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Body size correlates negatively with the frequency of distress calls and songs of Neotropical birds

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ABSTRACT. The allometric relationship between body size and song frequency has been established in previous studies of temperate and tropical bird communities. However, the relationship between body size and the frequency of distress calls has been examined in only one study of temperate birds. We examined size-frequency relationships in the distress calls and songs of a Neotropical bird community in northwestern Costa Rica. In 2008 and 2009, we recorded distress calls and determined the body mass of 54 mist-netted birds representing 38 species, 35 genera, and 14 families. We obtained songs for these same species from sound libraries and commercially available compact discs. For each vocalization, we measured minimum frequency and frequency of maximum amplitude. Larger birds produced lower-frequency distress calls and songs than smaller birds. Phylogenetically controlled analyses revealed that the frequency of maximum amplitude was negatively correlated with body mass for both distress calls and songs. Minimum frequency was negatively correlated with mass for distress calls, but not songs. Our analyses suggest that the influence of phylogeny on the relationship between frequency characteristics and body size is modest. Pair-wise comparisons across 37 species revealed that distress calls and songs had similar minimum frequencies, but songs had significantly lower frequencies of maximum amplitude than distress calls. This difference may arise from differences in signal function. Lower-frequency sounds should transmit farther through forest habitats and songs must often transmit longer distances to reach their intended audience than distress calls. Our results support the general theory that body size is negatively correlated with the frequency of acoustic signals by demonstrating that this pattern holds true for both distress calls and songs in a Neotropical bird community.

RESUMEN. **El tamaño de cuerpo correlaciona negativamente con la frecuencia de llamadas y cantos de angustia en aves Neotropicales**
Las relaciones alométricas entre tamaño del cuerpo y frecuencia de cantos ha sido establecido en estudios previos en comunidades de aves tropicales y de zona templada. Sin embargo, la relación entre tamaño corporal y la frecuencia de llamadas de angustia o desespero ha sido examinada en solo un estudio con aves de la zona templada. Examinamos las relaciones de tamaño, llamadas y cantos de angustia en una comunidad de aves Neotropicales de Costa Rica. En el 2008 y 2009, grabamos llamadas de angustia y determinamos la masa corporal de 54 aves capturadas con redes de niebla representando 38 especies, 35 géneros y 14 familias. Obtuvimos el canto de estas especies de bibliotecas de grabaciones y de CD comerciales disponibles. Para cada vocalización, medimos la frecuencia mínima y la frecuencia de mayor amplitud. Las aves más grandes produjeron cantos y llamadas de angustia de frecuencias mas bajas que las aves pequeñas. Un análisis de control filogenético reveló que las frecuencias de máxima amplitud estaban negativamente correlacionadas con la masa corporal, tanto para llamadas como para cantos angustiosos. Las frecuencias mínimas fueron negativamente correlacionadas con la masa corporal para llamadas de angustia, pero no así para cantos. Nuestro análisis sugiere que la influencia de la filogenia en la relación entre las características de la frecuencia de los sonidos y el tamaño corporal es modesta. Comparaciones pareadas entre 37 especies reveló que las llamadas y los cantos de angustia tienen frecuencias mínimas similares, pero que los cantos tienen frecuencias significativamente menores, pero de máxima amplitud, que las llamadas angustiosas. Estas diferencias pueden originarse de diferencias en la función de las señales. Los sonidos de baja frecuencia deben transmitirse más lejos a través del hábitat de bosque y los cantos deben transmitirse a mayor distancia para llegar a la audiencia pertinente, que las llamadas de angustia. Nuestros resultados apoyan la teoría general que el tamaño corporal está negativamente correlacionado con la frecuencia de señales acústicas, al demostrar que este patrón se sostiene tanto para llamadas como para cantos de angustia en comunidades de aves Neotropicales.

Key words: allometry, bird song, body size, call frequency, distress call, tropics

As a rule, the frequency of animal vocalizations is negatively correlated with body size. The allometric relationship between the frequency of vocalizations and body size arises because of physical and energetic constraints; animals cannot efficiently produce sound waves larger than the size of their body or their sound-producing apparatus (Bradbury and Vehrencamp 1998).

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This pattern holds across many taxa and many types of vocalizations (e.g., Bee and Perrill 1996, Jones 1999, Russ et al. 2004, May-Callado et al. 2007), including the songs and begging calls of birds (among-species comparisons: Wallschläger 1980, Ryan and Brenowitz 1985, Wiley 1991; within-species comparisons: Appleby and Redpath 1997, Laiolo and Rolando 2002, Patel et al. 2010). Both natural selection and sexual selection may lead to deviations from this relationship (e.g., Cardoso and Mota 2007, Peters et al. 2009), but ultimately the frequency components of most animal vocalizations are expected to show this pattern.

Birds produce a variety of acoustic signals, ranging from short, noisy distress calls to complex songs. Distress calls are often given by birds when captured by a predator or captured in a mist-net and handled by a human (e.g., Stefanski and Falls 1972a, Perrone 1980, Greig-Smith 1984, Jurisevic and Sanderson 1998). Distress calls show comparable structure across taxonomic groups, typically exhibiting a harmonic or noisy structure with little frequency modulation (Aubin 1991, Neudorf and Sealy 2002). Several hypotheses have been proposed to explain the function of distress calls, including startling attacking predators (Stefanski and Falls 1972a, Conover 1994, Wise et al. 1999, Neudorf and Sealy 2002), attracting secondary predators (Perrone 1980, Högstedt 1983, Koenig et al. 1991), warning conspecifics of the presence or location of a predator (Stefanski and Falls 1972a, b, Conover 1994), or eliciting help from nearby conspecifics and heterospecifics (Stefanski and Falls 1972a, b, Rohwer et al. 1976, Perrone 1980, Greig-Smith 1984). Jurisevic and Sanderson (1998) found that body size and distress-call frequency were negatively correlated in a south-temperate bird community, but this is the only study where the allometric relationship between body size and frequency of distress calls has been examined. Further research is needed to determine if this relationship is consistent across a diversity of different bird groups or habitats.

Avian distress calls and songs differ in a number of important ways. Although distress calls are thought to be similar across species, bird songs vary among species and sometimes between individuals within a species (Catchpole and Slater 2008). Whereas distress calls may function in a variety of contexts, bird songs are widely understood to function in territory defense (e.g.,

Krebs 1977), mate attraction (e.g., Ericksson and Wallin 1986), or in both contexts (e.g., Mennill et al. 2002). Finally, whereas distress calls are primarily under the influence of natural selection, bird songs are thought to be strongly influenced by sexual selection. These differences between distress calls and songs could result in different allometric relationships between body size and frequency.

We examined relationships between body size and the frequency of distress calls and songs in a Neotropical bird community. Little is known about the distress calls of tropical birds; only Neudorf and Sealy (2002) have comprehensively examined the distress calls of tropical birds. Based on the pattern observed in a south-temperate bird community (Jurisevic and Sanderson 1998), we predicted that tropical birds would exhibit a negative correlation between body size and distress-call frequency. Based on patterns observed in previous studies in Europe (Wallschläger 1980), Panama (Ryan and Brenowitz 1985), and North America (Wiley 1991), we also predicted that birds would exhibit a negative correlation between body size and song frequency. Because the frequency of bird songs varies both within and among individuals and species (Catchpole and Slater 2008) and that, within species, the allometric relationship between body size and frequency is greater for calls than songs (Patel et al. 2010), we predicted that the size-frequency relationship would be stronger for distress calls than songs.

METHODS

Study site.   We captured birds in mist nets at Ecolodge Las Bromelias, a private tropical premontane rainforest preserve located at an altitude of 725 m on the Caribbean slope of Rincon de la Vieja volcano at a site contiguous with the Guanacaste Conservation Area in the province of Guanacaste, Costa Rica (10°51.980′N, 85°19.580′W). Data were collected from 25 to 28 February 2008 and 22 to 26 February 2009.

Distress call recordings.   We operated six to eight mist nets from 06:00 to 18:00 daily, checking nets every 20 to 25 min. A recordist (JPM or RCK) accompanied the person removing birds from nets and recorded distress calls while each bird was being removed. Birds were carried in holding bags from the site of

the mist nets to a temporary weighing station, and additional recordings were collected when birds were removed from the bags. Birds were weighed with a spring scale ($\pm$0.25 g; Pesola, Baar, Switzerland) and then released. To avoid resampling the same individuals, we clipped a small portion of the tip of the right outer rectrix of each individual recorded. Mist nets were set up in different locations each year, and we assumed birds captured in different years were different individuals. All distress calls were recorded as uncompressed, 16-bit, 44-kHz WAV files using an omnidirectional microphone (ME62/K6; Sennheiser, Wedemark, Germany) and a solid-state digital recorder (PMD660; Marantz, Kanagawa, Japan); the same microphone and recording unit was used in both years.

We included in our analyses only distress calls given by birds in mist nets, being removed from nets, or in the hand. Vocalizations that did not resemble typical distress calls (i.e., harsh, noisy, and harmonic) were excluded; specifically, a Passerini's Tanager (*Ramphocelus passerinii*) and a Variable Seedeater (*Sporophila americana*) produced only a few short *peeps* that were not considered distress calls. Recordings with poor signal-to-noise ratios were also excluded. In a few cases where more than one type of distress call was recorded for a species, we analyzed the most frequently recorded call type. We combined data from males and females because we did not expect distress-call structure to vary with sex (Koenig et al. 1991).

Song recordings. For species where we recorded distress calls (Appendix 1), we also located a recording of their song. Most recordings came from a compact disc available from the Cornell Lab of Ornithology (Voices of Costa Rican Birds; Ross and Whitney 1995; $N = 20$ species) and the Xeno-Canto Bird Sounds of the Americas online sound library (www.xeno-canto.org; $N = 13$ species). We obtained recordings of four North American migratory species from a commercially available compact disc (Stokes Field Guide to Bird Songs; Stokes et al. 1997). For one species (Bronze-tailed Plumeleteer, *Chalybura urochrysia*), we could not locate a good quality recording, so sample sizes for distress calls ($N = 38$ species) and songs ($N = 37$ species) differed. For all species, we selected recordings that best represented songs typically encountered in the field, based on 9 yr of

experience working in this region by SMD and DJM.

Sound analysis. To standardize the amplitude of recordings prior to measurement, recordings of distress calls and songs were normalized to -1 dB (relative to maximum) using Audition software (Adobe, San Jose, CA). For each call and song, we measured the two frequency characteristics most likely to be constrained by body size: minimum frequency and frequency of maximum amplitude. We measured sounds with the automatic-parameter measurements tool of AviSoft SASLab Pro (R. Specht, Berlin, Germany). We established settings that would calculate one measurement for each distinct call or song (settings: hold time $= 250$ ms; threshold relative to maximum amplitude $= -15$ dB; we chose this threshold because it encompassed most of the sound energy above background noise levels). The automated measurement tool allowed us to calculate frequency measurements without human bias. When more than one distress call or song was recorded for a single bird, both features were measured for each exemplar and an average was calculated (6.6 $\pm$ 3.7 [SE] distress calls per individual; 7.9 $\pm$ 0.4 songs per species). When we had distress calls from multiple individuals of a given species, we calculated an average value for that species based on the average values of each individual (1.4 $\pm$ 0.2 individuals per species). Repeatability (r) of call frequency measurements within a species was high for both variables ($r = 0.89$–0.95; Lessels and Boag 1987), suggesting that even a single individual can provide a good approximation of the characteristics of calls for a species. For recordings of songs obtained from sound libraries and commercial compact discs, we could not determine if songs were recorded from single or multiple individuals; we assumed that songs we measured were typical for each species.

Phylogenetic comparisons. Because closely related species tend to exhibit more similar patterns than expected by chance (Garland and Ives 2000, Freckleton et al. 2002), we used phylogenetic generalized least squares analyses (PGLS, Grafen 1989), implemented in R 2.10.1 (Ihaka and Gentleman 1996) using the "ape" (analysis of phylogenetics and evolution) and "nlme" (nonlinear mixed effects) packages (Paradis et al. 2004). We constructed a hypothesis of phylogeny based on Sibley and

Ahlquist (1990) for basal nodes, supplemented with recently published phylogenies to characterize species relationships within nodes (Burns 1997, Cicero and Johnson 2002, Mann et al. 2006, Klicka et al. 2007, McGuire et al. 2007, Voelker and Klicka 2008, Ohlson et al. 2008, McGuire et al. 2009). Relationships were coded as polytomies when more specific phylogenetic information was unavailable. We used body mass as our measure of body size (Jurisevic and Sanderson 1998, Patel et al. 2010), determining body mass for each species by calculating the mean mass of individuals measured in the field. We log-transformed body mass for our PGLS analyses. In each PGLS analysis, we entered body mass as the independent variable and frequency characteristics as the dependent variable. The maximum-likelihood lambda values produced by PGLS analyses indicate the degree of phylogenetic dependence of the data according to a Brownian motion model. Low values (near 0) indicate that traits are evolving independently of phylogeny whereas high values (near 1) indicate trait evolution is highly dependent on phylogeny (Pagel 1999). We present statistical results of PGLS analysis, although we show raw data with a line-of-best-fit to provide a visual representation of the patterns.

Statistical analysis. Nonphylogenetic statistical analyses were performed using JMP 8.0 (SAS Institute, Cary, NC). Values are reported as means ± SE.

RESULTS

We captured 121 individuals (53 in 2008 and 68 in 2009) and recorded good-quality distress calls from 54 individuals representing 38 species, 35 genera, and 14 families (Appendix 1). All distress calls recorded were from adult birds. Distress calls of most species were loud, usually given repeatedly, and their structure was harmonic or noisy or a combination of the two (Fig. 1).

Larger species produced lower-frequency distress calls and songs than smaller species (Fig. 2). Phylogenetically controlled analyses revealed significant negative relationships between body mass and the minimum frequency of distress calls (PGLS; $\lambda = 0.17$, $t = -2.2$, $P = 0.03$, $N = 38$), frequency of maximum amplitude of distress calls ($\lambda = 0.11$, $t = -2.2$, $P = 0.04$, $N = 38$), and frequency

of maximum amplitude of songs ($\lambda = 0.21$, $t = -2.3$, $P = 0.03$, $N = 37$). The relationship between body mass and the minimum frequency of songs was also negative, but not significant ($\lambda = 0.27$, $t = -1.4$, $P = 0.16$, $N = 37$).

Pair-wise comparisons across 37 species revealed no difference between the minimum frequency of distress calls ($\bar{x} = 3247 \pm 272$ Hz) and songs ($\bar{x} = 2934 \pm 264$ Hz; paired t-test: $t_{36} = 0.9$, $P = 0.36$). Songs, however, had lower frequencies of maximum amplitude ($\bar{x} = 4613 \pm 307$ Hz) than distress calls ($\bar{x} = 5230 \pm 327$ Hz; paired t-test: $t_{36} = 2.0$, $P = 0.05$).

DISCUSSION

Analysis of the distress calls and songs of 38 species of birds in a Costa Rican premontane rainforest community revealed negative correlations between body size and vocal frequency. Specifically, the minimum frequency and frequency of maximum amplitude of distress calls were negatively related to body mass, and the frequency of maximum amplitude of songs was negatively related to body mass. Generally, body size sets a lower limit on the frequency of an acoustic signal, with smaller animals producing lower frequency sounds less efficiently than larger ones (Bradbury and Vehrencamp 1998). The size of the vocal apparatus constrains minimum frequency, and the common practice of using body size as a proxy for the size of the vocal apparatus introduces additional variability. Nevertheless, we found that larger birds produced lower-frequency distress calls and songs than smaller birds. Our results are consistent with those of previous studies where the size-frequency allometry of a variety of avian vocalizations has been examined (among-species comparisons: Wallschläger 1980, Ryan and Brenowitz 1985, Wiley 1991; within-species comparisons: Appleby and Redpath 1997, Laiolo and Rolando 2002, Patel et al. 2010).

Body size is one of several factors that can influence acoustic signal structure. Avian vocalizations have been shaped by multiple selective pressures that may drive frequency characteristics in different directions. For example, the structure of avian vocalizations is influenced by morphological features such as bill and gape size (Podos 2001, Podos et al. 2004). Habitat
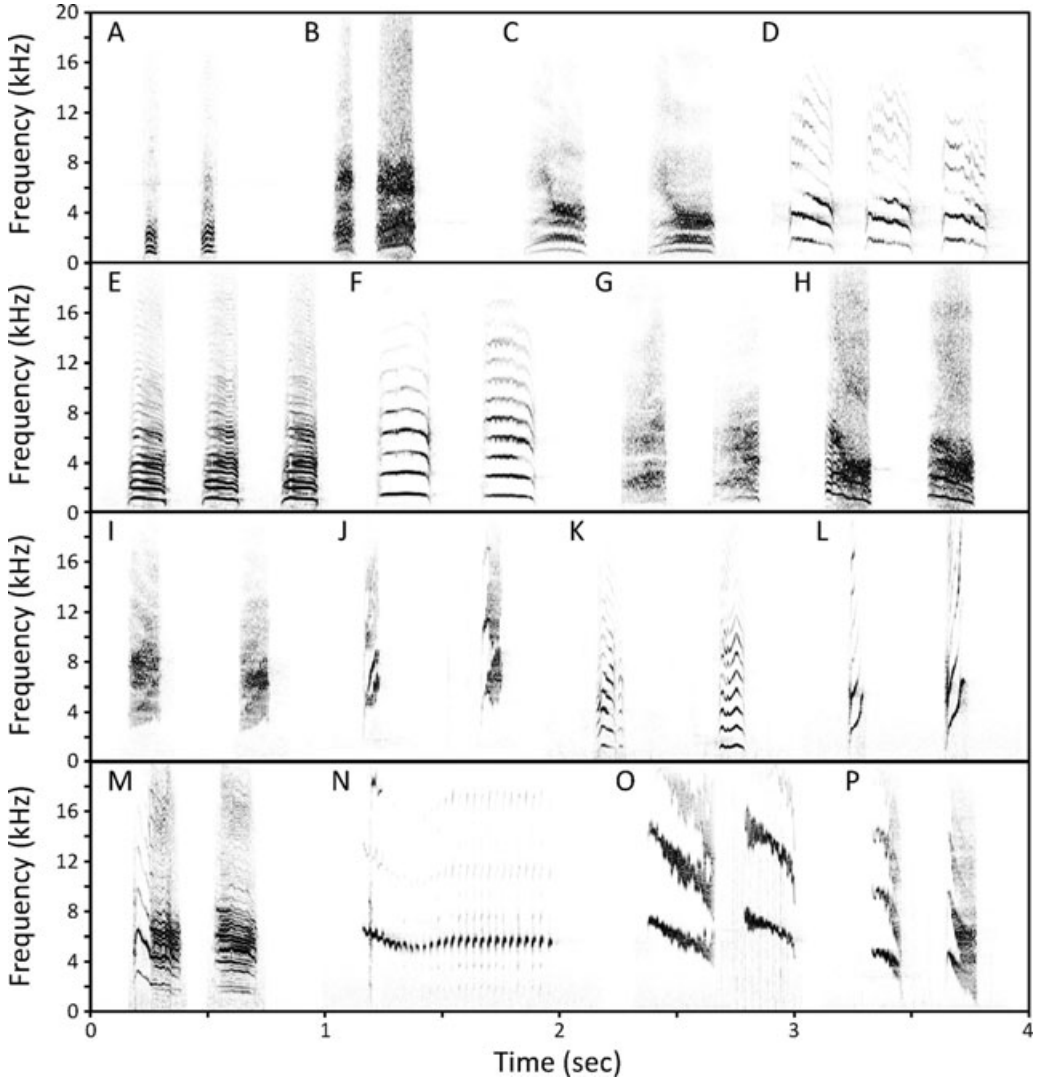
Fig. 1.   Sound spectrograms of the distress calls of 16 of the 38 species recorded in Costa Rica. Birds are arranged from largest to smallest on the basis of our measurements of body mass. (A) Clay-colored Robin, (B) White-throated Robin, (C) Black-striped Sparrow, (D) Scaly-throated Leaftosser, (E) Swainson's Thrush, (F) Olive Tanager, (G) Bay Wren, (H) Black-throated Wren, (I) Common Bush-tanager, (J) Tawny-capped Euphonia, (K) Ochre-bellied Flycatcher, (L) Slaty Antwren, (M) Lesser Greenlet, (N) Golden-crowned Spadebill, (O) Band-tailed Barbthroat, and (P) Green Hermit (see Appendix 1 for scientific names).

features can also shape the structure of distress calls (e.g., Mathevon et al. 1997) and songs (e.g., Ryan and Brenowitz 1985, Wiley 1991) by selecting for signals that minimize distortion and maximize transmission of information through the environment. In general, species in closed habitats produce vocalizations with lower emphasized frequencies than species in more open habitats (Slabbekoorn 2004). In addition, differ-

ences in territory sizes, ambient noise levels, and the acoustic properties of temperate and tropical forests may generate stronger selection pressures for songs with lower emphasized frequencies in the tropics (Barker 2008). All species in our study were captured in the same habitat so each should experience similar habitat-induced limitations to communication. Further study of the effects of different canopy strata and the
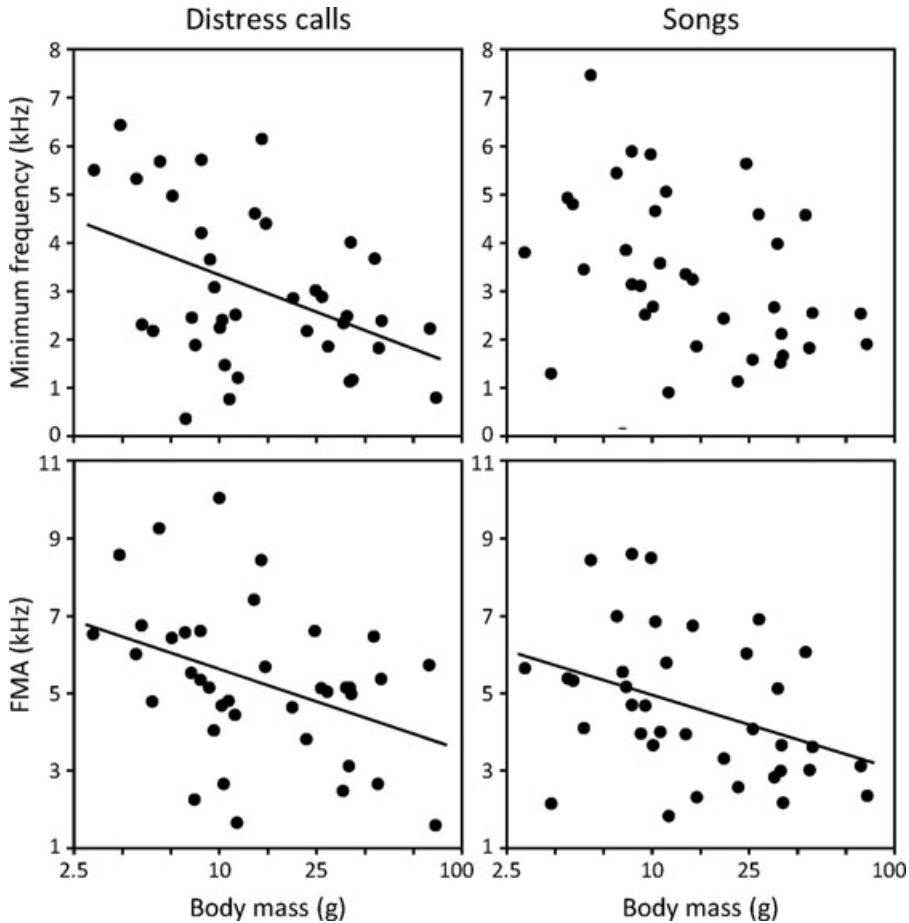
Fig. 2.   Body size shows a negative relationship with the frequency components of distress calls for 38 species of birds (left) and songs for 37 species of tropical birds (right) captured in premontane tropical forest in Costa Rica, including minimum frequency (top) and frequency of maximum amplitude (bottom). Values on the *x*-axis are presented on a log scale.

influence of microhabitat on sound transmission may help explain variation in the extent to which birds adhere to the body size/frequency relationship.

We found that the minimum frequency characteristics of distress calls and songs did not differ significantly across species. The frequency of maximum amplitude, however, was significantly lower for songs than for distress calls. This may be related to the transmission features of each type of vocalization. Songs must often transmit long distances through forests to reach their intended audience, that is, adjacent territorial conspecifics or distant potential mates. In contrast, distress calls may have a more immediate audience, to communicate with an

attacking predator or nearby conspecifics and heterospecifics. Because lower frequencies experience less attenuation than higher frequencies in forests (Wiley and Richards 1982), songs with lower frequencies may be advantageous for effective communication across greater distances, contributing to the lower frequencies of maximum amplitude of songs compared to distress calls.

The function of acoustic signals may also help shape their structure. Unlike distress calls, songs are strongly influenced by sexual selection. Sexual selection may drive changes in song frequency in directions that may affect the relationship between body size and frequency (Catchpole and Slater 2008). For example,

selective pressures to produce low-frequency sounds has favored the evolution of unusually large vocal apparatuses as a means of overcoming body size constraints, for example, the elongated tracheas of Trumpet Manucodes (*Manucodia keraudrennii*), Whooping Cranes (*Grus americana*), and Great Curassows (*Crax rubra*; Bradbury and Vehrencamp 1998, Fitch 1999). In other species, such as Serins (*Serinus serinus*), sexual selection has favored higher-frequency vocalizations (Cardoso and Mota 2007, Cardoso et al. 2007), demonstrating that sexual selection can act to either increase or decrease vocal frequency.

We found that, with one exception, relationships between body size and frequency characteristics were similar for distress calls and songs; the exception was that the minimum frequency of songs was not statistically related to body size. Together with our observation that songs had lower frequencies of maximum amplitude than distress calls, these results suggest that song may not be as strongly constrained by body size as distress calls, but this pattern requires further study, possibly involving song and distress calls recorded from the same individuals.

Although the influence of phylogeny was rather low for size-frequency relationships for both distress calls and songs, lambda values in our study were higher for songs than distress calls. Such a comparison should be made cautiously because a number of different selective factors could affect the magnitude of the phylogenetic influence on these size-frequency relationships. Nevertheless, this observation suggests that the relationship between body size and distress-call frequency is more labile than the relationship between body size and song frequency (Pagel 1999). Such a pattern could be a result of greater phylogenetic constraints on the evolution of song. Alternatively, songs may be more similar among closely related species because species experience similar intra- and intersexual pressures and their songs must propagate effectively through similar habitats.

Several studies have demonstrated that body size has a significant effect on song frequency in birds (Wallschläger 1980, Ryan and Brenowitz 1985), even after controlling for phylogenetic relationships (Wiley 1991). However, only Jurisevic and Sanderson (1998) have examined the relationship between body size and distress-call structure in birds and, although they exam-ined the influence of phylogeny on the slope of the relationship, they did not control for phylogenetic relatedness. In a review of the relationship between body size and tonal signal frequency in cetaceans, May-Callado et al. (2007) found that phylogenetically controlled analyses had reduced explanatory powers compared to uncontrolled analyses. Our study is the first to analyze the allometry of body size and distress-call frequency with phylogenetically controlled analyses, and our results demonstrate that this pattern holds true when controlling for the effects of phylogeny.

In conclusion, our results demonstrate that the frequency characteristics of both the distress calls and songs of tropical birds are negatively correlated with body size. Further research will serve to clarify the relative importance of body size and other selective pressures in shaping the structure of distress calls and songs in temperate versus tropical habitats.

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APPENDIX 1

List of 38 species captured during our study in a premontane tropical forest in Costa Rica

Species	Family	N (captured)	N (called)	N (analyzed)	Body mass (g)
Order Apodiformes					
Band-tailed Barbthroat, *Threnetes ruckeri*	Trochilidae	1	1	1	6.8
Green Hermit, *Phaethornis guy*	Trochilidae	2	2	2	6.4
Violet-crowned Woodnymph, *Thalurania colombica*	Trochilidae	1	1	1	5.5
Blue-throated Goldentail, *Hylocharis eliciae*	Trochilidae	1	1	1	3.8
Rufous-tailed Hummingbird, *Amazilia tzacatl*	Trochilidae	3	2	1	5.8
Bronze-tailed Plumeleteer, *Chalybura urochrysia*	Trochilidae	9	6	3	7.6
Ruby-throated Hummingbird, *Archilochus colubris*	Trochilidae	1	1	1	4.8
Order Passeriformes					
Scaly-throated Leaftosser, *Sclerurus guatemalensis*	Furnariidae	1	1	1	36.8
Plain Antvireo, *Dysithamnus mentalis*	Thamnophilidae	1	1	1	13.5
Slaty Antwren, *Myrmotherula schisticolor*	Thamnophilidae	1	1	1	10.5
Ochre-bellied Flycatcher, *Mionectes oleagineus*	Tyrannidae	2	1	1	12.5
Golden-crowned Spadebill, *Platyrinchus coronatus*	Tyrannidae	2	1	1	8.5
Sulphur-rumped Flycatcher, *Myiobius sulphureipygius*	Tyrannidae	3	1	1	13.3
Tawny-chested Flycatcher, *Aphanotriccus capitalis*	Tyrannidae	2	1	1	11.8
Tropical Kingbird, *Tyrannus melancholicus*	Tyrannidae	1	1	1	45.5
Thrushlike Schiffornis, *Schiffornis turdina*	Tyrannidae	1	1	1	34.5
White-collared Manakin, *Manacus candei*	Pipridae	2	1	1	22.0
White-ruffed Manakin, *Corapipo altera*	Pipridae	8	1	1	12.0
Lesser Greenlet, *Hylophilus decurtatus*	Vireonidae	1	1	1	9.8
Black-throated Wren, *Thryothorus atrogularis*	Troglodytidae	1	1	1	25.0
Bay Wren, *Thryothorus nigricapillus*	Troglodytidae	1	1	1	28.5
Stripe-breasted Wren, *Thryothorus thoracicus*	Troglodytidae	2	1	1	17.3
Swainson's Thrush, *Catharus ustulatus*	Turdidae	3	1	1	36.5
Wood Thrush, *Hylocichla mustelina*	Turdidae	2	2	1	47.0
Clay-colored Robin, *Turdus grayi*	Turdidae	3	3	3	78.7
White-throated Robin, *Turdus assimilis*	Turdidae	1	1	1	74.5
Chestnut-sided Warbler, *Dendroica pensylvanica*	Parulidae	1	1	1	9.0
Slate-throated Redstart, *Myioborus miniatus*	Parulidae	1	1	1	9.3
Bananaquit, *Coereba flaveola*	Parulidae	7	1	1	11.5
Common Bush-Tanager, *Chlorospingus ophthalmicus*	Thraupidae	5	2	1	16.8
Olive Tanager, *Chlorothraupis carmioli*	Thraupidae	16	8	8	35.5
Passerini's Tanager, *Ramphocelus passerinii*	Thraupidae	3	3	2	27.0
Blue-gray Tanager, *Thraupis episcopus*	Thraupidae	1	1	1	30.0
Variable Seedeater, *Sporophila americana*	Emberizidae	11	5	2	11.0
Orange-billed Sparrow, *Arremon aurantiirostris*	Emberizidae	1	1	1	9.8
Black-striped Sparrow, *Arremonops conirostris*	Emberizidae	3	3	3	37.2
Buff-throated Saltator, *Saltator maximus*	Cardinalidae	2	1	1	48.5
Tawny-capped Euphonia, *Euphonia anneae*	Fringillidae	4	1	1	15.8

N = number of individuals; body mass values represent mean body mass of individuals from which recordings were obtained.