Independent evolution of song structure and note structure in American wood warblers

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SUMMARY

This study addresses the issue of how evolutionary convergence within shared environments shapes some features of bird song while leaving others unaffected, using as an example the songs of 51 North American wood warblers (Parulinae). I combined published information on breeding habitats and evolutionary relationships to show that the structure of warbler songs is correlated with habitat, whereas the structure of the notes that comprise the songs is relatively unaffected by habitat and more closely related to phylogenetic history. The results confirm known relationships between bird song and habitat, including correlations between song frequency and the type and density of canopy foliage, and between the number and arrangement of notes in the song and foliage density and moisture. More importantly, the results suggest that individual notes and whole songs are to some extent functionally independent, because the configuration of notes shows more evidence of evolutionary constraint than does the way notes are assembled into songs.

1. INTRODUCTION

Bird song has long played a central role in the study of adaptation, partly because the connection between physical properties of the environment and acoustic properties of songs offer an opportunity to understand functional relationships underlying adaptation. But not all features of songs are shaped by natural selection for efficient acoustic propagation, and an important issue centres around how different components of bird song are integrated from different kinds of selection and constraints. This study takes a comparative approach to this issue, using the songs of American wood warblers (Emberizidae, subfamily Parulinae).

The diversity of avian songs results from a number of evolutionary influences and compromises between competing trade-offs. Comparative analyses of songs across many species, combined with studies of the functional consequences of variation within particular species, have illustrated some of the trade-offs relevant to singing birds. For example, loud songs are audible at great distances, but may be energetically expensive (Wiley & Richards 1978; Reid 1987). The acoustic properties of the habitat tend to favour certain arrangements of notes and dominant frequency, leading to consistent differences among habitats in average properties of songs (Chappuis 1971; Morton 1975; Wiley 1991). Vocalizations are also produced for social purposes, and the identity and location of the intended recipient of the song may affect the song's properties (Wiley & Richards 1978; McGregor 1991).

Environmental and social factors alone are not sufficient to explain the diversity of avian songs because groups of closely-related species frequently have songs with similar acoustic properties (Ryan & Brenowitz 1985; Wiley 1991). Presumably, some song features evolve in response to selection while others change very little, either because they are neutral with respect to fitness or because evolutionary change is constrained by genetic correlations or lack of genetic variance. This implies that evolutionary relationships must be included within comparative studies of adaptation in bird song (Read & Weary 1992).

How multiple factors combine to influence the evolution of functionally complex phenotypes such as bird song is poorly known. I undertook this study to address the issue of how shared ancestry combines with selection due to shared environments to shape variation in territorial song within the wood warblers, a diverse and closely-related group of birds with well-known ecology and behaviour (Ficken & Ficken 1962; Morse 1989). My goal is to measure the extent of song convergence within sets of species that share habitats, after first accounting for known evolutionary relationships within the group, and to estimate the relative contributions of habitat and ancestry to song diversity. Habitat-related vocal convergence is taken as evidence of selection originating from interspecific social interactions or physical properties of the habitat, and differences in response to habitats among song components suggest that they are functionally independent.

2. METHODS

(a) Song measurements

The study included 50 paruline species plus one subspecies breeding north of Mexico, excluding the yellow-breasted chat (*Icteria virens*) because of its uncertain taxonomic affinities (Morse 1989; Escalante-Pliego 1991). I obtained recordings of songs from a commercially available tape

Table 1. *List of variables used to measure the structure of notes and songs of North American wood warblers*

structure of notes	structure of songs
duration of the note (ms)	duration of the song (s)
proportion of time from beginning to minimum frequency	number of notes
	mean interval between notes (ms)
maximum bandwidth (kHz)	maximum frequency (kHz)
number of inflection points in the slope of frequency modulation	minimum frequency (kHz)
	frequency range (kHz)
number of different kinds of notes	proportion of notes adjacent an identical note

(Borror & Gunn 1985), and made audiospectrograms of songs from each of two birds (usually the first two individuals on the tape) using a DSP Sona-Graph Model 5500 kept at the same settings for all species. For species that produce two types of songs, I used only 'accented-ending' or 'type I' songs to standardize the context in which songs were produced (Ficken & Ficken 1962; Kroodsma 1981; Lemon *et al.* 1987). I made a total of 12 measurements on each song, which were used to describe either the individual notes within the song or the overall structure of the song. The general structure of songs can vary independently from the notes that compose them, and may convey different information (Lemon *et al.* 1983; Van Buskirk 1984; Nelson 1989).

Five measurements were designed to reflect the duration, complexity, clarity of tone, and diversity of notes (table 1, Appendix). A note was defined as a distinct tracing on an audiospectrogram, separated from other notes by a period of time in which no sound was produced. Songs were composed of between one and eight different kinds of notes, and the five measures were taken from each kind of note. The time from the beginning of the note to its minimum frequency, expressed as a proportion of the total duration of the note, reflected whether the note ascended or descended in frequency. The maximum bandwidth of the note reflected the clarity or 'buzziness' of the note, and the number of inflection points in the direction of frequency sweep reflected its complexity. The number of different kinds of notes reflected the diversity of note types.

I quantified the structure of songs using seven variables that measured duration, frequency, and the way notes were combined to construct the song (table 1, Appendix). The number of notes and the interval between notes reflected whether the song sounded staccato or measured. The frequency variables reflected the register at which the notes occurred and the frequency range over which they were distributed. The proportion of notes that occurred adjacent to an identical note reflected the extent to which the song was composed of series of notes that were either repeated or unique/alternating.

The collection of variables in table 1 is a subset of a larger number initially measured, but I eliminated redundant variables after inspecting a preliminary correlation analysis. I tested for departure from normality for all variables under five types of transformation, and found that the best results were given by a natural log transformation for all measurements except for proportions (time from beginning to minimum frequency), which did best when angularly transformed. Sampling from two birds was adequate to estimate species differences because only 10.1% (range 5.4–16%) of the variance in song and note measures arose from variation between samples within species. Of course, my characterizations of songs and habitats (see below) necessarily overlook much intraspecific variation, but they also reflect real differences among species.

(b) Habitat measurements

I gathered descriptions of warbler breeding habitats from published sources (Roberts 1936; Griscom & Sprunt 1957; Phillips *et al.* 1964; Small 1974; Collins *et al.* 1982; AOU 1983; Laughlin & Kibbe 1985; Brewer *et al.* 1991). I derived a quantitative habitat measure by scoring each species' preferred or most frequent breeding habitat on five axes, chosen to capture features of vegetation and moisture level that vary among warbler habitats (table 2, Appendix). Intermediate scores on an axis were assigned to species that are either variable in preference or are found in habitats intermediate between the extreme values.

(c) Comparative analyses

I began by testing whether characteristics of the territorial song were associated with features of the breeding habitat, after correcting for phylogenetic non-independence of species. Next, I estimated how variance in song similarity is associated with phylogeny, habitat similarity, and other factors.

I performed phylogenetic regression (Felsenstein 1985; Grafen 1989; Harvey & Pagel 1991) to determine whether birds that shared habitats sang similar songs, after first accounting for song similarity arising from common ancestry. The approach treats every radiation within the phylogeny as an independent observation, and uses regression to test whether evolutionary divergence among daughter taxa in song features is associated with divergence in habitat use. Although no comprehensive phylogeny of the Parulinae exists, I constructed an estimate of relationships among the 51 taxa by combining data from published sources (Mengel 1964; Avise *et al.* 1980; Escalante-Pliego 1991; Bermingham *et al.* 1992). Uncertain relationships were reflected as polychotomies in the working phylogeny, ensuring that all groups were monophyletic. Because the scheme represents a 'valid coarsening' of the true phylogeny (Grafen 1989), it will not be judged seriously incorrect if its polychotomies are resolved by future work. I reconstructed ancestral character states by assigning them the average of the song and habitat values of all their daughter taxa. This is equivalent to assuming that all branch lengths within the phylogeny are of equal length, which is an incorrect but necessary assumption in the absence of other information. Following Grafen's (1989) method, I examined the correlation among contrast scores for song and habitat variables, to determine whether evolutionary change in habitat use was consistently associated with change in song features. To eliminate multiple comparison problems I began with a multivariate correlation (canonical) analysis between contrast scores for habitat variables and song characteristics, after first reducing dimensionality with principal components analysis (PCA). The PCA summarized the pattern of multivariate correlation among measures and reduced the dimensionality of descriptions to a smaller system of uncorrelated responses. Separate

Table 2. *Five measures of foliage density, moisture, and tree species composition used to score the breeding habitats of wood warblers*

habit feature	score			
	1	2	3	4
tree type	coniferous	mixed or no preference	deciduous	
canopy height	low	intermediate or no preference	tall	
canopy density	open	intermediate or no preference	dense	
understory density	open	intermediate or no preference	dense	
moisture	dry	intermediate or no preference	moist	streams/bogs

analyses for song structure, note structure, and habitat were performed on the correlation matrices of normalized measurements.

A second analysis estimated the relative importance of phylogenetic and habitat effects on song features by comparing matrices representing similarity among species for song and note structure, habitat use, and evolutionary distance. Each matrix consisted of 51 rows and columns (one for each taxon) and 1275 unique elements, each a pairwise similarity value calculated as one minus the Euclidean distance between the two species in the multivariate space defined by song structure, note structure, or habitat scores. The similarity matrix expressing evolutionary relationships was generated by assigning numerical values to different levels of taxonomic association. Well-accepted sister species pairs were assigned a similarity value of 0.75; groups of closely-related species within genera (Mengel's (1964) species groups) received a value of 0.50; other congeners were assigned a value of 0.25; and all other elements in the matrix were set to zero.

I tested the hypothesis that similarity in song structure or note structure was correlated with habitat and evolutionary similarity using multivariate Mantel tests (Mantel 1967; Smouse *et al.* 1986). First, I regressed the unique elements of either the song structure or note similarity matrices upon the elements of the habitat and evolutionary similarity matrices. Each regression yielded two coefficients, expressing the extent to which the vocal similarity between any pair of species could be predicted by habitat or evolutionary similarity. I assigned significance values to coefficients by comparing them with a null distribution generated by performing 1000 similar regressions after permuting the rows and columns of the response matrix at random.

3. RESULTS

(a) Relationship between song and habitat

Evolutionary change in breeding habitat was not accompanied by change in note structure (Wilks's $F_{16,49.5} = 1.07$, $p = 0.411$, canonical correlation analysis of phylogenetic contrast scores), whereas the association between contrasts in habitat and song structure was nearly significant (Wilks's $F_{16,49.5} = 1.82$, $p = 0.057$). This implies that evolutionary shifts in breeding habitat have been accompanied by consistent changes in song features.

Univariate correlations between phylogenetic contrasts for the original song structure measurements and the habitat axes indicate that the association between

song structure and habitat arose from two separate relationships, involving song frequency and the time interval between notes (figure 1). First, evolutionary shifts toward habitats with more open canopy or coniferous tree species composition were accompanied by concurrent increases in maximum or minimum frequency (figure 1*a*, *b*). For example, within the genus *Wilsonia*, the species found in habitats with the most open canopy (*W. pusilla*) have the highest maximum frequency, and the species found in forests with dense canopy (*W. citrina*) sings a low-frequency song. This three-species radiation is represented by a single point in the lower right portion of figure 1*a*.

There was an increase in the interval between notes in songs of species that evolved to use wet habitats with open understorey (figure 1*c*, *d*). For example, within *Seiurus*, the species which inhabits drier habitats (*S. auricapillus*) sings many notes which are expressed at shorter intervals. Further, the habitat shifts represented by figures 1*c* and 1*d* were accompanied by a slight decrease in the number of notes within the songs of species inhabiting moist habitats ($p = 0.062$). This was expected since the interval between notes is negatively related to note number ($r = -0.64$, $p = 0.001$). Within *Oporornis* and the *Dendroica virens* group, for example, species found in moist habitats or more open understorey sing fewer notes.

Associations between song and habitat cannot be explained by variation among species in body size. Vocal traits are known to vary with mass in birds, and even across the relatively narrow range of sizes found within wood warblers there are relationships between song features and mass (data from Dunning 1984). None of these relationships altered the conclusions from phylogenetic regression: results were similar when the analyses reported above were repeated using residuals after regression against mass.

(b) Relative contributions of habitat and phylogeny

Mantel tests of association between similarity matrices for song, habitat, and phylogeny were in general agreement with the results of the phylogenetic regression. Similarity among species in the structure of notes within songs was more closely related to phylogenetic similarity than to habitat similarity (phylogeny, $p = 0.056$; habitat, $p = 0.446$; based on
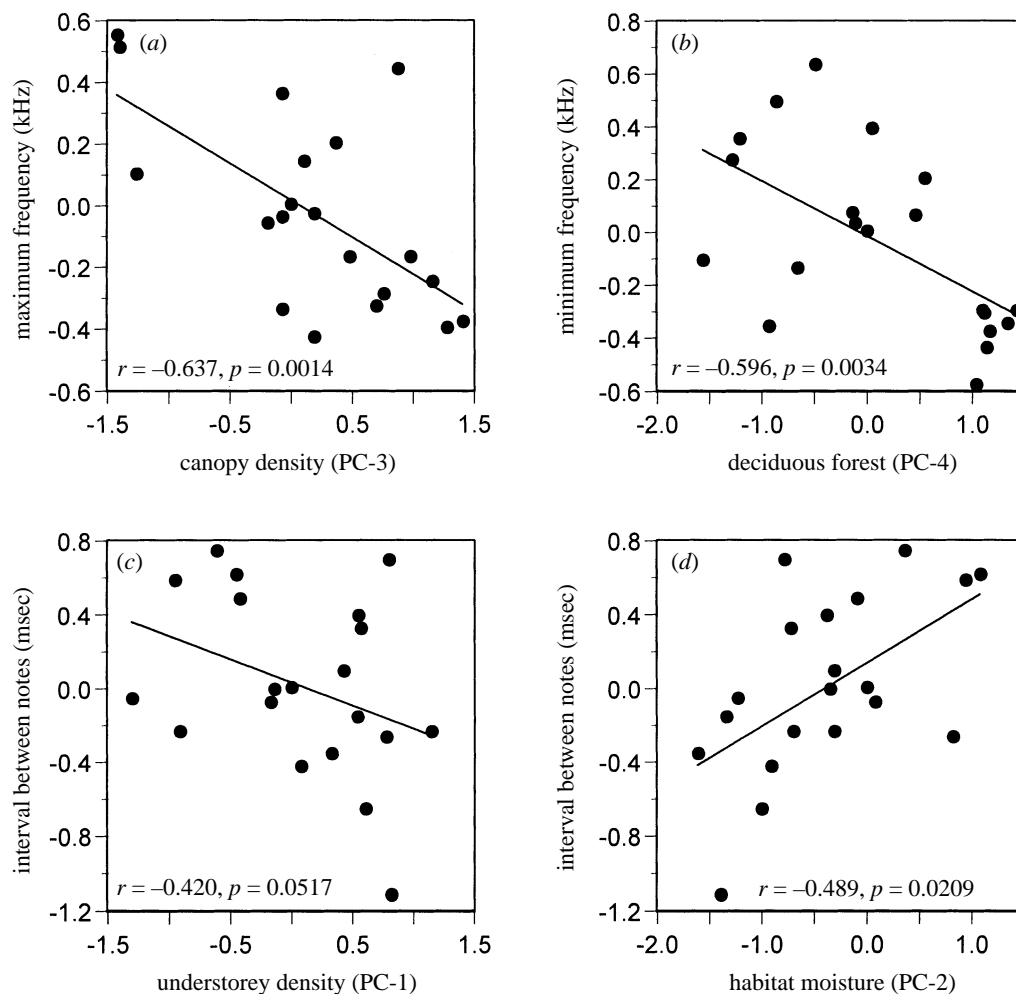
Figure 1. Relationships between sets of contrast scores for song structure and habitat, showing the results of phylogenetic regressions using original song structure variables. Each point represents a single radiation in the working phylogenetic hypothesis, composed of one parental species and between two and 13 daughter taxa. Contrast scores reflect directionality of evolutionary change in daughter taxa relative to one another in the trait in question; a correlation between contrast scores for two traits suggests that evolutionary change in the two traits was correlated.

1000 permutations of the response matrix). In contrast, similarity in song structure was more closely related to habitat similarity than to phylogeny, although neither effect was significant (phylogeny, $p = 0.470$; habitat, $p = 0.100$). These tests should be considered tentative because the phylogenetic similarity data were based in part on taxonomy.

4. DISCUSSION

There is a clear relationship between bird song and habitat (e.g. Wiley 1991). I have shown that within one group of closely related species this relationship has resulted from a pattern of correlated evolutionary changes in habitat associations and song features. The pattern arises from convergence within habitats of general features of songs, such as their frequency and the repetition rate of notes, but not from convergence of the structure of the individual notes that comprise songs. The results illustrate how functional differences between different levels of organization in a complex phenotype may lead to natural selection acting in different ways on the different levels, causing them to show disparate patterns of variation across species.

Convergent vocal characteristics in bird species that occur together in similar habitats may originate from either interspecific interactions or physical constraints imposed by the environment. Social interactions could cause either convergence or divergence of territorial signals among syntopic species. Divergence may be favoured to facilitate the ability of listeners to distinguish songs of syntopic species, an important component of species recognition in forested habitats (Nelson 1989; Naugler & Ratcliff 1994). Convergence may be favoured in any circumstance that requires two species to pay attention to one another, including, for example, interspecific territoriality (Cody 1969). Wood warblers apparently do not defend interspecific territories (Morse 1989), so socially mediated convergence of territorial signals within habitats is unlikely.

Vegetational features of the habitat are known to correlate with certain acoustic properties of animal vocalizations, and the functional relationships underlying these patterns are well understood (Morton 1975; Wiley & Richards 1978; Wiley 1991). For example, birds that perch low in the forest when singing are characterized by low frequency songs, because degradation with distance is reduced at low

frequency, especially in habitats with dense vegetation (Wiley & Richards 1978; Lemon *et al.* 1981). Likewise, birds that sing in closed habitats avoid producing notes with short repetition periods, because accumulated reverberation off vegetation degrades songs and makes rapidly-repeated notes indistinct (Richards & Wiley 1980; Wiley 1991). Taken together, these studies demonstrate that the vegetational features of certain habitats causes selection favouring particular acoustical organization of songs in the species found in those habitats.

My results for wood warblers are in general agreement with known mechanisms of sound propagation. For example, I have confirmed relationships between the frequency of songs and several aspects of the habitat, including canopy density and broad-leaved versus coniferous forests (Wiley 1991). The positive correlation between the average time interval between notes and habitat moisture originated because species that breed in swamps and along rivers have songs composed of few notes spaced far apart. The fact that wet habitats often contain relatively dense vegetation may explain this pattern, or perhaps interference from the noise of rushing water favours songs with distinct notes. One result appears puzzling in the context of earlier studies. While songs with closely-spaced syllables are typical of birds in open habitats, I found that the evolution of rapid note repetition was accompanied by use of dense under-storey (figure 1*c*). Understorey density and canopy height and density are negatively correlated across wood warbler habitats, so species in thick brush may in fact sing in the relatively open habitat at the tops of shrubs and short trees. These birds may experience an acoustic environment similar to that found in marshes or grasslands.

The relative importance of phylogenetic constraint on bird song may differ for higher and lower levels of song organization. The structure of individual notes shows a closer relationship with phylogeny than with habitat, whereas the way notes are put together into complete songs is more closely explained by habitat than phylogeny. These results are relevant to the study of how complex phenotypes are integrated from a set of interdependent traits (Bonner 1988; Wake & Roth 1989; Roth 1996). The possibility that some features of the song respond to selection imposed by habitat while other features are more phylogenetically conservative implies a surprising degree of independence among song features, in terms of their function or ability to respond to selection. Clearly, more detailed studies of genetic variation and selection on avian song features would help to interpret the evolution of species' differences highlighted by this study. In general, though, one should expect this sort of asymmetric contribution of selection and phylogenetic constraints to the level of notes and whole songs if design constraints or genetic correlations are more prevalent at one level than at another.

Other results on the mechanisms underlying vocal mimicry and perception in birds support the interpretation that whole song organization is more flexible than the structure of individual notes, and at the same time is more critical for conveying certain types of information. For example, interspecific song mimicry in the warbler *Dendroica coronata* is accomplished by adjustment of the tempo and frequency of songs, while the structure of notes is held constant (Van Buskirk 1984). Vocal differences among coexisting species are typically manifested in song structure rather than the exact configuration of notes (Lemon *et al.* 1983; Nelson 1989), and there are constraints on variation within species in the combinatorial arrangement of notes in songs (Hailman *et al.* 1987; Nowicki & Nelson 1990). These observations imply that critical information about species' identity is contained within the overall structure of the song, which may explain why song structure evolves to show acoustic properties suitable for the habitat.

The approach I have followed represents only one part of a pluralistic programme aimed at understanding how variation in vocalizations is shaped by selection and constrained by ancestry. In some sense, these results represent a set of hypotheses requiring experimental verification. Field studies should attempt to map traits to their function and estimate how selection is currently operating. Results such as mine provide a clear set of predictions about what kinds of song features will contribute to fitness in specific situations.

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APPENDIX

species	structure of notes[a]					structure of songs[b]							habitats[c]				
	DURA	BEGMN	BANDW	INFL	KINDS	DURA	NOTES	INTER	MAXFQ	MINFQ	RANGE	ADJAC	TREE	CANH	CAND	UND	MOIST
Cardellina rubrifrons	85	0.49	38.5	1.2	7.5	1.51	10.5	64.5	7.64	3.03	4.61	0.52	2	2	2	2	2
Dendroica caerulescens	401	0.22	118.5	0.0	2.0	1.23	3.0	89.5	6.03	3.30	2.75	0.67	3	2	3	3	2
Dendroica castanea	148	1.00	43.0	2.5	2.0	1.21	7.0	38.5	9.23	6.16	3.08	0.00	1	2	1	2	1
Dendroica cerulea	147	0.32	86.0	4.2	3.0	1.34	9.5	27.5	7.68	2.68	5.01	0.90	3	3	3	1.5	2
Dendroica chrysoparia	230	0.23	120.1	1.1	5.5	1.76	10.0	38.0	8.48	2.63	5.85	0.40	2	2	2	2	1
Dendroica c. auduboni	136	0.56	52.0	6.0	3.0	1.65	9.5	41.0	6.11	2.66	3.45	0.90	1	2	2	2	2
Dendroica c. coronata	105	0.45	49.7	4.1	2.5	1.68	11.5	47.0	6.30	3.02	3.28	0.96	2	2	2	2	2
Dendroica discolor	153	0.00	109.5	0.0	1.0	1.94	11.0	76.0	7.19	4.26	2.93	1.00	2	3	1	3	1
Dendroica dominica	116	0.57	39.6	2.4	2.5	2.20	8.5	61.0	7.07	3.13	3.94	0.83	2	3	2	1.5	3
Dendroica fusca	118	0.68	37.1	5.6	4.0	2.15	18.0	45.0	9.40	3.84	5.56	0.11	1.5	3	2	2	2
Dendroica graciae	80	1.00	32.0	3.0	1.0	1.77	15.0	44.0	6.50	2.90	3.60	1.00	3	2	2	3	2
Dendroica kirtlandii	57	0.65	36.3	1.7	3.0	1.24	8.0	93.0	5.35	2.31	3.05	1.00	1.5	2	1	3	2
Dendroica magnolia	105	0.70	37.0	1.8	3.0	0.73	5.5	53.0	7.00	3.09	3.91	0.38	2	2	2	3	1
Dendroica nigrescens	142	0.61	82.6	7.0	4.0	1.30	7.5	39.5	6.36	2.63	3.74	0.36	2	2	2	2	2
Dendroica occidentalis	148	0.62	57.7	0.8	3.5	1.67	9.5	44.0	7.70	3.33	4.37	0.80	1	3	2	1.5	3
Dendroica palmarum	51	0.55	57.5	2.5	2.0	1.88	26.5	24.0	7.08	3.25	3.84	0.00	3	2	1	3	3
Dendroica pensylvanica	105	0.75	36.2	1.6	4.0	1.21	9.0	50.0	8.10	3.08	5.02	0.52	3	1	3	3	3
Dendroica petechia	100	0.35	37.8	1.3	3.5	1.35	8.5	65.5	8.21	3.51	4.71	0.94	3	2	2	3	3
Dendroica pinus	27	0.00	40.5	1.0	1.0	1.86	38.0	19.5	5.19	3.61	1.58	1.00	1	3	1	1	2
Dendroica striata	54	0.23	38.5	2.0	1.0	1.77	15.0	105.5	9.82	7.85	1.97	1.00	1	2	2	2	2
Dendroica tigrina	193	0.04	35.5	0.5	1.0	1.14	5.0	72.5	8.61	7.08	1.54	1.00	1	2.5	1.5	2	2
Dendroica townsendi	180	0.80	91.3	1.2	3.0	1.29	7.5	57.0	6.83	3.41	3.42	0.81	1	3	2	1.5	2
Dendroica virens	184	0.50	80.7	0.2	3.0	1.19	6.0	48.0	7.54	3.91	3.64	0.68	2	2	2	2	2
Geothlypis trichas	90	0.56	38.7	1.3	3.0	1.58	10.0	64.5	7.29	2.85	4.44	0.00	2	1	2	3	2.5
Helmintheros vermivorus	40	0.51	26.5	3.0	1.0	1.99	32.0	20.0	8.60	4.24	4.36	1.00	3	2	3	3	2
Limnothlypis swainsonii	116	0.80	34.7	0.9	5.5	1.66	8.5	77.0	7.35	2.29	5.06	0.54	3	2	3	3	4
Mniotilta varia	106	0.33	40.0	1.8	2.0	2.10	13.0	43.5	8.50	5.07	3.44	0.00	3	2	2	2	2
Myioborus pictus	106	0.77	40.5	2.0	3.0	1.56	9.0	54.0	5.28	2.61	2.68	0.59	2	2	2	3	3
Oporornis agilis	72	0.81	36.0	1.0	3.0	1.51	9.0	79.0	6.61	1.87	4.74	0.00	2	1	1	3	3
Oporornis formosus	96	0.15	39.5	2.5	2.0	1.78	12.5	48.5	4.84	2.20	2.65	0.00	3	2.5	3	3	3
Oporornis philadelphia	57	0.49	35.9	1.9	4.5	1.20	14.5	25.5	6.09	2.04	4.05	0.00	2	2	2	2	2
Oporornis tolmei	60	0.34	36.4	3.3	3.0	1.37	13.5	44.5	7.10	3.05	4.05	0.09	2	3	1	2	3
Parula americana	62	0.96	45.8	3.5	2.0	1.46	31.0	17.0	8.11	3.69	4.42	0.97	3	2	2	2	2
Parula pitiayumi	70	1.00	125.0	2.8	2.0	1.59	34.0	16.5	8.19	4.05	4.14	0.97	3	2	1	2	2
Protonotaria citrea	144	0.00	35.5	4.0	1.0	1.81	8.0	92.5	9.23	3.47	5.76	1.00	3	2	3	3	4
Seiurus aurocapillus	79	0.61	34.8	2.3	2.0	2.30	16.5	61.5	9.03	2.75	6.28	0.00	3	3	2	1.5	2
Seiurus motacilla	89	0.64	31.4	0.8	7.5	1.99	11.0	69.5	7.24	2.60	4.64	0.54	3	2.5	3	2	4
Seiurus noveboracensis	56	0.69	34.1	1.1	4.0	1.70	14.0	72.5	7.71	2.40	5.31	0.42	2	2	2	3	4
Setophaga ruticilla	124	0.66	45.9	0.4	2.5	0.86	5.5	52.5	8.77	3.68	5.09	0.74	3	2	1.5	2	2
Vermivora bachmanii	76	0.16	179.3	0.0	1.5	1.63	14.0	44.5	8.22	4.70	3.52	0.94	3	3	2	3	3.5
Vermivora celata	35	0.79	38.8	1.5	2.0	1.49	26.0	22.0	8.23	3.65	4.58	1.00	3	3	1	3	2
Vermivora chrysoptera	298	0.71	110.0	0.0	2.0	1.30	4.0	55.0	8.66	5.42	3.25	0.74	2	2	2	3	3
Vermivora crissalis	49	0.57	35.5	2.5	1.0	1.59	19.5	27.0	6.52	3.96	2.56	1.00	2	1	1	3	2
Vermivora luciae	62	0.89	37.0	1.3	2.0	1.43	14.0	49.5	6.59	3.22	3.38	1.00	2	2	2	3	1
Vermivora peregrina	43	0.75	40.3	1.0	4.5	3.26	27.5	14.5	9.89	3.24	6.65	0.57	2	1	1	3	3
Vermivora pinus	212	0.01	110.8	0.8	2.0	1.11	25.0	15.0	8.77	3.94	4.83	0.96	3	2	1	3	3
Vermivora ruficapilla	59	0.61	32.0	1.3	3.0	1.73	16.5	44.5	8.51	3.38	5.14	0.30	2	2	1	3	2
Vermivora virginiae	74	0.52	35.2	1.8	3.0	2.09	16.0	66.0	7.03	2.90	4.13	0.22	2	1	1	3	1
Wilsonia canadensis	70	0.56	37.0	1.0	7.5	1.03	8.0	54.5	8.05	3.18	4.88	0.11	2	2	2	3	3
Wilsonia citrina	129	0.60	42.2	2.0	3.0	1.02	5.0	72.5	6.69	2.67	4.02	0.60	3	2.5	3	3	3
Wilsonia pusilla	56	0.59	33.4	1.7	2.5	1.52	13.5	47.5	7.03	3.41	3.62	0.96	2	2	1	3	3

[a] Variables describing the structure of notes: DURA = duration (ms), BEGMN = location of minimum frequency as a proportion of duration, BANDW = maximum bandwidth (kHz), INFL = number of infection points, KINDS = number of different kinds of notes.

[b] Variables describing the structure of songs: DURA = duration (sec), NOTES = number of notes, INTER = mean interval between notes (ms), MAXFQ = maximum frequency (kHz), MINFQ = minimum frequency (kHz), RANGE = frequency range (kHz), ADJAC = proportion of notes adjacent to an identical note.

[c] Variables describing breeding habitats (see table 2): TREE = tree type, CANH = canopy height, CAND = canopy density, UND = understorey density, MOIST = moisture.