

Increases in avian diversity associated with COVID-19 lockdowns in urban Colombia

I. MacGregor–Fors, E. Arbeláez–Cortés, F. A. Estela, D. Ocampo, C. E. Sánchez–Sarria, M. García–Arroyo, G. K. Aguirre–Samboní, D. Cortés–Díaz, J. C. Franco Morales, C. D. Gaitán–García, S. Guerrero–Pelaez, Y. Gutiérrez Parodys, M. Holguín–Ruiz, E. Meza–Angulo, H. A. Vides, J. D. Wilches–Vega

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Abstract

Increases in avian diversity associated with COVID-19 lockdowns in urban Colombia. Research on urban biodiversity has primarily addressed the effects of urbanization and human activity synergistically as it has been virtually impossible to dissociate their impact on city wildlife. However, the anthropause resulting from COVID-19 lockdowns provided an unprecedented scenario to study the relative role of human activity on avian communities. Here we provide evidence of the relationships between human activity and bird species richness in urban areas of Colombia during its strict and subsequent relaxed lockdowns. Once the strict lockdown was lifted and human activity increased, avian species richness decreased by 32% in 46% of our sampling sites. Although the strict lockdown lasted only six weeks, local assemblages (mainly from low-intensity urbanization peri-urban sites) swiftly became more diverse. Our findings highlight the importance of taking human activity into account when planning cities, with important focus on greenspaces, if our aim is to conserve and enhance urban biodiversity. Such plans will require not only the cooperation of local governments but also greater awareness among the local population regarding the importance of creating livable, healthy, biodiverse, and resilient cities.

Key words: Bird surveys, Coronavirus, Data-intensive science, Neotropic, Urban ecology

Resumen

Aumento de la diversidad de aves asociada con los confinamientos impuestos a raíz de la COVID-19 en ciudades Colombianas. El estudio sobre la biodiversidad urbana ha abordado primordialmente los efectos combinados de la urbanización y las actividades humanas, ya que ha sido prácticamente imposible disociar el papel del cambio físico de la urbanización y el de las actividades diarias en relación con la fauna silvestre de las ciudades. La antropausa producida por los confinamientos impuestos a raíz de la COVID-19 generó una situación sin precedentes que permitió estudiar el papel relativo de la actividad humana en las comunidades de aves. En el presente estudio aportamos evidencia sobre las relaciones entre la actividad humana y la riqueza de especies de aves en zonas urbanas de Colombia durante el confinamiento estricto y el subsecuente confinamiento relajado. Una vez que el confinamiento estricto concluyó, la riqueza de especies decreció 32% en 46% de nuestros sitios de muestreo. A pesar de que el confinamiento estricto únicamente duró seis semanas, la diversidad de las aves, mayoritariamente en sitios periurbanos con una baja intensidad de urbanización, aumentó rápidamente. Nuestros resultados subrayan la importancia de los planes urbanos futuros en relación con la actividad humana, particularmente en espacios verdes si se desea conservar y mejorar la biodiversidad en las ciudades. Para llevar a cabo estos planes, será necesario que los gobiernos locales cooperen, pero también que se conciencie a la población local de la importancia de crear ciudades vivibles, saludables, biodiversas y resilientes.

Palabras clave: Muestreos de aves, Coronavirus, Ciencia con utilización intensiva de datos, Neotrópico, Ecología urbana



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Ian MacGregor–Fors, Michelle García–Arroyo, University of Helsinki, Lahti, Finland.– Enrique Arbeláez–Cortés, Universidad Industrial de Santander, Bucaramanga, Colombia.– Felipe A. Estela, Gianni K. Aguirre–Samboní, Pontificia Universidad Javeriana–Cali, Colombia.– David Ocampo, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Villa de Leyva, Colombia and Princeton University, New Jersey, USA.– Camilo E. Sánchez–Sarria, Instituto de Ecología, A.C., Xalapa, México.– Daniela Cortés–Díaz, Universidad del Quindío, Armenia, Colombia.– Juan C. Franco Morales, Universidad Autónoma de Occidente, Cali, Colombia.– Cristhian D. Gaitán–García, Universidad del Tolima, Ibagué, Colombia.– Sebastian Guerrero–Pelaez, Pontificia Universidad Javeriana–Bogotá DC, Colombia.– Yossama Gutiérrez Parodys, Fundación Ecológica Los Besotes, Colombia.– Maira Holguín–Ruiz, Universidad de los Llanos, Colombia.– Enrick Meza–Angulo, Universidad de Caldas, Manizales, Colombia.– Hugo A. Vides, Universidad de Cartagena, Colombia.– Juan D. Wilches–Vega, Universidad de Santander, Campus Cúcuta, Colombia.

Corresponding author: I. MacGregor–Fors. E–mail: ian.macgregor@helsinki.fi

ORCID ID: Ian MacGregor–Fors 0000-0003-3198-7322; Enrique Arbeláez–Cortés 0000-0002-4350-1564; Felipe A. Estela 0000-0003-2090-1386; David Ocampo 0000-0003-1597-4038; Camilo E. Sánchez–Sarria 0000-0001-7990-7366; Michelle García–Arroyo 0000-0002-9167-4777; Gianni K. Aguirre–Samboní 0000-0002-3526-7253; Daniela Cortés–Díaz 0000-0002-7363-5547; Juan C. Franco Morales 0000-0001-8363-8314; Cristhian D. Gaitán–García 0000-0002-3852-8615; Sebastian Guerrero–Pelaez 0000-0003-3008-0139; Maira Holguín–Ruiz 0000-0001-8360-3779; Enrick Meza–Angulo 0000-0002-0268-5029; Hugo A. Vides 0000-0002-3935-3319; Juan D. Wilches–Vega 0000-0003-1067-4079

Introduction

Beyond the profound and long-lasting shifts intrinsic to the urbanization process, the metabolism of urban areas is considered one of the major environmental threats to date (Maxwell et al., 2016). Cities drive environmental change at multiple spatiotemporal scales, altering hydro-systems, biogeochemical cycles, climate, and biodiversity (Grimm et al., 2008). The impact of cities on biodiversity is so extensive that urban development itself, not accounting for extrinsic urban metabolism, has been regarded as the third most influential cause of species endangerment worldwide (Maxwell et al., 2016). Evidence has shown that biodiversity plummets in cities when contrasted with non-urban counterparts (Aronson et al., 2014), with the remaining assemblages non-randomly filtered into cities (taxonomically/phylogenetically and functionally); a pattern that holds globally (La Sorte et al., 2018). However, wildlife species have been shown to respond differently to urbanization (MacGregor-Fors et al., 2022). While some species avoid cities, others use the resources and live therein, with intriguing behavioral adjustments (e.g., Quesada et al., 2022). The latter often represent sink populations of non-urban species, however, and few thrive within urban centers (Fischer et al., 2015).

Studies focused on biodiversity shifts in urban systems have mostly addressed the role of urbanization and human activity synergistically (Forman, 2014). Findings have shown general patterns such as decreases in overall species richness with urbanization and increases in total bird abundances (MacGregor-Fors and Escobar-Ibáñez, 2017; Pena et al., 2017). Except for some local experiments (e.g., Bötsch et al., 2017, 2018) it has been virtually impossible to separate the role of the physical change imposed to the landscape through urbanization and day-to-day human activity on wildlife inhabiting or seeking to inhabit cities (Magel et al., 2019; Zellmer et al., 2020). Although currently increasing, our understanding of the magnitude and the ways in which human activity drives urban biodiversity has been heavily biased by correlational studies and small-scale experiments. Previous studies have focused on human activity as a wildlife driver, mostly in the form of passing pedestrians, recreational activities, vehicle traffic, and other proxies (e.g., noise; Gil and Brumm, 2014). Findings have shown that human activity can have negative effects on several wildlife groups, with consequences that span from changes in behavior (habituation processes) to changes in health and fitness (Stankowich and Blumstein, 2005; Schlesinger et al., 2008; Corsini et al., 2017; Morelli et al., 2018). Interestingly, some species well-adapted to urban life not only tolerate but also profit from the conditions at sites where human activity peaks (Sol et al., 2002). Thus, on the one hand, species that do not adjust to urban habitats are often more specialist (rather than generalist) or species have basic needs that cannot be met in urban settings, and are incapable of making the necessary adaptations that confer tolerance to urban life (Sol et al., 2013). On the other hand, previous studies have

shown that some of the positive responses to urbanization are related to the capacity of some species to adjust their behavior, or to natural history traits, such as diet or nesting strata (Sol et al., 2013).

The COVID-19 anthropause (scenario resulting from COVID-19 country lockdowns; Rutz et al., 2020) altered the scenario of human activity at a global scale. With the majority of the population confined to their homes, cities suddenly became less active and quieter. Billions of people worldwide sheltered-in-place intermittently for months due to COVID-19 pandemic lockdowns and ordinances (Thomas et al., 2020). In Colombia, the government decreed a strict nationwide lockdown starting on March 23, 2020 (referred to as 'strict lockdown' hereafter) that lasted for six weeks (decrees 457 and 636, respectively; Consejería Presidencial para las Regiones, 2020), and affected approximately 80% of the population (~40 million Colombians) (Thomas et al., 2020). On May 6, several economic sectors were reactivated with Colombians gradually, and partially, returning to the streets (referred to as 'relaxed lockdown' hereafter). The sharp reduction in human activities in cities during the strict COVID-19 lockdown period provided an unprecedented urban scenario in modern history, offering the opportunity to assess the role of human activity in relation to urban avian diversity.

After considering two windows of time during the anthropause, we here provide empirical evidence concerning the effect of human activity on bird diversity in urban areas in Colombia, the country with the richest avian diversity worldwide (Avendaño et al., 2017). We centered our study on birds as they are bioindicators and could feasibly be surveyed under lockdown conditions (Pollack et al., 2017). Birds have long been the most studied animal group in urban areas for a myriad of reasons, including their conformity to complex assemblages, their well-known natural history, and their rapid response to the changing dynamics in urban sites (Marzluff et al., 2001; Gil and Brumm, 2014; MacGregor-Fors and Escobar-Ibáñez, 2017).

To assess whether bird assemblages responded to this unique window of time in which cities were unprecedentedly calmer than usual, we used a standardized quantitative procedure to survey birds, starting a few days after the lockdown decree was put in place and continuously sampled throughout the strict lockdown and for several weeks after the first reactivation of human activities during the relaxed lockdown. We focused on species richness as it is a highly informative variable that relates to avian shifts in urban settings (Blair, 1996; Escobar-Ibáñez et al., 2020). Given that human activity has been shown to drive urban bird presence/absence and behavior (Sol et al., 2014; Spelt et al., 2021), and that a particular set of resources within the city are both abundant and predictable (Shochat, 2004), we predicted that the drop-off in outdoor human activity across urban Colombia would prompt the use of urban habitats by a larger number of bird species. We also expected to find a decrease in bird species richness as human activity increased after the strict lockdown in well-vegetated areas within Colombian cities (e.g., residential areas), where resources are more diverse than in heavily-built up areas (Faeth et al., 2005).

Material and methods

Study area

We conducted this study across urban Colombia, a mid-sized country (1.1 million km²) with at least 3,822 human settlements (cities, towns, villages) distributed across six major biomes and 29 ecological regions, but with an evident bias toward the Andes and the Caribbean (IGAC, 2008). We performed avian surveys in 13 locations within nine urban systems distributed across the country (fig. 1). Given the lockdown mobility restrictions, survey sites corresponded to the locations of observers' homes or nearby areas. Health and safety regulations were met to prevent transmission of the coronavirus. The sprawl of the involved cities varies in size, ranging from 7 to 137 km². Sprawl was quantified by freehand digitized polygons of built-up continuum using high-resolution satellite images provided by Google Earth Pro ([google.com/intl/en/earth](https://www.google.com/intl/en/earth/)) and following parameters of building aggregation and communication used by Lemoine–Rodríguez et al. (2019). The resulting polygons represented the urban fringe used to determine the survey site location in our study. This set of urban centers is located in a broad elevation range (9–1,298 m a.s.l.) across seven Colombian ecoregions (Olson et al., 2001). The distances between survey sites varied between 2 and 818 km.

Data collection

We retrieved data from a country-wide scale citizen-science monitoring scheme that aimed to compile bird records during the COVID-19 anthropause in Colombia (Arbeláez–Cortés et al., 2021). Data collection started on March 30, 2020, in response to the governmental lockdown decree enacted on March 23, which was continued until June 30, 2020 (Arbeláez–Cortés et al., 2021). Bird surveys consisted of 10 min fixed radius (50 m) circular or semi-circular point-counts between 06:00–09:00 h. All birds seen or heard during the time and space of the point-count were recorded; we only recorded individuals that were actively using the surveyed area (Bibby et al., 2000). The country-wide scheme included 45 survey sites from 22 urban systems (Arbeláez–Cortés et al., 2021).

The information used in this study comprises only data collected through circular point-counts at ground level at sites where observers recorded observations at least 4 times per week (average $6.3 \pm \text{SD } 2.4$; range: 5–7 surveys/week) over the course of at least 12 weeks (average $12.9 \pm \text{SD } 0.3$; range: 12–13 weeks). This assessment thus includes information on the patterns found at 13 locations (located in nine cities), which were repeatedly surveyed in search of local patterns among replicates, for a total of 668 point-count repetitions. All observers were experienced in identifying bird species in the surveyed regions, with field experience ranging from 1.5–28 years (average 6.7 years). A few migrant species, austral and boreal, recorded during the first and last weeks of the survey were excluded from further analyses.

Survey sites traits

Given the relevance of the intensity of urbanization of sites within cities and their spatial location in relation to the core and periphery of the urban sprawl, we quantified built cover (% in 50 m radius) and classified the location of all survey sites. To quantify built cover, we freehand digitized all vegetation components from high-resolution satellite images (provided by Google Earth Pro) in the same 50 m radius circular plots where birds were surveyed and considered all of the remaining areas as built. We classified the location of survey sites following MacGregor–Fors (2010): peri-urban sites were those located along the urban–wildland ecotone that has been shown to represent an ecological barrier for birds, intra-urban areas were those located in the core of the city (inside the peri-urban belt), and extra-urban areas were those located outside the peri-urban belt, representing human settlements that are connected to larger urban centers.

Data analysis

We used a quantitative comparable dataset published by Google (2020) as a proxy for human activity in our study sites. Although we recognize that the information was only available to the regional (departmental) level, it was the best measurement of human activity available at a fine scale during and after the COVID-19 lockdown (Cot et al., 2021). Specifically, these data contrast mobile phone movement and activities after lockdowns began worldwide with baselines calculated using information of a five-week period before lockdowns began (i.e., January 3–February 6). Human mobility values were quantified as the difference between the baseline and the measured activity during the studied period. Thus, the more negative a value, the more it differed from human activity before the lockdowns. Given that the surveys analyzed here are mostly from weekdays, we excluded information provided by Google (2020) at weekends. It is notable that mobile phones, wearables (e.g., smartwatches), and other geolocated devices had reached most of the human population by 2014 (Blondel et al., 2015), allowing retrieval of highly reliable real time information concerning human movement with unprecedented spatial resolution (Meekan et al., 2017).

Given that our aim was to assess shifts in avian richness across time (the surveyed weeks represent two different scenarios of lockdown, and therefore of human activity: strict lockdown = March 23–May 5, 2020; relaxed lockdown = May 6–June 30, 2020), we calculated Pearson correlation coefficients between human activity and the weekly accumulated bird species richness recorded at each survey site (fig. 1s in supplementary material). The tendencies of such results, representing the pattern that species richness followed in the surveyed time, varied among the sampled sites. Thus, we considered coefficients > 0.35 and < -0.35 to represent moderate to strong correlations (Rubin, 2012).

We later related the Pearson correlation coefficients for the relationships between human activity and the

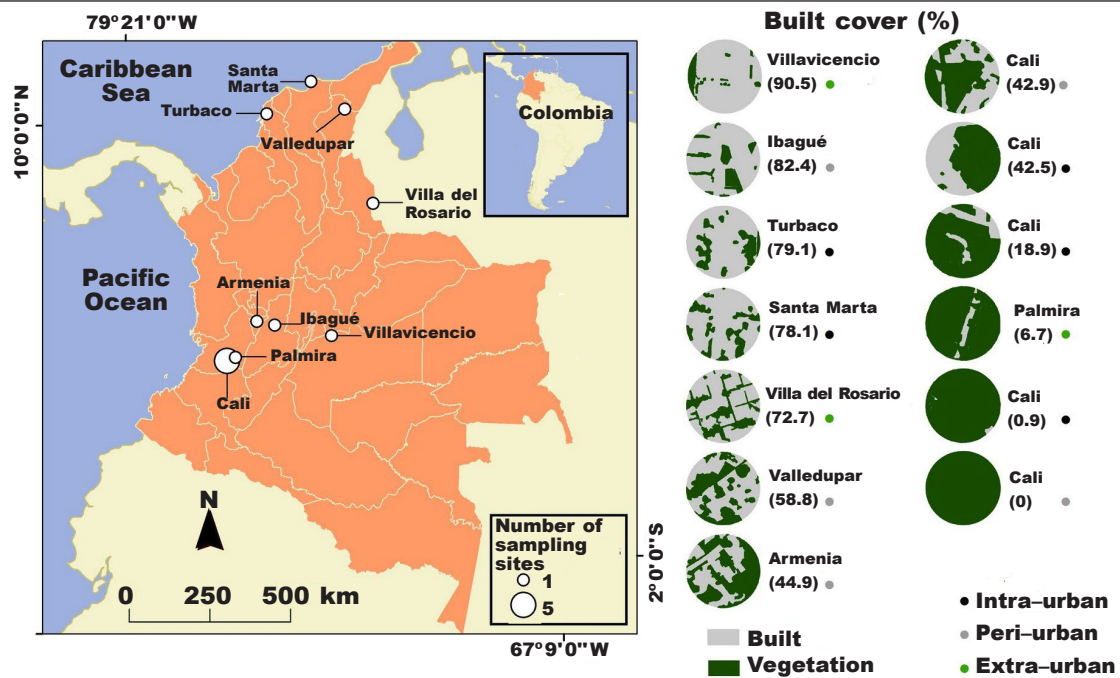


Fig. 1. Geographic location of survey sites and depictions of their built cover and location within the nine Colombian cities studied.

Fig. 1. Localización geográfica de los sitios de estudio y representación de la superficie construida y su localización dentro de las nueve ciudades colombianas estudiadas.

weekly accumulated bird species richness at each survey site to its built cover and spatial location using a generalized additive mixed model. We considered the correlation coefficients for the relationships between human activity and the weekly accumulated number of avian species recorded at each survey site as the dependent variable, built cover as the independent variable considering 'smoothers' for the three site location categories, and the identity of the studied cities and time (i.e., weeks since the strict lockdown decree) as random factors. Generalized additive models have different error structures and link functions able to provide a better fit for different types of variables. This allows non-parametric 'smoothers' to describe non-linear relationships by estimating the curves through the data and not based on predetermined equations (Crawley, 2013). All analyses were run in R (R Core Team, 2020).

Detectability

We acknowledge that ecological assessments focused on biodiversity changes can be biased by extrinsic factors that could affect detectability. Here, we assessed changes in bird species richness in relation to shifts in human activity as a result of the COVID-19 lockdown. However, such changes in human activity could also have decreased our ability to detect birds during the surveys, representing a con-

founding factor to take into account. Previous studies have shown that increasing human activity can also increase the amount and type of stressor stimuli for urban wildlife (Slabbekoorn and Ripmeester, 2008). For instance, noisy scenarios can have important effects on the measurement of urban diversity, such as decreases in the ability to detect birds in field surveys (Ortega and Francis, 2012) and birds avoiding such conditions for a plethora of reasons (e.g., limitations in their vocal communication; Perillo et al., 2017). Although the response of birds to changes in human activity and its consequences was the central aim of this study, changes in detectability related to factors such as anthropogenic noise could represent a confounding factor.

We were unable to directly measure detectability because observers did not have rangefinders to calculate effective radial distances using distance sampling and estimations, for instance. We were also unable to quantify passing pedestrians and/or cars given the bio-sanitary restrictions in place. However, we performed a couple of ad hoc indirect assessments to evaluate whether our ability to detect birds changed with human activities.

Magnitude of human activity

The human activity data we retrieved from Google (Google, 2020) for the 6-7 weeks of the relaxed

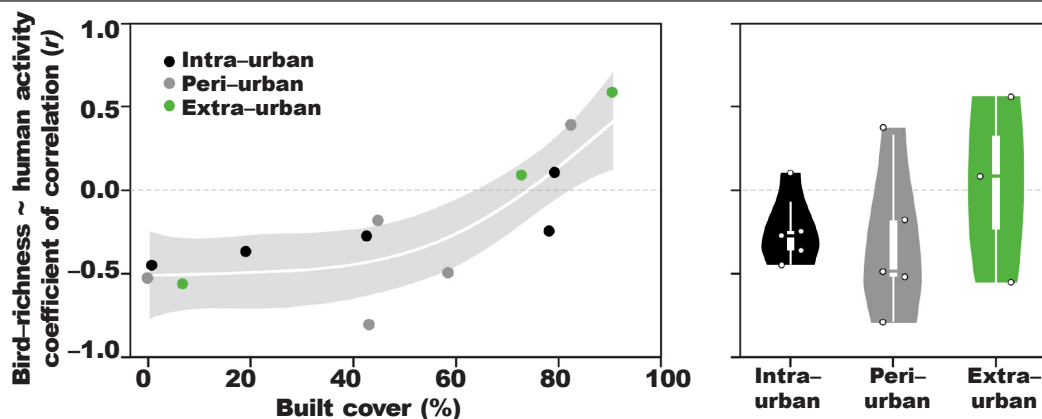


Fig. 2. Relationship between built cover and the location of survey sites within the nine studied Colombian cities and the correlation coefficients for the relationships between human activity and the weekly accumulated bird species richness at each survey site (left panel). Density plots for the coefficients of correlation of survey sites at each location within the studied cities (right panel).

Fig. 2. Relación entre la superficie construida y la ubicación de los sitios de estudio dentro de las nueve ciudades colombianas estudiadas y los coeficientes de correlación para las relaciones entre la actividad humana y la riqueza acumulada de especies de aves registrada en cada sitio de estudio (a la izquierda). Gráficos de densidad de los coeficientes de correlación de los centros del estudio en cada tipo de ubicación en las ciudades estudiadas (a la derecha).

lockdown remained negative (average $-35.81 \pm \text{SE } 0.72$), showing that although human activity changed notably in relation to activity during the strict lockdown (average $-50.96 \pm \text{SE } 0.53$), values were still lower than those of normal anthropogenic stimuli—mostly noise—that may affect the birds in the surveyed habitats. This was basically due to the type of reactivation allowed by the government, in which telecommuting and online education at all academic levels remained mandatory (decree 636, Consejería Presidencial para las Regiones, 2020).

Bird survey time and vehicle traffic

Vehicle traffic, even under regular conditions (i.e., before the COVID-19 lockdown), was relatively low during most of our surveys ($07:36 \text{ h} \pm \text{SD } 49 \text{ min}$) compared to earlier and later periods. To address this, we analyzed the typical traffic in the surveyed cities using data provided through Google Maps. Specifically, we took screenshots of city-wide traffic in each city hourly from 0600–1000 h and at noon using the same zoom framing for each city. For practical reasons, we randomly chose one day a week (i.e., Friday) to measure vehicle traffic in the cities. We then quantified the number of pixels reflecting the 'medium amount of traffic' (orange coded) and 'traffic delays' (red coded) categories using Gimp (a free and open-source image editor available at www.gimp.org). After deleting all visual elements of the screenshot with those colors to avoid miscalculations, we used a selection by color tool (Select-By color) using a threshold of 30 (which

allowed us to quantify as many pixels related to road and street traffic as possible without selecting other components of the map). We then added the amount of red- and orange-coded traffic pixels using a 2x factor for the red-coded pixels to denote the increase in traffic. Finally, we averaged the values in all the cities for the assessed times. As shown in figure 2s in supplementary material, the majority of surveys (75%) were performed between 07:00 h and 09:00 h, hours that correspond with the averages of regular traffic values. The most frequent time of our surveys was around 07:00 h (06:45–07:15 h), when traffic conditions are lowest under normal circumstances in the studied cities.

Aural records and human activity

Both these data (assessed through mobile phones and vehicle movements) show that our surveys were not performed under relatively high human activity scenarios. However, we tested whether increasing human activity (and the related noise stimuli that could reduce our ability to detect birds) caused by the lifting of restrictions during the relaxed lockdown after the strict lockdown was associated with our ability to detect birds in the field. To do this we analyzed shifts in the proportion of aural records in relation to visual records, which we use here as a proxy of our ability to record birds in noisier scenarios. We calculated the weekly proportion of aural and visual bird records by survey site (to avoid observer biases), assuming that if aural records were negatively correlated with human activity, our detection ability could affect our

Table 1. Generalized additive mixed model showing the relationship between Pearson correlation coefficients for the relationships between human activity and bird species richness with built cover by survey location.

Tabla 1. Modelo aditivo generalizado mixto en el que se muestra la relación entre los coeficientes de correlación de Pearson para las relaciones entre la actividad humana y la riqueza de especies de aves con la superficie construida por tipo de ubicación en los sitios de estudio.

Variables	Estimated df	F	P
Built cover × extra-urban	1.416	9.354	0.007
Built cover × peri-urban	1.938	6.233	0.021
Built cover × intra-urban	1.000	2.971	0.124

surveys in different human activity scenarios. To assess for a potential relationship between aural records and human activity, we correlated these variables per survey site and calculated the slope of the relationship (indicating its direction and magnitude). We then correlated the slopes of these relationships with the correlation coefficients for the relationships between human activity and the weekly accumulated bird species richness, assuming that if we found a positive relationship, then detectability could be an important confounding factor of our main results. This relationship was weak and non-significant ($r = 0.143$, $P = 0.639$).

We were particularly concerned about detectability at sites where we recorded negative correlation coefficients ($r \leq 0.35$) for the relationships between human activity and weekly accumulated bird species richness. Thus, we performed a similar correlation between the slopes of the aural records–human activity relationships with the correlation coefficients for the relationships between human activity and weekly accumulated bird species richness that were ≤ -0.35 . This correlation was also weak and non-significant ($r = 0.180$, $P = 0.731$). Two of the correlation coefficients ≤ -0.35 were related to positive slopes of the aural records–human activity relationships (i.e., a site in Cali and that of Valledupar). In the remaining four sites, the negative aural records–human activity relationships represented species richness losses of an average of 31.3% (\pm SE 2.4%). Thus, to provide conservative values for these sites, together with those observed, we also report these in our results to consider the loss in aural records as a correction factor of the decrease in species richness with increasing human activities. In doing so, we assume that decreases in aural records were caused by increases in the noise generated by human activity. For instance, for the peri-urban site of Cali that showed a 75% decrease in bird species richness when contrasting the first two and last two survey weeks, we calculated a relative decrease in aural records of 26.5%, and thus subtracted this proportion from the recorded decreases, as follows: $75 \times [(100 - 26.5) / 100] = 55.12$.

Results

We recorded 142 bird species across our survey sites in nine Colombian urban centers (table 1s in supplementary material). The average species richness per site was 36.4 species (\pm SD 10.0). Our analyses linking COVID-19 modifications in human activity to weekly accumulated bird species richness per site showed a negative relationship between human activity in 46% of the surveyed sites (average correlation coefficient $-0.54 \pm$ SE 0.06), with the remaining 39% being neutral (average correlation coefficient $0.09 \pm$ SE 0.08), and 15% being positive (average correlation coefficient $0.48 \pm$ SE 0.09) (fig. 1s in supplementary material). Considering the aforementioned coefficients of correlation, results of the generalized additive mixed model showed that, when controlling for city identity and survey week as random factors, the coefficients decreased significantly in relation to human activity with increasing built cover in extra- and peri-urban sites, but not in intra-urban sites (table 1, fig. 2, 3s in supplementary material).

Negative coefficients ($r \leq -0.35$) indicated a higher relationship between human activity and bird species richness in peri-urban areas, most of which were recorded at sites with less than 60% built cover. On the contrary, the two sites with the highest built cover (82.4 and 90.5%) showed positive associations between human activity shifts and weekly accumulated bird species richness per survey site. To provide a perspective of the magnitude of our results, we calculated the average bird species richness in the first two weeks and in the last two weeks of the survey at sites that showed negative correlation coefficients. After the strict lockdown, the decrease in average species richness in these sites was 32% (\pm SE 9.8%), with one site having 75% more species when contrasting the initial and final survey weeks, representing a ~55% conservative increase after aural assessment correction.

Discussion

Evidence provided here shows that bird species richness in well-vegetated urban sites was more sensitive

to human activity than that in heavily–built conditions, which generally foster less diversity (Gil and Brumm, 2014). The rapid avian response to use well–vegetated survey sites during such an unprecedented reduction of human activity as result of the COVID–19 strict lockdown was probably due to the resources available at these sites, resources that are often scarce in heavily–built sites (Fischer et al., 2015). The finding that well–vegetated peri–urban sites were among those with the highest decreases in bird species richness as human activity increased highlights the ecological importance of urban peripheries, at least in landscapes where the human footprint is not as intense. There, in such circumstances, urban and non–urban systems interact, and a higher number of bird species inhabiting nearby non–urban habitats may facilitate the incursion into urban habitats (MacGregor–Fors, 2010). Our findings also show that well–vegetated intra–urban sites experienced a decrease in bird species richness, although smaller in magnitude, with increased human activity following the strict lockdown, underlining the importance of urban vegetation beyond greenspace networks (Wood and Esaian, 2020).

Many urban–related species, often human commensals, have been shown to use and even depend on people and the consequences of the modern urban lifestyle. Apparently, individuals of some of the recorded species started using well–vegetated sites in the absence of the resources and conditions they typically rely on in heavily–built sites (Rodewald and Shustack, 2008). Although little evidence is yet available, individuals of a species as dependent on urbanization as the rock pigeon (*Columba livia*) were only recorded at the site with the highest vegetation cover in this study during the strict lockdown. These observations of urban–related species add to the existing evidence of the dependency that some urban species have on human activity and its consequences, suggesting that this association could be tighter than previously thought (Murgui and Hedblom, 2017).

However, considering that our ability to detect birds could have decreased at some survey sites as human activity increased, a conservative average value for such a decrease is 25% (\pm SE 7.6%; see the methodological section for detectability). This indicates that the severe reduction in human activity during the COVID–19 lockdown in almost half of our survey sites was drastic, showing an increase of at least one–fourth in species richness during the strict lockdown period. It is noteworthy that the strict lockdown lasted only six weeks, and in this short window of time many bird species responded swiftly –as seen in other studies (Gordo et al., 2021, Sanderfoot et al., 2022)– and with a similar pattern for nocturnal species (Estela et al., 2021), making local assemblages more diverse, particularly those from low–intensity urbanization sites.

An example of the importance of human activity recorded in this study is that of a residential peri–urban location in the city of Cali where we recorded a 75% decrease in bird species richness when comparing the accumulated richness from the first two weeks surveyed during the strict lockdown with

that of the last two surveyed weeks (~55% when accounting for potential detectability issues; see the Detectability section in the Material and methods for further detail), that is, seven weeks after the initial reactivation of activities and the consequent increase in human activity during the relaxed lockdown. Such an increase in bird species richness was partially associated with the arrival of flycatcher species (family Tyrannidae) at the beginning of our surveys. Besides some very common generalist flycatchers (tropical kingbird *Tyrannus melancholicus*), we frequently recorded species such as the yellow–olive flatbill (*Tolmomyias sulphureus*) and the piratic flycatcher (*Legatus leucophaeus*), but only when human activity was low. This observation illustrates how species that are absent or scarce during regular human activity scenarios may still use urban habitats, yet seem to be driven away by our activity.

Given the unexpected nature of the pandemic itself, which molded the nature of our surveys (and thus the data), we recognize that many potential confounding factors, such as noise or seasonality, could play a role in our findings. We tried to consider the potential biases related to detectability in indirect ways, but were unable to measure them directly. Neither were we able to generate a comparable dataset from pre–pandemic times. However, having found the three types of relationships across our survey sites leads us to believe that a change in detectability in both our time windows (although not negligible) does not seem to be a key factor, and thus our results are reliable.

Conclusions

Addressing the emerging mechanistic processes behind the patterns related to urbanization has become a major goal in urban ecology (McDonnell and Hahs, 2015). Our findings show that human activity was related to a considerable loss of bird species richness in urban systems. Such activity acts synergistically with urbanization, with profound effects on well–vegetated peri–urban sites. This highlights the importance of developing activity plans in urban greenspaces if our aim is not simply to maintain but to enhance biodiversity in cities. In doing so, human activity management plans in urban greenspaces will need to balance the positive and negative effects of visitation rates. Materializing such plans will require not only the cooperation of local governments but also increased awareness among the local population regarding the importance of creating livable, healthy, biodiverse, and resilient cities that can provide increasing ecosystem services to urbanites (McDonnell and MacGregor–Fors, 2016). Our findings may prompt future research on the response of avian communities and other wildlife groups for which information is available before, during, and/or after COVID–19 lockdowns. Did the COVID–19 lockdowns have only a momentary effect on bird diversity, or will they be sufficient to drive further behavioral or functional consequences? Together with our results, future studies focused on

disentangling the effect of human activities from the rest of the urban-related environmental changes will increase our understanding of the consequences of our day-to-day activities in limiting the biodiversity that surrounds us urbanites.

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Supplementary material

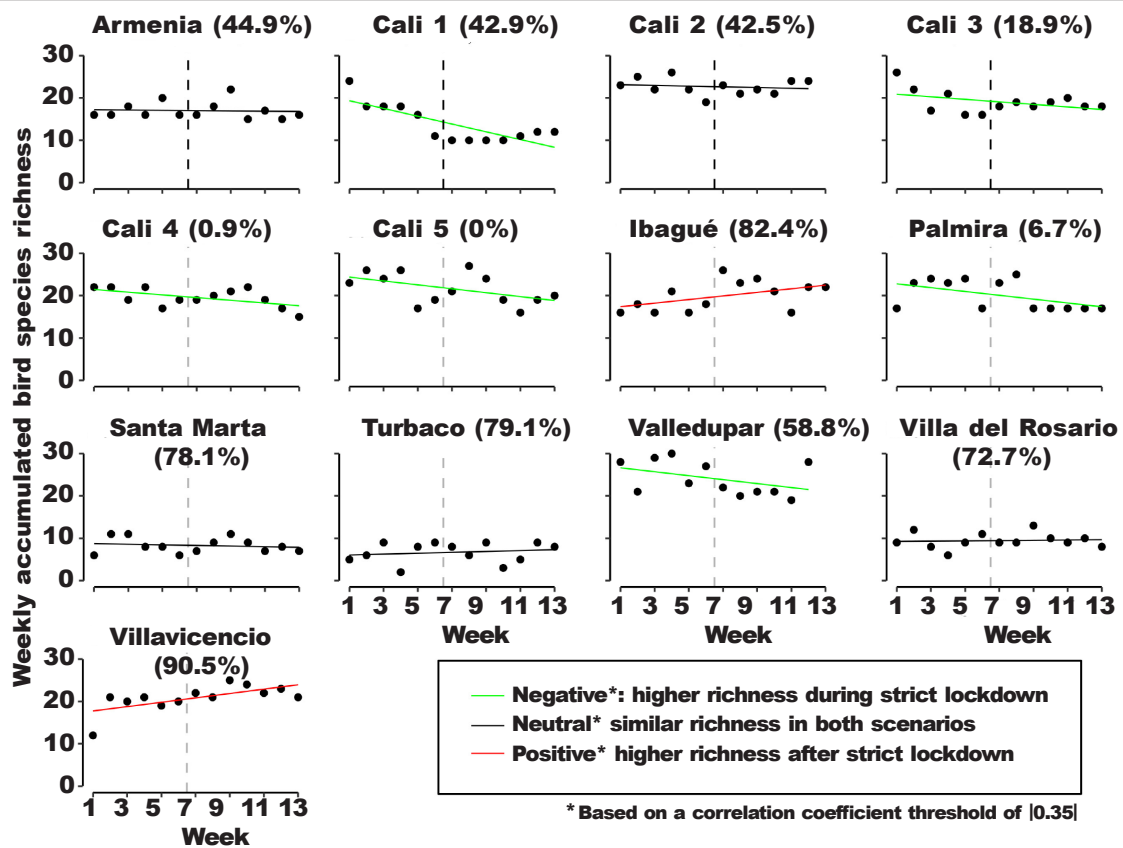


Fig. 1s. Patterns of weekly accumulated bird species richness during the COVID–19 strict lockdown in Colombia and subsequent relaxed lockdown for each of the 13 studied sampling sites. Three main patterns were found: decrease (green trend lines), remain stable (black trend lines), and increase with time (red trend lines) in weekly accumulated bird species richness. Dashed lines represent the date when the strict lockdown was lifted between weeks 6 and 7. Built cover per site is provided in parenthesis after the site's ID.

Fig. 1s. Patrones semanales de la riqueza de especies de aves durante el confinamiento estricto y el posterior confinamiento relajado para cada uno de los 13 sitios muestreados. Encontramos tres patrones principales: disminución (líneas de tendencia verdes), estabilización (líneas de tendencia negras) y aumento (líneas de tendencia rojas) de la riqueza acumulada semanal de especies de aves. Las líneas discontinuas representan la fecha en que se levantó el confinamiento estricto entre las semanas 6 y 7. La superficie construida por sitio se indica entre paréntesis.

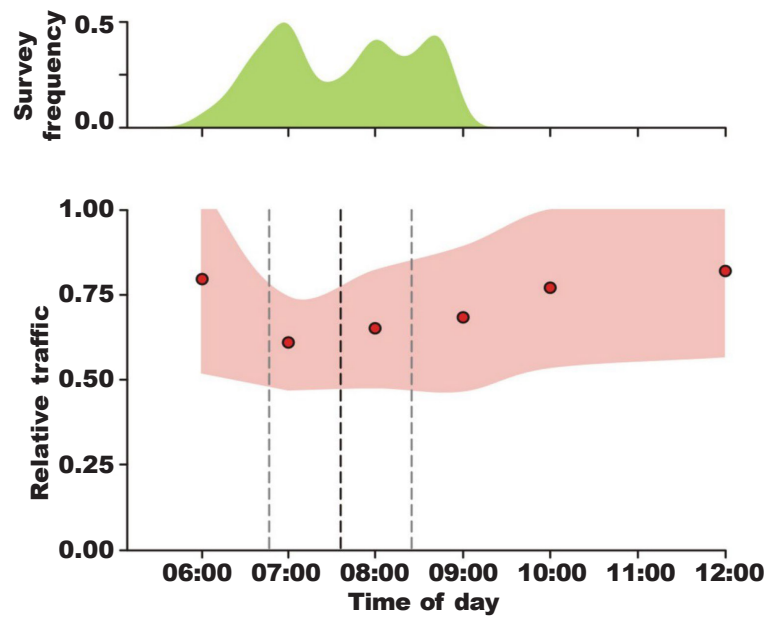


Fig. 2s. Avian surveys across cities and time (upper panel). Relative traffic (standardized to the highest value per city) from 06:00–10:00 h and noon. Red dots represent average vehicle traffic values, shaded pink area depicts SD values, and vertical segmented lines the average (black) and SD (gray) of the time of our surveys (lower panel).

Fig. 2s. Densidad de muestreos de aves en todas las ciudades y su hora de muestreo (gráfico superior). Tráfico relativo (estandarizado respecto al valor máximo por ciudad) de 06:00 a 10:00 h y a mediodía. Los puntos rojos indican los valores medios del tráfico de vehículos, el área rosada representa los valores de DE y las líneas discontinuas verticales negras y grises indican, respectivamente, el promedio y la DE de la hora de nuestros estudios (gráfico inferior).

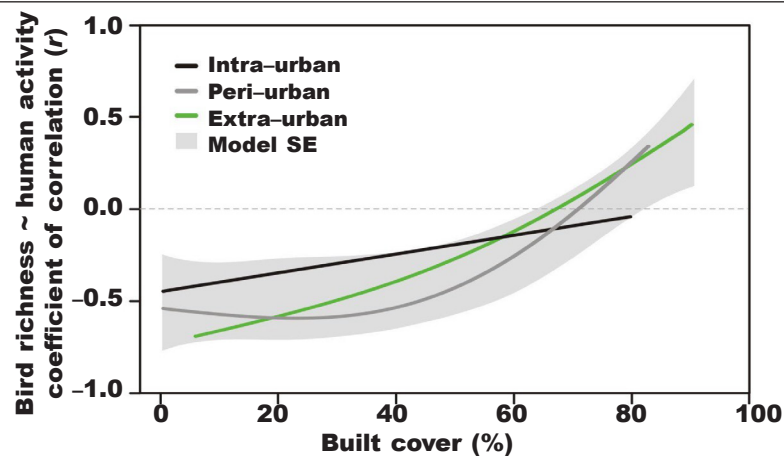


Fig. 3s. Slopes of the GAM for the relationship between built cover and the location of survey sites within the nine studied cities and the correlation coefficients for the relationships between human activity and the weekly accumulated bird species richness recorded at each survey site.

Fig. 3s. Pendientes del modelo aditivo generalizado para la relación entre la superficie construida y la localización de los sitios de muestreo en las nueve ciudades estudiadas con los coeficientes de correlación para las relaciones entre la actividad humana y la riqueza acumulada semanal de especies de aves registrada en cada sitio del muestreo.

Table 1s. List of the bird species recorded in this study. Dots represent the presence of species in our surveys in each city: AR, Armenia, CA, Cali; IB, Ibagué; PAL, Palmira; SM, Santa Marta; TUR, Turbaco; VALLE, Valledupar; VRO; Villa del Rosario; VILLA, Villavicencio. Nomenclature and order of appearance follow the one proposed by Remsen et al. (2017).

Tabla 1. Lista de especies de aves registradas en este estudio. Los puntos representan la presencia de especies en nuestros sitios de muestreo en cada ciudad: AR, Armenia, CA, Cali; IB, Ibagué; PAL, Palmira; SM, Santa Marta; TUR, Turbaco; VALLE, Valledupar; VRO; Villa del Rosario; VILLA, Villavicencio. La nomenclatura y el orden de aparición de las especies sigue la propuesta por Remsen et al. (2017).

Species	City									
	AR	CA	IB	PAL	SM	TUR	VALLE	VRO	VILLA	
<i>Dendrocygna autumnalis</i>			•							
<i>Ortalis ruficauda</i>							•			
<i>Ortalis columbiana</i>		•								
<i>Columba livia</i>					•				•	
<i>Patagioenas corensis</i>							•			
<i>Patagioenas cayennensis</i>	•								•	
<i>Leptotila verreauxi</i>							•			
<i>Zenaida auriculata</i>	•	•	•	•		•				
<i>Columbina passerina</i>						•				
<i>Columbina talpacoti</i>	•	•	•	•	•		•	•	•	
<i>Columbina squammata</i>					•		•			
<i>Crotophaga major</i>								•		
<i>Crotophaga ani</i>	•	•		•			•	•	•	
<i>Crotophaga sulcirostris</i>							•			
<i>Tapera naevia</i>	•						•			
<i>Piaya cayana</i>		•						•		
<i>Nyctibius griseus</i>		•								
<i>Streptoprocne zonaris</i>			•				•			
<i>Florisuga mellivora</i>			•							
<i>Phaethornis anthophilus</i>			•							
<i>Anthracothorax nigricollis</i>		•	•	•					•	
<i>Chlorostilbon melanorhynchus</i>		•								
<i>Chalybura buffonii</i>			•							
<i>Amazilia tzacatl</i>	•	•	•	•		•	•	•		
<i>Chionomesa fimbriata</i>									•	
<i>Saucerottia saucerottei</i>		•		•						
<i>Aramides cajaneus</i>	•									
<i>Vanellus chilensis</i>	•	•		•			•	•	•	
<i>Pelecanus occidentalis</i>					•					
<i>Nycticorax nycticorax</i>		•								
<i>Bubulcus ibis</i>				•			•			
<i>Ardea alba</i>				•			•			
<i>Egretta thula</i>		•								
<i>Egretta caerulea</i>							•			
<i>Phimosus infuscatus</i>	•	•	•				•			
<i>Theristicus caudatus</i>	•						•			
<i>Cathartes aura</i>					•		•			

Table 1s. (Cont.)

Species	City								
	AR	CA	IB	PAL	SM	TUR	VALLE	VRO	VILLA
<i>Coragyps atratus</i>	•	•		•	•	•	•		
<i>Rupornis magnirostris</i>	•	•		•					•
<i>Glaucidium brasilianum</i>						•	•		
<i>Megasceryle torquata</i>		•							
<i>Momotus aequatorialis</i>	•								
<i>Hypnelus ruficollis</i>								•	
<i>Picumnus granadensis</i>		•							
<i>Melanerpes formicivorus</i>	•								
<i>Melanerpes rubricapillus</i>		•	•	•	•	•	•	•	
<i>Colaptes punctigula</i>	•	•							
<i>Dryocopus lineatus</i>		•		•					
<i>Herpetotheres cachinnans</i>							•		
<i>Milvago chimachima</i>	•	•		•	•	•	•	•	
<i>Falco sparverius</i>		•							
<i>Falco ruficularis</i>						•	•		
<i>Falco deiroleucus</i>									•
<i>Falco femoralis</i>		•							•
<i>Pionus menstruus</i>	•	•	•	•			•		
<i>Brotogeris jugularis</i>		•			•	•	•		
<i>Amazona autumnalis</i>		•							
<i>Amazona ochrocephala</i>		•	•	•	•				
<i>Forpus xanthopterygius</i>						•			
<i>Forpus conspicillatus</i>	•	•	•	•			•		
<i>Eupsittula pertinax</i>						•	•	•	
<i>Ara severus</i>		•		•				•	
<i>Thamnophilus doliatus</i>								•	
<i>Thamnophilus multistriatus</i>	•	•							
<i>Xiphorhynchus susurrans</i>							•		
<i>Lepidocolaptes souleyetii</i>	•	•	•						
<i>Furnarius leucopus</i>							•		
<i>Tyrannulus elatus</i>		•							
<i>Elaenia flavogaster</i>		•	•	•			•	•	•
<i>Elaenia chiriquensis</i>		•							
<i>Camptostoma obsoletum</i>		•							
<i>Phaeomyias murina</i>		•		•					
<i>Zimmerius chrysops</i>	•								
<i>Todirostrum cinereum</i>	•	•	•						
<i>Tolmomyias sulphurescens</i>		•							
<i>Sayornis nigricans</i>		•							
<i>Pyrocephalus rubinus</i>	•	•	•	•					•
<i>Machetornis rixosa</i>				•			•		
<i>Legatus leucophaeus</i>		•							•

Table 1s. (Cont.)

Species	City								
	AR	CA	IB	PAL	SM	TUR	VALLE	VRO	VILLA
<i>Myiozetetes cayanensis</i>	•	•	•	•					•
<i>Myiozetetes similis</i>			•			•	•	•	•
<i>Pitangus sulphuratus</i>	•	•	•	•	•	•	•	•	•
<i>Myiodynastes maculatus</i>		•							
<i>Megarynchus pitangua</i>			•			•	•		•
<i>Tyrannus melancholicus</i>	•	•	•	•	•	•	•	•	•
<i>Tyrannus savana</i>				•			•		
<i>Myiarchus apicalis</i>		•							
<i>Myiarchus tyrannulus</i>							•		
<i>Cyclarhis gujanensis</i>			•						
<i>Hylophilus flavipes</i>									•
<i>Vireo chivi</i>		•							
<i>Cyanocorax violaceus</i>									•
<i>Pygochelidon cyanoleuca</i>		•	•	•					
<i>Stelgidopteryx ruficollis</i>	•							•	
<i>Progne tapera</i>						•			
<i>Progne chalybea</i>							•		
<i>Troglodytes aedon</i>	•	•	•	•		•		•	•
<i>Campylorhynchus zonatus</i>							•		
<i>Campylorhynchus nuchalis</i>							•		
<i>Campylorhynchus griseus</i>					•	•	•		
<i>Turdus leucomelas</i>							•		•
<i>Turdus grayi</i>						•	•		
<i>Turdus ignobilis</i>	•	•	•	•					•
<i>Mimus gilvus</i>									•
<i>Hemithraupis guira</i>		•		•					
<i>Sicalis flaveola</i>	•	•	•	•				•	•
<i>Volatinia jacarina</i>	•								
<i>Ramphocelus carbo</i>									•
<i>Sporophila intermedia</i>									•
<i>Sporophila nigricollis</i>	•	•	•	•					•
<i>Sporophila schistacea</i>	•								
<i>Saltator maximus</i>								•	
<i>Saltator striatipectus</i>	•	•	•						
<i>Saltator coerulescens</i>			•		•		•		
<i>Coereba flaveola</i>	•	•	•			•		•	•
<i>Tiaris olivaceus</i>	•								
<i>Melanospiza bicolor</i>			•						
<i>Stilpnia vitriolina</i>	•	•	•	•					
<i>Stilpnia cyanicollis</i>			•						
<i>Thraupis episcopus</i>	•	•	•	•		•	•	•	•
<i>Thraupis glaucocolpa</i>						•	•		

Table 1s. (Cont.)

Species	City									
	AR	CA	IB	PAL	SM	TUR	VALLE	VRO	VILLA	
<i>Thraupis palmarum</i>	•	•	•	•				•	•	
<i>Ammodramus aurifrons</i>									•	
<i>Cyanoloxia cyanooides</i>	•									
<i>Setophaga pitiayumi</i>		•		•						
<i>Setophaga petechia</i>		•								
<i>Myiothlypis fulvicauda</i>		•								
<i>Sturnella magna</i>									•	
<i>Leistes militaris</i>									•	
<i>Icterus chrysater</i>	•									
<i>Icterus nigrogularis</i>	•	•		•	•		•			
<i>Molothrus oryzivorus</i>				•			•			
<i>Molothrus bonariensis</i>	•	•		•			•			
<i>Quiscalus lugubris</i>							•			
<i>Quiscalus mexicanus</i>					•	•				
<i>Spinus xanthogastrus</i>	•									
<i>Spinus psaltria</i>			•	•						
<i>Euphonia chlorotica</i>									•	
<i>Euphonia trinitatis</i>							•			
<i>Euphonia concinna</i>			•							
<i>Euphonia laniirostris</i>	•	•	•	•				•		
<i>Lonchura malacca</i>	•									

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