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THE ROLE OF BODY SIZE, PHYLOGENY, AND AMBIENT NOISE IN THE EVOLUTION OF BIRD SONG

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Any biological trait may evolve under the influence of a variety of selective forces, and often these selective forces act in opposition. Thus, an observed trait will be the outcome of a compromise among different selective forces, as well as among constraints on the ability of that trait to respond to selection (e.g., Gould and Lewontin 1978; Oster and Wilson 1979). This is especially important in acoustic communication systems. To understand the evolution of such systems, it is necessary to consider the various selective forces and constraints acting on the transmission, production, and detection of signals.

Recently, there has been considerable interest in factors influencing the evolution of bird song. The majority of these studies (e.g., Morton 1970, 1975; Chappuis 1971; Marten and Marler 1977; Marten et al. 1977; Wiley and Richards 1978, 1982; Bowman 1979, 1983) have addressed how environmental constraints on sound transmission influence the evolution of the frequency components of acoustic signals used by birds for communication over relatively long distances. These studies have shown that some sound frequencies transmit with less energy loss per unit distance, and suggest that maximizing the transmission distance has led to concentration of the energy in bird songs at those frequencies that are least attenuated.

Although the environment may influence the evolution of song frequency, other factors need to be considered. From our own research (e.g., Brenowitz 1982 a,b ; Ryan 1985 a,b), we know that there are important constraints on the production and detection of animal acoustic signals. For example, the mass of the vibrating structure that produces the sound influences the frequency of the sound; in many animals, this mass is correlated with body size (Wallschager 1980; Bowman 1983). In at least some animals, the size-frequency allometry differs among groups of closely related species (anurans, Ryan 1985 b); thus, phylogenetic relationships must be considered in analyzing the evolution of the frequency structure of bird song. Also, Brenowitz (1982 a,b) has shown that the frequency distribution of

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ambient noise influences those signal frequencies that can be detected over distance, and this seems to influence the frequencies used by birds in long-range communication.

Morton (1970, 1975) investigated the frequency structure of the songs of birds in three Panamanian habitats. He found differences in the song frequencies emphasized (i.e., those frequencies containing the greatest amount of energy) by birds in different habitats, and suggested that these differences correlated with differences in sound transmission among habitats. Specifically, he found a "frequency window" in low-forest habitats, that is, an intermediate range (1585 Hz–2500 Hz) within which frequencies attenuate less rapidly than do higher or lower frequencies. Furthermore, Morton found that the mean emphasized frequency of bird songs in low-forest habitat occurred within this frequency range. The mean emphasized frequency of song in this habitat was significantly lower than those in edge and grassland habitats where no frequency windows were observed.

Although Morton and others (e.g., Wiley and Richards 1982; Bowman 1983) have also discussed the potential influence of body size and phylogeny in the evolution of bird song, we wish to quantify the contribution of these factors and of ambient noise to the habitat-correlated differences in song frequency observed by Morton.

MATERIALS AND METHODS

Morton (1970) presented a list of the species that were used in his later analysis (Morton 1975), along with their emphasized song frequencies and preferred habitats. For our analysis we obtained the sizes of 159 species (the length of the bird from the tip of its bill to the end of its tail in inches) from Ridgely (1976), de Schauensee (1964), Land (1970), and de Schauensee and Phelps (1978). If a range of sizes was presented for a species we used the median, and if the sexes were of different size we used the size of the male.

We calculated the regression equations for emphasized frequency on the logarithm of body size for all habitats combined, and for each habitat separately. Regressions also were calculated for taxonomic units combining habitats, and for low-forest and grassland-edge habitats considered separately. Species were placed in one of three taxonomic categories: non-Passeriformes, suboscine Passeriformes, or oscine Passeriformes (Welty 1979). Regressions were determined by the least-squares method.

Regressions were compared using analysis of covariance techniques (Snedecor and Cochran 1967). We tested for significant differences in residual variance, slope, and adjusted means. If there was a significant difference in any one of the parameters between regressions, the regressions were considered different and subsequent parameters were not compared. (The comparison of slopes assumes no significant difference between residual variances, and a comparison of adjusted means assumes no significant difference between slopes.) The differences in the sizes of birds among habitats were tested with a Kruskal-Wallis test (Siegel 1956). A *G*-test (Sokal and Rohlf 1969) was used to determine if, within a taxonomic unit, species in low-forest habitat produced songs with emphasized frequencies that were lower than predicted by the regression of emphasized frequency on size.

Analyses were restricted to birds found in low-forest, edge, and grassland habitats, and did not consider species in high-forest habitat. We did this because Morton found differences in emphasized frequency of song only among the former three habitats, and because the sample size of species in high-forest habitat was too small for analysis after being subdivided by taxonomic unit.

Ambient noise was recorded in forest and grassland habitats near Pipeline Road in the Parque Nacional Soberano, Republic of Panama, during July 1983. Noise was recorded near the ground and 1.5 m above the ground for a period of several minutes at 0600 h, 0700 h, and 0800 h with a Sony TCD5M cassette tape recorder using metallic tape and a Sennheiser ME 80 microphone with a K3-U power module. Spectral analysis of the noise was conducted with a Bruel and Kjaer model 2033 digital real-time spectrum analyzer, which provides a measure of relative amplitude versus frequency. Furthermore, we measured the absolute sound-pressure level of ambient noise. This was done by recording a 1-kHz tone of known sound-pressure level (SPL, re: 2×10^{-5} N/m²) at 1 m from the microphone just before recording ambient noise. The test tone and the ambient noise were recorded at the same record level on the tape recorder. Peak-to-peak voltage of the test tone was measured on a Tektronix storage oscilloscope and was used to determine the maximum root-mean-square (RMS) sound-pressure level of the ambient noise.

THE ROLE OF BODY SIZE IN THE EVOLUTION OF BIRD SONG

Among species of birds there can be a correlation between the emphasized frequency of the song and the size of the bird: larger birds have songs with lower emphasized frequencies. For example, Wallschager (1980) has shown that body mass explains 59% of the observed variation in frequency for the songs of 90 passerine species in Europe. In relation to this phenomenon, we addressed two questions regarding Morton's demonstration of differences in the emphasized frequency of bird songs in different habitats. Is there a relationship between size and song frequency for the species analyzed by Morton? If so, can lower average emphasized frequency of bird songs in low-forest habitat be attributed merely to the fact that larger birds reside in this habitat?

For the species analyzed, the regression analysis reveals that body size does explain a significant amount of the observed variation in the emphasized frequency of bird song (fig. 1, table 1). This leads us to consider the second question: are Morton's observations confounded by differences in the average size of birds among habitats? In fact, the average size of birds that sing in the low-forest habitat, where Morton found the lowest emphasized frequency, is larger than the average size in the grassland and edge habitats (table 1). A Kruskal-Wallis test shows that these differences are statistically significant ($H = 12.3$; $P < .01$). Thus, Morton's conclusion, that songs with lower emphasized frequencies in the low-forest habitat are a result of selection to maximize transmission distance, is confounded by the fact that body size was not considered.

Our results do not necessarily contradict Morton's conclusion, but do demonstrate that the constraint of body size on song frequency also needs to be consid-

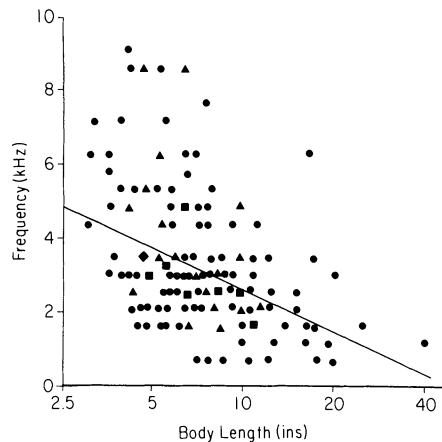


FIG. 1.—Regression of frequency on the logarithm of body size for all species included in the study. Circle = 1; triangle = 2; square = 3; diamond = 4.

TABLE 1
AVERAGE SIZE, AVERAGE EMPHASIZED FREQUENCY, AND THE RELATIONSHIP OF FREQUENCY TO THE LOGARITHM OF SIZE FOR ALL BIRD SPECIES ANALYZED, AND FOR SPECIES AS A FUNCTION OF PREFERRED HABITAT

Habitat	N	Size		Frequency		Regression Equation	r^2	F	(P)
		\bar{x}	(s^2)	\bar{x}	(s^2)				
All	159	7.57	(20.9)	3.30	(3.5)	$Y = 7.10 - 4.57 X$.23	45.8	(.0000)
Low forest	69	8.94	(36.4)	2.22	(1.0)	$Y = 4.49 - 2.56 X$.32	31.8	(.0000)
Edge	69	6.08	(4.5)	4.09	(3.8)	$Y = 8.58 - 5.87 X$.17	13.9	(.0004)
Grassland	21	7.92	(11.5)	4.24	(3.8)	$Y = 8.74 - 5.23 X$.23	5.9	(.0247)

ered. Instead of comparing the mean emphasized frequencies of songs in different habitats, Morton’s hypothesis predicts that the mean emphasized frequency adjusted for body size should be lower for residents in low-forest habitat than for residents in either grassland or edge habitats, and should not differ between the latter two habitats.

Inspection of the regressions for each habitat suggests that, as Morton’s results predict, there is no difference between the size-frequency relationship in songs of species in grassland and edge habitats (fig. 2). Analysis of covariance demonstrates that there are no significant differences in residual variance ($F = 1.07, P > .10$), slope ($F = 0.05, P > 0.25$), or adjusted means ($F = 2.83, P > .10$) between these two regressions. The regression for the low-forest habitat, however, differs in residual variance from the regressions of both grassland ($F = 4.34, P < .005$) and edge ($F = 4.63, P < .005$) habitats, and thus prohibits further comparisons of the regressions. Therefore, we cannot employ an analysis of covariance to compare the mean emphasized frequencies, adjusted for body size, among habitats.

The fact that the regressions of frequency on size differ among habitats, and that different taxonomic groupings of birds tend to predominate in different

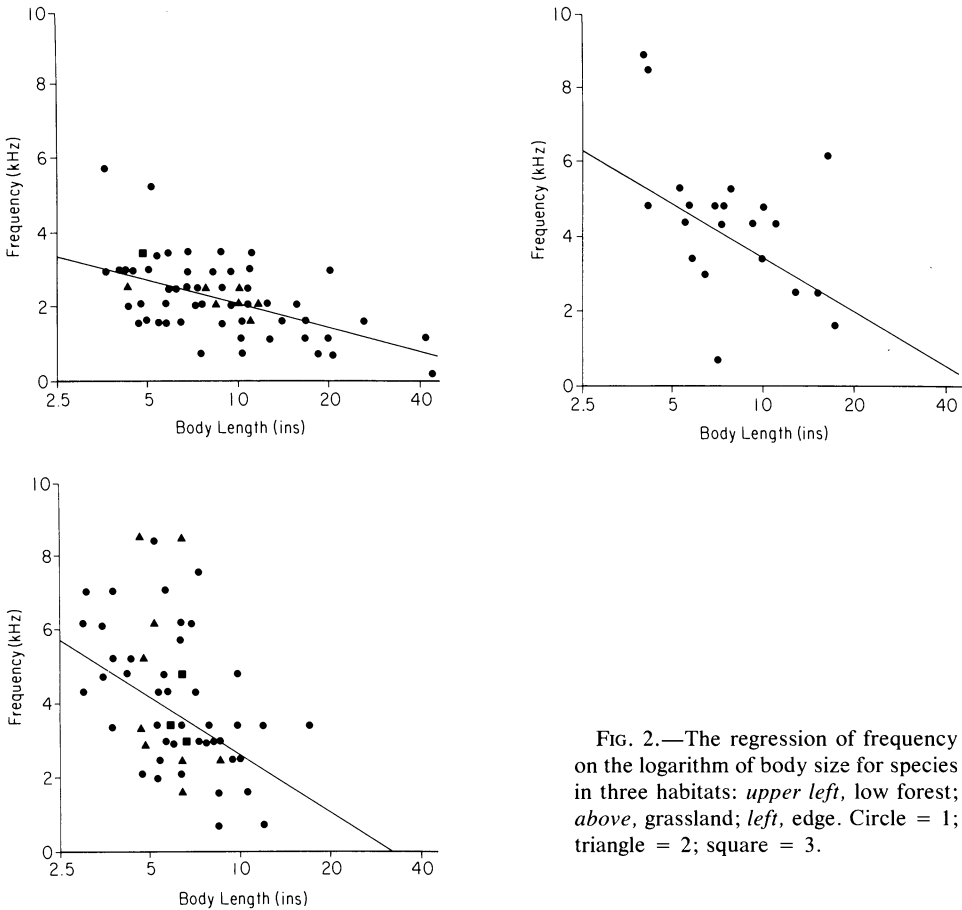


FIG. 2.—The regression of frequency on the logarithm of body size for species in three habitats: *upper left*, low forest; *above*, grassland; *left*, edge. Circle = 1; triangle = 2; square = 3.

habitats (see Morton 1975, table 1), suggests that there might be different allometric relationships between frequency and size for different taxonomic groups. We explore this in the next section.

THE ROLE OF PHYLOGENY IN THE EVOLUTION OF BIRD SONG

Many studies have emphasized the importance of choosing the correct taxonomic level for the analysis of cross-species comparisons, assuming that different taxonomic groups represent monophyletic lineages (e.g., Clutton-Brock and Harvey 1977; Harvey and Mace 1982; Ridley 1983). This is of particular concern here. If evolutionary history affects the size-frequency allometry, then it is not appropriate to examine the deviation from an expected frequency for species with different evolutionary histories if the expected frequency is derived from a common regression. The passerines are thought to be a monophyletic group, and within the passerines, the suboscines and oscines are each thought to be monophyletic (Raikow 1982). Therefore, we compared the size-frequency allometries

TABLE 2
THE RELATIONSHIP BETWEEN EMPHASIZED FREQUENCY AND THE
LOGARITHM OF SIZE AS A FUNCTION OF TAXONOMIC UNIT

Taxonomic Unit	N	Regression Equation	r^2	F*
		$Y = a + b X$		
Nonpasserines	32	$Y = 7.05 - 4.52 X$.35	15.9
Suboscines	69	$Y = 5.28 - 2.83 X$.09	7.4
Oscines	58	$Y = 9.26 - 6.69 X$.16	11.0

* $P < .01$.

among suboscines, oscines, and nonpasserines, even though the latter taxon probably is not monophyletic (e.g., Cracraft 1981).

It would be surprising if there were not differences in relationships between size and the emphasized frequency of songs among these groups since they are separated in part by differences in syrinx morphology (Nottebohm 1975; Gaunt 1983), morphological differences that might affect the allometric relationship between size and frequency. If this is true, then a comparison of the emphasized frequencies of bird songs in different habitats must control for phylogeny as well as body size. Although Morton (1970, 1975) did discuss the potential influence of body size and phylogeny, the interaction of these variables was not used to test his hypothesis.

Body size does explain a significant amount of the variation in frequency for nonpasserines, suboscines, and oscines (all $P < .01$), although the coefficients of determination are very low (table 2, fig. 3). Furthermore, all the regressions are significantly different from each other. The residual variance of the regression for suboscines is significantly different from that for both nonpasserines ($F_{(56,67)} = 2.86$, $P < .01$) and oscines ($F_{(30,67)} = 1.77$, $P < .05$). Although there were no significant differences in residual variance ($F_{(56,30)} = 1.64$, $P > .05$) or slope ($F_{(1,87)} = 0.88$, $P > .05$) between the regressions of nonpasserines and oscines, the adjusted means were significantly different ($F_{(88,89)} = 2.22$, $P < .01$). These results suggest that at the taxonomic levels we employed, phylogeny influences the size-frequency allometry. Although analysis at a finer taxonomic level may be appropriate (e.g., Harvey and Mace 1982), small sample size prohibited this. Therefore, we tested Morton's hypothesis by asking, *Within nonpasserines, suboscines, and oscines*, do species that reside in low-forest habitat produce songs with emphasized frequencies that are lower in relation to *their body size* than do birds that reside in grassland and edge habitats?

Since the relationships between size and frequency were not significantly different for grassland and edge habitats, these data were combined in the following analyses. Morton's hypothesis predicts that within each taxonomic unit, species in low-forest habitat should have emphasized frequencies that are relatively low for their size and their taxonomic unit. That is, their frequencies should tend to fall below the regression of frequency on size (i.e., they should have negative resid-

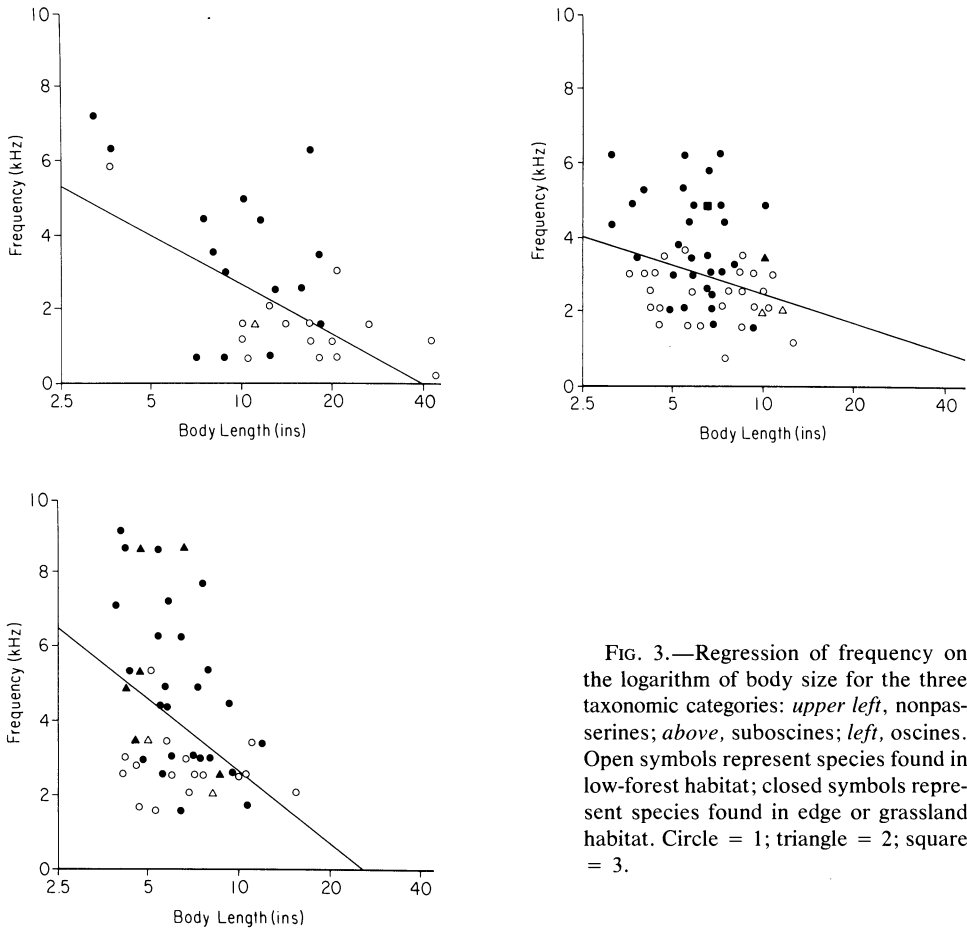


FIG. 3.—Regression of frequency on the logarithm of body size for the three taxonomic categories: *upper left*, nonpasserines; *above*, suboscines; *left*, oscines. Open symbols represent species found in low-forest habitat; closed symbols represent species found in edge or grassland habitat. Circle = 1; triangle = 2; square = 3.

uals) for that taxonomic unit (fig. 3). Similarly, species in grassland and edge habitats should have frequencies above the regression line (i.e., they should have positive residuals).

The analyses seem to support Morton's hypothesis (table 3). For each of the taxonomic units, species in low-forest habitats are more likely to have negative residuals than are species in grassland and edge habitats. Therefore, even after controlling for the confounding effects of body size and, to some extent, phylogeny, birds in low-forest habitats tend to produce songs with emphasized frequencies lower than those of birds in grassland or edge habitats.

THE ROLE OF AMBIENT NOISE IN THE EVOLUTION OF BIRD SONG

The results of our analyses are consistent with Morton's hypothesis, but we suspect this is not solely because of the frequency window near the ground in low-forest habitat, as proposed by Morton. Birds in this habitat tend to produce tonal

TABLE 3
SPECIES WITH EMPHASIZED FREQUENCIES THAT HAVE POSITIVE RESIDUALS
AND NEGATIVE RESIDUALS AS A FUNCTION OF TAXONOMIC UNIT AND
PREFERRED HABITAT

HABITAT	TAXONOMIC UNIT								
	Non-passerines ^{a*}			Sub-oscines ^{b**}			Oscines ^{c**}		
	+	-	N	+	-	N	+	-	N
Low forest	5	12	17	8	24	32	4	16	20
Edge-grassland	10	5	15	27	10	37	22	16	38
Total	15	17	32	35	34	69	26	32	58

NOTE.—See fig. 3.
^a $G = 4.54$.
^b $G = 16.46$.
^c $G = 8.04$.
* $P < .05$.
** $P < .005$.

songs with frequencies that match the frequency window. In the grassland habitat, however, there is no frequency window (but see Marten and Marler 1977; Marten et al. 1977). All else being equal, in this habitat there also should be selection for songs with low emphasized frequencies since, in the absence of a frequency window, lower frequencies transmit better (Wiley and Richards 1978, 1982). The mean emphasized frequency of songs in this habitat, however, is higher than in low-forest habitat. Perhaps this is because birds in grassland habitats are smaller (table 1), and their small body size constrains their ability to produce low-frequency sounds efficiently (Kinsler and Frey 1962; Morton 1970; Wiley and Richards 1982; Ryan 1985*a,b*). Therefore, Morton (1970, 1975) suggests that these species rely on temporal information for long-range communication, and that this is best achieved with broad-band signals. This consequently increases the mean emphasized frequency of the songs of species in grassland habitats relative to those of species in low-forest habitats. We believe that there is another important environmental constraint in long-range communication that needs to be considered: ambient noise.

A receiver can only respond to an acoustic signal if it is detected and discriminated (see Wiley and Richards 1982), and studies of animal sound transmission are based on the assumption that signals with certain acoustic structures are more likely to be detected over distance than are others, because of differential attenuation through the environment. Brenowitz (1982*b*), however, demonstrated that ambient noise also can play an important role in signal detection. He showed that the portion of the advertisement song that the red-winged blackbird (*Agelaius phoeniceus*) uses for long-range communication has a narrow frequency range that falls in a relatively quiet region of the acoustic environment. This window in the noise is bounded on the low-frequency side by wind-generated noise. (The movement of air past the ground, vegetation, and an animal's head generates ambient noise, predominantly at low frequencies.) There is less wind in low-forest habitats than in other habitats (Wiley and Richards 1982). This suggests that songs with low emphasized frequencies are less likely to be masked by wind-generated

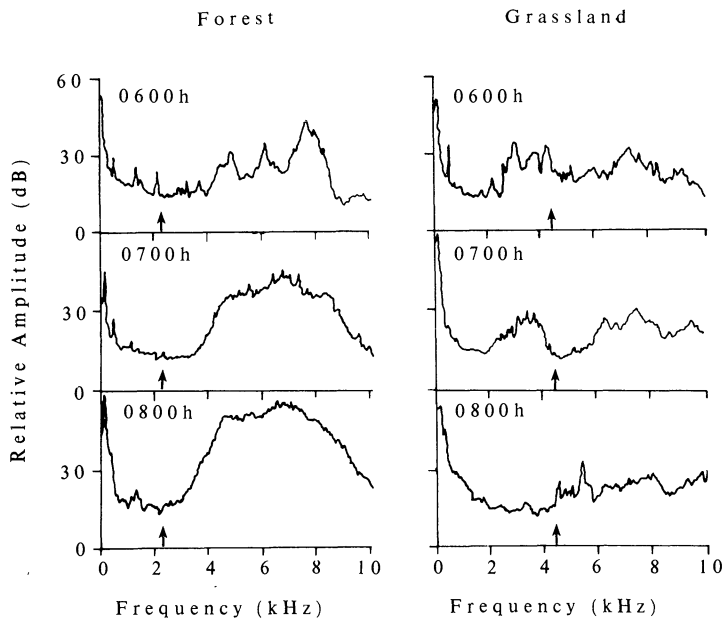


FIG. 4.—Amplitude spectra (relative amplitude vs. frequency) measured at ground level for forest and grassland habitats during the morning. Arrows indicate the mean emphasized frequency of bird song in each habitat.

noise in low-forest habitats than in more open habitats. Therefore, we recorded ambient noise at ground level and at 1.5 m in low-forest and grassland habitats.

In both the low-forest and grassland habitats there were two frequency distributions of high relative amplitude in the ambient noise spectrum (fig. 4). The first is about 100–200 Hz, and a second, much broader concentration occurs about 4–7 kHz. There is a substantial difference in the ambient noise spectra between the two habitats. In the low-forest habitat there is an area of relatively low amplitude in the ambient noise environment around 2 kHz. The amplitude in this area is as much as 60 dB less than that at the low-frequency end of the spectrum, and 30–40 dB less than the high-frequency end. (Decibels are based on a logarithmic scale and an increase in amplitude of 6 dB corresponds to a doubling of energy.) As figure 4 shows, the average emphasized frequency in the songs of birds in the low-forest habitat falls in the relatively quiet spectral region. This is not the case in the grassland habitat. Although there also is a decrease in the energy around the 2-kHz region, the level differs by only 30 dB from the low-frequency peak and by 10–15 dB from the high-frequency peak. (These results are almost indistinguishable from the recordings of ambient noise at a height of 1.5 m.) Also, Morton (1975, table 3) reported that low-frequency (500-Hz) ambient sound amplitude is considerably greater, on an absolute scale, in the grassland habitat (30 dB SPL) than in the low-forest habitat (23 dB SPL), and that noise in the 4–8-kHz range was greater in the forest (31–38 dB SPL) than in the grassland (20 dB SPL).

These results demonstrate that, at least at the time and place measured, a low-frequency region of relatively low ambient noise level is much more prevalent in

low-forest habitat than in grassland habitat. This is probably due to the reduction of atmospheric turbulence by vegetation and the abundance of insect noise at high frequencies in the low-forest habitat. Our measurements were made in early morning when turbulence is at a relatively low level; had they been made at midday, when turbulence from ground heating is maximal, one would expect the pronunciation of low-frequency ambient noise in the grassland relative to the forest to be even greater (see Brenowitz 1982*a*). Also, the higher-frequency peak has a greater relative amplitude in the low-forest habitat because of the abundant presence of calling insects, especially during the hours between 0700 and 0800. In addition, it is of interest that the average maximum RMS sound-pressure level of ambient noise (for the entire frequency spectrum measured) during the 3 h sampled was greater in the low-forest habitat (64 dB SPL) than in the grassland habitat (55 dB SPL); this is probably due largely to the incredible din produced by calling insects in the low-forest habitat. Therefore, a bird song of a given amplitude produced in the more intense region of the ambient noise spectrum is more likely to be masked in the low-forest habitat than in the grassland habitat. Thus, it might be more important for animals to communicate in a relatively quieter portion of the ambient noise spectrum in the low-forest habitat than in the grassland habitat. All of these results are consistent with the observed differences in the emphasized frequency of bird song between these two habitats.

DISCUSSION

Previous studies have demonstrated that habitat-dependent patterns of sound transmission exert an important influence upon the evolution of avian vocalizations (Morton 1970, 1975; Bowman 1979, 1983; Gish and Morton 1981). Our present analysis, however, indicates that body size and evolutionary history constrain the ability of birds to evolve emphasized frequencies that optimally match the sound transmission characteristics of the environment. Furthermore, other environmental factors, such as the spectral distribution and intensity of ambient noise might also influence signal structure.

Acoustic signals used for long-range communication should be more constrained by environmental limitations on sound transmission and detection than signals used for short-range communication (e.g., Brenowitz 1982*b*). In the absence of a frequency window, there should be selection for low-frequency songs since these frequencies transmit better. In the presence of a frequency window, songs with emphasized frequencies above the window should also experience selection for lower frequencies. This includes 27 of the 69 species in low-forest habitat listed by Morton (1970). He suggested that many of the remaining species evolved emphasized frequencies that match this frequency window (1585–2500 Hz). By similar reasoning, for many species in low-forest habitat and for all species in other habitats, selection to maximize transmission distance favors birds that produce low-frequency sounds at high intensities. It is in this sense that the influence of body size on emphasized frequency of bird song becomes important.

As we have shown, body size is correlated with the emphasized frequency of bird song. This is largely due to the correlation of body size with the mass of the

vibrating structures used to produce sound (Bowman 1983). Song frequency could be decreased by an increase in the mass of these structures independently of body size, as has been demonstrated in some anurans (Drewry et al. 1982; Ryan 1985*b*). Our analysis suggests that this has happened to some extent in birds of the low-forest habitat. Body size, however, constrains the lower range of frequencies that can be produced efficiently, that is, at a given output intensity for a given input of energy. For a sound to be transmitted, not only must it be produced by the vibrating membranes, but it also must be coupled to the large volume of air surrounding the bird from the bird's relatively small volume of internal air. This large difference in air volume results in a large acoustic impedance mismatch; thus, much energy is lost by the inefficient coupling of acoustic energy from bird to environment (see Brackenbury 1977). The efficiency of this coupling is partially dependent on the size of the structures that radiate the sound. In general, the larger these structures are relative to the wavelength of the sound, the greater the efficiency of radiation (Beranek 1954). Therefore, even if a small bird had vibrating structures that produced low-frequency sounds, these sounds would be radiated at relatively lower intensities than would be possible for higher frequencies. Since transmission distance is a function of both frequency and source intensity, for smaller species, lower frequencies will not necessarily transmit farther because they are radiated from the bird at lower intensities. To some extent, this constraint of body size can be circumvented by adding air sacs or other mechanical features that improve sound radiation (Wiley and Richards 1982). In general, body size and environment result in opposing selective forces. Each favors different frequencies that are optimum for long-range communication. This constraint of body size has been emphasized for other animals as well (Michelson and Nocke 1974; MacNally and Young 1981; Ryan 1985*a*).

Morton (1970, 1975) and Bowman (1979, 1983) share our view that body size and evolutionary history influence the emphasized frequency of bird song. However, they utilize an approach different from ours, to test the hypothesis of an evolutionary response to selection for lower emphasized frequencies. They predict that the emphasized frequencies should coincide with those frequencies that transmit with the least energy loss. In our analysis, we assume that in the absence of selection, emphasized frequency can be predicted by body size and evolutionary history. We then test the hypothesis that selection has changed the frequency from that predicted by these two variables. We feel that our approach is more applicable for two reasons: (1) since body size and evolutionary history have a demonstrable effect on song frequency, these variables must be applied quantitatively to tests of the hypothesis; (2) our approach views selection as a biasing force rather than an optimizing force. This view is more realistic when there are known constraints on an evolutionary response to selection, and when there are opposing selection forces.

Brenowitz (1982*a,b*) suggested that ambient noise might influence the evolution of signal structure in bird songs used for long-range communication. Our results show that even after controlling for body size and evolutionary history, birds in low-forest habitat have songs with lower emphasized frequencies than do birds in other habitats. Furthermore, there is a low-frequency region of relative quiet in

the ambient noise spectrum. These results are consistent with the hypothesis that ambient noise influences the evolution of bird song. We emphasize, however, that these results do not contradict Morton's hypothesis regarding the effect of the frequency window on bird song in low-forest habitat. Hypotheses that environmentally induced selection on bird song is caused by either a frequency window or a window in the ambient noise make the same prediction in this study. Therefore, we are not able to partition the quantitative effects of each variable.

We think that ambient noise plays an important role in environmental bioacoustics. Differences in the physical structure of the habitat, especially between forested and open habitat, influence the amount of wind-generated low-frequency noise in the environment. Biotic contributions to the ambient noise spectrum, especially those of sound-producing insects, also are important. Insect faunas probably vary among habitats. Since insect-generated sounds tend to be of higher frequencies, the combination of these sounds with low-frequency, wind-generated noise is likely to create a window in the ambient noise spectrum (Brenowitz 1982*b*). We suggest that the presence of these discrete frequency bands of relative quiet in some habitats but not in others could influence the evolution of acoustic signals produced by birds and other animals. Additional factors, such as territory size (Bowman 1979, 1983; Brenowitz 1982*a*), undoubtedly influence the evolution of signal structure and vocal behavior. Bowman (1983) discusses many of these factors in detail.

By suggesting the importance of ambient noise in the evolution of song, we feel that our study has amplified Morton's original suggestion that the environment can influence the evolution of acoustic signal structure. We also hope that we have made a contribution, both in perspective and in methodology, by indicating the important influence of body size and evolutionary history on the emphasized frequency of bird song, and demonstrating how these variables can be used to test the hypothesis that environmental selection influences the evolution of bird song.

SUMMARY

Morton found that the average emphasized frequency in the songs of tropical bird species in low-forest habitats was lower than that of species in grassland or edge habitats. He suggested that this was due to a frequency window around 1585–2500 Hz in low-forest habitats, and that there was selection to produce songs with frequencies in this window in order to increase the transmission distance of the songs. In the present study, we analyze the constraints of body size and evolutionary history on the ability of avian species to respond to this selection. Also, we examine the spectral distribution of ambient noise as an additional selective factor.

There is a correlation between body size and the emphasized frequency of the song for the species analyzed by Morton. Larger birds produce songs with lower emphasized frequencies. Morton's demonstration that birds in the low forest produce songs with lower frequencies is confounded by the fact that larger birds also live in this habitat. Phylogeny is also a potentially confounding factor, since the allometry of size and frequency differs among taxonomic units. Our analyses,

however, control for body size and, to some extent, phylogeny, and suggest that there has been an evolutionary response to selection for low-frequency songs by birds in low-forest habitats. Our analysis of ambient noise in low-forest and grassland habitats suggests that this selection might result in part from a relatively quiet region of the ambient noise spectrum in low-forest habitat because of the comparative lack of wind-generated noise and of the abundance of insect-generated sound.

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LITERATURE CITED

- Beranek, L. L. 1954. *Acoustics*. McGraw-Hill, New York.
- Bowman, R. I. 1979. Adaptive morphology of song dialects in Darwin's finches. *J. Ornithol.* 120: 353–389.
- . 1983. The evolution of song in Darwin's finches. Pages 237–537 in R. I. Bowman, M. Berson, and A. E. Leviton, eds. *Patterns of evolution in Galápagos organisms*. American Association for the Advancement of Science, San Francisco.
- Brackenbury, J. H. 1977. Physiological energetics of cock-crow. *Nature* 270:433–435.
- Brenowitz, E. A. 1982a. The active space of red-winged blackbird song. *J. Comp. Physiol.* 147: 511–522.
- . 1982b. Long-range communication of species identity by song in the red-winged blackbird. *Behav. Ecol. Sociobiol.* 10:29–38.
- Chappuis, C. 1971. Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'évolution des chants en forêt équatoriale. *Terre Vie* 25:183–202.
- Clutton-Brock, T. H., and P. H. Harvey. 1977. Primate social organization. *J. Zool. (Lond.)* 183:1–39.
- Cracraft, J. 1981. Toward a phylogenetic classification of Recent birds of the class Aves. *Auk* 98:681–714.
- de Schauensee, R. M. 1964. *The birds of Colombia*. Livingston, Narbeth, Pa.
- de Schauensee, R. M., and W. H. Phelps, Jr. 1978. *A guide to the birds of Venezuela*. Princeton University Press, Princeton, N.J.
- Drewry, G. E., W. R. Heyer, and A. S. Rand. 1982. A functional analysis of the complex call of the frog *Physalaemus pustulosus*. *Copeia* 1982:626–645.
- Gaunt, A. S. 1983. An hypothesis concerning the relationships of syringeal structure to vocal abilities. *Auk* 100:853–862.
- Gish, S. L., and E. S. Morton. 1981. Structural adaptations to local habitat acoustics in Carolina wren songs. *Z. Tierpsychol.* 52:74–84.
- Gould, S. J., and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptive programme. *Proc. R. Soc. Lond. B* 205:581–598.
- Harvey, P. H., and G. M. Mace. 1982. Comparisons between taxa and adaptive trends: problems of methodology. Pages 343–361 in King's College Sociobiology Group, eds. *Current problems in sociobiology*. Cambridge University Press, Cambridge.

- Kinsler, L. E., and A. R. Frey. 1962. Fundamentals of acoustics. Wiley, New York.
- Land, H. C. 1970. Birds of Guatemala. Livingston, Wynnewood, Pa.
- MacNally, R., and D. Young. 1981. Song energetics of the bladder cicada, *Cystosoma saundersii*. J. Exp. Biol. 102:1–12.
- Marten, K., and P. Marler. 1977. Sound transmission and its significance for animal vocalizations: I. Temperate habitats. Behav. Ecol. Sociobiol. 2:271–290.
- Marten, K., D. Quine, and P. Marler. 1977. Sound transmission and its significance for animal vocalizations: II. Tropical forest habitats. Behav. Ecol. Sociobiol. 2:291–302.
- Michelson, A., and H. Nocke. 1974. Biophysical aspects of sound communication in insects. Adv. Insect Physiol. 10:274–296.
- Morton, E. S. 1970. Ecological sources of selection on avian sounds. Ph.D. diss. Yale University, New Haven, Conn.
- . 1975. Ecological sources of selection on avian sounds. Am. Nat. 109:17–34.
- Nottebohm, F. 1975. Vocal behavior in birds. Pages 287–332 in D. S. Farner and J. R. King, eds. Avian biology. Vol. 5. Academic Press, New York.
- Oster, G. F., and E. O. Wilson. 1978. Caste and ecology in social insects. Princeton University Press, Princeton, N.J.
- Raikow, R. J. 1982. Monophyly of the Passeriformes: test of a phylogenetic hypothesis. Auk 99: 431–445.
- Ridgely, R. 1976. A guide to the birds of Panama. Princeton University Press, Princeton, N.J.
- Ridley, M. 1983. The explanation of organic diversity, the comparative method and adaptations for mating. Cambridge University Press, Cambridge.
- Ryan, M. J. 1985a. Energetic efficiency of vocalization by the frog *Physalaemus pustulosus*. J. Exp. Biol. 116 (in press).
- . 1985b. The túngara frog, a study in sexual selection and communication. University of Chicago Press, Chicago.
- Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York.
- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State University Press, Ames.
- Sokal, R. R., and F. J. Rohlf. 1969. Biometry, the principles and practice of statistics in biological research. Freeman, San Francisco.
- Wallschager, D. 1980. Correlation of song frequency and body weight in passerine birds. Experientia (Basel) 36:412.
- Wiley, R. H., and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav. Ecol. Sociobiol. 3:69–94.
- . 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pages 132–181 in D. E. Kroodsma and E. H. Miller, eds. Acoustic communication in birds. Vol. 1. Production, perception, and design features of sound. Academic Press, New York.