UNIVERSIDAD DE COSTA RICA

SISTEMA DE ESTUDIOS DE POSGRADO

ANÁLISIS DE LAS VARIACIONES ESPECTROTEMPORALES INTRAINDIVIDUALES EN LOS CANTOS DE UN AVE EVASORA URBANA DENTRO DE UN GRADIENTE URBANO-RURAL A LO LARGO DEL TIEMPO

Tesis sometida la consideración de la Comisión del Programa de Estudios de Posgrado para optar al grado de Maestría Académica en Biología

PABLO ANDRÉ SOSA NEGRÓN

Ciudad Universitaria Rodrigo Facio, Costa Rica

2026

Dedicatoria

A mi familia entera por brindarme su apoyo incondicional y enseñarme a perseverar, ante todo.

A mis padres y hermanos, Pablo, Miriam, Andrea y Alejandro, por motivarme a alcanzar mis metas y cumplir lo que me llena. A mi madrina, Charito, por siempre inculcarme el aprecio a la naturaleza.

A mi país, Puerto Rico, en el cual espero lograr aplicar en algún momento lo aprendido durante estos años en esta institución, y a todos los compatriotas alrededor del mundo forjando su futuro con las esperanzas de regresar.

Agradecimientos

Agradezco a mis padres por apoyarme en todos los sentidos durante estos dos años y confiar en mi proceso. Establecerse en un país distinto conlleva sus sacrificios y ellos hicieron que el proceso fuera mucho más llevadero. Aun a la distancia, su acompañamiento no se dejó de sentir. También, a mi mejor amiga Ariana, quien también a la distancia nunca ha dejado de motivarme y creer en mi potencial.

Agradezco a mi novio Felipe por ser el apoyo primordial en Costa Rica durante este proceso y por actuar como editor, revisor y asesor facultativo. En momentos de desaliento y bloqueos, fue él quien me recordaba la razón por la que comencé este camino. Con su conocimiento, también me ayudó a aclarar ideas y, de cierto modo, me retaba a ser mejor científico. Agradezco también a su familia, que me acogió y siempre estuvo en disposición de brindar cualquier tipo de ayuda.

Agradezco a mi director de tesis, Luis, por su paciencia, por fungir como guía y por asegurarse de formarme como científico con una visión crítica. También a mis asesores, Gibi y Roberto, por aportar su conocimiento a este proyecto. Gracias a mis compañeros de laboratorio, Montserrat, Lorena y Alex, por servir también de maestros en la elaboración del proyecto aportando ideas esporádicas. A las amistades que formé en estos años por ampliar mi perspectiva y visión del mundo, y por también hacer sentir el proceso de maestría más llevadero. A José Pablo, quien me ayudó a aliviar mucho del peso del procesamiento de datos. Gracias a todos los profesores y profesoras que, a través de sus cursos y con sus conocimientos, abundaron en mi formación profesional y lo aprendido de ellos lo logré aplicar a este proyecto de alguna forma u otra.

Agradezco a la Universidad de Costa Rica, al Sistema de Estudios de Posgrado y a Vicerrectoría de Investigación por permitirme desarrollar este proyecto y proveer financiamiento para el mismo.

Finalmente, agradezco a este país, Costa Rica, que desde el 2021 ha cambiado mi vida y, ya habiéndome establecido aquí, me ha ayudado a forjarme como individuo. Pura vida.

"Esta tesis fue aceptada por la Comisión del Programa de Estudios de Posgrado en Biología de la Universidad de Costa Rica, como requisito parcial para optar al grado y título de Maestría Académica en Biología."

G. Avalos

Dr. Gerardo Ávalos Rodríguez

Representante de la Decana del Sistema de Estudios de Posgrado

Dr. Luis Sandoval Vargas

Director de Tesis

Dr. Gilberth Barrantes Montero

Asesor de Tesis

Dr. J. Roberto Sosa López

Asesor de Tesis

Marcelo Araya S

Dr. Marcelo Araya Salas

Representante del Director Programa de Posgrado en Biología

Pablo A. Sosa Negrón

Candidato

Contenidos

Resumen

La urbanización ha producido cambios en los paisajes que a su vez ha afectado aspectos de la biología de especies que logran persistir en dichos espacios. La urbanización ha traido consigo alteraciones en el paisaje acústico, con la inserción de altos niveles de ruido antropogénico que potencialmente afectan la comunicación de especies. En aves, se ha encontrado que han modificado los parámetros acústicos de sus cantos con tal de aseguarar la comunicación efectiva entre individuos de una misma especie. No obstante, aún se conoce poco sobre el impacto a largo plazo que tiene el ruido antropogénico en la evolución cultural de las especies de aves al provocar cambios en sus parámetros acústicos. Mi objetivo fue analizar las variaciones intraindividuales en los cantos de una especie evasora urbana, *Melozone leucotis*, en los pasados 13 años dentro de un gradiente urbano rural. Específicamente, cuantificamos la variación intraindividual en cantos comunes con tal de determinar su estabilidad temporal y cuantificamos las modificaciones en el paisaje acústico para determinar cómo ha afectado los cantos. Utilizamos datos históricos de grabaciones de cantos comunes de *M. leucotis* de cuatro poblaciones ubicadas dentro del Gran Área Metropolitana de Costa Rica que varían en su nivel de desarrollo urbano y de ruido antropogénico. Encontramos que los cantos de machos en la población de alta urbanización fueron más consistentes en comparación al de las otras tres poblaciones. Esto se le atribuyó al ruido antropogénico, que potencialmente afecta en distintas magnitudes cada uno de los territorios estudiados. En el segundo capítulo encontramos que el ruido antropogénico limita a los machos en producir sus cantos comunes con parámetros acústicos variables con tal de asegurar la transmisión efectiva de sus señales. No obstante, las respuestas varían entre individuos, por lo cual no parece haber una respuesta generalizada al ruido antropogénico en el sitio de alta urbanización. Este proyecto brinda hallazgos sobre los efectos del desarrollo urbano continuo sobre especies que habitan estos espacios y de cómo puede producir trayectos divergentes en la evolución cultural en poblaciones de una misma especie según el nivel de los disturbios.

Lista de tablas

Capítulo 1

Supplemental material

Capítulo 2

Lista de figuras

Capítulo 1.

Capítulo 2.

Introducción

La urbanización ha sido la alteración más drástica al paisaje inducida por los seres humanos (Ellis et al. 2010; Ellis 2011). La urbanización ha crecido a una taza acelerada y se espera que aumente un 60% en los próximos 20 años (Naciones Unidas 2018). El surgimiento de ambientes urbanos ha causado cambios en las estructuras de los hábitats, composición de comunidades y condiciones microclimáticas (Carreiro & Tripler 2005; Pickett et al. 2011). Esto ha hecho que diversos organismos se enfrenten a condiciones distintas a las que poseían sus entornos no alterados (Charmantier et al. 2017). Así mismo varios aspectos de la historia de vida de las especies, tales como la comunicación, son afectados directamente (Luther & Derryberry 2012; Marín-Gómez & MacGregor-Fors 2021). Sin embargo, aún se entiende muy poco la capacidad que tienen los organismos para enfrentar y adaptarse a estos cambios (MacGregor-Fors & Escobar-Ibáñez 2017).

Las aves dependen de señales acústicas a larga distancia para aparearse, disuadir rivales o evitar ser depredadas (Leavesley & Magrath 2005; Marler & Slabbekoorn 2004; Vignal et al. 2008). La transmisión y recepción de estas señales pueden ser limitadas por varios factores, incluyendo la estructura del hábitat (Boncoraglio & Saino 2007; Ey & Fischer 2009). En el caso de las ciudades, se ha documentado que las aves han desarrollado frecuencias mayores y duraciones más largas en sus cantos a causa de los constantes ruidos antrópicos de baja frecuencia que predomina en estos ambientes (Lowry et al. 2012; Narango & Rodewald 2016; Nemeth et al. 2013). Del mismo modo, la modificación en los cantos de las aves podría deberse a la presencia de estructuras antropogénicas puesto a que pueden actuar como agentes de reverberación y refracción de los cantos emitidos (Dowling et al. 2012; Job et al. 2016). El constante cambio en el paisaje acústico en ambientes urbanos dado al desarrollo continuo podría explicar el surgimiento de variaciones en los cantos según transcurre el tiempo (Bradbury & Vehrencamp 1998).

Las señales acústicas distintivas de cada individuo permiten que la comunicación entre emisor y receptor sea efectiva (Dale et al. 2001; Ellis 2008). En aves, los rasgos individuales en vocalizaciones son más pronunciados en especies con aprendizaje vocal puesto a que, tales como algunos psittácidos, trochilidos y paserinos (Jarvis 2004; Petkov & Jarvis 2012). Durante la etapa de aprendizaje, los individuos pueden cometer errores o improvisar, introduciendo así elementos distintivos en la estructura de las vocalizaciones (Catchpole & Slater 2003; Hultsch et al. 2004).

Asimismo, estos rasgos característicos entre individuos son fundamentales para los comportamientos sociales, tales como la disuasión de competidores, comunicación entre parejas y cuidado parental (Mateo 2004; Tibbets & Dale 2007), pues permite el reconocimiento individual (Kennedy et al. 2009; Paz-y-Miño et al. 2004). En gran parte, el reconocimiento individual es gracias a la consistencia en las estructuras de las vocalizaciones a través de los años, como es el caso de algunas especies (Ballentine 2009; Nelson & Poesel 2009).

Las características de señales individuales pueden permanecer constantes según transcurre el tiempo (Sandoval et al. 2014). Sin embargo, existe evidencia de que pueden surgir cambios 8 debido a cambios en morfología o por modificaciones en la estructura del hábitat (Derryberry 2009). A pesar de que el hábitat puede ser un factor importante en el surgimiento de variaciones individuales en comportamientos, dichas variaciones dependen de cuánta plasticidad posee cada individuo (Dingemanse et al. 2010; Jablonszky et al. 2022). Todavía hace falta explorar si el grado de plasticidad se debe a patrones evolutivos fijados o si son el resultado de plasticidad fenotípica y la aptitud de un individuo (Van de Pol & Wright 2009; Zollinger et al. 2017).

Con tal de distinguir si las vocalizaciones exhibidas por aves urbanas son el producto de adaptaciones o plasticidad, es oportuno examinar si ocurren variaciones intraindividuales en cantos de aves que habiten ecosistemas en estos ecosistemas. El Cuatro-ojos de Cabeza Negra (*Melozone leucotis*) es un paserino territorial que habita naturalmente en matorrales densos de hábitats premontanos y es considerada una especie evasora urbana (Sandoval & Mennill 2023). Cada macho de esta especie puede poseer un repertorio de alrededor de dos a ocho cantos, los cuales son emitidos principalmente para atracción de hembras (Sandoval & Mennill 2012; Sandoval et al. 2013, 2014, 2016). Sumado a esto, cada individuo posee rasgos distintivos en las estructuras finas de sus cantos, las cuales se han documentado que pueden permanecer constantes entre una temporada reproductiva y la otra (Sandoval et al. 2014). Considerando que los cambios en la estructura del hábitat pueden causar alteraciones en la estructura de las vocalizaciones de aves, nos preguntamos si al habrá variaciones en los cantos de individuos de *M. leucotis* al analizarlo a lo largo de un período de tiempo prolongado.

Objetivo general:

Analizar las variaciones espectrotemporales intraindividuales en los cantos de *M. leucotis* dentro de un grandiente urbano-rural en los pasados 13 años.

Objetivos específicos:

(1) Cuantificar la consistencia de las frecuencias y duración de los cantos de los machos de *M. leucotis* durante los últimos 13 años.

Hipótesis (1): La consistencia de los cantos de aves depende de la edad y se ve reflejado en la variación intraindividual, la cual aumentará a través del tiempo y será más prominente en sitios con mayor urbanización.

(2) Cuantificar cómo la modificación del paisaje acústico que se dio en los pasados 13 años ha alterado los cantos de *M. leucotis.*

Hipótesis (2): Las aves en sitios más urbanizados compiten con mayores disturbios acústicos para transmitir sus cantos por lo cuál habrá mayor variación intraindividual en los cantos de estas poblaciones a través del tiempo.

Capítulo I: Consistency and individual variation in the common song types of an urban surviving bird species: a multi-population comparison over a decade

Abstract

Individual variation in singing behavior is influenced by cultural evolution, environmental constraints, and population dynamics. In closed-ended songbird species, aging may drive temporal song variations in individual birds due to vocal apparatus deterioration. However, song variations may also arise as a result of extrinsic factors that induce behavioral changes. In this study, we aimed to examine song-type consistency, limited song spectral variation between renditions, over 13 years in four populations of the White-eared Ground-sparrow (*Melozone leucotis*, Aves: Passerellidae) distributed along an urban-rural gradient and compared within and between-individual variation to determine potential population-level responses. We used long-term data from singing males to quantify five fine structure characteristics (minimum frequency, maximum frequency, frequency range, frequency of maximum amplitude, and song duration) for two common song types from each population. Song consistency differed between fine-structure characteristics, song types, and populations. Contrary to our expectations, we found that the highly urbanized population had greater between-individual variance, while the medium, low-urbanized, and rural populations had higher levels of within-individual variance. Between-individual variance in the highly urbanized population was attributed to anthropogenic disturbances such as habitat structure and noise pollution, suggesting non-uniform individual responses. In contrast, within-individual variance from the rest of the population was consistent with senescence or with morphological traits under constraints. Our study brings insight into how both intrinsic and extrinsic factors can influence song consistency and highlights how cultural evolution within a species can diverge across populations experiencing distinct environmental contexts.

Introduction

Animals produce acoustic signals in non-sexual (i.e., signaling food, predator, or location) and sexual contexts (i.e., competing for mates) (Searcy & Andersson 1986; Dreher & Pröhl 2014; Liu et al. 2021). Consequently, acoustic signals are under constant selective pressures (Podos et al. 2004; Sierro et al. 2023). In the case of birds, males may announce to other males their dominance or may indicate females the quality of their their physical condition using vocalizations (Kroodsma & Byers 1991). This is especially relevant for social interactions with conspecifics to secure their reproductive success and survival (Warrington et al. 2014; Keen et al. 2016). Furthermore, communicating between conspecifics is facilitated by individual distinctiveness, which are signals that differentiate traits associated with their dominance status, health, or size between individulas (Gil & Gar 2002; Tibbets & Dale 2007; Schmidt et al. 2014).

Vocalizations in song learning bird species may vary in three scales (Podos & Warren 2007; Medina & Francis 2012). First, differences between populations, in the form of dialects, arise in geographically separated populations within distinct environmental and social contexts (Wilkins et al. 2013) and are maintained if they are effectively communicated within the local environment (Luther & Baptista 2011). Second, individuals vary from each other because of errors or improvisations in songs acquired during their learning phase, or because of physical features that are intrinsic to the individuals (Wilson & Mennill 2010; Mennill 2011). Third, variations within individuals occur in terms of song consistency — the ability to produce songs, syllables, or elements with limited spectral variation across renditions — and have been previously related to male quality in certain species ( ). Song variations within individuals can occur across both short temporal scales (i.e., within the same year or breeding season) and longer temporal scales (i.e., between years).

Bird songs that remain consistent over years are fundamental for social communication because they facilitate individual recognition (Wiley 2013). Such consistency is often observed in dialects that persist for decades in the same locations, despite individuals' turnover in the population (Planqué et al. 2014). Maintaining this stability is costly, since singing demands repeated physiological effort (Zollinger et al. 2011) and increases exposure to predators (Schmidt & Belinsky 2013). Therefore, the preservation of fine structural features in songs likely reflects individual fitness or performance (Narango & Rodewald 2018). Further, songs are not entirely static: subtle variations can emerge through environmental influences, when plastic adjustments provide greater benefits than costs (Gross et al. 2010), or due to age-related factors such as ontogenetic changes or deterioration of the vocal apparatus (Rivera-Gutierrez et al. 2012). These modifications can function as honest signals of a male's condition, reflecting aspects such as fitness, reproductive potential, or age (Slabbekoorn 2013). Nevertheless, the implications of variation in song production of bird species remain theoretical, highlighting the need to determine whether song variation with age is indeed significant.

Studying between and within-individual variance in behavior has gained interest in behavioral ecology as it can provide insight on microevolutionary processes, population dynamics, and how animals may respond to their environmental contexts (Bolnick et al. 2011; Westneat et al 2015). In birds, not only does birdsong serve as an honest signal of a male's body condition, but it can also reflect their habitat conditions since vocalizations can fluctuate due to aggressiveness, magnitude of intersexual competition, and resource availability (Szymkowiak & Kuczyński 2007). Variation in behavior between individuals can occur when the same genotypes produce different phenotypes in response to various stimuli, representing adaptive plasticity (Alonzo 2015). Likewise, within-individual variation can also indicate the underlying mechanisms behind selection of plasticity and consistency (Nussey et al. 2007; Martin et al. 2017). However, plasticity can also be the result of adaptive responses, such as morphological or physiological constraints caused by environmental changes that may alter trait expression, but that are not sufficient to cope with such environmental variation (Gotthard & Nylin 1995; Friis et al. 2022). Whichever the case, song variation or consistency in individuals may indicate how bird populations respond to changing environments.

Song consistency can be used to determine how behavioral variation in birds inhabiting under distinct environmental conditions and how song dialects may evolve within and between populations. For this study, we aimed to examine individual male song type consistency over 13 years in an urban surviving species, the White-eared ground sparrow *(Melozone leucotis*, Aves: Passerellidae). This species exhibits individually distinctive traits in its solo songs, and it has been demonstrated that males maintain certain stability in their structure between short time periods (Sandoval et al. 2014; Bonilla-Badilla 2021). They are year-round territorial species and males produce their solo songs primarily for territorial defense and mate attraction (Sandoval & Mennill 2012; Sandoval et al. 2013, 2016).

White-eared ground sparrows present microgeographic variations in their songs, with populations presenting different song types (Sandoval et al. 2014; Bonilla-Badilla 2021). For our study, we selected four populations within a rural-urban gradient, which allowed us to compare how solo songs may vary throughout time depending on their environmental context. We analyzed the partitioning of variance to compare the levels within and between-individual level variation, which permitted determining whether singing males express behavioral consistency and have a collective response to their respective environments. Although song stability may be important to maintain social status, we predict that within-individual variance in common song types from males will increase over time, leading to a decrease in consistency. Specifically, we expect that within-individual variation in spectro-temporal characteristics, such as minimum frequency, maximum frequency, frequency range, frequency of maximum amplitude, and song duration, will increase over time. This study allows also to examine the course of cultural evolution in different populations of the same species that potentially face varying degrees of environmental disturbances.

Methods

Study sites

We recorded White-eared Ground-sparrows in four populations within the Costa Rican Central Valley during 14 consecutive breeding seasons from 2011 to 2024: (1) Universidad de Costa Rica, Rodrigo Facio Campus in San Pedro (**UCR:** 09°56’N, 84°03’W, 1200m), composed of secondary forest growth, fragmented green patches, gardens, and surrounded by a high volume of buildings (Biamonte et al. 2011; Juarez et al. 2020). (2) Instalaciones Deportivas, Universidad de Costa Rica in San Pedro (**DEP:** 9°56’N, 84° 03’W, 1200m), which is a mix of secondary forest growth, gardens, and surrounded by few buildings (Juarez et al. 2020). (3) Jardín Botánico Lankester, Cartago (**JBL:** 9°50’N, 83°53’W, 1370m), an area composed of secondary growth forest, gardens, and sparsely located buildings (Piza & Sandoval, 2016; Juarez et al. 2020). (4) Getsemaní, Heredia (**HDA:** 10°01’N, 84°05’W, 1350m), primarily composed of coffee plantations, fragmented thickets and secondary growth forest (Sandoval et al., 2015).

Song recordings

We recorded White-eared Ground Sparrow male solo songs between April and June of 2011-2024, at the onset of the species' breeding season (Sandoval & Mennill 2012). Recordings were conducted between 0500 and 0600 h, when this species is most vocally active (Sandoval et al. 2016), using the focal recording method (Sandoval et al. 2024) with Sennheiser ME66 shotgun microphones and Marantz PMD661digital recorders (recording format: WAVE; sampling rate: 44.1 kHz; 16-bit accuracy). Males were previously banded with a unique colored ring combination and a metallic number ring. This allowed us to identify and record them during consecutive years. We used information of 40 males (10 from each population) that were recorded two or more years to analyze if their common song types varied significantly during these 13 years. We defined common song types as those songs that were produced by at least 68% of males within a population and persist for consecutive years (Bonilla-Badilla 2021). These songs vary according to each population's dialect (Sandoval et al. 2014; Bonilla-Badilla 2021). We selected males that sang for at least 2 years and that had at least 10 songs recorded from each year.

Song classification and measurements

We classified songs based on their syntactic structure observed on spectrograms using Raven Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA) following Sandoval et al. (2014). To ensure accurate identification of song types, we compared the recorded songs to a song type catalog developed by Sandoval et al. (2014). Song types vary between individuals since each male added or omitted introductory elements or varied the length of the terminal trill. Nonetheless, we classified as the same song type, all songs that had similar overall fine structural features and contained the same number of elements in the middle section following Sandoval et al. (2014) classification. We measured five fine structure features in each song: 1) minimum frequency (Hz), 2) maximum frequency (Hz), 3) frequency range (Hz), 4) frequency of maximum amplitude (Hz), and 5) song duration (s). At the end, we selected only the two common song types of each population for analyses since these were common among males through the years (Bonilla-Badilla 2021). These were: T14 and T18 for UCR; T13 and T35 for DEP; T21 and T42 for JBL; and T2 and T3 for HDA.

Statistical analysis

To quantify the degree of temporal variation (over years) in male songs, we performed linear mixed models (LMM) for each common song type. In these models, we included *Year* as a fixed factor, male individuals were added as random factors, and the fine structure features as response variables. We interpreted the models' Random Effect Variance (σ^2) and Residual Variance (RV) as representing between-individual and within-individual variance, respectively (Van de Pol & Wright 2009; Dingemanse & Dochtermann 2013). By performing separate models for each common song type, we ensured that σ^2 specifically captured individual distinctiveness without the confounding effects of common song type differences. A higher variance in RV than σ^2 would thus indicate if there were indeed temporal intraindividual variance in the selected song parameters. In cases where RV was greater than σ^2, we also performed an ANOVA to determine how distinct males were from one another and a Tukey test to verify where exactly the difference occurred.

Results

From the 40 males recorded, 34 males accomplished the requirements for the analyses: 9 males from UCR, 8 from DEP, 7 from JBL, and 10 from HDA. We processed a total of 118 h of recordings and measured a total of 5,143 songs. There was data available for nearly every year, except for 2020, because of limitations due to the COVID-19 lockdown.

Temporal trends were different among fine-structure features and among song types. UCR and DEP song types had a mean minimum frequency above 3000 Hz, whereas JBL and HDA were mostly between 2000 and 4000 Hz (Figure 1). For the common song T14 of UCR population, minimum frequency and song duration increased over time, while maximum frequency and frequency range decreased (Table 1). For the UCR T18 common, maximum frequency and frequency range decreased over time, and song duration increased (Table 1). In T13 and T35, both songs of DEP, minimum frequency and song duration increased, while maximum frequency and frequency range decreased for T13 through the years (Table 1). Minimum frequency decreased temporally in songs of HDA (T2 and T3) and of JBL (T21 and T42) (Table 1). Frequency of maximum amplitude decreased in T2-HDA and T35-DEP, but it increased in T3-HDA, T13-DEP, and T21-JBL (Table 1). Frequency range increased in T3-HDA and T42-JBL (Table 1). No type of variance or temporal trends were observed on maximum frequency and song duration from T2-

HDA, and T21 and T42, both of JBL (Table 1). Also, frequency range did not change for T2-HDA and T21-JBL, as well as frequency of maximum amplitude in T42-JBL (Table 1).

Significant between-individual variation was present in nearly all fine-structure features of both UCR common song types, whereas in DEP, this was only observed for a single feature in one song type (Table 1). Within-individual variation (RV > σ^2) was mostly observed in DEP, HDA, and JBL common song types (Table 1). For T14-UCR specifically, there was more between-individual variance (β_0 > RV) in minimum frequency (Table 1; $F_{5,475}$=62.7, p<0.001), maximum frequency (Table 1; $F_{5,475}$=95.8, p<0.001), frequency range (Table 1; $F_{5,475}$=125.4, p<0.001), and song duration (Table 1; $F_{5,475}$=66.4, p<0.001). In T18-UCR, there was more between-individual variation in maximum frequency (Table 1; $F_{6,598}$=79.6, p<0.001), frequency range (Table 1; $F_{6,598}$=99.9, p<0.001), and song duration (Table 1; $F_{6,598}$=78.9, p<0.001). Lastly, in T35-DEP there was more between-individual variation in frequency range (Table 1; $F_{4,445}$=15.5, p<0.001). To observe the specific differences between individuals, refer to Table S1.

Discussion

We analyzed the song-types temporal stability in the White-eared Ground-sparrow common during a 13-year period and found significant variation in both within and between-individual variation on fine spectro-temporal characteristics over time. The same types of variation were detected in common song types from the same population, suggesting that song stability over time might be a population-level trait. Previous studies about White-eared Ground-sparrow songs have found more between-individual variation than within (Sandoval et al. 2014). But by examining these songs in a wider temporal context, overall, we found more within-individual variation than between. Our prediction that songs would exhibit more within-individual variance over time due to senescence was asserted for three populations (DEP, HDA, and JBL). In the case of UCR, temporal song variations could be mediated by extrinsic factors, such as each male’s life history or level of urbanization in each territory.

Variation between individuals in behavioral traits may arise due to environmental conditions during their development or genotypic differences (Dingemanse et al. 2010; Ghalambor et al. 2010). We expect some degree of between-individual variation in White-eared Ground-sparrow populations, as this species exhibits post-natal dispersal (Rodríguez-Bardía et al., 2022) and males may therefore experience different environmental contexts when they arrive to the territories and learn the local population's songs (Sandoval et al., 2014; Jones et al. 2025). Moreover, because males originate from different breeding populations (Rodríguez-Bardía et al., 2022); Cueva et al., 2025), both genetic inheritance and the environmental conditions experienced during development may influence body size and brain development, leading individuals to produce the same song types with distinct spectrotemporal characteristics (Mets & Brainard 2018). However, we detected larger between-individual variation in the highly urbanized population UCR, which may be caused by habitat characteristics (i.e., more open vegetation and impervious surfaces) that affect sound transmission (Cueva et al. 2024).

Our results suggest that territory variation due to habitat structure may be driving higher between-individual variation in the spectro-temporal features of common song types from UCR, with the level of urbanization playing a critical role. White-eared ground-sparrow territories in this site are surrounded by anthropogenic structures and are more open compared to the less urbanized site (Juárez et al. 2020), which ultimately limits transmission of certain acoustic traits (Gall et al. 2012; Cueva et al. 2024; Grimes et al. 2024). Considering that territories in this site are not homogeneous, and some resemble their original habitat, males could be adjusting their songs according to their territory's song transmission characteristics. In turn, males emit the same song types with varying spectral features, thus causing higher variation between-individuals. Moreover, variation in habitat structure between territories of the same population may also determine how concealed males are from anthropogenic disturbances. In Collared Flycatchers (*Ficedulla albicollis*), there were among individual differences in singing males depending on their perceived predation risk due to their singing position (Jablonsky et al. 2022). Given this, there is a chance that between-individual variation in UCR is also caused by how proximate males are to humans, which could be viewed by White-eared Ground-sparrows as potential predators. Nonetheless, it has been argued that ambient noise rather than habitat structure poses as a stronger selective pressure on song transmission (LaZerte et al. 2015), suggesting that in urban spaces, anthropogenic noise might be mediating differences in song production between individuals (Harding et al. 2019).

Temporal within-individual variation was larger at the middle urbanized (DEP), low urbanized (JBL), and rural (HDA) populations. Meanwhile, the highly urbanized population (UCR) showed very low within-individual variation over time. We expected to find similar levels of within-individual variation between the highly and medium urbanized populations, but these two sites, separated by only 800 m (UCR from DEP), showed two completely different patterns, which were unexpected. This difference may be caused by differences in habitat structure or in the soundscape. The UCR site has been demonstrated to have high levels of anthropogenic noise compared to DEP (Méndez et al. 2000; Juarez et al. 2017) and could be forcing White-eared ground-sparrow males to limit the range of variation of their solo songs to avoid masking. For example, Common Blackbirds (*Turdus merula*) tended to produce more high-frequency elements to increase their songs' salience in noisy urban environments (Nemeth et al. 2012). As well, territories at the highly urbanized site are more open than those at the medium urbanized site, and perhaps males could be striving to emit their solo songs more consistently to ensure proper transmission, since their original habitats are closed thickets (Cueva et al. 2024). White-eared Ground-sparrow males in the UCR site could thus be responding to anthropogenically induced environmental pressures (see Chapter II of this thesis).

Our results indicate that DEP and HDA had the most within-individual temporal variation in their common song types (T13 and T35; T3), followed by JBL in two song characteristics for both of its song types (T21 and T42), which suggests less temporal consistency (Wilson 2018). Within-individual temporal variations in songs can emerge as males age, a trade-off that may occur to prevent further physiological deterioration rather than allocating resources to maintain their singing performance (Hunt et al. 2004; Bonduriansky et al. 2008). Previous studies suggested that great tits (*Parus major*) males at advanced ages tended to produce less consistent songs, while males of intermediate ages were more consistent (Rivera-Gutiérrez et al. 2012). Furthermore, temporal variations in songs associated with senescence can also arise due to physical constraints of atrophied syrinxes that may ultimately affect motor performance and thus, song traits (Linville 1996). If this is the case, White-eared Ground-sparrow common song types from these three populations seem to vary through time because of aging in males. However, if within-individual variation increases with age in this species, it fails to explain why males from UCR showed higher levels of between-individual variation, considering that they have higher survival rates than their rural counterparts (Juárez et al. 2022).

In the case of both JBL song type (T21 and T42) and one HDA song type (T2), temporal variations were detected in only three of their fine spectrotemporal characteristics (minimum frequency and frequency of maximum amplitude for T2 and T21; minimum frequency and frequency range for T42). These song types could be considered the most temporally stable among White-eared ground sparrow populations in our study. Temporal song consistency is relevant in intrasexual encounters because males advertise their competitiveness and dominance to conspecifics (Botero et al. 2009; Rivera-Gutierrez et al. 2009). Song consistency in this species is subject to habitat quality, which may determine what song parameters are considered dominant within males. For example, male black-capped chickadees (*Poecile atricapillus*) from high-quality habitats responded less to playbacks from dominant males of low-quality habitats (Grava et al. 2013). This could be the case for white-eared ground sparrows, considering that JBL is a less urbanized area compared to UCR and DEP. Thus, standards for male-dominant signals may vary between populations. By observing how song types from the same population exhibited the same trends, our results could support this hypothesis. However, it is unclear why HDA song types (T2 and T3) had such contrasting temporal variations while belonging to a rural location.

The contrasting differences between the more (UCR and DEP) and less (JBL and HDA) urbanized populations can also be caused by differences in the soundscape (Juárez et al. 2020; Méndez et al. 2021; Cueva et al. 2024). For instance, increases in amplitude in white-crowned sparrows were thought to be adopted by juveniles due to increased ambient noise levels (Derryberry et al. 2020). However, Mikula et al. (2021) argued that frequency shifts are more likely attributed to morphological constraints rather than to the acoustic adaptation hypothesis. In fact, it has recently been found that males from JBL have increased their exposed culmen, which can be attributed to changes in feeding behavior (Cueva et al. 2025), and larger beaks can be associated with lower frequencies in songs (Huber et al. 2006). This could explain why song types from JBL and HDA had decreased minimum frequencies, although in White-crowned Sparrows (*Zonotrichia leucophrys*), it was primarily associated with decreasing peak frequencies (Derryberry 2009). Longer exposed culmen was also only found in JBL males, which fails to explain why minimum frequencies in HDA males also decreased in solely one song type. Thus, we cannot fully attribute variations over time in these to traits since fine structure features did not concur with functionality when comparing with other species.

In this study, we found that whether male White-eared Ground-sparrow showed between or within-individual variance over time in their common song types depends on their location.

Between-individual variance was mostly found in the UCR population, a highly urbanized site, and this may be because of individuals with distinct past life histories that may influence their song production. In turn, male responses to anthropogenic disturbances, like habitat structure modification and noise pollution, do not seem to be uniform among males. High urbanization levels may act as a threshold at which populations deviate from population-level responses and favor more varied individual behaviors. In contrast, males from DEP (medium urbanized), JBL (low urbanized), and HDA populations (rural) presented more within-individual variation, which suggests a more generalized trend within populations. Within-individual variation in common songs from these populations can be attributed to intrinsic traits of each male instead of responses to external pressures. This comes to show how singing males in less disturbed sites may have the chance to vary their song production, which creates the notion of more plastic behaviors. It demonstrates as well how microgeographic dialects from the same species are both shaped by the individuals that produce them, as well as by the specific external pressures in which their populations are located. Our study brings insight into how the course of cultural evolution from the same species may vary depending on each population's environmental context. Future research could focus on how newly arriving juvenile males learn these local songs to fully understand the long-term implications of these variations on song evolution.

References

Bonduriansky, R., Maklakov, A., Zajitschek, F., & Brooks, R. (2008). Sexual selection, sexual conflict and the evolution of ageing and life span. *Functional ecology*, 443-453.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... & Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, *26*(4), 183-192.

Bonilla Badilla, K. (2021). Variación cultural en los cantos del cuatro ojos de jupa negra (Melozone leucotis) a través del tiempo.

Botero, C. A., Rossman, R. J., Caro, L. M., Stenzler, L. M., Lovette, I. J., De Kort, S. R., & Vehrencamp, S. L. (2009). Syllable type consistency is related to age, social status and reproductive success in the tropical mockingbird. *Animal Behaviour*, *77*(3), 701-706.

Byers, B. E. (2007). Extrapair paternity in chestnut-sided warblers is correlated with consistent vocal performance. *Behavioral Ecology*, *18*(1), 130-136.

Catchpole, C. K., & Slater, P. J. (2003). *Bird song: biological themes and variations*. Cambridge University Press.

Cueva, L., Fuchs, E. J., Barrantes, G., Madrigal-Brenes, R., & Sandoval, L. (2025). Effect of Spatial and Temporal Urban Isolation on the Genetic Diversity, Acoustic Variation, and Morphological Characteristics of an Urban Survivor Bird Species. *Ecology and Evolution*, *15*(4), e70972.

Derryberry, E. P. (2009). Ecology shapes birdsong evolution: variation in morphology and habitat explains variation in white-crowned sparrow song. *The American Naturalist*, *174*(1), 24-33.

Derryberry, E. P., Seddon, N., Derryberry, G. E., Claramunt, S., Seeholzer, G. F., Brumfield, R. T., & Tobias, J. A. (2018). Ecological drivers of song evolution in birds: disentangling the effects of habitat and morphology. *Ecology and evolution*, *8*(3), 1890-1905.

Dingemanse, N. J., Kazem, A. J., Réale, D., & Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in ecology & evolution*, *25*(2), 81-89.

Dingemanse, N. J., & Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39-54.

Dreher, C. E., & Pröhl, H. (2014). Multiple sexual signals: calls over colors for mate attraction in an aposematic, color-diverse poison frog. *Frontiers in Ecology and Evolution*, *2*, 22.

Friis, J. I., Sabino, J., Santos, P., Dabelsteen, T., & Cardoso, G. C. (2022). Ecological adaptation and birdsong: how body and bill sizes affect passerine sound frequencies. *Behavioral Ecology*, *33*(4), 798-806.

Gall, M. D., Ronald, K. L., Bestrom, E. S., & Lucas, J. R. (2012). Effects of habitat and urbanization on the active space of brown-headed cowbird song. *The Journal of the Acoustical Society of America*, *132*(6), 4053-4062.

Ghalambor, C. K., Angeloni, L. M., & Carroll, S. P. (2010). Behavior as phenotypic plasticity. *Evolutionary behavioral ecology*, 90-107.

Gil, D., & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, *17*(3), 133-141.

Gotthard, K., & Nylin, S. (1995). Adaptive plasticity and plasticity as an adaptation: a selective review of plasticity in animal morphology and life history. *Oikos*, 3-17.

Grava, T., Grava, A., & Otter, K. A. (2012). Vocal performance varies with habitat quality in black-capped chickadees (Poecile atricapillus). *Behaviour*, *149*(1), 35-50.

Grimes, S. E., Lewis, E. J., Nduwimana, L. A., Yurk, B., & Ronald, K. L. (2024). Urbanization alters the song propagation of two human-commensal songbird species. *The Journal of the Acoustical Society of America*, *155*(4), 2803-2816.

Gross, K., Pasinelli, G., & Kunc, H. P. (2010). Behavioral plasticity allows short-term adjustment to a novel environment. *The American Naturalist*, *176*(4), 456-464.

Hall, M. L., Kingma, S. A., & Peters, A. (2013). Male songbird indicates body size with low-pitched advertising songs. *PloS one*, *8*(2), e56717.

Harding, H. R., Gordon, T. A., Eastcott, E., Simpson, S. D., & Radford, A. N. (2019). Causes and consequences of intraspecific variation in animal responses to anthropogenic noise. *Behavioral Ecology*, *30*(6), 1501-1511.

Huber, S. K., & Podos, J. (2006). Beak morphology and song features covary in a population of Darwin's finches (Geospiza fortis). *Biological Journal of the Linnean Society*, *88*(3), 489-498.

Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of evolutionary biology*, *22*(1), 13-26.

Hunt, J., Brooks, R., Jennions, M. D., Smith, M. J., Bentsen, C. L., & Bussiere, L. F. (2004). High-quality male field crickets invest heavily in sexual display but die young. *Nature*, *432*(7020), 1024-1027.

Irwin, D. E., Thimgan, M. P., & Irwin, J. H. (2008). Call divergence is correlated with geographic and genetic distance in greenish warblers (Phylloscopus trochiloides): a strong role for stochasticity in signal evolution?. *Journal of evolutionary biology*, *21*(2), 435-448.

Jones, T. M., Kaiser, S. A., & Sillett, T. S. (2025). Post-fledging ecology of birds: emergent patterns, knowledge gaps, and future frontiers. *Biological Reviews*.

Juárez, R., Chacón-Madrigal, E., & Sandoval, L. (2020). Urbanization has opposite effects on the territory size of two passerine birds. *Avian Research*, *11*(1), 1-9.

Juárez, R., Ruiz-Gutiérrez, V., & Sandoval, L. (2022). Surviving in cities: the case of a year-round territorial bird in the Neotropics. *Journal of Urban Ecology*, *8*(1), juac006.

Keen, S., Meliza, C. D., Pilowsky, J. A., & Rubenstein, D. R. (2016). Song in a social and sexual context: vocalizations signal identity and rank in both sexes of a cooperative breeder. *Frontiers in ecology and evolution*, *4*, 46.

Kroodsma, D. E., & Byers, B. E. (1991). The function (s) of bird song. *American Zoologist*, *31*(2), 318-328.

LaZerte, S. E., Otter, K. A., & Slabbekoorn, H. (2015). Relative effects of ambient noise and habitat openness on signal transfer for chickadee vocalizations in rural and urban green-spaces. *Bioacoustics*, *24*(3), 233-252.

Linville, S. E. (1996). The sound of senescence. *Journal of voice*, *10*(2), 190-200.

Liu, Z. D., Wickham, J. D., & Sun, J. H. (2021). Fighting and aggressive sound determines larger male to win male-male competition in a bark beetle. *Insect Science*, *28*(1), 203-214.

Luther, D., & Baptista, L. (2010). Urban noise and the cultural evolution of bird songs. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1680), 469-473.

Martin, J. G., Pirotta, E., Petelle, M. B., & Blumstein, D. T. (2017). Genetic basis of between-individual and within-individual variance of docility. *Journal of Evolutionary Biology*, *30*(4), 796-805.

Medina, I., & Francis, C. D. (2012). Environmental variability and acoustic signals: a multi-level approach in songbirds. *Biology Letters*, *8*(6), 928-931.

Méndez, C., Barrantes, G., & Sandoval, L. (2021). The effect of noise variation over time and between populations on the fine spectrotemporal characteristics of different vocalization types. *Behavioural Processes*, *182*, 104282.

Mennechez, G., & Clergeau, P. (2006). Effect of urbanisation on habitat generalists: starlings not so flexible?. *Acta Oecologica*, *30*(2), 182-191.

Mennill, D. J. (2011). Individual distinctiveness in avian vocalizations and the spatial monitoring of behaviour. *Ibis*, *153*(2), 235-238.

Mets, D. G., & Brainard, M. S. (2018). Genetic variation interacts with experience to determine interindividual differences in learned song. *Proceedings of the National Academy of Sciences*, *115*(2), 421-426.

Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., ... & Albrecht, T. (2021). A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecology Letters*, *24*(3), 477-486.

Narango, D. L., & Rodewald, A. D. (2018). Signal information of bird song changes in human-dominated landscapes. *Urban Ecosystems*, *21*(1), 41-50. Planqué, R., Britton, N. F., & Slabbekoorn, H. (2014). On the maintenance of bird song dialects. *Journal of Mathematical Biology*, *68*(1), 505-531.

Nemeth, E., Pieretti, N., Zollinger, S. A., Geberzahn, N., Partecke, J., Miranda, A. C., & Brumm, H. (2013). Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), 20122798.

Nussey, D. H., Wilson, A. J., & Brommer, J. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of evolutionary biology*, *20*(3), 831-844.

Piza, P., & Sandoval, L. (2016). The differences in transmission properties of two bird calls show relation to their specific functions. *The Journal of the Acoustical Society of America*, *140*(6), 4271-4275.

Podos, J., Huber, S. K., & Taft, B. (2004). Bird song: the interface of evolution and mechanism. *Annu. Rev. Ecol. Evol. Syst.*, *35*(1), 55-87.

Rivera-Gutierrez, H. F., Pinxten, R., & Eens, M. (2011). Songs differing in consistency elicit differential aggressive response in territorial birds. *Biology Letters*, *7*(3), 339-342.

Rivera-Gutierrez, H. F., Pinxten, R., & Eens, M. (2012). Tuning and fading voices in songbirds: age-dependent changes in two acoustic traits across the life span. *Animal Behaviour*, *83*(5), 1279-1283.

Rodríguez-Bardía, M., Fuchs, E. J., Barrantes, G., Madrigal-Brenes, R., & Sandoval, L. (2022). Genetic structure in neotropical birds with different tolerance to urbanization. *Scientific Reports*, *12*(1), 6054.

Sandoval, L., & Mennill, D. J. (2012). Breeding biology of White-eared Ground-sparrow (*Melozone leucotis*), with a description of a new nest type. *Ornitología Neotropical*, *23*(2), 8.

Sandoval-Vargas, L. A. (2014). Acoustic communication in thicket habitats: Vocal behaviour and vocal divergence in mesoamerican Melozone ground-sparrows.

Sandoval, L., Dabelsteen, T., & Mennill, D. J. (2015). Transmission characteristics of solo songs and duets in a neotropical thicket habitat specialist bird. *Bioacoustics*, *24*(3), 289-306.

Sandoval, L., Méndez, C., & Mennill, D. J. (2016). Vocal behaviour of White-eared Ground-sparrows (*Melozone leucotis*) during the breeding season: repertoires, diel variation, behavioural contexts, and individual distinctiveness. *Journal of Ornithology*, *157*(1), 1-12.

Sandoval, L., Graham, B., Sosa-López, J. R., Laverde-R, O., & Araya-Ajoy, Y. G. (2024). The study of bird vocalizations in Neotropical habitats: Current knowledge and future steps. *Ornitología Neotropical*, *35*(2), 112-129.

Searcy, W. A., & Andersson, M. (1986). Sexual selection and the evolution of song. *Annual Review of Ecology and Systematics*, 507-533.

Schmidt, K. A., & Belinsky, K. L. (2013). Voices in the dark: predation risk by owls influences dusk singing in a diurnal passerine. *Behavioral Ecology and Sociobiology*, *67*(11), 1837-1843.

Schmidt, K. L., MacDougall-Shackleton, E. A., Kubli, S. P., & MacDougall-Shackleton, S. A. (2014). Developmental stress, condition, and birdsong: a case study in song sparrows. *American Zoologist*, *54*(4), 568-577.

Sierro, J., de Kort, S. R., & Hartley, I. R. (2023). Sexual selection for both diversity and repetition in birdsong. *Nature Communications*, *14*(1), 3600.

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour*, *85*(5), 1089-1099.

Szymkowiak, J., & Kuczyński, L. (2017). Song rate as a signal of male aggressiveness during territorial contests in the wood warbler. *Journal of Avian Biology*, *48*(2), 275-283.

Taff, C. C., & Freeman-Gallant, C. R. (2016). Experimental tests of the function and flexibility of song consistency in a wild bird. *Ethology*, *122*(4), 319-328.

Tibbetts, E. A., & Dale, J. (2007). Individual recognition: it is good to be different. *Trends in ecology & evolution*, *22*(10), 529-537.

Van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal behaviour*, *77*(3), 753.

Van Oort, H., Otter, K. A., Fort, K. T., & Holschuh, C. I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. *Ethology*, *112*(8), 772-778.

Warrington, M. H., McDonald, P. G., Rollins, L. A., & Griffith, S. C. (2014). All signals are not equal: acoustic signalling of individuality, sex and breeding status in a cooperative breeder. *Animal Behaviour*, *93*, 249-260.

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

Westneat, D. F., Wright, J., & Dingemanse, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation. *Biological Reviews*, *90*(3), 729-743.

Wiley, R. H. (2013). Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour. *Biological Reviews*, *88*(1), 179-195.

Wilson, A. J. (2018). How should we interpret estimates of individual repeatability?. *Evolution letters*, *2*(1), 4-8.

Wilson, D. R., & Mennill, D. J. (2010). Black-capped chickadees, Poecile atricapillus, can use individually distinctive songs to discriminate among conspecifics. *Animal Behaviour*, *79*(6), 1267-1275.

Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in ecology & evolution*, *27*(8), 452-461.

Zollinger, S. A., Goller, F., & Brumm, H. (2011). Metabolic and respiratory costs of increasing song amplitude in zebra finches. *PLoS One*, *6*(9), e23198.

Table 1. Temporal variance in the fine structure features of common song types of the White-eared Ground-sparrow inhabiting the Central Valley, Costa Rica.

Song-type	Minimum frequency (Hz)				Maximum frequency (Hz)				Frequency range (Hz)			
	σ^2	RV	*p*	β_{Year}	σ^2	RV	*p*	β_{Year}	σ^2	RV	*p*	β_{Year}
	UCR											
T14	**533536**	**191421**	**<0.001**	**160.7**	***1944837***	***748918***	***<0.001***	***-223.0***	***4288550***	***990000***	***<0.001***	***-387.6***
T18	***225653***	***243085***	***0.008***	***-35.8***	***1669453***	***1179091***	***<0.001***	***-162.1***	***2679250***	***1736082***	***<0.001***	***-128.6***
	DEP											
T13	**109738**	**214142**	**0.012**	**30.05**	***260254***	***1100715***	***<0.001***	***-176.4***	***624501***	***1561582***	***<0.001***	***-208.9***
T35	**456155**	**121565**	**<0.001**	**69.57**	***434237***	***686984***	***<0.001***	***-210.6***	***1159126***	***1020641***	***<0.001***	***-280.2***
	JBL											
T21	***184122***	***625069***	***<0.001***	***-120.3***	4514685	5958636	0.163	-114.5	2867617	5116307	0.862	13.18
T42	***433064***	***1021488***	***<0.001***	***-213.3***	248573	1223544	0.173	48.57	**1040245**	**2536488**	**<0.001**	**264.6**
	HDA											
T2	***133186***	***266755***	***<0.001***	***-35.6***	513379	1113548	0.0857	-30.95	835389	1614285	0.864	3.73
T3	***49102***	***257820***	***<0.001***	***-52.9***	**131972**	**725524**	**<0.001**	**112.6**	**265135**	**1306718**	**<0.001**	**165.4**

Bold values indicate a positive relationship; bold and italicized values indicate a negative relationship.

Table 1. Continued.

Song-type	Frequency of maximum amplitude (Hz)				Duration			
	σ^2	RV	p	β_{Year}	σ^2	RV	p	β_{Year}
	UCR							
T14	***192609***	***1313889***	***0.002***	***-116.2***	**0.3198**	**0.1881**	**0.008**	**0.0410**
T18	246328	693234	0.490	-14.9	***0.5892***	***0.2370***	***<0.001***	***0.0854***
	DEP							
T13	**109738**	**214142**	**0.012**	**30.05**	***260254***	***1100715***	***<0.001***	***-176.4***
T35	**456155**	**121565**	**<0.001**	**69.57**	***434237***	***686984***	***<0.001***	***-210.6***
	JBL							
T21	***184122***	***625069***	***<0.001***	***-120.3***	4514685	5958636	0.163	-114.5
T42	***433064***	***1021488***	***<0.001***	***-213.3***	248573	1223544	0.173	48.57
	HDA							
T2	***133186***	***266755***	***<0.001***	***-35.6***	513379	1113548	0.0857	-30.95
T3	***49102***	***257820***	***<0.001***	***-52.9***	**131972**	**725524**	**<0.001**	**112.6**

Bold values indicate a positive relationship; bold and italicized values indicate a negative relationship.

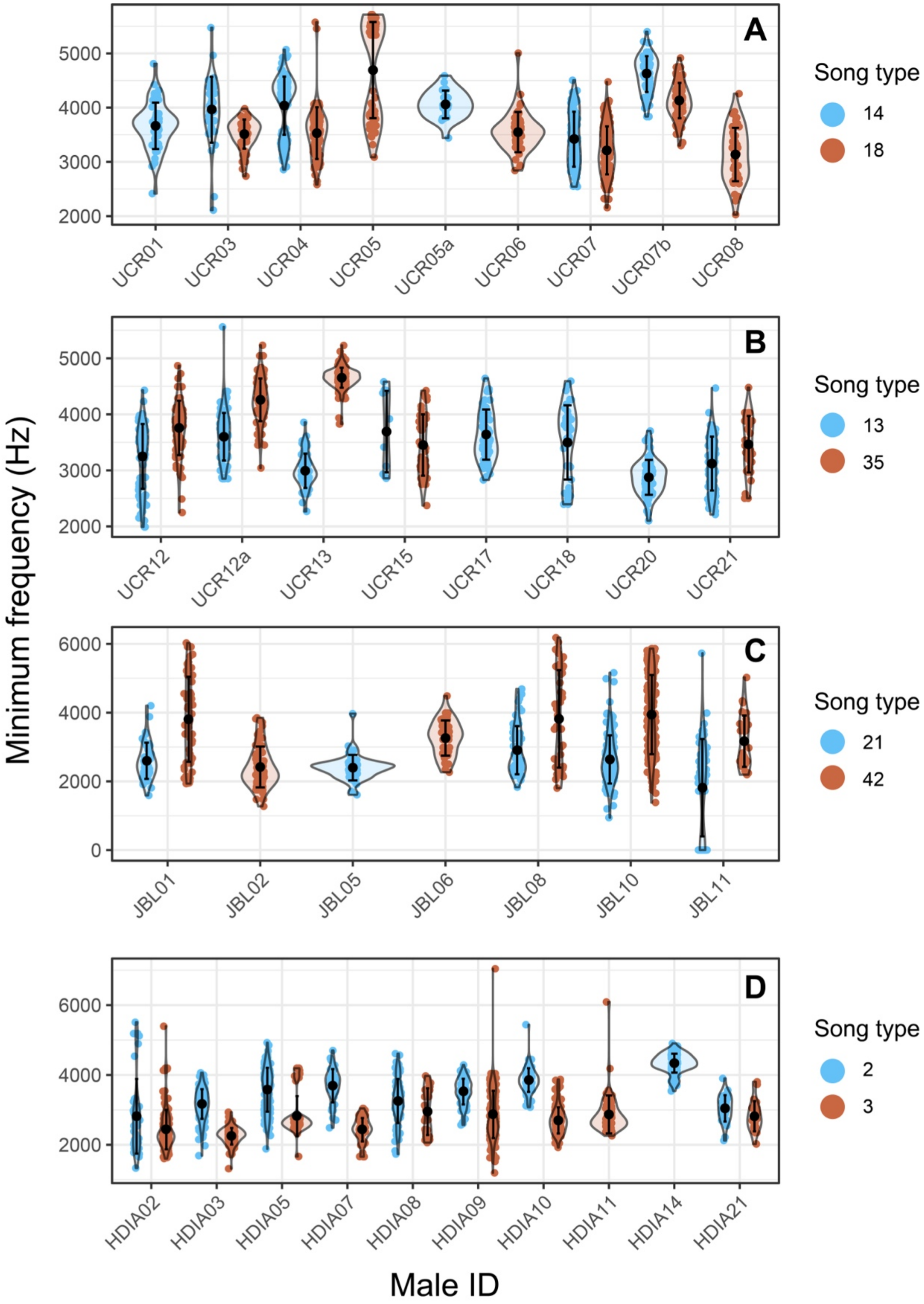

Figure 1. Temporal variance in minimum frequency in common song types from (A) UCR, (B) DEP, (C) JBL, and (D) HAD populations. Central black dots represent mean minimum frequency for each male within the 13-time frame, error bars represent the standard deviation, and colored points represent the measurements of the minimum frequency

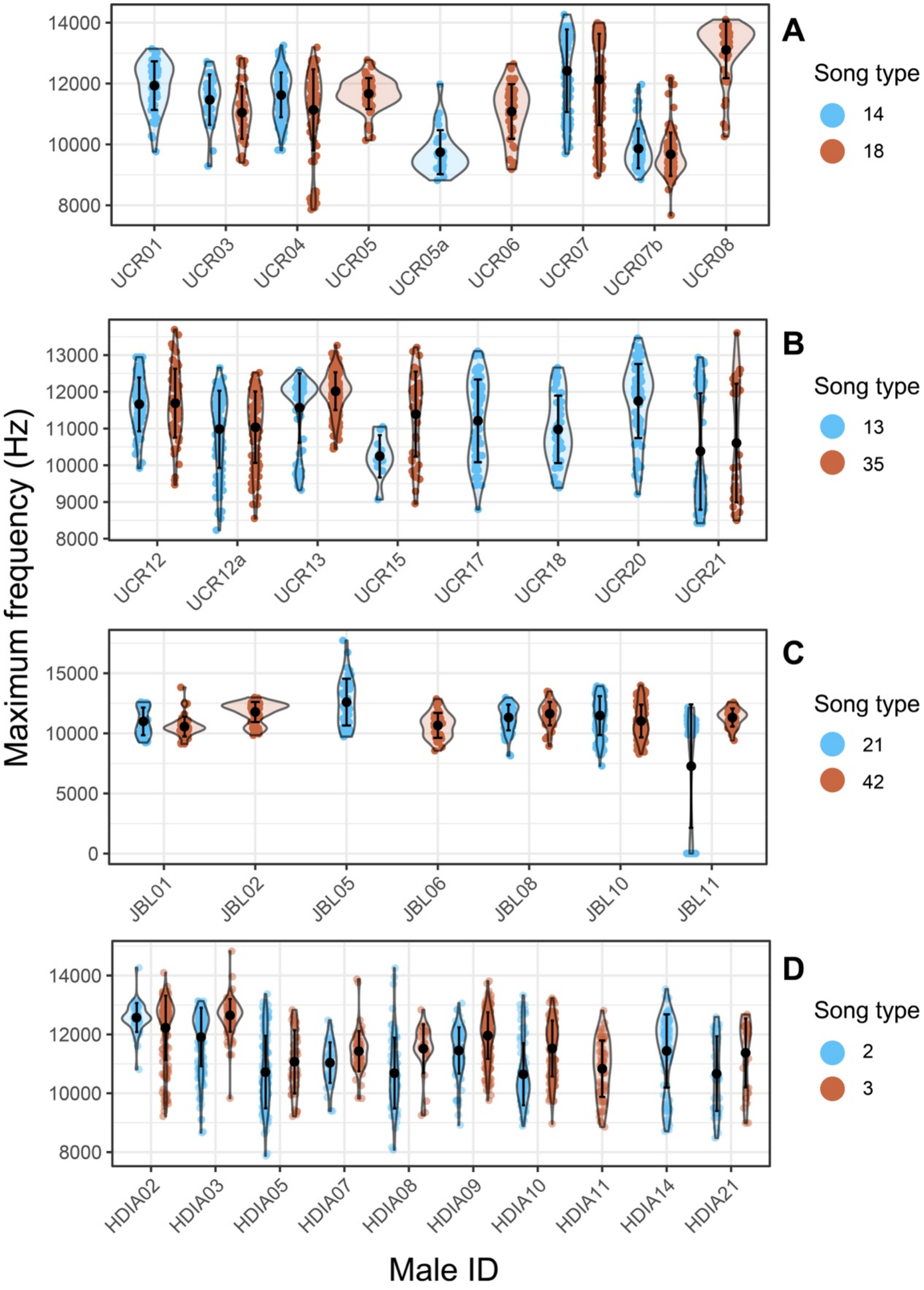

Figure 2. Temporal variance in maximum frequency in common song types from (A) UCR, (B) DEP, (C) JBL, and (D) HAD populations. Central black dots represent mean maximum frequency for each male within the 13-time frame, error bars represent the standard deviation, and colored points represent a measurement.

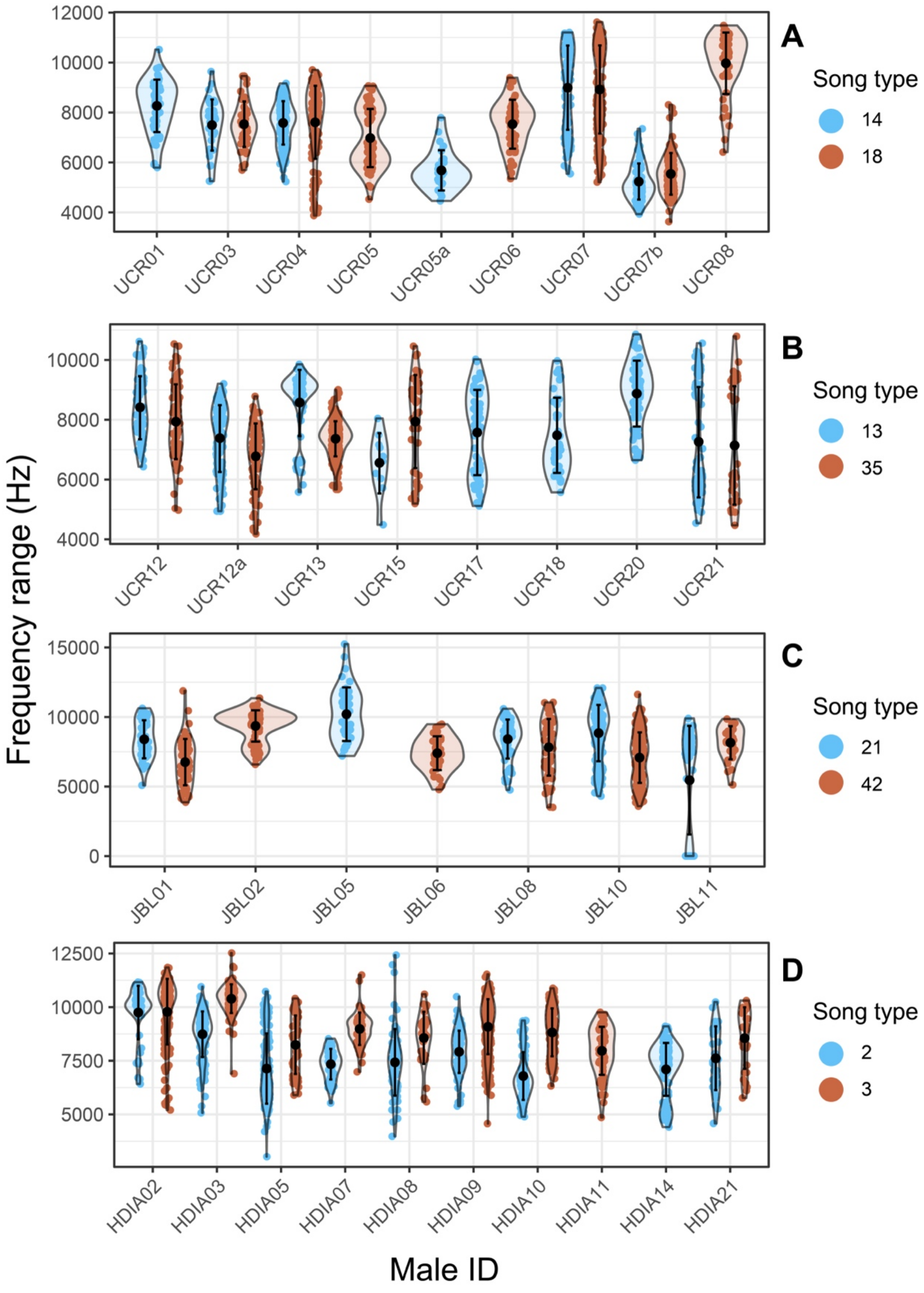

Figure 3. Temporal variance in frequency range in common song types from (A) UCR, (B) DEP, (C) JBL, and (D) HAD populations. Central black dots represent mean frequency range for each male within the 13-time frame, error bars represent the standard deviation, and colored points represent a measurements.

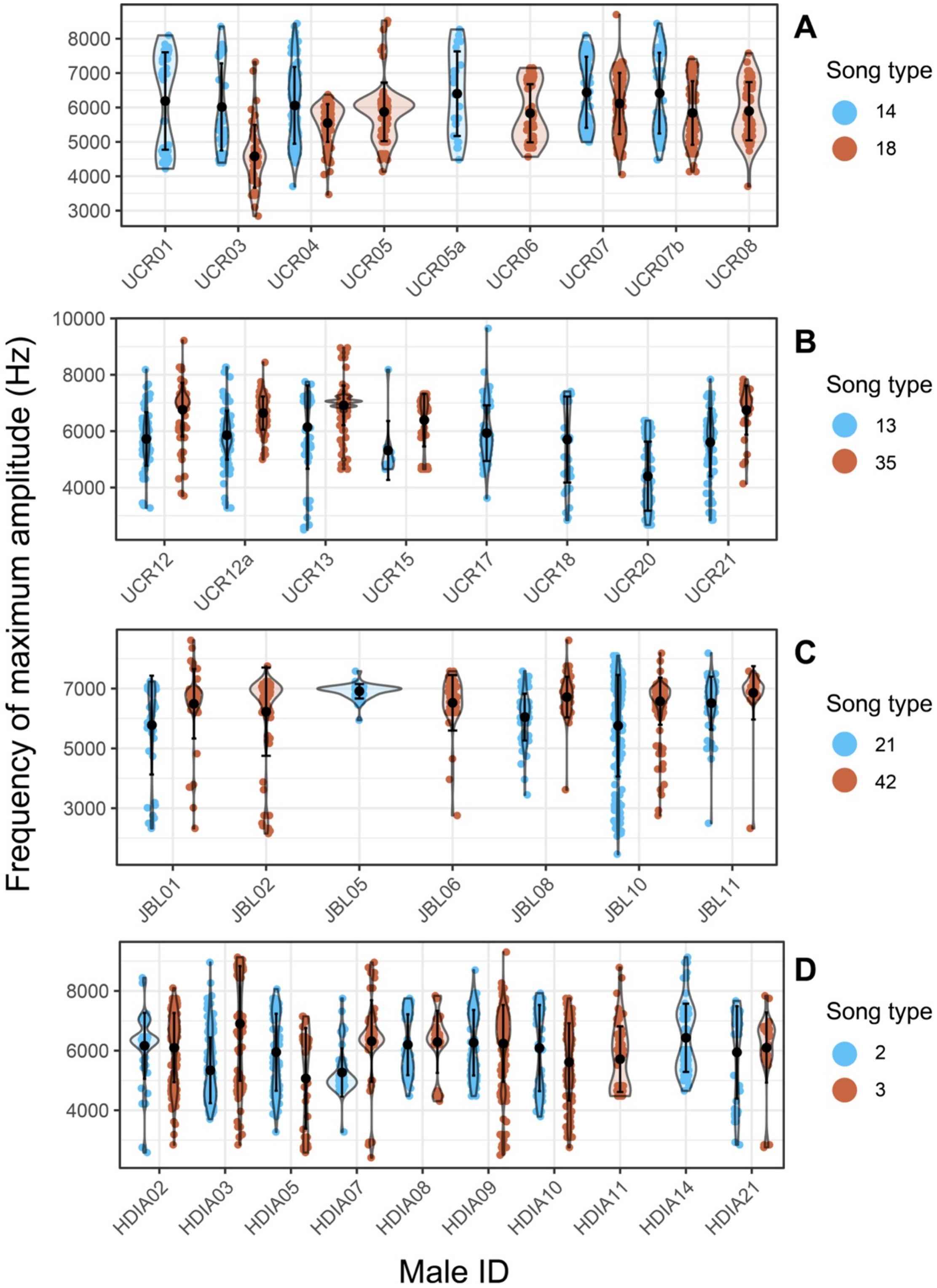

Figure 4. Temporal variance in frequency of maximum amplitude in common song types from (A) UCR, (B) DEP, (C) JBL, and (D) HAD populations. Central black dots represent mean frequency of maximum amplitude for each male within the 13-time frame, error bars represent the standard deviation, and colored points represent a measurements.

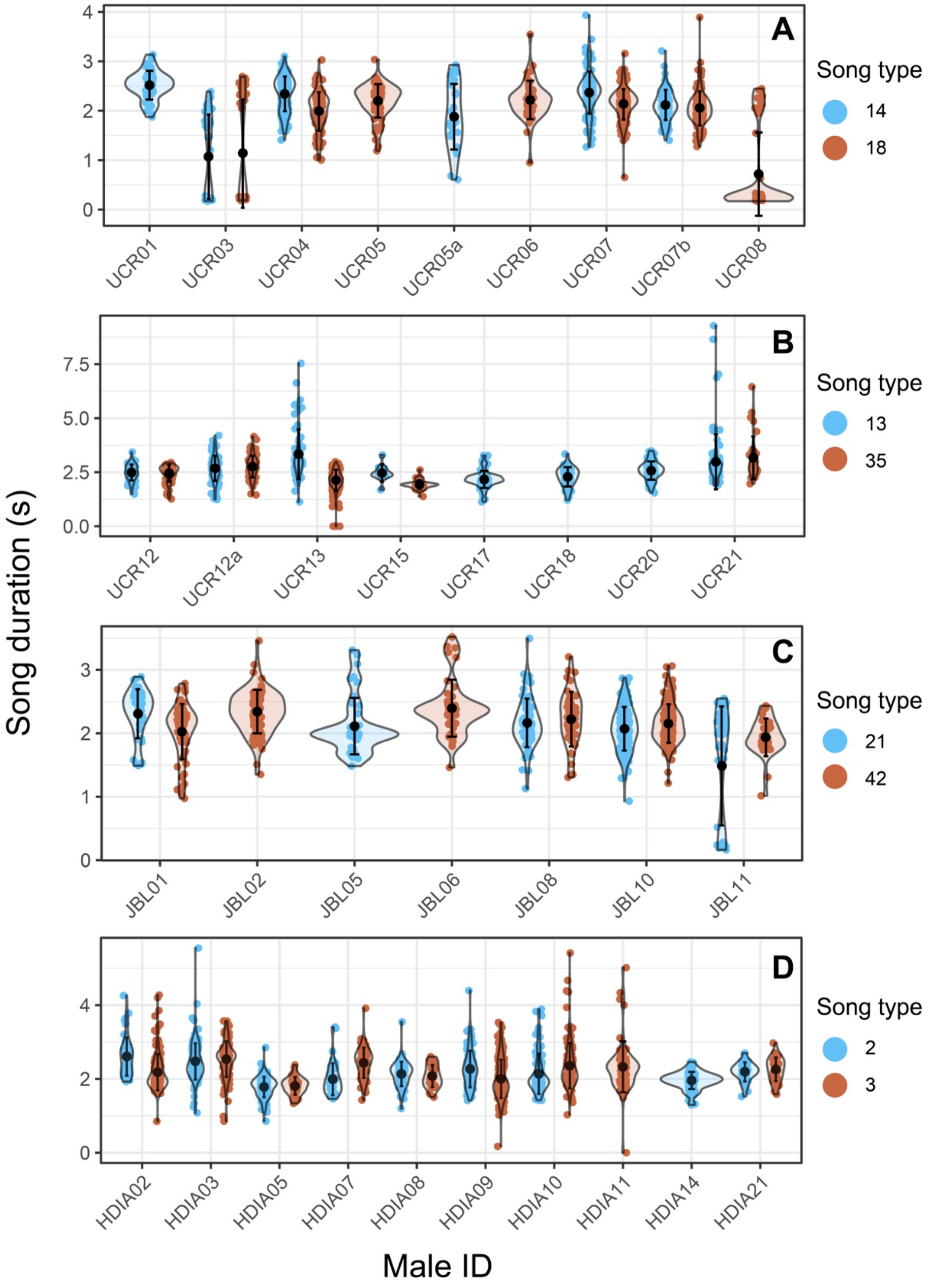

Figure 5. Temporal variance in song duration in common song types from (A) UCR, (B) DEP, (C) JBL, and (D) HAD populations. Central black dots represent mean song duration for each male within the 13-time frame, error bars represent the standard deviation, and colored points represent a measurements.

Supplemental material

Table S1. Differences between white-eared ground sparrow males in fine structure features from song types that presented between-individual variance.

Population	Song type	Interactions	LF *p adj*	HF *p* adj	DF *p adj*	DT *p adj*
UCR	T14	UCR03-UCR01	0.041	0.157	0.016	<0.001
		UCR04-UCR01	<0.001	0.260	0.002	0.110
		UCR05a-UCR01	0.010	<0.001	<0.001	<0.001
		UCR07-UCR01	0.038	0.022	0.002	0.324
		UCR07b-UCR01	<0.001	<0.001	<0.001	<0.001
		UCR04-UCR03	0.962	0.929	0.998	<0.001
		UCR05a-UCR03	0.976	<0.001	<0.001	<0.001
		UCR07-UCR03	<0.001	<0.001	<0.001	<0.001
		UCR07b-UCR03	<0.001	<0.001	<0.001	<0.001
		UCR05a-UCR04	0.999	<0.001	<0.001	<0.001
		UCR07-UCR04	<0.001	<0.001	<0.001	0.997
		UCR07b-UCR04	<0.001	<0.001	<0.001	0.002
		UCR07-UCR05a	<0.001	<0.001	<0.001	<0.001
		UCR07b-UCR05a	<0.001	0.992	0.467	0.150
		UCR07b-UCR07	<0.001	<0.001	<0.001	0.002
	T18	UCR04-UCR03	-	0.999	0.999	<0.001
		UCR05-UCR03	-	0.043	0.274	<0.001
		UCR06-UCR03	-	0.999	1.000	<0.001
		UCR07-UCR03	-	<0.001	<0.001	<0.001
		UCR07b-UCR03	-	<0.001	<0.001	<0.001
		UCR08-UCR03	-	<0.001	<0.001	0.001
		UCR05-UCR04	-	0.023	0.027	0.091
		UCR06-UCR04	-	0.999	0.999	0.138
		UCR07-UCR04	-	<0.001	<0.001	0.231
		UCR07b-UCR04	-	<0.001	<0.001	0.962
		UCR08-UCR04	-	<0.001	<0.001	<0.001
		UCR06-UCR05	-	0.072	0.281	0.999
		UCR07-UCR05	-	0.053	<0.001	0.978
		UCR07b-UCR05	-	<0.001	<0.001	0.487
		UCR08-UCR05	-	<0.001	<0.001	<0.001
		UCR07-UCR06	-	<0.001	<0.001	0.964
		UCR07b-UCR06	-	<0.001	<0.001	0.523
		UCR08-UCR06	-	<0.001	<0.001	<0.001
		UCR07b-UCR07	-	<0.001	<0.001	0.851
		UCR08-UCR07	-	<0.001	<0.001	<0.001
		UCR08-UCR07b	-	<0.001	<0.001	<0.001
DEP	T35	UCR12a-UCR12	-	-	<0.001	-
		UCR13-UCR12	-	-	0.001	-

Table S1. (Continued)

Population	Song type	Interactions	LF *p adj*	HF *p* adj	DF *p adj*	DT *p adj*
DEP	T35	UCR15-UCR12	-	-	0.999	-
		UCR21-UCR12	-	-	0.005	-
		UCR13-UCR12a	-	-	<0.001	-
		UCR15-UCR12a	-	-	<0.001	-
		UCR21-UCR12a	-	-	0.461	-
		UCR15-UCR13	-	-	0.015	-
		UCR21-UCR13	-	-	0.814	-
		UCR21-UCR15	-	-	0.014	-

Capítulo 2: Song plasticity in response to noise: Evidence from within and between-individual variation along a rural-urban gradient

Abstract

Anthropogenic noise can often thwart certain species from communicating effectively within urban environments, while others persist by modifying their acoustic signals. Birds may modify their songs to avoid being masked by persistent low-frequency noise and communicate between conspecifics. It remains unclear whether these responses are a result of behavioral plasticity or due to cultural microevolutionary processes. For this study, we examined how songs from an urban avoiding bird species may vary within an urban to rural gradient during a 13-year time frame. We compared within and between-individual behavioral variance to determine if variations in songs are a result cultural microevolutionary processes or due to differences in plasticity between singing males. We used long-term data from male songs and ambient noise levels at four sites within the Costa Rican Great Metropolitan Area, classified as highly urbanized, medium-urbanized, low-urbanized, and rural. The effects of anthropogenic noise were more pronounced on both ends of the urban-rural gradient, indicating that responses to noise levels may depend on the urbanization level. Males from the highly urbanized site presented greater between-individual variance and thus less behavioral plasticity, possibly because the soundscape in this site restricts them from emitting their songs in varying parameters. Overall, most modifications in songs were likely done to avoid acoustic masking, but the strength of their responses varied by population. However, other unaccounted constraints may be acting upon these spectral features apart from anthropogenic noise. This study demonstrates how ongoing human development is impacting the communication of a tropical urban bird species.

Introduction

Bird songs are strongly shaped by habitat conditions because their transmission depends on habitat structure and background noise (Morton 1975; Hansen 1979; Goutte et al. 2018). Urbanization alters both factors simultaneously (Gill et al. 2015; Perillo et al. 2017; Hao et al. 2024), introducing high levels of low-frequency noise and creating more open and reflective habitats that challenge song transmission (Grabarczyk & Gill 2020). While these conditions disadvantage some species (Chace & Walsh 2006), others persist by modifying their songs, often altering spectro-temporal traits (Francis et al. 2011b; Luther et al. 2016; Serrano et al. 2024). Indeed, urban birds commonly increase the minimum frequency of their songs to avoid masking by low-frequency noise (<3 kHz), and may also adjust song length, amplitude, or repertoire use to improve detectability (Slabbekoorn 2013; Luther et al. 2016; Juárez et al. 2021; Méndez et al. 2021; To et al. 2021). Since songs are crucial for territory defense, mate attraction, and other aspects of avian life history (Nowicki et al. 1995; Mower et al. 2025), these adjustments may influence how receivers perceive signals and ultimately affect reproductive success and fitness (Catchpole & Slater 1995; Luther et al. 2016; Phillips & Derryberry 2018).

Responses to noise, however, vary considerably across species, and it remains unclear whether such modifications represent immediate behavioral plasticity during an individual's lifetime or longer-term ontogenetic adjustments and microevolutionary cultural shifts in populations to adapt to urban environments (Brumm & Slabbekoorn 2005; Miranda et al. 2013; Reichard et al. 2020). For instance, white-crowned sparrow (*Zonotrichia leucophrys*) males decreased frequency bandwidth in their songs in response to experimental noise, possibly optimizing their signal-to-noise ratio during song transmission (Gentry et al. 2017). Temporal modifications in acoustic parameters, like minimum frequency, may result from passive acquisition (Derryberry et al. 2020) or be shaped by sexual and natural selection on, for example, frequency bandwidth because it improves transmission in noisy settings and becomes more salient to conspecifics (Halfwerk et al. 2011; Derryberry et al. 2020; Williams 2021; Marcolin et al. 2022; Villarreal et al. 2024). At the individual level, variation often reflects labile traits that fluctuate plastically in response to changing environmental conditions (O'Dea et al 2021; Araya-Ajoy et al. 2023). Although such within-individual variation can be a key driver of behavioral evolution, it has received comparatively little attention in evolutionary biology (Westneat et al. 2015; Mitchell et al. 2021). Recognizing its role is essential to understand how urban bird populations may continue, or not, to adjust their songs under ongoing environmental change.

Distinguishing whether variations in songs are more prominent between or within individuals can help us to elucidate which environmental constraints are acting upon avian acoustic signals (Alonzo 2015). Between-individual variance suggests that individual birds are producing more consistent signals, possibly due to stable habitat conditions (Mathot et al. 2012), or because they are facing costlier stressors than noise masking (Weir et al. 2012). On the other hand, within-individual variance suggests more plastic or flexible behaviors (Westneat et al. 2013). Behavioral plasticity often serves as a precursor to urban adaptation, since it allows individuals to respond to novel disturbances, like anthropogenic noise, and ensures population persistence (Caspi et al. 2022). These plastic behavioral shifts can eventually lead to microevolutionary cultural shifts, with traits that could be subject to natural or cultural selection (Lugo et al. 2018). We could expect that higher within-individual variance would occur in urban environments, which are notorious for their high levels of disturbance that may drive permanent acoustic adaptations (Lowry et al. 2013; Redondo et al. 2013; Thompson et al. 2022).

In this study, we examined how songs from an urban-avoiding species, the white-eared ground-sparrow *(Melozone leucotis*: Passerellidae), might be changing over time due to anthropogenic noise. The white-eared ground-sparrow is a neotropical song-learning species that occurs in forest patches or thickets of urbanized and rural spaces (Juárez et al. 2022). Males use songs primarily for mate attraction (Sandoval et al. 2016) and are year-round territorial species with prolonged lifespans (Juárez et al. 2022). Previous studies have found that anthropogenic noise influences the fine spectrotemporal characteristics of white-eared ground-sparrow solo songs (Méndez et al. 2021). Given this, we aimed to compare how individual males have potentially varied their solo songs in response to anthropogenic noise within an urban-rural gradient in a 13-year period. Méndez et al. (2021) also found that shifts in the fine spectrotemporal characteristics of the songs due to anthropogenic noise depended on the level of urbanization in which males inhabited. We also compared within and between-individual song variation to determine whether there have been microevolutionary cultural shifts in populations to adapt to noise pollution. Considering that these males have been chronically exposed to anthropogenic noise (Sandoval et al. 2016; Méndez et al. 2021; Rodríguez-Bardía et al. 2021), we expect them to exhibit higher levels of within-individual than between-individual variation as urbanization increases, since individuals from the same population should be similarly adapted to the population's environmental context.

Methods

Study area

We conducted this study in the Costa Rican Great Metropolitan Area (GAM). We selected four places that varied in urban development and anthropogenic noise and were classified according to the degree of urbanization. (1) Universidad de Costa Rica, Rodrigo Facio Campus in San José: Highly urbanized area (**UCR:** 09°56'N, 84°03'W, 1200 m). This site is composed of buildings, green recreational areas with ornamental vegetation, and contains a secondary forest known as the Leonelo Oviedo Reserve. It is also surrounded by busy roads and human settlements. (2) Instalaciones Deportivas, Universidad de Costa Rica in San José: Medium urbanized area (**DEP:** 9°56'N, 84° 03'W, 1200m). This site is comprised of extensive green areas, a secondary forest, and multiple buildings. It is also surrounded by roads and housing and is about 1.5 km away from UCR. (3) Jardín Botánico Lankester in Cartago: Low urbanized area (**JBL:** 9°50'N, 83°53'W, 1370m). It is composed of multiple gardens and thickets and is surrounded by roads and other human structures. (4) Getsemaní in Heredia: Rural (**HDA:** 10°01'N, 84°05'W, 1350m). This site is mainly composed of coffee plantations, thickets, and forest patches.

Data collection

We used recorded songs from the white-eared ground-sparrows breeding season (April and June) and the beginning of the wet season between 2011 and 2024, archived in the Bioacoustics Laboratory from the *Centro de Investigación en Biodiversidad y Ecología Tropical* (CIBET) at the University of Costa Rica. Data has been previously used by one of the manuscript's authors in past research (see Sandoval et al. 2011, 2014, 2015, 2016). Individuals were previously banded with a unique color ring combination, which facilitated identification and recording sessions during each breeding season. For each study site, ten males were recorded between 0500 - 0600 h using the focal recording method (Sandoval et al. 2024) with a Sennheiser ME66 shotgun microphones and Marantz PMD661 solid digital recorders.

During each recording session, the maximum and minimum levels of environmental noise were also measured every 10 minutes, resulting in six measurements per hour recording, using a Sper Scientific 840014 mini sound meter in rapid response and with *A Weighted* noise level. This adjustment was chosen because sparrows presumably have a hearing range between 1 and 8 kHz (Okanaya & Dooling 1988). After obtaining the noise values, we calculated a logarithmic mean per hour, using the minimum and maximum levels since both values can suddenly change due to traffic and people influx, resulting in sub- or over-estimates of environmental noise.

Acoustic analysis

We analyzed song recordings using sound spectrograms in Raved Pro 1.6.5. We first visually classified songs by song type based on the catalog developed in our laboratory to annotate the song types. Only males that sang for at least 2 years and had at least 10 song recordings per year were selected for analysis. We measured five fine structural features in each song: minimum frequency in Hz, maximum frequency in Hz, frequency range in Hz, frequency of maximum amplitude in Hz, and song duration in s. We selected these features since they vary between individuals in male white-eared ground sparrow songs (Sandoval et al. 2014).

Statistical analysis

We first conducted a linear mixed-effects model (LMM) to determine if noise levels differed between white-eared ground-sparrow territories. We employed noise levels as the response variable, population (rural, low, medium and highly urbanized) and year as fixed effects, and male territories as random effects. To test if noise levels have affected fine-structure features in songs, we also performed LMMs for each population. We separated the models by population to isolate the effects of noise and time. In this case, we used the fine-structure features as response variables, the interaction between year and noise levels (year*noise) as the fixed effect, and male identity as a random effect. The models' Intercept Variance (σ^2) and Residual Variance (RV) were interpreted as between-individual and within-individual variance, respectively (Van de Pol & Wright 2009; Dingemanse & Dochtermann 2013). Higher σ^2 than RV would be interpreted as greater between-individual variance, and vice versa.

Results

We obtained a total of 5,345 songs from 40 male white-eared ground-sparrows. However, only 29 males met the requirements to be analyzed: 7 for the high urbanized area, 7 for the medium urbanized area, 5 for the low urbanized area, and 9 for the rural area. We ended up with a total of 2,619 songs for the subsequent analyses.

Noise levels among study sites

Overall, the sites had similar noise level mean within the 13-year period, though the low urbanized site was marginally lower than the rest ($p = 0.07$). Noise levels have decreased throughout the years in the medium urbanized and rural sites (- 0.55 dB/year, $p < 0.001$; -0.36 dB/year, $p < 0.05$ respectively) and marginally for the highly urbanized site (-0.83 dB/year, $p = 0.057$), but they increased in the low urbanized site (+0.62 dB/year, $p < 0.001$). Noise levels have overlapped over the years, but recently, the highly urbanized site has had the highest levels, followed by the medium, rural, and low (Fig. 1).

Within and between individual variances

Males from the highly and medium-urbanized sites exhibited more between-individual variance than those from the low-urbanized site and rural site. Males from the highly urbanized site presented more between-individual variance in minimum frequency, maximum frequency, frequency range, and song duration (Table 1). In the medium-urbanized area, males had more between-individual variance in maximum frequency, frequency range, and song duration (Table 1). We observed more within-individual variance in frequency of maximum amplitude in both the highly and medium-urbanized sites, and minimum frequency for the medium-urbanized site (Table 1). Males from the low-urbanized and rural sites exhibited more within-individual variance in all their fine-structure features (Table 1).

Birds in highly urbanized areas may be responding to acoustic masking

Minimum frequency in songs from males at the highly urbanized site has been decreasing through time ($\beta = -448.5$, $p = 0.032$). However, we also observed that the interaction between time and noise levels, minimum frequency increases ($\beta = 8.79$, $p = 0.024$). Furthermore, males are producing songs with lower maximum frequencies as noise levels increase ($\beta = -251.4$, $p < 0.001$). Hence, frequency range decreases as noise levels increase ($\beta = -249.2$, $p < 0.001$). Song duration, however, increases as noise levels increase ($\beta = 0.126$, $p < 0.001$) and through the years ($\beta = 2.53$,

$p < 0.001$). Nonetheless, in the interaction between year and noise levels, song duration decreased temporally ($\beta = -0.044$, $p < 0.001$). No changes were detected in frequency of maximum amplitude ($p > 0.05$).

Response to noise depends on the population

Minimum and maximum frequency increased as noise levels increased in the medium ($\beta = 166.3$, $p < 0.05$) and low urbanized sites ($\beta = 22.4$, $p = 0.04$). Frequency range ($\beta = 118.6$, $p < 0.001$) and song duration ($\beta = 0.02$, $p < 0.001$) increased as noise levels increased in the low urbanized site, and song duration also increased at the rural site ($\beta = 7.76$, $p < 0.05$). In the medium urbanized site, minimum frequency ($\beta = -288.8$, $p < 0.001$), frequency of maximum amplitude ($\beta = 165.4$, $p < 0.05$), and song duration ($\beta = 0.101$, $p < 0.05$) increased over years, but maximum frequency ($\beta = -440.4$, $p < 0.001$) and frequency range decreased ($\beta = -752.6$, $p < 0.001$). For the low urbanized site, minimum ($\beta = -78.6$, $p < 0.001$) and maximum frequency ($\beta = -51.4$, $p < 0.05$) decreased over years, whereas frequency of maximum amplitude ($\beta = -65.9$, $p < 0.001$) and song duration ($\beta = 0.027$, $p < 0.001$) increased. In the rural site, minimum frequency ($\beta = -35.2$, $p < 0.05$), maximum frequency ($\beta = -789.9$, $p < 0.001$), frequency range ($\beta = -1246.7$, $p < 0.001$), and frequency of maximum amplitude ($\beta = -805.6$, $p < 0.001$) decreased over years. Song duration ($\beta =0.21$, $p < 0.001$) increased over years in the rural site.

The interaction between year and noise levels produced different patterns. In the medium-urbanized site, we found that maximum frequency ($\beta = -107.8$, $p < 0.001$) and frequency range ($\beta = -83.7$, $p < 0.05$) decreased over the years at higher noise levels. In the low-urbanized site, maximum frequency ($\beta = -37.3$, $p < 0.001$), frequency range ($\beta = -37.5$, $p < 0.001$), and frequency of maximum amplitude ($\beta = -16.9$, $p < 0.05$) decreased over the years with temporal noise trends. In the rural site, minimum frequency ($\beta = -10.5$, $p < 0.001$) and song duration ($\beta = -0.004$, $p < 0.05$) have decreased through the years with temporal noise trends. Lastly, maximum frequency ($\beta = 17.0$, $p < 0.001$), frequency range ($\beta = 29.0$, $p < 0.001$), and frequency of maximum amplitude ($\beta = 18.7$, $p < 0.001$) have increased temporally at higher noise levels over the years.

Discussion

Our results indicate that white-eared ground-sparrows responded to anthropogenic noise, but the patterns are most pronounced at the two extremes of the urban–rural gradient. Contrary to our expectations, males in the most urbanized sites showed less song plasticity and greater consistency, as reflected by higher between-individual variance. In contrast, males from low-urbanized and rural sites exhibited greater within-individual variance. Although noise levels did not differ greatly among populations, some variation in fine-structure features appears to have emerged to reduce masking, yet the strength of responses to noise varied across sites. Moreover, several fine-structure features did not vary or adjust with noise levels, suggesting that white-eared ground-sparrow males may face additional, unmeasured constraints on their acoustic communication.

Male solo songs from the most urbanized sites of the urban-rural gradient were more consistent and showed more variance between individuals of the same population than those from the less urbanized sites. This pattern was opposite to our prediction, even though males from this site seem to be adjusting all their spectral characteristics, except frequency of maximum amplitude, in response to temporal noise level dynamics. Anthropogenic noise, primarily composed of low frequencies (Slabbekoorn & Ripmeester 2008; Halfwerk & Slabbekoorn 2014), occupies the lower range of frequencies in the soundscape, which in turn directly competes with species that emit low-frequency acoustic signals (Proppe et al. 2013; Roca et al. 2016). Hence, to avoid masking, birds often increase their minimum frequency (Slabbekoorn 2013; Reichard et al. 2020), but since they are producing higher frequency songs or characteristics, they might face morphological limitations that impede them from producing further increases (Catchpole & Slater 2003; Patricelli & Blickley 2006). This restriction likely reduces the variation of acoustic parameters between singing bouts, resulting in greater behavioral consistency. Thus, male white-eared ground-sparrows may show more uniform singing patterns as anthropogenic noise compresses their functional acoustic space.

Within-individual variance was more prominent in the less urbanized sites (low-urbanized and rural) than in the more urbanized sites. This type of variance is associated with behavioral plasticity (Westneat et al. 2015), indicating that males in these sites have produced varying responses to environmental cues. In fact, noise levels in both the low-urbanized and rural sites were the most dynamic (Fig 1), suggesting that varying noise levels could have mediated variances within individuals in their acoustic signals, an opposite effect to that of males in the highly and medium urbanized sites. For instance, southern house wrens (*Troglodytes musculus*) tended to produce more high-frequency elements and to increase the minimum frequency in low-frequency elements in sites with higher noise levels (Juárez et al. 2020). Furthermore, southern house wrens from sites with lower noise levels had the chance to produce a wider range of song elements with varying frequencies because they were less masked and thus less limited in the acoustic space (Juárez et al. 2020). The same might be occurring with white-eared ground-sparrows, where males in the low-urbanized and rural sites can produce their songs at varying parameters since noise levels might not fully mask them. Considering that white-eared ground sparrow males from these sites exhibit more behavioral variation within individuals, our results might suggest that urban spaces may be selecting individuals with less behavioral plasticity, whereas more plastic individuals are favored in the less urbanized sites. It is worth noting the distinction between behavioral plasticity and trait variability, which could also be a possibility. Trait variability could represent less precision in signal production caused by other intrinsic factors (i.e., senescence, vocal apparatus deterioration) and not necessarily plasticity (Hunt et al. 2009; Rivera-Gutiérrez et al. 2012). Nonetheless, given the relationship between fluctuating noise levels and song feature variation, it is likely that this is a result of a plastic response rather than mere motor imprecision.

Our results suggested that temporal trends in noise have influenced minimum frequency primarily at both ends of the urban-rural gradient (highly urbanized and rural), though in the rural site minimum frequency decreased. In the case of the highly urbanized area, males seem to be increasing minimum frequencies in common songs as noise levels increase through time and could be exhibiting local cultural adaptations to chronic noise exposure (Derryberry et al. 2016). Spectral shifts in songs as a response to chronic noise exposure have been observed in several urban-dwelling bird species in the form of increasing minimum frequencies to avoid acoustic masking (Hu & Cardoso 2009; Dowling et al. 2012), including template species such as white-crowned sparrows *(Zonotrichia leucophrys*), song sparrows *(Melospiza melodia*), dark-eyed juncos *(Junco hyemalis*), and common blackbirds *(Turdus merula*) *(*Wood & Yezerinac 2006; Nemeth et al. 2013; Reichard et al. 2020). In line with these studies, our results suggest that white-eared ground-sparrows increased their minimum frequencies to avoid acoustic masking and transmit their songs effectively in highly urbanized settings. Reflecting this trend, decreases in minimum frequencies in the rural site seem to be associated with decreases in noise levels through the years, expanding their acoustic active space (Fig. 1). This underscores the potential for species to reverse noise-induced vocal changes when acoustic conditions improve, a phenomenon recently documented in white-crowned sparrows (Derryberry et al. 2020).

White-eared ground-sparrow males from the medium and low urbanized sites tend to produce songs with high minimum frequencies in territories with high noise levels. This also supports the notion that males that inhabit territories with high noise levels could be avoiding low-frequency acoustic masking (Nemeth & Brumm 2009; Slabbekoorn 2013; Dowling et al. 2015). Minimum frequency also increased through time in songs from males in the medium-urbanized site, but the opposite was true for males in the low-urbanized site. Songs with higher minimum frequencies transmit better and are more salient in conditions with high noise levels but are less effectively transmitted in conditions with low noise levels (Luther & Magnotti 2014; Duquette et al. 2021; Villareal et al. 2024), directly affecting how potential mates perceive them (Halfwerk et al. 2011; Luther et al. 2016). Given this, though males in noisier territories tend to sing with higher minimum frequencies, anthropogenic noise might still not be a strong selective pressure on songs from the low-urbanized, and sexual selection could be influencing temporal decreases in this characteristic instead. This could also be the reason there were no trends with respect to the interaction between time and noise levels, because noise has not reached a certain threshold for them to respond. The same could be true for the medium-urbanized site, since we did not find any trends in minimum frequency related to the interaction between time and noise levels. Perhaps noise might have to reach the same levels as the highly urbanized site so that white-eared ground-sparrows reflect temporal increases in their minimum frequency.

We found that male white-eared ground-sparrows tend to sing in higher maximum frequencies in the medium and low-urbanized sites when noise levels increase. However, it decreases through time in the medium, low-urbanized, and rural sites. Higher maximum frequencies in noisier territories may avoid being masked by low-frequency anthropogenic noise, but it can also be a trade-off for maintaining increased minimum frequencies, since it is energetically costly (Hu & Cardoso 2009; Sandoval 2011). However, temporal decreases in this spectral characteristic could be due to sexual selection (Mikula et al. 2021). White-eared ground-sparrow males' song are used mostly for mate attraction (Sandoval et al. 2014, 2016), and in general, female birds mostly prefer lower frequencies since it is related to male quality (Gil & Gahr 2002; Mikula et al. 2021), though this has not been confirmed for our study species. In fact, the results we found associated with the interaction between time and noise could support the idea that sexual selection is acting as a stronger selective pressure for maximum frequency since trends are not consistent with the acoustic adaptation hypothesis (Ey & Fischer 2009; Mikula et al. 2021;

Cueva et al. 2024; Budka 2025). Hence, although males seem to be producing higher maximum frequencies in noisier territories, females could still be selecting males that produce songs with lower maximum frequencies. However, we cannot rule out the role of impaired cultural transmission. If pervasive anthropogenic noise masks critical portions of the tutor’s song, juveniles may fail to perceive and accurately learn these spectral characteristics (Rabin & Greene 2002). This 'cultural erosion' could lead to a progressive loss of low-frequency components or a narrowing of the vocal bandwidth over generations (Luther & Baptista 2010).

Maximum frequency could also be facing pressures from physical structures like impervious surfaces or buildings, which occur at higher densities in the highly urbanized area (Juárez et al. 2020). Indeed, increasing maximum frequencies could be an adjustment to reduce reverberation caused by buildings that surround territories in the highly urbanized area. Dowling et al. (2012) indicate that simultaneous adjustments to minimum and maximum frequency can affect communication between conspecifics, since transmission would not be optimal for either noise or reverberating structures. Considering this, it is likely that noise is posing as a stronger selective pressure because, although males in noisier territories tended to produce higher maximum frequencies, there were no temporal trends in this acoustic feature. Thus, they may be presenting a trade-off in which they are less likely to adjust transmission for reverberation if high noise levels are present (Dowling et al. 2012). We cannot be completely certain of this since we did not include impervious surfaces in our analyses, so further research on the matter could focus on how acoustic signals respond to the presence of anthropogenic structures.

Song duration in male solo songs decreased when noise increased over time at both ends of the urban-rural gradient. Decreases in song length can also serve as a strategy for urban-dwelling birds to avoid acoustic masking (Gil et al. 2015). Shortening of song lengths can also come as a trade-off for modifications in other spectral features, such as increases in minimum or maximum frequency (Francis et al. 2011a; Ritschard & Brumm 2012). On the other hand, song output is energetically costly and could be restricted if birds inhabit low-quality habitats (Van Oort et al. 2006). This possibility is likely, considering that noise levels did not differ significantly between locations. Therefore, spectral modifications in songs can emerge due to other environmental constraints, such as limited resources or low-quality habitats, that males may face in their territories (Narango & Rodewald 2016).

White-eared ground-sparrow's response to chronic noise exposure seems to depend on the population's location. As opposed to what we expected, males presented less behavioral plasticity in the most urbanized sites, possibly because the urban soundscape limits birds from emitting songs at varying parameters. This demonstrates that responses to urbanization depend on species' locations. Furthermore, though some fine-structure features seem to coincide with modifications to avoid masking, it is likely that these spectral shifts are also being pressured by other environmental constraints. Maximum frequency, for example, appears to be a trait sexually selected as opposed to minimum frequency, since variations in the latter have been consonant with previous studies. This highlights the need to consider other external factors (i.e., territory density, anthropogenic structures, resource availability) when studying birdsong in urban spaces. Our study gives insight into how urban surviving tropical species may be coping with ongoing human development, and further research should focus on possible impacts on their reproductive behavior and success.

References

Alonzo, S. H. (2015). Integrating the how and why of within-individual and among-individual variation and plasticity in behavior. *Current opinion in behavioral sciences*, *6*, 69-75.

Araya-Ajoy, Y. G., Dingemanse, N. J., Westneat, D. F., & Wright, J. (2023). The evolutionary ecology of variation in labile traits: selection on among- and within-individual components. *Evolution*, *77*(10), 2246-2256.

Brumm, H., & Slabbekoorn, H. (2005). Acoustic communication in noise. *Advances in the Study of Behavior*, *35*, 151-209.

Budka, M. (2025). Thrush nightingales adjust the peak frequency and structure of their songs in response to different types of experimental noise. *Scientific Reports*, *15*(1), 2652.

Caspi, T., Johnson, J. R., Lambert, M. R., Schell, C. J., & Sih, A. (2022). Behavioral plasticity can facilitate evolution in urban environments. *Trends in Ecology & Evolution*, *37*(12), 1092-1103.

Catchpole, C. K., & Slater, P. J. (2003). *Bird song: biological themes and variations*. Cambridge University Press.

Chace, J. F., & Walsh, J. J. (2006). Urban effects on native avifauna: a review. *Landscape and urban planning*, *74*(1), 46-69.

Cueva, L., Bartolo, R., & Sandoval, L. (2024). The Acoustic adaptation hypothesis does not support the occurrence of common songs in a neotropical urban bird species. *Bioacoustics*, *33*(6), 510-526.

Derryberry, E. P., Danner, R. M., Danner, J. E., Derryberry, G. E., Phillips, J. N., Lipshutz, S. E., ... & Luther, D. A. (2016). Patterns of song across natural and anthropogenic soundscapes suggest that white-crowned sparrows minimize acoustic masking and maximize signal content. *PLoS One*, *11*(4), e0154456.

Derryberry, E. P., Phillips, J. N., Derryberry, G. E., Blum, M. J., & Luther, D. (2020). Singing in a silent spring: Birds respond to a half-century soundscape reversion during the COVID-19 shutdown. *Science*, *370*(6516), 575-579.

Diniz, P., & Duca, C. (2021). Anthropogenic noise, song, and territorial aggression in southern house wrens. *Journal of Avian Biology*, *52*(10).

Dowling, J. L., Luther, D. A., & Marra, P. P. (2012). Comparative effects of urban development and anthropogenic noise on bird songs. *Behavioral Ecology*, *23*(1), 201-209.

Duquette, C. A., Loss, S. R., & Hovick, T. J. (2021). A meta-analysis of the influence of anthropogenic noise on terrestrial wildlife communication strategies. *Journal of Applied Ecology*, *58*(6), 1112-1121.

Ey, E., & Fischer, J. (2009). The "acoustic adaptation hypothesis"—a review of the evidence from birds, anurans and mammals. *Bioacoustics*, *19*(1-2), 21-48.

Francis, C. D., Ortega, C. P., & Cruz, A. (2011a). Different behavioural responses to anthropogenic noise by two closely related passerine birds. *Biology letters*, *7*(6), 850-852.

Francis, C. D., Ortega, C. P., & Cruz, A. (2011b). Vocal frequency change reflects different responses to anthropogenic noise in two suboscine tyrant flycatchers. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1714), 2025-2031.

Gentry, K. E., Derryberry, E. P., Danner, R. M., Danner, J. E., & Luther, D. A. (2017). Immediate signaling flexibility in response to experimental noise in urban, but not rural, white-crowned sparrows. *Ecosphere*, *8*(8), e01916.

Gil, D., & Gahr, M. (2002). The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution*, *17*(3), 133-141.

Gil, D., Honarmand, M., Pascual, J., Pérez-Mena, E., & Macias Garcia, C. (2015). Birds living near airports advance their dawn chorus and reduce overlap with aircraft noise. *Behavioral Ecology*, *26*(2), 435-443.

Gill, S. A., Job, J. R., Myers, K., Naghshineh, K., & Vonhof, M. J. (2015). Toward a broader characterization of anthropogenic noise and its effects on wildlife. *Behavioral Ecology*, *26*(2), 328-333.

Goutte, S., Dubois, A., Howard, S. D., Márquez, R., Rowley, J. J. L., Dehling, J. M., ... & Legendre, F. (2018). How the environment shapes animal signals: a test of the acoustic adaptation hypothesis in frogs. *Journal of Evolutionary Biology*, *31*(1), 148-158.

Grabarczyk, E. E., & Gill, S. A. (2020). Anthropogenic noise masking diminishes house wren (Troglodytes aedon) song transmission in urban natural areas. *Bioacoustics*, *29*(5), 518-532.

Halfwerk, W., Bot, S., Buikx, J., van der Velde, M., Komdeur, J., ten Cate, C., & Slabbekoorn, H. (2011). Low-frequency songs lose their potency in noisy urban conditions. *Proceedings of the National Academy of Sciences*, *108*(35), 14549-14554.

Halfwerk, W., & Slabbekoorn, H. (2014). The impact of anthropogenic noise. *Avian urban ecology*, 84.

Hansen, P. (1979). Vocal learning: Its role in adapting sound structures to long-distance propagation, and a hypothesis on its evolution. *Animal Behaviour, 27*(4), 1270–1271.

Hao, Z., Zhang, C., Li, L., Gao, B., Wu, R., Pei, N., & Liu, Y. (2024). Anthropogenic noise and habitat structure shaping dominant frequency of bird sounds along urban gradients. *iScience*, *27*(2), 109056.

Hu, Y., & Cardoso, G. C. (2009). Are bird species that vocalize at higher frequencies preadapted to inhabit noisy urban areas?. *Behavioral Ecology*, *20*(6), 1268-1273.

Hunt, J., Breuker, C. J., Sadowski, J. A., & Moore, A. J. (2009). Male–male competition, female mate choice and their interaction: determining total sexual selection. *Journal of evolutionary biology*, *22*(1), 13-26.

Juárez, R., Chacón-Madrigal, E., & Sandoval, L. (2020). Urbanization has opposite effects on the territory size of two passerine birds. *Avian Research*, *11*(1), 11.

Juárez, R., Araya-Ajoy, Y. G., Barrantes, G., & Sandoval, L. (2021). House Wrens *Troglodytes aedon* reduce repertoire size and change song element frequencies in response to anthropogenic noise. *Ibis*, *163*(1), 52-64.

Juárez, R., Ruiz-Gutiérrez, V., & Sandoval, L. (2022). Surviving in cities: the case of a year-round territorial bird in the Neotropics. *Journal of Urban Ecology*, *8*(1), juac006.

K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology. (2024). Raven Pro: Interactive Sound Analysis Software (Version 1.6.5) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from https://www.ravensoundsoftware.com/.

Lewis, R. N., Williams, L. J., & Gilman, R. T. (2021). The uses and implications of avian vocalizations for conservation planning. *Conservation Biology*, *35*(1), 50-63.

Lowry, H., Lill, A., & Wong, B. B. (2013). Behavioural responses of wildlife to urban environments. *Biological reviews*, *88*(3), 537-549.

Lugo, A. E., Winchell, K. M., & Carlo, T. A. (2018). Novelty in ecosystems. *The Encyclopedia of the Anthropocene, vol. 3, p. 259-271. Oxford: Elsevier.*

Luther, D., & Baptista, L. (2010). Urban noise and the cultural evolution of bird songs. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1680), 469-473.

Luther, D., & Magnotti, J. (2014). Can animals detect differences in vocalizations adjusted for anthropogenic noise?. *Animal Behaviour*, *92*, 111-116.

Luther, D. A., Phillips, J., & Derryberry, E. P. (2016). Not so sexy in the city: urban birds adjust songs to noise but compromise vocal performance. *Behavioral Ecology*, *27*(1), 332-340.

Marcolin, F., Cardoso, G. C., Bento, D., Reino, L., & Santana, J. (2022). Body size and sexual selection shaped the evolution of parrot calls. *Journal of Evolutionary Biology*, *35*(3), 439-450.

Mathot, K. J., Wright, J., Kempenaers, B., & Dingemanse, N. J. (2012). Adaptive strategies for managing uncertainty may explain personality-related differences in behavioural plasticity. *Oikos*, *121*(7), 1009-1020.

Méndez, C., Barrantes, G., & Sandoval, L. (2021). The effect of noise variation over time and between populations on the fine spectrotemporal characteristics of different vocalization types. *Behavioural Processes*, *182*, 104282.

Mikula, P., Valcu, M., Brumm, H., Bulla, M., Forstmeier, W., Petrusková, T., ... & Albrecht, T. (2021). A global analysis of song frequency in passerines provides no support for the acoustic adaptation hypothesis but suggests a role for sexual selection. *Ecology Letters*, *24*(3), 477-486.

Miranda, A. C., Schielzeth, H., Sonntag, T., & Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity?. *Global change biology*, *19*(9), 2634-2644.

Miranda, A. C. (2017). Mechanisms of behavioural change in urban animals: the role of microevolution and phenotypic plasticity. In *Ecology and conservation of birds in urban environments* (pp. 113-132). Cham: Springer International Publishing.

Mitchell, D. J., Beckmann, C., & Biro, P. A. (2021). Understanding the unexplained: The magnitude and correlates of individual differences in residual variance. *Ecology and Evolution*, *11*(12), 7201-7210.

Morton, E. S. (1975). Ecological sources of selection on avian sounds. *The American Naturalist*, *109*(965), 17-34.

Mower, P. C., Vazquez-Cardona, J., Krause, S. W., Bonnell, T. R., & Logue, D. M. (2025). Fight song: variation in singing behaviour and song structure during natural agonistic interactions in a tropical songbird, Adelaide's Warbler (*Setophaga adelaidae*). *Ibis*.

Narango, D. L., & Rodewald, A. D. (2016). Urban-associated drivers of song variation along a rural–urban gradient. *Behavioral ecology*, *27*(2), 608-616.

Nemeth, E., & Brumm, H. (2009). Blackbirds sing higher-pitched songs in cities: adaptation to habitat acoustics or side-effect of urbanization?. *Animal behaviour*, *78*(3), 637-641.

Nemeth, E., Pieretti, N., Zollinger, S. A., Geberzahn, N., Partecke, J., Miranda, A. C., & Brumm, H. (2013). Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1754), 1471-2954.

Nowicki, S., Searcy, W., & Hughes, M. (1998). The territory defense function of song in song sparrows: a test with the speaker occupation design. *Behaviour*, *135*(5), 615-628.

O'Dea, R. E., Noble, D. W., & Nakagawa, S. (2022). Unifying individual differences in personality, predictability and plasticity: a practical guide. *Methods in Ecology and Evolution*, *13*(2), 278-293.

Patricelli, G. L., & Blickley, J. L. (2006). Avian communication in urban noise: causes and consequences of vocal adjustment. *The Auk*, *123*(3), 639-649.

Perillo, A., Mazzoni, L. G., Passos, L. F., Goulart, V. D., Duca, C., & Young, R. J. (2017). Anthropogenic noise reduces bird species richness and diversity in urban parks. *Ibis*, *159*(3), 638-646.

Phillips, J. N., & Derryberry, E. P. (2018). Urban sparrows respond to a sexually selected trait with increased aggression in noise. *Scientific reports*, *8*(1), 7505.

Proppe, D. S., Sturdy, C. B., & St. Clair, C. C. (2013). Anthropogenic noise decreases urban songbird diversity and may contribute to homogenization. *Global change biology*, *19*(4), 1075-1084.

Rabin, L. A., & Greene, C. M. (2002). Changes to acoustic communication systems in human-altered environments. *Journal of Comparative Psychology*, *116*(2), 137.

Redondo, P., Barrantes, G., & Sandoval, L. (2013). Urban noise influences vocalization structure in the House Wren *Troglodytes aedon*. *Ibis*, *155*(3), 621-625.

Reichard, D. G., Atwell, J. W., Pandit, M. M., Cardoso, G. C., Price, T. D., & Ketterson, E. D. (2020). Urban birdsongs: higher minimum song frequency of an urban colonist persists in a common garden experiment. *Animal Behaviour*, *170*, 33-41.

Ritschard, M., & Brumm, H. (2012). Zebra finch song reflects current food availability. *Evolutionary Ecology*, *26*(4), 801-812.

Rivera-Gutierrez, H. F., Pinxten, R., & Eens, M. (2012). Tuning and fading voices in songbirds: age-dependent changes in two acoustic traits across the life span. *Animal Behaviour*, *83*(5), 1279-1283.

Roca, I. T., Desrochers, L., Giacomazzo, M., Bertolo, A., Bolduc, P., Deschesnes, R., ... & Proulx, R. (2016). Shifting song frequencies in response to anthropogenic noise: a meta-analysis on birds and anurans. *Behavioral Ecology*, *27*(5), 1269-1274.

Rodríguez-Bardía, M., Fuchs, E. J., Barrantes, G., Madrigal-Brenes, R., & Sandoval, L. (2022). Genetic structure in neotropical birds with different tolerance to urbanization. *Scientific Reports*, *12*(1), 6054.

Sandoval, L. (2011). Male–male vocal interactions in a territorial neotropical quail: which song characteristics predict a territorial male's response?. *Behaviour*, *148*(9-10), 1103-1120.

Sandoval, L., & Mennill, D. J. (2012). Breeding biology of White-eared Ground-sparrow (*Melozone leucotis*), with a description of a new nest type. *Ornitología Neotropical*, *23*(2), 8.

Sandoval, L., Méndez, C., & Mennill, D. J. (2016). Vocal behaviour of White-eared Ground-sparrows (*Melozone leucotis*) during the breeding season: repertoires, diel variation, behavioural contexts, and individual distinctiveness. *Journal of Ornithology*, *157*(1), 1-12.

Sandoval, L., Graham, B., Sosa-López, J. R., Laverde-R, O., & Araya-Ajoy, Y. G. (2024). The study of bird vocalizations in Neotropical habitats: Current knowledge and future steps. *Ornitología Neotropical*, *35*(2), 112-129.

Serrano, J. M., Vázquez-Hernández, Z. K., Hernández-Jiménez, C. A., Villarreal-Olvera, E. T., & Ochoa-Ochoa, L. M. (2024). Assessing the impact of engine and non-engine urban noises on the calls of urban frogs: a natural experiment. *acta ethologica*, *27*(3), 177-187.

Slabbekoorn, H. (2013). Songs of the city: noise-dependent spectral plasticity in the acoustic phenotype of urban birds. *Animal Behaviour*, *85*(5), 1089-1099.

Slabbekoorn, H., & Ripmeester, E.A.P. (2008). Birdsong and anthropogenic noise: implications and applications for conservation. *Molecular ecology*, *17*(1), 72-83.

Thompson, M. J., Capilla-Lasheras, P., Dominoni, D. M., Réale, D., & Charmantier, A. (2022). Phenotypic variation in urban environments: mechanisms and implications. *Trends in ecology & evolution*, *37*(2), 171-182.

To, A. W., Dingle, C., & Collins, S. A. (2021). Multiple constraints on urban bird communication: both abiotic and biotic noise shape songs in cities. *Behavioral Ecology*, *32*(5), 1042-1053.

Van Oort, H., Otter, K. A., Fort, K. T., & Holschuh, C. I. (2006). Habitat quality, social dominance and dawn chorus song output in black-capped chickadees. *Ethology*, *112*(8), 772-778.

Villarreal, M., Barrantes, G., & Sandoval, L. (2024). Song frequency shifts in an urban bird species optimize acoustic transmission inside noisy urban areas. *Ornitología Neotropical*, *35*(2), 80-86.

Weir, J. T., Wheatcroft, D. J., & Price, T. D. (2012). The role of ecological constraint in driving the evolution of avian song frequency across a latitudinal gradient. *Evolution*, *66*(9), 2773-2783.

Westneat, D. F., Wright, J., & Dingemanse, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation. *Biological Reviews*, *90*(3), 729-743.

Williams, H. (2021). Mechanisms of cultural evolution in the songs of wild bird populations. *Frontiers in Psychology*, *12*, 643343.

Wood, W. E., & Yezerinac, S. M. (2006). Song sparrow (Melospiza melodia) song varies with urban noise. *The Auk*, *123*(3), 650-659.

Table 1. Within and between-individual variance in the five spectro-temporal features from common song types in response to temporal fluctuations in noise levels from the four study sites within the urban-rural gradient. HU = Highly urbanized, MU = Medium urbanized, LU = Low urbanized, and RU = Rural. RV represents within-individual variance, β_0 represents between-individual variance, and p represents significance between the interaction of year and noise.

Population	Minimum frequency (Hz)			Maximum frequency (Hz)			Frequency range (Hz)		
	RV	σ^2	p	RV	σ^2	p	RV	σ^2	p
HU	**186390**	***981689***	**0.0237**	845862	1413166	0.634	1104968	2833650	0.227
MU	320157	254516	0.195	**664619**	***5265508***	**<0.001**	**1076197**	***5637145***	**0.005**
LU	988010	245586	0.958	***3645306***	**2733361**	**<0.001**	***3955488***	**2032635**	**<0.001**
RU	***286160***	**229668**	**<0.001**	***708181***	**686170**	**<0.001**	***1320514***	**922714**	**<0.001**

Bold values indicate significant interactions; RV and σ^2 are italicized when one value is greater than the other.

Table 1. Continued.

Population	Frequency of maximum amplitude (Hz)			Song duration (s)		
	RV	σ^2	p	RV	σ^2	p
HU	1002653	404340	0.255	**0.1773**	***0.898***	**<0.001**
MU	1117799	600723	0.452	0.440	1.3553	0.782
LU	***1487377***	**41947**	**0.001**	0.190	0.056	0.23
RU	***1575409***	**61534**	**<0.001**	***0.186***	**0.0476**	**0.002**

Bold values indicate significant interactions; RV and σ^2 are italicized when one value is greater than the other.

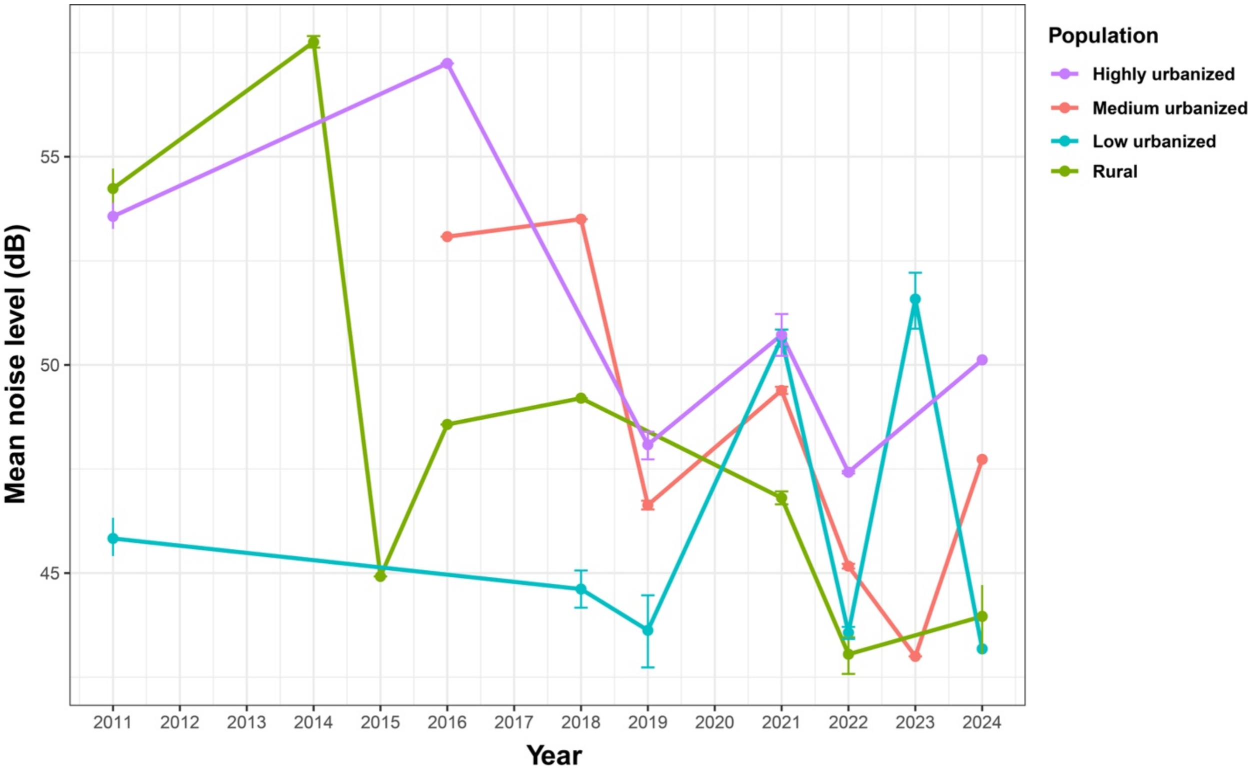

Figure 1. Mean noise level trends from the four study sites within the Great Metropolitan Area of Costa Rica over 13 years. Points represent mean noise values, and error bars represent standard deviation.

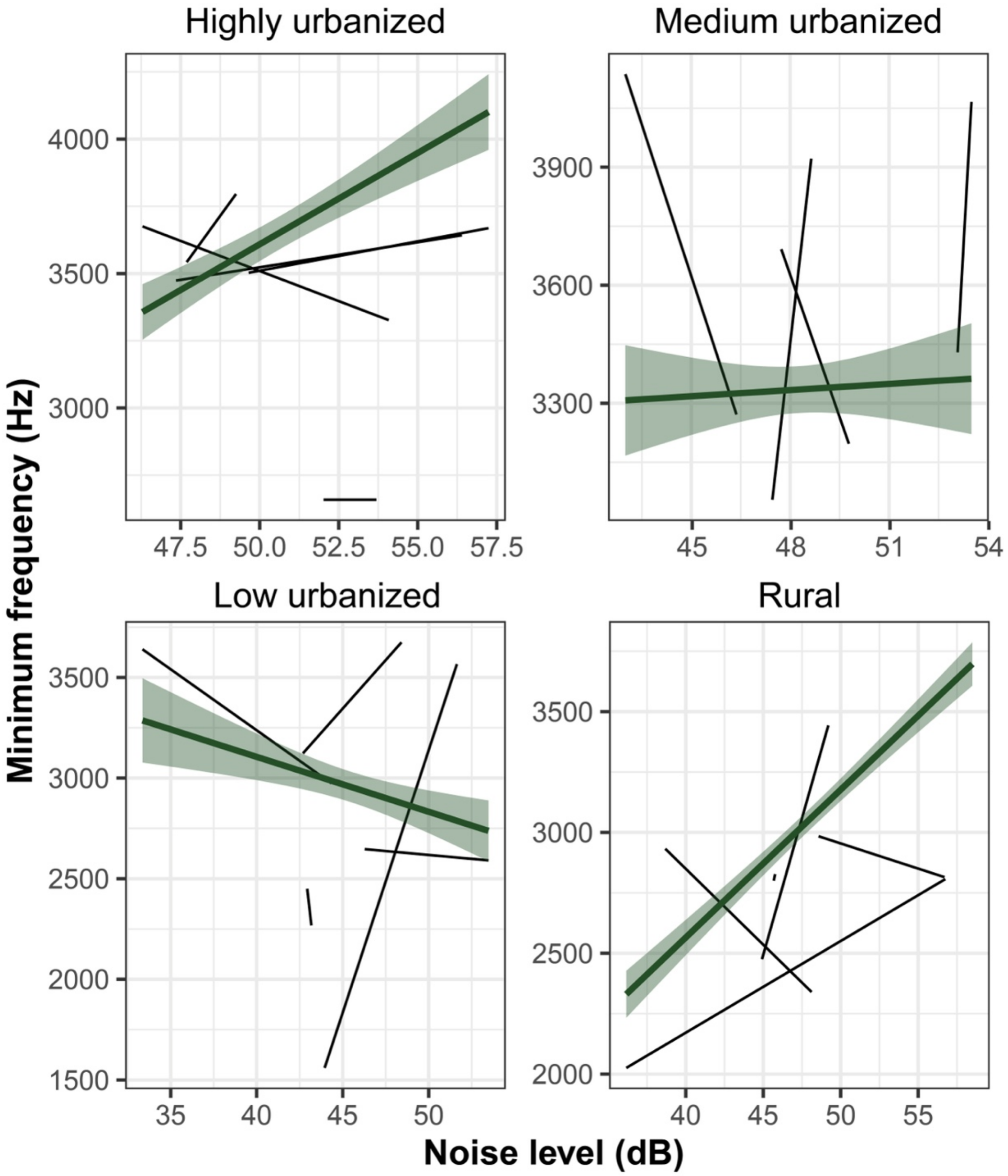

Figure 2. Within-individual and population variation of minimum frequency in response to noise levels. Thinner lines represent within-individual variation.

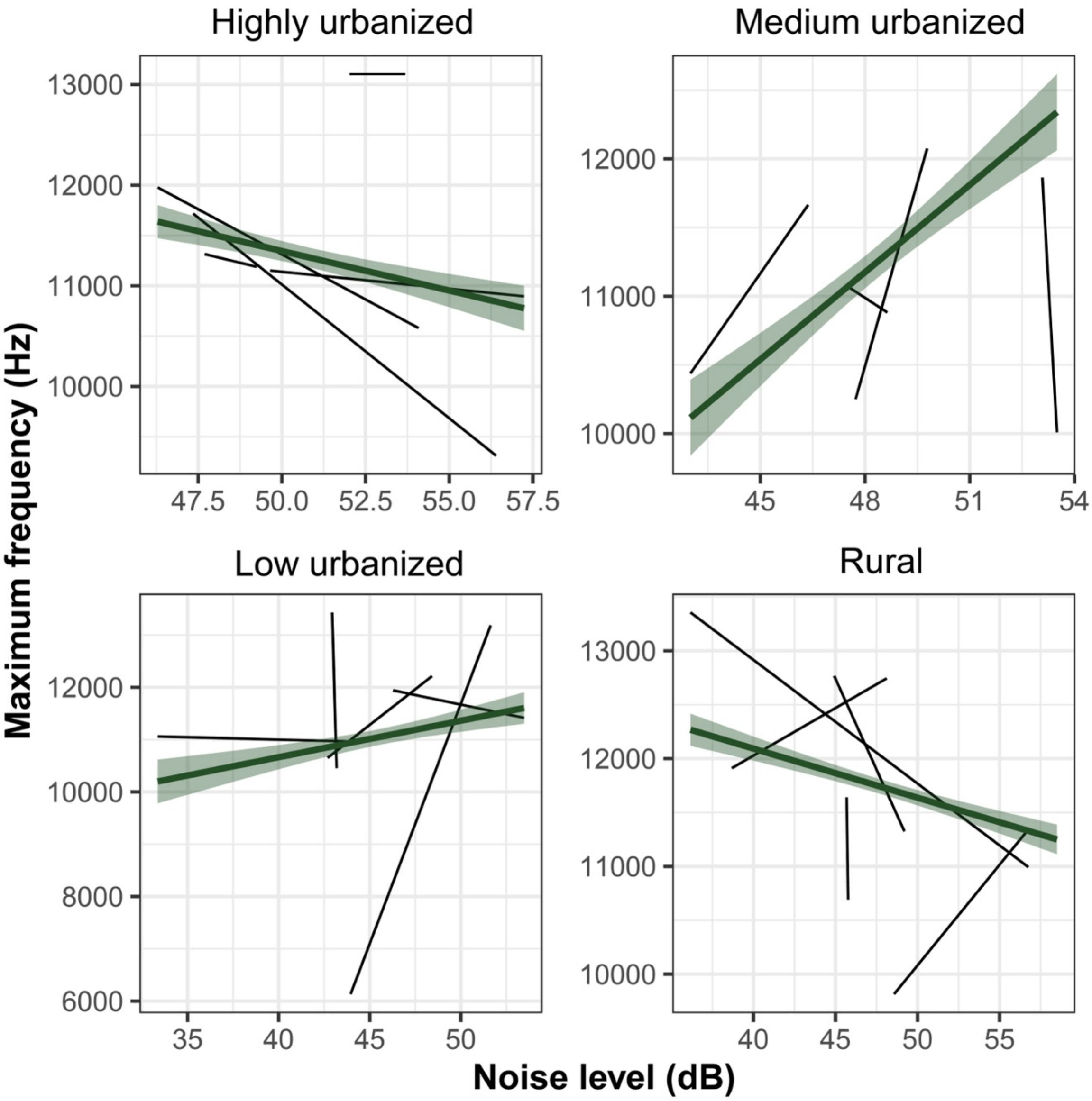

Figure 3. Within-individual and population variation of maximum frequency in response to noise levels. Thinner lines represent within-individual variation.

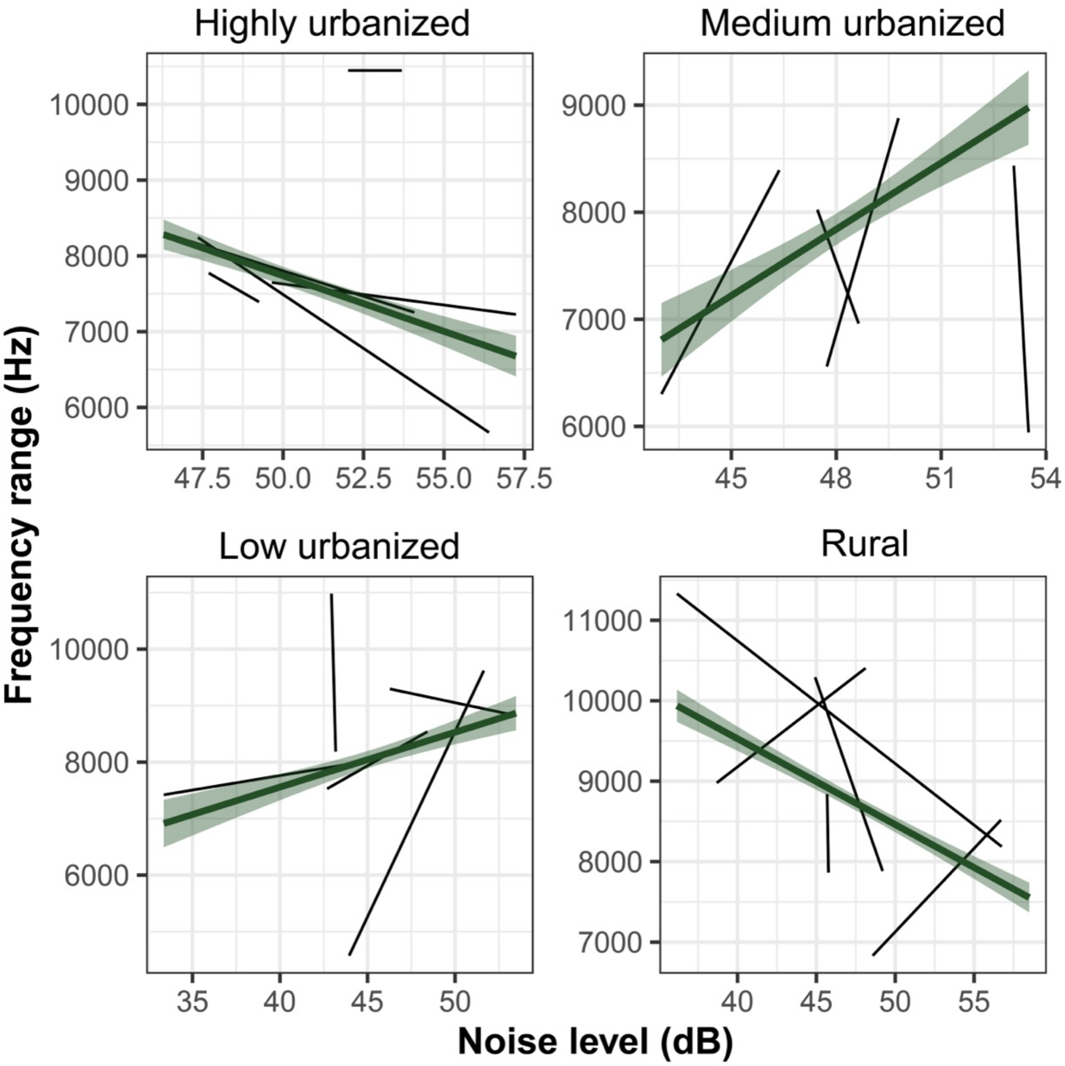

Figure 4. Within-individual and population variation of frequency range in response to noise levels. Thinner lines represent within-individual variation.

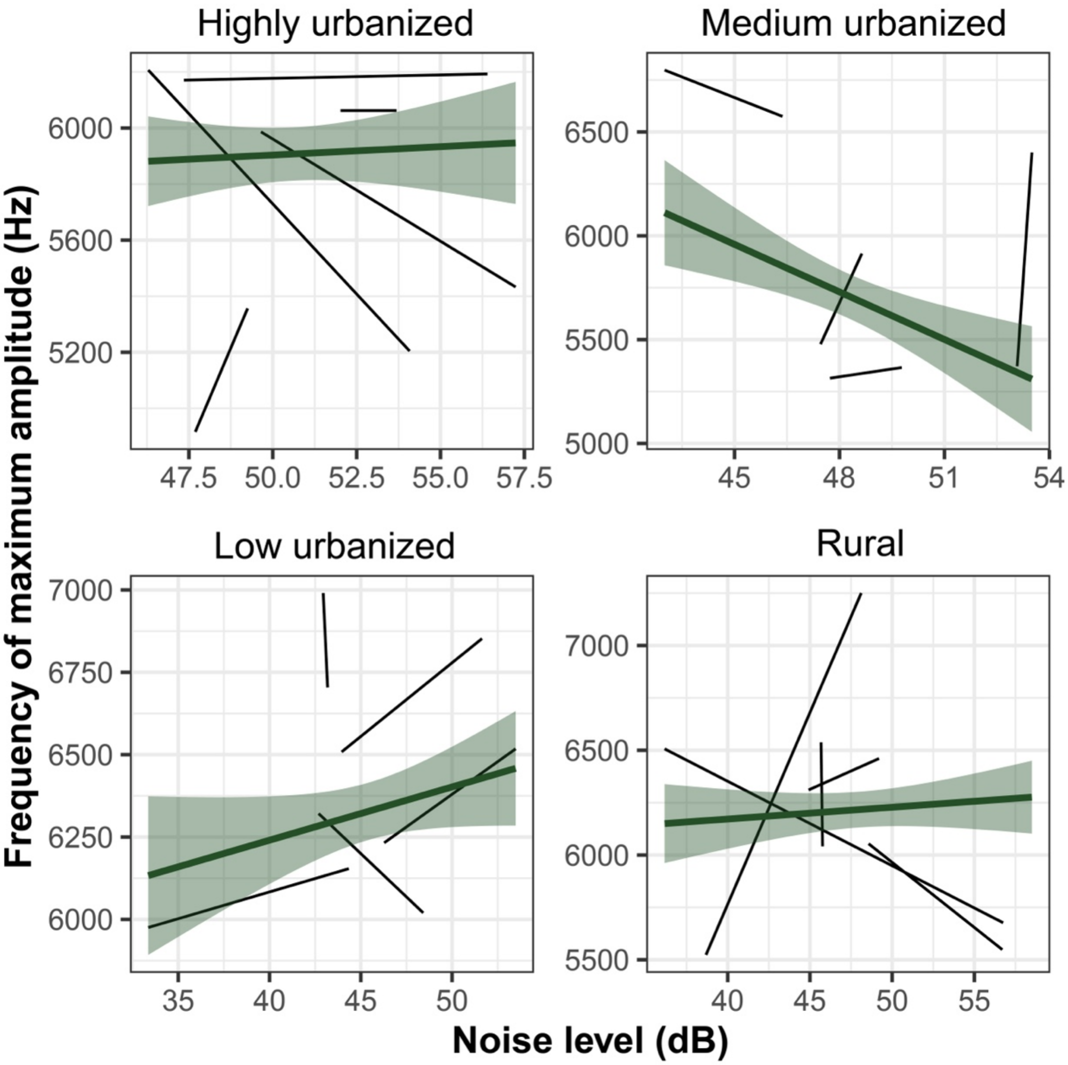

Figure 5. Within-individual and population variation of frequency of maximum amplitude in response to noise levels. Thinner lines represent within-individual variation.

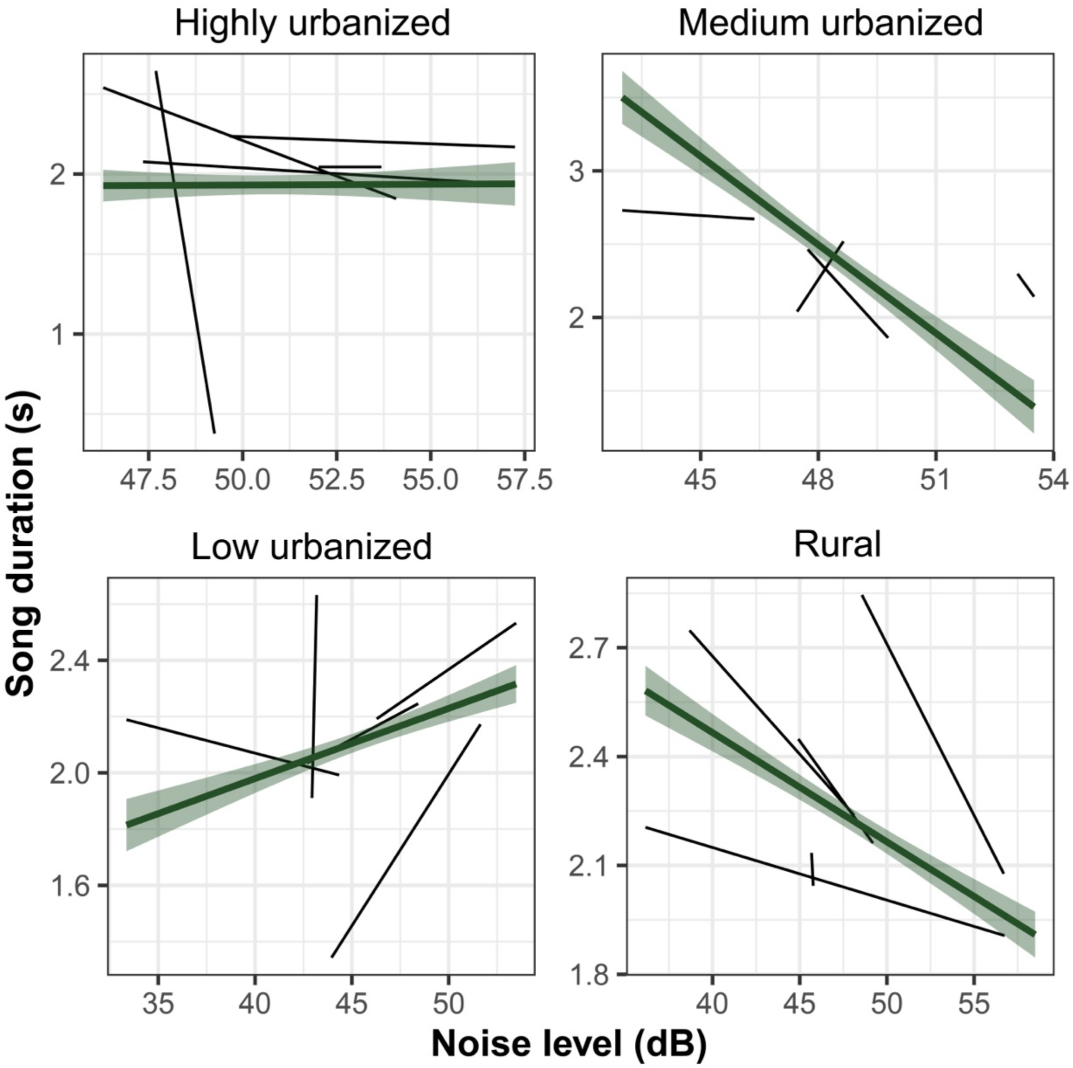

Figure 6. Within-individual and population variation of song duration in response to noise levels. Thinner lines represent within-individual variation.

Conclusiones

A través de este estudio, logramos determinar que la urbanización ha tenido efectos directos en los cantos de la especie evasora urbana *Melozone leucotis* durante los pasados 13 años. Encontramos que el tipo de variación en las características espectrotemporales de cantos comunes que surgieron a través de los va a depender de su población. En el sitio de alta urbanización, los machos presentaron mayor variación interindividual en comparación al resto de las poblaciones, posiblemente porque están enfrentando mayores disturbios antropogénicos. Tanto la estructura del hábitat como el paisaje acústico podrían estar frenando a los machos en producir cantos inconsistentes con tal de transmitirlos mejor en sus territorios. Por otra parte, encontramos que los machos de los sitios de media y baja urbanización, y rural demostraron mayor variación intraindividual. Dado a que posiblemente enfrentan menores disturbios antropogénicos en sus respectivos territorios, asociamos este tipo de variación a la senescencia. Por lo tanto, es posible que el desgaste de sus aparatos vocales esté afectando la consistencia de sus cantos a través de los años.

En cuanto a los cambios a través de los años en el paisaje acústico, encontramos apoyo al planteamiento de que la respuesta al ruido antropogénico de parte de machos cantores de *M. leucotis* también va a variar por población. Los machos pertenecientes a los sitios de alta y media urbanización demostraron mayor variación interindividual en comparación al de baja urbanización y rural. Esto demuestra que no ocurre una respuesta al aumento del ruido a nivel poblacional y que los machos producen cantos con características espectrotemporales más consistentes. Al haber menos espacio disponible en el paisaje acústico, es posible que los macho se vean obligados a producir cantos más consistentes con tal de no ser enmascarado por el ruido antropogénico. Apoyando esto, encontramos que la frecuencia mínima ha aumentado, el rango de frecuencias ha disminuido y la duración en los cantos de alta y media urbanización, lo cual es consistente con la evasión del enmascaramiento por ruido. Sin embargo, en casos como el sitio de alta urbanización, ciertas variaciones en algunas de sus características espectrotemporales no se ajustaban a la evasión del enmascaramiento por ruido. Por lo tanto, es posible que en adición estén respondiendo a factores estructurales que les dificulte la transmisión efectiva de sus cantos. En los sitios de baja urbanización y rural, hubo mayor variación intraindividual lo cual fue atribuido a las fluctuaciones inconsistentes en los niveles de ruido o nuevamente por senescencia. Según esto, los machos en los sitios de baja urbanización y rural demostraron mayor plasticidad conductual. No obstante, nuestros resultados podrían indicar también que los machos en estos dos sitios simplemente producen cantos con más variación y no necesariamente indican mayor plasticidad. Con base en esto, podríamos interpretar también que los ambientes urbanos sirven de filtro para la producción de comportamientos más consistentes.

En conjunto, encontramos cómo el trayecto de la evolución cultural en diferentes poblaciones de una misma especie va a ser determinado por sus contextos ambientales. En efecto, encontramos que las diferencias en el ruido antropogénico van a causar que los cantos varíen a través de los años de manera distinta por población. Este estudio nos da un vistazo del impacto de la urbanización en una especie de ave tropical y de cómo ajustan sus comportamientos con tal de lograr continuar persistiendo en estos espacios. Estudios futuros se podrían enfocar las posibles repercusiones que podrían traerle a la aptitud reproductiva de individuos dentro de estos espacios y de cómo las generaciones entrantes logran ajustarse al continuo desarrollo urbano según aprenden los cantos locales dentro de sus poblaciones.