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SISTEMA DE ESTUDIOS DE POSGRADO

CAMBIOS EN EL COMPORTAMIENTO TERRITORIAL Y VOCALIZACIONES DE LA AVIFAUNA A LO LARGO DEL GRADIENTE URBANO Y DE RUIDO ANTROPOGÉNICO

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

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Dedicatoria

Este trabajo y tiempo invertido lo dedico de todo corazón a mi familia, quienes, sin su apoyo incondicional desde muchos aspectos, no podría haber llegado hasta donde me encuentro, por su paciencia y cariño, a mi hermana quien es muy importante para mí y a quien adoro. Mis amigos y mi amado gato, que en paz descanse. Muchas gracias a todos por sus palabras y tiempo durante todo este proceso.

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Resumen

La urbanización a impulsado diferentes cambios drásticos en los hábitats naturales por el aumento de las áreas urbanas, generando gradientes urbanos y gradientes de ruido antropogénico. Como consecuencia de los cambios provocados en estos nuevos ambientes habrá una variación no solo en la comunidad de especies asociadas al hábitat sino en como responden a las nuevas variables urbanas como el ruido. Lo que provocará cambios no solo en la respuesta e identificación de las vocalizaciones, sino en su comportamiento asociado a la supervivencia, comunicación y territorialidad. En este estudio se evaluó como el gradiente de ruido antropogénico afecto en el grado de sincronización asociado al tamaño de territorio en el Cuatro-ojos de Cabeza Negra (*Melozone leucotis*) y como la comunidad de aves responde a dos diferentes llamadas de alarma en sitios donde varía el ruido antropogénico, así como la composición de las aves asociadas. Para el primer estudio se realizaron grabaciones de duetos las parejas, niveles de ruido, tamaño del territorio y medición de parámetros de sincronización, mientras que en el segundo se realizaron experimentos de playback donde se midieron la respuesta de la comunidad. Encontramos que, para el primer capítulo, existe una relación entre los niveles de ruido antropogénico con los territorios y la sincronización de los duetos con el tamaño de los territorios. En el segundo capítulo encontramos que la comunidad aves urbanas responde a las dos llamadas de alarma, sin embargo, varía cuando aumento el ruido antropogénico. Mientras que la comunidad de aves asociadas, la complejidad fue mayor en áreas más urbanizadas contrario a lo que esperábamos.

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individuals, species, time closer to the speaker, faster approach to the speaker, and first vocalization in response to the stimulus). Then the effect of anthropogenic noise in each study site where bars with the same letters mean non-significant difference between playback stimulus in a posteriori comparison.

Figure 4. Non-metric multidimensional scaling based on Bray-Curtis distance of the bird community response to the playback of House Wren alarm call in five sites with different urban development.

Figure 5. Changes in the bird community complexity response in five sites with different urban development, four playback stimuli (two controls and two House Wren alarm call types), and the interaction between both. Higher values of community complexity mean more individuals, species, and diversity. Bars with the same letters mean non-significant differences between playback stimulus in a posteriori comparison.

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Introducción

La urbanización es considerada como el segundo problema más serio para la fauna silvestre después del cambio climático (Sala et al. 2000; Isaksson 2018). Esto se debe a que un aumento acelerado y desordenado de las áreas urbanas, en parte impulsado por la migración de las personas del campo a la ciudad, genera cambios directos en el paisaje y en la estructura de las comunidades (Wilcox & Murphy 1985; Turner et al. 2004). Como consecuencia de este desarrollo antropogénico, se produce un gradiente urbano definido como la variación espacial de los factores ambientales, tales como cobertura natural, número de especies nativas, tamaño y conectividad de parches, en relación con la intensidad de urbanización (cantidad de edificios, automóviles y personas, y niveles de ruido antropogénico y luz artificial, o contaminantes sólidos), desde paisajes naturales hacia áreas densamente urbanizadas (Lee 2007; McDonnell & Hahs 2008; Sol et al. 2014). En este gradiente se da una disminución del proceso de urbanización (zonas con alta densidad de edificios, casas, y calles) desde el núcleo de la ciudad hacia la periferia ocupada por zonas rurales (zonas con una matriz agrícola muy desarrollada y baja densidad de casas y edificios) o naturales (zonas donde diferentes tipos de hábitats no creados por el ser humano como estadios tempranos de sucesión, bosques secundarios y maduros, pastizales naturales, o humedales son los dominantes) (Torres-Gómez 2009). Además, dentro del gradiente de ruido antropogénico se genera una variación de los niveles de ruido que puede o no coincidir con el gradiente urbano (Brown 1991; Patricelli & Blickley 2006; Luther & Baptista 2010). Lo anterior propicia la creación de parches heterogéneos de hábitats naturales, y antropogénicos, los cuales son utilizados por diversas especies de aves, algunas de las cuales se benefician por el incremento de las áreas urbanas y el ruido antropogénico (Slabbekoorn et al. 2006; Murgui & Hedblom 2017; Juárez et al. 2020).

El ensamble de especies varía entre sitios urbanos y a lo largo del gradiente inclusive si son cercanos (Blair 1996; Grimm et al 2008; Marzluff & Ewing 2001; McKinney 2002; Rotenberry 2002; Møller 2009; Isaksson 2018), debido al nivel de tolerancia y a la interacción de las especies que arriban y sobreviven dentro de estos hábitats (Yahner 1998; Donnelly and Marzluff 2004; Sánchez et al. 2004; Møller 2009; Biamonte et al. 2011). Por ejemplo, la presencia de depredadores urbanos como gatos, perros, o roedores puede ejercer una alta presión sobre las poblaciones de aves urbanas, afectando la densidad y presencia de estas (Chace & Walsh 2006; Isaksson 2018). También varía según la abundancia de recursos (alimento o perchas para reproducirse) naturales y antropogénicos ya que puede afectar de manera negativa el desarrollo y sobrevivencia de muchas especies (Charmantier et al. 2017; Murgui & Hedblom 2017). Finalmente, la abundancia de contaminantes como el ruido o luz artificial puede hacer que las especies migren de las zonas urbanas a otras con menor efecto de estos contaminantes para reducir el impacto negativo en la comunicación o en los ritmos circadianos (Murgui & Hedblom 2017).

Las características y el tamaño del territorio también influyen en la abundancia y densidad de especies en los ambientes urbanos, y afectan la estructura de las comunidades, (Lowry et al. 2013; Sol et al. 2014; Juárez et al. 2020). Esto porque limita o aumenta el espacio disponible para otras especies territoriales en los parches remanentes de hábitat natural o en los nuevos hábitats creados por la urbanización (Muñoz et al 2021). Por ejemplo, el tordo (*Turdus merula*) tienen territorios más grandes en zonas con un alto nivel de urbanización porque pueden utilizar perchas más altas que hacen que su canto llegue a mayor distancia (Luniak et al. 1990; Ripmeester et al. 2010), mientras que el comemáiz (*Zonotrichia capensis*) tiene territorios más pequeños en zonas con un alto nivel de urbanización porque es aquí donde puede encontrar una mayor cantidad de alimento (Leveau & Leveau 2005; MacGregor-Fors & Escobar-Ibáñez 2017).

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Capítulo 1

Territory size is associate to duet coordination along an anthropogenic noise level gradient

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Territory size, synchronization, anti-predator behaviour, masking effect, anthropogenic disturbance, structural acoustic features

Abstract

Territory size in birds depends on the balance of the cost animals invest in defence and the benefit they obtain. In urban areas, defending territories might be more complex because other variables such as urban noise interfere with the acoustical signal's birds use to defend territories. Noise can degrade and mask acoustic signals of many species, and have the potential to interfere communication between species. Urban noise can be classified as chronic (minimum noise) or instant noise (maximum noise). In birds, vocalization may have a difficulty to transmit in an effectively way for the possible overlap with the urban noise when they try to communicate with their congeners. It will become more complicate if the species use duet that require certain synchronization to defend their territories. Our goal was to determine whether duet synchronization correlates with territory size along an urban gradient on the white-eared ground-sparrow (*Melozone leucotis*). We conducted the experiment in 29 territories in four sites along an urban gradient in Costa Rica. We measured the territory size by tracking birds with GPS, recording duets, and measuring noise levels every 10 minutes. We found that territory size decrease when chronic noise increase, but territory size was not influenced by instant noise. Duet pairs with lower duet synchronization had smaller territories, but this change depending on the urban development. In low and medium-low urban degree is true, but there is no relationship between synchronization and territory size in medium-high and high urban development. The variable synchronization level change according to the interaction between noise type and population. For instant noise, synchronization only decreased when noise increased in the low-development population, and in the other three populations, synchronization increased with noise increase. In case of chronic noise, when noise level increased, the synchronization in high and medium-low urbanized population did not change. However, when the noise level increased, the synchronization increased in medium-high and decreased in low-urbanized populations. Thus, the increase of chronic anthropogenic noise affects negatively the White-eared Ground-sparrow. This is the first report of chronic noise influencing the size territory in any bird.

Introduction

Territories are protected areas that contain resources which are protected from individuals of the same specie or another species (Tinbergen 1936; Brown 1969; Salomonson & Balda 1977; Juárez et al. 2020). The territory defence may occur by males, females, both sexes, or a group of individuals using agonistic behaviours such as vocalizations, displays, or physical attacks (Tinbergen 1936; Morse 1941; Brown 1963; Duca & Marini 2014). For example, in hyenas, groups of females defend its hunting and roosting territories from other groups of females and single males chasing and attacking intruders (Wallander et al. 2001). In fishes like *Variabilichromis moori*, both members of the pair defend nesting territories from individuals of the same and other species displaying the fins and realizing different body movements first and chasing intruders if they approach closer (Nakano & Nagoshi, 1990; Sturmbauer et al. 2008). In some bird species such as Red-winged Blackbird (*Agelaius phoeniceus*), white-rimmed warbler (*Myiothlypis leucoblephara*), and Common nightingales (*Luscinia megarhynchos*) males defend its breeding territories from others males of the same species using songs (Brumm & Todt 2004; Mathevon et al 2008; Searcy & Beecher 2009).

Territory size is a variable within and between species because depend of the physical characteristics of the individuals (e.g., body size, hormone levels, sex; Hau et al 2004; Slabbekoorn 2013; Isaksson et al 2018), the characteristics of the resource selected for protection (e.g., food availability and quality, vegetation density; Marler & Slabbekoorn 2004; MacGregor-Fors & Escobar-Ibañez 2017), season of the year (e.g., breeding, non-breeding, dry season, rain season, Langen & Vehrencamp 1998; Duca &Marini 2005), or community interactions (e.g., neighbours, predators, other species). However, in general it is a positive relationship between the quality of the individuals with the benefits obtained from the territories they defend (Fedy & Stutchbury 2005; Marzluff et al. 2016; Weiner & Wingreen 2019) and with the capacity that individuals have to defend it (Duca 2005; Abbey-lee et al. 2016). But this relationship is not linear, because in good territories (territories with best benefits) after a certain size, the amount of energy necessary to protect larger territories is higher than the benefits and territory size decrease (Pyke 1979; Beletsky 1992; Minias & Janiszewski 2016). In Sanderling (*Calidris alba*), Red-eyed Vireos (*Vireo olivaceus*), and Buzzard (*Buteo buteo*), the territory increased as food availability increases but the size decreased when the territory intrusion increased, although food availability was larger (Myers et al. 1979; Both & Visser 2000; Krüger 2004). In Great Tits (*Parus major*), an increase in territory size positively affects territorial pair nested, major growth rate of chicks, and recruitment to the breeding population, where territory size directly affects fitness. However, clutch size will also not increase (Both & Visser 2000).

Factors that interfere in the capacity to protect territories, like higher noise levels and dense vegetation in species that use vocalizations (i.e., songs or duets), may also influence the territory size (Slabbekoorn & Boer-visser 2006; Slabbekoorn 2013). This because the information transmitted by vocalizations reaches short distances in territories with a higher noise levels or denser vegetation in comparison with territories with low noise levels or more open vegetation (Richards & Wiley, 1980; Wiley, 1991; Patricelli & Blickley, 2006; Wood & Yezerina, 2006). Therefore, it is expected that individuals of the same species that inhabit in territories with different noise levels (e.g., city vs rural zone) have territories with different sizes (Ripmeester et al. 2010; Juárez et al 2020). Noise level also may affect territory size, in species that use duets to defend the territory, because at higher noise levels individuals may not be able to hear well the partner that start the duet, delaying its start and producing less synchronized duets (Méndez et al. 2021) or not producing duets at all (Rivera-Cáceres 2015). Given that higher synchronizations in duets influence positively the territory defence (Koloff & Mennill 2011; Rivera-Cáceres 2015), less synchronized pairs may have smaller territories than more synchronized pairs (Hall 2009; Mendez & Sandoval 2019; Quirós-Guerrero 2021).

Our main goal is to find the relationship between duet synchronization and territory size along an anthropogenic noise level gradient on the year-round territorial white-eared ground-sparrow (*Melozone leucotis*). This species only uses duets for territory defence and duet synchronization change between pairs (Sandoval et al. 2016, Méndez & Sandoval 2021), and territories varied in size within and between populations over an urban gradient that vary in noise level (Juarez et al. 2020a, 2020b; Méndez et al. 2021). We predict that pair in nosier territories will have less synchronized duets, they will perceive the beginning of duet contribution too late, because noise might avoid or diminish perception's receivers. Noise overlaps low frequencies in each duet affecting duet coordination. Consequently, we predict small territories of pairs that inhabit areas with high anthropogenic noise will produce less coordinate duets, which are less effective in territory defence (Juárez et al 2020; Mendez 2021). However, if territories are smaller in nosier sites and duet synchronization is not affected by noise, we predict that the cause of low level in synchronization is because duets degrade faster at shorter distances more than the effect of synchronization.

Methods

We studied four populations that varied in anthropogenic development from April-June 2021 and 2022. 1) Universidad de Costa Rica, San Jose province (9°56´N, 84°05´W; altitude 1200 m) that is classify as high urban development. 2) Jardín Botánico Lankester, Cartago province (09°50´N, 83°53´N; altitude 1400 m) that is classify as medium-high urban development. 3) Getsemaní, Heredia province (10°01´N, 84°05´W; altitude 1200-1500 m) that is classify as medium-low urban development. 4) Monteverde, Puntarenas province (10°18´N, 84°48´; altitude 1600 m) that is classified as lower urban development (see Sandoval et al. (2016), Juárez et al. (2020), and Méndez et al. (2021), for a more detail of the four sites).

We measured 15 territories in Universidad de Costa Rica, 7 in Jardín Botánico Lankester, 7 in Norte de Heredia, and 6 in Monteverde during the White-eared Ground-sparrow breeding season (March-June 2021 and 2022) when territorial interactions are more common, and thus, easier to define the territory limits between pairs. The pairs we studied are part of a long-term study and each individual has a unique colour band code (Sandoval et al. 2016; Juarez et al. 2020). We collected coordinates within each territory where we observed a white-eared ground-sparrow singing or duetting from 05:00-9:00 h, using a Garmin MAP64 GPS (precision = 3 m) to establish the territory limits. We followed each pair at least two days (one week apart) per breeding season to mark a minimum of 13 points for territory (Juárez et al. 2020). We estimated the area of each territory using the minimum convex polygon method according to Juárez et al. (2020), using “adehabitat” package in R (Marshall & Cooper 2004; Calenge 2006; Ruiz-Sánchez et al. 2017).

Duet recording and analysis

We recorded each pair at least 1 h per year (mean ± SE) using the focal recording method, which consists in follow a pair from 5:00-6:00 h, when this pair was most vocal active (Sandoval et al. 2016). We recorded duets using a Marantz solid state recording PMD661 with a K6/ME66 Sennheiser shotgun microphone. Vocalizations were stored in wave format, 44.1 kHz sampling rate, accuracy 16-bit. We select 3-5 duets from pair that vocalized on contact context to obtain coordination measurements (white-eared ground-sparrow’ vocalization in contact context there is not variation in duet and in territorial context there is a variation in response to other pairs interaction) (Mendez & Sandoval 2021). We used in the analyses only duets with a high proportion of signal-to-noise ratio (≥30 dB of difference between duet and background noise energy) and without overlap with another sounds.

From each duet, we measured six synchronization measurements following the protocol established by Méndez and Sandoval (2021). This divides the duet into three sections: the start section, the middle section, and the final section (Fig. 1). We preferred this protocol over other methods (e.g., degree of temporal precision, Farabaugh 1982; characterizes a precision phrase, Levin 1996; or duet creation and stimuli, Diniz et al. 2021) because contribution of male and female white eared ground sparrows overlap in frequency and time, making almost impossible to separate the elements of one bird from the other (Fig. 1). In each section, we measured (1) duration in s, (2) minimum frequency in Hz, and (3) maximum frequency in Hz (Fig. 1). We also measured (4) frequency difference in Hz between the minimum frequency of the start and middle duet section and (5) difference in frequency between the maximum frequencies of the middle and final duet section (Fig. 1). We conducted all measurements in Raven Pro 1.6.1 (Cornell Lab of Ornithology, Ithaca, NY, USA), using a combination of waveform, sonogram, and power spectrum windows as has been suggested by Podos (2001). We estimated the coefficient of variation (CV) for each duet measurement per pair and breeding season. Then we estimated an average CV for all measurements and used that value as our synchronization measurement value. Pairs with lower average CV have higher duet synchronization.

Anthropogenic noise measurements

We measured anthropogenic noise level every 10 min during the focal recording hour using a mini sound meter Sper Scientific (Model 850014 with measurement range 32-130 dB) with the fast response and type A weight. We obtained the maximum and minimum noise measurements oriented the sound meter in the opposite direction of the recording male and a 1 m height. For our analysis we used the two noise measurements: 1) minimum noise that represent the chronic noise inside territories and 2) maximum noise that represent the instant noise, because is short in time, and is produced by other sound sources like a car passing, a wind current, other animals vocalizing, or people talking.

Statistical analysis

We conducted three generalized lineal mixed-effect models (GLMM) with Gamma distribution and logit link function to compare if size of the territories of the White-eared Ground-sparrow changes among pairs according to duet synchronization and anthropogenic noise level. In the four GLMM we used territory size as our dependent variable, and year of data collection (2021 and 2022) and territory number as random factors. We used both variables as random factors for the fact that each pair was sampled repeatedly. We used as independent continuous variables the two noise measurements and the average CV. We also used the population as a categorical variable (four levels), and the second order interaction between population, each noise measurement (minimum and maximum), and average CV. We also compared how both noise types affect the duet synchronization (CV values) using two GLMM. In both GLMM we used the average CV value per pair as our response measurements, and year of data collection (2021 and 2022) and territory number as random factors. We used as independent continuous variables the two noise measurements, population, and the second order interaction between population and each noise measurement. We reported the results of GLMM using the analysis of variation (ANOVA) type 3. GLMM were conducted using lme4 library (Bates et al., 2015) and ANOVA using car library (Fox and Weisberg 2019) in R.

Results

We sampled a total of 29 pair territories, eight at the higher urban development site, five at medium-highly urban development site, eight at medium-low urban development, and eight at lower urban development site. We found that territory size decreased when increased the chronic noise (GLMM: $X^2 = 49.51$, df = 1, $p < 0.001$; Fig. 2), and this hold true in the interaction of chronic noise within the four populations ($X^2 = 264.16$, df = 3, $p < 0.001$; Fig. 3). However, territory size was not influenced by instant noise (instant noise: $X^2 = 2.21$, df = 1, $p = 0.14$, Fig. 4; instant noise x population: $X^2 = 3.41$, df = 3, $p = 0.33$; Fig. 5). We found that pair with lower duet synchronization had smaller territories ($X^2 = 16.27$, df = 1, $p < 0.001$; Fig. 6). But this pattern only holds true in the two populations with lower urban development, because in the two with higher urban development, we found not relationship between territory size and duet synchronization ($X^2 = 30.53$, df = 3, $p = 0.33$; Fig. 7). Territory size between populations were lower in the medium-high urban development site compared with the other three populations ($X^2 = 11.66$, df = 3, $p = 0.009$; Fig. 8).

We found that noise levels inside territories did not influence the duet synchronization (chronic noise: $X^2 = 3.29$, df = 1, $p = 0.07$; instant noise: $X^2 = 0.19$, df = 1, $p = 0.66$; Fig. 9). But synchronization changed when we compared the interaction between population and noise type (chronic noise: $X^2 = 21.10$, df = 3, $p < 0.001$; instant noise: $X^2 = 14.23$, df = 3, $p = 0.003$; Fig. 9), but not in the expected ways. For chronic noise, when increase the noise level, synchronization did not change in high and medium low urbanized sites, but decrease in the medium-high site and increase in the low urbanized site (Fig. 9). For instant noise, when increased the noise level increased the synchronization in the low urbanized site contrary to our expectation, meanwhile in the other three sites synchronization decreased when increased the instant noise (Fig. 9). Duet synchronizations was similar between populations ($X^2 = 4.09$, df = 3, p = 0.25; Fig. 9).

Discussion

We found that territory size decreases when chronic noise increases, but it was not influenced by instant noise. Duet pairs with lower duet synchronization had smaller territories in low and medium low urban development. But size of territories was not affected by synchronization medium-high and high urban development. We also found that synchronization level change according to the interaction between noise type and population, but not in the predicted way. For instant noise synchronization only decreased when noise increased in the low development population, and in the other three populations synchronization increased as noise increase. For chronic noise, when noise level increased synchronization in high and medium-low urbanized populations did not change. But when the noise level increased the synchronization increased in medium-high and decreased in low urbanized populations.

Noise can be a difficult pollutant that affect establishment and maintenance of territories, because bird rely on acoustic signals to transmit information with conspecifics or heterospecific individuals; affect detection of possible predators; and difficulty to protect territories because they become incapable to detect or distinguish correct signals (Slabbekoorn et al. 2018; Isaksson et al. 2018). Therefore, establish a territory in habitats with high chronic noise may affect directly vocalization transmissions by overlapping the vocalization frequencies (totally or partially), reducing the distance of sound travel, and interfering with territorial behaviours (Naguib 2013; Lenis & Guillermo-Ferreira 2019). For example, the Great Kiskadee (*Pitangus sulphuratus*) in territories with higher level of noise pollution respond slower to simulated territory intrusions (Lenis & Guillermo-Ferreira 2019). Meanwhile, the European Robin (*Erithacus rubecula*) males reduced the production of low frequency elements in response of simulated intrusion under higher noise levels sacrificing signal efficacy for deter intruder in benefit of signal detection (Zwart et al. 2016). As in the previous two species, we showed that White-eared Ground-sparrow also have smaller territories under higher noise level. This may be produced because under higher noise levels territorial pairs are not capable to produce long distance vocal signals (i.e., duets) to deter intruders or reduce the capability of recognize intruder vocalization signal faster (Myers et al. 1979; Brumm 2004; Lenis & Guillermo-Ferreira 2019). Consequently, a way to deal with those problems, especially inside dense vegetated habitats like the ground-sparrows (Sandoval & Mennill 2012; Sandoval et al. 2015, 2016), is to reduce the territory size to reduce energy and time patrolling territory borders and conducting visual and physical displays to avoid intrusions or producing vocalizations that will not reach the intendent receiver.

The instant noise represents high energy sound produced randomly in short time periods (e.g., a car horn sound, truck motors, screaming or sing people, high volume music) (Wright 2010; Ortega 2012). Therefore, birds may not respond to instant noise in the same way that they respond to chronic noise when setting up territory borders. For example, territorial birds may produce longer vocalizations to increase the chance to be hearing by the receivers (Slabbekoorn & Boer-Visser 2006; Geberzahn et al. 2009; Luther et al. 2016), or stop to vocalizing when instant noise occur and continue vocalizing after finish the interference (Brumm 2006; Dominoni et al. 2016; Tomasek et al. 2023). Territory size may not have any affect by both behaviours explained before (increasing time in vocalization or avoid overlapping noise), because vocal transmission is occurring after noise masking so instant noise is already finish because of the shorter duration.

We found that pairs with lower synchronization had smaller territories in the two populations of low and medium-low urban development, but a lack of relationship in the populations of medium-high and high urban development. Therefore, our prediction was partially supported for these results. These differences probably are cause for differences in territory quality over the urban development gradient. Previously, papers have been showed that pairs of White-eared Ground-sparrows have larger territories inside more urbanized areas, because the quality of territory (e.g., food resources and nesting sites) are lower than more natural habitats (Juárez et al. 2020). Consequently, territory size may reduce due to other factors in urban areas more than duet synchronization, probably pair would not get enough resources to survive. Additionally, in urban populations, pair density is lower than in more natural habitats (unpub. data). The lower pair density inside urban areas may have effects like reduction on pressure for defence territories and synchronization that is an important signal in pair-pair interaction, the couples will play duets in a relaxed role than a real feature and a key to territory protection (Méndez & Sandoval 2020). In the opposite, there is a higher pair density inside more natural habitats, have more synchronize duets will increase the defence of territory. Therefore, in the two populations with less urban development we found that pairs with less synchronized duets had smaller territories.

Contrary our predictions, we did not find a clear pattern between noise level and duet synchronization. Only in low urban development population pairs decreased duet synchronization as we expected when increased chronic and instant noise. But synchronization increased in the other three populations when increased instant noise, and in the medium-high urban development for the chronic noise. Finally, the last two populations for chronic noise did change synchronization with noise level change. This lack of relationship in some populations between synchronization and noise level changes was surprising, given that noise would mask the communication between both pair members (Halfwerk et al. 2018; Méndez et al. 2021). However, previous studies on White-eared Ground-sparrows showed that different noise levels did not affect the spectrotemporal characteristics of duets because the minimum frequency is over 5 kHz (Sandoval et al. 2016; Méndez et al. 2021). Another possible cause for the lack of relationship is ground-sparrows pairs expend the majority of time foraging and moving inside the territory together (<1 m between both), so noise levels would not make any effect at all in the communication between pairs which make easy to coordinate duet production (Méndez & Sandoval 2021). But we found in low urban development a relationship between noise increase and synchronization decrease, this show that in this population (low urban development) exposed to a lower number of anthropogenic noises sources, the increment in noise level is an obstacle for communication between pair members. The probably reason of noise as obstacle on this population is the noise increment occur recently, so pairs are not adapted yet to this new source of pollution (Lazerte et al. 2017). Other possible reason is that pair members in this population (low urban development) did not move closer as the other and noise affect the detection of the duet initiation decreasing the synchronization. However, this last idea needs to be tested in the future.

In conclusion, our study showed that territory size of White-eared Ground-sparrow is influenced negatively by the increase of chronic anthropogenic noise, and to our best knowledge this is the first time that this effect is detected. We also found a relationship between synchronization and territory size, but in this case, synchronization only affects territory in sites with lower urban development. This is one of the first studies that try to connect vocalization characteristics with territory size in urban environments. Our results highlight the importance to analyse in a comparative way over urban gradient how anthropogenic noise affect other aspect of bird biology and how individuals adjust to those changes to survive. Given that urban settlements are continuing extend, the implement of comprehensive management plans to guarantee the maintenance of fragmented areas and green patches inside urban areas will give more opportunities to conservate diversity and richness of those habitats, as well as, incentive the knowledge about the effect of urban noise.

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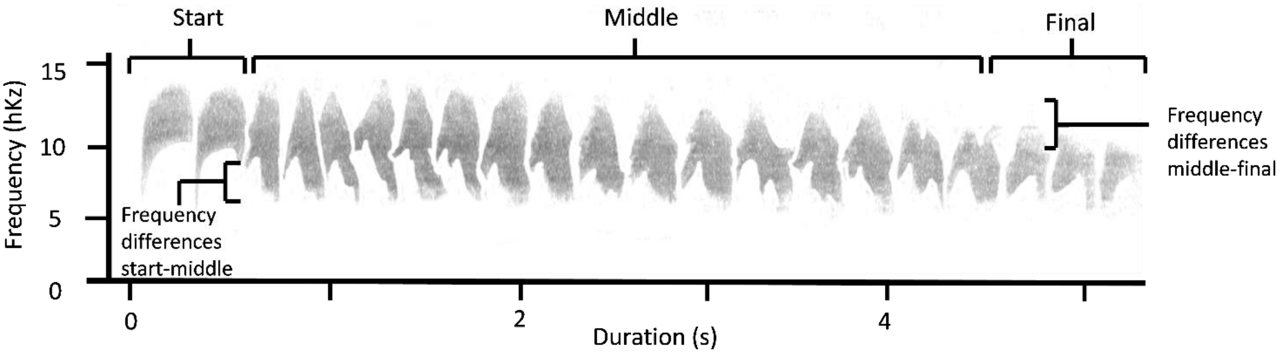

Figure 1. Sound spectrogram of a typical duet of White-eared Ground-sparrows signalling the sections used to analyse synchronisation

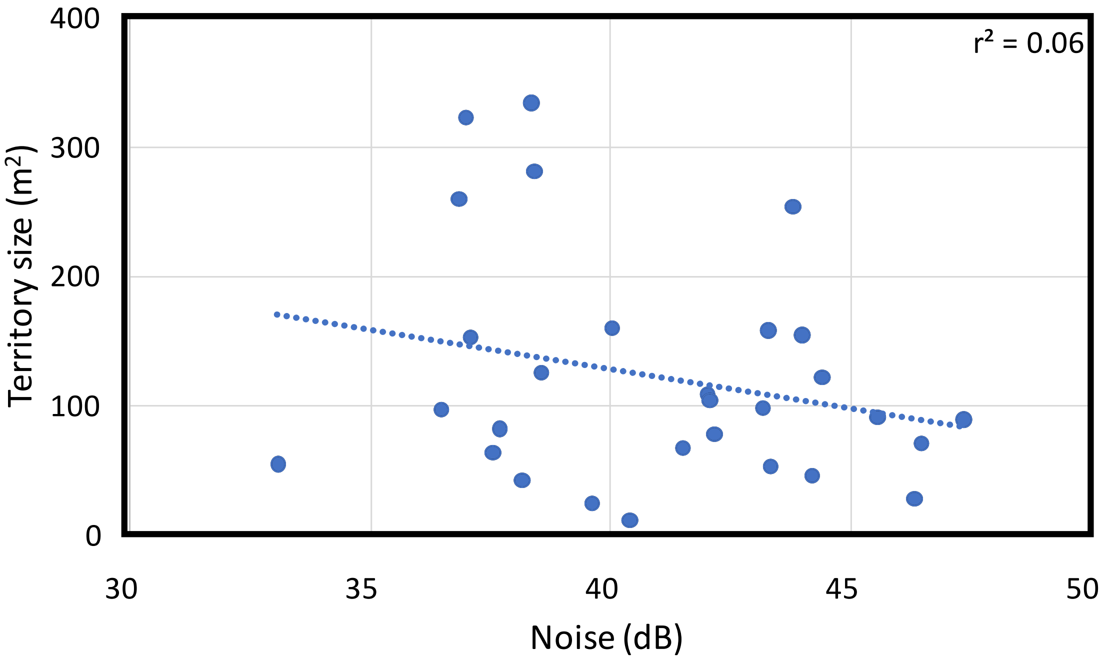

Figure 2. Linear relationship between chronic noise level and territory size of White-eared Ground-sparrow pairs ($p < 0.001$).

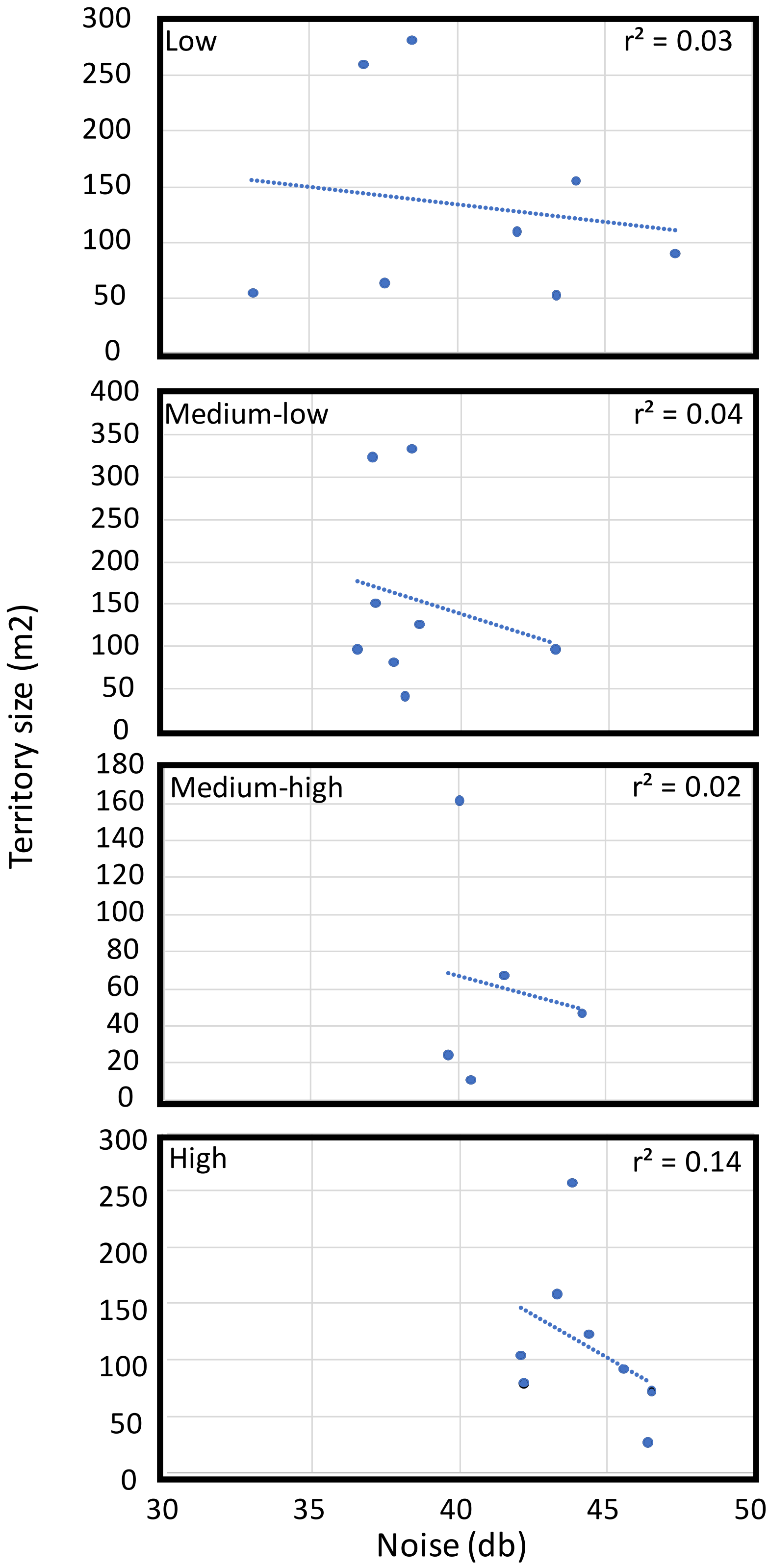

Figure 3. Linear relationship between chronic noise and territory size of White-eared Ground-sparrow pairs over four populations that vary in the urban development (p < 0.0001).

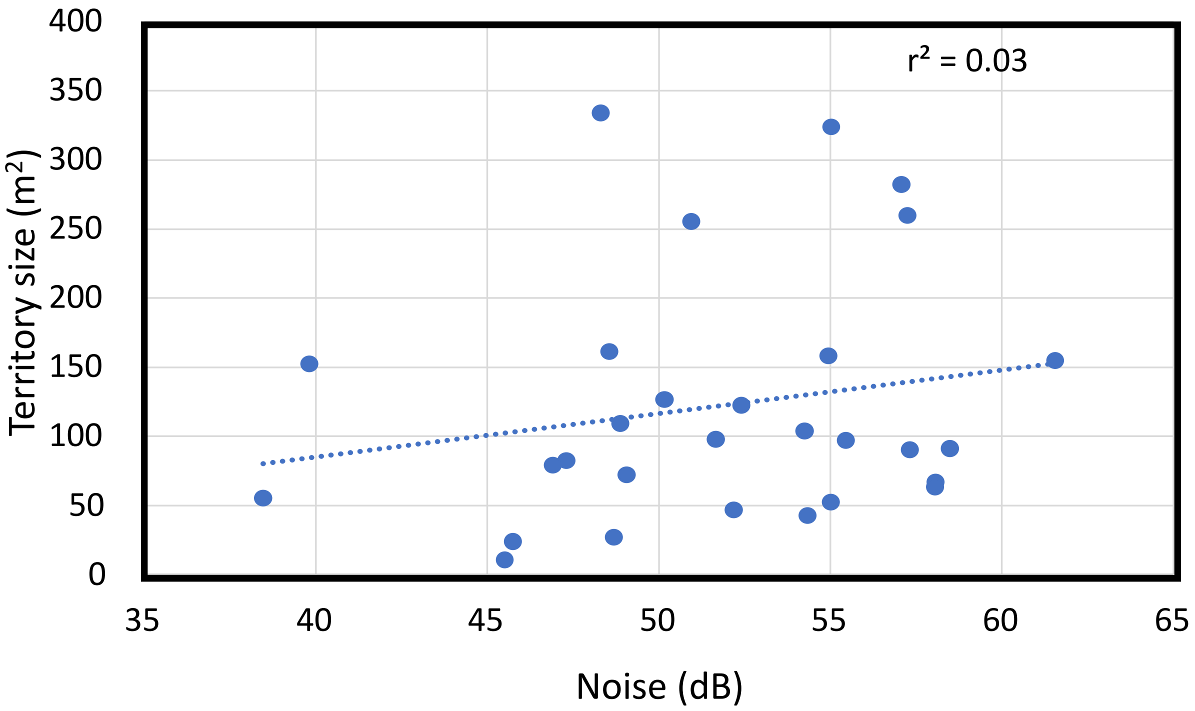

Figure 4. Linear relationship between instant noise and territory size of White-eared Ground-sparrow pair (p = 0.14).

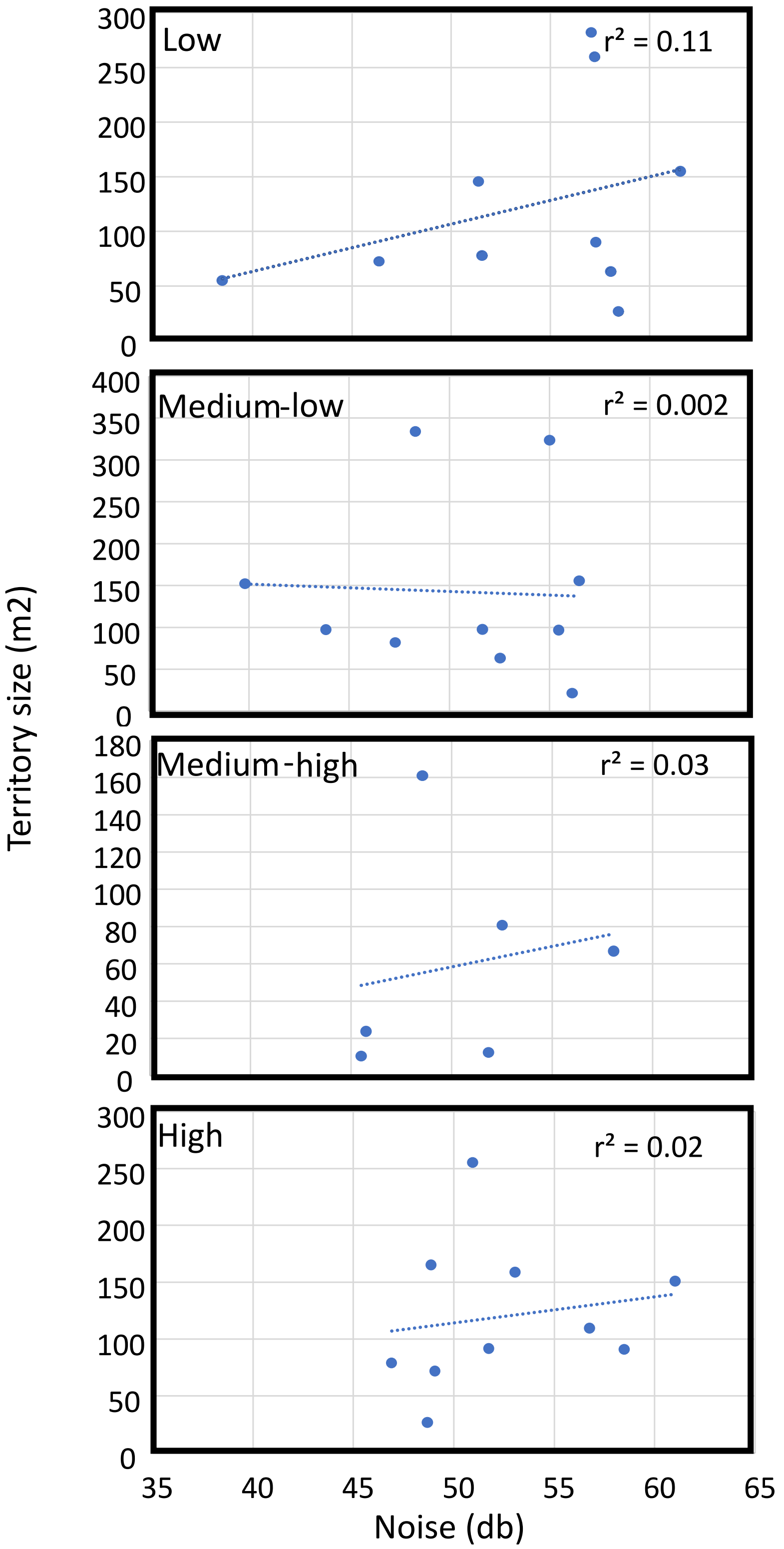

Figure 5. Linear relationship between instant noise and territory size of White-eared Ground-sparrow pair over four populations that vary in the urban development (p = 0.33).

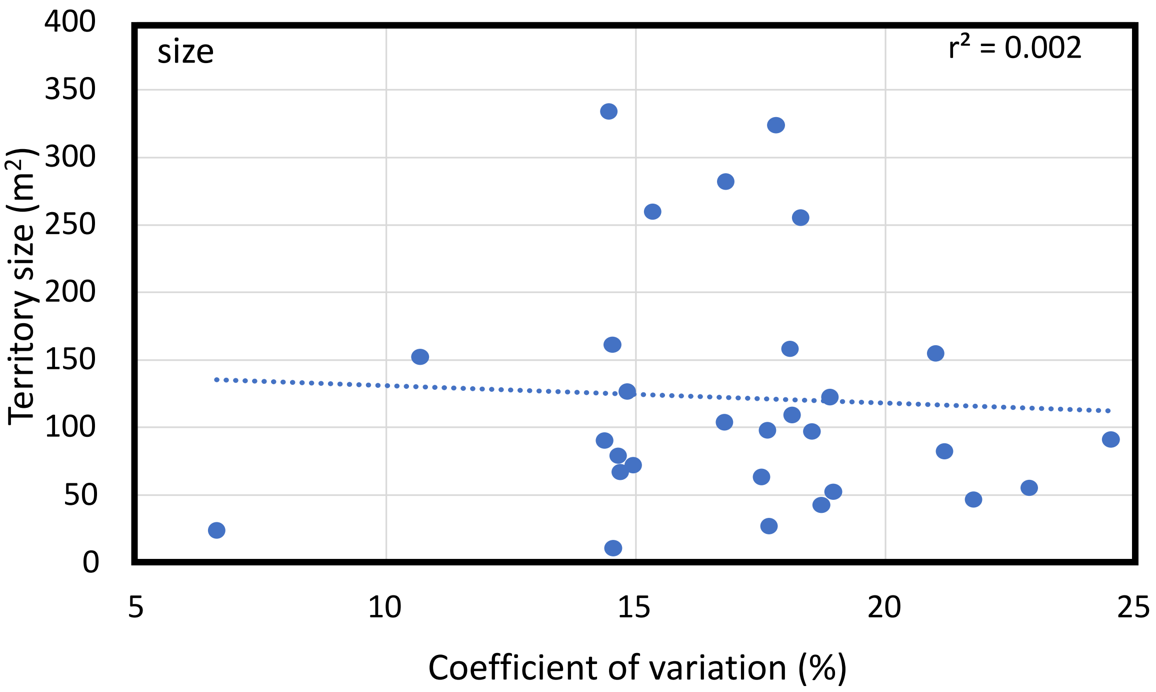

Figure 6. Linear relationship between duet synchronization and territory size of White-eared Ground-sparrow pair ($p < 0.001$).

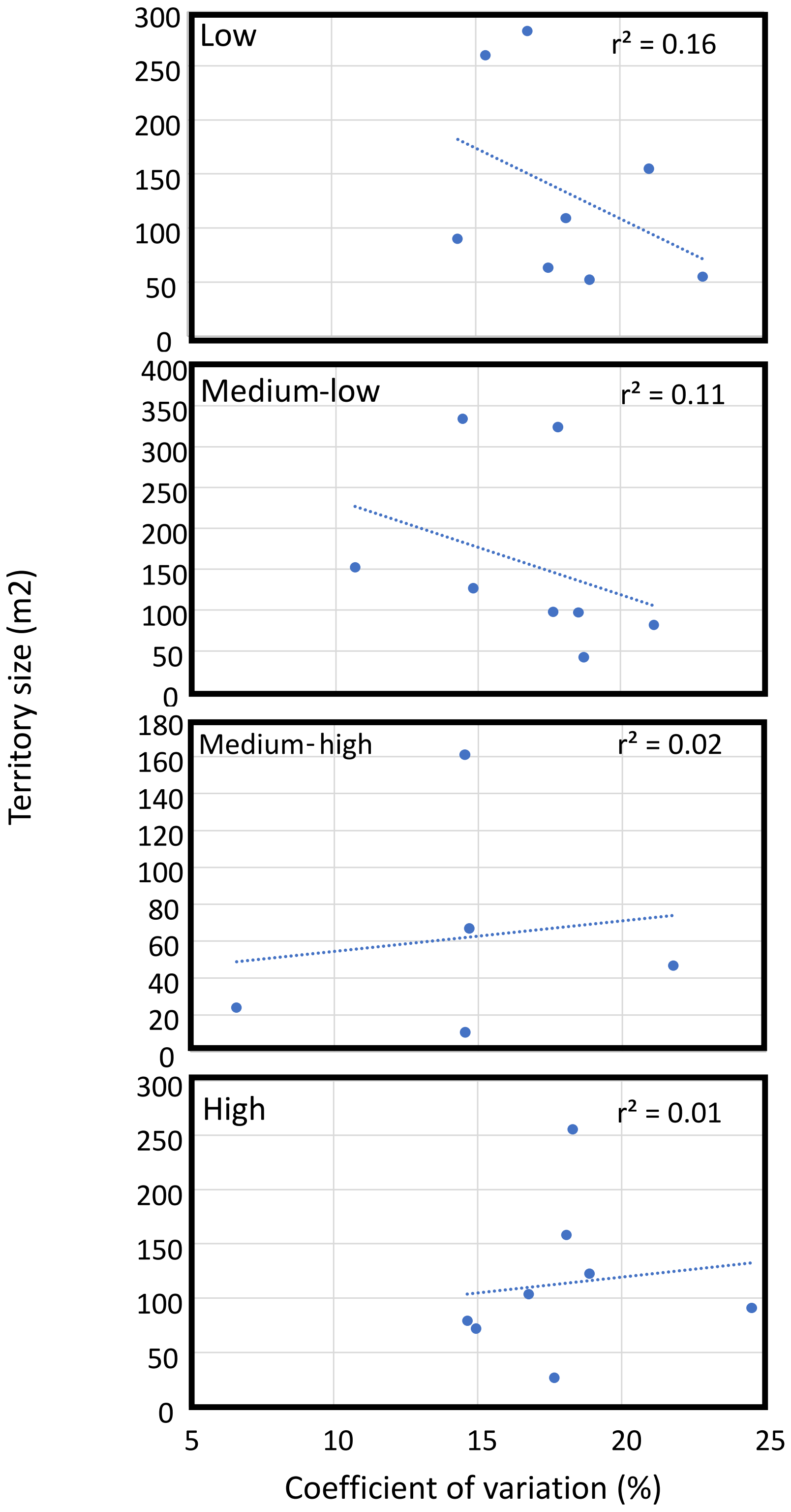

Figure 7. Linear relationship between duet synchronization and territory size of White-eared Ground-sparrow pair over four populations that vary in the urban development (p = 0.33).

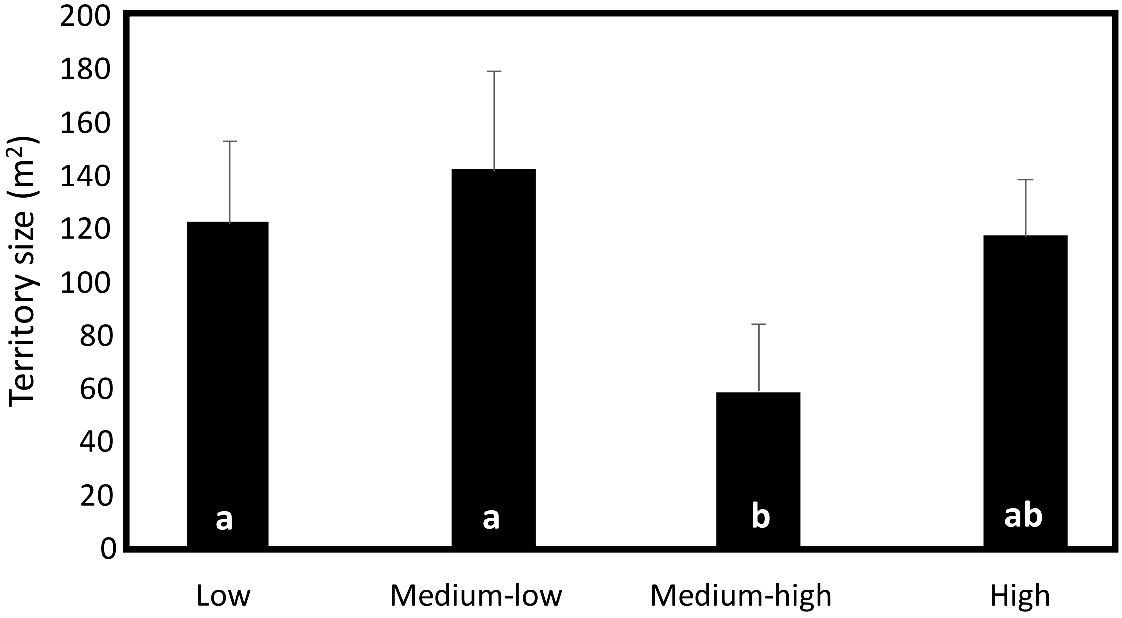

Figure 8. Difference of White-eared Ground-sparrow pair territory size (mean + SE) over four populations that vary in the urban development. Bars connected with the same letter mean a non-significant pair comparison under a post hoc test (p = 0.009).

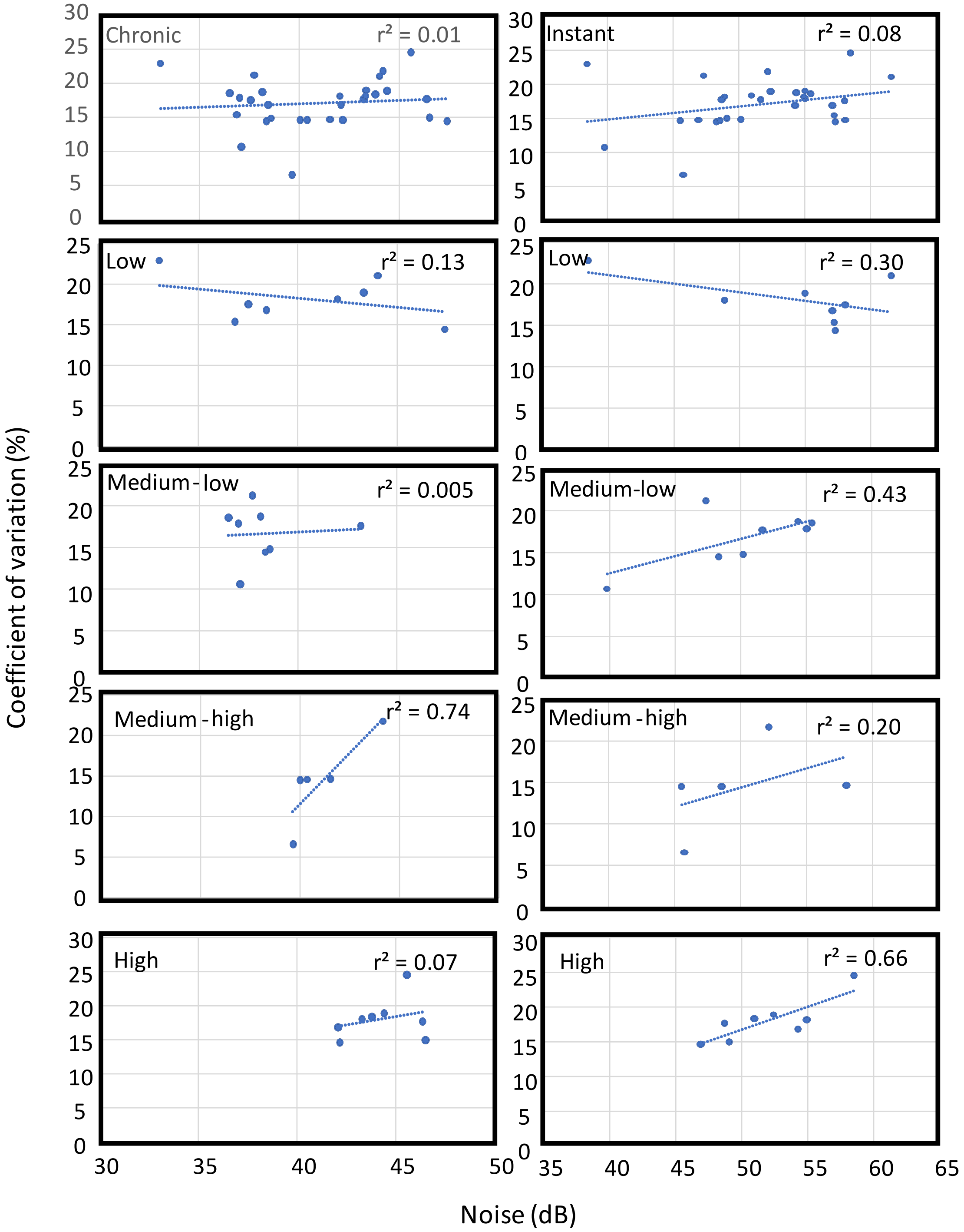

Figure 9. Differences in linear relationship between type of noise (Chronic and Instant noise) and duet synchronization over four populations that vary along the urban development

Capítulo 2

Urban development and noise interference on alarm calls in a bird community

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Urban noise levels, calls, community, composition, response, gradient

Abstract

Anthropogenic noise level has become an important selective force shaping animal communication in urban environments. Birds that inhabit urban areas must communicate effectively to survive and reproduce. However, the noise level is usually high in urbanized areas. It varies between sites, with some sites noisier and thus more challenging for birds to recognize acoustic signals than others. Noise is particularly critical when it interferes with acoustic signals used to indicate the presence of predators or danger because receptors' survivorship is directly related to the quality of the signal received. Our goal in this study was to test how bird species in a community respond to two different alarm calls of a common urban bird species across sites that varied in anthropogenic noise (urban gradient). We conducted 74 playback experiments of two alarm calls in five locations along the urban gradient in Costa Rica. Before and after each experiment, we measured the noise level inside each point. The result showed that the bird community responds to low-frequency alarm calls in urban sites, but this response decreases when the noise level increases, likely due to noise masking the low-frequency calls. Contrary to our expectations, complexity was higher in the three more urbanized sites compared to the two more natural ones because they have more open areas that avoid degradation and attenuate calls, so bird communities have more responses to the signal source. We suggest that urban noise could affect bird response and recognition potential threats as it interferes with the information conveying by mobbing calls; also, bird experience would play an important factor in recognizing alarm calls as bird community change along the urban gradient. We must go through priority management strategies to preserve at least part of the diminished bird biodiversity that inhabit urban areas is imperative to reduce the noise level.

Introduction

The alarm calls are a fundamental part in animal communication since they inform receivers of actual and potential threats (Marler & Slabbekoorn 2004; Isaksson et al 2018; Landsborough 2020; Suzuki 2020; To et al. 2021; Tietze 2021; Szymkowiak 2021). These calls are directly related to the emisor's direct and indirect fitness as they can inform offspring and relatives of the presence of predators (Farrow et al. 2017). Alarm calls often attract conspecific and heterospecific species to the site where they are emitted and cooperatively mob or distract the predator (Manser 2001; Templeton & Greene 2007; Fallow et al. 2011; Wilson & Mennill 2011; Sandoval & Wilson 2012), allowing conspecifics to scape or hide (Carro & Fernández 2021). In urban areas, anthropogenic noise (frequently higher than in natural areas) and less diverse animal communities may affect how receivers respond to alarm calls (Marler et al. 1986; Clergeau et al. 2006; Méndez & Sandoval 2017). Anthropogenic noise mask and degrade alarm call signals (Slabbekoorn 2018; Isaksson et al 2018) and community composition may influence the number of species and individuals that respond to the alarm call (Blair 1996; Nava-Díaz et al 2020; Chace & Walsh 2006).

Anthropogenic noise (higher levels close to the city core) may affect the number of individuals and species that respond to alarm calls under the predator presence because these calls reach a variable number of receivers (fewer receivers in noisier environments) (Curio 1978; Wood & Yezerinac 2006, Lowry et al. 2013, Slabbekoorn 2013). Alarm calls could degrade faster by noise masking affecting call information (Perla & Slobodchikoff 2002; Derryberry 2009). Thus, incomplete transmission or an incorrect message produces no response or incorrect response from the receivers, a waste of energy and time, and high exposure to predators from the sender (Suzuki 2016). For example, House Wrens (*Troglodytes aedon*) in cities showed fewer approaches to predator location as a consequence of anthropogenic noise because at higher noise levels birds likely had more difficulties in discriminating or assessing predator threats (Grabarczyk & Gil 2019). Other studies, showed that noise produced by chainsaws and traffic jam affect mobbing behavior in birds nesting close to roads, because noise overlaps the acoustic signals of the alarm calls (Diniz & Duca 2021; Tilger et al 2022).

The composition of a bird community that perceives the alarm calls is another factor that influences the number of species and individuals that respond to these calls (Slabbekoorn 2013; Méndez et al. 2021). Differences in composition in urban communities tend to be more accentuated (MacGregor-Fors & Escobar-Ibáñez 2017), because they are often shaped by different ecological processes, time periods, and composition of the urban/natural matrix (MacGregor-Fors & Escobar-Ibáñez 2017; Nava-Díaz et al. 2020). Thus, species richness in urban habitats is lower and very different from other urban communities and from nearby communities occupying rural and natural habitats (Curio 1978; Wood & Yezerinac 2006, Lowry et al. 2013, Slabbekoorn 2013). Additionally, there is a rapid species turnover in urban communities, so native locally-extinct species are substituted by opportunistic species (Curio 1978; Wood & Yezerinac 2006, Lowry et al. 2013, Slabbekoorn 2013). Consequently, alarm calls inside urban areas will be responded by a lower number of species, but probably for a larger number of individuals of the same species (Perla & Slobodchikoff 2002; Derryberry 2009; Méndez et al. 2021). Therefore, community homogenization and lower species richness may affect the response to alarm calls inside cities (Marler et al. 1986; Clergeau et al. 2006; Méndez & Sandoval 2017).

Our goal with this study was to test how the bird community responded to two different alarm calls of a common urban bird species, in sites that varied in the level of anthropogenic noise and bird composition over an urban gradient. We used calls of the House Wren, a common species that occupy a wide variety of natural, seminatural, and anthropogenic habitats (Skutch 1953, Redondo et al. 2013), with different noise levels (Juarez et al. 2020). House Wrens produce two different alarm calls that vary in their minimum frequency which are regularly responded by conspecific and heterospecific individuals in the habitats occupied by this species (Carro & Fernandez 2021). Consequently, if the response of heterospecific (species richness and individual quantity) to alarm calls vary between habitats, the differences cannot be attributed to the lack of experience with the calls. Both call types differ in the minimum frequency values; the frequency range of one call overlaps with the range of anthropogenic noise that has more energy (<3 kHz), but the range of the second call is above that frequency range (Lowry et al. 2013; dos Santos et al. 2016). Consequently, if noise affects each call differently, we expect, in the noisiest site, a higher response to the call with a higher minimum frequency (lesser overlap) compared with the ring with lower minimum frequency.

Specifically, we will respond to the following two questions: 1) Will the bird community respond more to alarm calls with higher minimum frequency in territories with higher anthropogenic noise levels? If noise affects call transmission, we predict that the bird community will respond to alarm calls with higher frequencies because this call is less masked by anthropogenic noise. If noise level does not affect the response to alarm calls, the bird community will be like both call types. 2) Will the bird species responding to House Wren alarm calls vary between urban and natural sites? We predict that the number of species responding to alarm calls will increase from more to less urbanized sites, because bird communities have fewer species in more urbanized areas (Chace & Walsh 2006; MacGregor-

Fors & Escobar-Ibáñez 2017). We also predict more individuals responding in urban areas than in less urbanized sites, because urban species have a higher density of individuals than species in natural habitats (Leveau & Leveau 2005; Murgui & Hedblom 2017).

Methods

We collected data in five sites that varied in the degree of urban coverture (hardspace) from September-October 2021. 1) Universidad de Costa Rica main campus, San Jose province (9°56´N, 84°05´W; 1200 m elevation) is highest urban developed site with a 66% of urban coverture that include 2-5 floor buildings, main roads, parking lots, and gardens. 2) Instalaciones Deportivas, Universidad de Costa Rica, San Jose province (9°56’N, 84°02’W; 1200 m elevation) is a medium-high urban site with a 52% of urban coverture that include 1-2 floor buildings, main and secondary roads, and sport fields. 3) Jardín Botánico Lankester, Cartago province (09°50´N, 83°53´W; 1400 m elevation) is a medium urban site with a 22% of urban coverture that include houses, buildings, warehouses, gardens, and main and secondary roads. 4) Getsemani, Heredia province (10°01´N, 84°05´W; altitude 1400 m) is a low urban site with 1% of urban coverture that include several 1-2 floor houses, gardens, and secondary roads. 5) Estación Biológica Monteverde, Puntarenas province (10°18´N, 84°48´W; altitude 1600 m) is a non-urban site with <1% urban coverture that include the biological station, four houses, and a dirt road. See Sandoval et al. (2016), Juárez et al. (2020), Rodríguez-Bardía et al. (2022), and Méndez et al. (2021), for a more detail description of the five sites based in vegetation characteristics.

Stimulus production

We used as our stimuli the two alarm calls (Type I and Type II; Fig. 1) of House Wren, which occurred in the five study sites (Skutch 1953, Redondo et al. 2013). It is known that several bird species respond, approaching and vocalizing to both call types (Caro & Fernández 2021). This allowed us to compare birds’ responses among sites with different urban noise levels along the urban gradient. The Type I call is produced when House Wrens harass a predator that is nearby the nesting territory (Corral et al. 2012). The Type II call is produced in presence of predator, but far from the nest (Carro & Fernández 2021).

For this experiment, we created two call stimuli and two control stimuli. All stimuli consisted of tracks with a particular call repeated several times. Each stimulus differs in length; and rather than holding playback rate constant, we held duty cycle constant. We used the natural duty cycle to create each stimulus following the average call rates previously used by Carro & Fernández (2021) in another playback study: 64 call/min for alarm call Type I and 305 call/min for alarm call Type II. Calls used to create the stimuli were obtained from recordings from Colección de Bioacústica, CIBET, Universidad de Costa Rica. We used calls with the higher possible relation signal-to-noise ratio that did not overlap with other sounds in the frequency range. After selected the calls, we filtered external noise under 1 kHz and above 9 kHz to call Type I; and under 1 kHz and above 6 kHz for call Type II using the Fast Fourier Transform filter (FFT) in the program Adobe Audition 1.0 (Adobe System incorporated). Then, we normalized both calls to -1dB to standardize its amplitude and the result of each call was repeated according to the respective call rate.

We created one control stimuli for each alarm call type using white noise. For call Type I control, we created a white noise call of 0.5 s duration in Adobe Audition 1.0. Then, we filtered using the FFT filter all the white noise below 1 kHz and above 9 kHz. After that, we normalized to -1dB to standardize its amplitude and repeated at the same call rate of the call Type I (64 rate call/min). For call Type II, we created a white noise call of 0.1 s duration. Then, we filtered the white noise below 1 kHz and above 6 kHz using the FFT filter. After that, we normalized to -1dB to standardize its amplitude and repeated at the same call rate of the call Type II (305 call/min). We storaged all stimuli in a portable audio player (iPod nano, Apple).

Playback Experiment

We conducted 74 experiments in total (14 at higher, medium-high, and low urban site, and 16 at medium and non-urban site). All trials were conducted between 6:00-9:00 h, when birds were more active. In each ensemble we placed the loudspeaker between 25 and 100 m apart (average ± SD = 51.5 ± 30.5 m), in sites with different noise levels. We conducted half of playbacks per site one day and the other half the next day. This allowed us to maximize the distance between playback locations in each site and prevented playback familiarization of bird community. We selected randomly the stimulus presentation for each experiment, but taking into account the broadcast order in neighbour experiments to avoid repetition. We displayed the loudspeaker at 1.5 m from the ground that is common height where House Wrens vocalize in the study sites (pers. obs.). We used an active loudspeaker Minivox Anchor Audio; frequency response: 100-20000 Hz, and playback volume was held constant across all trials at 60dB SPL, measured at 1 m from the speaker with a digital sound meter Sper Scientific (Digital Mini Sound Meter NIB – 850014) using A weighting and fast response. We used this playback amplitude because was similar to the amplitude of House Wren alarm calls, and was the amplitude used previously in other House Wren alarm call experiments (Carro & Fernández 2021).

We placed 30 cm long orange flagging tape at 5 m from the speaker on the four cardinal points to facilitate our estimates of the distance between the speaker and approaching birds at each stimulus and recorded the behaviour responses (see below). During each experiment, we conducted the observations at 8 m from the speaker without any movement to prevent any interference on avian responses. Finally, we measured noise inside the experimental area before and after each experiment, using the same digital sound meter and configuration used to measure the playback volume amplitude. We took a total of seven noise measurement 1 min before and 1 min after the experiment and then we estimated the average noise value for each experiment. To estimate noise level, we recorded noise measurements each 10 s in different orientations and positions inside the 5 m radius from the speaker.

Response Measures

We broadcasted the four playback stimuli consecutively following this procedure: 1 min of stimulus followed by 3 min of silence (Fig. 2). During the first 2 min (1 min stimulus and 2 min silence), we measured the following community responses: (1) time in seconds for the first vocalization of any individual since the start of the stimuli (if birds did not vocalize we assigned a value of 181 s); (2) time to approach in seconds (first species) within 5 m of the speaker since the start of the stimuli (if any individual approach we assigned a value of 181 s); (3) time in seconds that all birds that respond were in 5 m radius from the speaker; (4) total number of species that were within 5 m radius from the speaker; and (5) maximum number individuals per species that were in 5 m radius from the speaker. Finally, we estimated a (6) diversity index from the community in each site to represent the complexity of community response. This index was the ratio between species number and individuals' number, a value of 1 mean highest diversity because all species had the same number of individual responding, close to 0 mean the lowest diversity because a species have the larger amount of individual responding the stimulus. We let 1 min as a recovery period after birds' departure of the 5 m radius from the speaker and stopped the first stimulus before start the next. None bird stayed during the 1 min of recovery time inside the 5 m radius or kept calling in an alarm behaviour.

Statistical Analysis

We conducted two Principal Component Analyses (PCA) to reduce the original number variables; in this case to two new multivariate response variables. The first multivariate response is called "*community perception*" and included the time for the first vocalization, time to approach to the speaker, time that all birds that respond were closer the speaker; total number of species, and maximum number individuals per species. This new multivariate response variable explained the 54.5% of the original variance and correlated a positively with time closer the speaker (r = 0.31, this represents correlation coefficients between the raw variables and pc1), number of species approaching (r = 0.53), and individuals per species (r = 0.52); and negatively with time for the first vocalization (r = -0.38), and time to approach the speaker (r = -0.45). Therefore, higher values of *community perception* indicate more individuals, species, and time closer the speaker, and faster approach to the speaker and producing the first vocalization in response to the stimulus. The second multivariate response is called *"community complexity"* and included the total number of species, maximum number individuals per species, and diversity index value. This second multivariate response variable explained the 71.1% of the original variance and showed a positive relationship with total number of species (r = 0.66), maximum number individuals per species (r = 0.59), and diversity index value (r = 0.47). Therefore, higher values of *community complexity* indicate more individuals, species, and diversity.

We conducted a lineal mixed-effect model (LMM) to determine if community aggressiveness changed according to stimulus (4 levels), territory noise level (continuous variable), and the interaction between both. We conducted a second LMM to determine if community complexity changed according to stimulus type (4 levels), the sites that varied in the degree of urban coverture (5 levels); and the interaction between both. In both LMM, we used the code of each site where the playback was conducted and as a random factor to take into account multiple measurements in the same site. We also compared the composition of bird community that respond in the five studied sites using non-metric multidimensional scaling analysis (NMDS) with a Bray-Curtis distance. This analysis is based on the species presence and abundance. We compared community compositions between sites, using one-way PERMANOVA with 10000 permutations, a posterior pairwise comparisons. Principal components analysis and LMM were conducted using JMP 7.0, and NMDS and PERMANOVA using PAST 4.11.

Results

Community perception

The response of the bird community was stronger to call Type II than to call Type I, and stronger for each of the two calls than for the control ($F_{3,252}$ = 13.31, p < 0.001; Fig. 3). The response of the community decreased as noise increased ($F_{1,88}$ = 4.32, p < 0.001; Fig. 3). However, we did not find a significant interaction between stimulus type and noise level on the response of the bird community ($F_{3,252}$ = 0.10, p = 0.96). We also found that noise level did not directly correlate with the urban gradient; the max level of noise was founded in Monteverde (MV) (55.09 ± 0.56 dB), the least urbanized site. The noise in the other sites decreased from the Universidad de Costa Rica (UCR) (49.21 ±0.34 dB), Heredia (HER) (47.69 ± 0.22 dB), Jardín Botánico Lankester (JBL) (47.86 ± 0.53 dB) to Deportivas (DEP) (45.13 ±0.18 dB), which neither correlated with the extension of the urbanized area in each of the sites.

Community complexity

We observed a total of 48 bird species and 459 individuals approaching to the speaker in response to alarm call playbacks (Table 1). The site with less species observed was the non-urban site only with nine, the number of species approaching the speaker in the other four sites varied from 17 to 21 species (Table 1). We also observed fewer individuals approaching the speaker in the non-urbanized site, followed by the less urbanized; the three sites with larger urbanized area had the higher number of individuals (Table 1). The structure of bird community that responded to alarm call playbacks vary from more urbanized to non-urban site in a gradient (PERMANOVA: $F = 3.66$, $p < 0.001$; Fig. 4). Based on the pairwise comparison, the bird community that responded to the playback was similar between the higher urban and medium-high urban sites ($p = 0.06$), and between the low urban and non-urban sties ($p = 0.17$) (Fig. 4). The bird communities differed between the other sites (pairwise comparisons: $p < 0.04$; Fig. 4).

Complexity of the community varied in relation to each stimulus and urban development. The community that responded to call Type II was more complex than that responding to call Type I, and complexity of the communities responding to each call was higher than that responding to the control ($F_{3,207} = 18.15$, $p < 0.001$; Fig. 5). Contrary our expectations, we found that community complexity was higher in the three more urbanized sites than in those two sites with less urban development ($F_{4,69} = 6.22$, $p < 0.001$; Fig. 5). The effect of the interaction between stimulus and sites varied. The complexity of the community was higher when responding to call Type II on the middle-urbanized sites, but the complexity was low in communities responding to the control stimuli in the two more natural sites ($F_{12,207} = 8.32$, $p < 0.001$; Fig. 5).

Discussion

In this study, contrary to our prediction, alarm calls with lower minimum frequency (i.e., Type II) evoque a stronger response in the bird community too. Noise level did not affect differently the response to each alarm call, but the response of the communities to playbacks decreased in noiser territories. The complexity of the community that responded to the alarm call was higher in the three most urbanized sites (high, medium-high, and medium urbanization), contrary to our predictions. However, as expected more individuals responded in urban sites compared with those sites less urbanized.

Studies of anthropogenic noise effect on birds reported that acoustic signals with higher minimum frequency transmit better in noisier conditions (Marler & Slabbekoorn 2004, Slabbekoorn 2004, Derryberry et al 2017, Luther et al. 2016), because the overlap of higher minimum frequencies with the range of maximum interference of anthropogenic noise that occur below 3 kHz, is minimum. However, acoustic signals with higher minimum frequencies degrade faster than signals with lower minimum frequencies, because sound wave collide with more obstacles when travel in the ambient (Marler & Slabbekoorn 2004; Symes & Price 2015; Murgui & Hedblom 2017), therefore reach shorter distances and probably to a lower number of receivers (Vargas-Castro et al. 2017, Graham et al. 2016, Peake 2005). In our case, the alarm call Type I of the House Wren had higher minimum frequency and is expected to be more affected by anthropogenic noise than call Type II. Therefore, the faster degradation of alarm call Type I is likely the reason we found a lower response from the bird community to this alarm call than to the Type II. Another factor that could have affected the response of the bird community to this call type is its low call rate (64 call/min), which is the natural rate for this type of call (Carro & Fernández 2021). On the contrary, the high call rate (305 call/min) of the call Type II elicited a stronger response of the receivers (Wilson & Mennill 2011, Sandoval & Wilson 2012; Quirós-Guerrero et al 2021). Higher call rate also increases the probability of been hearing by receivers, because anthropogenic noise is not constant over time in field conditions, and signal could travel farther and attract more individuals of the community. However, is necessary to test this idea of call rate effect comparing both calls under different rates in habitats with different noise levels.

The target receivers of each alarm call type may also influence the responses observed. Alarm call Type I in House Wren is produced mainly close to the nest and have acoustic characteristics (i.e., broad frequency range and longer duration) that make it easily localizable (Corral et al. 2012), suggesting that this signal is designed to attract mostly conspecifics, including the other pair member, to help in the nest defense. Therefore, this call may not be perceived by a large number of other species as an alarm signal, or if it is perceived birds approach more slowly or not at all. On the contrary, the alarm call Type II of House Wrens is produced in predator contexts, far from the nesting site (Corral et al. 2012). This alarm call may be produced more frequently than Type I, because interactions with predators occurs year-round (during and outside of breeding season) and far from the nest, allowing other species in the community to recognize the alarm call Type II as a signal of predator presence, responding accordingly to that experience. This phenomenon has been observed in other communities that vary the intensity of response based on the previous experience with the signals (Sandoval & Wilson 2012, Wu et al. 2021, LaZerte et al. 2017).

We also found that the response of the community to alarm call varied among sites also higher species richness in more urbanized sites. Contrary to our expectations, because, bird community inside cities is less diverse than surrounded rural or natural habitats (MacGregor-Fors & Escobar-Ibáñez 2017). The lower bird species richness inside cities is result of the local extinction associated with natural habitat reduction or destruction (Lowry et al. 2013); and a reduced colonization in the new urban habitats by new species, a pattern observed in Higher urban and Medium-high urban studied sites (Biamonte et al. 2012). However, the difference in sound's transmission between sites (more urbanize and less urbanize) is the presence of more open habitats in the three urban sites (e.g., isolate trees, low vegetation, and grasses), and consequently less obstacles to degrade and attenuate the call. This will produce that alarm calls reach receivers that are far from the signal source compared to less urbanized sites that are denser in vegetation.

Another reason for the unexpected differences in community response may be related to the occurrence of House Wren’s along the urban gradient (Carro & Fernández 2021), and the recognition of the alarm call by other species inside the community (Wu et al. 2021). House Wren is more abundant in more urbanized sites (Juárez 2020a; 2020b); therefore, other birds in these sites have presumably the multiple opportunities to experience and learn the vocal aggressive displays of the House Wren, and thus to respond more intense than species in less urbanize areas, which have less experience recognizing the House Wren alarm call.

In conclusion, our study showed that the response of alarm calls over an urban gradient is affected by several factors: the acoustic characteristics of the call (lower frequency alarm call delivers a strong response), the community of potential receivers (inside more urbanize sites more species approach to the alarm call stimulus), and anthropogenic noise level (higher noise level reduce the response of potential receivers). This study also provides evidence that recognition of alarm calls is influenced by several factors acting simultaneously, thus, for a full understanding on how this type of signals are affected and perceived by different species and in different habitats, studies should compare the response of different communities of receiver to alarm calls with different acoustic characteristics and habitats.

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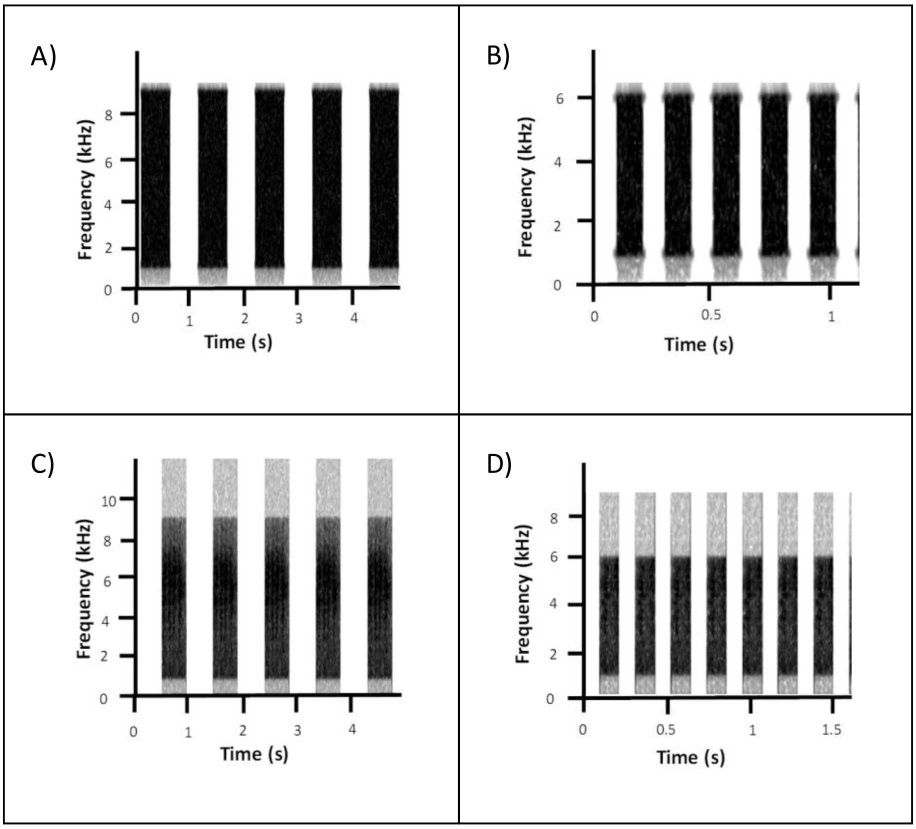

Figure 1. Spectrograms showing (A) Type I alarm call, (B) Type II alarm call, (C) Control I, and (D) Control II of house wren

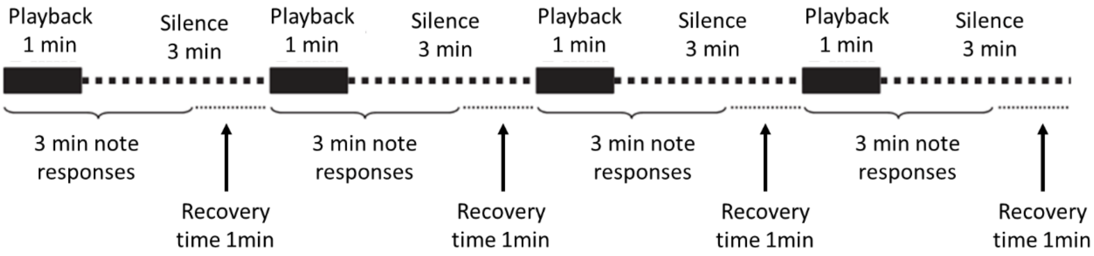

Figure 2. Schematic representation of the timing of playback trials of House Wren´s alarm calls. During each trial we broadcasted 4 treatments (Type I, Type II, control I, and control II).

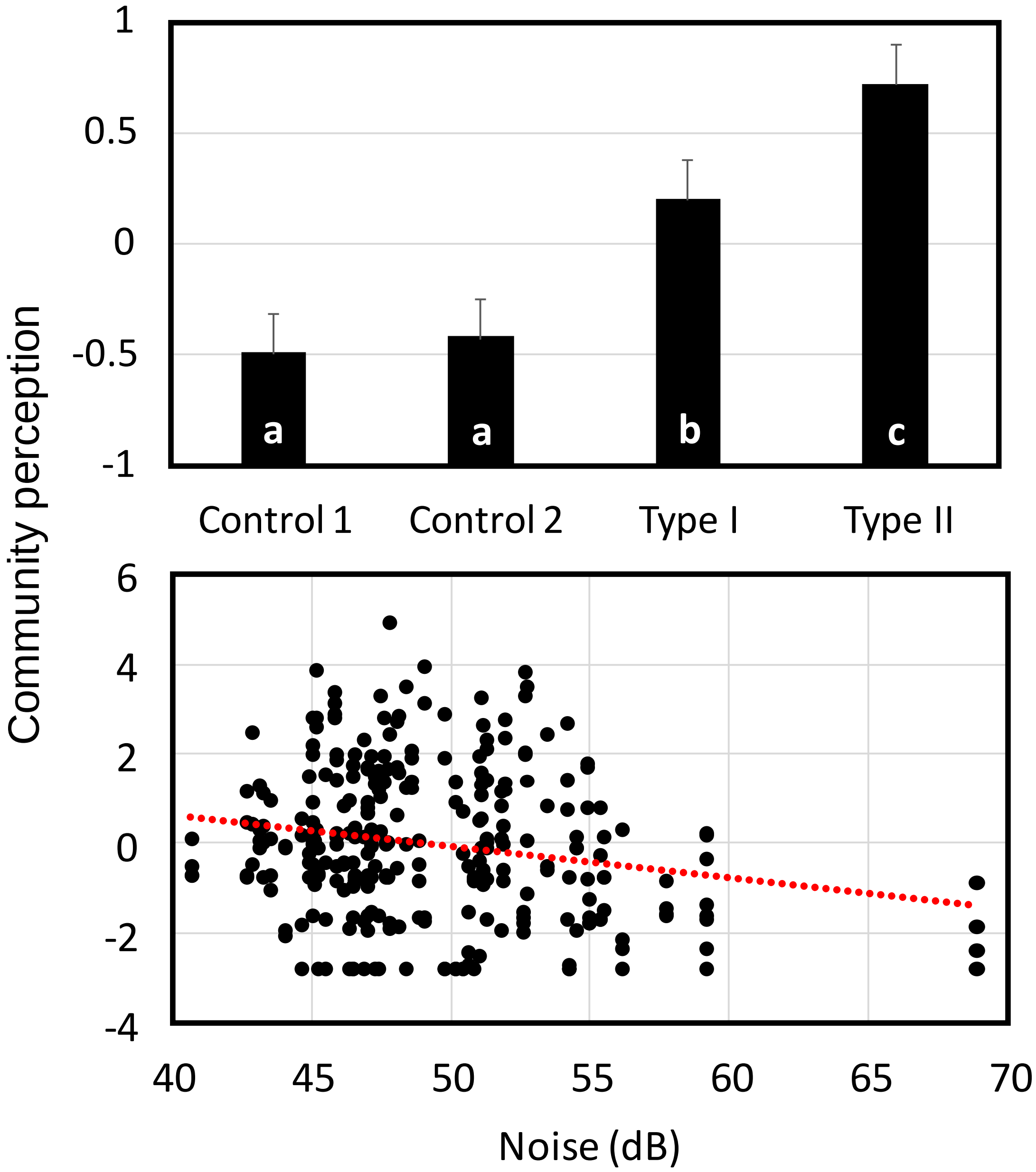

Figure 3. Changes in the response of bird community to four playback stimuli (two controls and two House Wren alarm call types) where higher values of community perception (i.e., more individuals, species, time closer to the speaker, faster approach to the speaker, and first vocalization in response to the stimulus). Then the effect of anthropogenic noise in each study site where bars with the same letters mean non-significant difference between playback stimulus in a posteriori comparison.

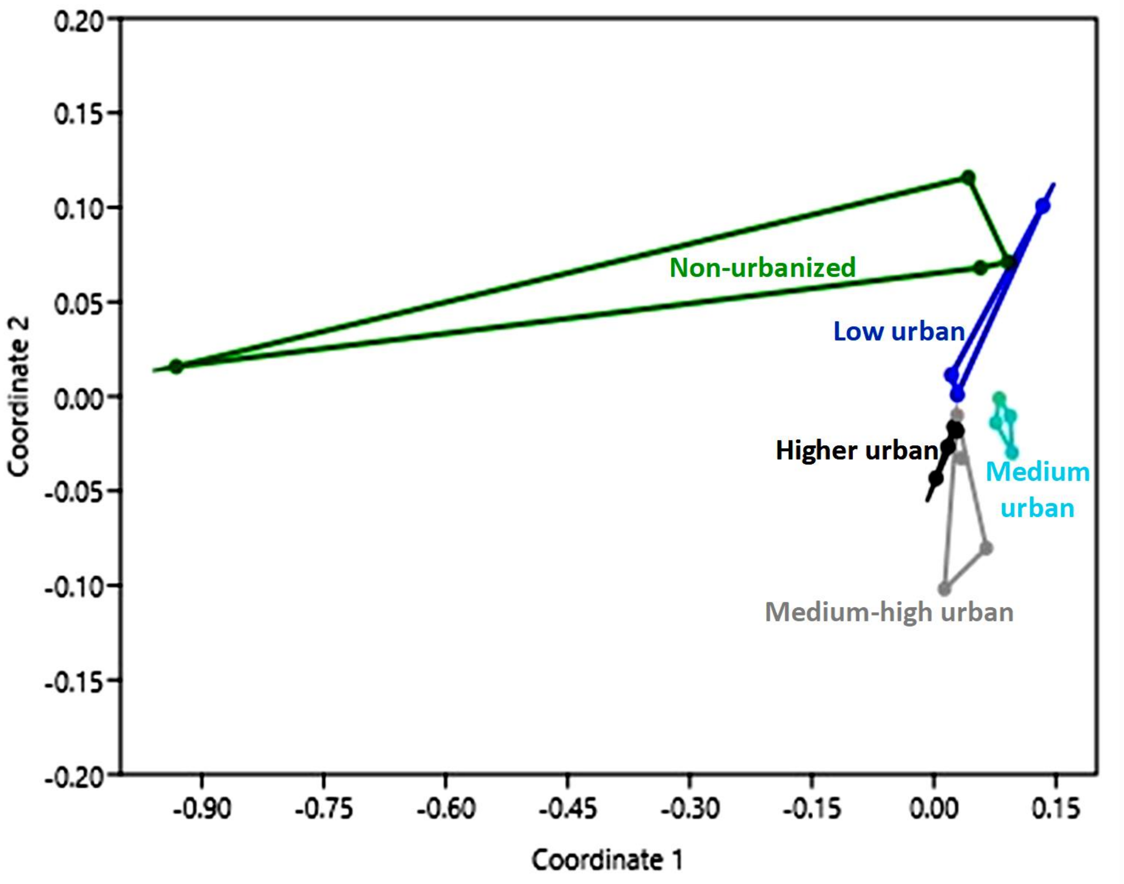

Figure 4. Non-metric multidimensional scaling based on Bray-Curtis distance of the bird community response to the playback of House Wren alarm call in five sites with different urban development.

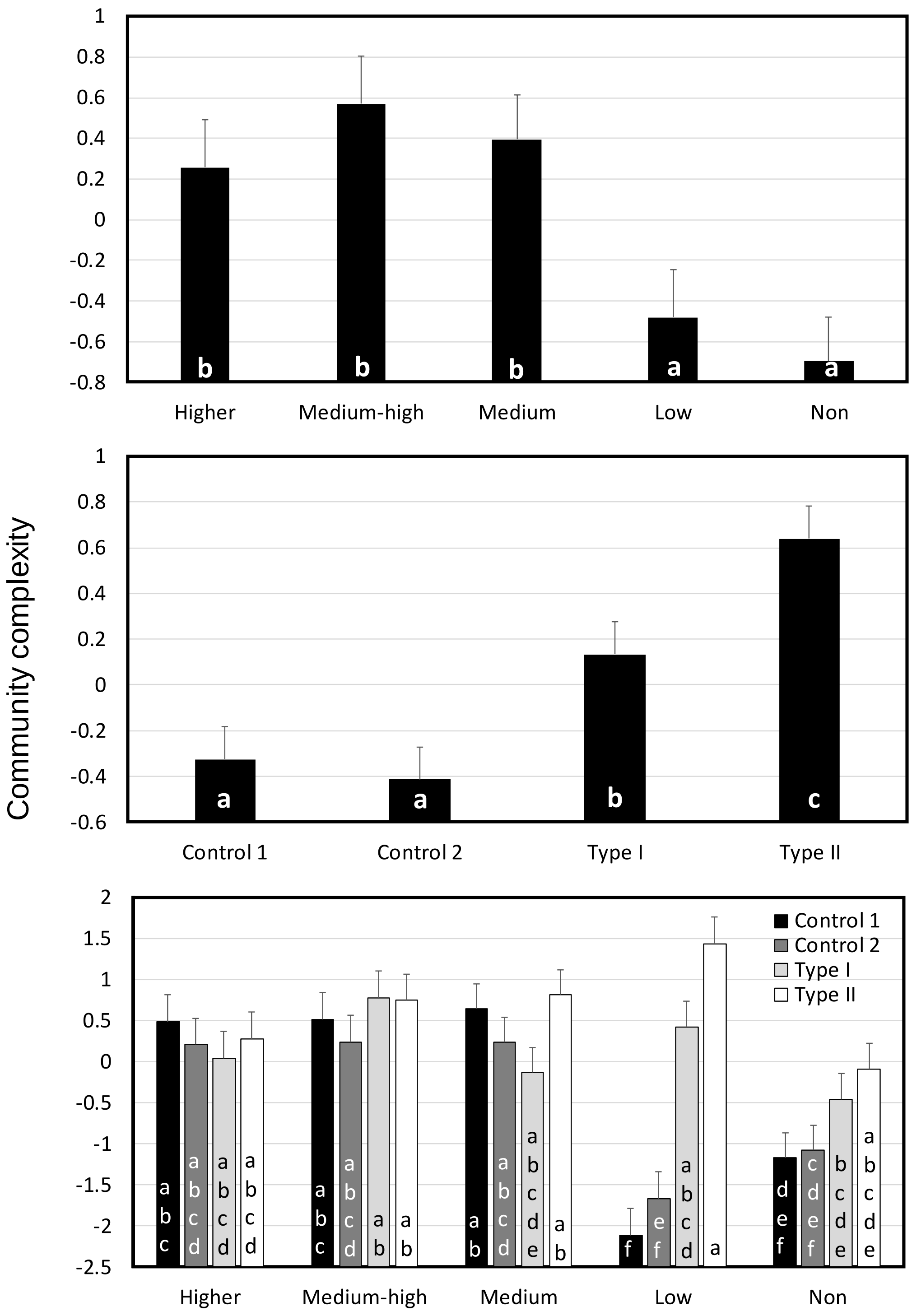

Figure 5. Changes in the bird community complexity response in five sites with different urban development, four playback stimuli (two controls and two House Wren alarm call types), and the interaction between both. Higher values of community complexity mean more individuals, species, and diversity. Bars with the same letters mean non-significant differences between playback stimulus in a posteriori comparison.

Table 1. List of the 48 bird species that responded to our 74 playback experiments in five sites with different urban development and bird communities.

Taxa	English name	Higher	High-medium	Medium	Low	Non	Total
Columbidae							
Columbina talpacoti	Ruddy Ground Dove			4			4
Zenaida asiatica	White-winged Dove	1	8				9
Cuculidae							
Piaya cayana	Squirrel Cuckoo	1					1
Trochilidae							
Saucerottia hoffmanni	Blue-vented Hummingbird	5	1		1		7
Amazilia tzacatl	Rufous-tailed Hummingbird	8	10	6	7		31
Lampornis calolaemus	Purple-throated Mountain-gem			7			7
Picidae							
Melanerpes hoffmannii	Hoffmann's Woodpecker	5			1		6
Tityridae							
Tityra inquisidor	Black-crowned Tityra		2				2
Tityra semifasciata	Masked Tityra	3	7				10
Tyrannidae							
Contopus virens	Eastern Wood-Pewee	2	4				6
Elaenia flavogaster	Yellow-bellied Elaenia	11		1			12
Elaenia frantzii	Mountain Elaenia			15			15
Empidorax traillii	Willow Flycatcher					1	1
Megarynchus pitangua	Boat-billed Flycatcher	12	7		1		20
Mionectes olivaceus	Olive-striped Flycatcher		6			1	7
Pitangus sulphuratus	Great Kiskadee		2	1			3
Tyrannus melancholicus	Tropical Kingbird	2	4	2	1		9
Todirostrum cinereum	Common Tody-Flycatcher		7	18			25
Vireonidae							
Vireo flavoviridis	Yellow-green Vireo		4				4
Vireo olivaceus	Red-eyed Vireo	22	19	12			53
Vireo olivaceus	Red-eyed Vireo			1			1
Troglodytidae							
Cantorchilus modestus	Cabanis's Wren				3	1	4
Henicorhina leucophrys	Gray-breasted Wood-Wren		2				2
Troglodytes aedon	House Wren			11	1		12
Turdidae							
Catharus ustulatus	Swainson's Thrush				2		2
Turdus grayi	Clay-colored Thrush	4	9		5		18
Passerillidae							
Melozone leucotis	White-eared Ground-Sparrow	16	11	16	13	8	64
Melozone cabanisi	Cabanis's Ground-Sparrow				2		2
Zonotrichia capensis	Rufous-collared Sparrow	6	3				9
Icteridae							
Icterus galbula	Baltimore Oriole				4		4
Parulidae							
Basileuterus delattrii	Chestnut-capped Warbler			15	9	3	27
Cardellina canadensis	Canada Warbler	4					4
Parkesia noveboracensis	Northern Waterthrush	5					5
Sethopaga virens	Black-throated Green Warbler			4			4
Setophaga castanea	Bay-breasted Warbler				1		1
Setophaga petechia	Yellow Warbler				4		4
Cardinalidae							
Habia rubica	Red-crowned Ant-Tanager				4		4
Piranga rubra	Summer Tanager				1	3	4
Thraupidae							
Coereba flaveola	Bananaquit					2	2
Ramphocelus passerinii	Scarlet-rumped Tanager			7			7
Ramphocelus passerinii	Scarlet-rumped Tanager			6			6
Saltator atriceps	Black-headed Saltator		4				4
Saltator coerulescens	Bluish-gray Saltator				1		1
Saltator grossus	Slate-colored Grosbeak		1				1
Sporophila corvina	Variable Seedeater					1	1
Thraupis episcopus	Blue-gray Tanager	4	4	2	19		29
Thraupis palmarum	Palm Tanager					4	4
Tangara dowii	Spangle-cheeked Tanager		1				1

Conclusiones

En mi primer capítulo logré demostrar que existió una relación entre los niveles de ruido antropogénico dentro de los territorios y la sincronización de los duetos del Cuatro-ojos de Cabeza Negra (*Melozone leucotis*) con el tamaño de su territorio. El tamaño de los territorios decreció cuando incrementó el ruido antropogénico crónico dentro de los territorios, pero el tamaño no fue influenciado por el ruido antropogénico instantáneo. Hasta donde sé, esta es la primera vez que se muestra este patrón para cualquier ave. Las parejas que tuvieron baja sincronización en los duetos tuvieron territorios más pequeños, pero únicamente en los dos sitios con menor desarrollo urbano. Este es uno de los primeros estudios que intentan relacionar las características de la vocalización con el tamaño del territorio en entornos urbanos.

Al analizar el efecto de los niveles de ruido antropogénico dentro de los territorios y su efecto en la sincronización de los duetos, no encontré una relación clara entre ambos. Para el ruido crónico, al aumentar el nivel de ruido, la sincronización no cambió en los sitios urbanizados alto y medio bajo, pero disminuyó en el sitio urbanizado medio-alto y aumentó en el sitio urbanizado bajo. Para el ruido instantáneo, cuando aumentó el nivel de ruido aumentó la sincronización en el sitio poco urbanizado contrariamente a mi expectativa, mientras que en los otros tres sitios la sincronización disminuyó cuando aumentó el ruido instantáneo.

En mi segundo capítulo demostré cómo responde la comunidad de aves urbanas a dos tipos de llamadas de alarma (que varían en frecuencia mínima) cuando varía el nivel de ruido antropogénico. Contrario a mi predicción, las llamadas de alarma con frecuencia más baja (Tipo II) provocaron respuestas más fuertes por parte de la comunidad de aves (más individuos y especies se aproximaron a la llamada). Sin embargo, la respuesta de la comunidad disminuyó si aumenta los niveles de ruido independientemente del tipo de llamada. La complejidad de la comunidad que respondió al llamado de alarma fue mayor en los sitios más urbanizados, contrario a mis predicciones. Sin embargo, como era de esperar, más individuos respondieron en sitios urbanos en comparación con los sitios menos urbanizados.

Mi estudio demostró que la respuesta de las llamadas de alarma sobre un gradiente urbano se ve afectada por varios factores: las características acústicas de la llamada (una llamada de alarma de baja frecuencia ofrece una respuesta fuerte), la comunidad de receptores potenciales (dentro de sitios más urbanizados más acercamiento de las especies al estímulo de la llamada de alarma), y nivel de ruido antropogénico (un mayor nivel de ruido reduce la respuesta de los receptores potenciales). Este estudio también proporciona evidencia de que el reconocimiento de las llamadas de alarma está influenciado por varios factores que actúan simultáneamente, por lo tanto, para una comprensión completa de cómo este tipo de señales se ven afectadas y percibidas por diferentes especies y en diferentes hábitats, los estudios deben comparar la respuesta de diferentes comunidades de receptores, llamadas de alarma con diferentes características acústicas y hábitats.

Mis resultados resaltan la importancia de analizar de manera comparativa sobre el gradiente urbano cómo el ruido antropogénico afecta otros aspectos de la biología de las aves y cómo los individuos se adaptan a esos cambios para sobrevivir. Dado que los asentamientos urbanos continúan extendiéndose a nivel global, se requieren estudios sobre este tema en un gran grupo de especies para tener una comprensión más completa de los efectos de los nuevos contaminantes que estamos generando como humanidad.