Universidad de Costa Rica

Sistema de Estudios de Posgrado

Variación anual en las vocalizaciones de las aves urbanas dentro y fuera de su época reproductiva

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

Andrew José Lindwedel Cruz

Ciudad Universitaria Rodrigo Facio, Costa Rica

2024

Dedicatoria

Esta tesis se la dedico a todos mis seres queridos, tanto familiares, como compañeros y por supuesto a mi pareja, los cuales de una u otra manera me han ayudado a seguir adelante a lo largo de este proceso, el cual ha sido difícil, pero a la vez también muy provechoso. A mis padres que han sido mi primer escuela de enseñanza, y me han forjado en la vida profesional gracias a todo su sacrificio. Quiero agradecerle a mi compañero Jordy, el cual, aunque no pudimos compartir mucho tiempo, me demostró que su lealtad es una de las cualidades más valiosas para un amigo. A mis hermanos porque han sido siempre un gran apoyo para mí persona, pero sobre todo a mi pareja Ashly, la cual ha sido un pilar muy importante en mi vida, y a veces, a pesar de la distancia, su cariño y su compromiso no tienen comparación.

Agradecimientos

Quiero agradecerle primero a Dios por haberme dado la oportunidad de estudiar y la resiliencia para continuar durante todo este proceso. A la Universidad de Costa Rica, por haberme dado la oportunidad de incorporarme al Posgrado de Biología para seguir con mi proceso de formación académica, y sobre todo a la Vicerrectoría de Investigación por brindarme la beca para poder sustentar mi educación. Quiero también agradecer a mis profesores Luis, Natalie y Gilbert, los cuales me han instruido y me han ayudado a culminar con éxito este proceso, pero sobre todo porque de ellos pude aprender y profundizar más sobre la ecología urbana, la bioacústica y también sobre las aves, lo cual me llevo por el resto de mi 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"

Dr. José Edgardo Arévalo Hernández

Representante de la Decana del Sistema de Estudios de Posgrado

Dr. Luis Andrés Sandoval Vargas

Director de Tesis

Dra. Natalie Viviana Sánchez Ulate

Asesora

Dr. Gilbert Barrantes Montero

Asesor

M.Sc. Ingrid Molina Mora

Representante de la Directora del Programa de Posgrado en Biología

Andrew José Lindwedel Cruz

Candidato

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Resumen

La urbanización es una de las principales causas de pérdida de diversidad biológica, ya que reemplaza hábitats naturales con ciudades. Sin embargo, las aves han logrado adaptarse a los ecosistemas urbanos, aunque enfrentan desafíos como la fragmentación del hábitat, transmisión de enfermedades, competencia con especies exóticas y contaminación acústica. Estos factores afectan su comportamiento, incluyendo la comunicación vocal, esencial para la reproducción y defensa territorial. Las aves urbanas emplean estrategias adaptativas, como cambiar horarios de canto o aumentar la frecuencia de sus vocalizaciones, para superar el ruido ambiental. Esto, sin embargo, implica un gasto energético mayor y puede impactar negativamente su éxito reproductivo y salud, incrementando el estrés y modificando sus ciclos circadianos.

El estudio se centra en evaluar el cambio en las vocalizaciones de las aves dentro y fuera de su época reproductiva, a lo largo de un gradiente urbano. En la primera sección, evaluamos el cambio en la producción de duetos, basados en el pinzón cuatro ojos (*Melozone leucotis*), un ave que habita en diversas zonas, incluyendo ambientes tanto rurales como periurbanos y urbanos. Su capacidad de vocalizar durante todo el año y su variado repertorio lo hacen ideal para estudiar los efectos de la urbanización en sus vocalizaciones. Por otro lado, en la segunda sección, evaluamos la cantidad de vocalizaciones nocturnas y los coros del amanecer durante un año a lo largo de un gradiente urbano. Para esto cuantificamos la cantidad de vocalizaciones nocturnas que eran emitidas por aves diurnas en horas de la noche, y además estudiamos cómo la riqueza y la composición de los coros del amanecer, puede variar con respecto al grado de urbanización, la época reproductiva, y también su relación con los niveles de contaminación lumínica y acústica.

Abstract

Urbanization is one of the main causes of biodiversity loss, as it replaces natural habitats with cities. However, birds have managed to adapt to urban ecosystems, although they face challenges such as habitat fragmentation, disease transmission, competition with exotic species and noise pollution. These factors affect their behavior, including vocal communication, which is essential for reproduction and territorial defense. Urban birds employ adaptive strategies, such as changing singing times or increasing the frequency of their vocalizations, to overcome environmental noise. This, however, involves greater energy expenditure and can negatively impact their reproductive success and health, increasing stress and modifying their circadian cycles.

The study focuses on evaluating the change in bird vocalizations within and outside their breeding season, along an urban gradient. In the first section, we evaluate the change in the production of duets, based on the four-eyed finch (*Melozone leucotis*), a bird that inhabits diverse areas, including rural, peri-urban and urban environments. Its ability to vocalize throughout the year and its varied repertoire make it ideal for studying the effects of urbanization on its vocalizations. On the other hand, in the second section, we evaluated the number of nocturnal vocalizations and dawn choruses during a year along an urban gradient. To do this, we quantified the number of nocturnal vocalizations that were emitted by diurnal birds during the night, and we also studied how the richness and composition of dawn choruses can vary with respect to the degree of urbanization, the reproductive season, and also their relationship with the levels of light and noise pollution.

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Capítulo I

Intra-annual Variation on Territorial Duet Production is Associated with Breeding Stage on a Neotropical Bird Specie

Abstract

Some bird species defend their territories in pairs producing duets; coordinated vocalizations between male and female that presumably provide them with a better territory defense compared to solo songs. Duets tend to be more frequent during the reproductive season, since they fulfill different functions linked to reproduction, such as avoiding the usurpation of the pair, safeguarding the nest, as well as manifesting their status within the neighborhood. Therefore, it is important that duets transmit well or in enough quantities for the message to reach the receivers. Our objective in this study is to quantify the White-eared Ground-sparrow (*Melozone leucotis*) duets throughout the year in three populations with different degrees of urbanization. We expected to find more duets during their reproductive season, because one of its main functions is linked to territory defense. We also expected more duets in the most urban areas because the anthropogenic noise can disturb their communication, inducing birds to sing more frequently. We used autonomous recorders to register the duets inside White-eared Ground-sparrow territories over one year, in three populations with different degree of urban development. We recorded and analyzed 1344 h of recordings to quantify the number of duets produced during two consecutive mornings (4:00 – 6:00) and afternoons (16:00 – 18:00) per month and per territory. We found showed that White-eared Ground-sparrow produced more duets during the reproductive season, and also more duets in the morning than in the afternoon. Furthermore, we found that the average production of duets correlates positively with the degree of urbanization among the populations, with birds in the most urban population producing the greatest number of duets. In conclusion, we were able to demonstrate that for White-eared Ground-sparrow duets are more frequent during the reproductive season, to likely defend better the resources within their territory (pair member, nesting site, and food resources). Additionally, duets tend to be more common during the morning and in urban areas, possibly to reduce interference from anthropogenic noise as well as agonistic interactions with other individuals.

Keywords: Urban ecology, vocalizations, reproduction, urban birds, bird songs, phenology

Introduction

A fundamental strategy that enables reproductive success in many vertebrate species is territoriality, which is defined as set of defensive behaviors aimed to prevent other individuals from accessing recourses within a particular area (Hinde, 1996; Maher, 1995; Brumm et al., 2023). The goal of territoriality is to defend limited resources such as breeding pairs, nests or shelters, and food sources (Grant, 1993; Davies and Sewall, 2016). Territoriality varies between bird species and from temperate to tropical zones, since tropical species tend to defend their territory throughout the year, while those from temperate zones do so mainly during the reproductive season, in spring (Slater, 2004; Brumm et al., 2023). This occurs because in temperate zones, birds return from migration ready to establish territories and attract mates (Whitaker and Warkentin, 2010). Territoriality is very strong and marked in this season, because the possibility of surviving another migration to reach the next breeding season can be low (Whitaker and Warkentin, 2010; Stutchbury and Morton, 2022). On the other hand, many tropical birds are social monogamous throughout the year, and have a higher level of survival (Morton 1996; Macedo, 2008; Stutchbury and Morton, 2022), which allows them to defend the same territory for much longer, although territorial defense becomes stronger during the reproductive season (Busch et al. 2008; Addis et al. 2010; Chiver et al., 2014).

In birds, territory defense relies heavily on vocalizations, which are acoustic signals that have a lower metabolic cost, compared to other more aggressive interactions like attack flies, physical interaction, territory patrol, or visual displays (Zollinger et al., 2011; Grafe et al., 2012; Ríos-Chelén et al., 2015; Partan, 2017; Akçay et al., 2020). In the tropics, some birds defend their territories using duets, temporally and/or frequency coordinated vocalizations between two individuals, mostly songs with songs, but also may occur between song and calls, and calls and calls (Hall, 2004; Hall, 2009; Douglas and Mennill, 2010; Trejos and Barrantes, 2015; Demko and Mennill, 2019). Several investigations have shown that duets are more effective when defending the territory than solo songs, in neotropical species such as the Barred Antshrike (*Tamnophilus doliatus*) (Koloff and Mennill, 2011), the Happy Wren (*Pheugopedius felix*) (Templeton et al., 2011), and also in afrotropical species, such as the Bangwa forest warbler (*Bradypterus bangwaensis*) (Budka et al., 2023) and the White-browed Sparrow-Weaver (*Plocepasser mahali*) (Voigt et al., 2006). This is because that the duet involves a higher level of competitiveness when defending a territory as a couple, compared to an individual singing alone (Odom and Omland, 2017).

Territoriality in birds varies throughout the year, mainly due to the reproductive season (Golabek et al., 2012). During the breeding season is important to defend reproductive pairs to avoid usurpation of the female (Rogers et al., 2007), safeguard nests (Sagario and Cueto, 2014), and indicate the status within the population (Hall, 2009), in order to ensure their reproductive success (Guedes, 2020). Another reason why territoriality is more restricted to the reproductive season is that defense involves a high energy cost (Stutchbury & Morton, 2022), given the decrease in foraging time and increase aggressions against other individuals (Golabek et al., 2012). In addition, the reproductive season in many tropical birds coincides with the change between the dry and rainy seasons, where food availability increases, providing energy that counteract the costs of reproduction (Sandoval, 2011). Another factor that influences territoriality is testosterone levels, since the increase of this hormone during the reproductive season, a product of the circadian rhythms of birds, is correlated with a seasonal increase in territoriality (Wingfield, 1994; Landys et al., 2010; Davies and Sewall, 2016). Outside the reproductive season, aggression due to territoriality decreases but in year-round territorial species may change little, because they will maintain the same partner or the area, they defend for the next reproduction season (Sandoval et al., 2016).

The degree of urbanization is another factor that may influence the territoriality on birds. For example, when the same species inhabit urban and rural environments, it is expected that territory vary in size and density (Hardman and Dalesman, 2018; Juárez et al., 2020), because the availability of nesting sites is different (James et al., 2019), the habitat availability change due to landscape fragmentation (Jung and Kalko 2010), exposure to different pollutants such as noise or light (Slabbekoorn and Ripmeester, 2007; Dominoni, 2015), as well as if the species if befitted (urban adapter) or harmed (urban avoider) for the urban development (Juárez et al., 2020). For these reasons, many bird species along an urban gradient maintain larger territories in more urban areas, leading to greater territorial density in rural areas where territories are smaller. The population density of a species can affect the number of duets when defending territories, because there may be greater interaction between neighbors (Levin, 1996; Hall, 2004; Mentesana et al., 2020).

However, studies that associate territorial vocalizations with the time of the year (i.e., breeding vs. non-breeding) in Neotropical urban birds remain scarce. Additional information may provide evidence of the adaptability of urban individuals to the challenges of surviving in urban areas. We focus on the White-eared Ground-sparrow (*Melozone leucotis*), a species that has been used as a model to study the variation in the territorial vocalization along an urban gradient. Previous research has demonstrated that territory size, territory structure, anthropogenic noise levels, and pair density vary over the urban gradient and affect differently the birds in each population (Sandoval and Mennill, 2012; Sandoval et al., 2016; Juárez et al. 2020).

In this study we focus in quantifying the change in the production of territorial vocalizations (duets) of the White-eared Ground-sparrow pairs, within and outside the breeding season in three populations that located in environments with different degree of urbanization. We predict that duets will be more frequent during the reproductive season (between March-July) (Sandoval and Mennill, 2012; Juárez et al., 2020), because during this period they intensely defend their territory to avoid the usurpation of the members and loss part of the territory used for breeding and feeding. We also predict that duets will be more frequently produced over the year in rural than in urban areas, because in rural areas the density of territories is higher and the territory size smaller (Juárez et al. 2020) increasing the pair-pair interactions. Moreover, we finally predict that duets will be more frequently produced over the year in urban areas because higher noise levels in these areas interferes in the pair-pair communication because duets degrade at shorter distances (Sandoval et al. 2016).

Materials and Methods

Study Area

We conducted this study from January to December 2022 at three sites that varied in urban development in Costa Rican Central Valley: (1) High urbanized site: Campus of the University of Costa Rica (UCR), San Pedro de Montes de Oca, San José province (09°56′ N, 84°02′ W, 1200 m elevation). This site comprises dense secondary forest about 50 years old and exposed to intense human disturbance, which is surrounded by gardens, remote groves, and buildings. (2) Medium urbanized site: Lankester Botanical Garden, province of Cartago (9°50′ N, 83°53′ W, 1370 m elevation). This site has a mixture of gardens, buildings, and medium-sized secondary forest with dense understory, where the avifauna are exposed to moderate human disturbance compared to the urbanized site. (3) Low urbanized site: Getsemani, Heredia province (10°02′ N, 84°06′ W, 1350 m). The site contains a mix of shade-grown and sun coffee plantation with advanced secondary and riverine forests, where birds are exposed to low human disturbance compared to the previous sites.

We used five autonomous recorders (2 SM2 and 2 SM3 Wildlife Acoustics, and 1 Swift Cornell Lab of Ornithology) in the medium and high urbanized sites, and four recorders in the low urbanized study site, due to security problems. We placed each autonomous recorder in the middle of a previously known territory of colored banded White-eared Ground-sparrow. The recorders were placed between 2-3 m above the ground, each one recorded for two consecutive days 59 min each hour per 24 h. Each recorder was configured to a frequency of 44.1 kHz, 24-bit precision, and WAVE file format.

Duet quantification

We quantified the number of duets per hour and day using the Raven Pro 1.6 software (Cornell Lab of Ornithology, Ithaca, NY, U.S.A). We counted the total number of high quality (>30dB of signal-to-noise ratio) duets per hour from 4:00-6:00 h and from 16:00-18:00 h, using spectrograms built using a Hann window with 50 % overlap and 256 Hz transform size, with a temporal resolution of 5.8 ms and a frequency resolution of 188 Hz. We selected those two recording periods, because during these periods the White-eared Ground-sparrows has the vocal activity peaks for duets (Sandoval et al. 2016).

Statistical Analysis

We conducted a linear mixed-effect model with a Poisson distribution of errors to compare the change in duet production in White-eared Ground-sparrow pairs per month (12 levels), sites (3 levels), and second order interaction between both variables using the library glmmTMB (Brooks et al., 2023), in the language statistical R. We used the number of duets as the response variable and the territory where the recorders were located as a random factor, since they may present an intrinsic variation depending on the spatial configuration of the site. Additionally, we conducted three additional linear mixed-effect models (one per study site) to compare duet production in pairs of White-eared Ground-sparrows among territories (4 or 5 levels), month (12 levels), duetting period (morning vs afternoon), and second order interactions. We used the number of duets as the response variable and the sites where the recorders were located as a random factor. Finally, an ANOVA was applied to calculate the significance of each factor in the linear models.

Results

Duet production in all populations

The production of duets in White-eared Ground-sparrows varied throughout the year ($F_{(2,11)=}$ 6.34, p <0.001; Fig. 1). We found a peak on duet production from March-July (Fig. 1.1), and the lowest duet production between November-February (Fig. 1.1). The population in the high urbanized site produced more duets than the population in the medium urbanized site, and the low urbanized site population produced the lowest quantity of duets of the three ($F_{(2,22)}$= 14.36, p <0.001; Fig. 1.2). We found that each population varied in the duet production peaks over the year ($F_{(2,22)}$= 2.39, p <0.001). In the high urbanized site the peak of duet production occurred between March-July, for the medium urbanized site population between April-October, and in the low urbanized site population the peak was from April-June (Fig. 1.3).

Duet production in low urbanized site

The duet production in the low urbanized site population varied throughout the year ($F_{(2,11)} = 1.89$, $p = 0.043$), showed a peak between April- June with, up to 7.06 ± 2.26 duets (Fig. 2.2). The average number of duets in all other months were less than 4.43 ± 1.2 duets (Fig. 2.2). The number of duets varied also between time windows ($F_{(2,1)} = 97.15$, $p < 0.001$; Fig. 2.3), with a greater production of duets during the morning (7.04 ± 0.63 duets) than during the afternoon (0.9 ± 0.13 duets). Nevertheless, the number of duets between the territories were similar ($F_{(2,3)} = 3.3$, $p = 0.07$; Fig. 2.1), as well as in the interactions between months with territories ($F_{(2,11)} = 0.97$, $p = 0.47$; Fig. 2.4), and month with time windows ($F_{(2,11)} = 1.07$, $p = 0.38$; Fig. 2.6). However, the interaction between territories with time windows was significant ($F_{(2,1)} = 4.8$, $p = 0.02$), where territory 1 showed a similar production of duets between the morning and the afternoon (Fig. 2.5).

Duet production in medium urbanized site

In the medium urbanized site population the duet production also varied throughout the year ($F_{(2,11)} = 3.54$, $p < 0.001$; Fig. 3.2), with peaks in January (7.81 ± 1.73 duets), May (7.06 ± 1.72 duets), August (8.75 ± 2.57 duets), and November (7.25 ± 1.72 duets). Similarly, the duets varied depending on the time window ($F_{(2,1)} = 103.59$, $p < 0.001$; Fig. 3.3), with a greater production of duets during the morning (7.95 ± 0.62 duets) than in the afternoon (1.65 ± 0.2 duets). However, there were no significant differences in the number of duets recorded between the territories ($F_{(2,3)} = 1.93$, $p = 0.16$; Fig. 3.1), nor in the interactions between months with territories ($F_{(2,11)} = 0.63$, $p = 0.79$; Fig. 3.4), territories with time window ($F_{(2,11)} = 0.76$, $p = 0.38$; Fig. 3.5) and months with day time ($F_{(2,1)} = 1.83$, $p = 0.05$; Fig. 3.6).

Duet production in high urbanized site

Similar to the other populations, the duet production in the high urbanized site population varied throughout the year ($F_{(2,11)} = 6.78$, $p < 0.001$; Fig. 4.2), presenting the highest averages on June and July (12.43 ± 2.89 and 11.81 ± 2.85 duets respectively), with a decline in duet production between October-December, with values as low as 4.06 ± 1.25 duets. Birds produced more duets during the morning (11.13 ± 0.79) than during the afternoon (2.11 ± 0.22) ($F_{(2,1)} = 167.68$, $p < 0.001$; Fig. 4.3). However, the production of duets was similar between the territories ($F_{(2,3)} = 3.01$, p= 0.08; Fig. 4.1), as well as in the interactions between territories with months ($F_{(2,11)} = 1.71$, p= 0.07; Fig. 4.4), and with the time window ($F_{(2,11)} = 2.04$, p = 0.15; Fig. 4.5). Nevertheless, the interaction between months with day time was significant ($F_{(2,1)} = 3.00$, $p < 0.001$), because between April-July the difference in duet production between morning and afternoon were greater (Fig. 4.6).

Discussion

Production of duets throughout the year

The number of duets recorded from White-eared Ground-sparrow varied throughout the year, with a peak between March and July, coupling with the reproductive season of the species (Sandoval and Mennill, 2013), as we predicted. In the case of White-eared Ground-sparrows, duets fulfill several functions related to reproduction such as defending territory (Sandoval et al., 2016), avoiding mate usurpation (Sandoval et al., 2018) or maintaining contact with the reproductive pair (Sandoval et al., 2015), so that it is expected to become more frequent during their reproductive season. Our results are congruent with the pattern described for other Neotropical species whose duets also serve for territory defense and pair coordination, such as Rufous Hornero (*Furnarius rufus*) (Diniz et al., 2018), Barred Antshrike (*Thamnophilus doliatus*) (Koloff and Mennill, 2013), Rufous-and-white wrens (*Thryothorus rufalbus*) (Topp and Mennill, 2008), and several species of wrens (Keenan et al., 2020). This indicates that duets have a cooperative function in these species, allowing pairs to better defend their resources and reduce extra-pair copulation with conspecifics during the breeding season (Topp and Mennill, 2008).

However, the tendency to produce more duets during the reproductive season does not occur inall species. For example, pairs of Chubb's Cisticola (*Cisticola chubbi*) and Yellow-breasted Boubou (*Laniarius atroflavus*) produce the same number of duets year-round (Szymański et al., 2021; Budka et al., 2023). Furthermore, Rufous-naped Wren (*Campylorhynchus rufinucha*), a Neotropical species, produced a similar number of duets in and out of their breeding season (Bradley and Mennill, 2009). The Venezuelan troupial (*Icterus icterus*) has the opposite pattern, a lower duet rate during the reproductive season than during the non-breeding period (Odom et al., 2016). It is likely than in these species the main function of the duet is to maintain the pair-bond and evaluate the mate´s quality, rather than defense of territory as happens in White-eared Ground-sparrows (Hall and Magrath 2007).

Production of duets among populations

The number of duets produced in the three populations of White-eared Ground-sparrows had a strong correlation with the urban development. Sparrows in the urban population produced a much larger number of duets over the year, than those from the other populations. There are currently not enough studies to demonstrate an association between the urban gradient and the duetting rate of birds, because most studies have focused on measuring the effect of anthropogenic noise on the adaptive response of birds' duets characteristics along the urban gradient (Mendes et al., 2017; Maldonado, 2022), or between male and female (Szymański et al., 2012). Therefore, white-eared ground sparrows have found more duets in urban areas compared to rural areas may improve the acoustic communication with neighbor pairs because a higher duets rate increases the probabilities that information reaches the receivers when anthropogenic noise decrease (Halfwerk and Slabbekoorn, 2018, Méndez et al., 2021). Recently was found that anthropogenic noise affects the synchronization of White-eared Ground-sparrow duets over an urban gradient with less synchronization in more urban sites (Bartolo, 2023), and duets in noisier territories decreased the minimum and maximum frequency contrary to the expected to avoid anthropogenic noise levels (Mendez et al., 2021).

Production of duets in periods during the day

The number of duets recorded was greater during the morning than during the afternoon as we predicted, regardless of the degree of urbanization. Our results are concordant agree with several other duetting species that vocalized more during the morning than in the afternoon such as Sclater's Wren (*Campylorhynchus humilis*) (Quirós and Sosa, 2022), White-browed Sparrow Weavers (*Plocepasser mahali*) (Voigt et al., 2021), and Chirruping Wedgebills (*Psophodes cristatus*) (Austin et al., 2019). Higher production of duets during the mornings may reinforce the territory boundaries, indicating the presence of the territory owners, and may reduce the probability of extra-pair copulations because signal the presence of both pair members (Voigt et al., 2021). During the rest of the day, White-eared Ground-sparrows minimize the vocal activity to contact during foraging, individual approaches and displacement within the territory (Sandoval et al., 2016). Furthermore, the small increase on duetting in the afternoon may be produce to coordinate pair behavior before roost (Logue, 2005; Templeton et al., 2011; Sandoval et al., 2015).

Conclusions

In conclusion, our study showed duets in White-eared Ground-sparrows were more frequent produced during the reproductive season than outside, as a possible defense of territories. Furthermore, birds dueted more frequently on urban sites, to likely have a more effective acoustic communication with neighbor pairs when anthropogenic noise interferes more strongly., White-eared Ground-sparrows also produce more duets during the morning, in order to defend territory, avoid mate usurpation, and reduce the agonistic interactions with neighbors' pairs.

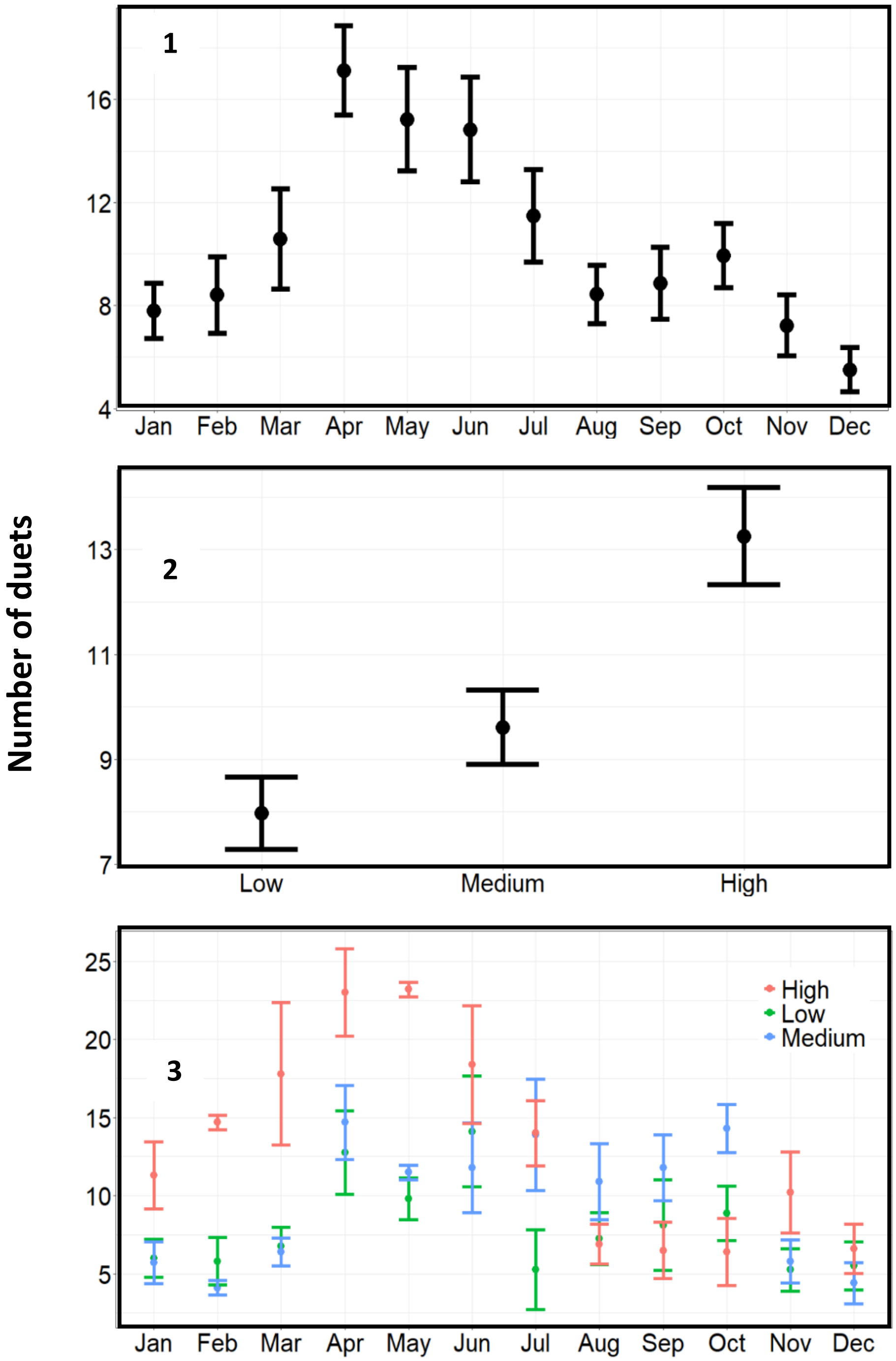

Figure 1. Average number of duets (points) and standard error (lines) of the White-eared Ground-sparrow according to: (1) the months of the year, (2) the three populations of *M. leucotis*, and (3) the interaction among the months and the populations.

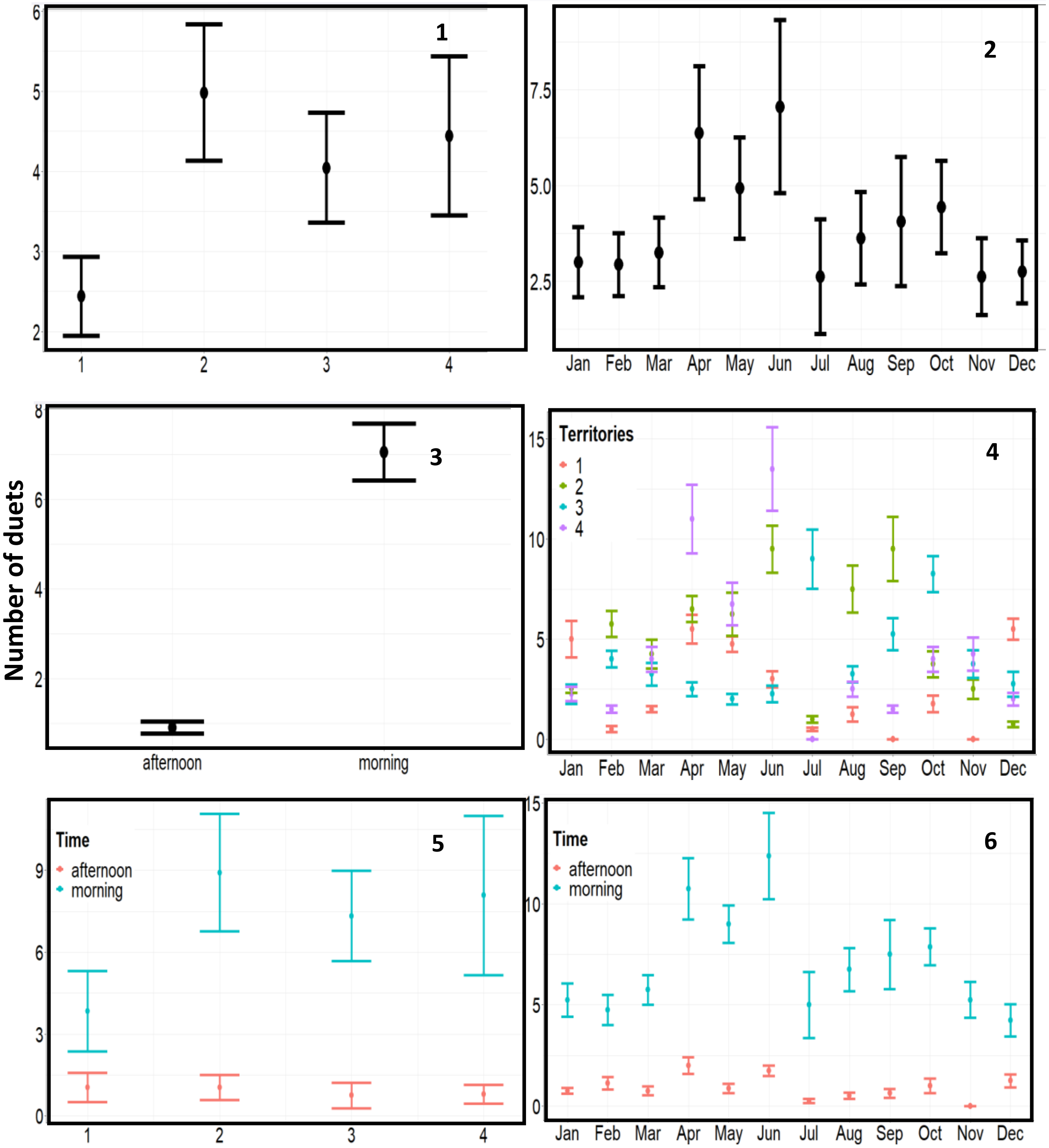

Figure 2. Average number of duets (points) and standard error (lines) of the White-eared Ground-sparrow within low urbanized population according to: (1) territories, (2) thorough the year, (3) day time, (4) interaction between months and territories, (5) interaction between territories and day time and, (6) interaction between months and day time.

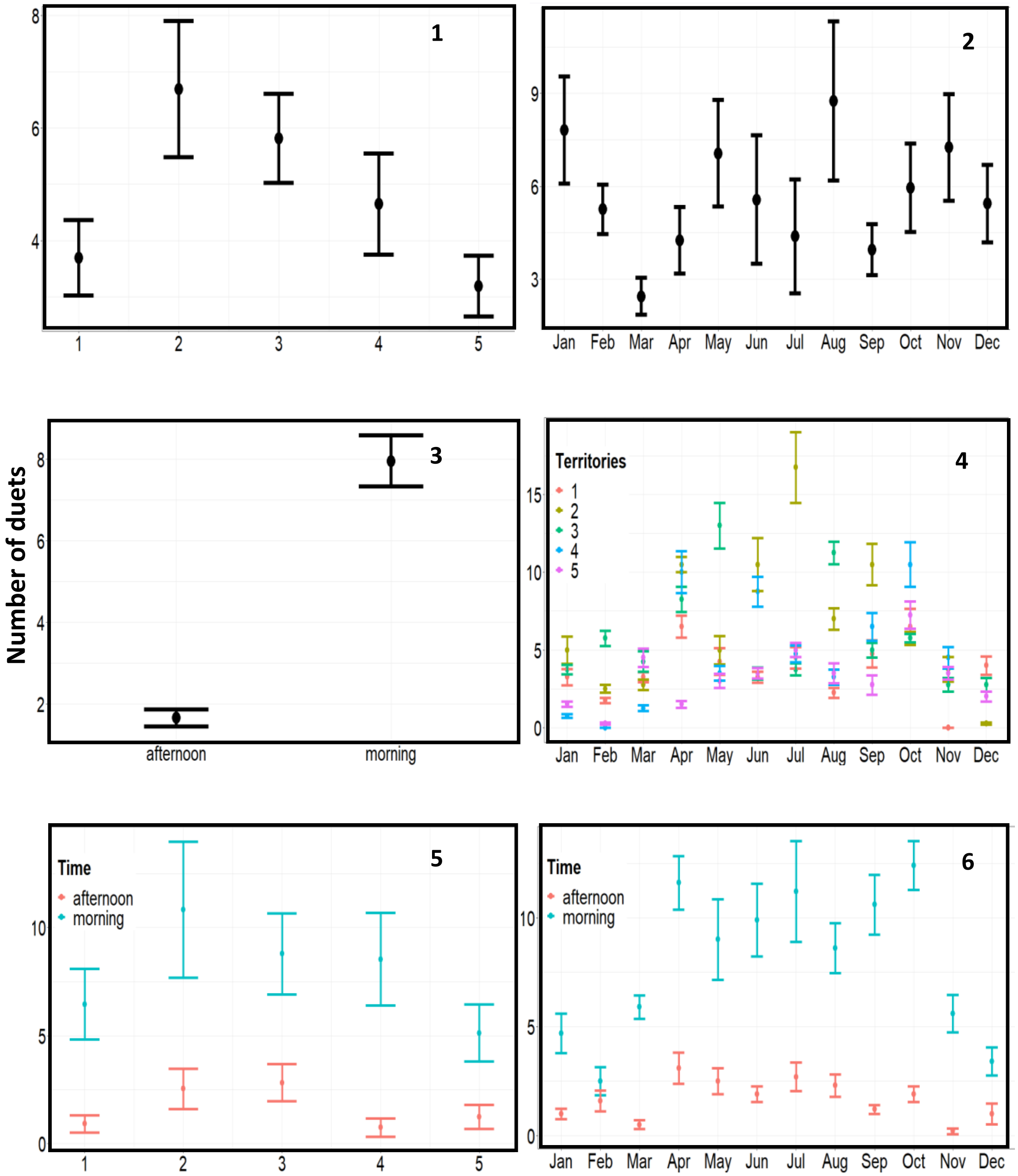

Figure 3. Average number of duets (points) and standard error (lines) of the White-eared Ground-sparrow within medium urbanized population according to: (1) territories, (2) thorough the year, (3) day time, (4) interaction between months and territories, (5) interaction between territories and day time and, (6) interaction between months and day time.

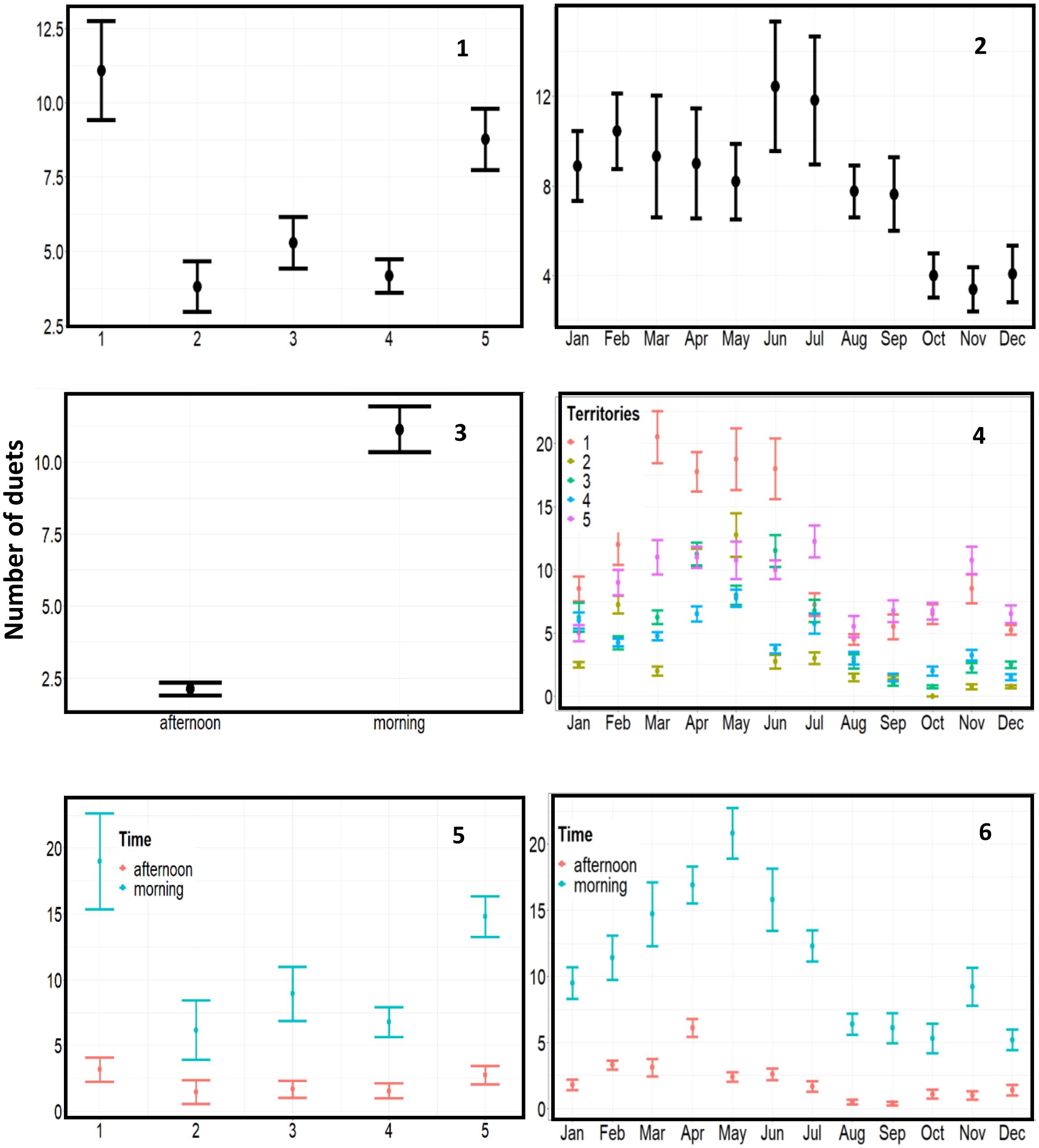

Figure 4. Average number of duets (points) and standard error (lines) of the White-eared Ground-sparrow within high urbanized population according to: (1) territories, (2) thorough the year, (3) day time, (4) interaction between months and territories, (5) interaction between territories and day time and, (6) interaction between months and day time.

Capítulo II

Light and Noise Pollution Affect Diurnal Birds Singing at Night and Dawn over the Year in an Urban Gradient

Abstract

Birds inhabiting urban areas are exposed to different types of pollution, which may affect their behavior and survival. Noise and light frequently induce birds to change behaviors for them to cope or counteract their negative effects. Noise interrupts the communication necessary for survival or reproduction, while artificial light alters circadian rhythms, reducing resting hours, which induces physiological stress. Our objective was to analyze whether light and noise levels affect number of vocalizations during the night emitted of diurnal birds and composition of dawn choruses throughout the year in three sites with different levels of urbanization. Using autonomous recorders, the vocalizations of the birds were recorded during the night and at dawn. Noise values were extracted from the recordings, while artificial light was recorded with a luxmeter during new moon nights. We found that the number of vocalizations of diurnal birds during the night vary with degree of urbanization, the hours of the night and throughout the year, and light pollution which had a strong effect on the number of vocalizations. For dawn choruses, the richness of birds varies depending on the hours and months, but not between levels of urbanization. In addition, both noise and light affected the composition of the community that makes up the choruses, altering not the richness, but the composition of species that vocalize during dawn. Hence, for neotropical urban areas, light and noise pollution strongly alter the vocalization behavior of birds during the night hours and dawn chorus, influencing the time and type of species that vocalize.

Key words: Urban ecology, breeding season, urban birds, phenology, bird songs, pollution

Introduction

Urbanization advance is considered one of the main causes of biological diversity loss globally during the last decades, as urban expansion fragments and replaces natural habitats (Chace and Walsh, 2006; Biamonte et al., 2011; Romero et al. al., 2014). Despite such drastic ambient deterioration, there is still likely to find different bird assemblages compose by species that survive and species that colonize the urbanscape (Guerrero et al., 2012). In urbanized areas, these species face drastic challenges such as habitat deterioration (Bolger, 2001; Smith et al., 2011), disease transmission (Riley et al., 2014; Zarco, 2019), competition with exotic species (Shochat et al., 2010; Hernández-Brito et al., 2014), nest predation (Reynolds et al., 2019; Broughton, 2020; Morozov, 2022), collision with structures (Grajales, 2009; Basilio et al., 2020; Van Doren et al., 2021), communication difficulties (Solís, 2012; Sheldon et al., 2020), and deal with different types of pollutants (Bauerová et al., 2017; Richard et al., 2021).

Birds that live within cities (urban birds), generally use strategies to reduce the negative effect of noise pollution and improve their communication such as: changing territories from stablishing territories in less-noisy sites (Curipaco, 2021), changing the diel time of singing to avoid the noisier time periods (Caycedo, 2010, Godet et al., 2023), increasing the frequency and amplitude of the songs to reach the intend receivers (Morán, 2018; De Magalhães et al., 2018; Sementili and Donatelli, 2021), or even make multimodal signals with visual displays to communicate (Barreira and García, 2019; Akçay and Beecher, 2019). Noise pollution also causes birds to spend more energy singing, mainly during the reproductive season, because singing individuals need to produce songs with longer duration and higher intensity to communicate in noisier habitats (Galeano and Stiles, 2006; Sandoval, 2011; León, 2019). This can induce a physiological stress that results in an increase on corticosterone levels which alters the normal singing activity (Slabbekoorn and Ripmeester, 2008), or in a poor diet due to less time foraging because need to vocalize more to increase the likelihood of reaching potential mate receivers (Reyes and Riveros, 2019).

There is some evidence that both light and noise pollution effect at the bird community level. Noise pollution affects the phenology of dawn choruses, since it induces birds to sing earlier to avoid anthropogenic noise (Slabbekoorn and Den Boer-Visser, 2006; Arroyo et al., 2013; Gómez & Fors, 2019). For example, Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*), change the timing of the dawn chorus in urban areas of Sevilla (Arroyo et al., 2013). Similarly, urban birds of Saint-Nazaire, France, start dawn choruses earlier when compared with less-noised sites (Godet et al., 2023). Another factor that presumably alter the phenology of birdsong is light pollution, which has increased as a result of urban expansion, generating a loss of natural nocturnal lightscapes (Holmes et al., 2017). This leads to behavioral alterations in their circadian rhythms, such as increases in foraging or vigilance time, but especially variation in diel singing (Da Silva et al., 2015; Dominoni, 2015; Carrasco and Flores, 2021). For example, in Seville, Spain, chickadees and tits (Paridae), blackbirds (Turdidae), and robins (Muscicapidae) start dawn choruses up to 60 min earlier in urban sites with higher artificial lighting (Kempenaers et al., 2010).

Despite the fact that the effects of noise and light pollution have been extensively studied in birds, most research has been carried out in North America and Europe cities, while in the Neotropics, the information is mainly restricted to Mexico, Argentina, and Brazil (Shannon et al, 2016), and only in a reduced number of species, such as Rufous-collared Sparrow (*Zonotrichia capensis*) (Dorado et al., 2016), House Sparrow (*Passer domesticus*) (Slabbekoorn, 2013) or House Wren (*Troglodytes aedon*) (Sementili and Donatelli, 2021). Thus, we consider reasonable to propose as the main goal of this study to analyze how noise and light pollution influence the production of vocalizations at night by diurnal urban bird species and during dawn choruses throughout the year in three places with different degree of urban development. These two factors, noise and light pollution, are unlikely mutually exclusive and may vary in concordance.

We have a two-fold objective for this study. The first objective was to analyze how light pollution, noise levels, and period of the year (months) affect the production of vocalizations at night by diurnal birds throughout the year. For this objective, we predict a higher number of vocalizations at night produced by diurnal bird in sites with a higher amount of light pollution, because light pollution changes circadian cycles and reduces resting hours for daytime birds (Dominoni and Partecke, 2015; Raap et al., 2015). We also expect a greater number of vocalizations at night for diurnal birds during the reproductive months (regardless of the degree of light pollution), since this change may benefit territory defense and mate attraction (Wilson and Bart, 1985; Catchpole and Slater, 2008; Davies and Sewall, 2016). We also expected a greater number of vocalizations at night produced by diurnal bird in sites with higher noise levels (high urbanized sites), because nights are less nosier than day, thus singing at night may benefit territory defense and mate attraction (Wilson and Bart, 1985; Catchpole and Slater, 2008; Davies and Sewall, 2016). Our second objective was to analyze how the beginning of the dawn choruses is influenced by light pollution, noise levels, and period of the year. For this objective, we predict that bird dawn choruses start earlier in the most noise-polluted sites to avoid the anthropogenic noise that masks their communication (Brumm and Slabbekoorn, 2005; Dorado et al., 2016). Besides, we predict that dawn choruses will begin earlier during the months of breeding season, as males sing more frequently to attract females and defend their territories (Catchpole and Slater, 2008; Cain and Langmore, 2015). We also predict that dawn choruses start earlier in more polluted sites because this factor likely affects the circadian rhythms in birds based in the photoperiods (Grunst et al., 2023).

Materials and Methods

Study Area

We conducted this study in three sites in the most human populate area of Costa Rica that varied in urban development level: (1) Highly urbanized site: Campus of the University of Costa Rica, San José province (09°56’N, 84°02’W, 1200 m). This site is dominated by human made constructions (e.g., buildings and streets), with some green areas like groves, gardens, and a small patch of a secondary forest, less than one hectare. In this zone the levels of light and noise pollution are high (Méndez et al., 2021). (2) Medium urbanized site: Lankester Botanical Garden, Cartago province (9°50’N, 83°53’W, 1370 m). This site has some buildings and streets, surrounded by gardens and a dense secondary forest, where the light and noise pollution are lesser. (3) Low urbanized site: Getsemani, province of Heredia (10°02’ N, 84°06’W, 1350 m). The site is dominated by dense secondary forest that is mixture with abandoned shade-grown coffee plantations, with a very low the pollution impact.

Recordings of vocalizations

We used five autonomous recorders (2 SM2, 2 SM3, and 1 Swift) on the High and Medium urbanized sites and four autonomous recorders (2 SM2 and 2 SM3) on the Low urbanized site. We placed the autonomous recorder between 2-3 m above the ground, separated for a minimum distance of 100 m, and set to a sampling rate of 44.1 kHz, 24-bit precision, and WAVE file format. Data was collected from 18:00-6:00 h a day for two consecutive days for each month, from January to December 2021. The recorders were placed haphazardly, some near to artificial light sources, close to the road, in forest edges or deeper in the forest.

We counted the number of vocalizations produced by diurnal birds during the night. To do this, we analyzed the recordings during two consecutive astronomic nights from 18:00-4:00 h per month. We annotated the number of vocalizations (i.e., calls and songs) emitted per hour for each species. Then, to determine the changes in the start time of the dawn choruses, we analyzed two consecutive mornings from 4:00-6:00 h per month, recording all the species that participated in the chorus using 20 min periods.

Noise and light pollution measurements

We measured noise pollution at night using the method published by Sánchez et al. (2022). For this method, we manually extracted the noise values at the beginning and end for each hour of recording analyzed, measuring the energy in dB during 1 s sections in the spectrogram window, where there is no bird vocalization. In each 1 s section, we obtained the average amplitude values in six frequency octave bands from 500-16000 Hz, using only the second third of each octave band to define the limits of the low and high frequencies of each section. Noise measurements were obtained using Raven Pro 1.6 software (Cornell Lab of Ornithology).

To obtain data on light pollution data, in each of the sites where the autonomous recorder was located, we took nine sampling points at 1.5 m above the ground, one at the point (central position) where the autonomous recorder was located, and the others eight spaced at 5 m and 15 m from the center and at 90 degrees from each other. At each point, we recorded the maximum and minimum light intensity (in lux) during new moon nights to avoid the effect of moonlight intensity on the amount of light recorded, using an EXTECH Instruments LightMeter LT 300 digital lux meter. From these data, we estimated the average of the minimum and maximum light intensity at each point for each autonomous recording sites.

Statistical Analysis

We first compared the light levels between study sites, using a Linear Mixed-effect Model with Gamma distribution and log link function, with the lme4 library (Bates et al., 2023). We included in the model the light levels as the response variable, studied sites as the fixed factor (3 levels), and the territories where the recorders were placed as a random factor. We also conducted a Generalized Linear Mixed-effects Model with a Poisson distribution of errors and zero inflated (library glmmTMB; Brooks et al., 2023) to evaluate which combination of factors best explain the variation in the number of vocalizations across sites. We included in the model the hours (10) at which birds vocalized, months of the year (12), populations sampled (3), noise level, the second order interactions between variables as fixed factors, and the territories where the recorders were placed as a random factor. Finally, an ANOVA was applied to calculate the significance of the linear model.

For the analysis of the choruses, we performed another Generalized Linear Mixed-effects Model with Poisson distribution of errors to analyze how species richness varies according to the time period, months, noise levels, studied site, and second order interactions, using the library lme (Bates et al., 2023). We considered the territories where the recorders were placed as a random factor. This analysis was conducted with the library lme4 of R (Bates et al., 2023). We used the R statistical language for these analyses (R Development Core Team, 2021). In the same way, an ANOVA was applied to calculate the significance of the linear model.

We also performed two Non-metric Multidimensional Scaling analysis (NMDS) to compare the composition of the community that participate on the dawn choruses across sites, based on the presence or absence of species. We used these two NMDS to compare species composition among the three sites, from matrices of which columns consisted of species and the rows of time periods or months (rows). In both NMDS, we included light pollution and noise levels to estimate the correlation with the NMDS scores calculated. NMDS significance was estimated with PERMANOVA analysis using Morisita as similarity distance. These analyses were conducted with PAST 4.14 (Warton and Wright, 2012).

Results

Light levels

Light level varied across populations according to the urban development. We found lower light levels at low urbanized site ($\beta = -2.19 \pm 0.15$ SE, $p < 0.001$; 0.11 ± 0.02 lux), followed by medium urbanized site ($\beta = 3.84 \pm 0.20$ SE, $p < 0.001$; 5.20 ± 2.61 lux), and the higher value was on the highly urbanized site ($\beta = 4.10 \pm 0.20$ SE, $p < 0.001$; 6.75 ± 3.01 lux).

Nocturnal Vocalizations

We found 18 species of diurnal birds vocalizing at night (Table 1). The number of vocalizations of diurnal birds recorded at night were variable over the year ($F_{(11,1510,)}$ = 5.50, p <0.001, Fig.1.1) with a greater quantity between March and July, reaching a peak on April with more than 2000 vocalizations, while in the other months the total vocalizations were less than 50. We also found differences between the number of vocalizations per hour, with two peaks, one at dusk with 557 vocalizations, and another before dawn with 3098 vocalizations ($F_{(9,1510)}$=9.39, p <0.001; Fig. 1.2). A significant difference was also found among populations ($F_{(2,1510)}$ = 7.20, p <0.001, Fig.1.3). Birds in the highly urbanized site vocalized more at night, with a total of 3186, followed by 712 vocalizations from medium urbanized site and 170 recorded in the low urbanized site. However, noise levels did not exert a significant effect in the number of vocalizations recorded ($F_{(1,1510)}$ = 2.71, p = 0.10).

Interactions

The number of nocturnal vocalizations varied between populations with respect to the hours of the night ($F_{(18,1510)}$ = 2.20, p = 0.003; Fig. 2.1), with a peak of vocalizations in the high and medium urbanized sites at 3:00 h, a second peak at 18:00 h, and the rest of the night vocalizations were lower and similar between hours. Conversely, the vocalizations on the low urbanized site were similar between hours (Fig. 2.1). In addition, we found differences in the amount of nocturnal vocalizations with respect to populations throughout the year ($F_{(22,1510)}$ = 1.79, p = 0.01; Fig. 2.2). Birds in the highly urbanized population vocalized more throughout the year, but number of vocalizations increased on March, April, and May. Similarly, there were differences between the hours throughout the year ($F_{(99,1510)}$ = 2.61, p <0.001; Fig. 2.3). The greatest number of vocalizations occurred at 18:00 h and 3:00 h, with a greater number between March and May. Noise did not differ across populations ($F_{(2,1510)}$ = 0.31, p = 0.74), neither between hours ($F_{(9,1510)}$ = 1.46, p=0.16), nor throughout the year ($F_{(11,1510)}$ = 0.56, p = 0.86).

Dawn Choruses Richness

The medium urbanized site showed the highest species richness, with a total of 57, followed by low urbanized site with 52 and high urbanized site with 41 (Table 2). Species richness on dawn choruses varied thorough the year ($F_{(11,995)} = 10.02$, $p < 0.001$, Fig. 3.1), with the higher richness between March and July, and the lowest between August and November. We found that species richness in dawn choruses increased over time periods ($F_{(5,1503)} = 254.29$, $p < 0.001$, Fig 3.2), which the lowest species richness before 5:00 h, and the peak at 5:20 h. However, the average species richness that participated on dawn choruses among populations was similar ($F_{(2,1004)} = 1.21$, $p = 0.30$, Fig. 3.3). Noise neither correlated with species richness($F_{(1,1007)} = 0.02$, $p = 0.87$); species richness that participated on the dawn choruses were similar among different noise levels.

Interactions

We found that the species richness of dawn chorus varied among time periods between populations ($F_{(10,988)} = 4.34$, $p < 0.001$, Fig. 4.1). In low and high urbanized sites, dawn chorus species richness was lowest before 4:40 h and had a peak at 5:20 h. At the medium urbanized site species richness was lowest before 5:00 h, then increased and remained nearly constant until 6:00 h. Species richness also varied between time periods in different months ($F_{(55,907)} = 8.57$, $p < 0.001$, Fig. 4.2). From January to July the choruses started at 4:00 h, while from August to November the choruses started until 4:40 h. Furthermore, the dawn choruses were different between the populations throughout the year ($F_{(22,984)} = 9,97$, $p < 0.001$, Fig. 4.3). For the low urbanized site, the peak of species richness that participated on dawn choruses occurred between March and June. For the medium urbanized site, the species richness peak occurred between March and April. While, in the highly urbanized site, the species richness peak occurred between March and July. In addition, we found differences of noise levels throughout the year ($F_{(11,984)} = 4.73$, $p < 0.001$, Fig. 5). From February to May, the number of species recorded in the choruses increased slightly as noise levels also increased. However, for the months of January and December the opposite occurred, the number of species decreased slightly as the noise increases, while for the rest of the year, the richness remained almost constant.

Dawn Choruses Composition

We found that the bird community composition that participated on dawn choruses per month was different between the three sites ($F_{(11,3)} = 5.22$, $R^2 = 0.49$, stress=0.19, $p < 0.001$, Fig 6). The greatest difference occurs between high and low urbanized sites which did not overlap on the bird community composition per month. Meanwhile, the medium urbanized site overlapped with the low urbanized site. Moreover, the community composition per month was apparently influenced by the levels of light and noise, because the high urbanized site had the largest difference, and also had the highest levels of both pollutants (Fig 6). Finally, when we analyzed the community composition between sites, but splitting the data by morning time periods, we still found differences between sites ($F_{(1,3)} = 2.82$, $R^2 = 0.65$, stress=0.09, $p < 0.001$, Fig. 6). In this case, the three sties overlapped in the community composition when had lower noise and light levels.

Discussion

Nocturnal vocalizations

The number of nocturnal vocalizations varied widely over the year, but with a maximum during March-July, which coincide with the reproductive season for the majority of species in the three sites (Stiles and Skutch, 1989; Sandoval, 2011, 2019; Biamonte et al; 2012). The species with more vocalizations registered during the night were Clay-colored thrush (*Turdus grayi*), White-eared ground sparrow (*Melozone leucotis*), Cabanis wren (*Troglodytes aedon*) same as Brow jay (*Psilorhinus morio*). Our results on vocalization activity at night are similar to those reported for diurnal Afrotropical birds, in that both bird assemblages vocalized more at night during the reproductive season months (Budka et al., 2021). Additionally, we found that vocal activity at night decreased over the months, as the reproductive season progresses, a pattern also found in species such as the Field Sparrow (*Spizella pusilla*) at Illinois, USA (Celis et al., 2016) and the Willie Wagtail (*Rhipidura leucophrys*) at Petite Camargue Alsacienne, France (Dickerson et al., 2020). Some diurnal birds vocalizing more at night during breeding seasons is congruent with the suggestion that vocalizations can be more effective for some species at night than during the day, due to the reduction of acoustic competition caused by anthropogenic noise and heterospecific songs interference, which can affect the territorial defense and the attraction of mates (Slabbekoorn and Boer-Visser 2006; Wiley 2006; La, 2012).

The number of nocturnal vocalizations was different over the hours, with peaks at dawn and dusk. This pattern is influenced by the retinal sensitivity of birds that is able to detect dim light at dusk and dawn, allowing birds maintaining the activity longer during the dusk and early at dawn (McNeil et al. 2005; La, 2012). Similar findings have been reported for the common Nightingale (*Luscinia megarhynchos*) (Thomas, 2002), redstarts and cuckoos (Cramp, 1998). However, there is not conclusive evidence why birds do not vocalize during the remaining hours of the night, although it has been suggested that predation risk may increase as night progress because nocturnal predators as owls and mammals may use vocalizations to localize the individuals in the roosting places (Schmidt and Belinsky, 2013). Birds produced more nocturnal vocalizations in high urbanize populations, probably as a strategy to reduce the acoustic interference of greater noise levels that occur during the day in more urban areas (Fuller et al., 2007). Another possible explanation is that light pollution and more open areas produce brighter nights and this may induce diurnal birds to vocalize more frequent at night (Raap et al., 2015; Holmes et al., 2017; Dickerson et al., 2022). For example, in more open areas the level of natural light at night is higher and this induce birds to vocalize more frequently in open than in closed spaces (Kulaga and Budka, 2020). These factors could explain the higher number of vocalizations we found in more urbanize sites.

Dawn choruses richness

The species composition of bird choruses was similar among the three populations, but richness was greater at the medium urbanized site and the lower species richness at the high urbanized site. Sites with intermedia disturbs is expected to have higher species richness, because allow a greater overlap between species of more disturbed sites (i.e., urban areas) with species of more natural sites (Pal et al., 2019; Lee et al., 2021). Whereas, more disturbed sites, include less species because habitat is more homogeneous and differ extensively from the natural habitats that occupied the same space prior to urbanization (Silva et al., 2015; Mbiba et al., 2021), thus reducing the number of species that may occur. Furthermore, inside more disturbed sites noise and artificial light levels were higher, reducing the number of bird species that participate in the choruses, because only a few the species tolerate high levels of light and acoustic pollution (Da Silva et al., 2015; Alquezar et al., 2015).

In our study, the number of species in dawn choruses increased as the morning progressed, a pattern also reported in dawn choruses in European birds, which started at 5:00 h and the number of species increased significantly until 6:00 h (Godet et al., 2023). On the contrary, studies in Canada and Colombia reported an earlier start of dawn choruses in more urbanized sites in Canada and Colombia (Marini et al., 2017; Sánchez et al., 2020), more species were recorded earlier at the low urbanized site. These studies indicate that anthropogenic noise is a factor that induce birds to sing earlier in urban areas, to avoid acoustic masking, mainly produced by car traffic (Bayne et al., 2008; Arroyo et al., 2013; Gil et al., 2015; Godet et al., 2023). Other authors also argue that artificial light is another factor that influences the start of dawn choruses, causing birds to sing earlier and longer in places with greater light pollution (Miller, 2006; Kempenaers et al., 2010; Carrasco and Flores, 2021), because likely birds perceive an earlier day start (Gil et al., 2015). However, these factors do not completely explain the differences on the beginning of dawn choruses in the study sites. A possible explanation for an early dawn choruses start in the low urbanized site in our study is the greater number of species that occur in the site (Sandoval et al. 2019) because having a greater number of neighbors encourages birds to start the dawn choruses at earlier hours for certain species (Stuart et al. 2019). For example, in the population of Heredia, the Brown Jay (*Psilorhinus morio*) that is very common (Sandoval 2019) began to sing 20 minutes before than in other studied sites. This happens because the song of some species could also be a source of masking noise for other species, inducing to sing earlier as a strategy to reduce the effect of acoustic masking by other species vocalizations (Marler and Slabberkoorn, 2004; Planque and Slabbekoorn 2008).

The dawn choruses began at different time over the year. From January to May, an increased number of species began to vocalize earlier, but from June to December the choruses began up to 40 minutes later. Similar results were found for the Rufous-collared Sparrows (*Zonotrichia capensis*) dawn choruses, whose dawn chorus started earlier between May and June, but much later by the end of the year (Dorado et al., 2020). The changes in the dawn choruses start were result of the day length seasonal change over the year, in the Northern Hemisphere; light hours increase gradually from March to June, decreasing after until December (Staicer et al., 1996; Gil and Llusia, 2020). The breeding season also influenced the start of dawn choruses. In the three study areas the breeding season starts on late March early April, and finish on late July early August (Stiles and Skutch, 1989; Sandoval, 2011, 2019; Biamonte et al; 2012; Da Silva et al., 2015). Consequently, since the functions of the choruses are associated with the defense of territory and mate attraction (Catchpole, 2008), singing earlier before and during the reproductive season may reduce the interference with other species or individuals (Pohl et al., 2009), thus increasing reproductive success (Francis et al., 2009).

Dawn choruses composition

The chorus species composition varied among the three sites according to the degree of urbanization and hour when birds vocalized, with the chorus species composition of the highly urbanized site been more different than the other two sites. In our case light and noise have a synergetic (non-exclusive) effect that separated the community's composition. Contrary to other studies, which reported that one of both pollutants had a larger effect on the choruses start and species composition. For example, in Colombia Rufous-collared Sparrows dawn choruses were more affected by noise than for light pollution (Dorado et al., 2016). But, in Colombia and EEUU light levels had a greater effect than noise on the start of dawn choruses (Lee et al., 2017; Marín-Gómez, 2022).

Conclusions

The number of vocalizations of diurnal birds during the night varies with the urban gradient, the hours of the night, and throughout the year; and light pollution had a major effect on this difference. For dawn choruses, the richness of birds varies among hours and months, but not among populations. However, both noise and light affected the composition of the bird community of choruses, influencing not the richness, but the composition of species that vocalize during dawn. We conclude that for neotropical urban areas, light and noise pollution induce changes (possibly negative) on the behavior of birds during the hours of night and dawn. Therefore, a reduction of both pollutants is required to contribute to biodiversity conservation in urbanscapes. In the case of noise pollution, a possible solution is implementing regulations to reduce noise produced by horns, music, vehicles, and loudspeakers; while for light pollution some simple regulations, e.g., use light sources in essential places, directing the light of public lighting down, or use lights through sensors, can reduce its negative effect.

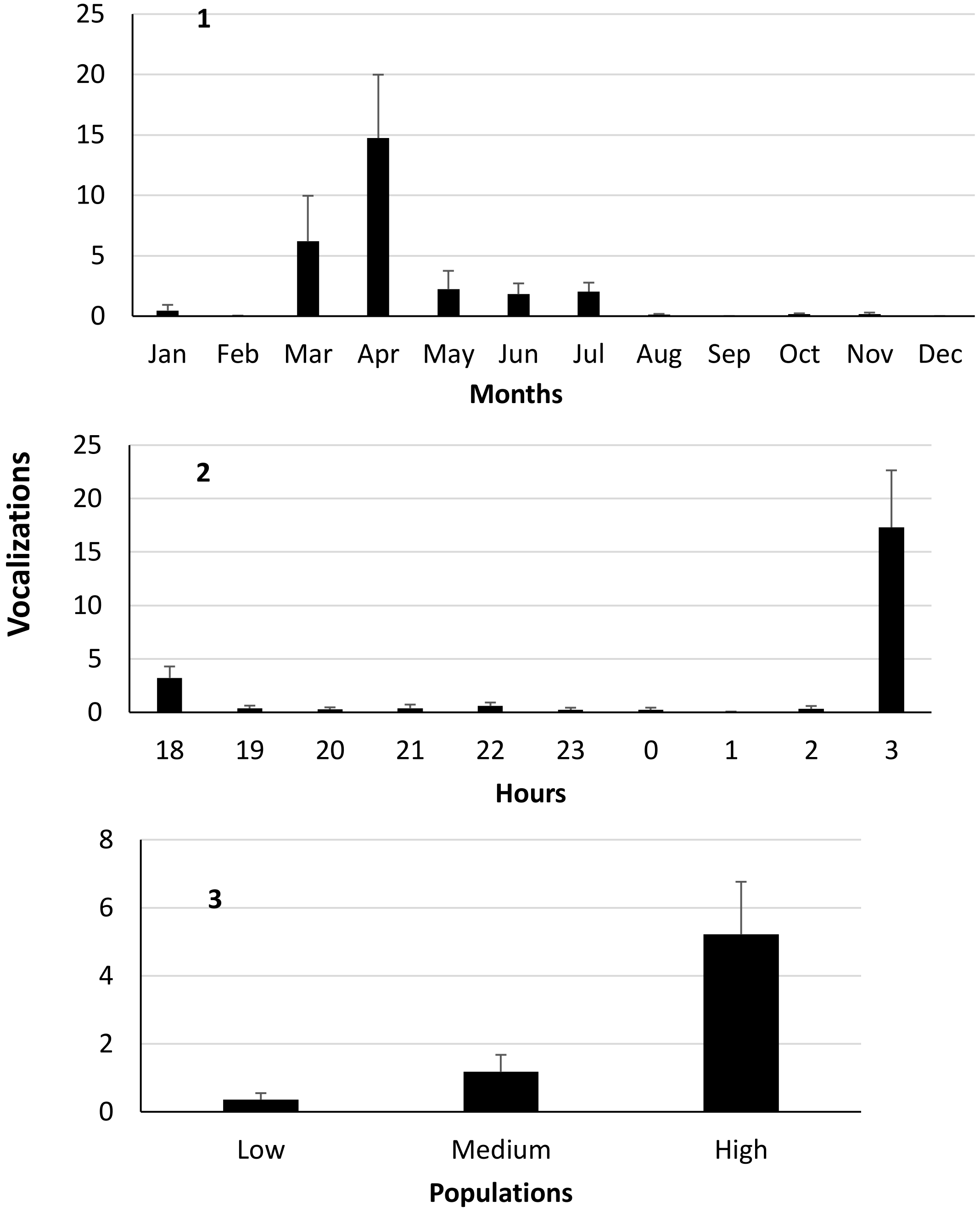

Figure 5. Mean number of nocturnal vocalizations with standard error (bars) produced by diurnal birds according to: (1) moths of the year, (2) between the night hours and (3) the urbanized sites

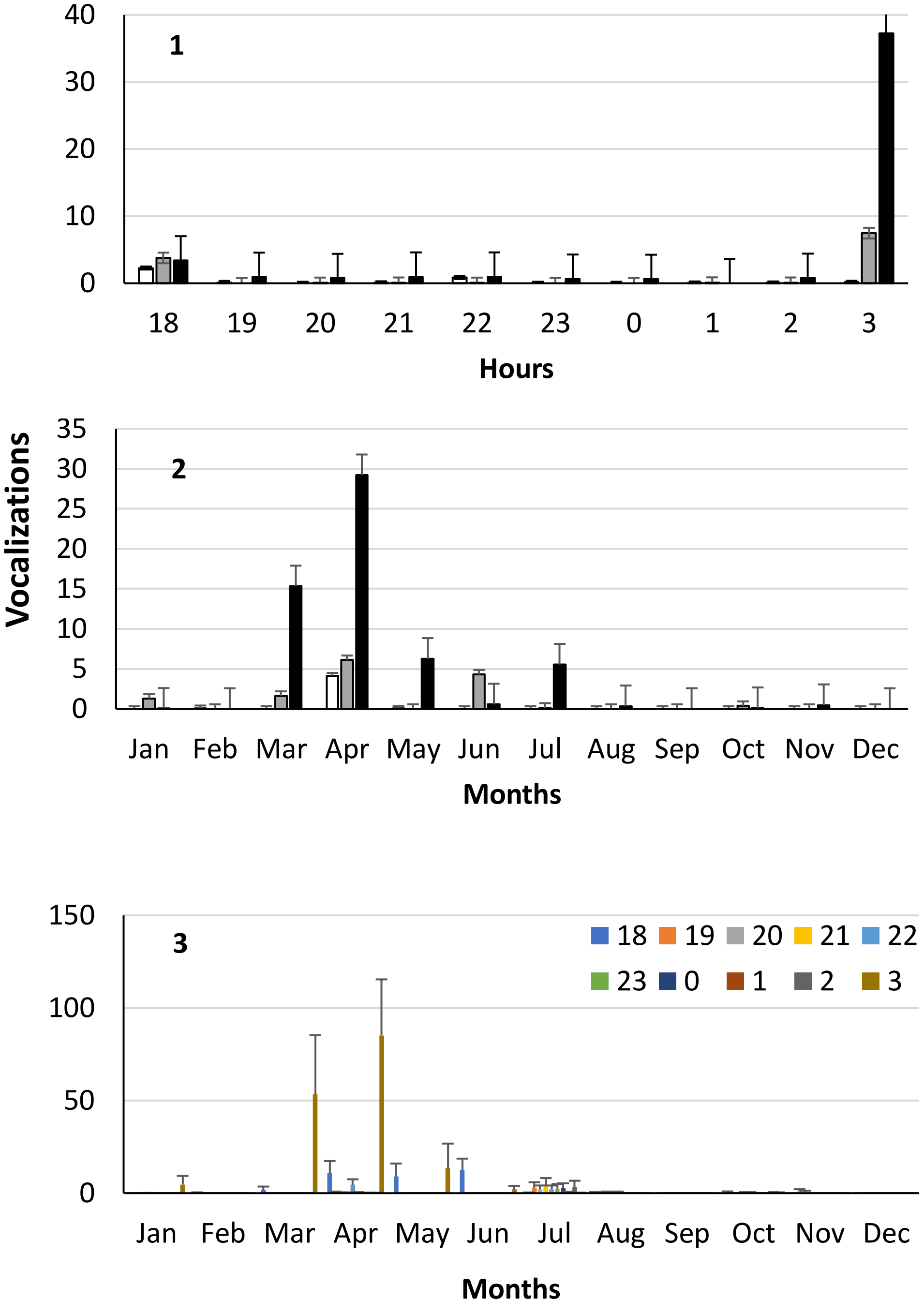

Figure 6. Interaction of nocturnal vocalizations produced by diurnal birds according to: (1) between populations and night hours, (2) months and populations, and (3) night hours and months

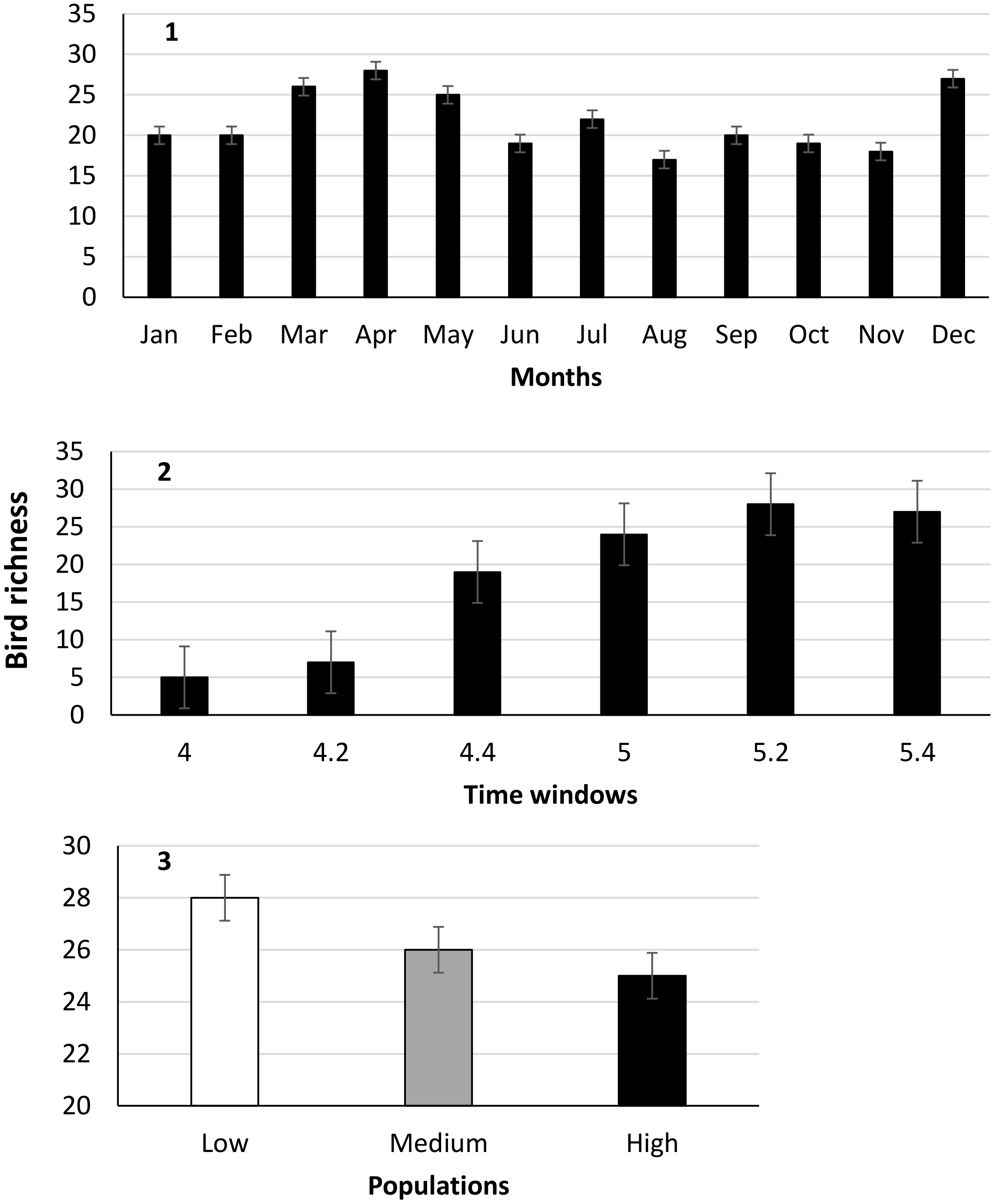

Figure 7. Mean bird richness registered during the morning choruses according to: (1) month, (2) the time windows from 4h to 6h, and (3) populations with different urbanized levels

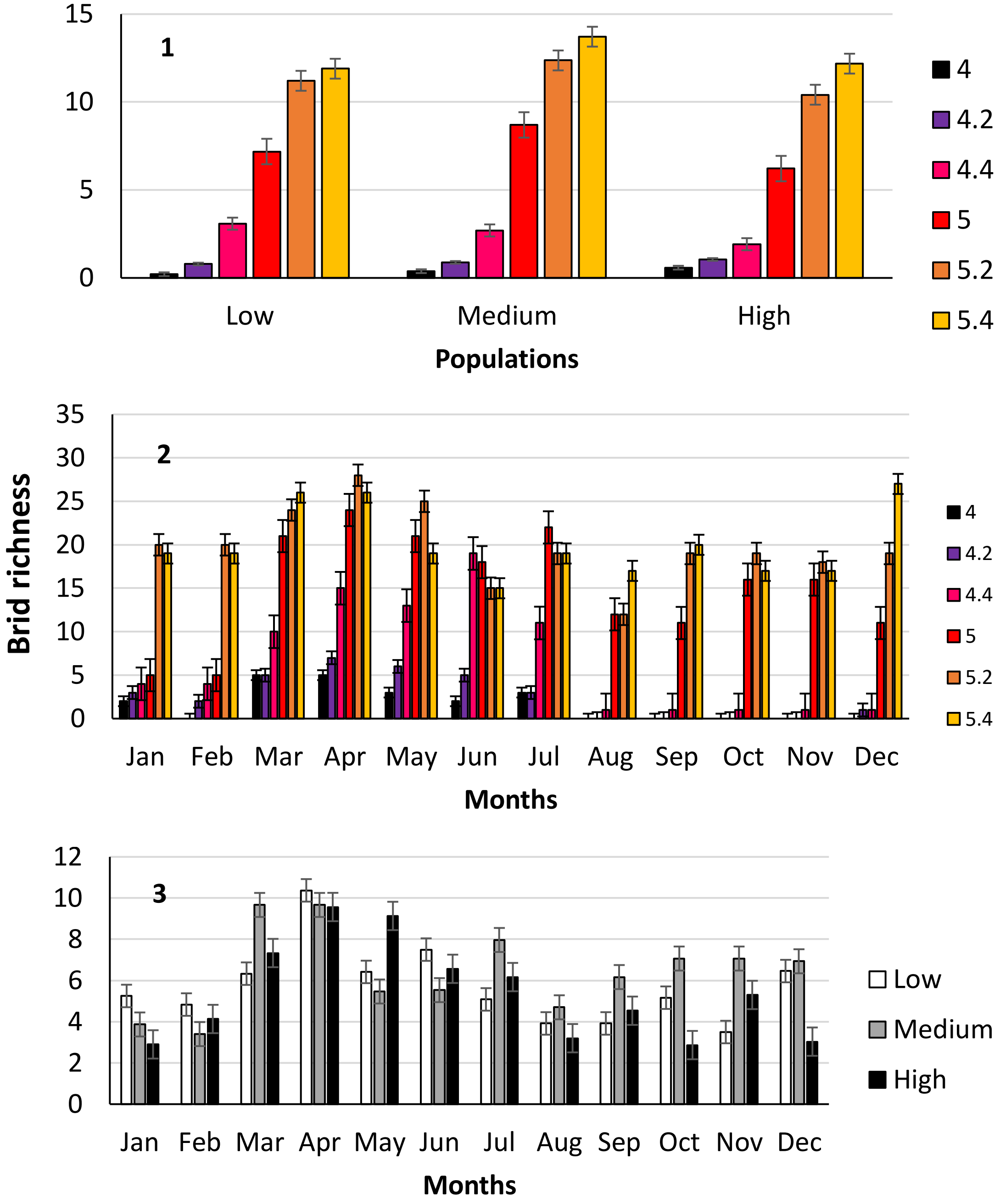

Figure 8. Interaction of bird richness in dawn choruses with standard error (bars) according to: (1) populations and time windows, (2) time windows and months, and (3) the populations and months.

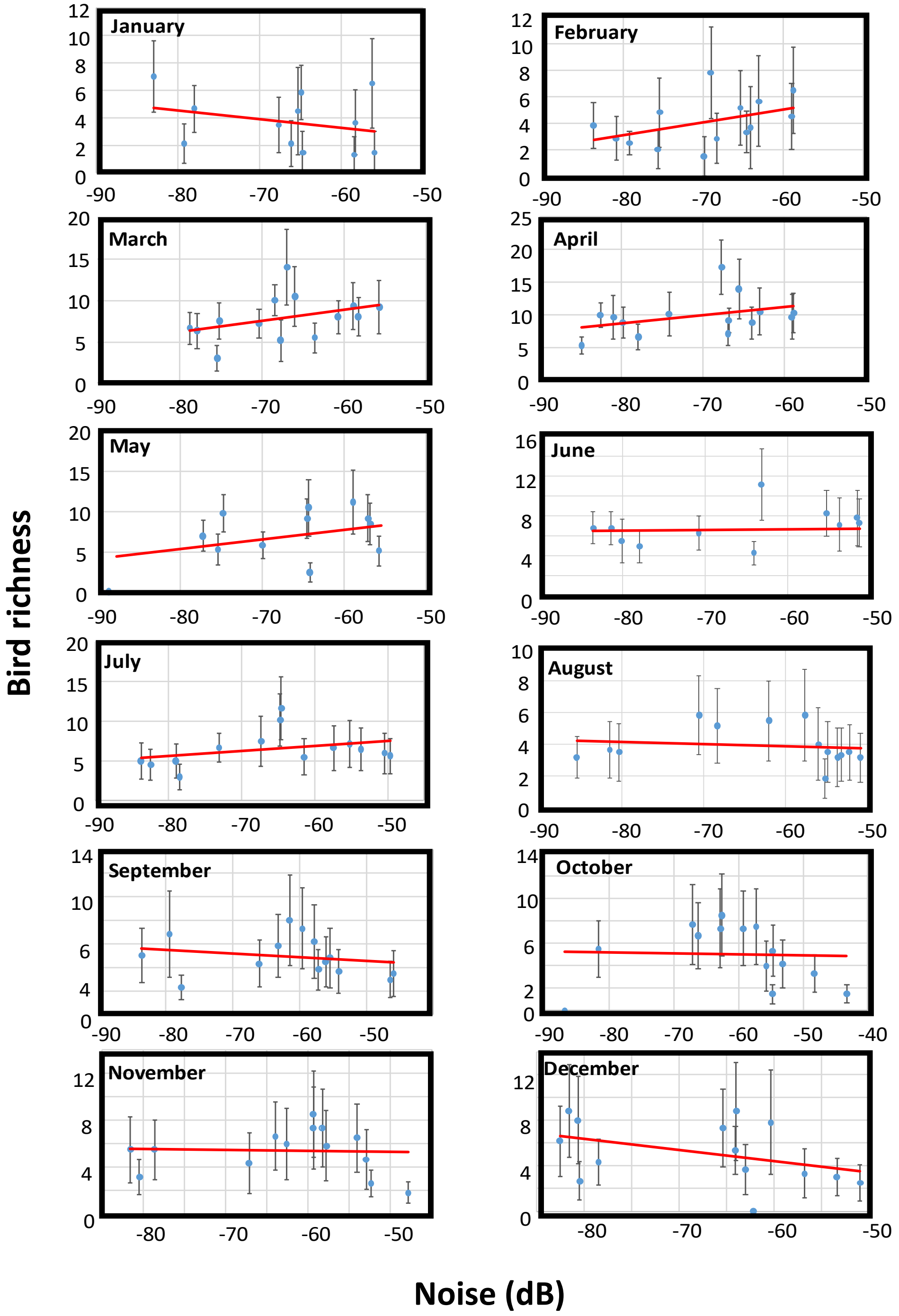

Figure 9. Relationship between bird richness of dawn choruses and noise levels registered throughout the year

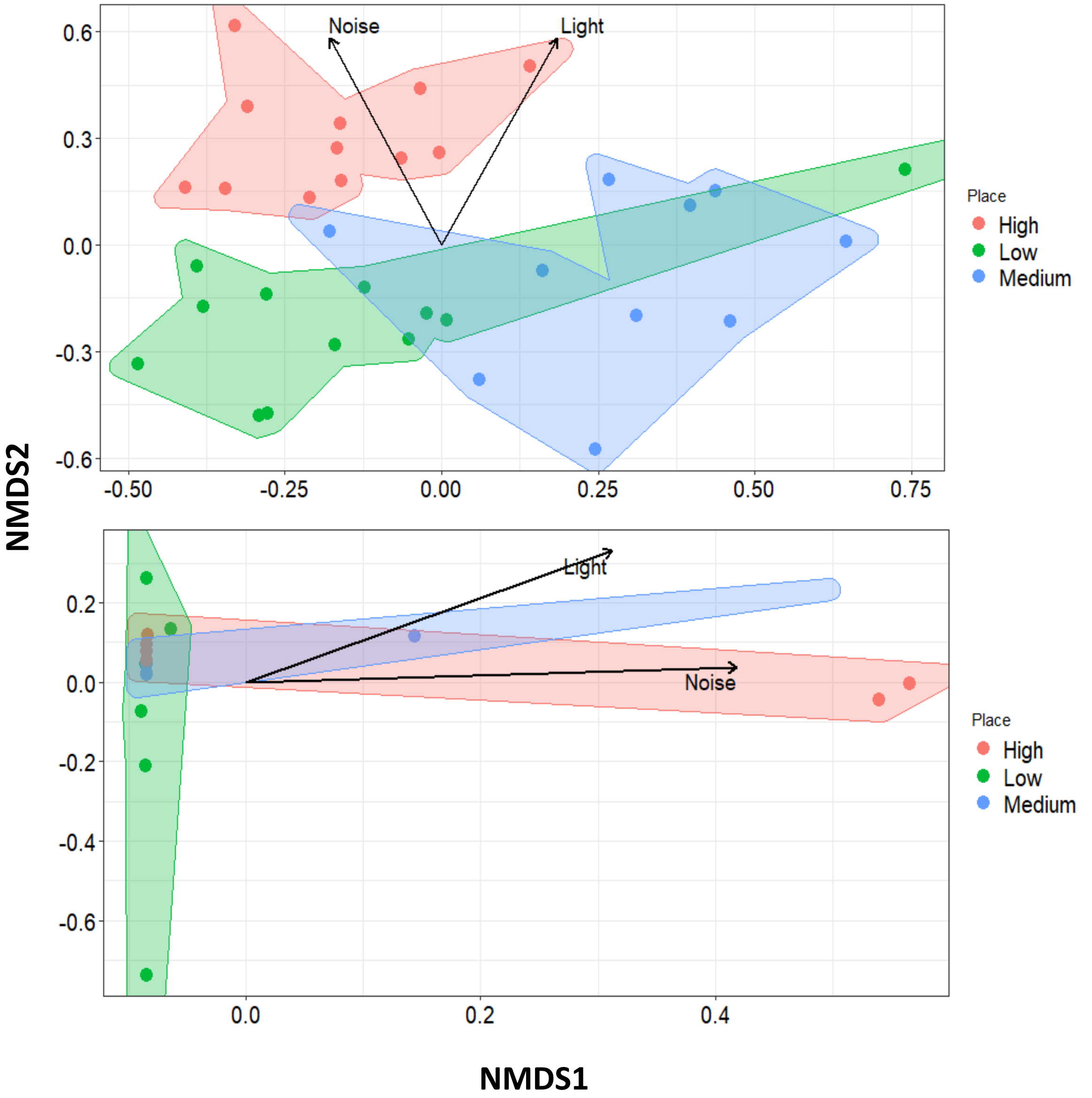

Figure 10. Dawn choruses composition in minimum convex polygons with the influence of light and noise pollution (arrows) according to: (upper panel) throughout the year between populations and (lower panel) the time windows between populations

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Anexos

Table 1. Diurnal bird species recorded during the night in sites with different urbanized levels

Order	Family	Scientific name	Low	Medium	High
Columbiformes	Columbidae	*Columba livia*			X
Gruiformes	Rallidae	*Aramides albiventris*			X
Passeriformes	Icteridae	*Psarocolius Montezuma*			X
Passeriformes	Icteridae	*Psilorhinus morio*			X
Passeriformes	Icteridae	*Quiscalus mexicanus*		X	
Passeriformes	Passerellidae	*Atlapetes albinucha*	X	X	X
Passeriformes	Passerellidae	*Melozone leucotis*	X	X	X
Passeriformes	Passerellidae	*Zonotrichia capensis*			X
Passeriformes	Thraupidae	*Habia rubica*	X		
Passeriformes	Thraupidae	*Thraupis episcopus*			X
Passeriformes	Troglodytidae	*Troglodytes aedon*		X	X
Passeriformes	Turdidae	*Catharus aurantiirostris*	X	X	
Passeriformes	Turdidae	*Turdus grayi*	X	X	X
Passeriformes	Tyrannidae	*Pitangus sulphuratus*			X

Passeriformes	Tyrannidae	*Tyrannus melancholicus*		X
Pelecaniformes	Ardeidae	*Cochlearius cochlearius*		X
Psittaciformes	Psittacidae	*Psittacara finschii*		X
Trochiliformes	Trochilidae	*Amazilia tzacalt*	X	

Table 2. Bird species recorded in dawn choruses in sites with different urbanized levels

Order	Family	Scientific name	Low	Medium	High
Accipitriformes	Accipitridae	*Buteo plagiatus*	X	X	X
Anatiformes	Anatidae	*Dendrocygna autumnalis*		X	
Caprimulgiformes	Caprimulgidae	*Nyctidromus albicollis*	X	X	
Columbiformes	Columbidae	*Leptotila verreauxi*	X	X	X
Columbiformes	Columbidae	*Patagioenas flavirostris*	X	X	X
Columbiformes	Columbidae	*Zenaida asiatica*			X
Coraciiformes	Coraciidae	*Megaceryle torquate*	X	X	X
Coraciiformes	Momotidae	*Momotus lessonii*	X	X	X
Cuculiformes	Cuculidae	*Piaya cayana*	X	X	X
Falconiformes	Falconidae	*Herpetotheres cachinnans*		X	
Galliformes	Cracidae	*Dendrortyx leucophrys*	X		
Galliformes	Cracidae	*Ortalis cinereiceps*	X	X	
Galliformes	Odontophoridae	*Odontophorus guttatus*		X	

Gruiformes	Rallidae	*Aramides albiventris*	X	X		X
Passeriformes	Corvidae	*Psilorhinus morio*	X	X		X
Passeriformes	Furnariidae	*Lepidocolaptes souleyetii*	X	X		
Passeriformes	Icteridae	*Dives dives*				X
Passeriformes	Icteridae	*Psarocolius montezuma*	X	X		X
Passeriformes	Icteridae	*Quiscalus mexicanus*	X	X		X
Passeriformes	Parulidae	*Protonotaria citrea*		X		
Passeriformes	Passerellidae	*Arremon brunneinucha*				X
Passeriformes	Passerellidae	*Arremonops conirostris*	X			
Passeriformes	Passerellidae	*Atlapetes albinucha*	X	X		X
Passeriformes	Passerellidae	*Melozone leucotis*	X	X		X
Passeriformes	Passerellidae	*Zonotrichia capensis*		X		X
Passeriformes	Pipridae	*Chiroxiphia linearis*	X	X		
Passeriformes	Pipridae	*Manacus candei*		X		

Passeriformes	Thamnophilidae	*Cymbilaimus lineatus*	X			
Passeriformes	Thamnophilidae	*Thamnophilus doliatus*	X	X		
Passeriformes	Thraupidae	*Coereba flaveola*	X	X		
Passeriformes	Thraupidae	*Habia rubica*	X	X		
Passeriformes	Thraupidae	*Piranga rubra*	X	X		X
Passeriformes	Thraupidae	*Saltator atriceps*	X	X		X
Passeriformes	Thraupidae	*Saltator coerulescens*	X	X		X
Passeriformes	Thraupidae	*Saltator maximus*	X	X		X
Passeriformes	Thraupidae	*Thraupis episcopus*	X	X		X
Passeriformes	Troglodytidae	*Cantorchilus modestus*	X	X		X
Passeriformes	Troglodytidae	*Cantorchilus thoracicus*		X		
Passeriformes	Troglodytidae	*Henicorhina leucophrys*	X	X		
Passeriformes	Troglodytidae	*Henicorhina leucosticta*	X	X		
Passeriformes	Troglodytidae	*Troglodytes aedon*	X	X		X

Passeriformes	Turdidae	*Catharus aurantiirostris*	X	X		
Passeriformes	Turdidae	*Turdus assimilis*	X			X
Passeriformes	Turdidae	*Turdus grayi*	X	X		X
Passeriformes	Turdidae	*Turdus plebejus*				X
Passeriformes	Tyrannidae	*Contopus cinereus*	X			
Passeriformes	Tyrannidae	*Contopus sordidulus*		X		
Passeriformes	Tyrannidae	*Contopus virens*	X			
Passeriformes	Tyrannidae	*Merarynchus pitangua*	X	X		X
Passeriformes	Tyrannidae	*Myiadestes melanops*		X		
Passeriformes	Tyrannidae	*Myiarchus tuberculifer*	X	X		X
Passeriformes	Tyrannidae	*Myiarchus luteiventris*		X		X
Passeriformes	Tyrannidae	*Myiozetetes similis*		X		X
Passeriformes	Tyrannidae	*Pitangus sulphuratus*	X	X		X
Passeriformes	Tyrannidae	*Tyrannus melancholicus*	X	X		X

Pelecaniformes	Ardeidae	*Butorides virescens*	X	X	X
Pelecaniformes	Threskiornithidae	*Mesembrinibis cayennensis*	X		
Piciformes	Picidae	*Melanerpes hoffmannii*	X	X	X
Piciformes	Ramphastidae	*Ramphastos sulfuratus*	X	X	
Psittaciformes	Psittacidae	*Brotogeris jugularis*	X	X	X
Psittaciformes	Psittacidae	*Pionus senilis*	X	X	X
Psittaciformes	Psittacidae	*Psittacara finschii*	X	X	X
Strigiformes	Strigidae	*Asio clamator*		X	
Strigiformes	Strigidae	*Ciccaba virgata*	X	X	X
Strigiformes	Strigidae	*Glaucidium costaricanum*		X	
Strigiformes	Strigidae	*Megascops choliba*	X	X	X
Strigiformes	Strigidae	*Tyto alba*			X
Trochiliformes	Trochilidae	*Amazilia tzacalt*	X	X	X
Trochiliformes	Trochilidae	*Phaeochroa cuvierii*	X	X	