., 1997), suggesting frequent North–South dispersal events that are at the base of several speciation events in this group (Irwin et al., 2005).

Phylloscopus males are highly vocal while defending territories (Martens, 1993), and sexual selection for particular song traits has been shown to be important in several species (Forstmeier et al., 2002; Gil et al., 2007; Radesäter et al., 1987). Thus, this genus seems to be a good model in which to study the evolution of song in a passerine group, and compare the different evolutionary forces that contribute to it. Previous studies have examined this problem in a limited number of species (Irwin, 2000, and also an unpublished MS by Liou, L. W., Tiainen, J., Higuchi, H., Richman, A. D., and Price, T. D.: ''Song variation in the genus Phylloscopus''). In this paper, we study the evolution of song in a much larger sample of taxa (30 species). In the first part of this study, we will compare the evolutionary lability of temporal, pitch, and repertoire characteristics. This will indicate whether

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song characters are the valuable traits in this group for predicting phylogenetic relationships between taxa. In the second part of the study, we will test a series of hypotheses concerning morphological constraints, song function, adaptation to habitat sound transmission, and character displacement between sympatric species. Explicitly, we predict: (1) song frequency and temporal characteristics to be correlated with body size and beak shape; (2) repertoire size and song complexity to increase with the intensity of sexual selection across species; (3) song frequency and temporal characteristics to be associated with niche and habitat characteristics that determine sound transmission; and (4) increased divergence of song characteristics in closely related species sharing distribution ranges.

II. Material and Methods

A. Taxa Sampled

We analyzed song for all *Phylloscopus* species for which mitochondrial DNA sequence data were available, basically those covered by a phylogeny based on these molecular data (Price et al., 1997), and additional information obtained from Richman (1996), Olsson et al. (2005), and Bensch et al. (2006). We excluded the Caucasian chiffchaff (*Phylloscopus lorenzii*), since song recordings could not be obtained from this species. We included an additional species not considered in this phylogeny, the Canary Islands chiffchaff (*Phylloscopus canariensis*), which is a sister species of the common chiffchaff (Helbig et al., 1996). In total, 30 species of the genus *Phylloscopus* were considered (Fig. 1).

B. Song Data and Analysis

We studied vocalizations emitted in seemingly territorial contexts, which we will refer to as songs. For most species, we succeeded in obtaining recordings from three different individuals, except for Hume's, Tytler's, and Ijima's leaf warblers (*Phylloscopus humei, P. tytleri*, and *P. ijimae*) and Eastern Bonelli's Warbler (*Phylloscopus orientalis)* for which only one individual was obtained, and the pale-legged and ashy-throated warblers (*Phylloscopus tenellipes* and *P. maculipennis*) for which only two individuals were available. Given the very high repeatability of song characteristics within species (see the following section), we are confident that the small sample size that we obtained for some species is not a problem. For each individual, measurements of acoustic variables were taken on five successive songs, or on the number of songs contained in the recording when they were less than five, and mean values

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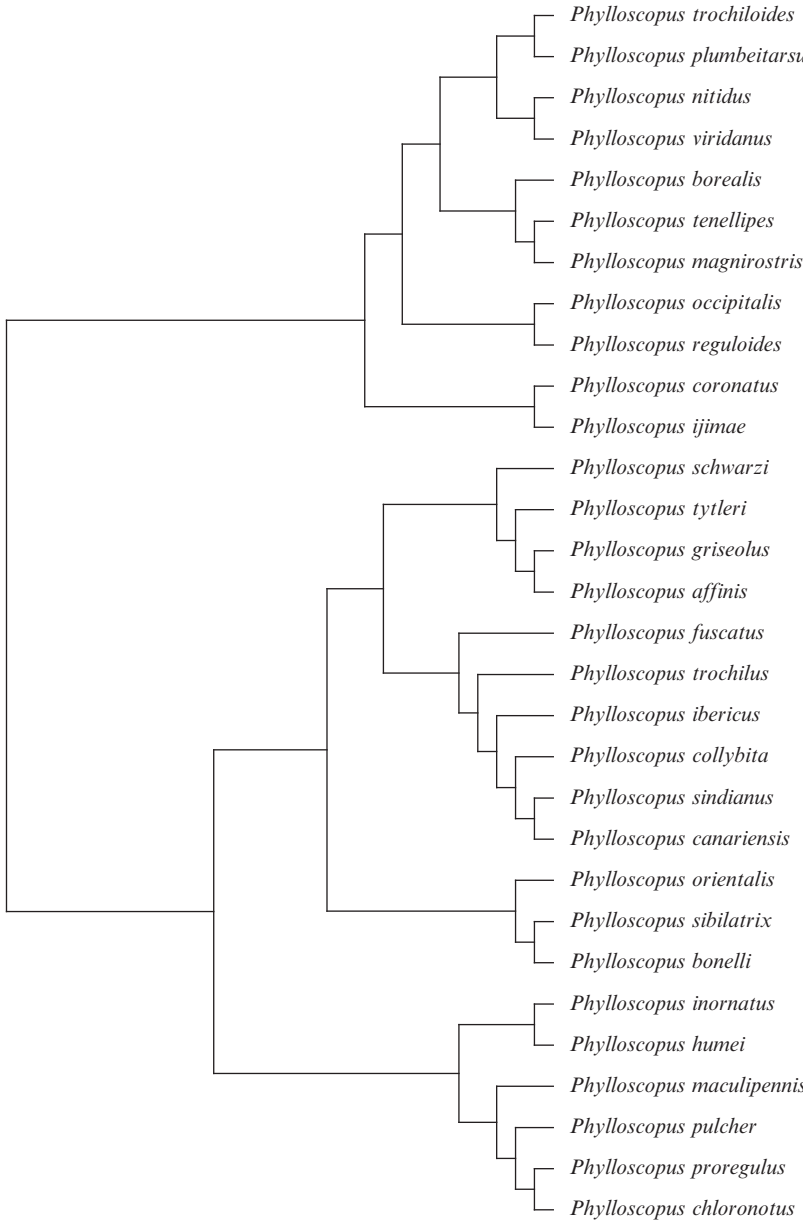

FIG. 1. Phylogenetic tree of the *Phylloscopus* species used in this study. This tree is based on Price et al. (1997), with additional information taken from Richman (1996), Olsson et al. (2005), Bensch et al. (2006), and Helbig et al. (1996).

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were calculated for each variable. In total, we analyzed recordings of 84 different birds belonging to 30 different species (Table I). Song recordings were obtained from several commercially available tapes and from sound libraries, mainly the National Sound Archive (London, UK) (Table I). Recordings for less common species were located by consulting Shaun Peters' web site catalog of recorded bird songs (http://aviandiscography.webs.com).

Recordings were digitized from CDs with Windows Media Player (Microsoft) and sonograms were created using Avisoft SASLab-Pro (www.avisoft-saslab.com) with the following parameters: FFT length 256; frame size 100%; Hamming window; frequency resolution 86 Hz; and temporal resolution 8 ms. Measurements of acoustic variables were performed on the sonograms. The smallest component of a leaf warbler's song is an element, defined as a continuous sound in time. Elements may be organized in syllables. We defined a syllable as a single element or a group of elements emitted consecutively forming a phrase. Introductory elements that are typical of some leaf warbler species were not considered in the analysis (Thielcke and Linsenmair, 1963). A group of elements emitted in the same successive order in different songs, forming a part or the whole song, was also considered a syllable. A phrase was defined as a repetition of one syllable two or more times.

Territorial song in the genus *Phylloscopus* varies markedly between species (Martens, 1980), and it is not straightforward to find a direct measure of complexity that could be applied to all species (see Fig. 2 for examples of songs). Additionally, previous studies in several species recommend a multivariate analysis of song (Gil and Slater, 2000b; Irwin, 2000). Thus, we established a comprehensive list of 29 song measurements, including temporal, structural, and frequency components of the songs which were taken on each song by BM. The precise definition of these measurements can be found in Table II.

All variables were highly repeatable among individuals of the same species (all $F_{25,\,53} > 3.31$, $P < 0.001$), except for the pause between songs, which varied greatly among individuals and between different songs of the same individual ($F_{25,\,52} = 1.19$, $P = 0.29$).

Inspection of the correlation matrix between all these variables led us to divide them in two categories: song complexity (temporal patterns and repertoire) and frequency characteristics, the former grouped since measures of repertoire size were highly correlated with many duration measurements. Thus, all measurements were categorized in two groups: song composition and frequency characteristics. Two different principal component analyses were performed upon each of these sets of variables.

The principal component analysis (PCA) on the song composition variables yielded up to five components of complexity. However, only the first component could be easily interpreted, and thus we restrict our analyses to

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TABLE I

SPECIES CONSIDERED IN THE STUDY AND RECORDINGS' SOURCES

Species	Individuals	Sources
Phylloscopus affinis	3	(1, 2)
Phylloscopus bonelli	3	(3–5)
Phylloscopus borealis	3	(1, 4, 6)
Phylloscopus canariensis	3	(2, 7)
Phylloscopus chloronotus	3	(1, 8)
Phylloscopus collybita	3	(4, 5, 9)
Phylloscopus coronatus	4	(2, 4, 10)
Phylloscopus fuscatus	3	(2, 4, 11)
Phylloscopus griseolus	3	(1, 2, 11)
Phylloscopus humei	1	(11)
Phylloscopus ibericus	3	(5, 6, 9)
Phylloscopus ijimae	1	(10)
Phylloscopus inornatus	4	(2, 11)
Phylloscopus maculipennis	2	(2)
Phylloscopus magnirostris	3	(1, 8, 12)
Phylloscopus nitidus	3	(2, 11, 12)
Phylloscopus occipitalis	3	(1, 2)
Phylloscopus orientalis	1	(4)
Phylloscopus plumbeitarsus	3	(2, 11)
Phylloscopus proregulus	3	(2, 11)
Phylloscopus pulcher	3	(1, 2)
Phylloscopus reguloides	3	(1, 13)
Phylloscopus schwarzi	3	(2, 4, 11)
Phylloscopus sibilatrix	3	(6, 9)
Phylloscopus sindianus	3	(1, 2, 4)
Phylloscopus tenellipes	2	(1, 10)
Phylloscopus trochiloides	3	(1, 2, 14)
Phylloscopus trochilus	3	(2, 4, 15)
Phylloscopus tytleri	1	(1)
Phylloscopus viridanus	3	(6, 9, 11)

Sources

1. Farrow, D., 2002. 24 Phylloscopus Species. Privately published.
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12. Warakagoda, D., 1998. The Bird Sounds of Sri Lanka. Part 2: Passerines. Library Nature Sounds, Sri Lanka.
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14. Scharringa, J., 2001. Birds of Tropical Asia. 2. Bird Songs International. BV, Westernieland.
15. Fonoteca Zoologica MNCN, Madrid.

it (Table III). This first component (hereafter ''song complexity'') can be described as a measure combining song repertoire size and complexity: birds with high scores in this component have large repertoires and sing long songs composed of many different syllables, which are also long and complex. The remainder of components does not have a straightforward biological interpretation. For instance, the second component is mostly loaded by switch rate, which is a measure of the turnover of new elements between consecutive songs, but also by measures of syllable length, reflecting thus some positive covariance between these measures. Only the first principal component will be used in the analysis.

The PCA of frequency measurements was simpler to interpret (Table III). The first principal component is loaded principally by maximum frequency and bandwidth (hereafter ''pitch1''), whereas the second component is explained by minimum and emphasized frequencies (hereafter ''pitch2'').

C. Morphological Data

Measurements of skin specimens were taken at the Bird Section of the British Museum of Natural History (Tring, UK) by DG, following standard procedures (Svensson, 1984). We aimed at obtaining measurements of 10 individuals in total, 5 per sex, and this was achieved for most species (for sample sizes, see Appendix 1).

Wing and tail lengths were measured with a wing ruler to the nearest 0.1 mm. Tarsus length was taken with the aid of a pair of dividers onto the wing rule to the nearest 0.1 mm. Beak measurements were taken with a digital caliper (Mitutoyo, Japan) to the nearest 0.1 mm. Repeatability of measurements as determined by ANOVAs performed on 12 repeated measures was high for all measurements (all tests: $F_{11,12} > 6.5$; $P < 0.001$; intraclass coefficient of correlations >0.72). Descriptive data (means and S.D.) are presented in Appendix 1 for each species.

1. Body Size

We performed a PCA on the correlation matrix of log-transformed morphological characters, including wing, tail, tarsus, and beak lengths; beak width; and beak depth. The results follow closely those of Price (1991), who

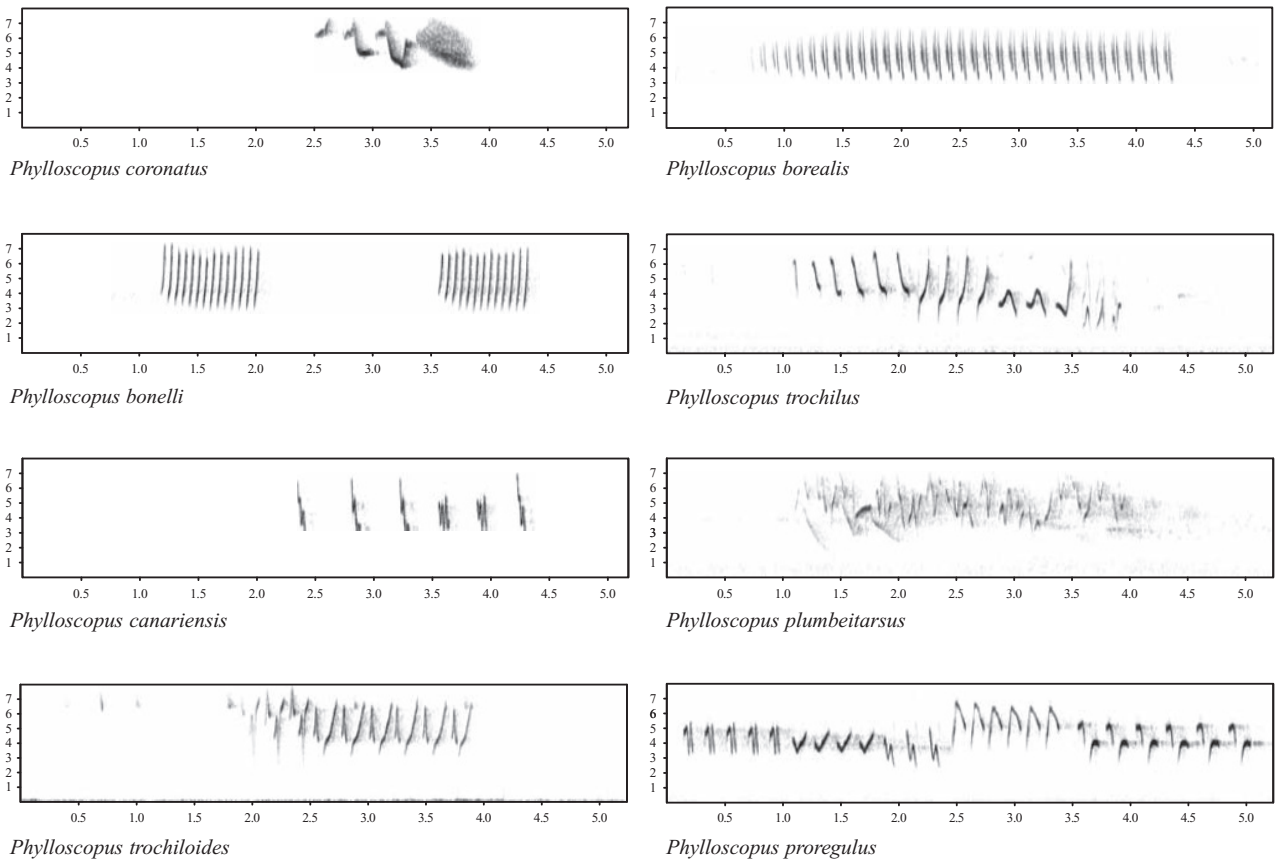

FIG. 2. Songs of eight of the *Phylloscopus* species included in this study, ordered in increasing complexity (from upper left to lower right), as defined by the song complexity measure used in this study (see text).

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TABLE II

DEFINITIONS OF THE DIFFERENT SONG MEASUREMENTS, WHICH CAN BE CLASSIFIED IN THREE TYPES: TEMPORAL (1–10), STRUCTURAL (11–21), AND FREQUENCY CHARACTERISTICS (22–29)

1	SONDUR	Song duration, measured from the beginning of the first to the end of the last element of the song
2	SONPAU	Pause between songs, measured from the end of the last element of one song to the beginning of the first element of the next consecutive song
3	SONPRO	Song proportion, calculated as the sum of the duration of the songs divided by the sum of the duration of the songs and the pauses between songs
4	DUSHOEL	Duration of the shortest element of the song
5	DULONEL	Duration of the longest element of the song
6	DUSHOSY	Duration of the shortest syllable of the song
7	DULONSY	Duration of the longest syllable of the song
8	SHOPAU	Shortest pause between elements of the song
9	LONPAU	Longest pause between elements of the song
10	SOUNPRO	Sound proportion, calculated as the sum of the duration of all the elements of one song divided by song duration
11	PRDIFSO	Number of different songs divided by the total number of analyzed songs
12	PRDIFSY	Number of different syllables present in all analyzed songs divided by the number of analyzed songs
13	PRDIFEL	Number of different elements present in all analyzed songs divided by the number of analyzed songs
14	REPBETSO	Repertoire between songs, measured as the number of shared elements by two consecutive songs divided by the total number of elements present in both songs (shared + different)
15	NPHRSO	Total number of phrases of one song
16	NDISYSO	Number of different syllables of one song
17	NTOSYSO	Total number of syllables of one song
18	NDIELSO	Number of different elements of one song
19	NTOELSO	Total number of elements of one song
20	SWITCH	Switch rate, measured as the transition to different syllables divided by the total number of pauses between syllables in one song (for the species in which the syllable composed the entire song, the switch ratio was calculated for the elements)
21	MODRAT	Modulation ratio, measured as the mean modulation of the elements of the song. The modulation was measured as the sum of the fragments of the element with ascending, descending, and constant frequencies
22	EMFREQ	Emphasized frequency, corresponding to the frequency with highest amplitude of the song
23	MAXFREQ	Maximum frequency
24	MINFREQ	Minimum frequency
25	ABSBNW	Bandwidth, measured as the difference between the maximum and minimum frequencies

(*Continued*)

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TABLE II (*Continued*)

26	MXBNWSO	Maximum bandwidth of one element of the song
27	MNBNWSO	Minimum bandwidth of one element of the song
28	MXBNWSY	Maximum bandwidth of one syllable of the song
29	MNBNWSY	Minimum bandwidth of one syllable of the song

TABLE III

SONG MEASUREMENTS AND THEIR CONTRIBUTION TO THE PRINCIPAL COMPONENT ANALYSES THAT WERE CARRIED OUT

	Song organization PCA		Frequency PCA	
	PC1 (song complexity)	PC2	PC1 (pitch1)	PC2 (pitch2)
SONDUR	0.67	0.17	–	–
SONPAU	0.26	0.25	–	–
SONPRO	0.37	−0.01	–	–
DUSHOEL	−0.64	0.17	–	–
DULONEL	−0.59	0.50	–	–
DUSHOSY	−0.67	0.62	–	–
DULONSY	−0.47	0.75	–	–
SHOPAU	0.11	−0.01	–	–
LONPAU	0.48	0.39	–	–
SOUNPRO	−0.65	0.04	–	–
PRDIFSO	0.65	−0.01	–	–
PRDIFSY	0.81	0.36	–	–
PRDIFEL	0.72	0.50	–	–
REPBETSO	−0.43	0.28	–	–
NPHRSO	0.42	−0.48	–	–
NDISYSO	0.61	0.65	–	–
NTOSYSO	0.69	−0.33	–	–
NDIELSO	0.80	−0.27	–	–
NTOELSO	0.56	0.75	–	–
SWITCH	0.18	0.84	–	–
MODRAT	–	–	0.41	−0.32
EMFREQ	–	–	0.25	0.90
MAXFREQ	–	–	0.77	0.56
MINFREQ	–	–	−0.32	0.89
ABSBNW	–	–	0.93	−0.14
MXBNWSO	–	–	0.87	−0.17
MNBNWSO	–	–	0.24	0.09
MXBNWSY	–	–	0.94	−0.11
MNBNWSY	–	–	0.70	0.19
Variance explained (%)	32.2	20.8	45.35	21.54

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performed a similar analysis on a smaller data set of species from Kashmir. The first two principal components explained 85.6% of the total variance. The interpretation of the loadings (Table IV) is that PC1 measures common variance in body size (and hereafter we will refer to as "body size"). PC2 is a bipolar component, positively loaded by tarsus and tail length and negatively by beak length and width (hereafter "tarsus/beak ratio"). We interpret this component similarly to Price (1991), agreeing that it represents a ratio between beak and tarsus length (although the direction of this ratio was inverted in Price's study). PC3 explained very little variance and was difficult to interpret functionally, and is thus not further discussed.

We decided to use body size instead of body mass in our analysis, because the latter was not available for some of the species. However, there is a very strong relationship between our measure of body size and body mass as reported in another study (Price et al., 1997): $F_{1,26} = 111.5$, $P < 0.0001$; $R^2 = 0.81$; regression equation: body mass $= 1.3 \times$ body size $+ 8.14$.

2. *Beak Shape*

Since we wished to specifically test the effect of beak shape on song structure, we performed an additional PCA including only the three beak measurements (length, width, and depth). The first two principal components explained 96% of the total variance. As expected, the first component was unidirectional, reflecting purely the size (Table IV). Since the scores of this component were highly correlated with body size ($r = 0.935$, $N = 30$, $P < 0.001$), it was not used further. On the contrary, PC2 provided us with a measure of beak shape unrelated to size, showing a ratio between beak width, length, and depth (hereafter "beak shape"). Although the percentage of variance explained by this component is low, it is functionally coherent and provides a useful size-free estimate of beak shape.

TABLE IV

COMPONENT LOADINGS OF LOG-TRANSFORMED MORPHOLOGICAL TRAITS OF THE 30 *Phylloscopus* SPECIES

	Morphology PCA			Beak PCA	
	PC1 (body size)	PC2 (tarsus/beak ratio)	PC3	PC1	PC2 (beak shape)
Wing length	0.86	0.15	−0.38	–	–
Tail length	0.80	0.43	−0.28	–	–
Tarsus length	0.34	0.84	0.40	–	–
Beak length	0.92	−0.24	0.10	0.96	−0.14
Beak width	0.81	−0.49	0.21	0.94	0.34
Beak width	0.92	−0.15	0.15	0.96	−0.19
Variance explained (%)	64.8	20.7	7.8	90.8	5.67

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D. Phylogenetic Signal of Song Variables

We studied the degree to which song characters and morphological measures are influenced by species relatedness using the software PHYSIG (Blomberg et al., 2003). We studied the phylogenetic signal of the characters by means of the statistic K using the algorithms implemented in the package. We also estimated the amount of variation of the song characteristics among species using coefficients of variation (CV). The CVs for types of variables (temporal, structural, and frequency) were compared using one-way ANOVA and pairwise comparisons were performed using a *post hoc* Tukey test.

E. Strength of Sexual Selection

Species-specific differences in the strength of sexual selection correspond to the average level of male reproductive skew (Kokko et al., 2002). This skew has been typically taken as equivalent to the degree of polygyny, but the discovery of highly variable levels of extra-pair paternity in birds has reduced the value of this measure (Birkhead and Møller, 1998). Unfortunately, estimates of extra-pair paternity are lacking for most *Phylloscopus* species, so we decided to use other possible surrogates of strength of sexual selection. We selected two different measurements: the degree of sexual size dimorphism and the average latitude of the species.

Sexual dimorphism is one of the basic correlates of sexual selection, given the contribution of male–male competition to selection for large male body size (Trivers, 1972). Furthermore, sexual size dimorphism has been found to be related to more direct measures of sexual selection, such as polygynous and promiscuous mating systems, or testis size (Dunn et al., 2001). We estimated average sexual size dimorphism by calculating the difference between male and female size [log (mean male trait)−log (mean female trait)] for wing, tail, and tarsus length. These data were available for all species except Ijima's leaf warbler, for which only one individual per sex was available. Dimorphism scores calculated for each trait correlated positively among them, so we ran a PCA and extracted a first principal component in which all dimorphism scores contributed in the same direction (wing length: 0.76; tail length: 0.84; tarsus length: 0.62; variance explained: 55.7%). Scores for this PC1 will be referred to as the index of size dimorphism.

In the Northern Hemisphere, sexual selection has been shown to increase in intensity with increasing latitude, possibly because increases in latitude lead to shorter reproductive seasons and higher abundance of nutrients and breeding densities (Irwin, 2000). These regimes would favor male competition (Catchpole, 1980). Similarly, comparative analyses have

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shown that levels of extra-pair paternity increase with migration distance and synchronous breeding in birds, and these two factors are known to increase with latitude (Spottiswoode and Møller, 2004).

F. Sound Characteristics of Niche and Habitat

Martens suggested that the particularly high-pitched song of the large-billed leaf warbler (*Phylloscopus magnirostris*) was an adaptation to sound transmission in the noisy conditions of the Himalayan springs (Martens, 1980). However, this is a rather unique habitat, and the wider variation in habitat usage in the genus *Phylloscopus* could be explained along a continuum between the open and closed forest (Badyaev and Leaf, 1997). A recent meta-analysis has shown that the song characteristic that is mostly affected by habitat structure is emphasized frequency (Boncoraglio and Saino, 2007). To test the hypothesis of acoustic adaptation, we tried to find reliable descriptions of the openness of typical species-specific habitat (e.g., Baker, 1997), but these were difficult to systematize and quantify (but see Badyaev and Leaf, 1997). However, several field studies have found that habitat selection and feeding niche in the *Phylloscopus* are strongly related to morphological adaptations (Forstmeier et al., 2001; Gaston, 1974; Price, 1991). Although there are several differences between studies conducted in different geographical areas in their results on the relationship of morphology to habitat, several main patterns are shared by most studies. Large tarsi and small beaks in *Phylloscopus* species have been shown to relate to terrestrial habitats, with short tarsi and relatively large beaks selected in birds feeding in high canopies (Gaston, 1974; Price, 1991; Richman and Price, 1992). We thus decided to use the morphological PC2 (tarsus/beak ratio) as an ecomorphological characteristic correlated with habitat and niche choice.

G. Character Displacement

A character reinforcement mechanism predicts that song should be more divergent between species in sympatry than in allopatry. We tested this prediction by comparing the differences in song variables between pairs of species differing in whether they were sympatric or not. For this, each pair of sister species was compared with the phylogenetically nearest species that is sympatric with one of them and allopatric with the other (Table V). This allowed us to control for differences related to divergence times. We did not include the pair composed by the Western-crowned and the Blyth's leaf warblers *(Phylloscopus occipitalis* and *P. reguloides)* because the nearest species on the tree fulfilling the requirement of sympatry was Hume's leaf warbler and this species is phylogenetically so distant that many factors other than sympatry might be responsible

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TABLE V

NEAREST SPECIES ON THE TREE (FIRST COLUMN) BEING ALLOPATRIC WITH ONE (SECOND COLUMN) AND SYMPATRIC WITH ANOTHER (THIRD COLUMN) SPECIES OF A PAIR OF SISTER SPECIES

	Allopatric	Sympatric
P. magnirostris	*P. plumbeitarsus*	*P. trochiloides*
P. borealis	*P. magnirostris*	*P. tenellipes*
P. plumbeitarsus	*P. ijimae*	*P. coronatus*
P. fuscatus	*P. griseolus*	*P. affinis*
P. affinis	*P. canariensis*	*P. sindianus*
P. ibericus	*P. sibilatrix*	*P. bonelli*
P. proregulus	*P. humei*	*P. inornatus*
P. pulcher	*P. proregulus*	*P. chloronotus*

for song differences. We considered a pair of species to be sympatric when they shared at least 20% of their distribution, otherwise they were considered allopatric.

H. STATISTICS AND DATA ANALYSIS

All morphological variables were log-transformed before use. Transformed variables were found to conform to normal distributions. Sound measurements were checked for normality and approached to normal distributions by transformations *ad hoc* (Sokal and Rohlf, 1995). We used parametric statistics throughout except for the test of sympatry–allopatry, where the small sample size made a sign test more appropriate (Siegel and Castellan, 1988). A priori hypotheses were tested using stepwise multiple regression procedures. Since species cannot be considered as the independent units in evolutionary terms, we used the method of independent contrasts to control for similarity due to common descent (Felsenstein, 1985). For this, we used the software CAIC, with the ''crunch'' algorithm and a phylogeny (Fig. 1) in which all branch lengths were considered of equal length (Purvis and Rambaut, 1995). Analyses of independent contrasts were conducted by multiple regressions through the origin (Felsenstein, 1985).

III. RESULTS

A. EVOLUTIONARY LABILITY OF SONG CHARACTERISTICS

Song characters were more labile than morphological traits (Mann-Whitney U-test: $Z = -2.45$, $P = 0.01$). The mean K value for song characters was 0.585 while for morphological characters it was 0.809. The K values closer to 1 indicate higher phylogenetic signal (Blomberg et al., 2003).

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Although K values were lower for song characters, the majority of them showed significant phylogenetic signal when analyzed individually, as did all the principal components that we studied: song complexity, pitch1, and pitch2. When the variation of temporal, structural, and frequency variables were compared, a significant difference in variation was found between types of variables ($F_{2, 24} = 13.56$; $P < 0.001$). The *post hoc* Tukey test showed that the CV of frequency variables (mean CV = 27%) was significantly lower than the CV of temporal (mean CV = 81%) and structural variables (mean CV = 84%; $P < 0.001$ for both comparisons), which did not differ significantly from each other ($P > 0.9$). Thus, song frequency characters are more conserved between warbler species than temporal and structural ones.

B. Morphological Constraints

Our initial hypotheses predicted that frequency characteristics could be affected by both the bird's overall body size and also by beak shape. Thus, we conducted stepwise regressions including these two predictors in the initial model. In the final model for the species data of pitch1, only body size remained in the model, showing the expected negative relationship ($F_{1, 28} = 6.53$, $P = 0.016$; β (S.E.) $= -0.43$ (0.17); $R^2 = 0.16$; Fig. 3). The same relationship was found in the analysis of independent contrasts ($F_{1, 28} = 5.97$, $P = 0.021$; β (S.E.) $= -0.49$ (0.20); $R^2 = 0.14$; Fig. 3). The exclusion of beak shape in these analyses was not due to collinearity with body size (tolerance > 0.95, FIV < 1.10).

Similarly, in the analysis of pitch2, the final model also included body size, after dropping beak shape for lack of significance ($F_{1, 28} = 5.75$, $P = 0.02$; β (S.E.) $= -0.41$ (0.17); $R^2 = 0.14$). The analysis of independent contrasts confirmed this relationship ($F_{1, 28} = 4.47$, $P = 0.043$; β (S.E.) $= -0.47$ (0.26); $R^2 = 0.10$). Again, collinearity between independent variables was not a problem in the analyses (tolerance > 0.90, FIV < 1.10).

C. Sexual Selection

1. *Size Dimorphism*

In the species data set, we found a nonsignificant trend toward a positive relationship between sexual size dimorphism and song complexity ($F_{1, 27} = 3.10$, $P = 0.089$; β (S.E.) $= 0.32$ (0.18); $R^2 = 0.10$). In the regression of independent contrasts through the origin, this pattern disappeared entirely ($F_{1, 27} = 0.16$, $P = 0.68$; β (S.E.) $= 0.07$ (0.17); $R^2 = 0.03$).

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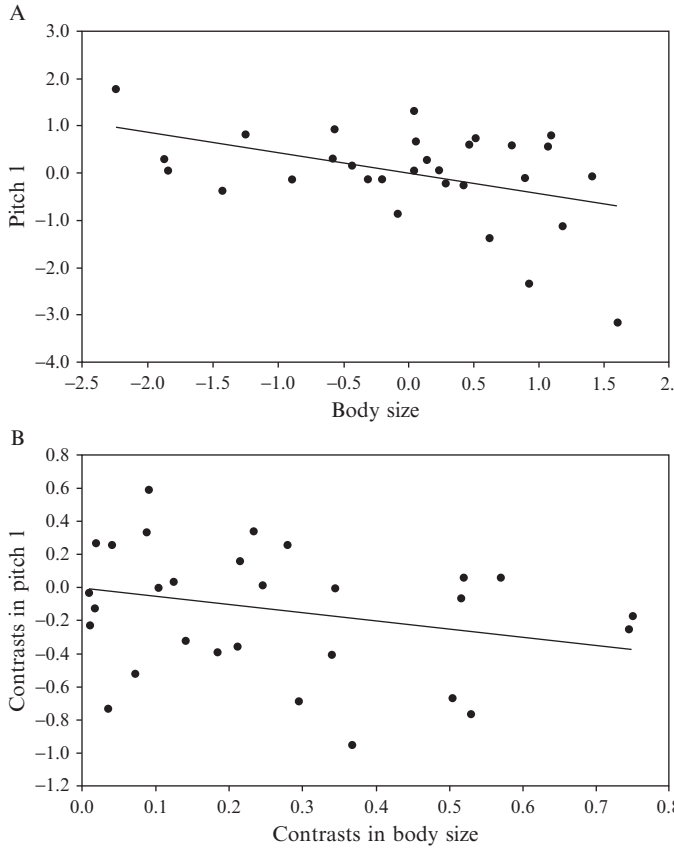

FIG. 3. Relationship between pitch1 and body size, as shown by linear regression using species data points (A) and linear regression through the origin using independent contrasts (B). See text for statistics.

2. *Latitude*

Midlatitude was positively, but not significantly related to song complexity in the species data set ($F_{1,\ 28} = 2.71$, $P = 0.11$; β (S.E.) = 0.030 (0.018); $R^2 = 0.05$; Fig. 4). However, the analysis of contrasts by means of linear regression through the origin showed a significant relationship in the same direction ($F_{1,\ 28} = 6.59$, $P = 0.016$; β (S.E.) = 0.032 (0.012); $R^2 = 0.16$; Fig. 4). Evolutionary transitions to higher latitudes have thus been followed by increases in song complexity. Body size was not significantly related to song complexity either in species data or contrasts, and was dropped from the models.

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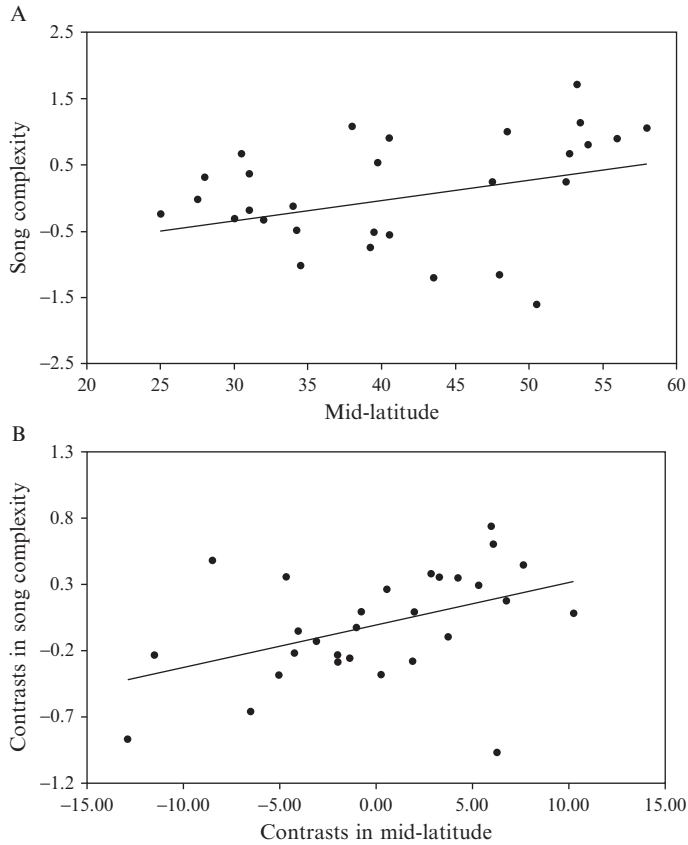

FIG. 4. Relationship between song complexity and midlatitude, as shown by linear regression using species data points (A) and linear regression through the origin using independent contrasts (B). See text for statistics.

D. HABITAT ACOUSTIC ADAPTATION

As predicted, the tarsus/beak ratio, an ecomorphological correlate of habitat use, was negatively related to pitch2 ($F_{1,\ 28} = 4.42$, $P = 0.045$; β (S.E.) $= -0.37$ (0.17); $R^2 = 0.10$; Fig. 5). However, the analysis of contrasts did not confirm this relationship ($F_{1,\ 28} = 0.21$, $P = 0.64$; β (S.E.) $= -0.09$ (0.20); $R^2 = 0.01$; Fig. 5).

We have previously shown (see Section III.B) that pitch2 is also affected by body size. Including the two predictors in a single model strengthens both relationships (overall model: $F_{1,\ 27} = 5.95$, $P = 0.007$, $R^2 = 0.25$; body size:

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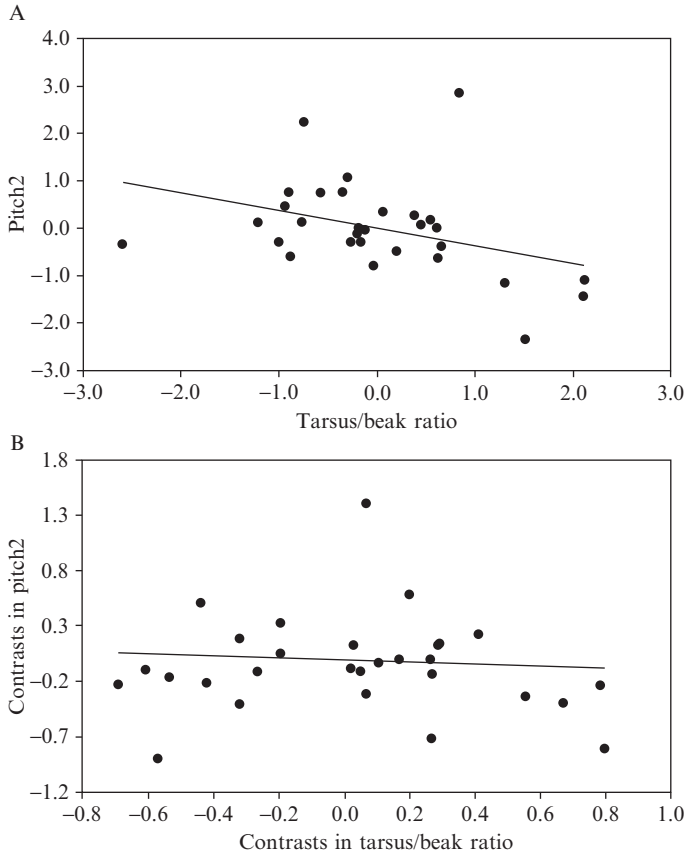

FIG. 5. Relationship between pitch2 and tarsus/beak ratio, as shown by linear regression using species data points (A) and linear regression through the origin using independent contrasts (B). See text for statistics.

β (S.E.) $= -0.41$ (0.16); tarsus/beak ratio: β (S.E.) $= -0.37$ (0.16)). When independent contrasts are analyzed, the effect of tarsus/beak ratio is dropped, and only body size remains in the model.

E. CHARACTER DISPLACEMENT

We did not find larger differences in frequency (pitch1: $N = 8$, $Z = 1.06$, $P = 0.28$; pitch2: $N = 8$, $Z = -0.35$, $P = 0.72$) or song complexity ($N = 8$, $Z = 0.35$, $P = 0.72$) between sympatric than between allopatric species.

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IV. Discussion

Previous comparative analyses have shown that the evolution of bird song is driven by a series of different selective pressures, both adaptive and nonadaptive (Read and Weary, 1992). Bird song is a complex set of multiple characters, and each of them is expected to be influenced by different selective pressures (Gil and Gahr, 2002). Our analysis of the song of 30 species of *Phylloscopus* warblers confirms previous studies in other bird groups in showing that phylogenetic drive, acoustic adaptation to the habitat, sexual selection, and morphological constraints have all played a role in shaping different aspects of the song of these species as we hear them today. Let us consider each of these mechanisms in turn.

A. Speciation and Differentiation

Ecological divergence between species of this group is not large (Price et al., 2000), and the extremely high number of species seems to have evolved through multiple invasions and dispersal events, but with limited habitat and niche specialization (Price et al., 2000; Richman, 1996). Detailed molecular analysis of mitochondrial DNA and amplified fragment length polymorphism (AFLP) markers within the greenish warbler superspecies (*Phylloscopus trochiloides*) shows that the formation of genetically isolated species in this group can be best explained by gradual dispersion and divergence in song characteristics (Irwin et al., 2005; Irwin et al., 2001). These data show that increased selection for song complexity following dispersal toward more Northern latitudes has led to reproductive isolation and formation of new species.

We found substantial phylogenetic signal in song characteristics, with lower among-species variance for frequency traits than structural or temporal characteristics. A similar conclusion was reached in a previous study in *Phylloscopus*, using a smaller sample size (Liou, L.W., Tiainen, J., Higuchi, H., Richman, A.D., and Price, T.D., unpublished: ''Song variation in the genus *Phylloscopus*''). Studies in other taxa also find significant phylogenetic signal in song variables, but studies differ in whether temporal or frequency characters are those which are better preserved.

For instance, in the herons, an evolutionarily very distant group, the largest phylogenetic information was contained in vocal traits that were not subjected to habitat adaptation processes (McCracken and Sheldon, 1997). However, since frequency components are highly dependent on morphology (see Section III), it is not surprising that these vocal characteristics are those that contain a higher phylogenetic signal. In the case of *Phylloscopus*, this pattern is expected because changes in body size have been shown to appear at the very

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start of the radiation, in the deepest part of the tree, with modifications of beak shape following shortly thereafter (Richman, 1996). A study on the song of *Regulus* warblers compared the phylogenetic signal of song characteristics that are present in birds that have been reared in acoustic isolation (Kaspar-Hauser birds) with that of signals that are due to learning (Päckert et al., 2003). Despite the rather arbitrary distinction (Kaspar-Hauser birds were not available for all species), the study suggests that higher phylogenetic signal is contained in unlearnt that in learned characters (Päckert et al., 2003). Similarly, in Paruline warblers, details of the fine note structure had a higher phylogenetic signal than song structure (van Buskirk, 1997).

In contrast, Price and Lanyon (2002) found that temporal components were more phylogenetically informative than frequency components in the Neotropical Oropendolas (suboscine Passerines). However, the authors selected characters that were judged to be phylogenetically informative a priori, and thus it is difficult to compare their results with studies in which no previous selection of variables is performed.

B. Habitat Adaptation

In the absence of good quality habitat selection data, we used an ecomorphological correlate of habitat, the tarsus/beak ratio, as an index of habitat selection (Price, 1991; Richman and Price, 1992). Data from the Himalayan leaf warbler guild shows that increases in this ratio have coevolved with changes in the use of coniferous trees (Richman and Price, 1992): species with high tarsus/beak ratios are more prone to use short understory vegetation and deciduous trees, whereas species with low ratios will be more frequently found foraging in taller coniferous trees. Sound transmission characteristics are expected to differ dramatically between these habitats, favoring low frequencies in leafy, understory habitats (Badyaev and Leaf, 1997; Morton, 1975; Wiley, 1991).

As expected, we found that tarsus/beak ratio was negatively related to pitch2, indicating that species with relatively large tarsus and a small beak in relation to their size, and thus preferring understory habitats, have songs with comparatively lower emphasized and minimum frequencies (cf. Badyaev and Leaf, 1997). However, this relationship was not confirmed when correcting for common descent, suggesting that the above relationship could be driven by the bias of a subgroup of highly related species.

Similar relationships have been found for the New World Parulid warblers, where species living in deciduous forests had songs with lower frequencies than those using conifers (van Buskirk, 1997).

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Interestingly, the beak/tarsus ratio was correlated with pitch2 and not with pitch1. This is in agreement with a recent meta-analysis in which the strongest effect of habitat on song was detected in the emphasized frequencies, much more strongly than in the maximum frequency (Boncoraglio and Saino, 2007). Despite maximum and minimum frequencies being strongly correlated, our principal component analyses separated the highest contribution of these two measurements in two distinct, uncorrelated components. The uncoupling of maximum frequency and bandwidth in pitch1 and minimum and emphasized frequency in pitch2 suggests that separate mechanisms are responsible for these two components. Indeed, physiological studies have shown that the left and right sides of the syrinx can contribute differently to song bandwidth, with each side specialized in a given frequency band (Suthers, 2004; Suthers et al., 1999). See the next section for additional evidence for dissociation between maximum and minimum frequencies.

The acoustic adaptation of song between different habitats has been shown to explain subspecific differences in song in *Melospiza melodia* (Patten et al., 2004), contributing to reproductive isolation in an area of sympatry. However, our results suggest that selection for songs with optimal sound transmission in populations expanding into new habitats has not considerably contributed to song differentiation and reproductive isolation.

C. Morphological Correlates

We found a negative relationship between both components of frequency (pitch1 and pitch2) and body size. This pattern corroborates previous studies on a large diversity of avian species which report similarly negative relationships between body mass and song frequency, although the slope of this relationship depends on the avian group that is being considered (Ryan and Brenowitz, 1985; Tubaro and Mahler, 1998; Wallschläger, 1980). Examining the graph for pitch1 (Fig. 3), we can see that in the genus *Phylloscopus*, small-bodied species consistently lack low frequencies, suggesting that low frequencies are constrained when the body size is small. This is in contrast to the larger study of Ryan and Brenowitz (1985), in which the general pattern suggests that large species are limited in the production of high-pitched sounds.

Body size can be subject to directional sexual or natural selection (Endler, 1986; Trivers, 1972) and, thus, such selective regimes could force song characteristics to trail along because of correlated change (Price and Langen, 1992). A major divergence in body size has been found at the root of the phylogenetic tree of *Phylloscopus* (Richman, 1996), suggesting that divergence for this characteristic had a determinant role in the evolution of

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the song in this group very early in their evolutionary history. Our data, thus, suggest that a correlated change in song frequency must have taken place from the onset of the evolution of this group.

Another morphological correlate that was examined in relationship to song frequency characteristics was beak shape; however, we found no evidence for beak shape to limit overall frequency patterns in the leaf warblers. Podos (2001) has found that evolutionary transitions toward deeper beaks in *Geospiza* finches are negatively associated with a measure of vocal agility, namely the capacity to produce quick trills encompassing a wide frequency range. This suggests that selection on beak morphology as a response to seed availability may have driven vocal characteristics during evolution, probably reinforcing prezygotic isolation and speeding up speciation processes. Similar trills are typical of some *Phylloscopus* species (e.g., Bonelli's, Wood warbler, etc.; Martens, 1980), so we do not discard the idea that beak shape may limit some trill performance measurements in some species.

D. Sexual Selection

We used two surrogates of intensity of sexual selection: size dimorphism and midlatitude. Of these two, only the expected positive relationship between midlatitude and song complexity was confirmed when controlling for common descent. This relationship shows that transitions to Northern latitudes have coevolved with increases in song complexity, the same pattern that has been found for a set of different populations and species included in the greenish warbler superspecies (Irwin, 2000; Irwin et al., 2001).

Furthermore, a previous comparative analysis on 165 species of birds provides similar evidence in showing that song complexity is positively related to migratory behavior (Read and Weary, 1992), which is itself a very good proxy of midlatitude (Newton and Dale, 1996). The interpretation of this pattern is not straightforward, since an increase in midlatitude involves a large series of changes in life history traits, and it is difficult to single out the most likely causal factor. Catchpole (1980, 1982) has argued that high latitude, migratory species have less time than resident species to obtain a territory and mate, and thus are subjected to higher levels of sexual selection. In agreement with this, extra-pair paternity rates are positively related to synchronous breeding and migratory distance, two traits that increase with increasing latitude (Spottiswoode and Møller, 2004).

Our measure of song complexity, encompassing increases in song length, versatility, and repertoire size, would suggest that species living in more Northern latitudes have developed more complex song repertoires. Additionally, Slater (1981) has argued that the two modes of sexual selection, male–male competition and mate choice, select for different song

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characteristics, the former favoring shorter songs which are more quickly perceived and used in countersinging by males. Although a specific test of this hypothesis is still lacking, a recent study in a *Sylvia* warbler provides some evidence by comparing two populations differing in latitude and migratory behavior (Collins et al., 2009). To the extent that this song divergence due to the two modes of sexual selection is real, our results could be interpreted in the same sense, namely an effect of mate attraction rather than male–male competition on song complexity.

Do the two modes of sexual selection correlate with latitude, or is this true just for mate choice? It is difficult to answer this question in the absence of more direct data, but some evidence does show that these two pressures may not correlate with each other. For instance, populations of the greenish warbler living in Northern latitudes have much lower densities than those in the south (Irwin, 2000). Although density should be a close correlate of the strength of male–male competition, intersexual selection for signals that attract females may be stronger at lower densities (Irwin, 2000).

However, not all studies are unanimous in finding a relationship between sexual selection and song complexity. A study relating levels of extra-pair paternity to song repertoire size in a large sample of species found a lack of support for this hypothesis (Garamszegi and Møller, 2004). This lack of relationship is reminiscent of the low power of song repertoire size as a predictor of reproductive success in many field studies (Byers and Kroodsma, 2009). Although the positive relationship between repertoire size and pairing success is strong in some species (e.g., Buchanan and Catchpole, 1997), it is remarkably absent in many others (e.g., Byers and Kroodsma, 2009; Gil and Slater, 2000a; Gil et al., 2007), questioning the current adaptive value of a trait that may have been used by sexual selection in the past (for evidence of temporal heterogeneity in the value of repertoire size for sexual selection, see Forstmeier and Leisler, 2004).

E. Character Displacement

We did not find evidence for a reinforcement of song differences (character displacement) across the genus. Differences in song were similar for allopatric and sympatric pairs of species. Although the sample size of this test was small, a similar lack of character displacement was found in the secondary contact zone of two morphs of the greenish warbler superspecies (Irwin, 2000). In their contact area in central Siberia, the difference between songs of the two morphs (*Phylloscopus plumbeitarsus* and *P. viridanus*) can be explained by the progressive change accumulated through evolutionary time along two South–North axes, and there seems to be no added differentiation that could be explained by character displacement.

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In contrast, a study on antbird acoustics (Thamnophilidae, suboscine Passeriformes) found evidence for higher differences in temporal and pitch characteristics of songs between sympatric than allopatric species (Seddon, 2005). Although the evidence is too scant to venture an explanation, future studies should consider whether greater selection for character displacement could be explained by the absence of song learning in the suboscines.

F. General Pattern of Song Evolution

Bird song is a remarkably difficult phenomenon to capture in quantitative measurements (Kroodsma, 1977), and thus our analysis can only attempt to explain some general patterns. Large species-specific differences in song content and overall syllable composition are probably due to stochastic events linked to colonization processes. In 1983, Gerhardt Thielcke proposed that the evolution of song in the common chiffchaff superspecies was due to colonization events by birds that had not properly crystallized their song (Thielcke, 1983). He reached this conclusion after finding that the song of common chiffchaff males that had been hand-reared in acoustic isolation resembled that of the Iberian and Canary islands chiffchaffs (*Phylloscopus ibericus* and *P. canariensis*). He proposed that such a mechanism (*Lernentzug:* withdrawal of learning) could be at the base of song differentiation between subspecies and song evolution in islands.

We can assume that the high evolutionary lability of midlatitude distribution in the genus *Phylloscopus* (Price et al., 1997) is an indication of the high frequency of dispersal events along North–South axes, and this is expected to have led to frequent and progressive degrees of allopatry where speciation can occur (Irwin et al., 2001, 2005). *Phylloscopus* warblers need to learn their songs (Schubert, 1976; Thielcke, 1983), and thus haphazard dispersal of song variants plus song learning by males and females could lead to new populations having distinctive songs and being isolated from each other (Lachlan and Servedio, 2004).

Although we cannot answer the question of why a given species sings a given syllable repertoire, we can offer some explanation about species differences in more quantitative estimates of song (Fig. 6). Thus, our study suggests that song frequency characteristics have coevolved with likely adaptive changes in body size (Gaston, 1974). Differences in minimum and emphasized peak frequencies show a relationship with a morphological character related to microhabitat choice, but this relationship disappears when controlling for common descent, suggesting that song is not adaptated to sound transmission characteristics of specific habitats.

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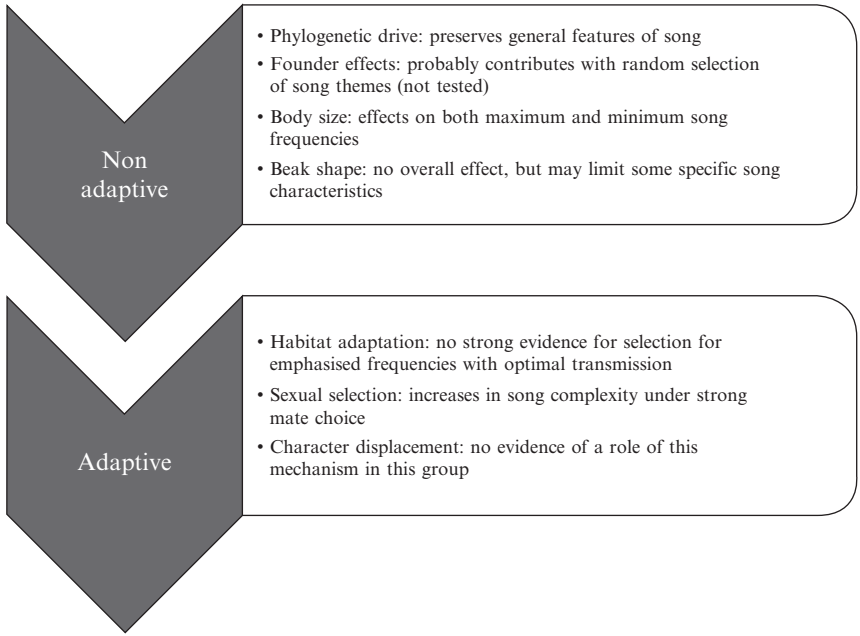

FIG. 6. List of different mechanisms that are likely to have influenced the evolution of song in the *Phylloscopus* warblers.

Song complexity, a wide-ranging measurement encompassing temporal and structural sound complexity estimates, is best explained by breeding latitude. We interpret this relationship as a correlate of increased sexual selection by mate choice toward more Northern latitudes. Thus, superimposed upon haphazard selection of themes, selective pressures for higher song elaboration in areas of high sexual selection, and correlative change in song brought about by natural selection of body size, would have lead to the diversity of songs that are found within the genus *Phylloscopus*.

Acknowledgments

We thank Trevor Price, who allowed us to examine an unpublished manuscript by Liu and coauthors, which tested some of the ideas of this study, and which was at the base of this research. Robert Prys-Jones and Katerina Cook at the bird collection of the British Museum kindly allowed access to the Tring bird skin collection, where the morphological data were taken. Richard Ranft provided recordings of some species from the British National Sound Archive. Rafael Márquez at the Fonoteca Zoologica of the Museo Nacional de Ciencias Naturales (Madrid, Spain) allowed access to commercial recordings held in the sound library. Peter Slater, Pablo Tubaro, Jose Luis Copete, and an anonymous referee provided valuable

APPENDIX 1

Morphological Data Obtained from Skins of the British Museum of Natural History

Species	Sample size		Wing length		Tail length		Tarsus length		Beak length		Beak width		Beak depth	
	Males	Females	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Phylloscopus affinis	5	5	56.2 (1.8)	55.4 (4.8)	43.6 (4.4)	42.6 (3.6)	17.4 (0.9)	17.9 (0.8)	12.22 (0.17)	12.71 (0.3)	3.49 (0.33)	3.35 (0.23)	2.55 (0.11)	2.55 (0.2)
Phylloscopus bonelli	6	4	63 (0.9)	61.3 (1.3)	46.2 (2.4)	46.5 (1.8)	16.8 (1.1)	16.7 (0.7)	12.41 (0.76)	12.85 (0.26)	3.82 (0.2)	3.51 (0.05)	2.71 (0.13)	2.63 (0.23)
Phylloscopus borealis	5	5	65.6 (1.6)	64.8 (2.6)	46.4 (2.5)	44.4 (2.3)	18 (1.2)	18.2 (0.5)	14.24 (0.41)	12.83 (1.17)	4.21 (0.33)	4 (0.11)	3.06 (0.14)	3.25 (0.2)
Phylloscopus canariensis	5	5	51.6 (2.3)	49.8 (2.3)	46.4 (1.7)	43.8 (1.3)	17.3 (1.6)	17.8 (1.4)	12.8 (0.47)	12.7 (0.84)	3.63 (0.42)	3.74 (0.26)	2.72 (0.21)	2.89 (0.21)
Phylloscopus chloronotus	5	5	49.6 (3.8)	48.2 (2)	38.4 (2.9)	33.4 (2.2)	15.5 (1.2)	14.7 (1.1)	10.56 (0.58)	9.57 (0.66)	3.21 (0.14)	3.24 (0.26)	2.31 (0.19)	2.25 (0.17)
Phylloscopus collybita	5	5	59.4 (1.4)	55 (1.9)	47.2 (1.3)	43 (1.5)	17.2 (1.9)	16.8 (0.4)	11.73 (0.32)	11.63 (0.26)	3.34 (0.32)	3.42 (0.37)	2.57 (0.19)	2.53 (0.12)
Phylloscopus coronatus	5	5	62.4 (1.9)	60.6 (2)	46.8 (1.3)	45 (3)	15.7 (0.3)	16.2 (1.1)	13.89 (0.57)	13.49 (0.35)	3.88 (0.27)	4.42 (0.41)	3.32 (0.2)	3.15 (0.06)
Phylloscopus fuscatus	5	5	59.6 (4.3)	56.2 (2.8)	46.8 (3.6)	45.2 (2.9)	20.9 (2.4)	20.7 (1.4)	12.51 (0.51)	12.81 (0.93)	3.39 (0.34)	3.69 (0.32)	2.64 (0.18)	2.66 (0.11)
Phylloscopus griseolus	7	3	62.5 (2.2)	62 (3.7)	47.9 (3.2)	48 (4.4)	19.4 (0.9)	19.3 (0.7)	13.57 (0.98)	13.22 (1.01)	3.42 (0.31)	3.43 (0.11)	2.9 (0.25)	2.54 (0.32)
Phylloscopus humei	5	5	55.6 (2.2)	53.4 (3.4)	40.8 (3.2)	37.6 (3.3)	17.3 (0.5)	16.6 (0.7)	10.73 (0.43)	10.8 (0.83)	2.9 (0.27)	3.43 (0.36)	2.34 (0.09)	2.35 (0.21)
Phylloscopus ibericus	5	5	59.4 (2.2)	53.8 (2)	45.4 (1.2)	41.8 (1.5)	18 (0.9)	16.2 (1.2)	12.24 (0.85)	12.07 (0.61)	3.51 (0.28)	3.49 (0.35)	2.66 (0.19)	2.7 (0.09)
Phylloscopus ijimae	1	1	62.0 (n/a)	64.0 (n/a)	42.0 (n/a)	45.0 (n/a)	15.3 (n/a)	18.1 (n/a)	15.1 (n/a)	15.7 (n/a)	4.8 (n/a)	4.7 (n/a)	3.09 (n/a)	3.21 (n/a)
Phylloscopus inornatus	5	5	55.2 (1.1)	52.6 (3)	39 (1)	36.2 (2.8)	16.3 (0.4)	16.8 (1.1)	11.36 (0.39)	10.54 (0.21)	3.23 (0.17)	3.16 (0.37)	2.37 (0.23)	2.37 (0.12)
Phylloscopus maculipennis	5	5	48.6 (2.2)	47.4 (2.9)	33.2 (1.7)	32.2 (1.8)	17.6 (1.2)	16.3 (1)	10.14 (0.61)	10.06 (0.77)	3.11 (0.25)	3.28 (0.28)	2.26 (0.15)	2.32 (0.17)
Phylloscopus magnirostris	6	4	67.5 (1.7)	67.3 (2.7)	49.4 (0.9)	49.5 (1.3)	17.6 (0.8)	17.7 (1.2)	14.74 (0.92)	14.34 (0.53)	4.23 (0.35)	4.61 (0.28)	3.31 (0.32)	3.32 (0.3)
Phylloscopus nitidus	5	5	62.2 (1.1)	59 (1.9)	46.8 (1.3)	43.6 (1.6)	17.9 (1)	16.6 (0.5)	12.67 (0.81)	12.51 (0.65)	3.71 (0.37)	3.6 (0.39)	2.92 (0.43)	2.92 (0.11)
Phylloscopus occipitalis	5	5	65.2 (3.5)	62.4 (2.3)	46.8 (2.9)	43 (1)	16.9 (1.3)	17 (1.1)	14.01 (0.31)	13.07 (0.65)	4.26 (0.51)	3.91 (0.5)	3.06 (0.13)	3.03 (0.28)
Phylloscopus orientalis	5	5	66.6 (1.4)	63.6 (1.2)	47.4 (2)	44.6 (0.9)	17.4 (1)	16.7 (0.9)	12.6 (0.26)	12.47 (0.43)	3.63 (0.32)	3.65 (0.27)	2.73 (0.14)	2.75 (0.15)
Phylloscopus plumbeitarsus	5	5	58.4 (2.9)	55.2 (2.2)	44.2 (2)	40.8 (1.5)	17 (0.6)	15.9 (0.9)	12.55 (0.1)	12.81 (0.48)	3.66 (0.35)	4.16 (0.24)	2.86 (0.19)	2.93 (0.28)
Phylloscopus proregulus	5	5	52.6 (1.4)	48.2 (1.3)	37.8 (1.7)	34.6 (1.4)	15 (1.5)	15.7 (1)	10.38 (0.5)	9.99 (0.52)	3.11 (0.29)	2.88 (0.18)	2.31 (0.11)	2.27 (0.18)
Phylloscopus pulcher	5	5	56.2 (2.4)	54 (3.3)	40.2 (2.3)	39.2 (2.3)	16.7 (0.5)	17.4 (1.9)	12.16 (0.34)	12.08 (0.9)	3.64 (0.33)	3.69 (0.2)	2.56 (0.21)	2.56 (0.23)
Phylloscopus reguloides	5	5	58.8 (2.8)	56.8 (3.7)	43.2 (1.7)	41.6 (2.3)	16.4 (1)	16.2 (0.9)	12.38 (0.37)	11.95 (0.55)	4.02 (0.28)	4.31 (0.15)	2.79 (0.07)	2.86 (0.17)
Phylloscopus schwarzi	5	5	63.6 (2.6)	58.4 (4.1)	52 (2.4)	49 (5.4)	20.6 (1)	19.5 (1.1)	12.81 (0.74)	12.73 (0.48)	4.07 (0.25)	3.89 (0.17)	3.4 (0.17)	3.41 (0.19)
Phylloscopus sibilatrix	5	5	72.6 (3.4)	69.2 (1.8)	47.6 (2.3)	44 (1)	16.6 (1.1)	17 (0.5)	12.71 (1.4)	12.98 (0.4)	3.86 (0.38)	3.89 (0.22)	2.84 (0.1)	2.82 (0.14)
Phylloscopus sindianus	5	5	58 (2.6)	51.8 (1.3)	46.2 (2.3)	44.6 (0.6)	16.4 (1.1)	16.5 (0.5)	11.37 (0.32)	11.14 (0.78)	3.04 (0.13)	3.05 (0.26)	2.36 (0.19)	2.42 (0.19)
Phylloscopus tenellipes	6	4	61.4 (1.3)	57.5 (0.6)	44.2 (1.8)	41.5 (2.1)	17.2 (0.7)	17.6 (0.6)	13.66 (0.48)	13.6 (0.6)	4.28 (0.22)	4.14 (0.14)	3.25 (0.27)	3.17 (0.15)
Phylloscopus trochiloides	5	5	62.8 (2.3)	57.8 (2.8)	50.2 (3.2)	46.2 (1.3)	17.4 (1.4)	16.9 (1.1)	12.86 (0.29)	12.21 (0.52)	3.57 (0.26)	3.7 (0.24)	2.84 (0.25)	2.81 (0.17)
Phylloscopus trochilus	5	5	66.4 (1.2)	62.4 (3)	48.8 (2.2)	44.2 (3.7)	19.6 (0.8)	18.9 (0.4)	12.29 (0.31)	12.15 (0.95)	3.13 (0.16)	3.3 (0.06)	2.71 (0.23)	2.75 (0.18)
Phylloscopus tytleri	5	5	56.4 (1.2)	55.6 (2.3)	38.2 (2.1)	38.2 (2.3)	16.3 (1.3)	16.2 (1.1)	12.79 (0.37)	12.2 (0.81)	3.49 (0.23)	3.32 (0.25)	2.68 (0.17)	2.58 (0.14)
Phylloscopus viridanus	5	5	60 (2.5)	56.4 (1.6)	45.6 (1.6)	44 (0.8)	16.6 (1.1)	17.5 (1.7)	12.69 (0.52)	12.09 (0.39)	3.5 (0.51)	3.36 (0.22)	2.79 (0.19)	2.66 (0.16)

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