Universidade de Brasília

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Ecologia

PROJETO DE MESTRADO

Latitude, clima e biodiversidade: o que influencia a complexidade do canto do tiziu *Volatinia jacarina*?

Edvaldo Ferreira da Silva Júnior

Orientadora: Regina H. F. Macedo

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“The Earth has music for those who listen”

George Santayana

SUMÁRIO

RESUMO

Animais podem codificar informações em seus sinais acústicos, em especial, o canto das aves pode ser notavelmente complexo, e ajustes nesse sinal acústico relacionados à frequência, duração e distribuição de energia podem indicar a identidade individual e a qualidade como parceiro. Hipóteses de seleção sexual e ecológica são comumente utilizadas para explicar a evolução de cantos complexos nas aves ao se considerar amplas áreas geográficas. Essas hipóteses predizem que a maior intensidade de seleção sexual e a maior disponibilidade do espaço acústico devem favorecer a evolução de cantos mais complexos em latitudes maiores, e em ambientes com sazonalidade acentuada e/ou menos espécies que compitam pelo espaço acústico. Entretanto, relativamente poucos estudos investigaram os padrões de complexidade do canto de aves para amplas escalas geográficas. Neste estudo, nós investigamos como a complexidade do canto do tiziu (*Volatinia jacarina*), espécie de ave Neotropical, varia ao longo de sua distribuição que se estende do México à Argentina. Para isso, utilizamos gravações disponíveis em bancos de dados *online*, e calculamos oito métricas do canto: largura de banda de frequência, duração do canto, entropia, frequência mediana, número de componentes do canto, número de inflexões por segundo, proporção de vibratos e taxa de canto. Nós observamos que a complexidade do canto do tiziu varia significativamente com a latitude, a sazonalidade climática, a riqueza de espécies de aves e o hemisfério. No entanto, contrário às nossas expectativas, a complexidade do canto prevalentemente diminuiu com o aumento da latitude, diminuiu com a sazonalidade climática, e aumentou com a riqueza de espécies de aves. Portanto, nossos resultados não corroboram o cenário de variação de complexidade do canto previsto pelas hipóteses de seleção sexual e ecológica. Nossos resultados também destacam que a complexidade do canto não varia uniformemente entre diferentes espécies de aves e entre diferentes parâmetros de complexidade do canto.

Estudos futuros que englobem mais espécies de aves irão ajudar a entender os padrões de complexidade do canto e fatores responsáveis pela evolução desses padrões para uma ampla escala geográfica.

Palavras-chave: adaptação acústica, gradiente latitudinal, Passeriformes, seleção sexual, variabilidade climática, variação geográfica no canto, *Volatinia jacarina*.

ABSTRACT

Animals can encode information within acoustic signals, particularly, bird songs can be remarkably complex and adjustments in this signal relative to features such as frequency, duration and energy can indicate individual identity and quality. There are two main sets of hypotheses that attempt to explain the evolution of increased song complexity across large-scale geographic ranges: (1) larger acoustic space availability, and (2) greater sexual selection intensity, both of which favor the evolution of more complex songs at higher latitudes, more seasonal and/or species-poor environments with less competition for the acoustic space. However, few studies have assessed patterns of birdsong complexity for birds with broad geographical ranges. Here, we investigated how song complexity varies across the distribution of the blue-black grassquit (*Volatinia jacarina*), a Neotropical bird that occurs from Mexico to Argentina and produces a monosyllabic song. Using recordings from online databases, we calculated song metrics, such as frequency bandwidth, duration, song rate and number of components of the song. We found that song complexity varies with latitude, climate variability, bird species richness and hemisphere. However, contrary to theoretical predictions, complexity mostly decreased with latitude and greater climate variability, while it was positively correlated with bird richness. Therefore, our findings did not support the main hypotheses proposed as explanations for song complexity. Our findings also highlight the fact that song complexity does not vary uniformly among songbird species and song parameters, and future studies encompassing more species should clarify patterns and drivers of song complexity evolution across broad geographic dimensions.

Key words: acoustic adaptation, environmental variability, geographical variation, latitudinal gradient, sexual selection, songbirds.

INTRODUÇÃO GERAL

REFERENCIAL TEÓRICO

Os sinais acústicos têm um importante papel na comunicação animal (Bradbury e Vehrencamp 2011). Nas aves, em particular, esses sinais podem codificar diversas mensagens e serem utilizados em diferentes contextos (Catchpole e Slater 2008; Geberzahn e Derégnaucourt 2020). O canto, por exemplo, pode ser usado no reconhecimento da espécie, defesa territorial e atração de parceiro sexual (Falls 1988; Nelson e Soha 2004; Catchpole e Slater 2008). As vocalizações também podem desempenhar um papel na sincronização de atividades reprodutivas (Schwabl e Sonnenschein 1992) e na sinalização contra predadores (Evans et al. 1993). Desta forma, é evidente que as diferentes funções dos sinais acústicos influenciam diretamente a capacidade de sobrevivência e reprodução das aves, sendo esses sinais importantes fatores na comunicação e sujeitos à evolução.

O canto das aves é um sinal acústico notavelmente complexo em algumas espécies e, de modo geral, métricas descritas em função da frequência, duração e energia do sinal acústico podem representar sua complexidade e estrutura (Kroodsma 2005; Catchpole e Slater 2008). Tais métricas incluem, por exemplo, a largura de banda de frequência, a duração, a entropia e a taxa de canto (i.e., cantos por unidade de tempo) (Figura 1). Além disso, métricas adicionais podem representar a variabilidade presente no canto, como o repertório de elementos produzidos ou a taxa de mudança dos elementos ao longo do tempo (veja Benedict e Najar 2019; Najar e Benedict 2019). Portanto, diferentes métricas podem caracterizar a complexidade do canto, mas não necessariamente todas essas estão sob pressões evolutivas convergentes (Benedict e Najar 2019).

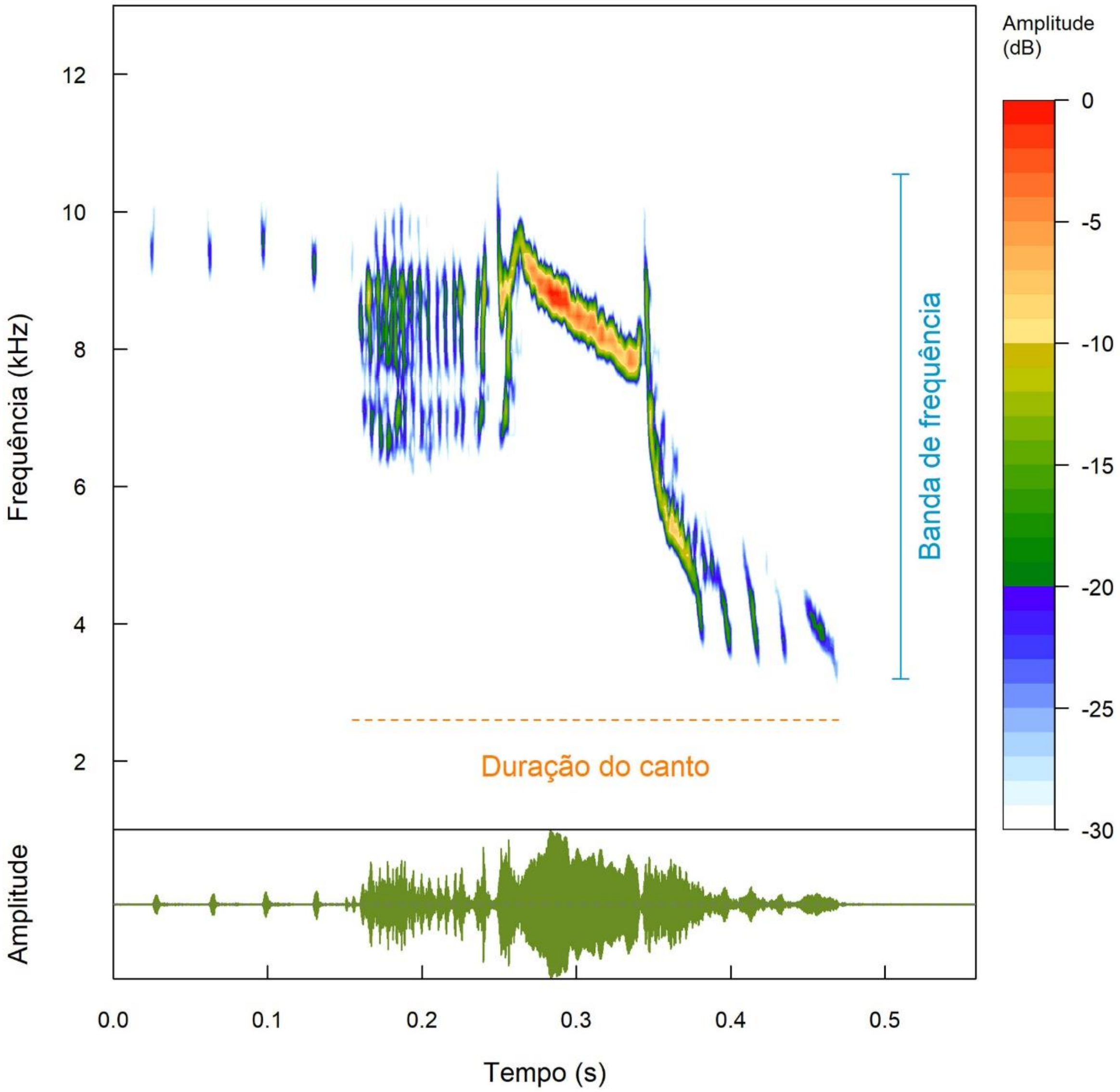

Figura 1. Espectrograma e oscilograma do canto do tiziu (*Volatinia jacarina*), espécie de ave Neotropical. A barra lateral indica a variação de amplitude da onda sonora em função de um gradiente de cores. Duas métricas do sinal acústico estão destacadas: a duração do canto e a largura de banda de frequência. Rodrigo Dela Rosa disponibilizou a gravação XC70652 na plataforma *online* de ciência cidadã Xeno-Canto.

Entender a relação entre a complexidade do canto e características ambientais, além de como esse sinal varia espacialmente ao longo da distribuição de uma espécie, pode nos ajudar a entender fatores ecológicos e evolutivos que moldaram a comunicação nas aves (Irwin 2000; Koetz et al. 2007; Weir et al. 2012; Kaluthota et al. 2016). No entanto, apesar da complexidade do canto das aves ser um tópico muito estudado, há relativamente poucos trabalhos de larga escala espacial sobre a variação da complexidade desse sinal, e os padrões relatados são diversos, pouco conclusivos e nem sempre comparáveis (Najar e Benedict 2019). Ademais, não há um consenso quanto aos mecanismos responsáveis pelos padrões observados (Najar e Benedict 2019). Há, pelo menos, 10 hipóteses propostas para explicar a variação de complexidade do canto nas aves (Singh e Price 2015). Porém, recentemente, Najar e Benedict (2019) dividiram essas explicações em dois grupos principais de hipóteses relacionadas à: (i) seleção sexual; e (ii) fatores ecológicos.

As hipóteses de seleção sexual apontam o aumento da complexidade do canto com a latitude, tendo como fundamento a intensidade da seleção sexual (Wei et al. 2017; Najar e Benedict 2019). Uma explicação para essa predição, por exemplo, é baseada na sazonalidade. Quanto mais distante dos trópicos (i.e., em latitudes maiores), mais acentuada é a sazonalidade e, portanto, menor o intervalo do período reprodutivo das aves (Wyndham 1986). Nesse contexto, a evolução de caracteres que indiquem a qualidade do indivíduo, como cantos mais complexos, seria favorecida visto que facilitaria a escolha do parceiro sexual e um rápido pareamento (Catchpole 1982). Por exemplo, observou-se que para espécies migratórias do gênero *Acrocephalus*, a felosa-palustre (*A. palustres*) é a última a chegar em sua área de reprodução e, portanto, tem um período reprodutivo curto. Em concordância com a hipótese de seleção sexual apresentada, os machos de felosa-palustre apresentaram os cantos mais elaborados entre as espécies do gênero estudadas (Catchpole 1982).

Sob outra perspectiva, mas com predições similares, as hipóteses ecológicas explicam o padrão de variação da complexidade do canto das aves com base no espaço acústico disponível e na eficácia de transmissão do sinal (Weir et al. 2012; Singh e Price 2015; Najar e Benedict 2019). Mais especificamente, em latitudes maiores há uma menor diversidade de animais potencialmente capazes de ocupar o espaço acústico utilizado pelas aves (Hillebrand 2004; Weir et al. 2012). Além disso, a vegetação costuma ser mais aberta e ter menos estruturas para atenuar e distorcer os sons produzidos por animais (Weir et al. 2012). Dessa forma, quanto mais próximo dos polos, maior a probabilidade e a possibilidade da evolução de cantos mais complexos e variados (Weir et al. 2012; Singh e Price 2015). Morton (1975), em um trabalho pioneiro, indicou que aves presentes em diferentes fisionomias vegetais (e.g., florestal, campestre) apresentam adaptações para transmissão do sinal acústico. Ademais, em ambientes com maior biodiversidade, a competição pelo espaço acústico pode ser acirrada e gerar pressões seletivas capazes de afetar o comportamento vocal das aves (Chitnis et al. 2020; Torres et al. 2020). Inclusive, em ambientes onde a interferência pelo ser humano no espaço acústico é alta, as aves podem apresentar adaptações, como cantos mais agudos (i.e., frequências maiores), de forma a evitar o mascaramento do sinal acústico pelo ruído antropogênico em frequências mais baixas (i.e., sons mais graves) ou vocalizar em horários alternativos, como pela noite (Slabbekoorn e Peet 2003; Fuller et al. 2007; Derryberry et al. 2020).

Conforme as predições das hipóteses de seleção sexual e ecológica, diferentes estudos apontam o aumento da complexidade do canto em direção às maiores latitudes (revisão em Najar e Benedict 2019). Por exemplo, para a corruíra (*Troglodytes aedon*), uma pequena ave de ampla distribuição na América – Canada à Terra do Fogo –, foi observado um aumento do número de elementos do canto em maiores latitudes tanto no hemisfério norte quanto no sul (Kaluthota et al. 2016). Em outro trabalho com aves do gênero *Phylloscopus*, na região dos Himalaias, também foi demonstrada a ocorrência de cantos mais complexos em latitudes maiores, tendo sido apontado que a menor diversidade de aves nessas latitudes deve ter sido uma condição importante para esse padrão observado (Singh e Price 2015). Entretanto, ressalta-se que há estudos que não indicaram variação latitudinal da complexidade do canto em algumas espécies de aves (Kroodsma e Verner 1987; Benedict e Bowie 2009), e, inclusive, estudos que apontaram um padrão de variação da complexidade do canto oposto ao predito pelas hipóteses de seleção sexual e ecológica (Pieplow and Francis 2011; Gordinho et al. 2015).

ESPÉCIE DE ESTUDO

Nós investigamos a relação entre a complexidade do canto, latitude, sazonalidade climática e riqueza de espécies em uma ave Neotropical de ampla distribuição, o tiziu (*Volatinia jacarina*). Essa espécie, um Passeriforme da família Thraupidae (Rising 2020), é comumente observada em áreas abertas, como formações campestres do bioma Cerrado ou áreas alteradas pelo ser humano (*e.g.* capinzais, arrozais) (Almeida e Macedo 2001; Sick 2001). Essa pequena ave granívora tem ampla distribuição, sendo observada do sul do México ao norte do Chile e da Argentina, e estando presente em todo o Brasil (Sick 2001; Rising 2020).

A espécie apresenta dimorfismo sexual (Figura 2). O macho tem asas e cauda maiores que a fêmea (Carvalho et al. 2007), além da plumagem nupcial negro-azulada e iridescente, resultado da deposição de queratina e de melanina durante a formação das penas (Sick 2001; Maia et al. 2009). Já a fêmea e machos jovens apresentam coloração críptica e amarronzada (Almeida e Macedo 2001; Maia et al. 2009). Provavelmente, o comportamento mais distinto e intrigante dessa espécie são os saltos dos machos durante o período reprodutivo, responsáveis pelo outro nome popular do tiziu, “saltador” (Sick 2001). Este comportamento faz parte do *display* sexual e multimodal da espécie que envolve tanto componentes visuais (e.g., salto e a exposição da coloração do macho), quanto componentes acústicos (e.g., canto e sons mecânicos produzidos pela batida de asas do tiziu) (Almeida e Macedo 2001; Sick 2001; Manica et al. 2014).

Figura 2. Adultos de tiziu *Volatinia jacarina*. Macho e fêmea (esquerda e direita, respectivamente).

Durante as exibições sexuais dos machos, três sinais acústicos são discerníveis (Webber 1985; Fandiño-Mariño e Vielliard 2004): (i) os elementos introdutórios; (ii) o canto que soa semelhante a "ti-síu" (Sick 2001); e (iii) o som mecânico produzido pelas asas durante o salto. De modo geral, o canto da espécie varia entre 2 e 13 kHz, dura cerca de meio segundo e é composto por uma única nota (Fandiño-Mariño e Vielliard 2004). Este canto tem três componentes principais, além dos elementos introdutórios (curtos chamados antes do típico "ti-síu"), sendo estes: (i) os vibratos; (ii) os arabescos; e (iii) as modulações simples. Estes componentes divergem principalmente quanto ao espectro de frequência que ocupam no tempo (Fandiño-Mariño e Vielliard 2004). Portanto, evidencia-se que o tiziu apresenta sinais acústicos distintos e que o canto, apesar de aparentemente simples, pode variar quanto à modulação de frequência e aos componentes principais (Fandiño-Mariño e Vielliard 2004).

Adicionalmente, destaca-se que o canto entre membros da espécie é altamente variado (Fandiño-Mariño e Vielliard 2004; Dias 2009). Um mesmo indivíduo adulto pode apresentar flexibilidade no canto entre estações reprodutivas, sendo a similaridade intra-individual deste sinal de cerca de 70%, e entre indivíduos (inter-individual), de 24% (Dias

2009; Rodrigues 2019). Dessa forma, pode haver dialetos para pequenas escalas geográficas (Dias 2009). Por fim, os machos ocupam pequenos territórios que variam entre 13 a 72 m^2 (Almeida e Macedo 2001). Observou-se que a abundância de alimento no território está correlacionada com o índice de desempenho do canto e a taxa de cantos por minuto (Dias 2009; Manica et al. 2014). Portanto, o sinal acústico pode indicar a qualidade dos machos no que tange à sua capacidade de defesa de um território rico em recursos.

OBJETIVOS DA DISSERTAÇÃO

Neste estudo, nós investigamos o padrão de complexidade do canto do tiziu em função da latitude, sazonalidade e riqueza de espécies de aves. Tivemos como objetivo verificar se as hipóteses de seleção sexual e ecológicas explicam a variação da complexidade do canto dessa espécie ao longo de sua área de ocorrência. Para abranger a ampla distribuição do tiziu, utilizamos gravações de canto dessa ave disponibilizadas em bancos de dados *online*, como em plataformas de ciência cidadã e em coleções audiovisuais. O estudo compreendeu duas abordagens, sendo que em um primeiro momento, investigamos a relação entre a complexidade do canto e a latitude. Posteriormente, em um segundo momento, investigamos a relação entre a complexidade do canto, a sazonalidade, e a riqueza de aves.

Para representar a complexidade e a estrutura do canto, calculamos oito métricas desse sinal acústico: largura de banda de frequência, duração do canto, entropia, frequência mediana, número de componentes do canto, número de inflexões por segundo, proporção de vibratos do canto, e taxa de canto (i.e., cantos por minuto). Para cada local onde a ave foi gravada, também coletamos dados de sazonalidade de precipitação e de temperatura a fim de representar a variabilidade climática. Também coletamos dados de riqueza de espécies de aves para representar o espaço acústico disponível ou ocupado.

Com base nas hipóteses de seleção sexual e ecológica, pode-se predizer um cenário de aumento da complexidade do canto com o aumento da latitude (Weir et al. 2012; Kaluthota et al. 2016; Wei et al. 2017), embora esse padrão não deva necessariamente se refletir em todas as métricas estudadas (Benedict e Najar 2019). Além disso, ao considerar as hipóteses ecológicas, tivemos como expectativa a ocorrência de cantos mais simples do tiziu em locais com maior riqueza de aves, dado que em tal condição, com mais espécies potencialmente capazes de ocupar o espaço acústico, haveria uma maior restrição para a evolução de sinais mais complexos (Weir et al. 2012; Singh e Price 2015). Por fim, ao considerar que é previsto uma maior intensidade de seleção sexual em ambientes com maior variabilidade climática (Macedo et al. 2008; Botero et al. 2009), tivemos como expectativa cantos mais complexos em locais com sazonalidade mais acentuada.

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CAPÍTULO 1

Song complexity varies with latitude, climate and species richness in a Neotropical bird

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LAY SUMMARY

Elaborate traits, such as complex bird songs, can encode information about individual identity and quality as a mate. Although birdsong is a well-studied topic, few studies have investigated how song complexity varies geographically across large-scale regions. Using recordings from online databases, we show that a broadly distributed tropical bird, the blue-black grassquit, usually sings simpler songs at higher latitudes. We also found that songs were mostly simpler in variable climates and/or in species-poor environments.

INTRODUCTION

Acoustic signals are used for communication in many animal taxa (Bradbury and Vehrencamp 2011; Fletcher 2014): from insects to mammals, vocalizations can be used for mate attraction and territorial defense (Catchpole and Slater 2008; Hou et al. 2017; Siracusa et al. 2017; Pettitt et al. 2020). Birdsong is a well-studied acoustic signal that can encode information about individual identity and quality (Catchpole and Slater 2008; Manica et al. 2017; Geberzahn and Derégnaucourt 2020). Additionally, birdsong traits can reflect phylogenetic relationships among species (Rendall and Di Fiore 2007; but see Cardoso et al. 2012). This signal can be remarkably complex and is subject to different mechanisms of evolution, such as cultural drift as well as natural and sexual selection pressures (Benedict and Bowie 2009; Weir et al. 2012; Kaluthota et al. 2016).

Assessing how song complexity varies across a species' distribution and its relationship with the environment can provide us with information about the evolution of organisms and their complex signals, besides providing a theoretical framework to predict ecological patterns of song variation (Irwin 2000; Koetz et al. 2007; Weir et al. 2012). However, despite the many existing studies about birdsong complexity, relatively few of them encompass extensive geographical dimensions, and the patterns of song complexity reported are not concordant and not always comparable (Najar and Benedict 2019). Song complexity is a broad concept that is variably defined in the scientific literature, and includes metrics such as repertoire size, song duration, bandwidth and song rate (i.e., songs per minute) (Benedict and Najar 2019; Najar and Benedict 2019). Nevertheless, these song metrics are not necessarily subjected to the same selective pressures, and thus they plausibly could vary in different directions, highlighting the fact that the song complexity concept should be clearly defined to become comparable between studies (Benedict and Najar 2019).

Different studies have shown that song complexity tends to increase towards the poles, or in temperate regions relative to the tropics (e.g., Irwin 2000; Weir et al. 2012; Kaluthota et al. 2016). Hypotheses to explain this pattern have been based on ecological and/or sexual selection pressures (Najar and Benedict 2019). The ecological hypotheses, which include the “acoustic adaptation hypothesis” and the “acoustic niche hypothesis”, consider the effective transmission of the signal under varying ecological conditions (Morton 1975; Rothstein and Fleischer 1987; Krause 1993; Ey and Fischer 2009; Najar and Benedict 2019). Environmental features, such as vegetation structure and frequency space availability, can affect acoustic communication and, therefore, song evolution (Weir et al. 2012). For instance, because there is a latitudinal gradient in species diversity for different organisms (Hillebrand 2004), more species tend to occupy the acoustic space (i.e., frequency window) available in lower latitudes (Weir et al. 2012; Singh and Price 2015). In addition, habitats with higher vegetation densities, such as tropical rainforests in lower latitudes, can attenuate higher frequencies (i.e., 6.5–10 kHz) (Morton 1975; Weir et al. 2012) and distort acoustic signals through reflection, reverberation and absorption (Morton 1975; Wiley and Richards 1978). It has been suggested that together, these environmental features may have restricted song complexity, driving the evolution of simpler bird songs in lower latitudes (Weir et al. 2012). Alternatively, lower competition for acoustic space associated with the lower levels of habitat attenuation and degradation of sounds in higher latitudes might have provided a better context for the evolution of more complex songs comprising multiple frequencies (Weir et al. 2012).

The sexual selection hypotheses, on the other hand, predict the evolution of more complex songs in higher latitudes due to the postulated higher intensity of sexual selection pressure in these regions (Kaluthota et al. 2016; Wei et al. 2017). One explanation for the higher intensity of sexual selection in higher latitudes entails its greater seasonality (i.e., higher climate variability), which constrains breeding opportunities during the year to a narrower window of time (Wyndham 1986). In this scenario, sexual selection pressure might have favored the evolution of elaborate traits, such as complex songs, which indicate individual quality, facilitating mate choice and rapid pair formation (Catchpole 1982). In addition, difficult and physically challenging songs can also be used as cues for mate choice (Vallet et al. 1998; Ballentine 2009), therefore under more intense selection pressure in higher latitudes.

Another explanation involves the presumed relation between extrapair fertilization (EPF) rates and breeding synchrony (Stutchbury and Morton 1995; but see Spottiswoode and Møller 2004). In seasonal habitats in higher latitudes (i.e., temperate regions), a high breeding synchrony could increase the availability of fertile females, as well as the opportunity for females to assess the sexual displays (i.e., quality) of multiple males simultaneously (Stutchbury and Morton 1995). In such a context, with more synchronous breeding opportunities, EPF may be relatively simpler to achieve, which could lead to increased sexual selection pressure (Stutchbury and Morton 1995). In aseasonal tropical habitats, however, animals can breed asynchronously, leading to higher costs to obtain extrapair mates. Furthermore, Macedo et al. (2008) pointed out that climate variability could increase EPF not only in temperate regions but also in high-seasonality localities in the tropics. Taken together, these predictions, which indicate greater intensity of sexual selection in environments with more variable climates, also encompass the idea that more intense selection on bird song should occur in regions with higher seasonality (Botero et al. 2009).

In this study, we investigated the relationship between song complexity metrics and latitude, climate variability and bird species richness across the distribution of the blue-black grassquit (*Volatinia jacarina*), a Neotropical bird that occurs from Mexico to

Argentina (Sick 2001; Rising 2020). Blue-black grassquits perform conspicuous sexual displays, including visual (i.e., leaps) and acoustic (i.e., song) signals, during its breeding season (Sick 2001; Manica et al. 2017). This socially monogamous bird occurs across the Neotropical region and is subject to different climatic conditions (Sick 2001; Manica et al. 2016; Rising 2020). There are indications that sexual selection shaped this bird's courtship display, because females prefer to pair socially with males that exhibit higher leaps in the display (Manica et al. 2016), and song duration is correlated positively with leap height (Manica et al. 2017). Additionally, females can potentially assess a male's territory quality through song metrics, such as song rate, which is correlated with territory food availability (Manica et al. 2014). Lastly, males with higher leaps and longer songs have more success in obtaining extrapair fertilizations (Manica et al. 2020), which occur in 11% to 47% of all broods in the species (Manica et al. 2016). The blue-black grassquit is well-suited as our model species because: 1) it occurs across a broad geographical scale encompassing different levels of climate variability; 2) it performs a conspicuous sexual display, enabling easy records of the behavior; 3) it produces a simple song, but which is remarkably variable among individuals (Figure 1) (Fandiño-Mariño and Vielliard 2004); and 4) there are indications that the species' song may be under sexual selection pressure (see Byers 2011).

To obtain song data to cover the entire geographic range of the blue-black grassquit, we retrieved recordings available in online databases from citizen science projects and audiovisual collections. We adopted two approaches to determine patterns of geographical variation of song. First, we assessed the relationship between song complexity metrics and latitude. Secondly, we investigated the relationship between song complexity, climate variability and bird richness considering the specific areas where the grassquits were recorded. To represent song complexity, we calculated

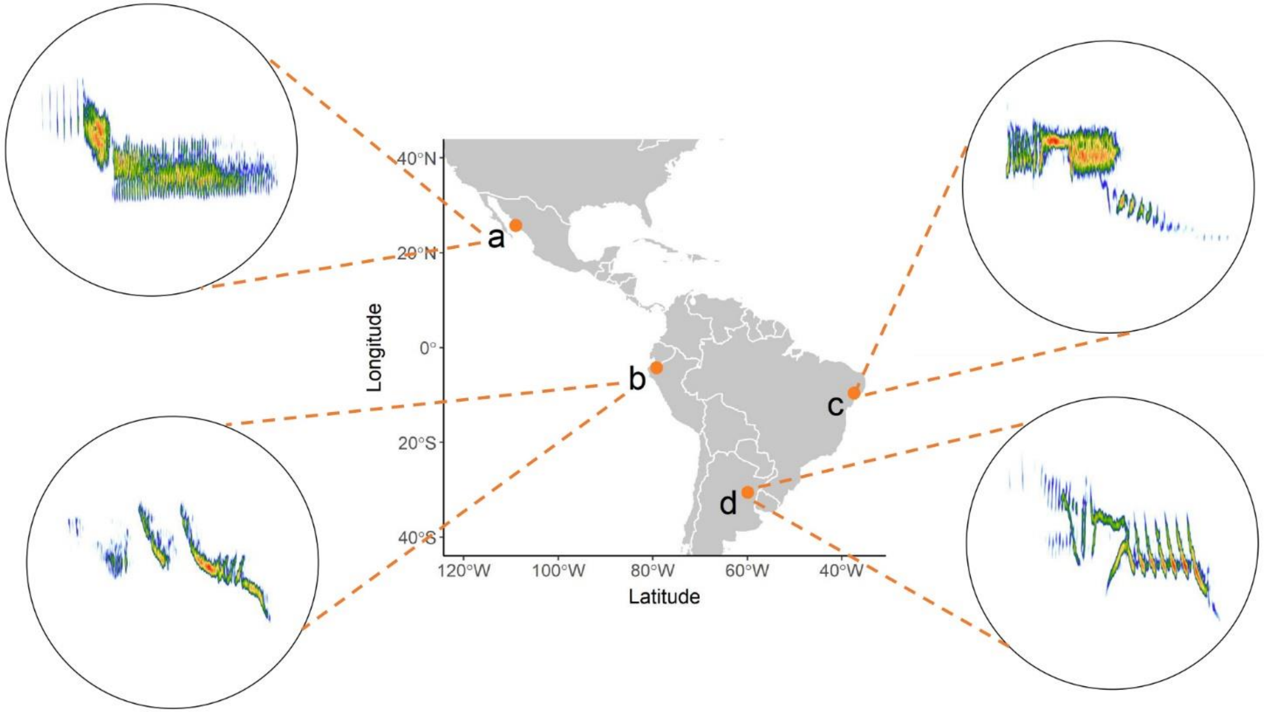

Figure 1. Spectrograms of blue-black grassquit songs recorded in different locations across the distribution range of the species. Notice the remarkable variability in the structure of the song among different individuals. (a) Manuel Grosselet, (b) Jerome Fischer, (c) Pedro Têia and (d) Bernabe Lopez-Lanus provided the recordings XC489743, XC207196, XC105631 and XC47146 to Xeno-Canto database, respectively.

metrics of song structure, elements and performance, such as song duration, frequency bandwidth, song rate and proportion of vibratos. To represent climate variability, we retrieved data on precipitation and temperature seasonality, and to represent the available acoustic space, we used data on bird species richness.

Based on the ecological and sexual selection hypotheses, we expected a positive correlation between blue-black grassquit song complexity and latitude, with more complex songs towards the poles (i.e., higher latitudes) (Weir et al. 2012; Kaluthota et al. 2016; Wei et al. 2017), although not necessarily for all complexity metrics (Benedict and Najar 2019). Moreover, specifically associated with the ecological hypotheses, we expected a decrease in song complexity as bird richness increased. A higher number of species occupying the acoustic space available in the environment could have increased acoustic interference and have constrained bird song evolution (Weir et al. 2012; Singh and Price 2015). Finally, based on the concept that sexual selection pressures may be greater in more variable environments (Macedo et al. 2008; Botero et al. 2009), we expected more complex songs in localities with higher seasonality.

METHODS

Study species

The blue-black grassquit is a small granivorous passerine that inhabits open areas, such as grasslands in natural and urban areas (Almeida and Macedo 2001; Sick 2001; Rising 2020). This species has a broad geographical range, occurring from southern Mexico to northern Chile and northern Argentina (Sick 2001; Rising 2020), with three recognized subspecies (Rising 2020). During its breeding season, males acquire an iridescent blue-black plumage and perform a conspicuous multimodal display, which entails visual (i.e., leap and plumage exhibition) and acoustic (i.e., song and wing mechanical sounds) signals (Sick 2001; Manica et al. 2017).

Males produce a short song with a single note usually preceded by introductory elements. The song varies from 2 to 13 kHz, and its frequency modulation decreases from the beginning to the end of the signal (Fandiño-Mariño and Vielliard 2004). Each male has a unique song that is repeated with high fidelity (i.e., high similarity), and which could be considered an individual signature (Fandiño-Mariño and Vielliard 2004). Despite being seemingly a simple song, it is remarkably variable among individuals and can be described as a function of different components (Fandiño-Mariño and Vielliard 2004) (Figures 1 and 2).

In this study, similarly to Fandiño-Mariño and Vielliard (2004), we also describe the blue-black grassquit song through three types of components: vibratos, isolated modulations and arabesques. We excluded introductory elements, because they are of low amplitude and low regularity (Fandiño-Mariño and Vielliard 2004; Dias 2009). Here, we defined vibratos as similar elements that are usually repeated more than 10 times, and which exhibit a compact structure i.e., short time interval between elements. We considered that songs contained two consecutive vibratos whenever the element types or elements' frequency interval (i.e., bandwidth) and degree of compression of the elements within each vibrato differed substantially. Our definition of vibrato matches the descriptions of "trills", "vibrations" and "slow and fast buzzes" presented in other studies (Podos 1997; Fandiño-Mariño and Vielliard 2004; Diniz et al. 2015). Isolated modulations were defined as variable structures repeated 2–10 times, with frequency intervals typically greater than that of vibratos, in addition to having a longer silent interval between repetitions. We considered that isolated modulations were independent when there were sets of repetitions with different element types in each one. However, a

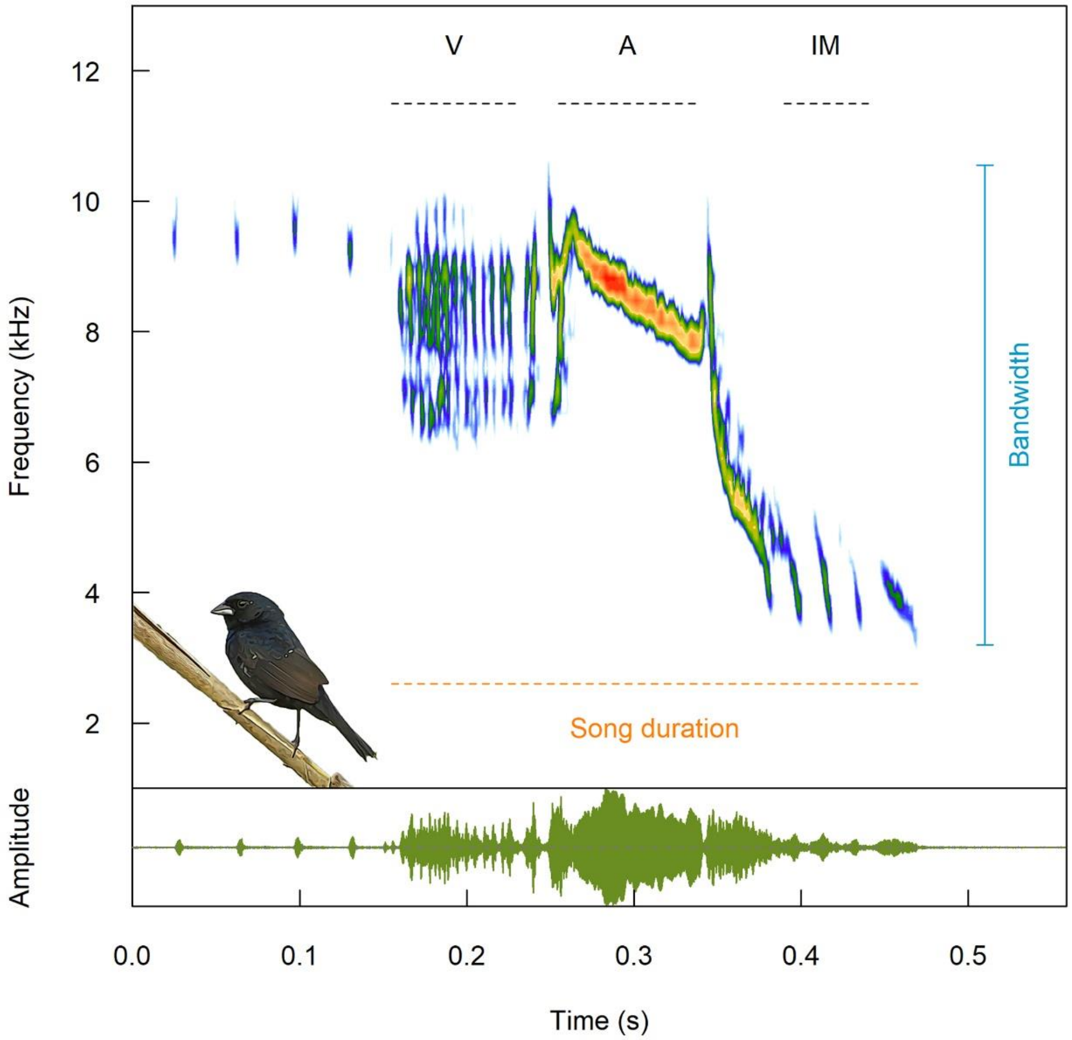

Figure 2. Spectrogram and oscillogram of a blue-black grassquit song with some measured metrics highlighted. Examples of the main components of the song are indicated: "V" = vibrato; "A" = arabesque; "IM" = isolated modulations. Introductory elements of the song can be seen before the vibrato. Rodrigo Dela Rosa provided this recording (XC70652) to Xeno-Canto database.

sequence of different elements, i.e., without the same-type elements repeated sequentially, was considered as a single isolated modulation. Our definition, although observing strict specifications, is similar to that of "isolated modulations" previously proposed for the species (Fandiño-Mariño and Vielliard 2004). Finally, arabesques were defined as components with a narrow frequency interval (~1 kHz) and a compact structure of repeated elements, following Fandiño-Mariño and Vielliard (2004). Whenever we found unusual song structures for the first time, we assessed the specific structure of its main component to determine the best fit considering the definitions above.

Song complexity

We measured eight acoustic metrics to represent complexity and structure of the blue-black grassquit song. For more details concerning the first six metrics, see Araya-Salas and Smith-Vidaurre (2017) and Benedict and Najar (2019):

1. Duration (s) = time elapsed between the beginning and the end of the song.
2. Entropy = measure of energy disorder through time and frequency spectrum of the song. Pure tones i.e., sounds with constant frequency have entropy values near zero, while noisy sounds that encompass a broad frequency spectrum tend to one.
3. Median frequency (kHz) = the frequency where the song is split in two frequency intervals with the same amount of energy (50%).
4. Bandwidth (kHz) = the frequency interval between maximum and minimum frequencies of the song.
5. Inflections per s = number of changes in a frequency contour of the song per second. For example, a shift from increasing to decreasing frequency in an acoustic signal is considered one inflection.

6. Song rate (songs per min) = number of songs produced per minute, also referred to as “delivery” (Benedict and Najar 2019) and “song output” (Manica et al. 2014).
7. Number of components = sum of the numbers of vibratos, arabesques and isolated modulations.
8. Proportion of vibratos (%) = number of vibratos divided by number of components.

Following other studies, we considered that more complex songs have longer duration, more elements, higher degree of frequency modulation and/or occupy a wider frequency interval (Singh and Price 2015; Kaluthota et al. 2016; Wei et al. 2017; Benedict and Najar 2019). Therefore, higher complexity could be expressed by higher values of duration, entropy, bandwidth, inflections per second and/or number of components. Because song rate is a vigor attribute, performing at higher rates may be difficult, costly and represent a trade-off with skill-based attributes (Manica et al. 2017). Moreover, frequency is negatively correlated with body size in birds (Bradbury and Vehrencamp 2011), and low-frequency vocalizations are less attenuated by habitat features (Morton 1975; Weir et al. 2012). Thus, median frequency could be a target of ecological and sexual selection. Finally, parts of a song can be challenging to produce in certain ways. For example, increasing trill rate, a vibrato-like structure, without changing frequency bandwidth can be anatomically challenging for the bird (Podos 1997). Regarding the specific components of the blue-black grassquit song, we only investigated the proportion of vibratos, because it is more strongly correlated with the other components of the song (proportion of arabesques and isolated modulations), and may be a difficult feature for the bird to produce.

Song data and measurements

To assess patterns of variation in song complexity of the blue-black grassquit across its entire range distribution, we used recordings available from online databases: Xeno-Canto (www.xeno-canto.org), Macaulay Library at the Cornell Lab of Ornithology (www.macaulaylibrary.org), WikiAves (www.wikiaves.com.br) and Fonoteca Neotropical Jacques Vielliard (FNJV) (www2.ib.unicamp.br/fnjv). We gathered these recordings in February and March 2020, except for FNJV, which were retrieved in July 2020. As a first quality filter of our dataset, we used only recordings with minimum values of sample rate (44.1 kHz) and bit depth (16-bits) (Abrahams 2018). Because the filtered recordings still contained different audio settings, we standardized file format (WAV), sample frequency (44.1 kHz) and bit-depths (16-bits) in Adobe Audition 8.0.0. We also filtered out frequencies below 1.5 kHz and above 14 kHz (i.e., bandpass filter) from the recordings to exclude low- and high-frequency noise and to facilitate acoustic measurements.

Whenever the metadata did not have specific geographical coordinates, we used the stated locality and recorders' comments to estimate the coordinates with Google Maps. We eliminated recordings that lacked information about the bird's location. Moreover, there were recordings for the same stated location, ranging from 1 to 6 recordings, but from different authors and/or dates. In such cases, we assumed that recordings were from different grassquits, and despite shared coordinates, the birds might have been recorded on different perches. Therefore, to be more accurate and avoid further statistical problems, we sequentially added 0.0001° in longitude values (~ 11.1 m) to recordings that had the same original coordinates. Thus, for a location with six recordings, for example, the last one identified had 0.0005° added to its longitude value (~55.5 m). Duplicated recordings and different recordings from the same individual were identified based on both metadata and sonograms (vocal signature). In such situations, we kept only the recording with the best quality.

We selected the beginning and the end of up to three songs per recording to calculate acoustic metrics. For song rate measurements, we used only recordings with duration of at least 21 s, and selected uninterrupted song bouts from 15 s to 120 s. Song bout duration was defined by the start of the first song and the start of the last song with good quality, considering signal energy and background noise. Thus, song rate was the number of songs within the song bout divided by bout duration. We considered the end of a song bout and the start of another when the silent interval between songs was ~15 s, but if there were several calls during this silent interval, we usually considered ~10 s as sufficient, because the animal could be exposed to an unusual context. We only considered one song bout per recording, usually the longest one, but for some recordings we kept the ones with less background noise. Finally, we verified if there was a relationship between song rate (natural log-transformed) and song bout duration (linear model, $F = 0.11$, df = 1, p = 0.74; *Anova* function, *car* package, Fox and Weisberg 2019), before further statistical analyses. All these acoustic measurements were conducted using the spectrogram and oscillogram in Raven Pro 1.6 (settings, window: blackman, window length: 256, overlap: 89.8) (Cornell Lab of Ornithology, www.ravensoundsoftware.com).

While we selected songs and song bouts, we assigned quality categories to each song and recording, based on signal energy, background noise and level of edition of the audio file. We eliminated poor quality recordings after this visual inspection. Before measuring song complexity metrics, we also filtered out recordings with signal-to-noise ratio (SNR) lower than 2 dB (*sig2noise* function, *warbleR* package; settings, margin: 0.1, type: 3) (Araya-Salas et al. 2017; Araya-Salas and Smith-Vidaurre 2017).

Duration, entropy, median frequency, bandwidth and inflections per second were calculated for each song with *warbleR* package in R (settings, window: blackman, window length: 256, window length for measurements on the frequency domain: 1024, overlap: 50) (Araya-Salas and Smith-Vidaurre 2017). For bandwidth, we calculated maximum and minimum frequencies using the threshold method, which is suggested over the "by-eye" approach and to estimate bandwidth for selected songs with different noise levels (Podos 1997; Ríos-Chelén et al. 2016; Araya-Salas et al. 2017; Ríos-Chelén et al. 2017). We adopted an amplitude threshold of -18 dB in relation to the peak frequency, and we smoothed the power spectrum to reduce the effect of amplitude peaks throughout the frequency interval of the song. We used the same settings as above, adding the smooth feature (smooth = 1). For further analyses, we eliminated samples with inaccurate selections of bandwidth. To calculate the complexity metric relative to inflections per second, we used dominant frequency values. Finally, we counted the number of each component of the songs during the inspection of spectrograms and oscillograms of the recordings.

In total, we compiled 992 recordings of blue-black grassquits. We eliminated 28 after the first quality filter based on sample rate and bit-depth, and one additional file was corrupted, which left us with 963 recordings from Xeno-Canto (n = 233), Macaulay Library (n = 223), WikiAves (n = 436) and FNJV (n = 71). After additional quality filtering and exclusion of duplicated recordings, the final sample was different for each song metric: n = 558 for duration, entropy, median frequency and inflections per second; n = 480 for bandwidth; n = 377 for song rate; n = 483 for number of components and proportion of vibratos. Presumably, each recording represents a song from a different blue-black grassquit male. To illustrate blue-black grassquits song, we used *seewave* package (Sueur et al. 2008) to generate spectrograms and oscillograms.

Climate and bird richness data

To determine patterns of variation in song complexity of the blue-black grassquit as a function of climate and bird species richness, we also collected data from the WorldClim v2 database (Fick and Hijmans 2017; www.worldclim.org) and BiodiversityMapping.org website (www.biodiversitymapping.org). Climatic data for each grassquit song recording locality included data on precipitation and temperature seasonality (i.e., bioclimatic variables 04 and 15 from WorldClim; spatial resolution of 4.6 X 4.6 km). These bioclimatic variables are based on monthly variation of precipitation and temperature for a temporal range of thirty years (1970–2000), where higher values indicate higher climate variability (seasonality) (O'Donnell and Ignizio 2012). We used these variables as indicatives of environmental variability, which we assume could reflect the pressure of sexual selection on bird song (Irwin 2000; Botero et al. 2009). Overall, WorldClim database is a global spatially interpolated climate surface, based on monthly measurements of temperature and precipitation (Hijmans et al. 2005).

Regarding species richness, we collected data on total bird species richness for each grassquit song recording locality. We used a spatial dataset with resolution of 10 X 10 km to retrieve richness data, previously published by Jenkins et al. (2013). This global dataset on bird richness was created from species' range maps gathered by BirdLife International (www.birdlife.org) and Handbook of the Birds of the World, now merged into the Birds of the World database (Billerman et al. 2020). In this study, we assume that bird richness represents acoustic space availability, a factor that can influence the evolution of complex bird songs (Singh and Price 2015; Weir et al. 2012). All climate and richness data were retrieved from raster data (GeoTIFF) using the *raster* package in R (Hijmans et al. 2020).

Statistical analyses

We analyzed our data using two approaches. First, to investigate the prediction that song complexity increases towards the poles (i.e., higher latitudes), we fitted models for each song metric as a function of latitude. Because land masses, oceans and other potential variables differ between hemispheres (Leslie et al. 2012; Kang et al. 2015), we fitted separate models for the northern and southern hemispheres. For ease of comprehension, we used the absolute value of latitude for the southern hemisphere. Second, to investigate the prediction that song complexity increases with sexual selection pressure but decreases with competition for available acoustic space, we fitted models for each song metric as a function of temperature seasonality, precipitation seasonality and bird richness. We also added hemisphere (northern or southern) as a predictor factor in our models to avoid a possible confounding variable. We analyzed our data in R environment v. 4.0.3 (R Core Team 2020).

Initially, we fitted Linear Models (LMs), Generalized Linear Models (GLMs) or "glmmTMB" models (Brooks et al. 2017) depending on the nature of the response variables. We also determined the family of error distribution based on the nature of the response variables (continuous: Gaussian; count: Poisson, Zero-truncated Poisson or Zero-truncated Conway-Maxwell-Poisson; proportion: Binomial or Quasi-Binomial) (Appendix Table A1) (Zuur et al. 2009; Brooks et al. 2017). We considered the number of inflections per second and song rate (i.e., number of songs per minute) as continuous variables, while the number of components was considered a discrete variable. Because we had up to three selected songs per recording, we dealt with pseudo replication by calculating the mean value of each metric per recording (Hurlbert 1984), an approach that was not applicable for song rate. Relative to the number of components, we subsequently rounded values before fitting the models. In addition, regarding the proportion of vibratos, we rounded the numbers of each main component of the song and recalculated the total number of components based on these values, then used this dataset to fit the model.

We checked model residuals and assumptions as follows: 1) normality was tested using a Kolmogorov-Smirnov test, and when that was not applicable we used a Shapiro-Wilk test; 2) homogeneity was verified through inspection of residuals versus fitted plots; 3) collinearity was checked using the variance inflation factor (VIF) after model fitting, and we considered values below 10 as acceptable levels (Kutner et al. 2004); 4) dispersion was checked with the *DHARMa* package that we also used to verify normality and homogeneity whenever possible (Hartig 2020). We also natural log-transformed response variables (for proportion data, we used arcsine transformation instead) to verify whether the model assumptions improved. We checked outliers using Cleveland's Dot plots of response variables, and Cook's distances (threshold = 1) (Dhakal 2017). Whenever we found visual outliers, we fitted additional models without them to verify whether model fitting improved. If not, we kept all sample units. The model regarding entropy as a function of latitude for the southern hemisphere was the only one that improved (see Appendix Tables A2), and we present results for both models i.e., with and without outliers. Finally, spatial autocorrelation was checked with Moran's I autocorrelation coefficient using the *ape* package in R (Paradis and Schliep 2019). Because several models showed spatial autocorrelation, we also fitted Generalized Least Square models (GLS) including spatial correlation structures (Zuur et al. 2009), and spatial models using Matérn function (hereafter "spaMM models") (Rousset and Ferdy 2014).

Since we fitted GLS models with different correlation structures for each acoustic metric, we selected the model with the lowest Akaike's Information Criterion (AIC) to proceed. Later, we selected one best model for each variable based on fulfilled assumptions. We determined the significance of predictors using Type II Wald chi-square tests (*Anova* function, *car* package, Fox and Weisberg 2019), and whenever this was unattainable, we used likelihood ratio tests based on χ^2 or F statistics (*drop1* function, *stats* package, Zuur et al. 2009) (Appendix Tables A1–A3). Because of multiple testing, after selecting the final best fitted models, we adjusted P values based on the False Discovery Rate approach (FDR) (Benjamini and Hochberg 1995; Jafari and Ansari-Pour 2019). The values were independently adjusted for each predictor. Despite fitting different models and selecting the best ones, not all models fulfilled all assumptions (see footnotes in Tables 1 and 2), and results from these models should therefore be interpreted with caution (see Appendix Tables A2 and A3).

Finally, all figures and maps were produced in R environment v. 4.0.3 (R Core Team 2020). To illustrate the spatial variation of song complexity across the blue-black grassquit distribution, we fitted spaMM models considering the predictors seasonality, bird richness and hemisphere. Subsequently, we used *filled.mapMM* function from *spaMM* package to perform interpolation and mapping (Rousset and Ferdy 2014). Regarding models including multiple explanatory variables, we also generated plots to show the relationship between song metrics and a single predictor. To produce these plots, we fixed the non-focal variables to their medians and then estimated the predicted values. We back-transformed number of inflections per second to produce the plots. Regarding GLS models, we used *AICcmodavg* (Mazerolle 2020) and *sjPlot* (Lüdecke 2021) packages to calculate predicted values, and their associated standard errors and 95% confidence intervals.

RESULTS

Song complexity mostly decreases with latitude

In general, our results are contrary to our prediction of an increase in song complexity with latitude (i.e., towards the poles) (Figures 3 and 4, Table 1). For the northern hemisphere, this decrease in song complexity included entropy (GLS, correlation structure: exponential, $\chi^2 = 5.91$, $P = 0.043$), bandwidth (GLS, correlation structure: rational quadratic, $\chi^2 = 7.92$, $P = 0.028$) and number of inflections per second (GLS, correlation structure: exponential, $\chi^2 = 5.95$, $P = 0.043$). The only exception was the proportion of vibratos that increased with latitude (GLS, correlation structure: linear, $\chi^2 = 75.66$, $P < 0.001$). Song duration, median frequency, song rate and number of components did not show a statistically significant relationship with latitude in the northern hemisphere.

For the southern hemisphere, song complexity as expressed by duration decreased with latitude (GLS, correlation structure: rational quadratic, $\chi^2 = 23.64$, $P < 0.001$), although entropy increased slightly with latitude (GLS with no correlation structure, $\chi^2 = 6.07$, $P < 0.043$). However, the best fitted model did not show a statistically significant effect of latitude on entropy (“scale entropy” without outliers; spaMM, $\chi^2 = 3.70$, $P = 0.103$). All other variables did not vary with latitude in the southern hemisphere.

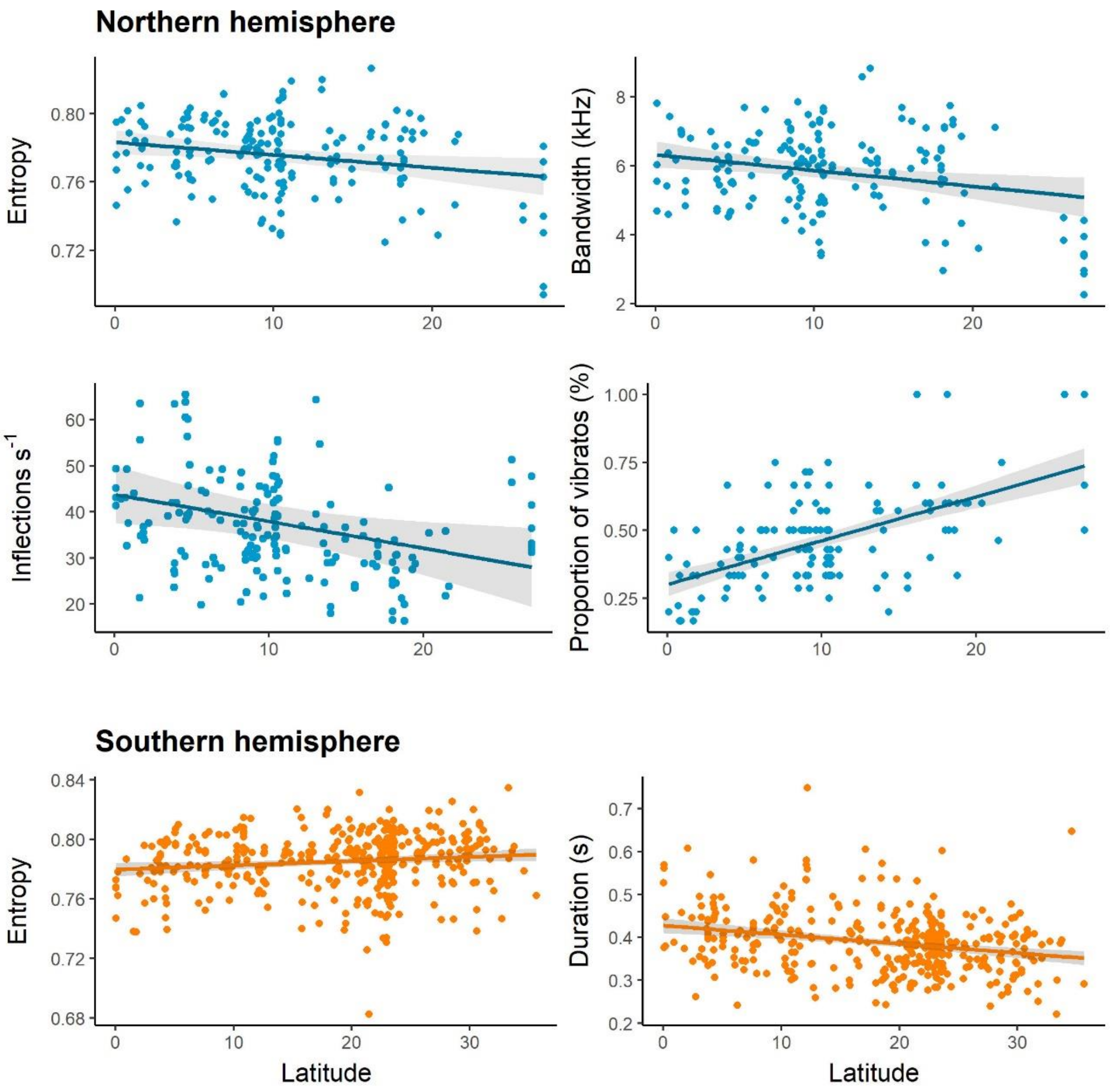

Figure 3. The relationship between latitude and song complexity metrics of the blue-black grassquit in northern and southern hemispheres across the Neotropical region. Entropy is a measure of energy disorder through the time and frequency spectrum of the song; bandwidth represents the difference value between maximum and minimum frequencies; inflections s^{-1} are the number of inflections per second; proportion of vibratos is the percentage of vibrato-like structures in the song; and duration is the song duration in seconds. The solid line indicates the predicted values from Generalized Least Squares models and ribbons show the 95% confidence intervals. Samples, average metric values from up to three songs per recording, are shown by dots (northern hemisphere: n = 179 recordings for entropy and inflections s^{-1}, n = 163 recordings for bandwidth, and n = 161 recordings for proportion of vibratos; southern hemisphere: n = 379 recordings for entropy and duration).

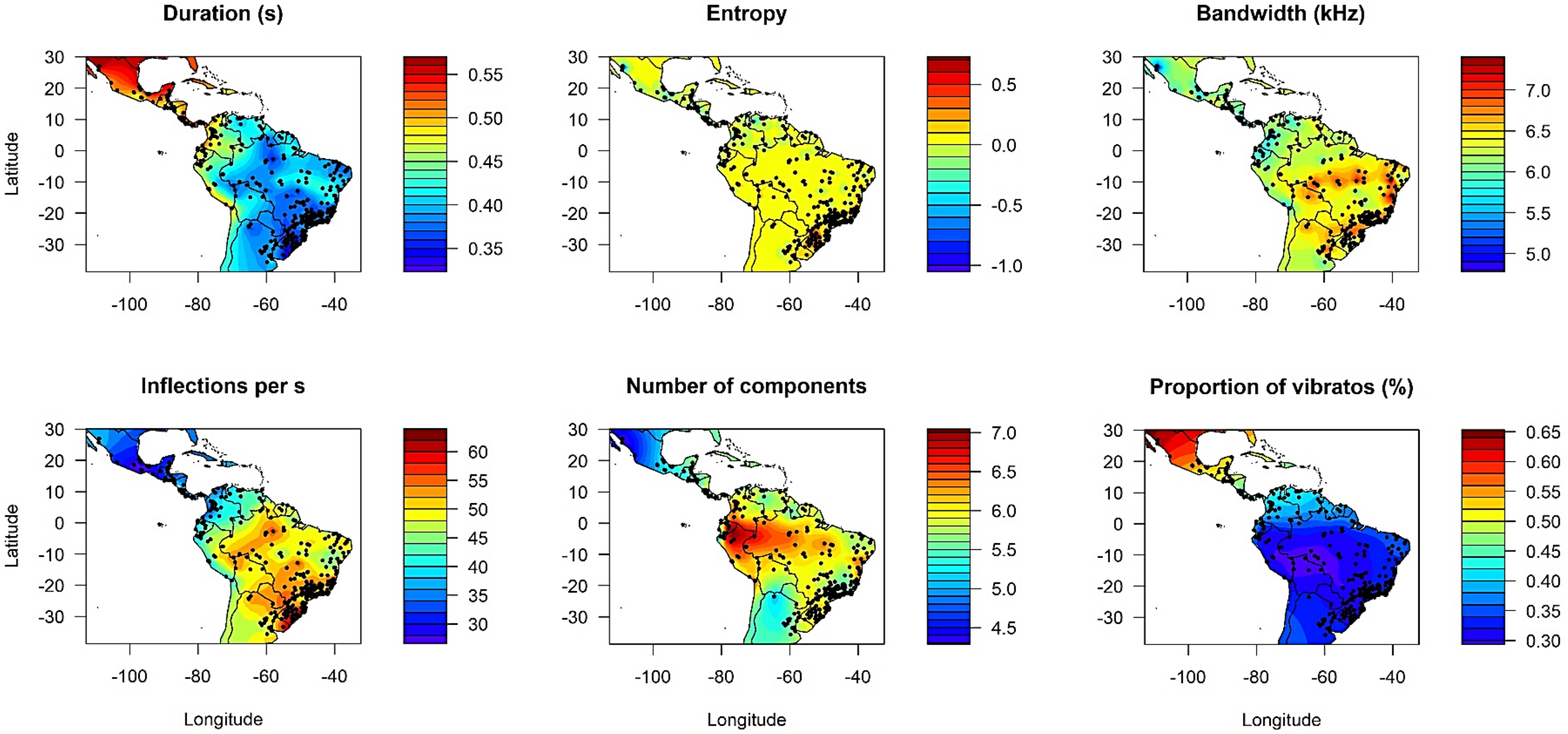

Figure 4. Maps of predicted values of song complexity metrics of the blue-black grassquit across its distribution range in the Neotropical region. Values for each song metric are indicated by a gradient from cool to warm colors i.e., dark blue and dark red indicate the lower and higher values, respectively. Duration is the song duration in seconds; entropy is a measure of energy disorder through the time and frequency spectrum of the song; bandwidth represents the difference value between maximum and minimum frequencies; inflections s^{-1} are the number of inflections per second; number of components is the average number of single components per song; and proportion of vibratos is the percentage of vibrato-like structures in the song. Spatial models (model formula: song metric ~

precipitation seasonality + temperature seasonality + bird richness + hemisphere) were used to estimate predicted values and make interpolation maps in R environment (filled.mapMM function, spaMM package). Samples, average metric values from up to three songs per recording, are shown by dots (duration, entropy and inflections s^{-1}: n = 558 recordings; bandwidth: n = 480 recordings; number of components and proportion of vibratos: n = 483 recordings).

Table 1. Results of best fitted models to test for effects of latitude on the song complexity metrics of the blue-black grassquit. All models are generalized least squares (GLS), except for scale entropy (spaMM), number of components for northern (spaMM) and southern (glmmTMB) hemispheres, and proportion of vibratos for southern hemisphere (GLM). We present results of Type II Wald chi-square tests or likelihood ratio tests based on χ^2 or F statistics, P values, model coefficient and correlation terms when applicable

	Hemisphere			χ^2 (*P*),	Estimate ± SE	Correlation terms	
Response variables	(sample size)	Mean ± SD	Range	df = 1	(latitude)	Range	Nugget
Duration	northern (179)	0.49 ± 0.09	0.31–0.75	4.76 (0.071)	0.005 ± 0.002	5.8	0.6
	southern (379)	0.39 ± 0.07	0.22–0.75	**23.64 (<0.001)**	-0.002 ± $4*10^{-4}$	$1*10^{-4}$	$3*10^{-10}$
Entropy	northern (179)	0.78 ± 0.02	0.69–0.83	**5.91 (0.043)**	-0.001 ± $3*10^{-4}$	0.3	0.7
	southern (379)	0.78 ± 0.02	0.68–0.83	**6.07 (0.043)**	$3*10^{-4}$ ± $1*10^{-4}$	–	–
Scale Entropy[a]	southern (378)	0.15 ± 0.93	-4.80–2.55	3.70 (0.103)	0.015 ± 0.007	16.7[c]	1.3[c]
Median frequency	northern (179)	7.18 ± 0.67	5.26–8.72	0.01 (0.908)	-0.001 0.010	0.3	0.5
	southern (379)	7.07 ± 0.84	4.56–9.03	0.59 (0.557)	-0.004 ± 0.005	–	–
Bandwidth	northern (163)	5.84 ± 1.19	2.27–8.82	**7.92 (0.028)**	-0.046 ± 0.016	$1*10^{-4}$	$5*10^{-8}$
	southern (317)	6.53 ± 1.35	2.19–10.15	0.47 (0.557)	0.007 ± 0.010	0.1	0.4
Inflections s^{-1}	northern (179)	36.27 ± 10.24	16.32–65.43	**5.95 (0.043)**	-0.585 ± 0.240	2.6	0.4
	southern (379)	51.40 ± 13.52	19.58–88.75	4.51 (0.072)	0.302 ± 0.142	2.0	0.8
Song rate	northern (141)	15.15 ± 3.51	8.82–30.17	0.11 (0.786)	-0.028 ± 0.085	9.1	0.8
	southern (236)	14.96 ± 3.38	7.11–24.76	1.30 (0.36)	-0.029 ± 0.026	–	–
Number of components	northern (161)	5.65 ± 1.89	2–13	2.20 (0.234)	-0.016 ± 0.006	16.7[c]	3.7[c]
	southern (322)	5.95 ± 1.52	2–13	1.30 (0.36)	-0.002 ± 0.002	–	–
Proportion of vibratos	northern (161)	0.47 ± 0.17	0.17–1	**75.66 (<0.001)**	0.016 ± 0.002	$2*10^{-4}$	$2*10^{-2}$
	southern (322)	0.33 ± 0.14	0–0.8	0.47 (0.557)[b]	-0.003 ± 0.004	–	–

Some models did not fulfill all assumptions for the northern hemisphere (bandwidth, inflections per second, number of components and proportion of vibratos) and for the southern hemisphere (entropy and proportion of vibratos). Additional information about model details, such as spatial correlation structure, family of error distribution, assumptions and tests of significance, are available in the Appendix Tables A1 and A2. Significant results are highlighted in bold. Asterisk (*) indicates multiplication operations.

[a] We excluded one outlier from the dataset to improve model assumptions and scaled the response variable before fitting a spaMM model.

[b] Because we fitted a GLM model (family function: Quasi-binomial; link = logit) for the proportion of vibratos for the southern hemisphere, we show F value, instead of $\chi2$ value.

[c] Because it regards spaMM models, we show the correlation parameters “nu” and “rho” of Matérn function, instead of “range” and “nugget”, respectively.

Song complexity varies with seasonality and bird richness

We found that song complexity usually decreased with increasing seasonality and decreasing bird species richness, contrary to our expectations based on sexual selection and ecological hypotheses. This decrease in song complexity included: the number of inflections per second that decreased as bird richness decreased (GLS, correlation structure: exponential, $\chi^2 = 8.39$, $P < 0.03$); song duration, which decreased as precipitation seasonality increased (GLS, correlation structure: linear or spherical, $\chi^2 = 12.22$, $P < 0.002$); and number of components of the song, which decreased as temperature (GLS, correlation structure: rational quadratic, $\chi^2 = 8.82$, $P < 0.012$) and precipitation seasonality increased ($\chi^2 = 11.75$, $P < 0.002$). The only exception to this general pattern was found for song complexity defined as the proportion of vibratos, which increased with temperature (GLS with no correlation structure, $\chi^2 = 11.05$, $P = 0.007$) and precipitation seasonality increase ($\chi^2 = 18.22$, $P < 0.001$) (Figures 4 and 5, Table 2). The other variables, i.e., entropy, median frequency, bandwidth and song rate did not vary with seasonality and bird richness.

Moreover, song complexity differed between northern and southern hemispheres. Entropy, bandwidth and number of components was higher in the southern hemisphere, while the proportion of vibratos was higher in the northern hemisphere (Table 2 and Appendix Figure A1). Summary descriptive statistics of the blue-black grassquit song for its entire distribution range across the Neotropical region are shown in the Appendix Table A4.

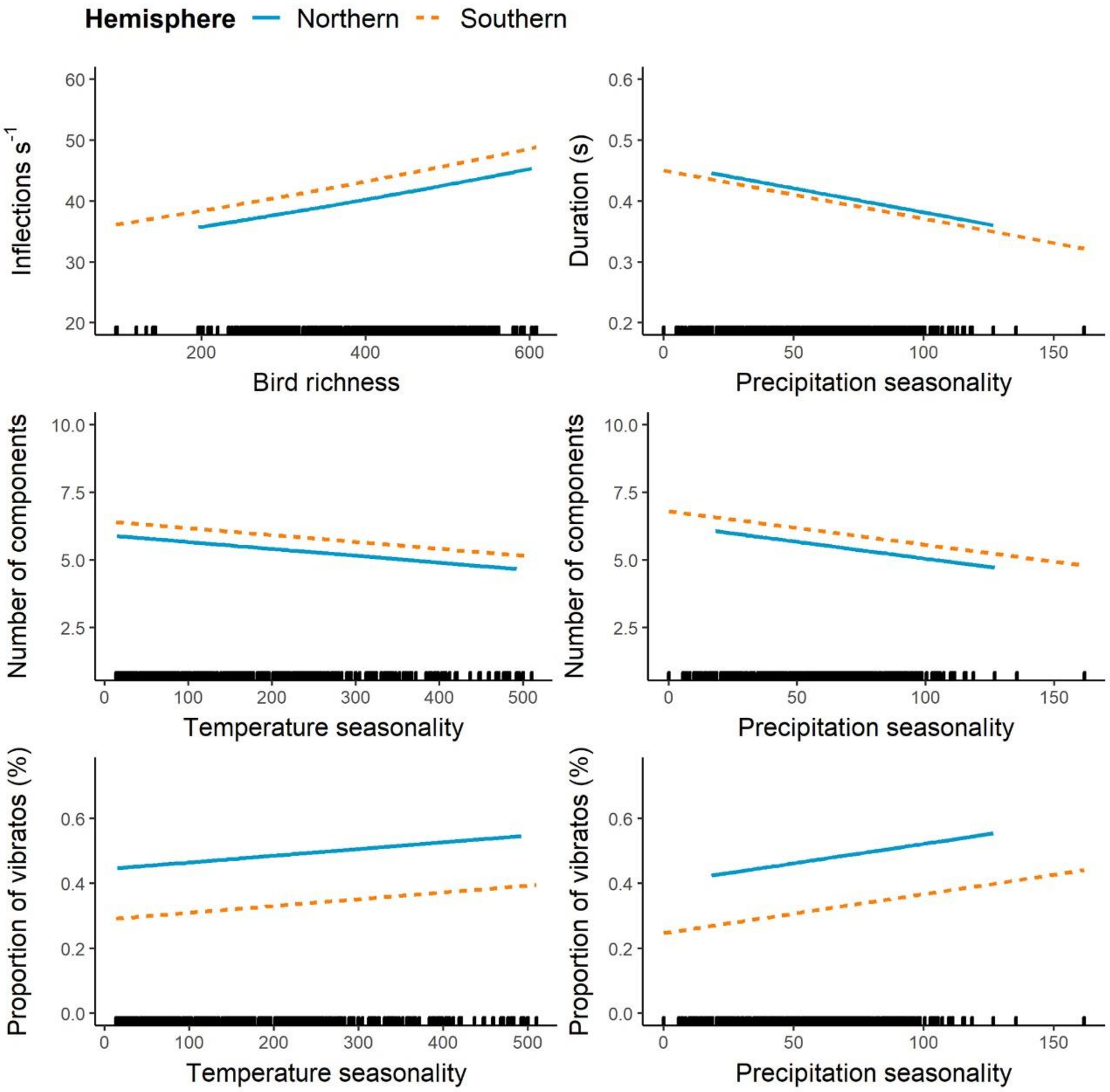

Figure 5. The relationship between bird richness, precipitation and temperature seasonality with song complexity metrics of the blue-black grassquit across its distribution range in the Neotropical region. Inflections s^{-1} are the number of inflections per second; duration is the song duration in seconds; number of components is the average number of single components per song; and proportion of vibratos is the percentage of vibrato-like structures in the song. Solid (northern hemisphere) and dashed (southern hemisphere) lines indicate the predicted values from Generalized Least Squares models (model formula: song metric ~ precipitation seasonality + temperature seasonality + bird richness + hemisphere). To produce these plots, the non-focal variables have been fixed to their medians for estimation of predicted values. The distribution of samples, average metric values from up to three songs per recording, are indicated by vertical marks in the x-axis in the rug plot (inflections s^{-1} and duration: n = 558 recordings; number of components and proportion of vibratos: n = 483 recordings).

Table 2. Results of generalized least squares (GLS) models to test for effects of seasonality, bird species richness and hemisphere on the song complexity metrics of the blue-black grassquit. We present results of Type II Wald chi-square tests, P values, model coefficients and correlation terms when applicable

	Wald test χ^2 (*P*), df = 1				Correlation terms	
Response variable (sample size)	Temperature seasonality	Precipitation seasonality	Bird richness	Hemisphere	Range	Nugget
Duration (558)	4.17 (0.11)	**12.22 (0.002)**	2.94 (0.346)	0.16 (0.785)	4115.2	$4*10^{-3}$
Entropy (558)	0.11 (0.985)	3.72 (0.108)	0.65 (0.498)	**13.53 (0.001)**	0.3	0.8
Median frequency (558)	3.00 (0.167)	0.17 (0.906)	0.75 (0.498)	0.26 (0.785)	–	–
Bandwidth (480)	0.13 (0.985)	0.03 (0.957)	1.65 (0.498)	**13.50 (0.001)**	$4*10^{-2}$	0.4
Inflections s^{-1} (558)[a]	$3*10^{-4}$ (0.987)	1.73 (0.301)	**8.39 (0.03)**	0.66 (0.667)	26.1	0.5
Song rate (377)	0.02 (0.987)	$3*10^{-3}$ (0.957)	0.61 (0.498)	0.04 (0.843)	–	–
Number of components (483)	**8.82 (0.012)**	**11.75 (0.002)**	1.06 (0.498)	**5.55 (0.037)**	0.1	0.5
Proportion of vibratos (483)	**11.05 (0.007)**	**18.22 (<0.001)**	0.20 (0.656)	**92.52 (<0.001)**	–	–

	Estimate ± SE			
Response variable (sample size)	Temperature seasonality	Precipitation seasonality	Bird richness	Hemisphere
Duration (558)	$2*10^{-4} \pm 1*10^{-4}$	$-0.001 \pm 2*10^{-4}$	$-1*10^{-4} \pm 1*10^{-4}$	-0.010 ± 0.026
Entropy (558)	$-3*10^{-6} \pm 1*10^{-5}$	$-1*10^{-4} \pm 4*10^{-5}$	$1*10^{-5} \pm 1*10^{-5}$	0.009 ± 0.003
Median frequency (558)	$-0.001 \pm 3*10^{-4}$	-0.001 ± 0.001	$-3*10^{-4} \pm 3*10^{-4}$	-0.042 ± 0.082
Bandwidth (480)	$-2*10^{-4} \pm 0.001$	$5*10^{-4} \pm 0.003$	0.001 ± 0.001	0.618 ± 0.168
Inflections s^{-1} (558)[a]	$-5*10^{-6} \pm 3*10^{-4}$	0.001 ± 0.001	$0.001 \pm 2*10^{-4}$	0.071 ± 0.087
Song rate (377)	$-3*10^{-4} \pm 0.002$	$-4*10^{-4} \pm 0.007$	-0.001 ± 0.002	-0.083 ± 0.419

Number of components (483)	-0.003 ± 0.001	-0.012 ± 0.004	-0.001 ± 0.001	0.510 ± 0.217
Proportion of vibratos (483)	$2*10^{-4} \pm 1*10^{-4}$	$0.001 \pm 3*10^{-4}$	$-3*10^{-5} \pm 1*10^{-4}$	-0.155 ± 0.016

Some models did not fulfill all assumptions: duration, entropy, number of components and proportion of vibratos. Additional information about model details, such as spatial correlation structure, assumptions and tests of significance, are available in the Appendix Table A3. Significant results are highlighted in bold. Asterisk (*) indicates multiplication operations.

[a] Natural log-transformed.

DISCUSSION

Our results show that song complexity varies with latitude, climate seasonality and bird species richness across the distribution of a Neotropical songbird, the blue-black grassquit. However, contrary to predictions based on classical hypotheses in the literature, song complexity expressed by different metrics mostly decreased with increasing latitude (i.e., towards the poles) in both northern and southern hemispheres. Additionally, song complexity was positively correlated with bird richness, and mostly negatively correlated with climate seasonality. Therefore, our results do not support ecological and sexual selection hypotheses. Similarly to our findings, other studies have also shown that some bird species sing simpler songs in higher latitudes compared to lower latitudes in different regions of the globe (Pieplow and Francis 2011; Gordinho et al. 2015; Xing et al. 2017; Crouch and Mason-Gamer 2019). Conversely, however, an increase in song complexity towards higher latitudes has also been reported for bird species (e.g., Irwin 2000; Weir et al. 2012; Greig et al. 2013; Kaluthota et al. 2016). Taken together, the data from this and other studies show inconsistent patterns of song complexity variation across the latitudinal gradient (Najar and Benedict 2019). One explanation for the contradictory results reported involves the inconsistent definition of song complexity among different studies (Benedict and Najar 2019; Najar and Benedict 2019). Bird song has a multifaceted nature and different song features can be under distinct evolutionary pressures (Gil and Gahr 2002; Benedict and Najar 2019), potentially blurring widespread spatial and ecological patterns of song variation.

Song complexity vs. latitude

For the northern hemisphere, the blue-black grassquit song expressed by frequency bandwidth, entropy and number of inflections per second became simpler towards higher latitudes. Thus, grassquits exhibited more complex songs regarding the frequency domain in lower latitudes; this result contradicted our expectations of simpler songs in less seasonal habitats based on the presumption of weaker intensity of sexual selection in these habitats (Macedo et al. 2008; Botero et al. 2009). Part of our expectations also considered that songs with higher frequency modulation and occupying a wide bandwidth should be exposed to higher levels of interference by the more diverse fauna that use the acoustic space in lower latitudes (Hillebrand 2004; Weir et al. 2012). Despite this general trend of decreasing complexity towards the pole in the northern hemisphere, the proportion of vibratos in the blue-black grassquit song was positively correlated with latitude. These antagonistic patterns of song complexity variation could be partially explained through a trade-off perspective. There are song features that may be physically challenging to produce together. In songbird species, for example, increasing song bandwidth limits an increase in trill rate (i.e., a vibrato-like structure) due to anatomical constraints, and a negative relationship between these song metrics was reported for different species (Podos 1997; Illes et al. 2006; Diniz et al. 2015). Accordingly, our findings show a latitudinal gradient where the proportion of vibratos increases, while the frequency bandwidth decreases. To clarify this pattern, future empirical studies are needed to focus on the relationship between possible male quality cues in the blue-black grassquit song, such as the proportion of vibratos and vocal performance (e.g., frequency excursion, Podos et al. 2016), and whether females use these song features as a basis for mate choice.

For the southern hemisphere, complexity as a function of song duration decreased toward higher latitudes i.e., blue-black grassquits sang longer songs in lower latitudes, contrary to theoretical predictions. Greater levels of background noise have already been reported for tropical rainforests at lower latitudes (Weir et al. 2012), and longer acoustic signals can enhance signal detectability both in silent and noisy environments (Pohl et al. 2013). In this context, although longer songs could facilitate acoustic communication in lower latitudes, we did not find a significant relationship between grassquit song duration and bird richness, which we used as a proxy for acoustic space availability. Moreover, we did not find a significant effect of latitude on the other song variables in the southern hemisphere. For these reasons, we consider that our findings do not provide support for the scenario predicted by ecological and sexual selection hypotheses i.e., positive correlation between song complexity and latitude.

Song complexity vs. seasonality and bird richness

Regarding climate variability, we found opposing patterns of variation for song complexity metrics. As expressed by duration and number of components of the song, complexity decreased with higher seasonality, in contrast to our primary expectation. However, the proportion of vibratos was higher in locations with higher seasonality. In general, previous studies show a pattern of song complexity that increases in locations with greater climate variability (Irwin 2000; Botero et al. 2009; Medina and Francis 2012; Karin et al. 2018), in accordance with sexual selection hypotheses. In addition, regarding ecological and sexual selection hypotheses, disparate results have also been reported for leaf warblers (Phylloscopidae), wherein the diversity of song elements decreased towards higher latitudes, while verse duration of songs became longer (Tietze et al. 2015). Xing et al. (2017) also found contradictory patterns of variation for different song complexity metrics in the marsh grassbird (*Locustella pryeri*). Our results, taken together with the findings of previous studies, highlight the necessity of further studies with different bird species to clarify the relationship between song complexity, climate variability and sexual selection. Considering this general divergence among results of several studies, we suggest that the ecological and sexual selection hypotheses do not fully explain song complexity variation. We suggest that other factors could also have shaped song features, affecting the evolution of song complexity in different species. For example, stochastic errors accumulated during song learning (Grant and Grant 1996; Benedict and Bowie 2009), historical isolation of a species' populations (Koetz et al. 2007), migratory behavior (Catchpole 1982; Collins et al. 2009) and food availability (Irwin 2000) may help to explain the divergent patterns of song complexity reported to date.

Moreover, contrary to our expectations, we found a positive correlation between song complexity (defined as the number of inflections per second) and bird species richness. In other words, there is a higher concentration of frequency modulations per unit of time within the grassquit song in environments where this animal coexists with more bird species. In such conditions, where the competition for acoustic space may be higher (Doutrelant et al. 2000; Chitnis et al. 2020; Torres et al. 2020), it could be worthwhile for birds to compress signal information to improve acoustic communication. Finally, we found that frequency bandwidth, entropy, number of components and proportion of vibratos differed between northern and southern hemispheres. Although not the focus of this study, differences of landmass and ocean features between these hemispheres might have determined climatic conditions that we did not consider, and which could have influenced patterns of song evolution in the blue-black grassquit and other birds (see Dingle 2008; Kang et al. 2015). Additionally, a possible geographical isolation of blue-black grassquit populations in the southern and northern hemispheres would have favored the accumulation of differences (e.g., through cultural drift; Grant and Grant 1996; Koetz et al. 2007) in distinct song metrics. For instance, between-hemispheres differences for avian taxa have already been shown relative to migration patterns (Dingle 2008) and parental investment (Heming and Marini 2015).

CONCLUSIONS

Previous studies investigating the evolution of bird song complexity across geographically broad areas have shown inconsistent patterns of song variation (Najar and Benedict 2019). Here, we found that attributes of song complexity in the blue-black grassquit, a Neotropical bird species, show correlations with latitude, climate variability and bird richness. Although ecological and sexual selection hypotheses predict greater song complexity in higher latitudes, more seasonal and species-poor habitats (Botero et al. 2009; Weir et al. 2012), our results are mostly contrary to these predictions. Thus, we highlight that these hypotheses do not fully explain song complexity variation for populations that have broad geographic ranges. In addition, our study demonstrates the usefulness of online databases, which provide the needed large samples to robustly investigate questions of ecology, evolution and animal behavior (see Silvertown 2009; Jarić et al. 2020). Indeed, data about the natural world are being gathered at unprecedented rates with millions of observations added to online databases annually (Sullivan et al. 2014). Future studies encompassing different species are needed to test the myriad hypotheses in the literature concerning patterns of bird song complexity and drivers of song evolution, and recordings available in online databases will constitute a valuable resource for such studies.

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Conflict of interest: The authors declare no conflict of interest.

Data availability: Analyses reported in this article can be reproduced using the data that will be provided by the authors as soon as the manuscript is accepted.

Author Contributions: E.F.S.J. and R.H.M. conceived and designed the study; E.F.S.J. collected the data, conducted acoustic and statistical analyses with input from P.D.; E.F.S.J. wrote the first draft of the manuscript, and all authors read, contributed and approved the final version of the text.

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APPENDIX

Appendix Figure A1

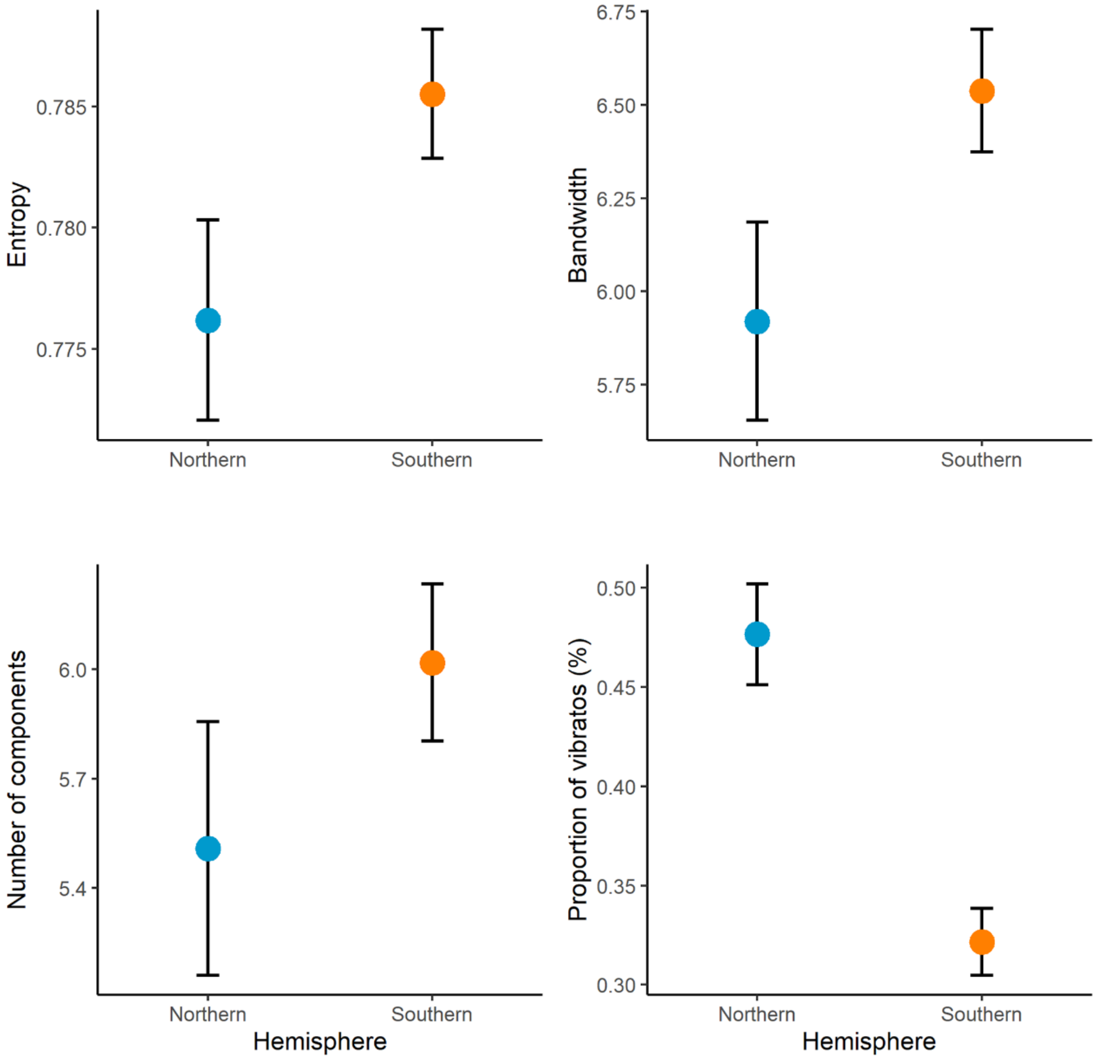

Figure A1. The relationship between hemisphere and song complexity metrics of the blue-black grassquit. We show predicted values with 95% confidence intervals for each hemisphere based on Generalized Least Squares models (model formula: song metric ~ precipitation seasonality + temperature seasonality + bird richness + hemisphere) (plot_model function, sjPlot package). Entropy is a measure of energy disorder through the time and frequency spectrum of the song; bandwidth represents the difference value between maximum and minimum frequencies; number of components is the average number of single components per song; and proportion of vibratos is the percentage of vibrato-like structures in the song. Samples were average metric values from up to three songs per recording (entropy: n = 558 recordings; bandwidth: n = 480 recordings; number of components and proportion of vibratos: n = 483 recordings).

Appendix Table A1

Table A1. General information of the fitted models that represents the relationship between acoustic complexity metrics of the blue-black grassquit song and latitude. We present the best correlation structure for Generalized Least Squares models (GLS) based on the lowest Akaike's Information Criterion (AIC) values, while we present the family of error distribution for Generalized Linear (GLM), glmmTMB and spaMM models

Response variable	Type of variable	Hemisphere (sample size)	Model	Best correlation structure/ Family of error distribution (*link*)	R functions for tests of significance, df = 1
Duration	Continuous	northern (179)	GLS	Rational quadratic	*Anova*, *car* package
		southern (379)	GLS	Rational quadratic	*Anova*, *car* package
Entropy	Continuous	northern (179)	GLS	Exponential	*Anova*, *car* package
		southern (379)	GLS	No correlation	*Anova*, *car* package
Scale Entropy[a]	Continuous	southern (378)	spaMM	Gaussian (*identity*)	*drop1* (test = "Chisq"), *stats* package
Median frequency	Continuous	northern (179)	GLS	Spherical	*Anova*, *car* package
		southern (379)	GLS	No correlation	*Anova*, *car* package
Bandwidth	Continuous	northern (163)	GLS	Rational quadratic	*Anova*, *car* package
		southern (317)	GLS	Spherical	*Anova*, *car* package
Inflections s^{-1}	Continuous	northern (179)	GLS	Exponential	*Anova*, *car* package
		southern (379)	GLS	Exponential	*Anova*, *car* package
Song rate	Continuous	northern (141)	GLS	Rational quadratic	*Anova*, *car* package
		southern (236)	GLS	No correlation	*Anova*, *car* package
Number of components	Count	northern (161)	spaMM	Zero-truncated Poisson (*log*)	*drop1* (test = "Chisq"), *stats* package
		southern (322)	glmmTMB	Zero-truncated COMPoisson[b] (*loglambda*)	*Anova*, *car* package

Proportion of vibratos	Proportion	northern (161) southern (322)	GLS GLM	Linear Quasi-binomial (*logit*)	*Anova*, *car* package *drop1* (test = "F"), *stats* package

[a] We excluded one outlier from the dataset to improve model assumptions and scaled the response variable before fitting a spaMM model.

[b] COMPoisson = Conway-Maxwell-Poisson.

Appendix Table A2

Table A2. Model assumptions of the fitted models that represent the relationship between acoustic complexity metrics of the blue-black grassquit song and latitude

Response variable	Hemisphere (sample size)	Model	Assumptions		
			Normality	Homoscedasticity	Dispersion
Duration	northern (179)	GLS	Ok	Ok	–
	southern (379)	GLS	Ok	Ok	–
Entropy	northern (179)	GLS	Ok	Ok	–
	southern (379)	GLS	Not ok	Ok	–
Scale Entropy[a]	southern (378)	spaMM	Ok	Ok	Ok
Median frequency	northern (179)	GLS	Ok	Ok	–
	southern (379)	GLS	Ok	Ok	–
Bandwidth	northern (163)	GLS	Ok	Not ok	–
	southern (317)	GLS	Ok	Ok	–
Inflections s^{-1}	northern (179)	GLS	Ok	Not ok	–
	southern (379)	GLS	Ok	Ok	–
Song rate	northern (141)	GLS	Ok	Ok	–
	southern (236)	GLS	Ok	Ok	–
Number of components	northern (161)	spaMM	Ok	Not ok	Not ok
	southern (322)	glmmTMB	Ok	Ok	Ok
Proportion of vibratos	northern (161)	GLS	Not ok	Not ok	–
	southern (322)	GLM	Not ok	Ok	Ok

[a] We excluded one outlier from the dataset to improve model assumptions and scaled the response variable before fitting a spaMM model.

Appendix Table A3

Table A3. General information of the fitted models that represent the relationship between acoustic complexity metrics of the blue-black grassquit song and seasonality, bird species richness and hemisphere. We present the best correlation structure for Generalized Least Squares models (GLS) based on the lowest Akaike's Information Criterion (AIC) values

Response variable		Best correlation	Assumptions			R functions for tests
(sample size)	Model	structure	Normality	Homoscedasticity	Multicollinearity	of significance, df = 1
Duration (558)	GLS	Linear and Spherical	Ok	Not ok	Ok	*Anova*, *car* package
Entropy (558)	GLS	Rational quadratic	Not ok	Ok	Ok	*Anova*, *car* package
Median frequency (558)	GLS	No correlation	Ok	Ok	Ok	*Anova*, *car* package
Bandwidth (480)	GLS	Gaussian	Ok	Ok	Ok	*Anova*, *car* package
Inflections s^{-1} (558)[a]	GLS	Exponential	Ok	Ok	Ok	*Anova*, *car* package
Song rate (377)	GLS	No correlation	Ok	Ok	Ok	*Anova*, *car* package
Number of components (483)	GLS	Rational quadratic	Not ok	Not ok	Ok	*Anova*, *car* package
Proportion of vibratos (483)	GLS	No correlation	Not ok	Not ok	Ok	*Anova*, *car* package

[a]Natural log-transformed.

Appendix Table A4

Table A4. Complexity metrics of the blue-black grassquit song for its entire distribution range across the Neotropical region

Response variable (sample size)	Mean ± SD	Range
Duration (558)	0.42 ± 0.09	0.22–0.75
Entropy (558)	0.78 ± 0.02	0.68–0.83
Median frequency (558)	7.1 ± 0.79	4.56–9.03
Bandwidth (480)	6.29 ± 1.34	2.19–10.15
Inflections s^{-1} (558)	46.55 ± 14.41	16.32–88.75
Song rate (377)	15.03 ± 3.43	7.11–30.17
Number of components (483)	5.85 ± 1.66	2–13
Proportion of vibratos (483)	0.37 ± 0.17	0–1

Appendix Table A5

We gathered 992 recordings of blue-black grassquits from Xeno-Canto (XC); Macaulay Library (ML) at the Cornell Lab of Ornithology; WikiAves (WA); and Fonoteca Neotropical Jacques Vielliard (FNJV) of the Universidade Estadual de Campinas. Recording IDs and URLs for these recordings are available below.

Recording ID	**URL - XC**
29425	//www.xeno-canto.org/29425
42513	//www.xeno-canto.org/42513
28458	//www.xeno-canto.org/28458
105806	//www.xeno-canto.org/105806
375830	//www.xeno-canto.org/375830
375831	//www.xeno-canto.org/375831
375832	//www.xeno-canto.org/375832
288261	//www.xeno-canto.org/288261
311995	//www.xeno-canto.org/311995
319273	//www.xeno-canto.org/319273
487476	//www.xeno-canto.org/487476
9626	//www.xeno-canto.org/9626
9627	//www.xeno-canto.org/9627
9628	//www.xeno-canto.org/9628
9629	//www.xeno-canto.org/9629
59972	//www.xeno-canto.org/59972
304500	//www.xeno-canto.org/304500
405861	//www.xeno-canto.org/405861
405862	//www.xeno-canto.org/405862
405865	//www.xeno-canto.org/405865
405866	//www.xeno-canto.org/405866
454484	//www.xeno-canto.org/454484
454485	//www.xeno-canto.org/454485
454486	//www.xeno-canto.org/454486
72324	//www.xeno-canto.org/72324
81387	//www.xeno-canto.org/81387
214834	//www.xeno-canto.org/214834
47146	//www.xeno-canto.org/47146
51124	//www.xeno-canto.org/51124
51125	//www.xeno-canto.org/51125
55748	//www.xeno-canto.org/55748
106476	//www.xeno-canto.org/106476
348692	//www.xeno-canto.org/348692
31977	//www.xeno-canto.org/31977
420059	//www.xeno-canto.org/420059
428141	//www.xeno-canto.org/428141
52881	//www.xeno-canto.org/52881
454581	//www.xeno-canto.org/454581
454582	//www.xeno-canto.org/454582
198179	//www.xeno-canto.org/198179
146538	//www.xeno-canto.org/146538
146540	//www.xeno-canto.org/146540
398968	//www.xeno-canto.org/398968
92184	//www.xeno-canto.org/92184
257148	//www.xeno-canto.org/257148
28494	//www.xeno-canto.org/28494
28784	//www.xeno-canto.org/28784
154989	//www.xeno-canto.org/154989
198855	//www.xeno-canto.org/198855
486813	//www.xeno-canto.org/486813
457241	//www.xeno-canto.org/457241
457245	//www.xeno-canto.org/457245
207618	//www.xeno-canto.org/207618
15524	//www.xeno-canto.org/15524
11171	//www.xeno-canto.org/11171
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DISCUSSÃO GERAL

Neste estudo, nós investigamos a complexidade do canto do tiziu ao longo de sua distribuição na região Neotropical. Em linhas gerais, as aves podem codificar mensagens nos sinais acústicos que emitem. Particularmente, o canto pode conter informações relativas a identidade individual, qualidade como parceiro e capacidade de defender um território (Catchpole e Slater 2008; Manica et al. 2017; Geberzahn e Derégnaucourt 2020). Tais informações podem ser representadas em características do comportamento vocal, como a taxa de produção do canto e a variação de frequência e de duração desse sinal (Catchpole e Slater 2008; Manica et al. 2014; Manica et al. 2017; Geberzahn e Derégnaucourt 2020). Apesar da complexidade do canto das aves ser um tópico bem estudado, relativamente poucos trabalhos investigaram a variação da complexidade desse sinal ao longo de amplas escalas geográficas, sendo os padrões relatados diversos e inconclusivos (Najar e Benedict 2019). Dessa forma, para explorar essa questão e investigar como fatores ambientais estão relacionados com a complexidade do canto, nós utilizamos o tiziu (*Volatinia jacarina*) como espécie modelo e bancos de dados *online* para obter gravações do canto dessa espécie ao longo de sua distribuição.

Hipóteses de seleção sexual e ecológica predizem um cenário em que cantos mais complexos devem ser produzidos pelas aves em maiores latitudes, e em ambientes com maior variabilidade climática e/ou menor riqueza de espécies que utilizam o espaço acústico. Neste contexto, primeiramente investigamos a relação entre a complexidade do canto do tiziu com a latitude. Posteriormente, exploramos a relação deste sinal acústico com a sazonalidade de precipitação, sazonalidade de temperatura e riqueza de espécies de aves onde o tiziu foi registrado.

Como resultado, observamos que a complexidade do canto representada por diferentes métricas prevalentemente diminuiu com o aumento da latitude, padrão contrário às nossas expectativas fundamentadas nas hipóteses de seleção sexual e ecológica. Mais especificamente, para o hemisfério Norte, a complexidade do canto diminuiu com a latitude quando expressa pela largura de banda de frequência, entropia e número de inflexões por segundo. Porém, a proporção de vibratos no canto do tiziu aumentou com a latitude. Não houve relação entre a latitude e as outras variáveis calculadas. Já para o hemisfério Sul, a complexidade, expressa pela duração do canto, diminuiu em direção as latitudes maiores. Não houve efeito da latitude sobre os outros parâmetros do canto nesse hemisfério.

Além disso, a complexidade do canto variou com a sazonalidade climática e a riqueza de espécies de aves onde o tiziu foi registrado. Nossos resultados apontam que a ave emite cantos mais complexos em ambientes com sazonalidade menos acentuada e/ou maior riqueza de espécies, padrão contrário às nossas predições. Observamos que o número e inflexões por segundo se correlacionou positivamente com a riqueza de espécies de aves; a duração do canto diminuiu com o aumento da sazonalidade de precipitação; e o número de componentes do canto diminuiu com o aumento da sazonalidade de precipitação e de temperatura. A única exceção foi a complexidade do canto representada pela proporção de vibratos, tendo sido maior em ambientes com sazonalidade de precipitação e de temperatura mais acentuada. As outras variáveis – isto é, entropia, frequência mediana, largura de banda de frequência e taxa de canto – não variaram significativamente com a sazonalidade e a riqueza de espécies. Por fim, a complexidade do canto variou entre hemisférios: largura de banda de frequência, entropia e número de componentes tiveram valores maiores no hemisfério Sul; ao passo que a proporção de vibratos foi maior no hemisfério Norte.

Nossos resultados destacam que o canto do tiziu varia em função da latitude, da sazonalidade climática e da riqueza de espécies de aves. No entanto, de forma contrária às nossas expectativas fundamentas nas hipóteses de seleção sexual e ecológica, a complexidade do canto majoritariamente diminuiu com o aumento da latitude, tanto no hemisfério Norte quanto no Sul. Ademais, a complexidade do canto do tiziu se correlacionou positivamente com a riqueza de espécies de aves, e, no geral, negativamente com a sazonalidade. Logo, nossos resultados não apoiam as principais hipóteses propostas para explicar o padrão de complexidade do canto das aves para amplas escalas geográficas. Outros estudos também relataram que diferentes espécies de aves produziram cantos mais simples em maiores latitudes em partes distintas do globo (Pieplow e Francis 2011; Gordinho et al. 2015; Xing et al. 2017; Crouch e Mason-Gamer 2019). Apesar de cantos mais complexos terem sido relatados em maiores latitudes para algumas espécies (Irwin 2000; Weir et al. 2012; Kaluthota et al. 2016; Wei et al. 2017), de modo geral, não há um padrão consistente de variação da complexidade do canto ao longo do gradiente latitudinal entre diferentes espécies de aves (Najar e Benedict 2019).

Considerando a relação entre a complexidade do canto e a latitude, observamos que os valores das métricas do canto do tiziu relativas ao domínio de frequência (i.e., largura de banda de frequência, entropia e número de inflexões por segundo) diminuíram com a latitude para o hemisfério Norte, de forma contrária ao que esperávamos. Porém, a proporção de vibratos aumentou com a latitude nesse hemisfério. Tal padrão de variação pode ser parcialmente interpretado sob uma perspectiva de *trade-off*. Mais especificamente, há características do canto que são difíceis e desafiadoras de serem produzidas e ampliadas em conjunto por uma ave. Em Passeriformes, aumentar a largura de banda de frequência do canto simultaneamente à taxa de trinados – parâmetro do canto similar ao vibrato – pode ser desafiador e, inclusive, impossível depois de um certo ponto, o que está relacionado a uma limitação anatômica das aves (Podos 1997). Uma relação negativa entre esses dois parâmetros foi relatada para diferentes espécies de aves (Podos 1997; Illes et al. 2006; Diniz et al. 2015) e, conforme esse padrão, nossos resultados para o hemisfério Norte mostram um gradiente latitudinal com aumento da proporção de vibratos à medida que a largura de banda de frequência do canto diminui.

Para o hemisfério Sul, há uma relação negativa entre duração do canto e latitude, sendo assim, os tizius produzem cantos mais longos em latitudes menores. Foi demonstrado maiores níveis de ruído ambiental em florestas tropicais em latitudes menores (Weir et al. 2012), o que reduziria o espaço acústico disponível. Adicionalmente, cantos mais longos potencialmente facilitam a detecção do sinal acústico em ambientes com maior nível de ruído (Pohl et al. 2013). Logo, cantos mais longos de tiziu em latitudes menores poderiam facilitar a detecção do sinal, mas não encontramos relação entre a duração do canto e a riqueza de espécies de aves, variável que utilizamos como um indicativo da disponibilidade do espaço acústico.

Considerando a relação entre a complexidade do canto e a sazonalidade climática, nós observamos padrões divergentes para a variação da complexidade do canto do tiziu. Em função da duração do canto e do número de inflexões por segundo, a complexidade do canto diminuiu com o aumento da sazonalidade. Porém, em direção oposta, a proporção de vibratos aumentou com a sazonalidade. Diferente dos nossos resultados, estudos prévios apontaram o aumento da complexidade do canto das aves em ambientes com condições climáticas mais variáveis e instáveis (Irwin 2000; Botero et al. 2009; Medina e Francis 2012; Karin et al. 2018), de acordo com a hipótese de seleção sexual. Por outro lado, resultados divergentes também foram relatados em trabalhos prévios (e.g., Tietze et al. 2015; Xing et al. 2017). Por exemplo, em aves da família Phylloscopidae, notou-se a redução da diversidade de elementos do canto concomitantemente ao aumento da duração dos versos desse sinal com o aumento da latitude (Tietze et al. 2015).

Por último, considerando a relação entre a complexidade do canto e a riqueza de espécies de aves, observamos uma correlação positiva entre o número de inflexões por segundo do canto do tiziu e a riqueza de espécies. Dessa forma, onde o tiziu coexiste com mais espécies, há mais modulações de frequência em seu canto por unidade de tempo. Neste cenário, onde a competição pelo espaço acústico deve ser maior (Doutrelant et al. 2000; Chitnis et al. 2020; Torres et al. 2020), acumular informações em menos tempo pode facilitar a comunicação entre tizius. Por fim, também encontramos diferenças significativas para parâmetros do canto do tiziu entre os hemisférios Norte e Sul. Apesar de não ser o foco desse estudo, diferenças nas características das massas continentais e características dos oceanos em cada hemisfério devem ter desempenhando um papel direto ou indireto sobre a evolução do canto do tiziu e de outras aves (veja Dingle 2008; Kang et al. 2015). Diferenças entre hemisférios também foram relatadas para outros aspectos comportamentais em aves, como padrões migratórios (Dingle 2008) e investimento parental (Heming e Marini 2015).

Em linhas gerais, destaca-se que os nossos resultados não coincidem com o cenário de variação da complexidade do canto previsto pelas hipóteses de seleção sexual e ecológica e, portanto, este estudo não corrobora tais hipóteses. Uma possível explicação para os padrões divergentes relatados neste estudo pode estar relacionada à definição variada e inconsistente do termo “complexidade” na literatura científica (veja Benedict e Najar 2019; Najar e Benedict 2019). O canto das aves apresenta natureza multifacetada, sendo que diferentes parâmetros desse sinal podem estar sob pressões seletivas distintas (Gil e Gahr 2002; Benedict e Najar 2019). Sendo assim, isso pode dificultar o estabelecimento de padrões claros de variação geográfica da suposta complexidade do canto. Além disso, fatores adicionais também podem ter influenciado a evolução desse sinal acústico. Por exemplo, o acúmulo de erros estocásticos nas características do canto durante o aprendizado vocal (Grant e Grant 1996; Benedict e Bowie 2009); o isolamento histórico de populações de aves (Koetz et al. 2007); o comportamento migratório da espécie (Catchpole 1982; Collins et al. 2009); e a disponibilidade de alimento (Irwin 2000).

CONCLUSÕES

1. As diferentes métricas de complexidade do canto do tiziu se relacionam significativamente com a latitude, a sazonalidade climática e a riqueza de espécies de aves.
2. O padrão de variação da complexidade do canto do tiziu é prevalentemente contrário ao previsto pelas hipóteses de seleção sexual e ecológica.
3. Hemisfério Norte: a complexidade do canto do tiziu – representada pela largura de banda de frequência, entropia e número de inflexões por segundo – diminuiu com o aumento da latitude. Porém, em direção contrária, a proporção de vibratos aumentou com o aumento da latitude.
4. Hemisfério Sul: complexidade, representada pela duração do canto do tiziu, diminuiu com o aumento da latitude.
5. Duração e número de componentes do canto do tiziu diminuíram com o aumento da sazonalidade. Ao contrário, a proporção de vibratos aumentou com o aumento da sazonalidade.
6. Número de inflexões por segundo do canto do tiziu aumentou com a riqueza de espécies de aves.

Por fim, este estudo demonstra a utilidade das plataformas *online* de ciência cidadã e de coleções audiovisuais, as quais fornecem registros do mundo natural para amplas áreas geográficas. Esses bancos de dados *online* possibilitam responder perguntas diversas nas áreas de ecologia, evolução e comportamento animal (veja Silvertown 2009; Toledo et al. 2015; Jarić et al. 2020). Estudos futuros que envolvam diferentes espécies são necessários para testar as diversas hipóteses da literatura científica referentes aos padrões de variação da complexidade do canto e os fatores que influenciaram a evolução desse sinal acústico. Gravações de cantos disponíveis em plataformas de ciência cidadã e de coleções audiovisuais constituirão um recurso valioso para tais estudos.

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