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ABSTRACT

Human-induced disturbances affect animal behaviours such as anti-predatory responses. Animals in urban environments exhibit a reduced escape response, measured as a shorter flight initiation distance (FID), compared to their rural counterparts. While FID has been evaluated in animals in habitats that are completely urban or rural, little is known about how this response vary within urban environments, especially in tropical cities. Here, I studied the FID of resident bird species in Bogota, Colombia, in 22 sites grouped in 3 categories with various levels of vegetation cover and building density (i.e., urbanization gradient) that represented the habitat heterogeneity experienced by urban wildlife. I evaluated whether extrinsic or intrinsic factors affected the escape response. The results showed that birds in larger flocks are more tolerant when being approach, and that the escape response differ between site categories. Birds found in residential areas and urban parks exhibited the shortest FID whereas birds in natural areas exhibited the longest. This indicates that birds in smaller flocks and those in natural areas are less tolerant to human presence than birds found in residential areas and urban parks. Understanding how animals respond to increasing levels of human intervention is important to maintain urban biodiversity.

RESUMEN

Los disturbios antropogénicos afectan la respuesta anti-depredatoria de los animales. Los animales urbanos exhiben distancias de escape (FID, por sus siglas en inglés) más cortas en comparación con sus contrapartes rurales. Las respuestas de escape han sido muy estudiadas en animales en hábitats completamente urbanos o rurales; sin embargo, poco se sabe acerca de cómo varía dentro de las ciudades, especialmente en el trópico. En este estudio investigué las respuestas anti-depredatorias de aves residentes de Bogotá, Colombia. Seleccioné 22 sitios con diferentes niveles de urbanización que representan la heterogeneidad del hábitat, y evalué cuáles factores extrínsecos e intrínsecos afectan la respuesta de escape y la variación del FID a lo largo del gradiente de urbanización. Los resultados indican que las aves que forrajean en bandadas más grandes son más tolerantes a las aproximaciones de humanos y que la respuesta de escape difiere entre sitios con diferentes niveles de urbanización. Contrario a lo esperado, solo se encontraron diferencias entre aves en zonas naturales y urbanas (parques y áreas residenciales), pero no entre parques y áreas residenciales. En general, las aves que se encuentran en áreas residenciales exhibieron distancias de escape más cortas que las aves en áreas naturales. Esto indica que las aves en áreas naturales son menos tolerantes a la presencia humana que las aves que se encuentran en áreas urbanas con mayor grado de intervención humana. Nuestros resultados nos permiten entender cómo los animales responden a los crecientes niveles de intervención humana y cómo estas respuestas son importantes para mantener la biodiversidad urbana.

KEYWORDS

Anti-predatory response, urban wildlife, tropical cities, anthropogenic disturbances

PALABRAS CLAVE

Respuesta anti-depredatoria, vida silvestre urbana, ciudades tropicales, disturbios antropogénicos

INTRODUCTION

Urbanization processes entail habitat destruction and transformation, which have significant impacts on wildlife. Some species are sensible to these changes and are forced to migrate once an area has been intervened (i.e., urban avoiders), while others are tolerant towards human presence and can exploit urban resources (i.e., urban-dwellers; Isaksson, 2018). Those individuals that remain in urban environments are exposed to human activities that could cause disturbances and affect activity patterns, behaviour or physiology (Weston et al., 2012). Thus, urban dwellers should exhibit mechanisms to cope with disturbances, including changes in anti-predatory behaviour. Urban birds usually exhibit a less sensitive escape response (i.e., slower reaction; response at a shorter distance) in contrast to their rural counterparts (Davey et al., 2019; Møller et al., 2013). Comparing contrasting habitats (i.e., fully urban vs. rural) may reveal the effects or urbanization. However, few studies have included the heterogeneity of habitats that birds experience within cities (i.e., urbanization gradients), which could reveal the effects of different habitat features on perception of risk and escape responses. I focused on the distance at which an animal reacts to a potential predator's presence (i.e. FID: flight initiation distance; Fernández-Juricic et al., 2001), of urban birds exposed to different levels of human-induced disturbances in Bogota, Colombia. This may give us insights into how animals are adapting to urban habitats with high level of human-induced disturbances and also on how to propose effective mitigation strategies to favor the persistence of wildlife in cities, villages and other human-transformed habitats.

Animals' response to human-induced disturbances could depend on the risk perceived by each individual

(Frid & Dill, 2002), and could be assessed through changes in their anti-predatory response. Risk perception is mainly influenced by intrinsic (e.g., life history traits) and extrinsic (e.g., habitat characteristics) factors. On the one hand, sensitive responses to approaches increase with group size (e.g. bigger flocks; Morelli et al., 2019), body size (Blumstein, 2006), outside of breeding season (Jorgensen et al., 2016), and during migration (Mikula et al., 2018). On the other hand, urban dwelling birds exhibit a less sensitive anti-predatory response when exposed to domestic animals (Cavalli et al., 2016), higher pedestrian densities (Mikula, 2014), and noise pollution (Petrelli et al., 2017).

Within urban areas, birds are exposed to heterogeneous ecosystems (Cadenasso, 2007), with different levels of vegetation cover (e.g., from urban wildlife reserves to bare concrete zones) and building density (e.g., from suburbs to densely populated zones). This variation in habitat represents an urbanization gradient. Since, habitat's characteristics (i.e., level of human intervention) can influence animals' risk-perception (Blumstein, 2006), it is expected that animals vary their anti-predatory response in this gradient (Clucas & Marzluff, 2012; Hall et al., 2020). For example, in Sydney, Australia, birds escaped at a greater distance when being approached by humans in areas with a low intervention level such as urban bushland reserves than individuals in areas with a higher intervention level such as urban streets and lawns (Hall et al., 2020). In temperate zones, urban birds exhibit a shorter response to humans relative to those living in fully rural habitats (Clucas & Marzluff, 2012). However, there is not much empirical information about animal's anti-predatory response variation in varying levels of anthropogenic disturbances in urban areas, especially in tropical ecosystems.

Tropical and temperate animal species differ in behaviour, ecology and life history traits that may influence their risk-perception and thus, their anti-predatory response. For example, tropical birds have small clutches, are long-lived, have a slow maturation and a low metabolic rate (Wiersma et al., 2007). Therefore, compared to temperate birds, tropical birds have a greater residual reproductive value (Moschilla et al., 2018) and a slow pace-of-life. Thus, to guarantee their survival and reproductive prospects, tropical birds are expected to be more cautious about the presence of a potential predator than temperate ones (Møller & Liang, 2012). This suggests that tropical birds might show a less tolerant anti-predatory response compared to their temperate counterparts. Yet, to date we lack empirical information that supports it.

Here, I aim to understand: 1) which intrinsic and extrinsic factors influence anti-predatory response in urban tropical birds, and 2) how does anti-predatory response vary in an urbanization gradient. For this, I measured anti-predatory responses in 22 study sites grouped in three categories along an urbanization gradient: natural areas, parks and residential areas; and I evaluated the extrinsic (environmental noise level, pedestrian and predator density) and intrinsic factors (body size, intra and heterospecific flock size) that could affect this response. First, I expected birds' FID to decrease from natural to residential areas. Second, I expected to find a negative correlation between FID and environmental noise level and, pedestrian and predator density since previous studies have reported that when environmental stimuli increase, birds tend to exhibit a less sensible response (Lin et al., 2012). I also expected a negative correlation between FID and intra and heterospecific flock size because birds in bigger flocks have a lower individual predation risk which can result in a "less cautious" behaviour and a shorter FID (Lima & Dill, 1990). Finally, I expected to find a positive correlation between FID and body size since previous studies have evidenced that bigger birds are less tolerant than small birds when being approached (Fernández-Juricic et al., 2001).

METHODS

Data collection

Study area

The study was carried out in Bogota, Colombia. This city offers an interesting opportunity to study changes in urban tropical bird's anti-predatory behaviour, because it has: 1) a considerable avian diversity (200 bird species: 136 residents and 64 migrants; ABO, 2000), 2) a highly urbanized area (Barrera, 2010), 3) a high population density (Wheeler, 2015), and 4) a heterogeneous landscape (Páramo, 2003). Therefore, Bogota's wildlife is exposed to different anthropogenic disturbance intensities. I categorized urban areas based on their vegetation cover status (disturbed/undisturbed) and the patterns of use (adapted from Hall et al., 2020). I identified three site categories: 1) *Natural sites* (NS) correspond to areas with relatively undisturbed vegetation cover where restricted recreational activities are allowed; 2) *Parks*, these areas are characterized by disturbed vegetation (mainly arboreal) and recreational infrastructure. Here, I considered metropolitan (MP) and zonal parks (ZP), defined as highly visited parks open to the public and parks used mainly by nearby population, respectively; and 3) *Residential areas* (RA), which are highly disturbed areas that have a high housing estate and low vegetation cover (see Fig. 1).

Anti-predatory response: Flight initiation distance

I measured anti-predatory responses in 22 study sites, three wetlands (NS), six metropolitan parks (MP) and six zonal parks (ZP), and seven residential areas (RA) (Fig. 1). At each site, I quantified the distance at which the focal bird reacted to my presence (i.e., bird's flight initiation distance; FID) using the protocol established by Blumstein (2003), as follows:

1) *Identification of focal individual:* The observer (MAV) walked, following random transects, around the study sites to identify focal birds (i.e., birds that were foraging in trees or soil, alone or in flocks, and have not been disturbed by the observer or other pedestrian's presence).

2) *FID estimation:* Once the focal bird was identified, the observer first, estimated if the bird was within a 10-30 meters range. This ensured that the observer was within the bird's vision range. Then, the observer marked with a stake the starting position, where it first identified the focal bird (i.e., the starting distance between bird and observer; SD). Right after that, the observer walked towards the focal individual at a constant speed (0.5-1 m/s) maintaining eye contact. When the focal bird exhibited an alert behaviour (i.e., bird extends its neck vertically, it directs its attention to the observer), the observer marked it with another stake without interrupting its path (i.e., the alert distance; AD). Once the focal bird exhibited an escape behaviour (e.g., walking fast, hopping, flying, jumping, moving away), the observer stopped and marked this place with another stake (i.e., the distance walked by the observer; DW).

At each event (i.e., an FID trial), the observer recorded the SD, AD, DW and the escape strategy that the birds exhibited (walked fast, walked away, hopped, flew). Each of these distances was measured using a laser rangefinder (BOSCH GLM 20) when possible or through steps. The FID was calculated as the starting distance (SD) minus the distance walked by the observer (DW). For birds that were foraging in arboreal vegetation, I estimated the perch height and used it in a formula correction to find the FID (see Blumstein, 2006).

To avoid data replication (i.e., sampling the same bird twice) the observer sampled birds that were at least 25 meters apart. FID measurements were conducted between 07:00 and 10:00 hours for four months

(February to June of 2021). To reduce human errors, the observer trained distance estimation, birds' alert and escape behaviour recognition routinely for a month (January 2021), before data collection began.

Factors affecting the anti-predatory response

To identify which factors affected the anti-predatory response, I characterized two types of factors associated with risk-perception construction: 1) intrinsic factors such as life history traits and animal's characteristics, and 2) extrinsic factors, compromised by the animal's environment characteristics. These factors were selected based on previous studies showing that they affected birds' anti-predatory response in human intervened ecosystems (Blumstein, 2003; Braimoh et al., 2017; Glover et al., 2011; Mayer et al., 2019; Petrelli et al., 2017). Thus, I expected them to also affect the study species' response.

I evaluated the following intrinsic factors: 1) Body size, defined as the body length of the focal bird, and 2) Foraging flock size (FFS), defined as the number of hetero-specific and inter-specific birds within a 10 meters radius from the focal individual (Clucas & Marzluff, 2012). The information regarding body size was obtained from the book "Guía de las aves de Colombia" (Hilty y Brown, 1986), whereas the information regarding FFS, was measured *in-site*. For the extrinsic factors I considered: 1) Environmental noise level, defined as the noise level in the study site and recorded using a sound level meter (UNI-T UT353-BT), and 2) Pedestrian and predator density: measured as the number of humans (pedestrian density) and domestic animals and/or raptors that walk/fly by the study sites in a 15-minute interval (following Mikula, 2014). I measured the noise level and pedestrian and predator density three times during a sampling session in different places of the study site to generate a sampling day average.

Statistical analysis

Which environmental factors and life history traits influence anti-predatory response in urban tropical birds?

To determine the intrinsic and extrinsic factors that influenced the anti-predatory response of birds, I fit a *linear mixed model* (LMM) with FID as the response variable. I included starting distance, heterospecific flock size, intraspecific flock size, body size, environmental noise level, pedestrian density, and predator density as covariates, and study site as a random effect. Order, family and genus were included as nested random effects to control for phylogenetic relationships (Braimoh et al., 2017). Additionally, to control for differences in sampling effort among species, I added the number of observations per species as a weighted factor.

How does anti-predatory responses vary in an urbanization gradient?

To analyse if the level of anthropogenic disturbances affects birds' FID (i.e., differences between the study sites categories), I fitted a *linear mixed model* (LMM) with FID as the response variable and site category and body size as covariates and their interaction, since body size influence on FID can change depending on the site category that birds were sampled (Braimoh et al., 2017). For this analysis, I only used the species registered in all site categories: *Zenaida auriculata*, *Turdus fuscater* and *Zonotrichia capensis*. Lastly, I performed a *post-hoc* pairwise comparison among site categories to determine which categories were different from each other.

For both models, I fit a Gaussian error structure, and I scaled the predictors to obtain effect size estimates that are comparable to Pearson's correlation coefficients (Nakagawa & Cuthill, 2007). The predictors, intra and heterospecific flock size, pedestrian and predator density were $\log_{10}$+1-transformed and starting distance $\log_{10}$-transformed to achieve normal distributions (Tätte et al., 2018). Also, because alert distance had a strong correlation with the FID (r=0.84, N=848), I excluded it from both models. I did not include the variable "escape strategy" because I did not have a specific prediction for this variable. All analyses were done in the statistical program R version 4.1 (R Core Team, 2021). Models were run using the package lme4 version 1.1-14 (Bates et al. 2015), p-values were estimated using the package lmerTest version 3.1-3 (Kuznetsova et al. 2017) and pairwise comparisons were done in the package lsmeans version 2.30-0 (Lenth, 2016).

RESULTS

I collected a total of 855 FID measures on 20 species from 12 families and 7 orders. The mean FID of the sampled species was 3.23 m±1.73, and the mean starting distance was 16.77 m±5.45. I excluded seven measurements from both analyses that belong an extreme value of intraspecific foraging flock size (N=1) and the escape type swim that did not have enough representation in the dataset (N=6). This left me with 848 FID measures.

Natural areas presented a lower pedestrian density, predator density, and environmental noise level in comparison to the other categories (Pedestrian density (mean±SD): 1.21±1.05 walkers/min; Predator density (mean±SD): 0.04±0.1 predators/min; Noise level (mean±SD): 52.76±5.24 dB). Parks were characterized by a high pedestrian density, predator density and environmental noise level (Pedestrian density (mean±SD): MP=6.6±3.15 walkers/min, ZP=5.42±1.71 walkers/min; Predator density (mean±SD): MP= 1.15±1.29 predators/min, ZP= 1.9±0.46 predators/min; Noise level (mean±SD): MP=56.02±3.5 dB, ZP=57.95±6.11 dB). Lastly, residential areas presented a high pedestrian density and environmental noise level but lower predator density when compared with the park category (Pedestrian density (mean±SD): 6.15±1.3 walkers/min; Predator density (mean±SD): 0.97±0.45 predators/min; Noise level (mean±SD): 60.45±5.55 dB).

Birds in larger interspecific flock size have a shorter FID

I found a significant negative correlation between FID and the intrinsic factor: interspecific flock size (p-value< 0.0001, N=848, Table 1). Birds that were foraging in larger interspecific flocks exhibited a shorter escape response when being approached (i.e., reacted slower) in comparison to birds in smaller flocks (Figure 2; Table 1). FID varied negatively with the intrinsic factors: heterospecific flock size, body size, and the extrinsic factors: predator and pedestrian density, although these relationships were not statistically significant (Table 1).

Birds in natural areas exhibit a longer FID compared with birds in residential areas

There was a significant influence of urbanization gradient on FID (p-value=0.008, N=638, Table 2). When comparing among site categories, I found that the FID in NS differ from all other evaluated site categories (Figure 3; Table 3). Birds found in NS exhibited longer escape responses than birds in ZP, MP or NS. Finally, I found a significant interaction effect between body size and site category (p-value = 0.024, Table 2) indicating that the effect of body size varies depending on site category. FID is more strongly affected by body size in RA than in ZP, MP or NS. In residential areas, the medium specie (*Z. auriculata*) exhibited the shortest escape response followed by the smallest specie (*Z. capensis*) and the biggest specie (*T. fuscater*) (Figure 4).

DISCUSSION

This study shows a link between intraspecific flock size and the escape behaviour of birds. Individuals in larger flocks escaped at a shorter distance when being approached, which suggests more tolerance to human-induced disturbances. Birds that inhabit natural areas within cities showed less tolerance when being approached compared to birds that used other types of habitats.

Patterns of sociality such as group size are an important predictor of predation risk and thus, escape decisions (Lima & Dill, 1990). This relationship between grouping patterns and escape responses can be explained by two hypotheses: the "many eyes" hypothesis and the "predation dilution effect" hypothesis. The first, establishes that larger groups have higher vigilance and thus, its individuals are more aware of the habitat's possible threats and tend to react faster than lonely individuals (Pulliam, 1973). Whereas the second hypothesis establishes that individuals that belong to larger groups have a lower risk of being predated and thus, should be less aware when being approach (react at shorter distances; Ydenberg & Dill, 1986). In this study, birds in larger flocks were less cautious about approximations, which is consistent with the "predation dilution effect" hypothesis. However, previous studies are more concordant with the "many eyes" hypothesis (Glover et al., 2011; Mayer et al., 2019; Morelli et al., 2019). This variation can be due to differences in predation risk between the birds that were analysed in this study and the mentioned studies. For example, birds' natural predators such as raptors, have a higher representation across European urban areas (18 species; Mak et al., 2021) than in Bogota (6 species; Hilty & Brown, 1986). Thus, tropical birds that associate in larger groups reacted at longer distances and therefore, are less responsive to their environment's stimuli because they do not have a strong natural predation pressure.

Urban animals exhibit shorter escape distances in comparison to their rural counterparts (Van Donselaar et al., 2018). Since escape responses have mainly been studied in areas that are totally rural or urban, in this study, I included areas with mixed characteristics such as parks. However, I only found differences between natural and urban (parks and residential) areas. This indicates that birds found in areas with mixed characteristics still exhibit a similar response to the birds found in residential areas. Therefore, contrary to my predictions, I did not find variation in FID along the urbanization gradient. This might be due to the fact that although parks have more vegetation cover than residential areas, these sites still have high levels of anthropogenic disturbance measured as pedestrian density and environmental noise level. Therefore, birds found in parks are also exposed to high frequency and intensity stimuli and thus, exhibit similar escape responses to birds in residential areas. In this study, birds in residential areas exhibited the shortest FIDs and the birds in natural areas had the longest, a trend that has already been reported in previous studies (Clucas & Marzluff, 2012; Hall et al., 2020; Lin et al., 2012; Mikula, 2014). This variation between these two categories is mainly attributed to residential birds "acclimation" to heavily disturbed areas (i.e., high pedestrian density and environmental noise level).

Human attitudes towards birds can also affect escape decisions (Clucas & Marzluff, 2012; Møller & Xia, 2020). In this study, *Z. auriculata* exhibited the shortest escape response across all study sites and especially, in residential areas (Figure 4). This specie is known to have a close relationship with humans (MAV personal observation). For example, humans feed these birds more often in RA than in other categories (MAV personal observation), which can increase its tolerance to human presence. In RA, FID was more strongly affected by body size than in other site categories, which can be a result of the strong relationship between *Z. auriculata* and humans in this site category.

Tropical birds were expected to be more cautious (i.e., exhibit longer escape distances) than temperate ones (as reported by Møller & Liang, 2012). However, when comparing the escape distance response of the rock dove (*C. livia*), a species that can be found in parks and residential areas of both temperate and tropical zones, I found that it exhibited a longer escape distance ($mean_{FID\text{-}Tropics}$=1.64 m±0.75) when compared to temperate areas ($mean_{FID\text{-}Temperate}$=5.3 m ± 0.4, Gendall et al., 2015). A potential explanation for this difference is that in tropical cities, birds can be exposed to greater human disturbances (stimuli) as a result of the rapid population growth rate and poor urban planning that characterizes Latin American cities (Wheeler, 2015). Birds found in highly disturbed areas are usually more tolerant to approaches (Clucas & Marzluff, 2012; Hall et al., 2020; Møller et al., 2013), which can be an underlying reason for the differences in the escape response of *C. livia* between temperate and tropical areas. Nonetheless, it is important to note that I only found one study that reported this specie's FID mean for comparison (Gendall et al., 2015), and therefore, further research is needed to explore differences between tropical and temperate birds.

Conservation implications

Urban biodiversity loss is a concern in Latin American cities (Bax & Francesconi, 2019), therefore it is important to design and implement conservation plans that aim maintaining tropical urban biodiversity. Anti-predatory response (measured as FID) has been widely used to quantify an individual's reaction to human disturbances (Guay et al., 2016), one of the main threats of urban wildlife (Dirzo et al., 2014). My results suggest that birds that live in natural areas exhibit longer escape response, and thus are less tolerant to human presence and the disturbances it causes. Therefore, I suggest that local stakeholders could regulate activities that might result in high intensity disturbances such as outdoor active recreation activities, especially in natural areas and urban nature reserves.

Conclusion

My study contributes to the understanding of the variation of anti-predatory responses of tropical birds in an urbanization gradient and the factors that affect it. The results indicate that birds in larger flocks and birds found in residential areas are more tolerant to approaching pedestrians. Understanding how animals respond to human presence can further our knowledge about species' adaptation to urban environments and can be a key step in the design of conservation plans that aim to manage human-induced disturbances in cities.

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FIGURES AND TABLES

Figures

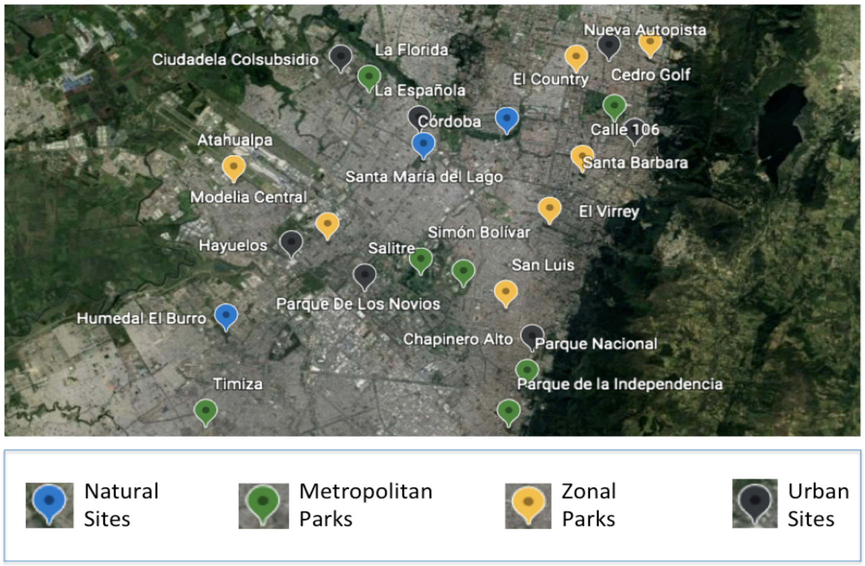

Figure 1. Location of study sites. The map (extracted from Google Earth) shows the location of 22 study sites from three categories. Within each site category several sites were evaluated. Residential areas (RA, dark grey bubble) included seven sites, Metropolitan parks (MP, green bubble) six sites, Zonal parks (ZP, yellow bubble) six sites, and Natural areas (NA), three sites. Site categories were selected based on their landscape physical traits, vegetation cover status (disturbed/undisturbed) and human use patterns.

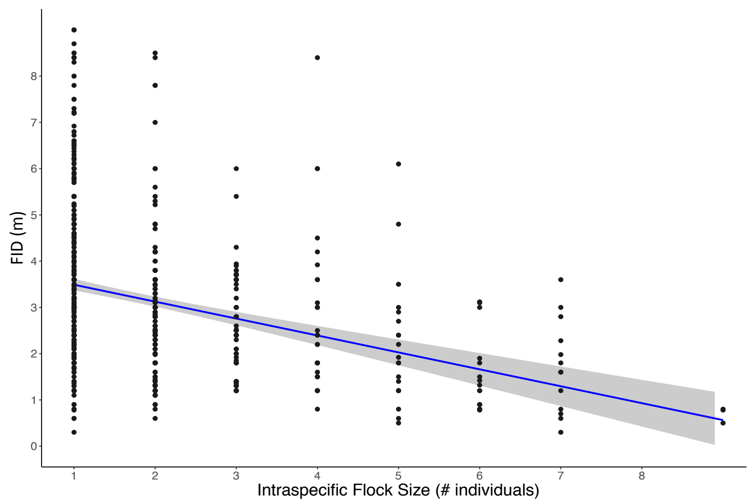

Figure 2. Relationship between interspecific foraging flock size and flight initiation distance. The plot shows the regression line for the main effect (blue line) and its corresponding 95% confidence interval (shaded zone). Dots represent the raw data (N=848).

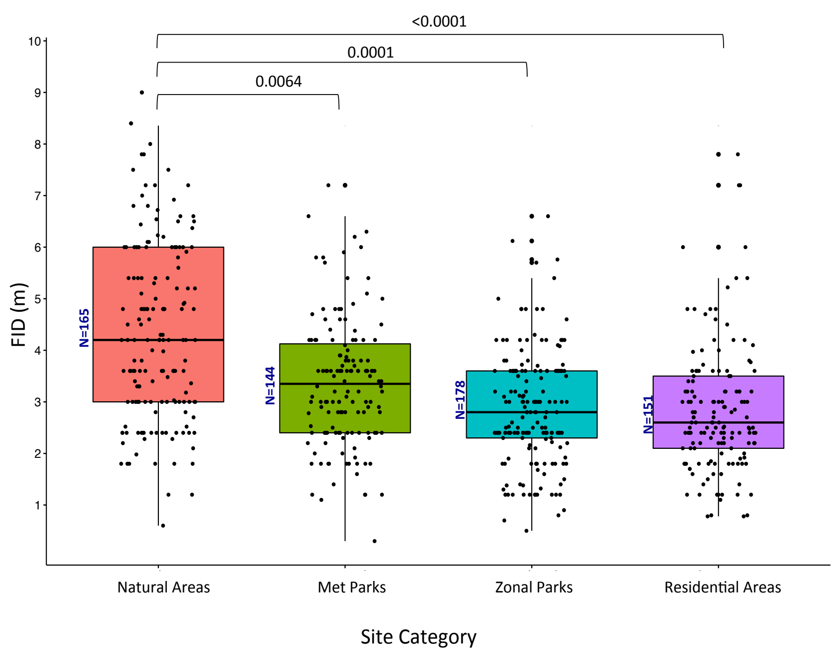

Figure 3. Differences in flight initiation distance (FID) along the urbanization gradient. The plot shows the medians (black line inside the box), with boxes showing the lower and upper quartile, black vertical bars showing the full range of the data, and dots showing the raw data (N=638). Numbers in blue at the

left of the box indicate the number of FID trials. Only significant comparisons were represented and indicated by the square brackets. Values above the square brackets indicate p-values.

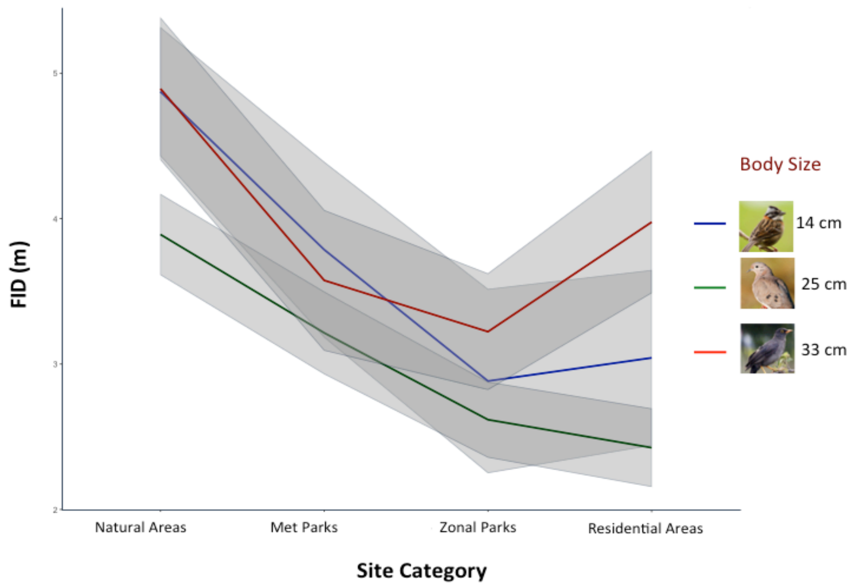

Figure 4. Effect of the urbanization gradient on flight initiation distance (FID). The regression shows the interaction effect of body size and site category (N=638, p-value = 0.024; Table 2). Lines represent the effects on each of the three species registered in all site categories: *Z. auriculata* (green line), *Z. capensis* (red line) and *T. fuscater* (blue line). Shaded zone correspond to a 95% confidence interval.

TABLES

Table 1. LMM coefficients and standard errors from linear-mixed models evaluating the influence of environmental noise level, pedestrian and predator density, body size, intra specific flock and heterospecific flock size (fixed effects) on flight initiation distance (FID). Bold values indicates statistical significance at α=0.05. N=855 corresponds to the total number of FIDs included in the regression model. The variance explained by the model was $R^2=6.88 \times 10^{-4}$

Fixed effect	Estimate	SE	*t-value*	*P-value*
Intercept	-0.12	0.23	-0.545	0.615
Starting distance	**0.093**	**0.025**	**3.693**	**0.0002**
Heterospecific flock size	-0.012	0.026	-0.454	0.65
Intraspecific flock size	**-0.2**	**0.024**	**-8.227**	**<0.0001**
Body size	-0.034	0.112	-0.302	0.773
Environmental noise level	-0.66	0.04	-1.659	0.098
Pedestrian density	-0.062	0.783	-0.788	0.432
Predator distance	0.016	0.088	0.187	0.852
Random effect		Variance		SE
Site		2.281×10^{-1}		0.478
sp:(family:order)		5.21×10^{-2}		0.228
Family:order		2.4×10^{-7}		0.0005
Order		6.668×10^{-2}		9.609
Residual		9.234×10^{1}		9.61

Table 2. LMM results for the evaluation of the influence of urbanization gradient on flight initiation distance (FID) of the three species that were represented in every site category. N=638 corresponds to the total number of FIDs included in the regression model. Bold indicates statistical significance at α=0.05. The variance explained by the model was R2=0.002

Fixed effect	Estimate	SE	*t-value*	*P-value*
(Intercept)	0.129	0.3	0.429	0.669
Starting distance	**0.112**	**0.033**	**3.371**	**0.0007***
Natural Areas	0.984	0.569	1.731	0.085
Residential areas	**-1.518**	**0.57**	**-2.665**	**0.008***
Zonal park	-0.688	0.559	-1.231	0.22
Natural area* Body size	0.002	0.018	0.089	0.929
Residential area* Body size	**0.044**	**0.019**	**2.266**	**0.024***
Zonal parks* Body size	0.013	0.019	0.721	0.47
Random effect		Variance		SE
Site		0.149		0.386
Residual		151.864		12.323

Table 3. Post-hoc pairwise comparison between site categories. Bold indicates statistical significance at α=0.05

Contrast	Estimate	SE	*t-value*	*P-value*
Metropolitan parks – Natural areas	**-1.026**	**0.316**	**-3.25**	**0.006***
Metropolitan parks – Residential areas	0.376	0.252	1.496	0.44
Metropolitan parks – Zonal parks	0.341	0.258	1.321	0.55
Natural areas – Residential areas	**1.403**	**0.307**	**4.569**	**<0.0001***
Natural areas – Zonal parks	**1.367**	**0.312**	**4.381**	**0.0001***
Residential areas – Zonal parks	-0.036	0.247	-0.144	0.999