ORNITOLOGIA NEOTROPICAL 23: 349–365, 2012

SONG ANALYSIS OF THE SOUTH AMERICAN THRUSHES (*TURDUS)* IN RELATION TO THEIR BODY MASS IN A PHYLOGENETIC CONTEXT

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Resumen. – Análisis del canto de los zorzales sudamericanos del género *Turdus* en relación con su masa corporal, en un contexto filogenético. – El canto de las aves es uno de los ejemplos de diversificación del comportamiento animal más estudiado, tanto por su rol en la comunicación como por su papel en el aislamiento reproductivo precopulatorio. Existe una conocida y aceptada relación negativa entre el tamaño corporal del ave y la frecuencia de las vocalizaciones, que ha sido identificada como una de las restricciones morfológicas actuando en la evolución del canto. En este trabajo evaluamos la influencia de la masa corporal en el canto de los zorzales sudamericanos del género *Turdus*, reconocidos por sus complejas y variables vocalizaciones. Se compararon cantos de 137 individuos de 25 especies y se midieron cuatro características temporales y cinco de frecuencia en cada espectrograma. El efecto de la masa corporal sobre las variables fue analizado mediante comparaciones de pares filogenéticamente independientes, basadas en la hipótesis filogenética de Voelker *et al.* (2007). Nuestros resultados evidenciaron una relación negativa entre la frecuencia enfatizada y la masa corporal, también descrita en otros grupos de aves, que estaría relacionada con factores anatómicos y fisiológicos de la siringe y del tracto vocal anterior al órgano fonador. Como es posible que otras fuerzas selectivas estén influyendo sobre la estructura del canto, discutimos algunas de ellas y el impacto de las mismas sobre nuestros resultados.

Abstract. – Bird song is one of the most studied examples of animal behavior diversification because of its role in communication and its function in premating reproductive isolation. There is a well-known negative relationship between bird body size and song frequency that has been identified as a vocal constraint playing a role in song evolution. Here we assessed the influence of bird body mass in the frequency and temporal features of the song of the South American *Turdus* thrushes, recognized by their complex and variable vocalizations. Songs from 137 individuals from 25 species were compared, and four temporal and five frequency features were measured on each spectrogram. The effect of body mass on these variables was analyzed through phylogenetically independent pairwise comparisons, based on the phylogenetic hypothesis of Voelker *et al.* (2007). Our results showed a clear negative relationship between song emphasized frequency and body mass, also reported in other groups of birds, that could be related to both anatomical and physiological features of the syrinx and the vocal tract anterior to the vocal organ. As other selective forces could be shaping the song structure, we discuss some of them and their implications for our results. *Accepted 16 August 2012.*

Key words: Thrushes, *Turdus,* body mass, comparative analysis, song structure.

INTRODUCTION

The acoustic sensory channel is essential for long distance communication in birds because, despite the great energetic cost involved in song production, sound travels in all directions and can penetrate through or round objects (Catchpole & Slater 1995). As other biological features, bird song has been evolving under the influence of a great diversity of selective forces that may or not act in opposition (Ryan & Brenowitz 1985). One of the most studied factors, assumed to play a role in the evolution of avian acoustic signals, is the variation in vocal performance due to physical constraints imposed by morphology.

Since the work of Wallschläger (1980), a well-accepted negative relationship between body mass and song frequencies has been shown for different kinds of vocalizations and across many avian groups. This association stands for comparisons made among songs and calls of both songbird species (Ryan & Brenowitz 1985, Wiley 1991, Badyaev & Leaf 1997, Laiolo & Rolando 2003, Martin *et al.* 2011) and species that lack vocal learning (Tubaro & Mahler 1998, Bertelli & Tubaro 2002, Seddon 2005). However, when comparisons were made between closely related species or restricted to intraspecific variation, larger body sizes were not always related to lower frequencies. So far, previous studies that analyzed this relationship within species have yielded mixed results (Shy 1983, Handford & Lougheed 1991, Irwin *et al.* 2008), and the strength of the association appears to vary depending on whether both sexes are pooled or not before the analysis, because this could increase or reduce, respectively, the range of variation in body size (Logue *et al.* 2007, Patel *et al.* 2010).

Larger birds with larger vocal organs should be able to generate lower frequency sounds more easily than smaller ones (Bradbury & Vehrencamp 1988). However, the anatomical or physiological causes of the relationship between body size and frequency are not clearly understood. It has been traditionally explained in terms of the mass of the vibrating structure that produces the sound, because heavier syringeal medial tympaniform membranes should vibrate at lower frequencies producing lower-pitched vocalizations (Ryan & Brenowitz 1985, Podos & Nowicki 2004). However, experimental studies have suggested that these membranes play a minor role in vocalizations since their removal or destruction produces only small changes to the song. In fact, direct endoscopic observations showed that the principal sound generating mechanism in songbirds involves vibration of two small masses of connective tissue, the medial and lateral labia (Larsen & Goller 1999, Larsen *et al.* 2006). Additionally, Handford & Lougheed (1991) reported that in the Rufous-collared Sparrow (*Zonotrichia capensis*) body size and syrinx size appear not to be related, despite the fact that they found a negative relationship between body size and song frequency (although not a linear one).

Unlike the association between frequency and body size, literature on the effect of body mass on the temporal features of bird vocalizations is sparse. Wiley (1991) reported no association between body mass and temporal structure of the song of 120 oscine species from the east of North America. On the other hand, Badyaev & Leaf (1997) showed that in the *Phylloscopus* and *Hippolais* warblers, heavier species have songs with more notes, which are also longer and separated by shorter internote intervals. Conversely, Podos (2001) found that species of Darwin's finches with larger beaks and body sizes have evolved songs with comparatively low rates of syllable repetition, and suggested that those differences in beak morphology and body mass could be explained as a diversification driven by strong selective pressure related to diet.

The *Turdus* thrushes (Passeriformes, Turdidae) constitute one of the most speciose (77 extant species; Clements *et al.* 2011) songbird genera, which has a widespread and cosmopolitan distribution with a high number of species occurring in the New World (36 spp.) and particularly in South America (25 spp., Voelker *et al.* 2007). This genus is recognized by the complex vocalizations which vary greatly between species, making the group an ideal target to the study of acoustic signals (Ince & Slater 1985, Clement 2000). In this paper, we present an analysis of the influence of body mass on the song of the South American *Turdus* thrushes taking into account the phylogenetic relationships among the species of the clade. Additional selective pressures may also have an impact on thrushes' songs, as expected for a complex behavioral character (Gil & Gahr 2002, Barker 2008), so we discuss some of them and their implications for our results.

METHODS

Recordings used in this study were obtained from Xeno-canto (www.xeno-canto.org) and three different compilations (Hardy & Parker 1992, López-Lanús 2008, Minns *et al.* 2010). The dataset included songs of 137 males (Appendix 1) from 25 *Turdus* species (Table 1), that belong to the "Largely South American Clade" from the phylogeny of Voelker *et al.* (2007), which is the one we follow in this paper (see below). Two species were not included the analysis, Tristan Thrush (*Nesosichla eremita*) and Lawrence's Thrush (*T. lawrenceii*). Recordings from the former were not available in any of the libraries used during this study. In the case of the Lawrence's Thrush, we decided not to include it in the database because it is considered one of the best mimic songbirds in the world, commonly including imitations of other bird species in its song (Clement 2000). This species constitutes an exceptional case in comparison to the rest of the thrushes, in which the analysis of song characteristics in relation to body mass might be misleading. Also, songs of the Eastern Slaty Thrush (*T. subalaris*), considered a subspecies of the Slaty Thrush (*T. nigriceps*) by some authors (Collar 2005, Clements *et al.* 2011), were not analyzed because this species was not sampled in the work of Voelker *et al.* (2007), and its phylogenetic relationship with the other South American species is unknown.

Songs from Hardy & Parker (1992) were digitalized at a sampling rate of 44,100 Hz with RavenPro 1.3 (Charif *et al.* 2007). Spectrograms of all songs were made with this same software and the conditions for the analyses were a "Hamming" window type, a frame size of 512 samples, and a bandwidth of 112 Hz. For the color scheme we chose the "grayscale" option, and brightness and contrast values were maintained at 50% in all cases to standardize the measurements. Only one song per individual was analyzed and it was selected favoring the best signal-to-noise ratio observed in each recording cut. On each spectrogram the following variables were measured (Fig. 1): song maximum and minimum frequencies (SMAX and SMIN), song bandwidth (SBAND = SMAX – SMIN), song emphasized frequency (SEMF: frequency with the higher amplitude in the song), mean note bandwidth (NBAND: average of the bandwidth of all notes), song length (SL), mean note length (NL: average of the length of all notes), mean internote interval (InI: average of the silence durations between the end of a note and the beginning of the next one), and number of notes (NN). SEMF was measured automatically, and all the other measurements were performed manually (selection-based measurements). All these measurements were performed before knowing the body mass of the species under study to avoid any potential bias. We defined a note as any continuous trace in the temporal axis of the spectrogram, and when harmonics were present we measured the frequency band with the highest energy. Body mass data, as a measure of body size, were obtained from Dunning (2008) and they correspond to the average body mass for each species.

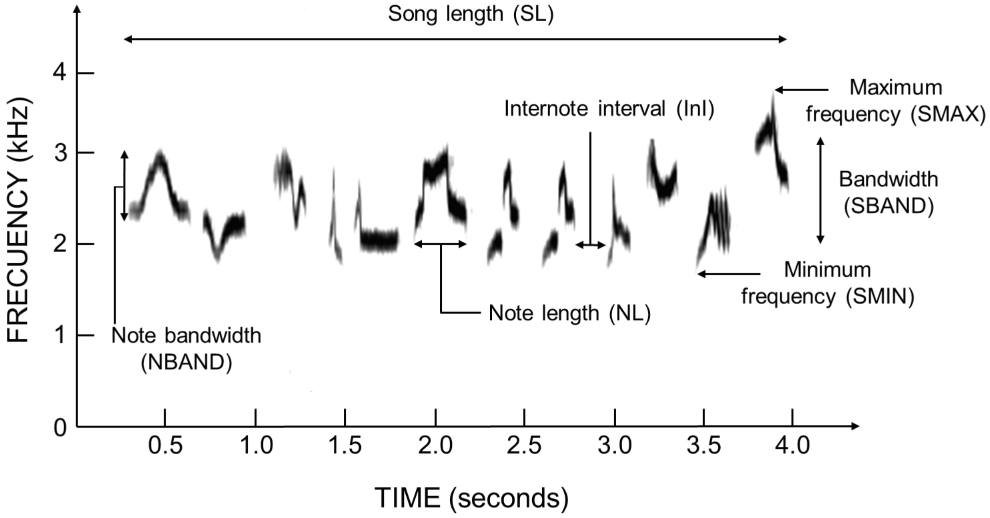

FIG. 1. Spectrogram from a portion of a song of the Rufous-bellied Thrush (*Turdus rufiventris*), showing the variables measured in this study (recorded by C. Hartshome in Buenos Aires, Argentina, on 18 November 1972.) Not shown in the figure but also measured were the number of notes (NN; 12 in this case) and the song emphasized frequency (SEMF).

Species are part of a hierarchically structured phylogeny and thus cannot be regarded for statistical purposes as if drawn independently from the same distribution. The non-independence problem can be sorted if adequate information on the phylogeny is available (Felsenstein 1985). However, methods that take into account the phylogenetic relationships among the species usually assume that branch lengths of the phylogenetic tree are known, that character evolution proceeds according to a specified stochastic model, or that ancestral states have been accurately reconstructed (Maddison 2000, but see Garland *et al.* 1992 for a detailed explanation of the assumptions and restrictions of phylogenetically independent contrasts). Because such assumptions may lead to incorrect results if they are not met, we decided to use the Maddison's (2000) method of pairwise comparisons (contrasts), as implemented in the pairwise module in Mesquite ver. 2.75 (Maddison & Maddison 2011). This analysis finds the maximum number of non-overlapping comparisons (phylogenetically independent) of terminal taxa, and uses a non-parametric sign test to find out whether changes in one character are associated with changes in the other character. We based our analysis on the "Largely South American" clade from the maximum likelihood phylogeny of Voelker *et al.* (2007) estimated from the combined analysis of three mitochondrial genes (ND2, ND3, and cytochrome b). Three species distributed mainly in Central America, Clay-colored Thrush (*T. grayi*), White-throated Thrush (*T. assimilis*), and Pale-vented Thrush (*T. obsoletus*), and the African Thrush (*T. pelios*) are included in this clade. Nevertheless, we decided to include those species in our analysis because the clade is well supported, as are most nodes within it. The clade also contains two species formerly considered to belong to another genus (*Platycichla*), which are now recognized as *Turdus* species, Pale-eyed Thrush (*T. leucops*) and Yellow-legged

Thrush (*T. flavipes*). Taxa mentioned above to be excluded from this study were pruned out of the tree, and the original variables for the remaining species (Table 1) were $\log_{10}$ transformed before the analyses because of the expected allometric relationship between song variables and body mass. This logarithmic transformation linearizes the mentioned relationship and also tends to equate the variances of song variables for different values of body mass (Harvey & Pagel 1991).

To provide a visual representation of the association found between body mass and emphasized frequency, we show the negative relationship between these variables through raw data with a trend line, and also using a standard linear regression adjusted to pass through zero among the phylogenetic independent contrasts of body mass and SEMF. In the second case, ancestral states for both traits were reconstructed following the procedure detailed in Felsenstein (1985), and all branch lengths were set to one since simulations have shown that, when true branch lengths are not known, arbitrary equal branch lengths have smaller Type I error than lengths generated through topological algorithms (Ackerly 2000). The analysis was done using the PDAP module ver. 1.15 (Midford *et al.* 2010) implemented in Mesquite ver. 2.75 (Maddison & Maddison 2011). As mentioned above, methodologies that rely in ancestral reconstructions can be error prone and depend on many assumptions. Consequently, we used this approach only to visually represent the relationship found through the pairwise comparisons, in which we accepted the structure of the phylogenetic hypothesis only at the lowest level because the comparisons are made among terminal taxa (Harvey & Pagel 1991).

To assess the variation within and among species we calculated the coefficient of variation (standard deviation divided by the mean) for all the song features measured. The intraspecific coefficient of variation (CV) was obtained using the mean and standard deviation (SD) values calculated for each song variable within each species. The interspecific CV was calculated using the mean and SD values of each song feature estimated through the species means of each variable. Differences among the intra- and interspecific CVs were evaluated through a Mann-Whitney *U*-test for each variable. We also compared the variation in frequency and temporal traits by computing a mean CV for all the frequency and temporal parameters together as two separate groups. For the within-species level of analysis, a mean CV for each species was obtained as an average of all frequency or temporal features CVs. Among-species mean CV for the two categories of parameters was calculated using the interspecific CVs obtained as previously explained. A nonparametric Friedman's ANOVA test was used to compare the variation of the features at both levels of analyses. All statistical tests were done using STATISTICA ver. 8.0 (StatSoft 2007).

RESULTS

Descriptive statistics for the variables analyzed are summarized in Table 1. We found variability within and among species in all the song features measured, with a tendency to higher variation at the interspecific level (Fig. 2). However, none of the comparisons made for each trait showed significant difference between the intra- and the interspecific degree of variation (Mann-Whitney *U*-test, all P values > 0.1). Temporal features of songs were more variable than frequency traits at both levels of analyses (Table 2). Within each group of parameters, NL was the less variable temporal feature and SBAND presented higher variation than the other frequency attributes of the song (Fig. 2).

Considering this variability, we reanalyzed the data using the species medians of the

TABLE 1. Descriptive statistics of the variables measured on the 137 individuals from 25 species of thrushes used in the comparative analysis of the relationship between body mass and song structure. Values are given as means ± standard deviation (SD). BM = body mass; for other acronyms, see Methods.

Species	N	SBAND (kHz)	SMAX (kHz)	SMIN (kHz)	SEMF (kHz)	NBAND (kHz)	SL (s)	NL (s)	InI (ms)	NN	BM (g)
Turdus albicollis	10	1.49 ± 0.22	2.78 ± 0.14	1.28 ± 0.13	2.06 ± 0.14	0.81 ± 0.11	10.90 ± 5.31	446 ± 77	333 ± 53	14.3 ± 5.9	54.0
T. amaurochalinus	10	2.25 ± 0.66	3.86 ± 0.64	1.59 ± 0.13	2.68 ± 0.25	1.39 ± 0.14	5.95 ± 4.10	232 ± 40	417 ± 84	9.9 ± 6.4	57.9
T. assimilis	5	2.16 ± 0.18	3.63 ± 0.25	1.47 ± 0.23	2.47 ± 0.11	1.23 ± 0.23	9.65 ± 9.56	268 ± 61	308 ± 135	19.3 ± 19.2	70.2
T. chiguanco	9	2.90 ± 1.66	4.68 ± 1.55	1.77 ± 0.22	2.91 ± 0.45	1.32 ± 0.70	1.76 ± 3.32	206 ± 46	131 ± 51	5.8 ± 1.4	93.3
T. falcklandii	10	2.68 ± 0.55	4.47 ± 0.49	1.79 ± 0.30	2.87 ± 0.35	1.52 ± 0.23	8.54 ± 10.81	239 ± 52	395 ± 119	12.6 ± 11.1	93.9
T. flavipes	8	7.15 ± 1.70	8.77 ± 1.58	1.62 ± 0.26	3.72 ± 1.52	2.85 ± 1.03	3.34 ± 1.75	158 ± 38	174 ± 115	11.1 ± 4.3	64.0
T. fulviventris	1	3.86	5.13	1.27	3.27	1.46	19.61	235	645	23.0	70.0
T. fumigatus	7	1.79 ± 0.35	3.19 ± 0.26	1.40 ± 0.23	2.21 ± 0.29	0.67 ± 0.14	9.61 ± 5.40	237 ± 56	210 ± 58	24.1 ± 16.6	72.0
T. fuscater	7	5.36 ± 1.56	6.77 ± 1.53	1.41 ± 0.26	2.78 ± 0.37	2.06 ± 0.59	2.78 ± 1.52	202 ± 29	159 ± 29	8.2 ± 4.2	143.0
T. grayi	7	2.12 ± 0.55	3.40 ± 0.35	1.28 ± 0.24	2.18 ± 0.17	0.99 ± 0.26	9.86 ± 3.96	284 ± 33	282 ± 82	18.9 ± 9.4	79.5
T. haplochrous	1	1.18	2.22	1.04	1.72	0.56	5.23	276	219	11.0	84.0
T. hauxwelli	10	1.79 ± 0.32	3.25 ± 0.40	1.45 ± 0.17	2.22 ± 0.16	0.76 ± 0.14	16.07 ± 15.30	269 ± 65	330 ± 76	27.2 ± 24.9	69.0
T. ignobilis	1	5.52	6.92	1.40	3.45	2.49	5.34	226	285	11.0	61.0
T. leucomelas	10	1.93 ± 0.47	3.31 ± 0.46	1.39 ± 0.17	2.46 ± 0.28	1.09 ± 0.21	3.42 ± 1.40	262 ± 30	202 ± 53	7.7 ± 2.3	69.1
T. leucops	5	5.71 ± 1.41	7.99 ± 1.33	2.28 ± 0.49	5.28 ± 2.13	2.60 ± 0.88	1.13 ± 2.32	188 ± 39	77 ± 8	4.6 ± 0.4	62.4
T. maculirostris	2	1.86 ± 0.27	3.13 ± 0.46	1.27 ± 0.19	2.28 ± 0.43	0.94 ± 0.07	9.70 ± 6.91	291 ± 31	183 ± 5	20.5 ± 13.4	69.6
T. maranonicus	1	2.34	3.75	1.41	2.53	1.27	58.60	262	476	80.0	70.0
T. nigriceps	5	5.73 ± 2.47	7.74 ± 2.17	2.01 ± 0.69	4.18 ± 1.83	2.43 ± 0.72	4.92 ± 3.50	214 ± 28	238 ± 63	11.8 ± 8.0	52.7
T. nudigenis	1	1.53	2.875	1.34	2.15	1.39	2.37	288	231	5.0	63.9
T. obsoletus	5	2.08 ± 0.43	3.50 ± 0.32	1.42 ± 0.17	2.26 ± 0.29	1.07 ± 0.26	8.55 ± 7.87	254 ± 14	292 ± 114	14.8 ± 10.2	74.8
T. olivater	2	5.93 ± 5.01	7.34 ± 4.40	1.42 ± 0.61	2.80 ± 0.18	2.19 ± 1.23	30.28 ± 4.61	243 ± 37	1436 ± 1028	24.5 ± 17.7	84.8
T. pelios	1	2.08	3.25	1.17	2.24	0.82	2.81	160	81	12.0	65.4
T. reevei	1	5.70	6.89	1.20	3.27	1.98	1.87	232	99	6.0	61.0
T. rufiventris	10	2.15 ± 0.39	3.42 ± 0.39	1.27 ± 0.18	2.27 ± 0.35	0.98 ± 0.22	7.00 ± 1.77	232 ± 26	150 ± 28	19.0 ± 4.8	66.8
T. serranus	8	5.31 ± 1.91	7.44 ± 1.56	2.13 ± 0.43	3.50 ± 0.23	2.21 ± 0.70	1.94 ± 1.91	141 ± 45	93 ± 47	7.7 ± 4.5	84.9

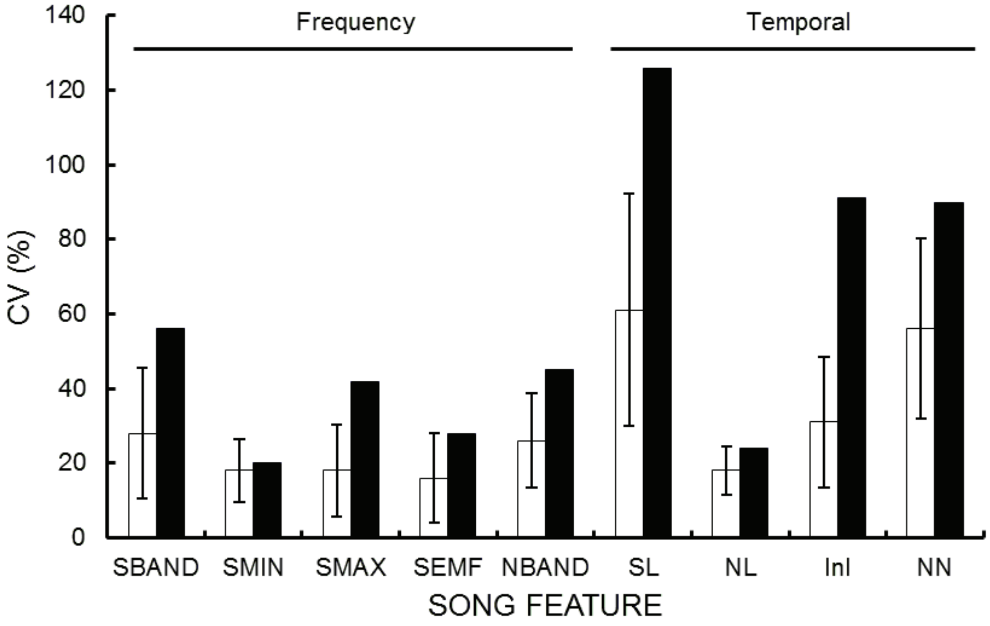

FIG. 2. Comparison of variation within and among species in frequency and temporal features of thrushes' songs. White bars represent the mean intraspecific coefficient of variation (CV), error bars indicate the standard deviation from the mean, black bars represent the interspecific CV. None of the comparisons showed significant differences between the two levels of analysis.

variables, instead of the mean, because the median is more resistant to outliers and can be a better estimator of the center of skewed distributions (Quinn & Keough 2002). The results were similar no matter which estimator was used, so we present those obtained using the mean.

There were 25 sets of 12 pairwise comparisons for each of the body mass and song trait combinations (Table 3). We found a clear negative relationship between body mass and SEMF (Fig. 3), although its range of probability values included some non-significant combinations (P = 0.0002–0.194). A closer examination revealed that in 19 of the 25 combinations there were between 12 and 10 negative SEMF contrasts associated with positive body mass contrasts, leading to significant results. Only five and one combinations with nine and eight negative SEMF contrasts, respectably, resulted in marginally or non-significant results. This is because there are a relatively small number of species pairs per combination, so a few comparisons showing an inversion in the association between the variables is enough for the result of a sign test not to be significant, despite the fact that the tendency is still clear. Also, the least-squares regression of 24 independent contrasts adjusted to pass through zero (Fig. 3), confirmed this result: there was a significant negative relationship between body mass and SEMF (t = –1.94, df = 23, P = 0.03, β = –0.412). In this case, 19 of the 24 comparisons were negative SEMF contrasts associated with positive body mass contrasts (P < 0.01).

Although other variables included significant values in their ranges (Table 3), the detailed analyses showed that there were no

TABLE 2. Results of the nonparametric Friedman's ANOVA to assess differences between temporal and frequency features variation. Frequency traits showed significantly lower variation than temporal traits for both levels of comparisons. Coefficients of variation (CV) are expressed in percentage as mean ± standard deviation (SD).

Analysis level	Song frequency features CV ± SD	Song temporal features CV ± SD	ANOVA χ^2	*P*
Within species	21 ± 10	41 ± 15	8	< 0.01
Among species	38 ± 14	83 ± 42	4	< 0.05

other discernible associations between body mass and the temporal or frequency song properties measured.

DISCUSSION

Despite the fact that *Turdus* thrushes are well known by their distinctive vocal abilities, the analysis of the relationship between continuity and versatility done by Ince & Slater (1985) is the only precedent of song comparative studies in this group. Here, we present the first interspecific analysis of song structure in this genus in relation to body mass, which is based on the South American species and accounts for their phylogenetic relationships.

We found a negative relationship between body size and emphasized frequency, which is one of the most relevant song frequencies because it is the one in which the bird deposits most energy. This relationship has been previously associated with the mass of the syringeal vibrating structure as birds with larger body sizes should have larger syringes with heavier tympaniform membranes that are expected to vibrate more slowly, thus producing vocalizations with lower frequencies (Ryan & Brenowitz 1985, Podos & Nowicki 2004). However, it has been shown that in some songbird species the medial tympaniform membranes play only a minor role in vocalization in comparison with other syringeal tissues (Larsen *et al.* 2006), and that in other cases body size and syrinx size do not even appear to be related (Handford & Lougheed 1991). In fact, even though the mechanisms responsible for sound production are not completely understood, it is clear that syringeal membranes are not the only structures that are associated with vocalizations that could be related to body size. Elements of the suprasyringeal vocal tract have resonating properties that modify the spectral structure of the song related to frequency. The trachea, larynx, and beak form a resonance filter tube which length is inversely associated to the song frequencies, so if larger or heavier species have larger vocal tracts they should evolve sounds with lower frequencies (Podos & Nowicki 2004). For example, beak morphology and gape have been shown to influence the length of the vocal tract anterior to the syrinx, shifting its resonance properties and then altering the frequencies of the song (Palacios & Tubaro 2000, Podos *et al.* 2004). However, the thrushes have a relatively unspecialized bill, which is moderately long, deep and broad at the base (Collar 2005) and similar in all species. Therefore, interspecific differences in beak morphology do not appear to be a suitable explanation to the variation in acoustic frequencies reported.

In regard to the influence of body size in temporal aspects of the song, we found no associations between the four temporal variables measured and the body mass of the 25 species analyzed. Little is known about the anatomical or physiological constraints that

TABLE 3. Pairwise comparisons results for the association between body mass and song traits. The predictor variable was the body mass and the direction of the subtraction for the contrast was heavier–lighter species. Ranges in *P* values (sign test) correspond to the 25 different combinations of 12 species pairs, and the most common pairing (MCP, third column) was the one that occurred most times in the total of combinations for each variable (fourth column).

Song feature	*P* (range)	Most common pairing (MCP)		No. of combinations with the MCP
		Positive	Negative	
SBAND	0.019–0.387	4	8	11
SMAX	0.073–0.613	4	8	14
SMIN	0.194–0.613	7	5	15
SEMF	0.0002–0.194	2	10	13
NBAND	0.073–0.613	4	8	12
SL	0.019–0.613	7	5	12
NL	0.194–0.613	6	6	11
InI	0.073–0.387	7	5	13
NN	0.073–0.613	6	6	12

body mass could directly impose to the temporal structure of the song. In fact, there are only a few studies that have previously investigated this relationship (Wiley 1991, Badyaev & Leaf 1997), and the evidence on this subject is not only limited but contradictory. According to other studies, temporal patterning appears to be more influenced by beak size (Podos 2001, Seddon 2005) rather than body mass, because of a biomechanical trade-off between force and speed in musculoskeletal systems (Herrel *et al.* 2002). Although it is reasonable to assume that beak size correlates with body size (Podos 2001, Palacios & Tubaro 2002), the lack of association between body mass and temporal features in our study, is in agreement with the aforementioned low variation in beak morphology among species of thrushes.

We observed significantly higher variation within and among species in temporal features than frequency ones. Bird song production involves neurologic coordination of respiratory, syringeal, and craniomandibular muscles, and also depends on intrinsic properties of the vocal organ (Suthers *et al.* 1999, Fee 2002). Ryan (1988) and Cocroft & Ryan (1995) have previously suggested, based on anuran vocalization analysis, that traits more related with morphology constraints (e.g., size of the vocal organ) might be less variable than characters which variation is linked to behavior or neurophysiological changes. This could at least partially explain the differences in variation in temporal vs. frequency features, if the frequency range that a bird can use mainly depends on the syringeal and vocal tract morphology, while the temporal pattern is largely determined by changes in the activity of the motor control pathways that coordinate the respiratory rhythm and syringeal muscle activity (Suthers *et al.* 1999). Because of their complex and variable vocalizations, we believe that it is worth including representatives of this genus in future anatomical and physiological studies that may help to better understand sound production, and the role played by the different syringeal tissues in the process.

Other factors, not related with body mass or other morphological features of the bird, could also influence the frequency and tem-

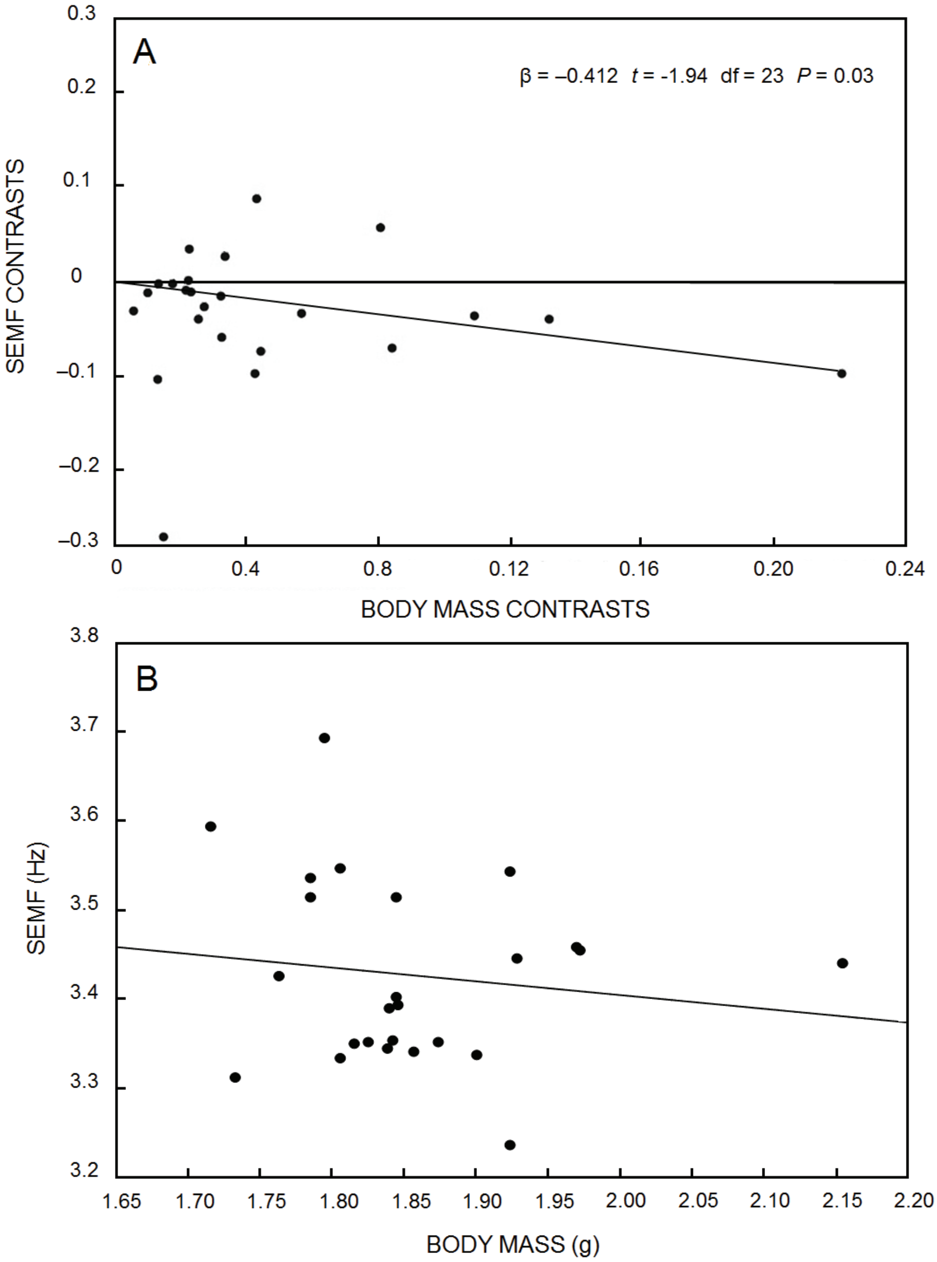

FIG. 3. Song emphasized frequency (SEMF) showing negative relationship with body mass for 25 species of *Turdus* thrushes. A) Scatterplot of 24 standardized contrasts of SEMF on body mass, with the slope (β) of the regression forced to pass through zero and its significance inside the graph. Horizontal line separates positive and negative SEMF contrasts. B) Raw data with a trend line, where each point corresponds to the body mass and SEMF of each species. Values on both axes are presented on a log scale.

poral structure of the song, and have been identified as selective forces driving bird song evolution. For instance, acoustic signals used for long-range communication could be adapted for minimizing attenuation and degradation suffered by the song as it crosses the native habitat of the sender (Ryan & Brenowitz 1985). It has been shown that birds living in closed habitats generally use lower frequency sounds and narrower bandwidths than species living in more open habitats (Wiley 1991, Bertelli & Tubaro 2002, Barker 2008). The species in our study are principally forest dwellers (Clement 2000) that occupy mainly closed habitats with resembling ecological and acoustic properties, so all songs should experience similar effects on their structure because of the type of habitat. However, transmission studies have shown that increasing the vertical position of the sender and the receiver can minimize the attenuation and distortion of the signal with distance in closed habitats (Dabelsteen *et al.* 1993, Barker *et al.* 2009). Specifically, Nemeth *et al.* (2006) reported that the attenuation of the song elements of the White-necked Thrush (*Turdus albicollis)* and the Cocoa Thrush (*T. fumigatus orinocensis*) was inversely height-dependent. The presence of longer notes and lower frequencies (usually associated with closed habitats) in the species singing closer to the ground (White-necked Thrush), compared to those of the higher perching species (Cocoa Thrush), suggests that the acoustic differences among the strata of a rainforest could be similar to those found between closed and open habitats (Nemeth *et al.* 2006). Additionally, frequency differences in this comparison could not be related to body size because the Cocoa Thrush is more than 30% heavier than the White-necked Thrush (see Table 1).

Some features of the song could have also evolved under sexual selective pressure as a consequence of the mate attraction function of the vocalizations. Female preferences for low or high frequency sounds (Fitch 1999, Cardoso *et al.* 2007, Irwin *et al.* 2008) could influence the structure of the song, and therefore have an impact on the relationship between body mass and song frequencies. In the particular case of the thrushes, Dabelsteen & Pedersen (1993) reported that high-frequency sounds elicited more copulation displays by females of the Eurasian Blackbird (*Turdus merula*). Moreover, if the differences in song frequency related with body size that appeared among species also exist within species, females could use song frequency as an indicator of male size and health condition (Gil & Gahr 2002). Additional studies regarding sexual preferences, sound transmission, and other selective pressures, should help to comprehend how the effect of body mass on the structure of thrushes' songs interacts with other several shaping forces.

In conclusion, our results showed a negative association between body mass and emphasized frequency of the songs of the South American *Turdus* thrushes. Although bird song structure has evolved under a great diversity of selective pressures, as we have discussed, our results support the previously reported negative relationship between body size and frequency features of the song, with the peculiarity that this morphological constraint has never been addressed in this particular group of birds until this study.

ACKNOWLEDGMENTS

We want to thank all the sound recordists that appear in the Appendix 1 who collected the songs that were used in this study. We also thank D. A. Lijtmaer for his comments and suggestions during different stages of the study and preparation of the manuscript. This work was supported by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (PIP 2009-2011 112-200801-00741, PLT), the

Agencia Nacional de Promoción Científica y Tecnológica (PICT 2010-0805), and the Universidad de Buenos Aires (UBACyT 2010-2012 01/1240, PLT), Argentina, and the International Developmental Research Centre of Canada (IDRC, PLT).

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APPENDIX 1. List of the 137 spectrograms from 25 species of *Turdus* thrushes used in this study. Acronyms indicate the source of the song analyzed, and numbers refer to the corresponding numerical identification that each cut has at its source. XC: Xeno-canto; BB: Birds of Brazil; BSA: Bird sounds from southern South America; NWT: Voices of the New World thrushes.

Species	Catalogue number	Location	Recordist
Turdus albicollis	XC 17408	Rio Grande do Sul, Brazil	F. Jacobs
Turdus albicollis	XC 457	Bolivia	J. van der Woude
Turdus albicollis	XC 13021	Rio de Janeiro, Brazil	L. Pimentel
Turdus albicollis	XC 5699	Saül, French Guiana	A. Renaudier
Turdus albicollis	XC 16331	Lavalleja, Uruguay	A. Riccetto
Turdus albicollis	BB 1	Pernambuco, Brazil	J. Minns
Turdus albicollis	BB 5	Rio de Janeiro, Brazil	J. Minns
Turdus albicollis	BB 6	Rio de Janeiro, Brazil	J. Minns
Turdus albicollis	BSA 03	Parana, Brazil	F. Gorleri
Turdus albicollis	NWT 1	São Paulo, Brazil	J. Vielliard
Turdus amaurochalinus	XC 42131	Rio Grande do Sul, Brazil	A. Eisen Rupp
Turdus amaurochalinus	XC 2741	Cochabamba, Bolivia	S. Mayer
Turdus amaurochalinus	XC 1770	Santa Cruz, Bolivia	S. Mayer
Turdus amaurochalinus	XC 16831	Ceará, Brazil	R. C. Hoyer
Turdus amaurochalinus	XC 12924	Rio de Janeiro, Brazil	L. Pimentel
Turdus amaurochalinus	XC 7387	Rio Grande do Sul, Brazil	F. Jacobs
Turdus amaurochalinus	BB 6	São Paulo, Brazil	J. Minns
Turdus amaurochalinus	BSA 01	Entre Ríos, Argentina	R. Fraga
Turdus amaurochalinus	BSA 04	Entre Ríos, Argentina	F. Gorleri
Turdus amaurochalinus	NWT	Argentina	M. Rumboll
Turdus assimilis	XC 6041	Distrito Federal, Mexico	M. Grosselet
Turdus assimilis	XC 2380	Cayo, Belize	D. Jones
Turdus assimilis	XC 29674	Tamaulipas, Mexico	D. Lane
Turdus assimilis	XC 11125	Peñas Blancas, Nicaragua	D. Knapp
Turdus assimilis	NWT 1	Sinaloa, Mexico	J. W. Hardy
Turdus chiguanco	XC 2090	La Paz, Bolivia	S. Mayer
Turdus chiguanco	XC 2126	La Paz, Bolivia	S. Mayer
Turdus chiguanco	XC 16145	Chuquisaca, Bolivia	N. Krabbe
Turdus chiguanco	XC 20158	Cuzco, Peru	N. Krabbe
Turdus chiguanco	XC 20667	Cuzco, Peru	I. Aragon
Turdus chiguanco	XC 8700	Lambayeque, Peru	W. P. Vellinga
Turdus chiguanco	XC 20839	Cuzco, Peru	I. Aragon
Turdus chiguanco	NWT 1	Cochabamba, Bolivia	R. A. Rowlett
Turdus chiguanco	NWT 2	Cuzco, Peru	M. Isler
Turdus falcklandii	XC 19506	Los Lagos, Chile	F. Schmitt
Turdus falcklandii	XC 994	Santiago de Chile, Chile	R. Valenzuela Aceval

APPENDIX 1. Continuation.

Species	Catalogue number	Location	Recordist
Turdus falcklandii	XC 962	Santiago de Chile, Chile	R. Valenzuela Aceval
Turdus falcklandii	XC 41506	Santiago de Chile, Chile	F. Cáceres
Turdus falcklandii	BSA 01	Chubut, Argentina	B. Lopez-Lanus
Turdus falcklandii	BSA 02	Neuquén, Argentina	F. Vidoz
Turdus falcklandii	BSA 03	Chubut, Argentina	F. Schmitt
Turdus falcklandii	BSA 10	Santiago de Chile, Chile	B. Lopez-Lanus
Turdus falcklandii	NWT 1	Isla Kidney, Islas Malvinas/Falkland Islands	O. S. Pettingill
Turdus falcklandii	NWT 2	Chile	G. Riveros Gomez
Turdus flavipes	XC 18101	Magdalena, Colombia	H. van Oosten
Turdus flavipes	XC 12221	Santander, Colombia	O. Laverde
Turdus flavipes	XC 12228	Santander, Colombia	O. Laverde
Turdus flavipes	XC 43260	Santa Catarina, Brazil	E. Legal
Turdus flavipes	XC 22271	Santander, Colombia	A. Spencer
Turdus flavipes	XC 12429	Santander, Colombia	J. de las Casas
Turdus flavipes	XC 10453	Rio de Janeiro, Brazil	R. A. de By
Turdus flavipes	BB 9	Santa Catarina, Brazil	J. Minns
Turdus fulviventris	NWT	Tachira, Venezuela	P. Schwartz
Turdus fumigatus	XC 5403	Amazonas, Brazil	R. C. Hoyer
Turdus fumigatus	XC 27217	Pará, Brazil	S. Dantas
Turdus fumigatus	XC 18751	Pará, Brazil	S. Dantas
Turdus fumigatus	XC 42740	Saül, French Guiana	O. Claessens
Turdus fumigatus	BB 2	Trancoso, Brazil	D. Buzzetti
Turdus fumigatus	BB 3	Mato Grosso, Brazil	D. Buzzetti
Turdus fumigatus	NWT	Arima, Trinidad & Tobago	R. Ward
Turdus fuscater	XC 37093	Cauca, Colombia	O. Cortes
Turdus fuscater	XC 11296	Bogotá, Colombia	D. Knapp
Turdus fuscater	XC 20781	San Martín, Peru	N. Athanas
Turdus fuscater	XC 18296	Caldas, Colombia	H. van Oosten
Turdus fuscater	XC 1967	La Paz, Bolivia	S. Mayer
Turdus fuscater	XC 11295	Bogotá, Colombia	D. Knapp
Turdus fuscater	NWT	Nariño, Colombia	B. B. Coffey, Jr.
Turdus grayi	XC 11126	Managua, Nicaragua	D. Knapp
Turdus grayi	XC 28496	Orange Walk, Belize	D. Lane
Turdus grayi	XC 322	Managua, Nicaragua	J. P. Kjeldsen
Turdus grayi	XC 6953	Ammo Dump Ponds, Panama	K. Allaire
Turdus grayi	XC 40977	San José, Costa Rica	L. E. Vargas
Turdus grayi	XC 578	Guanacaste, Costa Rica	D. Mennill
Turdus grayi	NWT	Campeche, Mexico	J. W. Hardy
Turdus haplochrous	NWT	El Beni, Bolivia	C. G. Schmitt
Turdus hauxwelli	XC 2211	Santa Cruz, Bolivia	S. Mayer
Turdus hauxwelli	XC 23385	Cuzco, Peru	D. Geale
Turdus hauxwelli	XC 541	Tambopata, Peru	J. van der Woude
Turdus hauxwelli	XC 18760	Acre, Brazil	S. Dantas
Turdus hauxwelli	XC 39839	Madre de Dios, Peru	D. Geale
Turdus hauxwelli	XC 994	Tambopata, Peru	B. Planqué

APPENDIX 1. Continuation.

Species	Catalogue number	Location	Recordist
Turdus hauxwelli	XC 14121	Madre de Dios, Peru	R. Ahlman
Turdus hauxwelli	XC 223	Santa Cruz, Bolivia	S. Mayer
Turdus hauxwelli	NWT 1	Madre de Dios, Peru	T. A. Parker
Turdus hauxwelli	NWT 3	Loreto, Peru	T. A. Parker
Turdus ignobilis	NWT	Ucayali, Peru	B. B. Coffey, Jr.
Turdus leucomelas	XC 12216	Santander, Colombia	O. Laverde
Turdus leucomelas	XC 8386	San Martín, Peru	H. van Oosten
Turdus leucomelas	XC 5435	Amazonas, Brazil	R. C. Hoyer
Turdus leucomelas	XC 11585	Ceará, Brazil	N. Athanas
Turdus leucomelas	XC 7777	Mato Grosso, Brazil	J. Menezes
Turdus leucomelas	XC 26149	Rio de Janeiro, Brazil	R. Gagliardi
Turdus leucomelas	BB 3	Piauí, Brazil	R. Parrini
Turdus leucomelas	BB 10	Bahia, Brazil	J. Minns
Turdus leucomelas	BSA 03	Amambay, Paraguay	M. Velazquez
Turdus leucomelas	NWT	Magdalena, Colombia	B. B. Coffey, Jr.
Turdus leucops	XC 15063	Napo, Ecuador	R. Ahlman
Turdus leucops	XC 2388	Cosanga, Ecuador	W. Halfwerk
Turdus leucops	XC 10690	Cajamarca, Peru	T. Mark
Turdus leucops	XC 9382	Pichincha, Ecuador	N. Athanas
Turdus leucops	NWT	San Martín, Peru	T. A. Parker
Turdus maculirostris	XC 6635	Pichincha, Ecuador	N. Athanas
Turdus maculirostris	XC 8056	Loja, Ecuador	N. Athanas
Turdus maranonicus	XC 17251	Zamora-Chinchipe, Ecuador	A. Spencer
Turdus nigriceps	XC 4035	Santa Cruz, Bolivia	S. K. Herzog
Turdus nigriceps	XC 419	Santa Cruz, Bolivia	J. van der Woude
Turdus nigriceps	XC 4672	Tarija, Bolivia	A. Maccormick
Turdus nigriceps	XC 1724	Tarija, Bolivia	S. Mayer
Turdus nigriceps	NWT 1	Rio Grande do Sul, Brazil	T. A. Parker
Turdus nudigenis	NWT	Caracas, Venezuela	P. Schwartz
Turdus obsoletus	XC 8055	El Oro, Ecuador	N. Athanas
Turdus obsoletus	XC 24215	Cocle, Panama	K. Allaire
Turdus obsoletus	XC 3307	Cocle, Panama	D. Bradley
Turdus obsoletus	XC 17702	El Oro, Ecuador	A. Spencer
Turdus obsoletus	NWT	Bolivar, Venezuela	M. L. Godwin
Turdus olivater	NWT 1	Aragua, Venezuela	R. J. Raitt
Turdus olivater	NWT 2	Bolivar, Venezuela	T. A. Parker
Turdus pelios	XC 34030	Abuko, Gambia	O. Jakobsen & N. Krabbe
Turdus reevei	XC 5567	Lambayeque, Peru	W. P. Vellinga
Turdus rufiventris	XC 1664	Tarija, Bolivia	S. Mayer
Turdus rufiventris	XC 8768	Rio Grande do Sul, Brazil	F. Jacobs
Turdus rufiventris	XC 8772	Rio Grande do Sul, Brazil	F. Jacobs
Turdus rufiventris	XC 8775	Rio Grande do Sul, Brazil	F. Jacobs
Turdus rufiventris	XC 7974	Rio Grande do Sul, Brazil	F. Jacobs
Turdus rufiventris	XC 62748	São Paulo, Brazil	R. De la Rosa
Turdus rufiventris	BB 8	Bahia, Brazil	J. Minns

APPENDIX 1. Continuation.

Species	Catalogue number	Location	Recordist
Turdus rufiventris	BB 9	Bahia, Brazil	D. Buzzetti
Turdus rufiventris	BB 15	São Paulo, Brazil	D. Buzzetti
Turdus rufiventris	NWT	Buenos Aires, Argentina	C. Hartshorne
Turdus serranus	XC 2017	La Paz, Bolivia	S. Mayer
Turdus serranus	XC 8086	Amazonas, Peru	D. Geale
Turdus serranus	XC 18322	Chocó, Colombia	H. van Oosten
Turdus serranus	XC 17740	Loja, Ecuador	A. Spencer
Turdus serranus	XC 38872	Cochabamba, Bolivia	F. Lambert
Turdus serranus	XC 12575	Santander, Colombia	O. Laverde
Turdus serranus	XC 12638	Santander, Colombia	O. Laverde
Turdus serranus	NWT	Huánuco, Peru	T. A. Parker