Surviving in cities: the case of a year-round territorial bird in the Neotropics

Roselvy Juárez ⬤ ,[1,]* Viviana Ruiz-Gutiérrez[2] and Luis Sandoval[1]

[1]Laboratorio de Ecología Urbana y Comunicación Animal, Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica and [2]Cornell Lab of Ornithology, Cornell University, Ithaca, NY, 14850, USA

*Corresponding author. E-mail: roselvy.juarez@gmail.com

Abstract

Urban expansion has been identified as one of the main threats to biodiversity because it can negatively affect wildlife populations. However, wildlife population dynamics have not been studied in one of the most rapidly urbanizing regions in the world—the Neotropics. To examine the effect of urbanization on the population dynamics of Neotropical wildlife, we used recapture data from a marked population (2011–2017) of White-eared Ground-Sparrow (*Melozone leucotis*) across an urban–rural gradient in the Costa Rican Central Valley. Additionally, we tested if this effect differed between males and females. Contrary to our prediction, ground-sparrow survival rates were higher in urban and suburban sites than in the rural site, and we found that survival was positively correlated to the proportion of urban surface inside each territory ($\beta = 0.90$, 95% CI: 0.71–0.97). We did not find differences in survival rates between the sexes and the mean survival rate was high overall (0.79 ± 0.06). Surprisingly, our results suggest that the survival rate of this urban avoider is positively influenced by urbanization, and therefore, suggest that the potential cost to some urban avoiders may not be driven by reduced survival in more urbanized environments, and could be driven by reductions in other vital rates. Therefore, we encourage research to evaluate multiple vital rates of urban avoiders and urban adapters to achieve more comprehensive knowledge on how urbanization is affecting avian populations in the Neotropics.

Key words: apparent survival, *Melozone leucotis*, urban avoider, urban–rural gradient, White-eared Ground-Sparrow

Introduction

Urbanization has been identified as one of the main threats for biodiversity because of the negative impacts it can have on wildlife populations, including birds (United Nations Secretariat 2015). Worldwide urbanization is expected to increase—by 2050, 66% of the world's population will inhabit urban areas (United Nations Secretariat 2015) and under any scenario, at least 1.1 million km^2 on Earth will become urban land by 2100 (Gao and O'Neill 2020). This increase in urbanization results in degradation, fragmentation or disappearance of habitats, leading to a reduction in biodiversity because many species are incapable of dealing with the demographic impacts of the environmental changes that urbanization implies (Biamonte et al. 2011; González-Lagos and Quesada 2017).

For the Neotropics, there is limited information on how urbanization affects specific aspects of life-history parameters in wildlife populations, such as breeding success or survival (Sepp et al. 2018). However, urbanization likely affects key vital rates of animals and plants anywhere in the world through changes in food availability and quality, abundance and diversity of predators, and changes in environmental conditions (Sorace 2002; Leston and Rodewald 2006; Chamberlain et al. 2009; Rodewald, Kearns, and Shustack 2011). Studies in North America and Europe focused on birds found that survival of individuals inhabiting urban and rural habitats differs among (Chamberlain et al. 2009; Evans et al. 2015) and within species (McGowan 2001). For example, in adults of Great Tit (*Parus major*) and Northern Mockingbird (*Mimus polyglottos*), the survival rate is higher in urban than in rural habitats (Hõrak and Lebreton

1998; Stracey and Robinson 2012). Similarly, the survival rate of American Crow (*Corvus brachyrhynchos*) juveniles is higher in suburban than in rural habitats (McGowan 2001). However, survival of adult American Crows is not known to be affected by urbanization—they survive in urban habitats just as well as in suburban or rural habitats (McGowan 2001; Leston and Rodewald 2006). Unfortunately, with one exception, the effect of urbanization on survival of Neotropical birds has not been well studied (Chamberlain et al. 2009; Rebolo-Ifrán et al. 2015; González-Lagos and Quesada 2017; Sepp et al. 2018). In Argentina, the survival rate of Burrowing Owl (*Athene cunicularia*) was much higher for individuals in urban versus rural sites (Rebolo-Ifrán et al. 2015). Outside of the urbanization context, annual survival rates in the Neotropics have been estimated for ∼ 4% of all avian resident species (Ruiz-Gutiérrez et al. 2012; Lees et al. 2020), even though life history theory would predict that adult survival likely drives much of the population growth rates of these generally long-lived species. A recent publication about the shortfalls in Neotropical ornithology highlights the need for research on survival rates for Neotropical species because little progress has been made since 2012 (Lees et al. 2020).

Survival rates of individuals of the same species can also vary among sites in response to resource availability, predation risk, and climatic conditions (Blake and Loiselle 2002; Ruiz-Gutiérrez, Gavin, and Dhondt 2008; Shogren et al. 2019; Juárez, Chacón-Madrigal, and Sandoval 2020). For example, the survival rate of Swainson's Thrush (*Catharus ustulatus*) is lower in the Northwestern Interior Forest than in the Northern Rockies and the Atlantic Northern Forest (Saracco et al. 2009). Survival rates may also vary among males and females of the same species resulting from differences in predation risk and body condition between sexes (Marra and Holmes 2001; Blake and Loiselle 2002; Evans et al. 2015). In Greater Sage-Grouse (*Centrocercus urophasianus*) and Red-capped Manakin (*Ceratopipra mentalis*), females have higher survival rates than males, whereas in American Redstart (*Setophaga ruticilla*), males have higher survival rates than females (Marra and Holmes 2001; Blake and Loiselle 2002; Zablan, Braun, and White 2003). However, in Ruddy-capped Nightingale-Thrush (*Catharus frantzii*), White-ruffed Manakin (*Corapipo altera*), Common Blackbird (*Turdus merula*) and Burrowing Owl, no evidence was found for differences in survival among the sexes (Rangel-Salazar et al. 2008; Ruiz-Gutiérrez, Gavin, and Dhondt 2008; Robinson, Kew, and Kew 2010; Rebolo-Ifrán et al. 2015). Furthermore, differences in survival among males and females may also be a result of variation in reproductive costs among the sexes. Females and males may differ in energy expenditure and/or in exposure to predators during reproduction, which can vary along an urban landscape due to changes in food density, nest site cover, and in response to human disturbance (Breitwisch 1989; Leston and Rodewald 2006; Rodewald and Shustack 2008; Stracey and Robinson 2012; Juárez, Chacón-Madrigal, and Sandoval 2020).

Here, we examine differences in apparent survival, i.e. the product of true survival and site fidelity (Lebreton et al. 1992; White and Burnham 1999; Ruiz-Gutiérrez, Gavin, and Dhondt 2008), of a year-round territorial bird, the White-eared Ground-Sparrow (*Melozone leucotis*), that inhabits urban, suburban and rural sites (Sandoval and Mennill 2012; Sandoval, Méndez, and Mennill 2016). In this ground-sparrow, males sing and pairs deliver duets to defend territories (Sandoval, Méndez, and Mennill 2016). We believe that our estimates of apparent survival, hereafter survival rate, are indicative of true survival rate in this species because site fidelity is exceedingly high (L.S. unpublished data for 11 years) and similar to other year-round territorial bird

species (Illera and Díaz 2008). In addition, this territorial bird is an ideal focal species to study the effects of urbanization on bird populations because it is a Neotropical resident with a limited range whose densities are lower in urban relative to rural environments (Blair 1996; Sandoval et al. 2017; Juárez, Chacón-Madrigal, and Sandoval 2020). We consider this species an urban avoider because of the differences in densities along the urban–rural gradient and because it has larger territory sizes in urban areas compared with rural and natural ones (Juárez, Chacón-Madrigal, and Sandoval 2020). Additionally, inside urban areas it only occurs in remaining natural habitats (e.g. thickets and secondary forest) and when those areas are changed the ground-sparrows disappear (Sandoval and Mennill 2012). In addition, life-history characteristics such as nest location and habitat preference render this species vulnerable to anthropogenic disturbance (Clergeau et al. 2006; Sandoval and Mennill 2012; Sandoval, Dabelsteen, and Mennill 2015). This ground-sparrow nests directly on or near the ground and inhabits unprotected early successional vegetation like dense thickets of young secondary forest, forest edges, riverside vegetation, coffee plantations, natural regeneration patches within cities and densely vegetated gardens of urban and suburban environments (Sandoval and Mennill 2012; Juárez, Chacón-Madrigal, and Sandoval 2020). We specifically addressed three questions: (i) Are there differences in survival of White-eared Ground-Sparrow along an urban–rural gradient? And if so, (ii) do these differences vary between males and females? (iii) Is survival correlated to urbanization in this species? We predicted that birds captured at urban sites will have lower survival rates relative to those captured in suburban and rural sites. In addition, we predicted that survival rates will be negatively correlated with the proportion of urban surface per territory (e.g. urbanization), since this ground-sparrow qualifies as an urban avoider and urban environments may be the lowest quality habitat for the species. If survivorship in this ground-sparrow is mostly affected by investment in reproduction (e.g. parental care behavior), we predicted that females would have lower survival resulting from additional costs of reproduction from egg production, incubation and feeding nestlings (Sandoval and Mennill 2012).

Methods

Study sites

We conducted this study in an urban–rural gradient using three sites within the Costa Rican Central Valley (Fig. 1). Universidad de Costa Rica, San José (9.937°N, 84.050°W; elevation: 1210 m asl)—hereafter: urban site—showed higher levels of urban development where ∼ 60% of the area is urbanized or covered by impervious surface, and 40% are green areas (i.e. house gardens, urban parks, small natural reserves and small patches of secondary forest). Lankester Botanical Garden, Cartago (9.840°N, 83.890°W; elevation: 1370 m asl)—hereafter: suburban site—showed medium levels of urban development where ∼ 30% of the area is urbanized and 70% are green areas (i.e. house gardens and small patches of secondary forest). Getsemaní, Heredia (10.035°N, 84.112°W; elevation: 1330 m asl)—hereafter: rural site—showed low levels of urban development where <1% of the area is urbanized and 99% are green areas (i.e. coffee plantations, abandoned pastures and natural remnant vegetation).

The urban site is separated from the rural site by 12.5 km and from the suburban site by 20.7 km (Fig. 1). These sites are
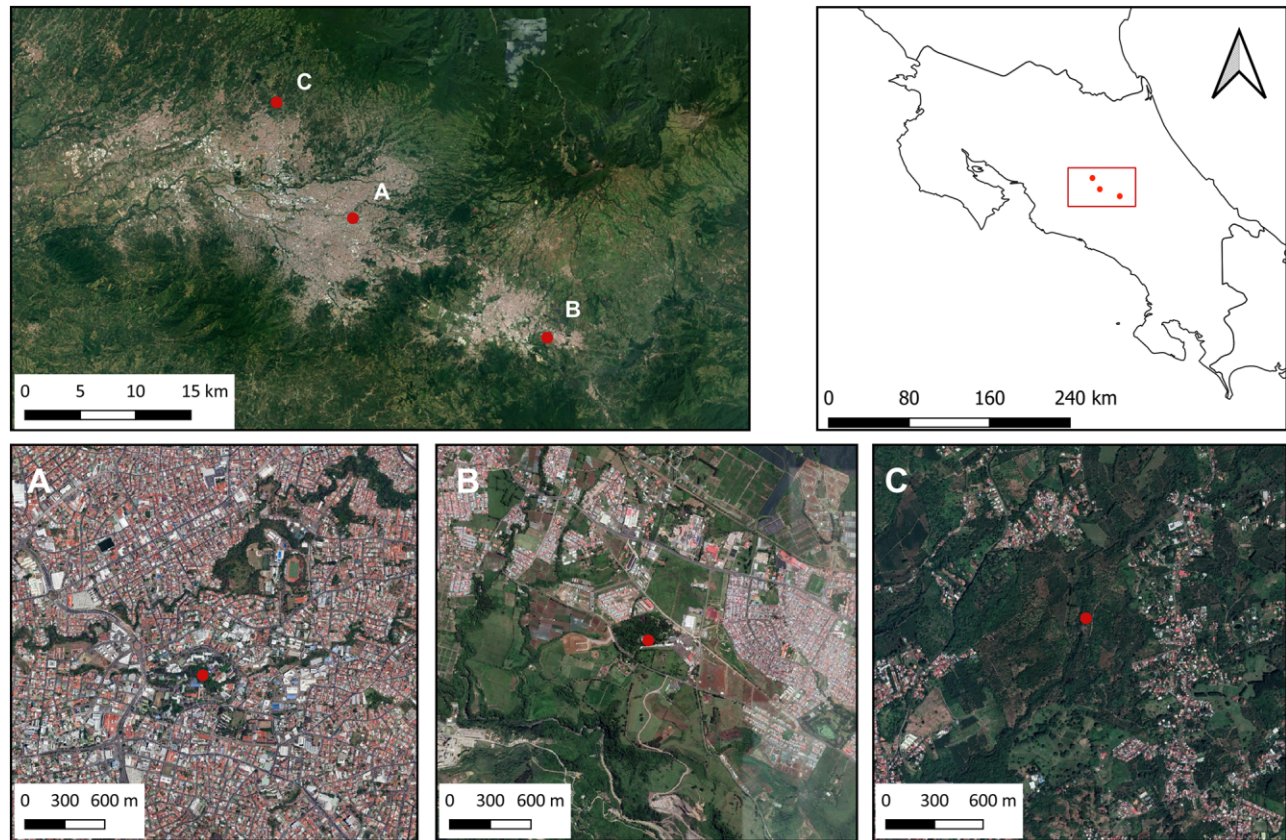
Figure 1: Map of the study sites within the Costa Rican Central Valley (upper left). The images at the bottom show the habitat of the urban (A), suburban (B) and rural (C) sites

located within the life zone known as Premontane Moist Forest (Tosi 1969). On average, these sites are subject to the same amount of precipitation and relative humidity (Supplementary Material). Further information about the habitats at these sites is presented in Juárez, Chacón-Madrigal, and Sandoval (2020).

Capture data

The study was carried out between March and July, from 2011 to 2017, during the species' breeding season (Sandoval and Mennill 2012). We visited each known territory twice per season between 5:00 and 9:00 am to capture, mark and resight each pair of individuals. This is the period when White-eared Ground-Sparrow is typically more active, and thus easier to observe and capture (Sandoval, Méndez, and Mennill 2016). We used mist-netting and playback (songs and duets of conspecifics) inside every territory to capture each individual. If birds were not captured after 5 min of playback, we visited another territory where at least one individual was not marked. If birds were not caught after a second attempt during the same breeding season, we tried again the following year, until the pair was successfully caught and marked. We marked each ground-sparrow with a numbered aluminum band and a unique combination of two-color bands. Following Sandoval and Mennill (2013), each bird was sexed by the combination of an incubation patch, present only in females, cloacal protuberance, present only in males, and wing length, since females have shorter wings. All individuals were released inside their territories.

We avoided recapturing banded individuals, since all marked birds are part of a long-term project that includes playback experiments for behavioral questions, and additional playbacks would have interfered with the experiments for that project. Therefore, we consider each time we observed an individual and identified the color band combination (i.e. resight) as a recapture event. Each pair was visited twice per breeding season for at least 1 h, between 5:00 and 9:00 am, to confirm their presence and identity. Therefore, our capture-resight data are annual. All individuals banded within a year remained in their territories during the entire study period. For each site, we studied at least 90% White-eared Ground-Sparrows that were present, since one or two pairs per site were in inaccessible locations.

Estimation of urban surface per territory

We first estimated the territory size of each pair by following and collecting Global Positioning System (GPS) points during two breeding seasons. We followed all focal individuals on two different days for 1 h, between 05:00 and 09:00 am. We avoided disturbing studied individuals by following them from a moderate distance (mean: 12 m, range: 8–16 m), and by wearing unobtrusive camouflage clothing. Using a GPS (GARMIN model map 62, accuracy $= 3$ m), we collected the coordinates of each location where focal individuals sang or perched after every period of observation. We collected the coordinates only when the GPS precision indicated ≤ 4 m. Then, we used the "adehabitat" package in R language and environment, version 3.3.3, to estimate the territory size as the minimum convex polygon using the sets of coordinates of each pair (Calenge 2006; R Core Team 2019). We calculated the minimum convex polygon for

individuals with at least five points per year (mean ± SE: 9 ± 0.6, range: 5–25). Finally, we classified the habitats available in each territory using two categories: (i) urban surface (roads, buildings and any other paved surface), and (ii) natural surface (thickets and secondary forest with well-developed understory). We measured the surface in every territory by manually drawing polygons of each type of surface using satellite images from April 2015, with a spatial resolution of 46 cm, and the land area calculator in Google Earth Pro. We used our field experience to distinguish between natural surface, lawns and gardens to draw the polygons.

Survival analysis

We estimated survival rate (ϕ, the probability that a marked individual was still alive and present within the territory) using the Cormack–Jolly–Seber (CJS) mark–recapture model (Lebreton et al. 1992). The CJS model is also parameterized to estimate recapture probability (P, the probability that an individual was observed, conditional of being alive and within the territory). As stated above, our recapture data correspond to annual resighting of banded individuals with a combination of color bands. For our first analysis, we used 82 individual capture histories to estimate survival rates and modeled survival as a function of sex and population type (urban, suburban and rural). The second analysis was restricted to estimate the survival rate only as a function of the proportion of urban surface per territory and included 47 individuals because for the other 35 individuals we were unable to collect enough data to estimate the proportion of urban surface per territory. We modeled survival and resighting probabilities as constant and as a function of the proportion of urban surface of each individual bird. We used Akaike's information criterion corrected for small sample sizes (AIC$_c$), and normalized Akaike weights (wi) for model selection (Burnham and Anderson 2002). For these analyses, we used the program MARK, version 9.0 (White and Burnham 1999). Survival rates are reported as mean ± SE (95% CI).

Mean life span

We estimated mean life span (MLS) from the estimated apparent survival rate (S), according to Brownie et al. (1985) using the function MLS = $1/-\ln(S)$. We use MLS because both pair members of White-eared Ground-Sparrow stay in and defend the same territory across multiple years (Brownie et al. 1985; Sandoval, Dabelsteen, and Mennill 2015).

Results

Captures, mean survival rate and mean resighting rate

From 2011 to 2017, we captured and banded 54 males and 28 females of White-eared Ground-Sparrow. We banded 27 individuals at the urban site, 22 at the suburban site and 33 individuals at the rural site. Mean annual survival probability for adults White-eared Ground-Sparrow in Costa Rican Central Valley was 0.79 ± 0.06 (0.72–0.85). The observed average resighting probability of marked White-eared Ground-Sparrows per year was 0.57 ± 0.24 (range = 0.33–0.88). During the last year of the study, 39% of marked birds were resighted alive. Mean annual resighting probability for this species was estimated as 0.65 ± 0.04 (0.61–0.69).

Survival rate along the urban–rural gradient

The analysis of survival for white-eared Ground-Sparrow along the urban–rural gradient suggests that survival probabilities differ among sites (Table 1). Although the model with survival as a function of site type received similar support as the one that specified survival as the same across sites, we believe that this is because survival did not differ among the suburban and urban sites. However, survival was estimated to be ~ 9% higher in the urban and suburban sites relative to the rural site (urban: 0.82 ± 0.10, 0.72–0.93; suburban: 0.82 ± 0.09, 0.72–0.90; rural: 0.72 ± 0.07, 0.64–0.80; Fig. 2B). This finding is more evident through the strong support we found for model that specified annual survival rates as a function of the proportion of urban surface inside each territory (AIC$_c$ weight = 87%; Table 1). Survival probabilities increased with an increase in the proportion of urban surface (β = 0.90, 95% CI: 0.71–0.97).

Survival rate by sex

The model with the most support informed by data from adults of known sex was one that specified constant survival and resight probabilities, i.e. $\phi(.)$ and $p(.)$. This is evidenced by overlapping confidence intervals of estimates of survival rates for adult males and females (males: 0.82 ± 0.09, 0.70–0.90; females: 0.75 ± 0.07, 0.67–0.83). Therefore, we do not have enough evidence to support a difference in survival rates among sexes (Fig. 2A and Table 1).

Life span and longevity records

Based on the resighting records of 82 banded individuals and the unambiguous identification of the color band combination, 10 were known to have survived at least 1 year, 17 at least 2 years, 23 at least 3 years and 16 at least 4 years, then rapidly declining to only 8 individuals surviving at least 5 years, 4 at least 6 years and 4 at least 7 years. The estimated MLS in years for this species is 5.3 ± 1.00 in the urban site, 5.3 ± 0.96 in the suburban site and 3.3 ± 0.91 in the rural site. MLS for adult White-eared Ground-Sparrow in the Costa Rican Central Valley was 4.2 ± 0.36 (3.0–6.2 years).

Discussion

Our results suggest that high survival rates may help year-round populations of territorial birds in the Neotropics persist in cities. We found that the survival rate of White-eared Ground-Sparrow is positively related to the proportion of urban surface inside the territories. In line with our result, a positive relationship between the proportion of urban surface and survival rates has been found in adults of Gray Catbird, *Dumetella carolinensis*, as well as in adults and juveniles of Northern Cardinal, *Cardinalis cardinalis* (Ausprey and Rodewald 2011; Evans et al. 2015). In White-eared Ground-Sparrow, this result may be explained by a positive correlation between the proportion of urban surface with territory size, which in turn is positively related to the availability of natural habitat, i.e. dense thickets of secondary growth, preferred by ground-sparrows (Juárez, Chacón-Madrigal and Sandoval 2020). It could also be argued that the positive correlation between White-eared Ground-Sparrow survival rate and urban surface is due to the lower predation pressure in urban environments (Chamberlain et al. 2009; Rodewald, Kearns, and Shustack 2011, Rebolo-Ifrán et al. 2015). Unfortunately, predation data on this species along the urban–rural gradient are lacking and we cannot confirm

Table 1: Model selection tables for CJS models of survival (ϕ) and resighting rates (p) for adult White-eared Ground-Sparrow inhabiting the Costa Rican Central Valley, from 2011 to 2017

Model	AIC_c[a]	ΔAIC_c[b]	AIC_c weight	Model likelihood	Parameters	Deviance
Sex						
$\phi(.)\,p(.)$	242.01	0.00	0.43	1.00	2	13.95
$\phi(s)\,p(.)$	242.77	0.76	0.29	0.68	3	12.66
$\phi(.)\,p(s)$	243.90	1.89	0.17	0.39	3	13.79
$\phi(s)\,p(s)$	244.81	2.81	0.11	0.25	4	12.63
Urban–rural gradient						
$\phi(.)\,p(.)$	242.01	0.00	0.50	1.00	2	60.90
$\phi(g)\,p(.)$	243.04	1.03	0.30	0.60	4	57.81
$\phi(g)\,p(g)$	244.90	2.89	0.12	0.24	6	55.46
$\phi(.)\,p(g)$	245.85	3.85	0.07	0.15	4	60.61
Proportion of urban surface						
$\phi(us)\,p(.)$	140.28	0.00	0.87	1.00	2	136.20
$\phi(.)\,p(.)$	144.14	3.85	0.13	0.14	2	140.05

Annual survival and resighting probabilities were modeled to evaluate differences among sex (s), urban–rural gradient (g), proportion of urban surface (us) or constant (.).
[a]Models were constructed by CJS model in Program MARK ranked by Akaike's information criterion corrected for small sample sizes (AIC_c).
[b]ΔAIC_c is the difference between each model and the best-fitting one.
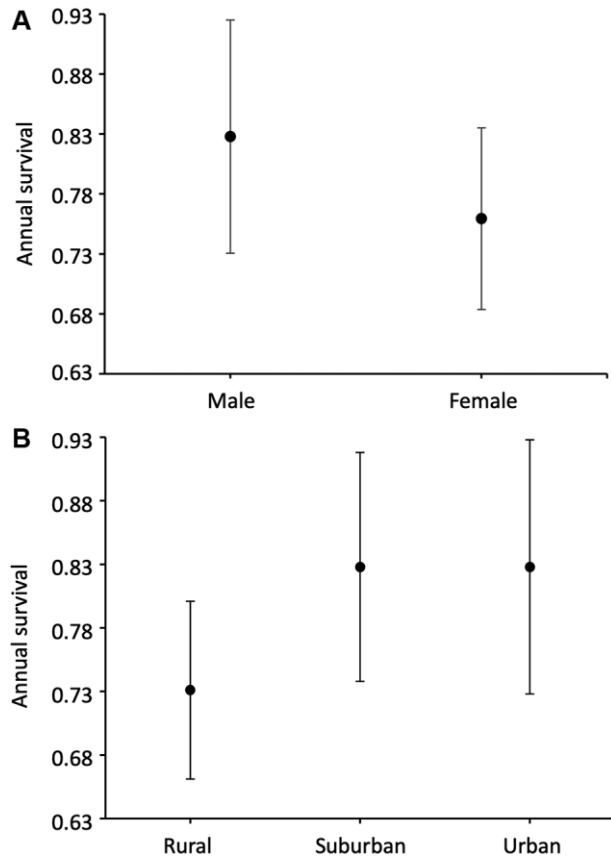
Figure 2: Model-averaged estimates of apparent adult survival rates ± SE by sex (A) and for each site (B) for White-eared Ground-Sparrow in the Central Valley in Costa Rica

that high survival rates are associated with low predation rates in more urbanized environments. For White-eared Ground-Sparrow, there is no information on predation or recorded predators, which impedes quantifying predation pressure along the urban–rural gradient. Supplemental food has also been shown to improve survival rates, and although some urban sites provide easily available food resources (Brittingham and Temple 1988; Chamberlain et al. 2009), food supplementation may not explain the positive correlation between urban surface and survival for our focal species. Because the diet of White-eared Ground-Sparrow consists of small seeds and fruits of native plants (e.g. *Bidens pilosa*, *Ficus* sp., *Stemmadenia donnell-smithii* and *Iochroma arborescens*), and insects (Sandoval and Mennill 2012). White-eared Ground-Sparrow does not scavenge for food scraps or approach to humans in urban areas for food.

Our analysis of survival rates along the urban–rural gradient in this species, an urban avoider, suggests that survival rates for this species group can be lower in rural environments compared with more urban settings. This result is evidenced by the positive relationship between the proportion of urban surface and survival found in our study, and supports similar results of survival rates along the urban–rural gradient (Hõrak and Lebreton 2008; McGowan 2001; Stracey and Robinson 2012). For example, higher survival rates in urban environments compared with rural have been documented in Great Tit and Northern Mockingbird (Hõrak and Lebreton 1998; Stracey and Robinson 2012). For the White-eared Ground-Sparrow, higher survival rates in urban environments may result from behavioral changes, such as defending larger territories, learning to distinguish disturbance from real danger, breeding when there are sufficient resources, and nesting in the safest places. Our findings of survival for a year-round territorial bird in the Neotropics are suggestive of the general trend of a slow pace-of-life, i.e. higher survival rate and low reproduction rate, of urban-dwelling birds found in temperate zones (Sepp et al. 2018).

We note that our estimated rates of survival of White-eared Ground-Sparrow are high. However, high survival similarly occurs in other genera of this family, as has been documented in Orange-billed Sparrow (*Arremon aurantiirostris*), as well as in other passerines (Wilson, Collister, and Wilson 2011; Shogren et al. 2019). Another aspect that we analyzed while reviewing these results is that some species of *Melozone* have a long-life span, i.e. more than 8 years (Klimkiewicz and Futcher 1987, Benedict et al. 2020), and at first it may seem that the time frame in which the study was carried out was not ideal to estimate differences in annual survival rates. However, based on our own estimation of the life span of White-eared

Ground-sparrow, 4.2 years on average, and considering that most individuals were only known to survive 3 years, our 7-year study is adequate to estimate survival in this species. Furthermore, the time frame used in this study is equal to that used in other survival studies of species with high survival rates (e.g. Wilson, Collister, and Wilson 2011) and is in line with what is suggested to estimate apparent survival for neotropical passerines (Blake and Loiselle 2013).

We expected to find a difference in survival rates among sexes since females invest more in reproduction than males (Sandoval and Mennill 2012). This increased investment may render females more vulnerable to predators, as has been shown in Wood Thrush (*Hylocichla mustelina*, Powell et al. 2000). However, our results did not show differences in survival rates between sexes. Similar survival rates for males and females have been documented in Ruddy-capped Nightingale-Thrush, White-ruffed Manakin and Common Blackbird (Rangel-Salazar et al. 2008; Ruiz-Gutiérrez, Gavin, and Dhondt 2008; Robinson, Kew, and Kew 2010). A lack of support for differences in survival rates might be due to low sample sizes, given the difference in estimates and high degree of overlap in the confidence intervals among females and males. Similarity in survival rates between the sexes may also reflect similar predation risks for either sex for this ground-sparrow, and because females and males inhabit the same territory year-round (Sandoval, Dabelsteen, and Mennill 2015), they may also have similar access to food resources. The pair cooperation extends to predator signaling, as either may give the same alarm call to which the partner responds, spreading predation risk equally (Sandoval, Méndez, and Mennill 2016). During the breeding season, males search and indicate the presence of food items to females (Sandoval and Mennill 2012).

In conclusion, our study of adult White-eared Ground-Sparrows in the Costa Rican Central Valley shows that the survival of this species increases with the proportion of urban surface within the territory. We also found differences in survival rates between rural and urban sites, but we did not find support for differences in survival rates between sexes. Our results suggest that investing in survival may help a Neotropical bird species with year-round territories to persist in urban environments. We encourage research to investigate whether urban environments are advantageous or constitute a demographic sink for White-eared Ground-Sparrow populations. Understanding the differences in survival rates and reproductive success of Neotropical birds along the urbanization gradient will contribute to the conservation of unique species restricted to urban environments.

Supplementary data

Supplementary data are available at *JUECOL* online.

Acknowledgements

Funding

Data availability

Data sets used for analyses in this study are available upon request to the corresponding author.

Conflict of interest statement. None declared.

References

Ausprey, I. J., and Rodewald, A. D. (2011) 'Postfledging Survivorship and Habitat Selection across a Rural-to-Urban Landscape Gradient', *The Auk*, **128**: 293–302.

Benedict, L. et al. (2020). 'California Towhee (*Melozone crissalis*)', in A. F. Poole (ed.) *Birds of the World*, Ithaca, NY: Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.caltow.01> accessed 21 January 2022.

Biamonte, E. et al. (2011) 'Effect of Urbanization on the Avifauna in a Tropical Metropolitan Area', *Landscape Ecology*, **26**: 183–94.

Blair, R. B. (1996) 'Land Use and Avian Species Diversity along an Urban Gradient', *Ecological Applications*, **6**: 506–19.

Blake, J. G., and Loiselle, B. A. (2002) 'Manakins (Pipridae) in Second-Growth and Old-Growth Forests: Patterns of Habitat Use, Movement, and Survival', *The Auk*, **119**: 132–48.

——, and —— (2013) 'Apparent Survival Rates of Forest Birds in Eastern Ecuador Revisited: Improvement in Precision but No Change in Estimates', *PLoS One*, **8**: e81028.

Breitwisch, R. (1989). 'Mortality Patterns, Sex Ratios, and Parental Investment in Monogamous Birds', in D. M. Power (ed.) *Current Ornithology*, pp. 1–50. New York: Springer Science+Business Media LLC.

Brittingham, M. C., and Temple, S. A. (1988) 'Impacts of Supplemental Feeding on Survival Rates of Black-Capped Chickadees', *Ecology*, **69**: 581–9.

Burnham, K. P., and Anderson, D. R. (2002). A Practical Information-Theoretic Approach. *Model Selection and Multimodel Inference*. New York: Springer.

Brownie, C. et al. (1985) 'Statistical Inference from Band Recovery Data: A Handbook. U.S. Fish and Wildlife Service', *Fish Wildlife Technicel Reports*, **156**: 1–305.

Calenge, C. (2006) 'The Package "Adehabitat" for the R Software: A Tool for the Analysis of Space and Habitat Use by Animals', *Ecological Modelling*, **197**: 516–9.

Chamberlain, D. E. et al. (2009) 'Avian Productivity in Urban Landscapes: A Review and Meta-Analysis', *Ibis*, **151**: 1–18.

Clergeau, P. et al. (2006) 'Avifauna Homogenisation by Urbanisation: Analysis at Different European Latitudes', *Biological Conservation*, **127**: 336–44.

Evans, B. S. et al. (2015) 'Characterizing Avian Survival along a Rural-to-Urban Land Use Gradient', *Ecology*, **96**: 1631–40.

Gao, J., and O'Neill, B. C. (2020) 'Mapping Global Urban Land for the 21st Century with Data-Driven Simulations and Shared Socioeconomic Pathways', *Nature Communications*, **11**: 12.

González-Lagos, C., and Quesada, J. (2017). 'Stay or Leave? Avian Behavioral Responses to Urbanization in Latin America', in I. MacGregor-Fors, and J. F. Escobar-Ibáñez (eds) *Avian Ecology in Latin American Cityscapes*, pp. 99–123. Cham: Springer International Publishing.

Hõrak, P., and Lebreton, J. D. (1998) 'Survival of Adult Great Tits *Parus major* in Relation to Sex and Habitat; A Comparison of Urban and Rural Populations', *Ibis*, **140**: 205–9.

Illera, J. C., and Díaz, M. (2008) 'Site Fidelity in the Canary Islands Stonechat *Saxicola dacotiae* in Relation to Spatial and Temporal Patterns of Habitat Suitability', *Acta Oecologica*, **34**: 1–8.

Juárez, R., Chacón-Madrigal, E., and Sandoval, L. (2020) 'Urbanization Has Opposite Effects on the Territory Size of Two Passerine Birds', *Avian Research*, **11**: 1–9.

Klimkiewicz, K., and Futcher, A. G. (1987) 'Longevity Records of North American Birds: Coerebinae Through Estrildidae', *Journal of Field Ornithology*, **58**: 318–33.

Lebreton, J. D. et al. (1992) 'Modeling Survival and Testing Biological Hypotheses Using Marked Animals: A Unified Approach with Case Studies', *Ecological Monographs*, **62**: 67–118.

Lees, A. C. et al. (2020) 'A Roadmap to Identifying and Filling Shortfalls in Neotropical Ornithology', *The Auk*, **137**: 1–17.

Leston, L. F., and Rodewald, A. D. (2006) 'Are Urban Forests Ecological Traps for Understory Birds? An Examination Using Northern Cardinals', *Biological Conservation*, **131**: 566–74.

Marra, P. P., and Holmes, R. T. (2001) 'Consequences of Dominance-Mediated Habitat Segregation in American Redstarts During the Nonbreeding Season', *The Auk*, **118**: 92–104.

McGowan, K. J. (2001). 'Demographic and Behavioral Comparisons of Suburban and Rural American Crows', in J. M. Marzluff, R. Bowman, and R. Donelly (eds) *Avian Ecology and Conservation in an Urbanizing World*, pp. 365–381. NY: Springer Science+Business Media LLC.

Powell, L. A. et al. (2000) 'Effects of Forest Management on Density, Survival, and Population Growth of Wood Thrushes', *The Journal of Wildlife Management*, **64**: 11–23.

Rangel-Salazar, J. L. et al. (2008) 'Population Dynamics of the Ruddy-Capped Nightingale Thrush (*Catharus frantzii*) in Chiapas, Mexico: Influences of Density, Productivity and Survival', *Journal of Tropical Ecology*, **24**: 583–93.

R Core Team. (2019). *A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rebolo-Ifrán, N. et al. (2015) 'Links between Fear of Humans, Stress and Survival Support a Non-Random Distribution of Birds among Urban and Rural Habitats', *Scientific Reports*, **5**: 1–10.

Robinson, R. A., Kew, J. J., and Kew, A. J. (2010) 'Survival of Suburban Blackbirds *Turdus merula* Varies Seasonally but Not by Sex', *Journal of Avian Biology*, **41**: 83–7.

Rodewald, A. D., and Shustack, D. P. (2008) 'Urban Flight: Understanding Individual and Population-Level Responses of Nearctic–Neotropical Migratory Birds to Urbanization', *The Journal of Animal Ecology*, **77**: 83–91.

——, Kearns, L. J., and Shustack, D. P. (2011) 'Anthropogenic Resource Subsidies Decouple Predator–Prey Relationships', *Ecological Applications*, **21**: 936–43.

Ruiz-Gutiérrez, V., Gavin, T. A., and Dhondt, A. A. (2008) 'Habitat Fragmentation Lowers Survival of a Tropical Forest Bird', *Ecological Applications*, **18**: 838–46.

—— et al. (2012) 'Survival of Resident Neotropical Birds: Considerations for Sampling and Analysis Based on 20 Years of Bird-Banding Efforts in Mexico', *The Auk*, **129**: 500–9.

Sandoval, L., and Mennill, D. J. (2012) 'Breeding Biology of White-Eared Ground-Sparrow (*Melozone leucotis*), with a Description of a New Nest Type', *Ornitología Neotropical*, **23**: 225–34.

——, and —— (2013) 'Morphometric Measurements Permit Accurate Sexing of Three Species of Mesoamerican Ground-Sparrow (Genus: *Melozone*)', *The Wilson Journal of Ornithology*, **125**: 471–8.

——, Dabelsteen, T., and Mennill, D. J. (2015) 'Transmission Characteristics of Solo Songs and Duets in a Neotropical Thicket Habitat Specialist Bird', *Bioacoustics*, **24**: 289–306.

——, Méndez, C., and —— (2016) 'Vocal Behaviour of White-Eared Ground-Sparrows (*Melozone leucotis*) during the Breeding Season: Repertoires, Diel Variation, Behavioural Contexts, and Individual Distinctiveness', *Journal of Ornithology*, **157**: 1–12.

—— et al. (2017) 'The Biogeographic and Evolutionary History of an Endemic Clade of Middle American Sparrows: *Melozone* and *Aimophila* (Aves: Passerellidae)', *Molecular Phylogenetics and Evolution*, **110**: 50–9.

Saracco, J. F. et al. (2009). 'Using the MAPS and MoSI Programs to Monitor Landbirds and Inform Conservation', in T. D. Rich, C. D. Thompson, D. Demarest, and C. Arizmendi (eds) *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics*, pp. 651–658. Edinburg, TX: University of Texas-Pan American Press.

Sepp, T. et al. (2018) 'A Review of Urban Impacts on Avian Life-History Evolution: Does City Living Lead to Slower Pace of Life?', *Global Change Biology*, **24**: 1452–69.

Shogren, E. H. et al. (2019) 'Apparent Survival of Tropical Birds in a Wet, Premontane Forest in Costa Rica', *Journal of Field Ornithology*, **90**: 117–27.

Sorace, A. (2002) 'High Density of Bird and Pest Species in Urban Habitats and the Role of Predator Abundance', *Ornis Fennica*, **79**: 60–71.

Stracey, C. M., and Robinson, S. K. (2012) 'Are Urban Habitats Ecological Traps for a Native Songbird? Season-Long Productivity, Apparent Survival, and Site Fidelity in Urban and Rural Habitats', *Journal of Avian Biology*, **43**: 50–60.

Tosi, J. A. (1969). *Mapa Ecológico, República de Costa Rica; Según la Clasificación de Zonas de Vida Del Mundo de L. R. Holdridge*. San José, Costa Rica: Tropical Science Center.

United Nations Secretariat. (2015). *World Urbanization Prospects: The 2014 Revision*. New York: Department of Economic and Social Affairs, Population Division.

Wilson, S., Collister, D. M., and Wilson, A. G. (2011) 'Community Composition and Annual Survival of Lowland Tropical Forest Birds on the Osa Peninsula, Costa Rica', *Ornitología Neotropical*, **22**: 421–36.

White, G. C., and Burnham, K. P. (1999) 'Program MARK: Survival Estimation from Populations of Marked Animals', *Bird Study*, **46**: S120–139.

Zablan, M. A., Braun, C. E., and White, G. C. (2003) 'Estimation of Greater Sage-Grouse Survival in North Park, Colorado', *The Journal of Wildlife Management*, **67**: 144–54.