

HABITAT ASSOCIATIONS OF SONG CHARACTERISTICS IN *PHYLLOSCOPUS* AND *HIPPOLAIS* WARBLERS

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ABSTRACT.—Bird-song functions, such as mate attraction, species recognition, and territory defense, are closely linked to individual fitness. Thus, habitat characteristics that affect song transmission and degradation should exert a strong influence on the evolution of song attributes. Whereas different acoustic environments may influence the evolution of song characteristics, factors such as body size and evolutionary history of taxa are expected to constrain the amount of environmental variation in song properties. In the present study, we controlled for phylogeny and examined the effects of body mass and habitat structure on variation in song structure of 30 taxa of *Phylloscopus* and *Hippolais* warblers, which are a closely related group of birds that occupy a wide variety of habitats and show high variation in vocalizations. Habitat structure was strongly correlated with temporal characteristics of songs but not with most of the frequency-related attributes that we measured. Only the highest frequencies of songs varied with habitat structure. As predicted, species occupying closed habitats avoided the use of rapidly modulated signals and had song structures that minimized reverberation. Body mass covaried significantly with most of the song attributes. Smaller species used higher frequencies and had more notes in their songs compared with larger species. Received 9 May 1996, accepted 26 July 1996.

THE MAJOR FUNCTIONS OF BIRD SONG, such as mate attraction, species recognition, and the establishment and defense of territories, are closely linked to individual fitness (Catchpole and Slater 1995). Thus, songs that maximize effective communication of signals to intended receivers should increase the fitness of the singing individual. Concurrently, songs and acoustic communication in general are subject to spherical-spreading and frequency-dependent attenuations, reverberations, and irregular amplitude fluctuations caused by habitat structure (Wiley and Richards 1982, Wiley 1991). Thus, the acoustic environment may exert a strong influence on the evolution of song attributes.

Previous studies of habitat associations of song properties led to predictions that lower frequencies should be favored more in closed habitats than in open habitats (Chappuis 1971, Morton 1975, Cosens and Falls 1984, Waas 1988), although, theoretically, lower frequencies should always be favored because they travel the farthest regardless of habitat (Wiley and Richards 1982, Wiley 1991). High frequencies have a greater tendency to be scattered by foliage than do low frequencies, which are affected only by objects larger than foliage (Wiley

1991). Thus, high frequencies may be more constrained by habitat (Wiley 1991). Reverberation is thought to influence the length of notes (also referred to as "elements") and the amount of time between notes (Tubaro and Segura 1995). Consequently, birds that live in habitats with numerous scattering surfaces (e.g. leaves and branches) may: (1) avoid using rapidly modulated signals, (2) use shorter notes, and (3) put more space between notes to avoid extensive reverberation (Nottebohm 1975, Wasserman 1979, Richards and Wiley 1980, Gish and Morton 1981, Handford 1981, Anderson and Conner 1985, Sorjonen 1986, Handford and Loughheed 1991, Wiley 1991).

Song frequencies also may be constrained by body size because the mass of a vibrating structure affects the frequency that is produced most efficiently (Morton 1975, Bowman 1979, Wall-schager 1980, Shy 1983, Ryan and Brenowitz 1985). Hence, inter-habitat variation in songs could be confounded by unequal distribution of different-sized birds among habitat types (Ryan and Brenowitz 1985). In addition, evolutionary history and relatedness of species can confound variation in song structures exerted by habitat parameters (Ryan and Brenowitz 1985), especially if different taxa are unevenly distributed among habitat types (Wiley 1991).

In this paper we use a phylogenetic approach

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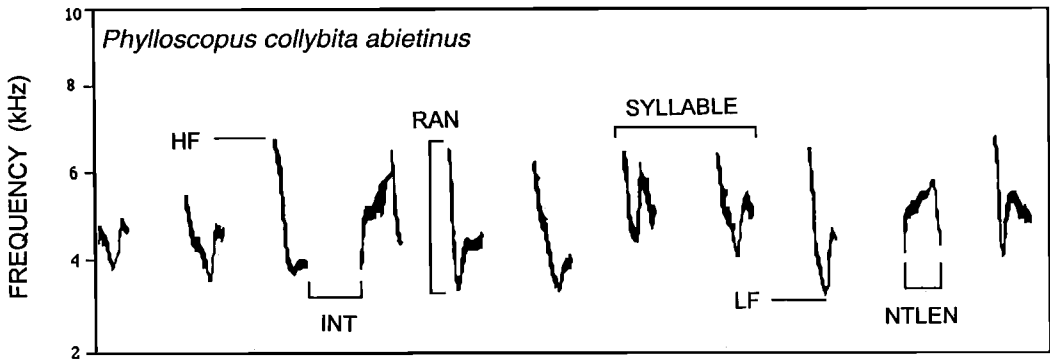


Fig. 1. Sonogram of *Phylloscopus collybita abietinus* showing variables measured. HF = highest frequency; INT = internote interval; RAN = frequency range; LF = lowest frequency; NTLEN = note length. A typical syllable consisting of two notes also is identified.

to examine habitat associations of 30 taxa of *Phylloscopus* and *Hippolais* warblers. These genera are especially well-suited for this study. Most of the *Phylloscopus* and *Hippolais* warblers are poorly differentiated in plumage characteristics and morphology but show extensive variation in vocalizations, even on a subspecies level (e.g. Dementiev and Gladkov 1954, Cramp 1992; see Appendix). These warblers are widely distributed and occupy a broad variety of habitats (Dementiev and Gladkov 1954, Cramp 1992). In addition, the phylogenetic relationships of these birds, especially *Phylloscopus* warblers, have been studied extensively (Ticehurst 1938, Martens 1980, Haffer 1991, Cramp 1992, Richman and Price 1992, Helbig et al. 1995), providing an opportunity to control for species and subspecies relatedness.

We statistically controlled for phylogeny and examined the effects of body mass and habitat structure on variation in song structure of *Phylloscopus* and *Hippolais* warblers. Specifically, we tested the following predictions: (1) frequency characteristics of song should correlate with body mass, and high frequencies should vary with habitat type; (2) temporal characteristics of songs should be affected by habitat structure.

METHODS

Songs used in the study were obtained from the song identification guide by Veprintsev (1987). Recordings on these disks contain complete songs and calls of several individual birds of each species. We used Canary 1.0 (Cornell Laboratory of Ornithology) software to measure the following variables (see Fig. 1): (1) highest frequency (HF; kHz), (2) lowest fre-

quency (LF), (3) range of frequency distribution (RAN), (4) dominant frequency (PEAK; i.e. the most prevalent frequency within a song), (5) number of notes (NT), (6) number of syllables (SYLL), (7) length of notes (NTLEN), (8) song length (SLEN), and (9) internote interval (INT). Means of songs of at least three to four individuals per species or subspecies were averaged to obtain values given in the Appendix.

We gathered published data on body size and habitat type for all 30 taxa (Dementiev and Gladkov 1954, Veprintsev 1987, Cramp 1992). We ranked nesting habitat from open to closed in the following sequence: (1) open fields, steppes, and deserts; (2) bushes and subalpine bushes; (3) intermediate between bushes and forest habitats, gardens; (4) coniferous forests; and (5) deciduous forests. Published data on habitat distribution were used in conjunction with habitat types listed on the source of the recordings (Veprintsev 1987).

The phylogeny of *Phylloscopus* and *Hippolais* species used in this study was constructed by summarizing available systematics data (Ticehurst 1938, Martens 1980, Haffer 1991, Cramp 1992, Richman and Price 1992, Helbig et al. 1995). Our phylogenetic hypothesis (see Fig. 2) was largely constructed based on molecular data for *Phylloscopus* warblers (Richman and Price 1992, Helbig et al. 1995). However, the resulting phylogenetic tree is consistent with findings in most other classification studies as well. Branch lengths were set as equal because they were available only for a few species in this study (Richman and Price 1992, Helbig et al. 1995). Plots of standardized contrasts against the variances of the untransformed contrasts showed no significant correlation, justifying the use of equal branch lengths (Purvis and Rambaut 1995).

To control for species relatedness, we calculated independent contrasts between nodes for the traits of interest (Felsenstein 1985) using the CAIC software package (Purvis and Rambaut 1995). We then examined the relationships between the variables by cal-

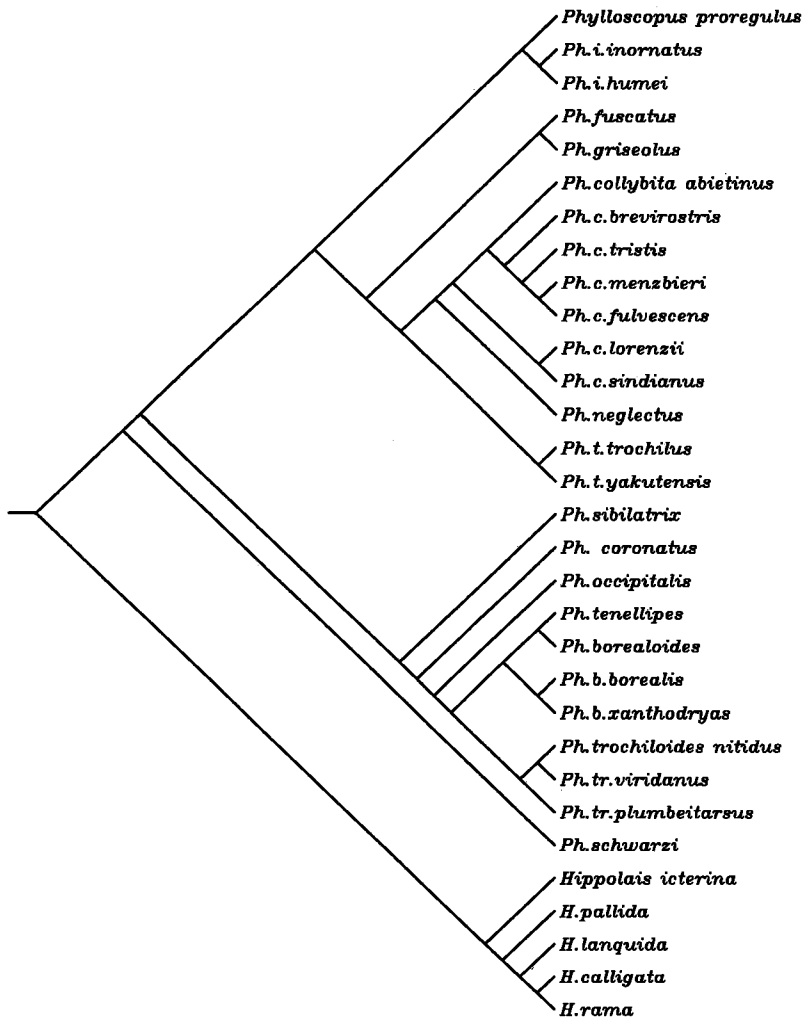


Fig. 2. Phylogenetic hypothesis for the *Phylloscopus* and *Hippolais* warblers.

culating linear regressions on these contrasts (Garland et al. 1992, Grafen 1992). All regressions were forced through the origin (Garland et al. 1992). Analyses of independent contrasts of habitat types were conducted following Martin and Badyaev (1996). The numbers of syllables and notes were square-root transformed; all other song parameters and body mass were log-transformed before the analyses.

RESULTS

Song characteristics were highly intercorrelated (Table 1). The taxa we studied used widely ranging types of syllables in songs, thereby complicating the direct comparison of original song variables among species. Therefore, we

used principal components (PC) analysis to describe variation in song characteristics (Table 1). Principal components were constructed such that PC I (32% of variation in the model) accounted for most of the variation in frequency-related variables, and PC II (22.5% of variation) accounted for most of the variation in temporal characteristics of songs (Table 1). *Phylloscopus* and *Hippolais* warblers of different size were equally represented across habitat types; body mass did not vary with habitat openness (Pearson $r = -0.1$, $P = 0.6$).

Among frequency-related song parameters, only the highest frequency varied significantly with habitat openness (Table 2). Frequency parameters were strongly affected by body mass;

TABLE 1. Pearson correlation coefficients of song properties and eigenvectors for principal components analyses of song variables (corrected for phylogeny using linear contrasts; Purvis and Rambaut 1995). See Methods for acronyms of song variables.

	SLEN	HF	LF	SYLL	NT	RAN	PEAK	INT	NTLEN
HF	0.34*								
LF	-0.10	0.01							
SYLL	0.43*	0.50**	-0.31						
NT	0.59**	0.01	-0.10	0.43**					
RAN	0.34*	0.76***	-0.58***	0.50**	-0.03				
PEAK	-0.00	0.20	0.50**	-0.14	-0.06	-0.12			
INT	0.00	0.17	0.02	-0.24	-0.49**	0.27	0.10		
NTLEN	0.25	0.28	-0.02	0.26	-0.35**	0.34*	-0.06	0.24	
HT ^a	-0.33*	0.16	0.07	-0.20	-0.51**	0.15	0.17	0.25	0.14
MASS ^b	-0.07	-0.33*	0.05	-0.17	0.20	-0.36**	-0.28	-0.37**	-0.46**
PC I ^c		0.42		0.47		0.50			
PC II ^c					-0.60			0.53	0.40

*, $P < 0.1$; **, $P < 0.05$; ***, $P < 0.001$.

^a Habitat type.

^b Body mass (g).

^c Only loadings $\geq |0.40|$ are shown.

smaller species used the highest frequencies and had the widest frequency range compared with larger species (Table 2, Fig. 3). Body mass also was strongly correlated with temporal characteristics of song; smaller species had shorter intervals between notes and used shorter notes compared with larger species (Table 2). In contrast to the frequency characteristics of songs, temporal parameters were strongly affected by habitat structure. Species in closed habitats used fewer notes and longer notes, and had longer intervals between notes compared with their open-habitat relatives (Table 2, Fig. 4).

TABLE 2. Standardized coefficients from multiple regression of song properties on habitat and body mass (corrected for phylogeny using linear contrasts; Purvis and Rambaut 1995).

Variable	F	Sources of variance	
		Habitat openness	Body mass
Frequency properties			
Highest frequency	3.78**	0.41**	-0.39*
Lowest frequency	0.04	0.03	0.03
Dominant frequency	2.31*	0.37	-0.27*
Frequency range	2.44**	0.14	-0.39**
PC I	3.67**	0.32	-0.39**
Temporal properties			
No. of syllables	1.09	-0.19	-0.16
No. of notes	1.69	-0.35	0.29
Internote interval	2.69*	0.22	-0.42**
Song length	0.82	-0.24	-0.04
Note length	3.56**	0.14	-0.48**
PC II	6.22**	0.45**	-0.52**

*, $P < 0.1$; **, $P < 0.05$.

DISCUSSION

The results support our predictions that temporal characteristics of song vary strongly with

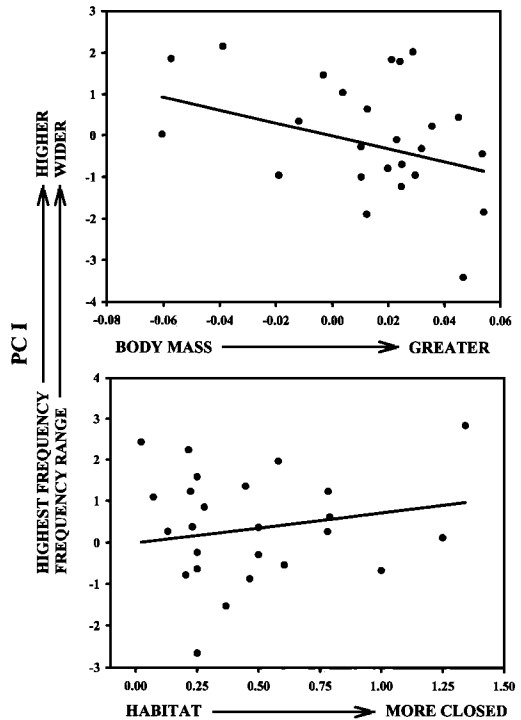


Fig. 3. Partial-regression residual plots of independent linear contrasts illustrating relationship between frequency-related characteristics of songs (i.e. PC I), body mass (upper), and habitat openness (lower).

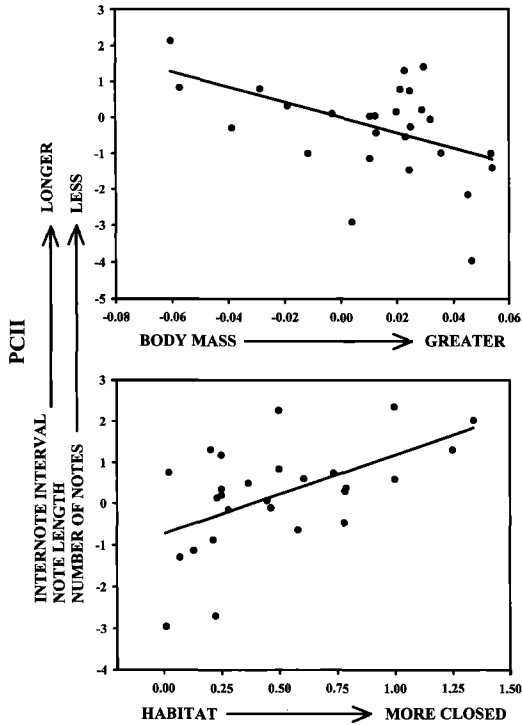


Fig. 4. Partial-regression residual plots of independent linear contrasts illustrating relationship between temporal characteristics of songs (i.e. PC II), body mass (upper), and habitat openness (lower).

habitat openness, whereas frequency attributes largely are unaffected by habitat structure. Only the highest frequencies varied significantly with habitat structure (Table 2). Closed habitats are thought to cause greater attenuation in songs, which in turn would affect the upper band of acceptable frequencies (Wiley 1991). Thus, only the highest frequencies are expected to vary with habitat. The highest frequencies might also be affected by different levels of background noise among habitat types (Ryan and Brenowitz 1985). Temporal attributes of song should vary with habitat because reverberation rises with increasing habitat closeness (e.g. Wiley and Richards 1982). As we have shown, birds in closed habitats avoid the use of rapidly modulated signals, use shorter notes, and have more space between notes (potentially to minimize reverberation). These findings are consistent with other studies (Wiley 1991, Tubaro and Segura 1995).

Body mass was a significant constraint on most

song attributes (Table 2, Figs. 3 and 4). In particular, smaller species use higher frequencies and shorter notes than do larger species (Table 2). This is consistent with the finding that body size is positively correlated with the mass of the song-producing structures in birds (Morton 1975, Ryan and Brenowitz 1985). It is thought that in vocalizations intended for long-range communication, body mass should strongly limit the lower range frequency because more energy is required to produce and transmit low-frequency sounds (Ryan and Brenowitz 1985). Although song structure predictably varied with habitat type, singing behaviors such as use of high perches and song-flights also could maximize song transmission (Jilka and Leisler 1974, Wilczynski et al. 1989). However, courtship song-flights, such as the one of *P. sibilatrix*, are very rare among these warbler species. We did not examine the relationship between singing height and song structure. These species used a wide variety of habitats, and taxa with greater number of species are needed to simultaneously control for effects of habitat, singing height, and body mass.

Although habitat structure and body mass significantly affected song properties in *Phylloscopus* and *Hippolais* warblers, a large amount of variance in song characteristics (46.9%) remained unexplained. These warblers, especially *Phylloscopus*, vary widely in such biological parameters as mating system, territory size, and population density (reviewed in Cramp 1992). These factors may determine functions of songs, i.e. whether songs are intended for long- or short-range communication, and thus can influence song structure and composition (e.g. Salomon and Hemim 1992).

Species recognition frequently is invoked to explain high variation in characteristics of vocalizations, especially in *Phylloscopus* warblers (e.g. Salomon and Hemim 1992). The degree of sympatry varies within *Phylloscopus* (Cramp 1992); thus, the variation we observed, especially among subspecies, may be influenced by the presence of closely related species (Salomon 1989, Salomon and Hemim 1992). Further reviews and experimental tests of potential mechanisms are needed to better address the ecological and evolutionary factors causing unusually high variation in song attributes among closely related species of *Phylloscopus* and *Hippolais* warblers.

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APPENDIX. Characteristics of songs (mean values) of *Phylloscopus* and *Hippolais* warblers. Song recordings were obtained from Veprintsev (1987). See Methods for acronym definitions.

Species	SLEN	HF	LF	SYLL	NT	RAN	PEAK	INT	NTLEN
<i>Phylloscopus proregulus</i>	2.192	7.738	2.735	3.7	19.3	5.005	4.35	57.01	94.39
<i>P. i. inornatus</i>	1.433	8.460	3.925	4.5	4.0	4.545	5.39	58.50	129.50
<i>P. i. humei</i>	2.192	8.200	3.400	3.0	7.0	4.800	5.30	53.00	89.00
<i>P. fuscatus</i>	1.160	6.003	2.773	1.3	6.7	3.230	5.16	91.10	118.57
<i>P. griseolus</i>	1.163	5.437	2.607	3.0	9.0	2.830	3.83	32.83	73.27
<i>P. collybita abietinus</i>	2.865	6.810	3.190	3.0	11.0	3.630	5.13	162.00	106.50
<i>P. c. brevirostris</i>	2.898	7.140	2.800	3.0	11.0	4.330	4.52	168.50	105.00
<i>P. c. tristis</i>	5.648	6.775	2.710	3.5	31.0	4.070	4.52	86.52	101.90
<i>P. c. menzbieri</i>	2.556	7.310	3.110	3.0	8.0	4.200	4.26	238.80	105.80
<i>P. c. fulvescens</i>	2.136	7.410	2.760	2.0	7.0	4.650	4.17	267.70	73.00
<i>P. c. lorenzii</i>	2.587	6.900	3.090	2.0	8.0	3.810	5.30	289.00	80.50
<i>P. c. sirdianus</i>	3.873	6.230	2.920	3.0	15.0	3.310	4.35	109.00	205.00
<i>P. neglectus</i>	1.113	6.450	2.400	10.0	11.0	4.050	4.35	34.80	69.30
<i>P. t. trochilus</i>	2.513	7.265	2.200	7.0	17.3	5.063	3.65	63.30	134.95
<i>P. t. yakutensis</i>	2.742	6.950	1.880	8.0	18.0	5.070	1.88	68.75	102.50
<i>P. sibilatrix</i>	2.823	7.620	3.070	1.0	29.0	4.550	4.87	98.30	36.30
<i>P. coronatus</i>	1.722	5.987	2.823	2.0	8.7	3.163	4.78	94.57	132.07
<i>P. occipitalis</i>	4.536	7.510	2.980	6.0	22.0	4.530	3.91	74.30	127.70
<i>P. tenellipes</i>	1.727	6.755	5.400	1.0	24.5	1.350	5.70	12.50	44.65
<i>P. borealoides</i>	2.584	7.887	4.290	1.3	9.3	3.590	4.67	47.87	256.27
<i>P. b. borealis</i>	2.316	6.360	2.040	2.0	18.0	4.320	4.61	41.00	32.80
<i>P. b. xanthodryas</i>	2.025	5.750	2.470	3.0	20.0	3.290	4.43	39.30	54.70
<i>P. trochiloides nitidus</i>	3.091	7.600	2.980	4.0	13.0	4.620	4.96	72.30	112.30
<i>P. t. viridanus</i>	1.507	6.570	2.880	3.0	14.0	3.690	3.82	112.50	83.00
<i>P. t. plumbeitarsus</i>	1.846	8.050	2.500	4.0	15.0	5.550	5.30	47.30	110.50
<i>P. schwarzi</i>	1.459	6.440	1.850	3.0	24.5	4.585	3.48	17.00	50.80
<i>Hippolais icterina</i>	5.951	7.520	1.540	5.0	23.0	5.990	3.48	63.50	145.00
<i>H. pallida</i>	2.881	7.280	1.700	6.0	18.0	5.580	—	—	—
<i>H. languida</i>	6.132	4.640	2.190	2.0	39.0	2.450	3.82	63.50	61.00
<i>H. c. caligata</i>	2.765	4.840	1.780	1.5	19.0	3.060	3.04	80.00	102.30
<i>H. rama</i>	5.816	6.520	1.670	15.0	47.0	4.850	3.82	54.50	109.00