Body mass and habitat correlates of song structure in a primitive group of birds

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We assessed relationships between acoustic frequency, body mass, and habitat in tinamous. This monophyletic group of primitive birds comprises *c.* 47 ground dwelling species whose habitats range from dense humid forest to open grasslands. The relationship between frequency and body mass was found to be negative, while the songs of open-habitat species exhibited higher frequencies and a wider bandwidth than the closed-habitat ones. Residual variation in song frequency, after controlling for the effect of body mass and phylogeny, tends to differ among habitats. However, a statistical test of this pattern was not possible because of the existence of only five pairs of sister species differing in habitat. In spite of this, positive contrasts of bandwidth were associated with positive contrasts of habitat, confirming that songs of open-habitat species have a wider bandwidth than those of their more closed habitat relatives. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **77**, 423–430.

ADDITIONAL KEYWORDS: adaptation – bioacoustics – Tinamidae – tinamous.

INTRODUCTION

Interspecific comparisons across a large number of Neognathous (mainly passerine) species have revealed the existence of different patterns of song variation. For example, there is a negative relationship between body mass and acoustic frequencies (Wallschläger, 1980; Ryan & Brenowitz, 1985; Tubaro & Mahler, 1998). In addition, closed-habitat species produce songs with lower frequencies, slower modulated notes and longer internote intervals than open-habitat species (Chappuis, 1971; Morton, 1975; Ryan & Brenowitz, 1985; Wiley, 1991).

The cause of the body size–frequency relationship has been related to both anatomical and physiological factors such as syrinx size, tracheal length, and vocal track resonance, which covary with body size and mass (Wallschläger, 1980; Baptista, 1996; Lambrechts, 1996). Morphology, including beak size and movements, seems to influence not only acoustic frequencies (Westneat *et al.*, 1993; Podos *et al.*, 1995; Palacios & Tubaro, 2000), but also some temporal aspects of bird-song (Podos, 2001).

In turn, the habitat–song relationship has been explained in terms of its advantages for long-range communication. According to current ideas about habitat acoustics, slowly modulated signals are favoured in forests because they avoid the acoustic degradation generated by the accumulation of echoes produced by relatively high 'clutter' (e.g. in the form of trees and leaves). In open fields, the main source of degradation is low rate amplitude fluctuations produced by moving cells of air with varying temperature and humidity. This tends to favour signals with high rates of repetition (Wiley & Richards, 1978; Richards & Wiley, 1980; Brown & Handford, 1996, 2000). Differences in mean acoustic frequencies among habitats are not easily explained because low frequencies always attenuate less with distance when broadcast at a height greater than a meter above the ground (Morton, 1975; Marten & Marler, 1977; Marten, Quine & Marler, 1977). However, for species singing at ground-level, there is a 'sound window' favouring propagation of frequencies

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between 1 and 3 kHz (Morton, 1975; Marten & Marler, 1977; Marten *et al.*, 1977). In this paper, we present an analysis of song structure in relation to body size and habitat for a monophyletic group of primitive birds, the tinamous. Together with ratites, tinamous represent the sister group of all other extant birds (Sibley & Ahlquist, 1990; Groth & Barrowclough, 1999). Because the patterns of song variation emerged from studies of derived birds, the study of tinamous is important in terms of expanding our understanding of song structure and testing its generality. In this context, it is also important to note that tinamous are ground dwellers and lack vocal learning (Hardy, Vielliard & Straneck, 1993), in contrast to the perching habits and learning capabilities of most of the species included in previous studies.

METHODS

SONG ANALYSIS

Analyses of tinamous vocalizations were based on recordings published by Hardy *et al.* (1993), Mayer (1996a), and on the following recordings obtained from the Library of Natural Sounds, Cornell University (USA): *Tinamus tao* (cut 00887); *Tinamus solitarius* (cut 18804); *Tinamus guttatus* (cut 31950); *Nothocercus bonapartei* (cut 00870); *Nothocercus nigrocapillus* (cut 33744); *Crypturellus cinereus* (cut 34189); *Crypturellus soui* (cuts 00859 and 00854); *Crypturellus noctivagus* (cut 00828); *Crypturellus boucardi* (cut 00816); *Crypturellus parvirostris* (cut 51850); *Crypturellus tataupa* (cut 18805); *Rhynchotus rufescens* (cut 35571); *Nothura maculosa* (cut 20279); *Nothoprocta cinerascens* (cut 43836); *Nothoprocta pentlandii* (cuts 46439 and 46168); *Nothoprocta ornata* (cut 43906) and *Eudromia formosa* (cut 50804). The whole sample included songs of 39 out of 47 traditionally recognized species of tinamous. For *Rhynchotus rufescens* the song of two different subspecies were considered (*R. r. rufescens*, *R. r. maculicollis*), because of their distinctiveness (Mayer, 1996b).

Sonograms and power spectra for the song of each recorded species were made using Canary v. 1.2 software (Charif, Mitchell & Clark, 1995). On each song we measured the following variables (Fig. 1): maximum and minimum frequencies (MAX and MIN), bandwidth (BAND = MAX–MIN), and emphasized frequency (EMF: frequency with the higher amplitude in the song). Body mass data were obtained from Dunning (1993), and completed (in a few cases) with unpublished information submitted by different ornithologists. We were unable to find information about the body masses of *Crypturellus brevirostris*, *C. casiquiare*, *C. duidae*, *C. kerriae*, *C. ptaritepui*, *Nothocercus julius*, *N. nigrocapillus*, *Nothoprocta curvirostris*, *N. kalinowskii*, *N. taczanowskii*, *Nothura bora-*

quira and *N. chacoensis*; these species were therefore deleted from the comparative tests, but still considered in the construction of the phylogeny as well as in the estimation of ancestral states of the characters.

COMPARATIVE ANALYSIS

For comparative analysis we used a phylogenetic hypothesis which is not based on the acoustic structure of the song, but on 80 integumentary characters (Bertelli, Giannini & Goloboff, 2002). This cladistic analysis resulted in a strict consensus of 36 most parsimonious trees, each of 444 steps (Fig. 2).

Based on the phylogeny, we estimated the ancestral states of song characters using two different models of evolution: random walk and punctuated (Harvey & Purvis, 1991). The random walk model assumes that changes have occurred at each time interval along the branches of the phylogeny and that the direction of that change is random. The ancestral values of the characters may be reconstructed according to the values of the derived species adjusted by their branch length. The punctuated model assumes that changes have occurred only at the nodes of a tree. Details of the general procedure for estimating the ancestral character values can be found in Felsenstein (1985). We also carried out non-directional comparative tests using independent contrasts (Felsenstein, 1985) and CAIC v. 2.0 (Purvis & Rambaut, 1995). This method is based on comparisons between pairs of sister species. Each comparison produces a new variable termed 'contrast', which is the difference between the values of the variable measured on the species within the pair. Contrasts may be 'standardized' if divided by the square root of the length of the branches being compared, or 'raw' if they are left uncorrected. These contrasts are independent among pairs of sister species, because they result from the evolutionary divergence which has occurred since the origin of each pair. Correct standardization and homogeneity of variance of standardized contrasts was confirmed using the method proposed by Purvis & Rambaut (1995). Thus, any association between contrasts belonging to different variables is statistically detectable using a standard linear regression model (adjusted to pass through zero). In computing comparative analyses, polytomies were solved using the method of Pagel (1992). Briefly, this method assumes that the true phylogeny is bifurcated, and splits the daughter taxa of each polytomy into two monophyletic groups according to their values on the independent variable.

We tested the robustness of our analyses by varying at random (increasing or decreasing by 10%) the body mass and the acoustic frequencies assigned to each species. Body mass and acoustic frequencies were treated independently. Because we have a complete
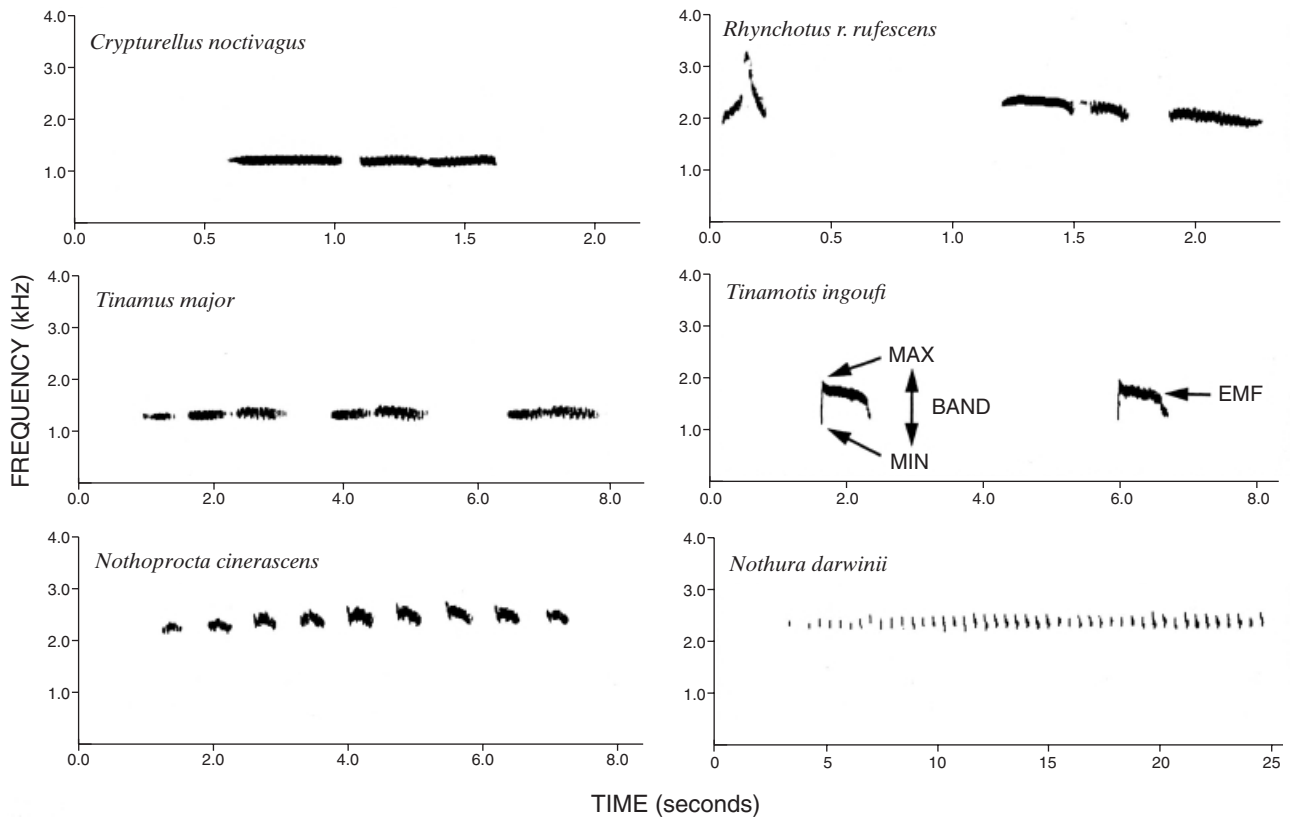
Figure 1. Representative songs of species living in closed (*C. noctivagus* and *T. major*), mixed (*N. cinerascens*), and open habitats (*R. r. rufescens*, *T. ingoufi* and *N. darwinii*). Acoustical variables measured are exemplified on the song of *T. ingoufi*. For acronyms see Methods.

set of song, body mass, and phylogenetic data for 35 species and subspecies, the theoretical number of possible matrices is about $1.18*10^{21}$. We made a random subset of 10 additional data matrices, like the one depicted in Table 1, and repeated the comparative analyses.

Data on habitat were obtained from Parker, Stotz & Fitzpatrick (1996); tinamous habitats were broadly divided into three categories: (1) closed, including tropical lowland, montane evergreen and river edge forest; (2) mixed, including forest edge and tropical deciduous forest, and (3) open, including all non-forest habitats *sensu* Stotz *et al.* (1996). For the comparative analysis, these three categories were coded as 0, 1 and 2, respectively. Although admittedly imperfect, we assumed that this generalized sketch of the main habitats reduced subjectivity to a minimum, while retaining enough ecological information to show any potential trend in the design of the songs. At the same time, the use of three categories (instead of only two) gave us a greater number of independent contrasts for comparison with residuals of song variables after discounting the effect of body mass. Robustness of the

results was assessed by calculating residuals of song variation using the subset of 10 additional matrices mentioned above. All statistical tests were two-tailed, and performed on the log-transformed values of the original variables.

RESULTS

BODY MASS AND SONG VARIABLES

The results of the independent contrast analyses were similar regardless of the model of character evolution employed; we therfore only present those obtained using the punctuated model. In particular, we found that acoustic frequencies varied negatively with body mass (slope of the regression forced to pass through zero B = −0.19); this relationship was significant for MAX, MIN, and EMF, but not for BAND (see Table 2).

Analysis of robustness using 10 replicates of the data matrix showed similar results. All acoustic frequency variables changed negatively with body mass, and in nine, eight, and 10 of the comparisons involving MAX, MIN, and EMF, the relationship was significant,

Figure 2. Phylogeny of tinamous based on the strict consensus tree of 36 optimal trees (each of 444 steps), resulting from the cladistic analysis of 80 integumentary characters (Bertelli, Giannini & Goloboff, 2002). The phylogenetic reconstruction of habitat is based on unordered parsimony.

Table 1. Database used in the comparative analysis of the relationship between body mass, habitat and the structure of the song. For acronyms see Methods

Species	MAX (Hz)	MIN (Hz)	EMF (Hz)	BAND (Hz)	Body mass[a] (g)	Habitat	Phylogenetic position[b]
Crypturellus atrocapillus	2090	1160	930	1127	453	Closed	BCBBA
Crypturellus bartletti	1889	1270	619	1530	241	Closed	BCBBABBCBB
Crypturellus berlepschi	1500	1340	160	1409	478	Closed	BCBBBBCDB
Crypturellus boucardi	815	680	135	779	418	Closed	BCBBBBBA
Crypturellus brevirostris	ND	ND	ND	ND	ND	Closed	BCBBABBCBA
Crypturellus casiquiare	1800	1390	410	1657	ND	Closed	BCBBABBCA
Crypturellus cinereus	1950	1600	350	1762	450	Closed	BCBBBBCDA
Crypturellus cinnamomeus	1440	1210	230	1315	419	Closed	BCBAB
Crypturellus duidae	ND	ND	ND	ND	ND	Closed	BCBBAA
Crypturellus erythropus	1190	950	240	1121	485	Closed	BCBBABA
Crypturellus kerriae	1250	1040	210	1094	ND	Closed	BCBBBBBB
Crypturellus noctivagus	1310	1060	250	1188	800	Closed	BCBBABBB
Crypturellus obsoletus	2960	1450	1510	2033	482	Closed	BCBBBBCEA
Crypturellus parvirostris	2800	1290	1510	2069	212	Mixed	BCBBBBCEBB
Crypturellus ptaritepui	ND	ND	ND	ND	ND	Closed	BCBBBBCC
Crypturellus soui	2230	1750	480	2016	198	Closed	BCBBBBCB
Crypturellus strigulosus	1440	1210	230	1348	390	Closed	BCBBBBA
Crypturellus tataupa	2710	1400	1310	2234	264	Closed	BCBBBBCEBA
Crypturellus transfasciatus	2780	1190	1590	1252	283	Closed	BCBAA
Crypturellus undulatus	1360	1060	300	1248	540	Closed	BCA
Crypturellus variegatus	1780	1440	340	1503	384	Closed	BCBBABBA
Eudromia elegans	1700	1460	240	1591	660	Mixed	BCCBBBBBBAB
Eudromia formosa	1730	1530	200	1657	640	Mixed	BCCBBBBBBAA
New sp.	ND	ND	ND	ND	ND	Mixed	BCCA
Nothocercus bonapartei	1590	1180	410	1468	763	Closed	ABA
Nothocercus julius	2397	1330	1067	2202	ND	Closed	AA
Nothocercus nigrocapillus	2352	1400	952	2012	ND	Closed	ABB
Nothoprocta cinerascens	2830	2080	750	2507	475	Mixed	BCCBBBBABBBB
Nothoprocta curvirostris	ND	ND	ND	ND	ND	Open	BCCBBBBABBAB
Nothoprocta kalinowskii	ND	ND	ND	ND	ND	Mixed	BCCBBBBABAB
Nothoprocta ornata	4420	2870	1550	3515	572	Open	BCCBBBBABAA
Nothoprocta pentlandii	4990	1990	2610	2610	293	Open	BCCBBBBABBBA
Nothoprocta perdicaria	4990	2540	2540	2659	458	Open	BCCBBBBABBAA
Nothoprocta taczanowskii	ND	ND	ND	ND	ND	Mixed	BCCBBBBAA
Nothura boraquira	2960	2420	540	2692	ND	Mixed	BCCBBAA
Nothura chacoensis	ND	ND	ND	ND	ND	Mixed	BCCBBBAA
Nothura darwinii	2600	2070	530	2289	245	Open	BCBBBABA
Nothura maculosa	2564	1999	565	2373	300	Open	BCBBBABB
Nothura minor	3578	2858	720	3374	166	Open	BCCBBAB
Rhynchotus rufescens maculicollis	3200	1500	1700	2144	890	Open	BCCBBBBBAA
Rhynchotus rufescens pallescens	ND	ND	ND	ND	850	Mixed	BCCBBBBBABA
Rhynchotus rufescens rufescens	3100	1900	1200	2287	900	Mixed	BCCBBBBBABB
Taoniscus nanus	ND	ND	ND	ND	43	Mixed	BCCBA
Tinamotis ingoufi	1880	1210	670	1718	730	Open	BCCBBBBBBBB
Tinamotis pentlandii	1990	1130	860	1306	895	Open	BCCBBBBBBBA
Tinamus guttatus	1130	930	200	1061	600	Closed	BA
Tinamus major	1500	1160	340	1315	1052	Closed	BBA
Tinamus osgoodi	1190	930	260	1033	1285	Closed	BCBBBBCA
Tinamus solitarius	1500	1130	370	1342	125	Closed	BBC
Tinamus tao	1520	1160	360	1248	2000	Closed	BBB

[a]Based on Dunning (1993).
[b]Phylogeny based on plumage characters (Bertelli *et al.*, 2002), and according to the convention of Purvis & Rambaut (1995). This convention consists in looking at each node of the phylogeny and lettering its daughter branches. When this is done for each node in turn, each species has a unique code formed by the sequence of letters on the branches leading to it, starting from the root (last common ancestor of all the species).

Table 2. Regressions of phylogenetically independent contrasts in song variables with contrasts in body mass. All original variables were log-transformed. Ancestor reconstruction was based in the punctuated model of character evolution. For acronyms see Methods

Comparison (df = 1,26)	B[a]	Student's t-test	P
MAX	−0.28	2.63	0.014
MIN	−0.19	2.60	0.015
BAND	−0.41	1.52	0.140
EMF	−0.24	3.18	0.004

[a]Slope of the regression forced to pass through zero.

respectively (B = −0.16, t_{26} = 2.10, $P < 0.05$). Instead, none of the comparisons involving BAND was significant.

HABITAT STRUCTURE AND ACOUSTIC FREQUENCIES

Closed-habitat species present significantly lower MIN and EMF than their open- and mixed-habitat counterparts (Table 3). In addition, they have lower MAX and narrow bandwidth songs compared to open-habitat ones; mixed habitat species were positioned between both groups.

To avoid confounding effects of body mass differences in comparisons involving habitat type, we calculated the residuals of variation using the slope of the regression (forced to pass through zero) among their respective contrasts and body mass contrasts (Garland, Harvey & Ives, 1992). Thus, residuals of variation in acoustic frequencies were compared to habitat, but controlled again for phylogeny. This produced five contrasts among pairs of related species differing in habitat. Since we needed a minimum of six cases in order to test the statistical significance of the result (using for example a Binomial test) we will only comment on the tendencies we observed. These contrasts were between: (1) *Crypturellus tataupa* and *C. parvirostris* (2) *Rhynchotus rufescens rufescens* and *R. r. maculicollis* (3) the common ancestors of *Eudromia* and *Tinamotis* (4) *Nothoprocta cinerascens* and *N. pentlandii*, and (5) the common ancestors of *Crypturellus* and the clade including *Eudromia* + *Tinamotis* + *Rhynchotus* + *Nothura* + *Taoniscus* + *Nothoprocta* + a new species. All contrasts of BAND were positive, indicating a tendency of open habitat species to sing wider band songs than their more closed habitat counterparts.

Robustness analysis showed that in the 10 replicates of the data matrix, BAND contrasts were always positive, confirming that open habitat species have wider bandwidth songs compared with more closed habitat ones.

DISCUSSION

We found a negative relationship between body size and acoustic frequencies in the songs of a monophyletic group of primitive birds, the tinamous, as reported in other groups of more derived birds such as doves (Tubaro & Mahler, 1998), woodcreepers (Palacios & Tubaro, 2000), and songbirds (Ryan & Brenowitz, 1985; Wiley, 1991; Badyaev & Leaf, 1997). This negative correlation is indicative of a general pattern that probably reflects basic anatomical and physiological processes involved in song production (Lambrechts, 1996).

We also found that the species living in closed habitats tend to use narrower bandwidth songs than their open-habitat relatives. This result was obtained irrespective of whether songs were corrected for interspecific body mass differences and phylogenetic relationships or not. However, the statistical significance of the result could not be assessed because of the small number of independent comparisons available in tinamousí phylogeny. All five contrasts among species differing in habitat were positive, indicating the use of

Table 3. Descriptive statistics of songs and body mass from tinamous species living in different types of habitats. Black horizontal lines indicate non-significant differences (ScheffÈ contrasts) among treatments. For acronyms see Methods

Variable	df	Closed (N = 25)	Mixed (N = 6)	Open (N = 9)	One-way ANOVA among habitats F	P
MAX[a]	2, 37	1747 ± 562	2520 ± 633	3357 ± 1214	15.38	<0.001
MIN[a]	2, 37	1217 ± 232	1780 ± 429	2019 ± 654	16.06	<0.001
BAND[a]	2, 37	530 ± 433	740 ± 527	1295 ± 816	6.40	<0.005
EMF[a]	2, 37	1452 ± 391	2134 ± 447	2443 ± 709	15.74	<0.001
Body mass[b]	2, 34	631 ± 439	540 ± 319	505 ± 280	0.38	>0.500

[a]In Hertz. [b]In grams.

wider BAND songs in more open habitats. This result was robust to variations in the model or character evolution (random walk or punctuated) and to variations in the song and body mass data (±10%).

It is interesting to note that this pattern of song variation, with wider bandwidths in open-habitat species, repeats that reported for songbirds (Ryan & Brenowitz, 1985; Wiley, 1991). In songbirds, acoustic adaptation of song structure to habitat acoustics is supposedly mediated by vocal learning, because young birds should hear and memorize song models which have been filtered by the environment (Hansen, 1979; Nottebohm, 1985). Since tinamous lack vocal learning (Hardy *et al.*, 1993), the cause of song variations among habitats must be sought elsewhere. Natural selection favouring different song structures in each habitat is one possibility. If long-range communication is important to attract mates and/or repel competitors, individuals with well-designed songs could achieve higher reproductive success, transmitting to their offspring the ability to produce such adapted signals. A second possibility is that morphological adaptation may drive signal evolution. In this case, we would not necessarily expect the signal to match the optimum structure for long-distance propagation in a particular medium, because this would depend on the exact relationship between morphology and song structure. In Darwin's finches, birds with large beaks and body sizes produce songs with comparatively low rates of syllable repetition and narrow frequency bandwidth (Podos, 2001), and there is evidence that both beak morphology and body size are under strong selective pressure related to diet (Gibbs & Grant, 1987). We believe that this scenario is a less suitable explanation for the habitat–song relationship found in tinamous, for two reasons: (1) while there is a significant relationship between acoustic frequencies and body mass, we could not find differences in body mass among habitats (Table 3); and (2) habitat-song relationship in tinamous was evident even on the size-free residuals of acoustic frequencies.

Experimental studies showed that near the ground, frequencies in the range of 1–3 kHz propagate better irrespective of habitat, thus creating an 'acoustic window' for long-range communication (Marten & Marler, 1977). Table 3 shows that almost all tinamous fall well inside this window, suggesting that song is well adapted for reaching distant receptors. This can be very important because of the higher attenuation of the sound near the ground (Morton, 1975; Marten & Marler, 1977; Marten *et al.*, 1977). However, we do not yet fully understand the advantages of using lower frequencies and narrower bandwidth songs in closed habitats compared to open ones. One possibility is the existence of subtle differences in the location and width of the acoustic window among habitats. Marten & Marler (1977) provided partial evidence for this, finding that the lowest attenuated frequencies are somewhat lower in forest than in grasslands. A second possibility is the existence of consistent differences in background noise among habitats as suggested by Ryan & Brenowitz (1985). Concentrating the acoustic energy of a song in a part of the spectrum which is free from environmental noise (including the sounds emitted by other species) can be a good strategy for long-range communication. In tropical forests, the absence of wind-generated noise and the abundance of calling insects could favour relatively lower maximum and narrow band songs compared to grasslands (Morton, 1975; Ryan & Brenowitz, 1985).

ACKNOWLEDGEMENTS

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