

Do beak volume and bite force influence the song structure of sympatric species of seedeaters (Thraupidae: *Sporophila*)?

N. S. Porzio, M. Repenning & C. S. Fontana

To cite this article: N. S. Porzio, M. Repenning & C. S. Fontana (2018): Do beak volume and bite force influence the song structure of sympatric species of seedeaters (Thraupidae: *Sporophila*)?, Emu - Austral Ornithology, DOI: [10.1080/01584197.2018.1535833](https://doi.org/10.1080/01584197.2018.1535833)

To link to this article: <https://doi.org/10.1080/01584197.2018.1535833>



View supplementary material [↗](#)



Published online: 29 Oct 2018.




Submit your article to this journal [↗](#)



View Crossmark data [↗](#)



Do beak volume and bite force influence the song structure of sympatric species of seedeaters (Thraupidae: *Sporophila*)?

N. S. Porzio , M. Repenning and C. S. Fontana

Programa de Pós-Graduação em Zoologia, Museu de Ciências e Tecnologia – Laboratório de Ornitologia, Pontifical Catholic University of Rio Grande do Sul (PUCRS), Porto Alegre, Brazil

ABSTRACT

Song structure can be constrained by morphological characters such as beak size. Studies have shown that songbirds with larger beaks produce songs with a lower frequency, narrower frequency range and lower note rates than birds with smaller beaks. We tested whether beak volume and bite force constrain song parameters in three Neotropical seedeaters that show a gradient of beak size and force (*Sporophila beltoni*, *S. caerulea* and *S. hypoxantha*). We also determined the relationship between body size and song structure. We evaluated the song structure of these species, measuring differences that may help them to segregate the acoustic space, since they occur in sympatry. These birds can be predicted to segregate the acoustic space to reduce overlapping of their songs, which is a possible result of the force of sexual selection. Individuals of each species had their beaks and bite forces measured and their own territorial songs recorded in the field. Only *S. caerulea* showed a positive relationship between beak volume and song parameters (maximum frequency and frequency bandwidth). No song parameters showed an association with bite force or body size. The use of acoustical space seemed to be unique to each species with respect to note rate and song duration. *Sporophila beltoni* and *S. hypoxantha* showed the most differences from each other in all song parameters analysed. In contrast to other studies of finch species with conical beaks, our findings suggested that for these three species, beak volume and bite force do not limit the song structure.

ARTICLE HISTORY

Received 5 April 2018
Accepted 8 October 2018

KEYWORDS

Acoustic communication;
animal behaviour; birdsong;
ecological segregation;
oscines

Introduction

The production of elaborate songs in oscine passerines, is a complex behaviour that is subject to multiple pressures including sexual selection, natural selection and drift (Catchpole and Slater 2008; Wilson *et al.* 2014). Acoustic signals are highly important for species recognition, acting as a reproductive barrier in the speciation process (Marler *et al.* 2004; Catchpole and Slater 2008). During bird communication, in order to reach the receiver, the transmission must overcome several obstacles, such as noise, the acoustic properties of the environment, and songs of other animals (Morton 1975; Linskins *et al.* 1976; Wiley and Richards 1978; Richards and Wiley 1980; Endler 1992).

Patterns in song structure (e.g. maximum and minimum frequencies, frequency bandwidth, number of notes and song duration) are a result of changes in variables that can act on the birdsong parameters (e.g. beak variations and body size) or phylogenetic relationships, and these characters (morphological and evolutionary) have been studied to elucidate birdsong

variations (Ryan and Brenowitz 1985; Podos 2001; Herrel *et al.* 2005; Martin *et al.* 2011; Mason and Burns 2015; García and Tubaro 2018).

Beak gape can indirectly affect the bandwidth in song structure, since it is assumed that a larger beak will open and close more slowly compared to a small beak, thus producing narrower bandwidths (Nowicki 1987; Westneat *et al.* 1993; Podos 2001; Podos *et al.* 2004; Podos and Nowicki 2004; Ballentine 2006; Catchpole and Slater 2008). Related to beak gape are the bite force and beak size, which can affect a bird's capacity to move its jaw while it is singing, thus constraining the song produced (Ratcliffe and Grant 1985; Hoese *et al.* 2000; Grenier and Greenberg 2005; Christensen *et al.* 2006; Huber and Podos 2006; Derryberry *et al.* 2012).

Beak morphology is generally an evolutionary consequence of an adaptation of the feeding habit, related to the environment, food availability and inter-specific competition. For example, birds that feed on large hard seeds have larger and stronger beaks than those that

feed on insects (Herrel *et al.* 2005; Genbrugge *et al.* 2011). Beak size and strength can affect how widely and rapidly the bird can move its beak, and consequently this adaptation acts as a song constraint, so that birds with larger beaks produce low rates of syllable repetition and narrow-frequency bandwidth compared to birds with smaller beaks (Westneat *et al.* 1993; Podos 2001; Herrel *et al.* 2009; Genbrugge *et al.* 2011). Body size is also related to song structure; smaller birds typically produce higher frequencies and wider-frequency bandwidths than larger birds, because the size of the vocal apparatus usually scales with overall body size (Ryan and Brenowitz 1985; Podos and Nowicki 2004; Martin *et al.* 2011; Giraudeau *et al.* 2014; Mason and Burns 2015).

The genus *Sporophila* (seed eaters; Thraupidae) includes about 40 species in the subtropical and tropical Americas which have evolved and diverged in the mainland (Burns *et al.* 2014, 2016; Barker *et al.* 2015). Although *Sporophila* passed through a continental speciation process, with coexistence of species that currently live in sympatry, members of this genus diverge widely in beak size, from small and slight (e.g. capuchino group) to large and strong (e.g. *Sporophila maximiliani* – Great-billed Seed-Finch). The seed eaters are a monophyletic group in which some members (capuchino group) have diversification rates comparable to Darwin's finches, making this group (*Sporophila*) a potentially useful system to study divergence and evolution in continental habitats (Mason and Burns 2013; Burns *et al.* 2014). Species of *Sporophila* have undergone this continental speciation process, with an allopatric period when pairs of populations evolve to species that can now live in sympatry after secondary contact, in which they tend to segregate ecological traits (e.g. acoustic space) to avoid the overlap of resources of each species (Grant and Grant 1979).

Coexisting species may adapt their songs in order to be heard and avoid overlapping in acoustic space. A species may increase the maximum frequency of the song when the sound has low frequency; or may invest in lower frequencies, which have longer wavelengths that diffract around obstacles more easily than do higher frequencies (Wiley and Richards 1978).

Understanding the role of morphological and ecological traits that limit vocal signals is therefore important to clarify the diversification and evolution of species. We studied three species of seed eaters that share the same environment in southern South America grasslands to try to understand the limits of vocal signals in birds with conical beaks that are continental and have radiated rapidly (Burns *et al.* 2014). The *Sporophila* group has not yet been evaluated by

tests of this sort, in which we analysed a set of species that vary in beak morphology, body size and song features.

Previous studies have focused on the link between beak size and shape with song (Nowicki 1987; Westneat *et al.* 1993; Hoese *et al.* 2000; Podos 2001; Podos and Nowicki 2004). However, most researchers have worked with Darwin's finches, which have passed through a single adaptive radiation process, an allopatric speciation on islands (Lack 1947; Podos 2001; Podos *et al.* 2004; Podos and Nowicki 2004; Huber and Podos 2006). Morphological changes in beak size and force are often followed by song divergence, in which larger and stronger beaks produce lower frequencies and slower note rates, compared to birds with smaller beaks. These patterns give rise to several questions: do variations in beak size/force and divergences in song structure interplay in sympatric closely related birds that vary widely in song structure? Do these birds adjust the acoustic parameters in order to be heard, due to the presence of related species that have overlapping songs? In this study we tested whether song parameters (e.g. maximum/minimum frequency, note rate and frequency bandwidth) are constrained by beak volume, bite force and body size, in three sympatric species of seed eaters. We also compared the song structures of these three species to evaluate how they differ in the acoustic space, where they coexist in syntopy. We expected differences in song parameters due to variations in beak and body size, as mentioned in the literature. Additionally, we expected variations in song structure of three sympatric species of Neotropical *Sporophila* seed eaters which coexist in breeding area and supposedly have to dispute acoustic space. We used morphological data (beak volume, bite force and body size) and acoustic data (song variables) to show relationships within and between them.

Methods

Study species and sites

We studied three sympatric species (Figure 1) of Neotropical mainland seed eaters that differ in size and breed in the same habitat, namely *Sporophila beltoni*, the Tropeiro Seed eater; *Sporophila caerulescens*, the Double-collared Seed eater; and *Sporophila hypoxantha*, the Tawny-bellied Seed eater. These three species differ widely in song structure (Figure 1).

Sporophila beltoni was described recently, as distinct from the taxon *Sporophila plumbea*. It is a rare, long-distance migrant that breeds from northern Rio Grande

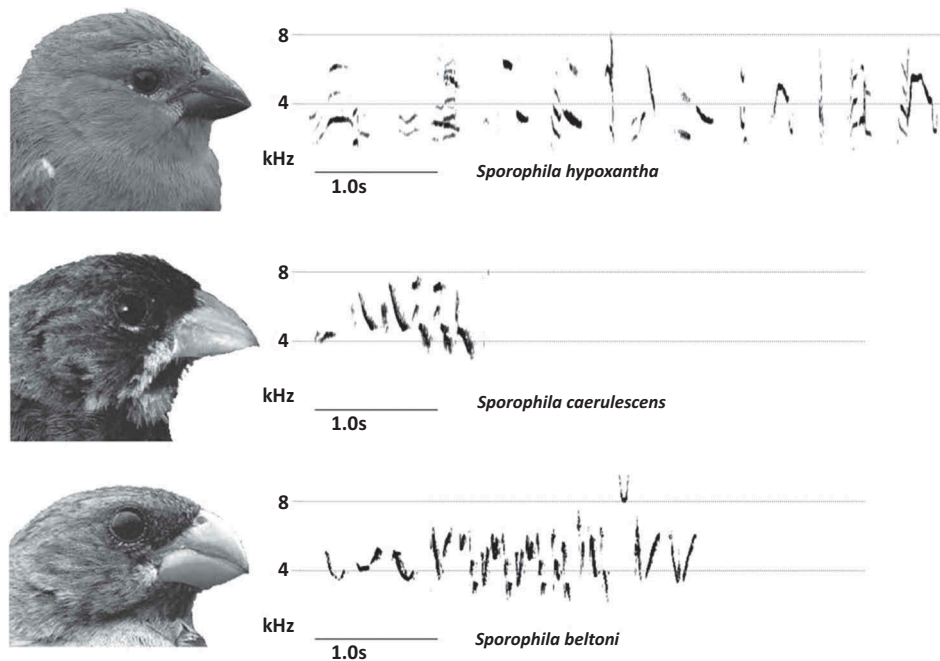


Figure 1. Illustration of beak morphology and representative sound spectrograms of songs from *Sporophila hypoxantha*, *S. caeruleascens* and *S. beltoni*, sympatric species of seedeaters.

do Sul to north-eastern Paraná and has a fragmented distribution (Repenning and Fontana 2013). It is the largest species in our study, with an average total length of 119.3 mm (114.1–126 mm) and body mass of 12.4 g (11.1–13.9 g) (Repenning and Fontana 2013; unpub. data). *Sporophila caeruleascens* has a wide distribution and is a partial migrant that breeds in Argentina, Paraguay, Uruguay and parts of Brazil. This species averages 109 mm (104.1–117 mm) in total length and 10.1 g (8.8–11.2 g) in body mass (unpub. data). *Sporophila hypoxantha* belongs to the capuchino group, which has undergone a rapid and recent radiation (Campagna *et al.* 2013). We studied only the easternmost population of *S. hypoxantha* (of five recognised allopatric populations) which breeds in the highlands of southern Brazil (Areta and Repenning 2011). This is the smallest of the three species analysed here, measuring 100.3 mm (97.5–105.1 mm) long and 8.6 g (7.8–9.6 g) in body mass (Franz and Fontana 2013).

We conducted our fieldwork in the municipalities of Bom Jesus (28°40' S, 050°28' W) and Jaquirana (28°52' S, 050°27' W), state of Rio Grande do Sul, Brazil, where the three species breed in syntopy. This area is located in an upland grassland of southern Brazil in the Atlantic Forest Biome.

Fieldwork

We recorded the territorial songs of five adult males of each species in December 2015, during their breeding

season. These data enabled us to evaluate the song structure of the species, since the birds in these populations basically sing the same song type almost without individual variation. We selected territorial adult males that were singing advertisement songs. Songs were recorded at a standard distance from the individuals (~20 m), using a Nagra LB digital recorder, at 96 kHz sampling rate and 24-bit depth in Wave format, with a Sennheiser ME62 external microphone, combined with a Telinga parabola (21.5 in./6.1 in. = 54.6 cm/15.5 cm). All sounds recorded for this study will be archived at the Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York.

First, each male was recorded and then captured with a mist-net (Ecotone) in order to take morphometric measurements and to test the bite force. This process was performed for each territorial male. After each male was recorded, captured, banded and released, we searched for the next one. This procedure allowed us to link the data for the beak and the song of each territorial male. We banded all birds with coloured and metal rings in order to distinguish them. We measured the height, width and length of the beak (exposed culmen), the total length, and the body mass with a metal calliper rule (Mitutoyo) and a precision balance (resolution 0.01 mm) and a dynamometer (Swiss Pesola Micro-Line spring scale, model 20 060, with 0.5 g precision) (Ballentine 2006; Roos 2010). The beak volume was calculated as a cone

$[v = (\pi.r^2.h)/3]$ where r = beak height/2 and h = beak length. The cone-shape measure was chosen in consultation with a technician in the Physics Department of Pontifical Catholic University of Rio Grande do Sul (PUCRS), considering the possible variables that best describe the beak shape of seedeaters. To measure the bite force, we used a Tekscan FlexiForce pressure sensor (Freeman and Lemen 2008) linked to a multimeter (2 V) mounted in a custom-built holder. The pressure sensor was calibrated with known masses (g) to allow conversion of the values from volts to grams. This equipment was developed together with the Physics Department. To test the bite force, we took the maximum value of each beak pressure applied by each bird. We were careful to standardise and accurately position the beak by aligning it with the middle part until the tip of the beak was in contact with the pressure sensor. We recorded the maximum value displayed on the pressure sensor, 15 times for each bird.

Sound processing

All acoustical measurements were made with a Raven Pro 1.5, using the following spectrogram parameters [window type: Hann; size: 512 samples (10.7 ms); time grid-overlap: 75%; frequency grid-DFT size: 1024 samples; bandwidth 270 Hz]. For each bird, we analysed three songs and calculated the mean values for each parameter. We evaluated seven acoustical variables: song duration, number of notes, note rate (number of notes per second), frequency bandwidth, peak frequency, and maximum and minimum frequencies. We used the spectrum amplitude to calculate the frequency bandwidth, as the difference between the maximum and minimum frequency, using -24 dB relative to the peak amplitude frequency in the song (Podos 1997, 2001). Variables over time (number of notes, song duration and note rate) were measured with an oscillogram, with which we delineated each song, and used an on-screen cursor to measure the song duration. We selected the notes based on visual inspection on unambiguous temporal-spectral shape. We defined a note as single whistles in a building block of songs (Baptista 1996).

Statistical analysis

We estimated performance constraints using a simple linear regression for each species, to describe how the song structure relates to beak volume and bite force. We also evaluated whether beak volume is associated with bite force, using the same analysis with allometric values (*sensu* West *et al.* 1997) to remove the effect of

body size, using the formula $x/\sqrt[3]{\text{body mass}}$, where x = beak volume and bite force. For bite-force values, we selected the five strongest bites (of at least 15 bites per individual) and averaged them to estimate the pattern of bite force per individual (Herrel *et al.* 2005). To evaluate the use of song space by the three species, we compared song duration, frequency bandwidth, number of notes, note rate, and maximum and minimum frequencies using a univariate analysis. We used the Shapiro test to check the normal distribution of data, followed by ANOVA ($P < 0.05$) and post hoc Tukey test. For non-normal distributions, we processed the data using Kruskal–Wallis and Dunn tests as post hoc. All statistical analyses were performed using R (R Core Team 2016). We used the package ‘arm’ for simple linear regression, ‘car’ for ANOVA, ‘coin’ and ‘dunn.test’ for Kruskal–Wallis, and ‘ggplot2’ for graphs.

Ethical note

All the bird manipulations were performed in accordance with Brazilian law. The study was authorised under licences from the National Center for Research on the Conservation of Wild Birds (CEMAVE No. 361,788), which provided the metal bands, and the Ethics Council of the PUCRS; and a permit from Chico Mendes Institute for Biodiversity Conservation (ICMBio) through the Brazilian System for Authorization and Information on Biodiversity (SISBIO No. 36,881).

Results

We found that *Sporophila caerulea* showed a statistically significant association between beak volume and song parameters. Maximum frequency ($P = 0.03$, $R^2 = 0.82$, $F_{1,3} = 13.49$) and frequency bandwidth ($P = 0.03$, $R^2 = 0.81$, $F_{1,3} = 13.63$) were strongly explained by beak volume, i.e. birds with larger beaks produced higher frequencies and wider-frequency bandwidths. *Sporophila beltoni* and *S. hypoxantha* did not show significant results ($P > 0.05$) for beak volume and song parameters. No variables were explained by the bite-force analysis. We found a strong positive association between bite force and beak volume ($P = 0.002$, $R^2 = 0.51$, $F_{1,3} = 13.72$) (Figure 2).

Considering the gradient of beak sizes, *S. beltoni* had the largest beak volume and bite force, followed by *S. caerulea* and *S. hypoxantha*; and their body masses averaged 12.2 g (11.5–12.5 g), 10.1 g (9.4–10.5 g) and 8.6 g (8.3–9.2 g), respectively. Five variables differed significantly between at least two species. *Sporophila beltoni* and *S. hypoxantha* showed the most differences from each other: beak volume, bite force, note rate and

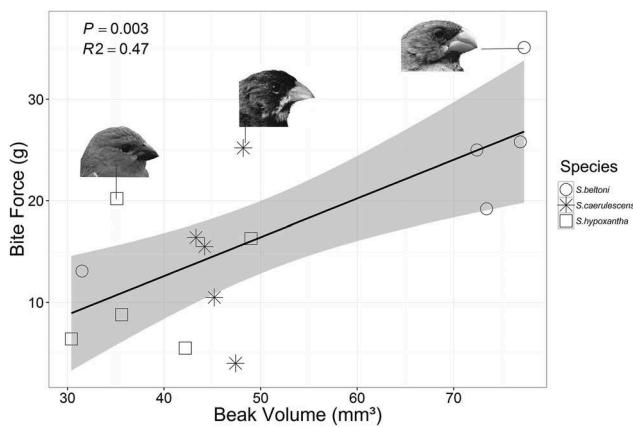


Figure 2. Positive relationship between the beak volume and bite force in *Sporophila beltoni*, *S. caerulea* and *S. hypoxantha*.

song duration. *Sporophila hypoxantha* and *S. caerulea* had two differences, in note rate and song duration. *Sporophila caerulea* and *S. beltoni* also showed two differences, in bite force and beak volume. The frequency parameters (peak minimum/maximum frequencies and frequency bandwidth) and the number of notes did not show significant differences ($P > 0.05$) among species (Tables 1 and 2). Beak volume, bite force, note rate and song duration were the most frequent differences among the three species (Figure 3).

Discussion

Many studies have shown that larger beaks with stronger bites are physically incompatible with rapid open-

Table 1. ANOVA results (P values) for the inter-specific analyses among *Sporophila beltoni* (*S. bel*), *S. caerulea* (*S. cae*) and *S. hypoxantha* (*S. hyp*). Statistically significant results are in bold.

	ANOVA – P values		
	<i>S. cae</i> – <i>S. bel</i>	<i>S. hyp</i> – <i>S. bel</i>	<i>S. hyp</i> – <i>S. cae</i>
Peak frequency	0.977	0.953	0.873
No. of notes	0.977	0.953	0.873
Frequency bandwidth	0.704	0.627	0.991
Bite force	<0.014	<0.001	0.723
Note rate	0.076	<0.001	<0.001

Table 2. Kruskal–Wallis results (P values) for the inter-specific analyses among *Sporophila beltoni* (*S. bel*), *S. caerulea* (*S. cae*) and *S. hypoxantha* (*S. hyp*). Statistically significant results are in bold.

	Kruskal–Wallis – P values		
	<i>S. cae</i> – <i>S. bel</i>	<i>S. hyp</i> – <i>S. bel</i>	<i>S. hyp</i> – <i>S. cae</i>
Minimum frequency	0.268	0.31	0.235
Maximum frequency	0.857	0.471	0.465
Beak volume	0.036	<0.001	0.09
Song duration	0.128	0.027	0.001

ing and closing movements, affecting the note rate and frequencies produced (Hoese *et al.* 2000; Podos and Nowicki 2004). Differently from other finches with conical beaks and that have songs constrained by morphological characters, we found that beak volume and bite force do not limit the production of higher frequencies and faster note rates for these three sympatric species of Neotropical seedeaters.

The most interesting result regarding song constraint by beak volume was shown by *Sporophila caerulea*. This species showed the opposite pattern compared with previous studies, since in the intra-specific analyses with *S. caerulea*, birds with larger beaks had higher maximum frequencies and wider frequency bandwidths. *Sporophila caerulea* had the widest variation in frequencies of the three species, with the lowest minimum frequency and the highest maximum frequency. In contrast, *S. beltoni* and *S. hypoxantha* did not show an intra-specific relationship between song parameters and beak variations (size and force). The pattern observed in these three seedeaters, in which beak size does not limit song structure, is also seen on a larger scale in the genus *Sporophila* as a whole, in which the members vary markedly in beak shape and size. Morphological characters such as body size, beak size and bite force have the potential to shape vocal evolution. However, in some cases these characters did not explain or correlate with song structure.

Regarding the characteristics of song structure, *S. hypoxantha* showed more stable song phrases than the others, since the individuals maintained a similar repertoire of notes and song duration. This species also had a lower note rate and longer song duration, characteristic of the stereotyped song previously observed in the capuchino clade (Areta 2008; Repenning *et al.* 2010; Areta and Repenning 2011). *Sporophila beltoni* has the capacity to mimic in addition to learning songs, showing strong vocal plasticity (Repenning and Fontana 2013). This species varied widely in the number of notes, song duration and consequently the note rate; although it had the largest beak and strongest bite force, *S. beltoni* showed no limitation in producing variations in song frequencies as well as trill note types. These results do not support the hypothesis postulated for the finches with conical beaks, since species with larger beaks and stronger bites, such as *S. beltoni*, produced higher frequencies and faster note rates compared to smaller species, *S. caerulea* and *S. hypoxantha* (Podos and Nowicki 2004).

Note rate and song duration were the most striking parameters that differed among the three species. These factors may help them in the competition for acoustic space, since they breed in the same habitat and have contiguous or overlapped territories (Morton 1975;

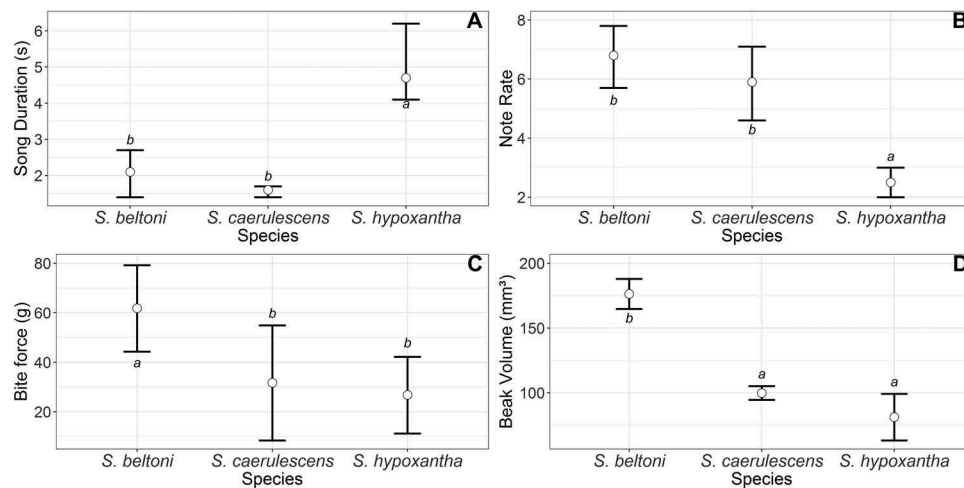


Figure 3. Intra-specific variations of (A) song duration, (B) note rate, (C) bite force and (D) beak volume, in three sympatric species of seedeaters, showing the differences among them.

Brumm and Zollinger 2011). These parameters differed significantly between *S. hypoxantha* and the other two seedeaters. The smallest one, *S. hypoxantha*, had a longer song with a lower note rate, unlike *S. beltoni* which produced a higher note rate in a shorter time. Although *S. caerulescens* did not show a significant difference from *S. beltoni*, the former's song was shorter with a lower note rate than the latter.

Beak size and bite force are a motor constraint on vocal performance in some oscine and suboscine birds (Podos 1997, 2001; Podos and Nowicki 2004; Ballentine 2006; Herrel *et al.* 2009; Derryberry *et al.* 2012; Giraudeau *et al.* 2014; García and Tubaro 2018). However, most of these studies were conducted with species that produce trilled songs, with a constant rate where the notes are equal. Our study demonstrates that *Sporophila* species may have more plasticity in song production, besides changes in beak morphology.

Regarding the coexistence of the three sympatric species, the differences found in song structure may facilitate the overlapping of their songs, so there is no inter-specific competition in the acoustic space. However, in this case, a different song feature (e.g. note rate and minimum frequency) might be better explained by their phylogenetic distance (Buskirk 1997; Price and Lanyon 2002; Cardoso and Mota 2007; Carsoso *et al.* 2012). Further studies with closely related species that differ significantly in beak size and shape would help to evaluate the influences of beak morphology on song structure that operate in passerines in general. For *Sporophila* seedeaters, identifying the roles of the other structures related to song production, such as the trachea or syrinx, separately from the influence of beaks, could be useful to explain the source of song complexity in this genus. Apparently, in some oscine birds, patterns in the

song structure can be better explained by the systematic relationships of the species than by ecological forces or morphological constraints.

Acknowledgements

We are grateful to technician Samuel Corvello Vilar from the Physics Department of Pontifical Catholic University (PUCRS) for his help in surveying pressure-sensor adjustments and his expertise. The Brazilian National Research Council (CNPq) provided fellowships to N.S.P. and M.R. and a grant to C.S.F. (process 310022/2015-0). To Cornell Lab. (Macaulay Library) for lending the sound recording material to M.R.

Funding

This work was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico [310022/2015-0]

ORCID

N. S. Porzio  <http://orcid.org/0000-0002-9981-7824>

References

- Areta, J. I. (2008). The entre ríos seedeater (*Sporophila zelichi*): A species that never was. *Journal of Field Ornithology* **79**, 352–363. doi:10.1111/jof.2008.79.issue-4
- Areta, J. I., and Repenning, M. (2011). Systematics of the Tawny-Bellied Seedeater (*Sporophila hypoxantha*). I. Geographic variation, ecology, and evolution of vocalizations. *The Condor* **113**, 664–677. doi:10.1525/cond.2011.100058
- Ballentine, B. (2006). Morphological adaptation influences the evolution of a mating signal. *Evolution* **60**, 1936–1944.

- Baptista, L. F. (1996). 'Apuntamientos para la historia natural de los pájaros Del Paraguai y Río de La Plata'. (Imprenta de La Viuda de Ibarra: Madrid.)
- Barker, F. K., Burns, K. J., Klicka, J., Lanyon, S. M., and Lovette, I. J. (2015). New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk* **132**, 333–348. doi:10.1642/AUK-14-110.1
- Brumm, H., and Zollinger, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behavior* **148**, 1173–1198. doi:10.1163/000579511X605759
- Burns, K. J., Shultz, A. J., Title, P. O., Mason, N. A., Barker, F. K., Klicka, J., Lanyon, S. M. et al. (2014). Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Molecular Phylogenetics and Evolution* **75**, 41–77. doi:10.1016/j.ympev.2014.02.006
- Burns, K. J., Unitt, P., and Mason, N. A. (2016). A genus-level classification of the family Thraupidae (Class Aves: Order Passeriformes). *Zootaxa* **4088**(3), 329–354. doi:10.11646/zootaxa.4088.3.2
- Buskirk, J. V. (1997). Independent evolution of song structure and note structure in American wood warblers. *Proceedings of the Royal Society B: Biological Sciences* **264** (1382), 755–761. doi:10.1098/rspb.1997.0107
- Campagna, L., Silveira, L. F., Tubaro, P. L., and Loughheed, S. C. (2013). Identifying the sister species to the rapid capuchino seedeater radiation (Passeriformes: *Sporophila*). *The Auk* **130**, 645–655. doi:10.1525/auk.2013.13064
- Cardoso, G. C., and Mota, P. G. (2007). Song diversification and complexity in canaries and seedeaters (*Serinus* spp.). *Biological Journal of the Linnean Society* **92**, 183–194. doi:10.1111/j.1095-8312.2007.00837.x
- Carso, G. C., Hu, Y., and Mota, P. G. (2012). Birdsong, sexual selection, and the flawed taxonomy of canaries, goldfinches and allies. *Animal Behavior* **84**, 111–119. doi:10.1016/j.anbehav.2012.04.015
- Catchpole, C. K., and Slater, P. J. B. (2008). 'Bird Song: Biological Themes and Variations', 2nd edn. (Cambridge University Press: Cambridge, UK).
- Christensen, R., Kleindorfer, S., and Robertson, J. (2006). Song is a reliable signal of bill morphology in Darwin's small tree finch *Camarhynchus parvulus*, and vocal performance predicts male pairing success. *Journal of Avian Biology* **37**, 617–624. doi:10.1111/jav.2006.37.issue-6
- Derryberry, E. P., Seddon, N., Claramunt, S., Tobias, J. A., Baker, A., Aleixo, A., and Brumfield, A. T. (2012). Correlated evolution of beak morphology and song in the Neotropical woodcreeper radiation. *Evolution* **69**, 2784–2797. doi:10.1111/j.1558-5646.2012.01642.x
- Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist* **139**, 125–153. doi:10.1086/285308
- Franz, I., and Fontana, C. S. (2013). Breeding biology of the Tawny-Bellied Seedeater (*Sporophila hypoxantha*) in southern Brazilian upland grasslands. *The Wilson Journal of Ornithology* **125**, 280–292. doi:10.1676/12-059.1
- Freeman, P. W., and Lemen, C. A. (2008). Measuring bite force in small mammals with a piezo-resistive sensor. *Journal of Mammalogy* **89**, 513–517. doi:10.1644/07-MAMM-A-101R.1
- García, N., and Tubaro, P. L. (2018). Dissecting the roles of body size and beak morphology in song evolution in the "blue" cardinals (Passeriformes: Cardinalidae). *The Auk* **135**, 262–275. doi:10.1642/AUK-17-146.1
- Genbrugge, A., Herrel, A., Boone, M., Hoorebeke, L. V., Podos, J., Dirckx, J., Aerts, P. et al. (2011). The head of the finch: The anatomy of the feeding system in two species of finches (*Geospiza fortis* and *Padda oryzivora*). *Journal of Anatomy* **219**, 676–695. doi:10.1111/j.1469-7580.2011.01437.x
- Giraudeau, M., Nolan, P. M., Black, C. E., Earl, S. R., Hasegawa, M., and McGraw, K. J. (2014). Song characteristics track bill morphology along a gradient of urbanization in house finches (*Hamorhous mexicanus*). *Frontiers in Zoology* **11**, 83. doi:10.1186/s12983-014-0083-8
- Grant, B. R., and Grant, P. R. (1979). Darwin's finches: Population variation and sympatric speciation. *Proceedings of the National Academy of Sciences of the United States of America* **76**, 2359–2363.
- Grenier, J. L., and Greenberg, R. (2005). A biogeographic pattern in sparrow Bill morphology: Parallel adaptation to tidal marshes. *Evolution* **59**, 1588–1595. doi:10.1554/04-502
- Herrel, A., Podos, J., Huber, S. K., and Hendry, A. P. (2005). Bite performance and morphology in a population of Darwin's finches: Implications for the evolution of beak shape. *Functional Ecology* **19**, 43–48. doi:10.1111/fec.2005.19.issue-1
- Herrel, A., Podos, J., Vanhooydonck, B., and Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: A biomechanical basis for ecological speciation? *Functional Ecology* **23**, 119–125. doi:10.1111/fec.2009.23.issue-1
- Hoese, W. J., Podos, J., Boetticher, N. C., and Nowicki, S. (2000). Vocal tract function in birdsong production: Experimental manipulations of beak movements. *The Journal of Experimental Biology* **203**, 1845–1855.
- Huber, S. K., and Podos, J. (2006). Beak morphology and song features covary in a population of Darwin's finches (*Geospiza fortis*). *Biological Journal of the Linnean Society* **88**, 489–498. doi:10.1111/bij.2006.88.issue-3
- Lack, D. (1947). 'Darwin's Finches'. (Cambridge University Press: Cambridge, UK.)
- Linsens, H. F., Martens, M. J. M., Hendrikssen, H. J. G. M., Roestenberg-Sinnige, A. M., Browsers, W. A. J. M., van der Staak, A. L. H. C., and Strik-Jansen, A. M. J. (1976). The acoustic climate of plant communities. *Oecologia* **23**, 165–177. doi:10.1007/BF00361233
- Marler, P., Slabbekoorn, H. V., and Bowman, R. I. (2004). 'Nature's Music: The Science of Birdsong'. (Elsevier Academic: Boston, MA.)
- Martin, J. P., Doucet, S. M., Knox, R. C., and Mennill, D. J. (2011). Body size correlates negatively with the frequency of distress calls and songs of Neotropical birds. *Journal of Field Ornithology* **82**, 259–268. doi:10.1111/jof.2011.82.issue-3
- Mason, N. A., and Burns, K. J. (2013). Molecular phylogenetics of the neotropical seedeaters and seed-finches (*Sporophila*, *Oryzoborus*, *Dolospingus*). *Ornitologia Neotropical* **24**, 139–155.
- Mason, N. A., and Burns, K. J. (2015). The effect of habitat and body size on the evolution of vocal displays in Thraupidae (tanagers), the largest family of songbirds.

- Biological Journal of the Linnean Society* **114**, 538–551. doi:[10.1111/bij.12455](https://doi.org/10.1111/bij.12455)
- Morton, E. (1975). Ecological sources of selection on avian sounds. *The American Naturalist* **109**, 17–34. doi:[10.1086/282971](https://doi.org/10.1086/282971)
- Nowicki, S. (1987). Vocal tract resonances in oscine bird sound production: Evidence from birdsongs in a helium atmosphere. *Nature* **325**, 53–55. doi:[10.1038/325053a0](https://doi.org/10.1038/325053a0)
- Podos, J. (1997). A performance constraint on the evolution of trilled vocalizations in a songbird family (Passeriformes: Emberezidae). *Evolution* **51**, 537–551. doi:[10.1111/j.1558-5646.1997.tb02441.x](https://doi.org/10.1111/j.1558-5646.1997.tb02441.x)
- Podos, J. (2001). Correlated evolution of morphology and vocal signal structure in Darwin's Finches. *Nature* **409**, 185–188. doi:[10.1038/35051570](https://doi.org/10.1038/35051570)
- Podos, J., Huber, S., and Taft, B. (2004). Bird song: The interface of evolution and mechanisms. *Annual Review of Ecology, Evolution, and Systematics* **35**, 55–87. doi:[10.1146/annurev.ecolsys.35.021103.105719](https://doi.org/10.1146/annurev.ecolsys.35.021103.105719)
- Podos, J., and Nowicki, S. (2004). Beaks, adaptation, and vocal evolution in Darwin's finches. *BioScience* **54**, 501–510. doi:[10.1641/0006-3568\(2004\)054\[0501:BAAVEI\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0501:BAAVEI]2.0.CO;2)
- Price, J. J., and Lanyon, S. M. (2002). Reconstructing the evolution of the complex bird song in the oropendolas. *Evolution* **56**(7), 1514–1529. doi:[10.1554/0014-3820\(2002\)056\[1514:RTEOCB\]2.0.CO;2](https://doi.org/10.1554/0014-3820(2002)056[1514:RTEOCB]2.0.CO;2)
- R Core Team. (2016). 'R: A Language and Environment for Statistical Computing'. (R Foundation for Statistical Computing: Vienna, Austria.)
- Ratcliffe, L. M., and Grant, P. R. (1985). Species recognition in Darwin's finches (*Geospiza*, Gould). III. Male responses to playback of different song types, dialects and hetero-specific songs. *Animal Behaviour* **33**, 290–307. doi:[10.1016/S0003-3472\(85\)80143-3](https://doi.org/10.1016/S0003-3472(85)80143-3)
- Repenning, M., and Fontana, C. (2013). A new species of gray seedeater (Emberezidae: *Sporophila*) from upland grasslands of southern Brazil. *The Auk* **130**, 791–803. doi:[10.1525/auk.2013.12167](https://doi.org/10.1525/auk.2013.12167)
- Repenning, M., Rovedder, C. E., and Fontana, C. F. (2010). Another color morph of *Sporophila* Seedeater from the *capuchinos* group (Aves. Emberezidae). *Iheringia Série Zoologia* **100**, 369–378. doi:[10.1590/S0073-47212010000400012](https://doi.org/10.1590/S0073-47212010000400012)
- Richards, D. G., and Wiley, R. H. (1980). Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. *The American Naturalist* **115**, 381–933. doi:[10.1086/283568](https://doi.org/10.1086/283568)
- Roos, A. L. (2010). Capturando aves. In 'Ornitologia e Conservação: Ciência Aplicada, Técnicas de Pesquisa e Levantamento'. 1st edn. (Eds S. Von Matter, F. C. Straube, V. Q. Piacentini, I. A. Accordi, and J. F. Cândido Jr.) pp. 79–104. (Technical Books Editora: Rio de Janeiro.)
- Ryan, M. J., and Brenowitz, E. A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. *The American Naturalist* **126**, 87–100. doi:[10.1086/284398](https://doi.org/10.1086/284398)
- West, G. B., Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126.
- Westneat, M. W., Long, J. H. Jr., Hoese, W., and Nowicki, S. (1993). Kinematics of birdsong: Functional correlation of cranial movements and acoustic features in sparrows. *The Journal of Experimental Biology* **182**, 147–171.
- Wiley, R. H., and Richards, D. G. (1978). Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* **3**, 69–94. doi:[10.1007/BF00300047](https://doi.org/10.1007/BF00300047)
- Wilson, D. R., Bitton, P. P., Podos, J., and Mennill, D. J. (2014). Uneven sampling and the analysis of vocal performance constraint. *The American Naturalist* **183**, 214–228. doi:[10.1086/674379](https://doi.org/10.1086/674379)