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ORIGINAL ARTICLE

Territory size, population density, and natural history of Cabanis's Ground Sparrow, an endemic species found in urban areas

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Abstract

Worldwide urban expansion threatens biodiversity inhabiting the original natural environments now being transformed, especially range-restricted species. Here, we provide estimates of population density, population size, and territory size of Cabanis's Ground Sparrow *Melozone cabanisi*, a Costa Rican endemic. Additionally, we provide information about its life history. We measured abundance and estimated density using the King model. We estimated population size using density data and available habitat. We estimated territory size by following 21 pairs during the breeding season. We followed every individual for 1–3 days, for at least 1 h per day, and geo-referenced their locations. We then estimated territory size using the minimum convex polygon method. Counts and territory size observations were carried out between 06:00 and 09:00 h, when this species is most active. We summarized natural history from opportunistic observations collected during 20 years in the field as well as data from museum specimens. Bird densities range from 0.06 to 0.24 mature individuals per hectare. We estimated that the global population of Cabanis's Ground Sparrow is between 2958 and 11,832 mature individuals. Territory size was larger at the suburban and urban sites than at the rural sites. The breeding season for this species spans 10 months with a peak in June–July. Nest architecture is less variable than that reported for other congeners. Both parents feed and defend their nestlings and provide nest sanitation. Since we found lower bird density and larger territory size at the suburban and urban sites, we propose that these represent lower-quality habitats for Cabanis's Ground Sparrows. Given its small population size, the reduction and fragmentation of its habitats due to urbanization, and its high conservation priority assigned by the Costa Rican government, we urgently recommend a careful re-evaluation of the species' IUCN status.

Keywords Breeding ecology · Conservation · IUCN status · *Melozone cabanisi* · New World sparrows · Urban areas

Introduction

Urbanization has been identified as one of the biggest threats to biodiversity as urban areas are expanding worldwide and transforming natural habitats (Seto et al. 2012; United Nations Secretariat 2015). Worldwide urbanization is expected to continue expanding, and by 2050, 66% of humans will inhabit urban areas and 34% rural areas (United Nations Secretariat 2015). As urbanization increases, natural habitats around or inside those areas are being lost or fragmented, which leads to a reduction in biodiversity (Bolger et al. 1997; Biamonte et al. 2011; Fontúrbel et al. 2015). In urban environments, besides the urban surface, other types of habitats are generally present including remnants of previous natural habitats, natural or artificial water bodies, lawns, gardens, and early successional habitats of cleared and undeveloped areas (Bolger et al. 1997; Biamonte et al. 2011; Sandoval et al. 2019).

Early successional habitats occur across almost all continents and are common on disused lands within urban areas. These habitats have been largely left unprotected in many countries because they are seen as states before the recovery of natural, uninteresting, or even unappealing habitats (Askins 2001; Sandoval et al. 2019). Early successional habitats are home to numerous generalists, e.g., Blue Grosbeak *Passerina caerulea*, Yellow-breasted Chat *Icteria virens*, or Common Nightingale *Luscinia megarhynchos*, and specialists, e.g., White-eared Ground Sparrow *Melozone leucotis*,

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or Golden-winged Warbler *Vermivora chrysoptera* (Shugart-Jr and James 1973; Wilson et al. 2005; Confer et al. 2020; Sandoval and Mennill 2013; Sandoval et al. 2019). For instance, Northern Cardinal *Cardinalis cardinalis*, a generalist species that breeds in North America, is found in habitats in different successional stages all year, while Wilson's Warbler *Cardellina pusilla*, another generalist species, is found in these habitats only during the breeding season (Dow 1969; Dettmers 2003). Resident and migratory species rely on these types of habitats for food and breeding sites (Shugart-Jr and James 1973; Sandoval et al. 2019).

Small fragments of natural and successional habitats in urban areas provide food, roosting, and reproductive sites for many species, but not for others, even though the habitat itself is right, because some species are sensitive to edge effects and isolation associated with fragmentation (Hoover et al. 1995; Askins 2001). The lack of connection between fragments, the edge effect, and environmental stochasticity may cause genetic drift, reduction in population sizes, and eventually local extinctions (Bolger et al. 1997; Delaney 2014). As urbanization increases, more predators, diseases, and invasive species arrive in the remaining fragments of natural and successional habitats, reducing the survival of the individuals that still inhabit them (Marzluff and Rodewald 2008; Robinson et al. 2010). Not all species respond equally to these changes produced by urbanization; while some species become more abundant and are called urban dwellers, other species become less abundant and are called urban utilizers if they keep living in urban areas or avoiders if they disappear entirely (Donnelly and Marzluff 2006; Rodewald and Shustack 2008; González-Lagos and Quesada 2017). However, utilizer species may become avoiders if the habitats they use inside urban areas disappear.

Cabanis's Ground Sparrow *Melozone cabanisi* is an urban utilizer species, endemic to Costa Rica, which inhabits dense thickets, young secondary successional habitats, and agricultural fields such as coffee and chayote plantations (Stiles 1990; Sandoval et al. 2014, 2019). This species occurs across the Costa Rican Central Valley, Orosí Valley, and Turrialba Valley where urbanization and human population have increased dramatically over a 37-year period between 1973 and 2010 (Joyce 2006; Biamonte et al. 2011; Pujol and Pérez 2012; Muñoz et al. 2021). The latest urban development report from Costa Rica indicates that 15,186 ha of vegetated surface was converted into urban surface, which represents a 93% increase in urbanization within the Central Valley between 1982 and 2012 (Martínez 2014). Furthermore, the report also suggests that the increase in urbanization did not slow down—in fact, the rate of urbanization even accelerated slightly during the last 7 years compared to the previous 20 years (Martínez 2014). During the same period, human population in the Central Valley increased by 74% (Pujol and Pérez 2012). Most areas where this ground sparrow occurs lack any protection under Costa Rican legislation (Sandoval et al. 2014; Muñoz et al. 2021), and therefore, its habitats are subject to constant changes and loss (Sánchez et al. 2009; Biamonte et al. 2011; Sandoval et al. 2019). Although the systematics, distribution, and vocalizations of this ground sparrow are relatively well known (Sandoval and Mennill 2013; Sandoval et al. 2014, 2017; Muñoz et al. 2021), other aspects of its natural history are less understood. There is little information about this species' diet, reproductive biology, territorial behavior, lifespan, survivorship, dispersal, and population size. Until recently, Cabanis's Ground Sparrow was considered a subspecies of Prevost's Ground Sparrow *Melozone biarcuata* (Sandoval et al. 2014; Chesser et al. 2017; Sandoval et al. 2017). As recent as August 2020, its IUCN status was Least Concern, and the number of mature individuals was unknown (BirdLife International 2020). In this study, we have three objectives: (1) to estimate population densities and population size of Cabanis's Ground Sparrow, (2) to estimate the territory size of Cabanis's Ground Sparrow, and (3) to improve our knowledge about the species' natural history (e.g., breeding season, nest and egg quantitative data, and juvenile plumage development).

Methods

Study area

We carried out fieldwork at four main sites within the Costa Rican Central Valley (Fig. 1), which vary in the amount of forest and urban surface (defined below in "Urban surface estimate and site classification").

(1) Ujarrás (09°49′30″N; 83°49′55″W; 1019 m a.s.l.), Cartago province. The habitat at this site is a mix of secondary forest patches, agricultural areas, and a few isolated buildings. The small forest fragments are dominated by trees such as *Ficus* spp. (Moraceae), *Inga* spp. (Fabaceae), *Lonchocarpus* spp. (Fabaceae), and *Erythrina* spp. (Fabaceae) with dense understories. An artificial lake, Lake Cachí, created by the Cachí Dam, is less than 1 km away.
(2) Getsemaní (10°01′44″N; 84°06′44″W; 1300 m a.s.l.), Heredia province. The habitat at this site is a mix of a large secondary forest, an abandoned shaded coffee plantation (*Coffea arabica*), and a few isolated buildings. The forest is dominated by trees such as *Ficus* spp. (Moraceae), *Inga* spp. (Fabaceae), *Lonchocarpus* spp. (Fabaceae), and *Erythrina* spp. (Fabaceae) with an understory of dense shrubs and vines (Juárez et al. 2020).
(3) Calle Hernandez (10°02′11″N; 84°05′09″W; 1600 m a.s.l.), Heredia province. The habitat at this site is a

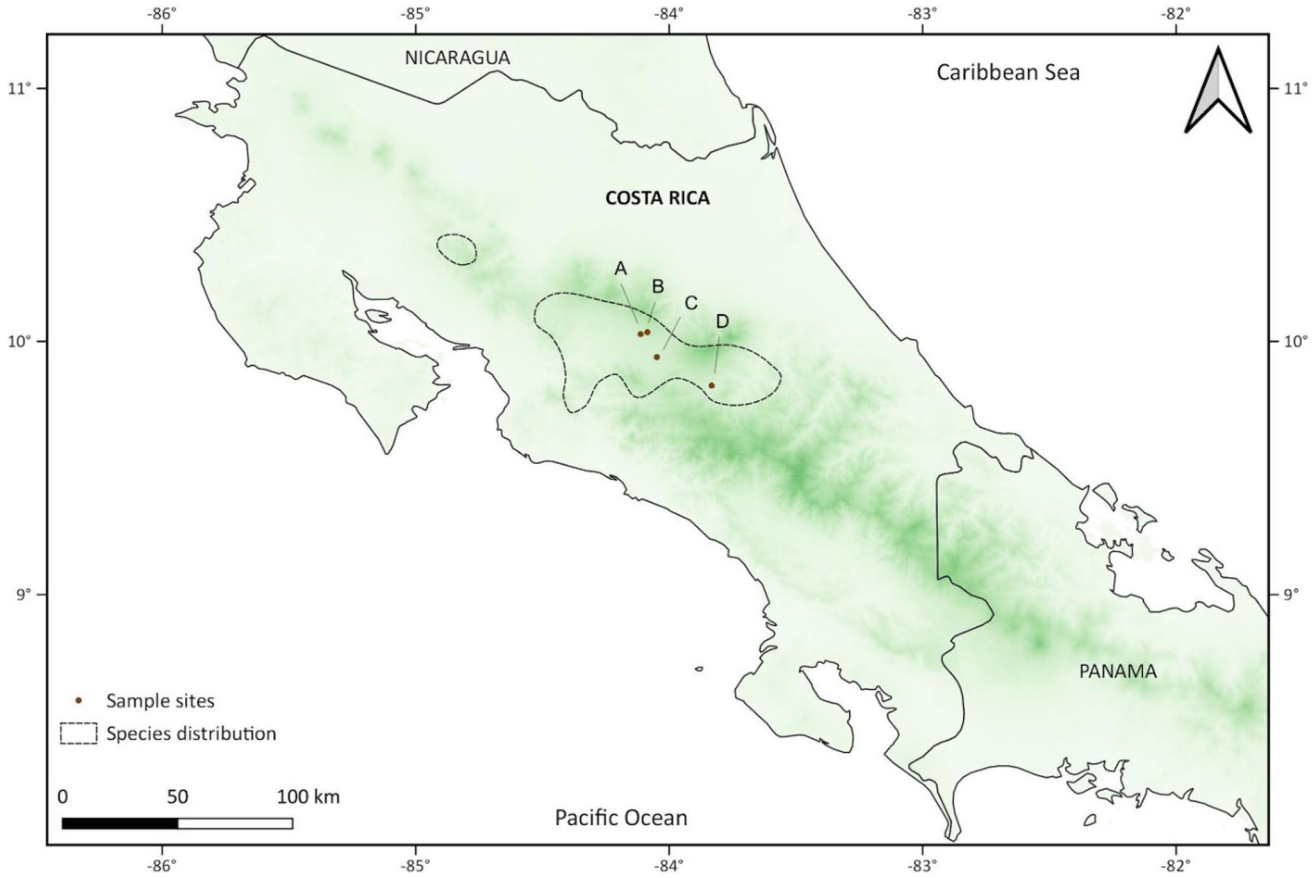

Fig. 1 Distribution range of Cabanis's Ground Sparrow, *Melozone cabanisi*. The solid brown dots indicate sample sites. The dotted area delimits the range for this Costa Rican endemic species according to BirdLife International and Handbook of the Birds of the World (2020). Letters represent the main localities sampled: (A) Getsemaní, Heredia province; (B) Calle Hernandez, Heredia province; (C) Universidad de Costa Rica, San José province; (D) Ujarrás, Cartago province

mix of secondary forest patches, residential areas with gardens, and industrial buildings. The small forest fragments are dominated by trees such as *Ficus* spp. (Moraceae) and *Inga* spp. with dense shrubs and vines.

(4) Universidad de Costa Rica (09°56′17″N; 84°02′54″W; 1200 m a.s.l.), San José province. The habitat at this site is a mix of secondary forest patches, including a 1.93-ha forest reserve, surrounded by residential and industrial areas with gardens, and few isolated trees. The reserve is a 50-year-old secondary growth forest composed of trees such as *Ficus* spp. (Moraceae), *Erythrina poeppigiana* (Fabaceae), and *Cordia eriostigma* (Boraginaceae) with an understory of palms, dense bushes, and some vines (Sandoval et al. 2019).

The Costa Rican Central Valley, originally covered by Premontane Moist Forest, was deforested almost two centuries ago (Tosi 1969; Stiles 1990; Biamonte et al. 2011). For most of the twentieth century, the predominant land use in the Central Valley was the cultivation of coffee (Stiles 1990). Since the late 1960s, the habitats there started changing from being dominated by traditional shaded coffee plantations and other agricultural systems to one dominated by urban and suburban developments (Stiles 1990; Pujol and Pérez 2012; Martínez 2014). The climate of the area is characterized by a dry season with little or no rain between December and April, and a wet season between May and November. In the Central Valley, the average annual precipitation and average temperature are 155 ± 120 mm and 20 ± 1 °C throughout the year.

Density and population size estimates

To estimate the population density of Cabanis's Ground Sparrow, we conducted line transects samples at four sites in Costa Rica with habitat for this species (Fig. 1; Table 1). The number of visits to each site varied from four to 89 from 2003 to 2018, between January and December. The number of visits varied in function of the type of studies conducted at each site over the 15-year period. Thus, sites where we conduct long-term avian studies (Getsemaní or Universidad de Costa Rica) were visited more often than other sites. Each

Table 1 Estimates of density and territory size for Cabanis's Ground Sparrow. Density per site (average ± SD) using a lineal transect with different lengths and 25-m width at each site is presented. Territory size per site (average ± SE) using the minimum convex polygon method is presented. It is worth noting that sampled size refers to the number of visits to each site during the sampling period. Each site was visited 4, 89, 5, and 70 times respectively, during the sampling period

Site	Habitat type	Urban surface (%)	Number of transects	Transect distance (km)	Sampling period	Density (individuals/ha)	Territory size (ha)
Ujarrás	Rural	3	2	0.5	2010–2012	0.24 ± 0.34	0.53 ± 0.19
Getsemaní	Rural	7	1	3	2003–2010	0.06 ± 0.10	0.60 ± 0.11
Calle Hernandez	Suburban	19	1	1	2010–2012	0.20 ± 0.28	0.85 ± 0.22
Universidad de Costa Rica	Urban	61	3	1	2004–2018	0.14 ± 0.23	0.79 ± 0.14

transect was replicated over the 15-year period to obtain a better abundance estimate, and therefore, a more precise density and population estimation. Although not all transects were equally replicated, note that the standard deviation is relatively low at each location (Table 1), which makes the population estimates more robust. In each visit, we conducted surveys by walking at a steady pace along transects that varied in length between 0.5 and 3 km and were 25 m wide at each side of the transect line (Table 1). We selected 25 m wide as our limit to avoid that variation in habitat density affected the individuals' detectability. Surveys were conducted between 06:00 and 09:00 h, when this species is more vocally and physically active (Sandoval et al. 2014). The minimum time between two consecutive samples in the same transect was 15 days. Cabanis's Ground Sparrow abundance was recorded by noting the number of mature individuals heard or seen during walks. Given that this species is territorial year-round (Stiles and Skutch 1989; Sandoval et al. 2014), any individual recorded at more than 100 m from the previous one was considered a different individual. The ground sparrow's density per site was estimated using the King model, as per Silva and Strahl (1997), with the following formula: $D = n / (2L\hat{a})$, where D is the density, n is the total number of individuals detected in each transect, L is the transect length, and $\hat{a}$ is the transect width. Using our data of density and the available habitat, i.e., 49,037.4 ha (Muñoz et al. 2021), we estimated the global population size for the Cabanis's Ground Sparrow. To avoid differences in detectability between observers, all surveys were conducted by one observer, L.S., who has years of experience working with Cabanis's Ground Sparrow (Sandoval and Mennill 2013; Sandoval et al. 2014, 2017; Muñoz et al. 2021).

Territory size estimate

We estimated the territory size by following 21 pairs from 2003 to 2015, between March and August, during the species' breeding season (Stiles and Skutch 1989). We followed one or both individuals of the pair between 07:00 and 09:00 h, on a different day from the transect count. We arrived at the sites where a pair had been detected and waited until we saw either or both individual(s). After that, from a moderate distance (range: 5–15 m), we followed the individuals by walking slowly and observing them with binoculars, while we wore unobtrusive clothing. This method did not appear to disturb the focal individuals. When birds noticed our presence, they almost immediately resumed their activities, they did not fly long distances, and they did not change their vocal behavior. The procedure described is similar to the one used to study the territorial behavior of other passerines with similar habits, like Chestnut-backed Antbird *Poliocrania exsul*,White-bellied Antbird *Myrmeciza longipes*, and White-eared Ground Sparrow (Stutchbury et al. 2005; Juárez et al. 2020).

At the end of the observation period, we collected the coordinates of each location used by each focal individual for singing or perching only if (1) we followed the pair or the male at least 1 h, (2) the individuals perched in more than five different locations separated by more than 10 m, and (3) GPS precision indicated ≤ 4 m (GARMIN model map 62, accuracy = 3 m). On average, we collected eight coordinates per territory (SD: 2; range: 6–12 points). We observed the birds either one morning (12 territories), two mornings (3 territories), or three mornings (4 territories). We estimated the territory size using the "adehabitat" package in R to measure the minimum convex polygon on the GPS coordinates collected per focal pair (Calenge 2006). This technique of territory estimation has been used to measure the territory sizes of other passerines such as House Wren *Troglodytes aedon*,

Wilson's Warbler *Cardellina pusilla*, Red-eyed Vireo *Vireo olivaceus*, and White-eared Ground Sparrow (Marshall and Cooper 2004; Ruiz-Sánchez et al. 2017; Juárez et al. 2020).

Urban surface estimate and site classification

We classified the four main sites used for collecting data on ground sparrow density and territory size according to the level of urbanization as urban, suburban, or rural sites (Table 1). Our designation of urban, suburban, and rural sites was based on the amount of urban surface (i.e.,

impervious surface cover, such as roads and rooftops), within a 500-m-radius circle around each site sampled. We used as circle center the centroid of all coordinates collected for each territory. Within each circle, we measured the urban surface area by manually drawing polygons over satellite images using the land area calculator in Google Earth Pro. The spatial resolution of the satellite images used was 46 cm, with an eye altitude of 1.50 km. The urban sites were locations with more than 50% of impervious surfaces. Suburban sites were locations with 10–50% impervious surface areas. Rural sites were locations with less than 10% of impervious surfaces. Our classification follows standard habitat classification for a gradient of urbanization (McKinney 2008).

Natural history observations

Natural history observations were conducted between 2000 and 2020 in several areas where this species occurs, including the four main sites where we collected data to estimate abundance and territory size. Since information about nesting for this species was scarce, we included data shared by colleagues (two observations), data taken from museum specimens deposited at Museo de Zoología, Universidad de Costa Rica (MZUCR; 12 dry skins, seven nests, and seven eggs), and data stored in the eBird database (Sullivan et al. 2009). We used the nest and egg collection to measure and describe the nests and eggs. We used dry skins from seven adults and five juveniles to describe the diet from stomach contents according to the label reports. We describe the nestling appearance, the juvenile, also known as first basic, and formative plumages following the standard definitions of these plumages (Howell et al. 2003; Johnson and Wolfe 2017) from the same 12 dry skins. In this section, we quantitatively describe the species' nest (external and internal diameter), eggs (length and width), parental care, nestling appearance, juvenile and formative plumage, parasitism, and diet. Additionally, we determined the duration of the breeding season using our observations and eBird data until December 2020. Most of the information presented in this section was collected opportunistically. Reported values are mean ± standard error.

Results

Density, population size, and territory size

We estimate a density of 0.06 to 0.24 mature individuals/ha, with an average of 0.16 ± 0.03 mature individuals/ha, at four sites in Costa Rica (Table 1). Based on these densities, we estimate that the global population of Cabanis's Ground Sparrow ranges from 2942 to 11,769 mature individuals with an average of 7846 ± 1663 individuals. The average territory size is 0.75 ± 0.10 ha (range: 0.15–1.93 ha, $n = 21$ territories). A further examination suggests that average territory size is smaller in the rural areas (0.56 ± 0.10 ha, $n = 6$) than in the urban areas (0.82 ± 0.13 ha, $n = 15$), because there is no range overlap in territory size.

Natural history observations

Nest Nests are built between branches or trunks of small bushes or on top of a grass tussock, inside dense vegetation in thickets, coffee or chayote plantations, and young secondary forest. In addition to the seven nests deposited at MZUCR (Table 2), we located and measured 13 nests on the field in Ujarrás, Cartago province (9° 49′ 32″ N; 83° 49′ 54″ W; at 1018 m a.s.l). All nests consist of two layers: the external layer is a dense cup of small twigs, grass fibers, dead leaves, and vines; the internal layer is composed of tightly woven thin plant fibers, including the fungal rhizomorphs of *Marasmius* sp. (Fig. 2). Measurements of the external cup are as follows (mean ± SD): 133.7 ± 34.1 mm in diameter, 69.3 ± 39.0 mm in height, and 36.0 ± 12.2 mm in the thickness of the wall. The internal cup measurements are as follows: 71.3 ± 4.7 mm of cup diameter and 25.3 ± 7.1 mm in the cup depth (Fig. 2). Nests are located at 1.2 ± 1.0 m above the ground (range: 0.3–2.8 m).

Eggs and clutch size Eggs are elliptical in shape with a glossy white or a light blue wash and irregular reddish-brown spots (Fig. 3). Egg length is 22.1 ± 0.1 mm and egg width is 16.2 ± 0.3 mm. Clutch size in the 25 active nests observed either with nestlings or eggs was two in 18 nests, three in three nests, and one in four nests (probably nests with an incomplete clutch). In three of these nests which we monitored from the time of construction, the duration between the laying of the first and second eggs was 1 day.

Breeding season We observed and recorded males singing from February to August with a peak in May (recordings are deposited in the Laboratorio de Bioacústica, Universidad de Costa Rica; Table 3). Nests and juveniles were observed from March to November, with a greater abundance between May and July (Table 3). On 10 November 2018, a juvenile attended by both parents was observed at Santo Domingo, Heredia province (09°58′39″N; 84°04′40″W; 1178 m a.s.l.; https://ebird.org/view/checklist/S50922264). On 6 October 2017, two juveniles were observed at Alajuelita, San José province (09°53′31″N; 84°05′59″W; 1186 m a.s.l.; https://ebird.org/checklist/S39578175).

Parasitism On 02 July 2018, we observed a nest with two Cabanis's Ground Sparrow eggs and oneBronzed Cowbird *Molothrus aeneus* egg in Ujarrás, Cartago province (9° 50′ 12″ N; 83° 49′ 52″W; 1031 m a.s.l.), in a coffee plantation

Table 2 Nest measurements for Cabanis's Ground Sparrow. These nests are deposited in the nest collection of Museo de Zoología, Universidad de Costa Rica. All measurements were obtained by the same investigator (L.S.) and data (date, location, coordinates, altitude, and height) were obtained from the labels of each nest

Date found	Location	Coordinates	Altitude (m)	Height above ground (m)	External diameter (mm)	External height (mm)	Internal diameter (mm)	Internal depth (mm)	Wall thickness (mm)	Catalog number
02 April 2012	Getsemaní	10°01′40″N; 84°06′54″W	1265	0.3	113.2	50.6	70.3	15.1	21.5	MZUCRN152
24 May 2012	Getsemaní	10°01′42″ N; 84°06′81″W	1288	0.6	112.6	46.2	73.9	26.7	19.4	MZUCRN166
25 August 1998	Universidad Nacional	09°59′58″N; 84°06′31″W	1156	0.5	184.2	43.8	75.5	22.1	54.3	MZUCRN026
25 August 2019	Getsemaní	10°02′27″N; 84°06′37″W	1418	2.8	124.9	69.2	63.7	34.2	30.6	MZUCR

(Fig. 4). On 15 June 2017, in Ujarrás, Cartago province (09°49′59″N; 83°49′84″W; 1014 m a.s.l.), a nest was found with one Cabanis's Ground Sparrow and one Bronzed Cowbird nestling in a bougainvillea bush in a garden (Fig. 4). This nest was monitored with a camera, and during 47 min of observation, the adults fed the Bronze Cowbird nestling 18 times and their own nestling only three times. We observed two pairs feeding a single juvenile Bronzed Cowbird inside shade coffee plantations. The first pair was observed on 07 July 2009 at Getsemani, Heredia province (10°01′39″N; 84°06′42″W; 1289 m a.s.l.). The second pair was observed on 29 June 2020 at Santo Domingo, Heredia province (9°58′55″N; 84°02′45″W; 1260 m a.s.l.). Finally, we observed a nestling with a *Philornis* sp. (Muscidae) larva on the left side of its bill (Fig. 4), at Getsemaní, Heredia province, on 02 April 2012.

Incubation and parental care In nests with two eggs, incubation began after the second egg was laid. We estimate the incubation period to be 12 ± 2 days. Nestlings remain in the nest for another 12 ± 2 days before fledging, which always occurred while the nestlings were still flightless (three observations). We were not able to confirm if incubation was carried out by both parents. However, both parents do feed the nestlings and remove fecal sacs. Whenever adults were accidentally flushed from nests, they would perform a distraction display by slowly fluttering to the ground and hopping in a way that is reminiscent of a bird with an injured wing. This distraction display appears to become more frequent and obvious as incubation progresses and after hatching. Food is given to the nestlings in two ways depending on the size of food items. Smaller items including seeds are regurgitated and larger items such as arthropods are given whole to the nestlings. We monitored two nests with cameras. At one nest, the parents brought food 21 times in 47 min and at the second nest 33 times in 380 min. Identified food items consisted of 32 larvae (mainly Lepidoptera), 8 grasshoppers (Orthoptera), 2 beetles (Coleoptera), 2 spiders (Araneae), and 4 moths (Lepidoptera). After leaving the nest, the juveniles follow the adults by hopping on the ground to approach them. Once in proximity, juveniles vocalize persistently before grabbing food from the parents. On one occasion when a farm worker approached the area where the family was foraging, the juvenile remained still and quiet beside a rock as the adults gave a repetitive, sharp "*tsik*." The fledgling did not move until the person walked away and the adults had stopped vocalizing.

Nestling appearance, juvenile, and formative plumage Cabanis's Ground Sparrow nestlings hatch with closed eyes, reddish skin, pinkish beak, cream-yellow gapes, reddish legs, and a small quantity of dark gray down feathers distributed equally along the whole body. One-week-old nestlings

Fig. 2 Upper and lateral views of two Cabanis's Ground Sparrow, *Melozone cabanisi*, nests from Getsemaní, Heredia province, Costa Rica

Fig. 3 Size, color, and pattern of Cabanis's Ground Sparrow, *Melozone cabanisi*, eggs

Table.3 Abundance of nests, juveniles, and singing males for Cabanis's Ground Sparrows per month. The numbers in each field are the total observations. The number in the parentheses refers to observations stored in the eBird database. Observations collected from 2004 to 2020

Month	Observation year	Nests/juveniles	Singing males
January			
February	2010		1
March	2005	2	1
April	2010–2012, 2020	2 (1)	3
May	2010–2012, 2017, 2018, 2020	3 (1)	8
June	2011, 2012, 2017, 2020	3 (1)	2
July	2004, 2009, 2018	3 (1)	1
August	2005, 2009, 2012, 2019	1 (1)	2
September	2020	(1)	
October	2015	1 (1)	
November	2018	2 (1)	
December			

have open eyes, blue-grayish beak, bright yellow gape, and pink legs; dorsal and side feathers are already developed but ventral feathers are still lacking, and wing feathers start to develop around that age. At the time of fledging and at least during the next 10 days, birds in juvenile plumage are brown above and creamy white below with heavy streaking throughout the underparts. In this plumage, the head and cheeks are reddish-brown, while the lesser, median, and greater wing coverts have rusty tips. After fledgling, birds quickly undergo a preformative molt, which varies in extent, to develop the formative plumage (Fig. 5). Formative plumage is similar to adult plumage (also known as definitive basic plumage) but has marked differences that allow us to distinguish age classes during the first year (Fig. 5). Compared to the basic plumage, in the formative plumage, the black on the forehead and in the malar region is reduced and duller; the white pre-ocular spot is smaller and the white post-ocular spot is absent; the rusty color in the cap and cheeks is less bright; the upperparts (back, wing,

Fig. 4 Cabanis's Ground Sparrow, *Melozone cabanisi*, nests parasitized by Bronzed Cowbird, *Molothrus aeneus*: (A) larger blue cowbird egg; (B) larger cowbird juvenile; (C) ground sparrow nestling with *Philornis* larvae

Fig. 5 Plumage development and plumages of Cabanis's Ground Sparrow, *Melozone cabanisi*. From left to right: (1) nestling developing the juvenile plumage; (2–3) juvenile plumage (also known as first basic plumage); (4–5) individuals molting from juvenile to formative plumage, (6) formative plumage, and (7) adult plumage (also known as definitive basic plumage)

and rectrices) are brown with obvious rusty tips to the lesser, median, and greater wing coverts absent in the basic plumage; the underparts are cream not white; and the black breast spot is smaller, duller, and less defined.

Diet We observed this sparrow consuming fruits on branches or from the ground of the following trees and bushes: *Stemmadenia donnell-smithii* (Apocynaceae), *Acnistus arborecens* (Solanaceae), *Morus nigra*, *Ficus pertusa*, *F. jimenezii* (Moraceae), *Cecropia obtusifolia* (Urticaceae), *Zanthoxilum ekmanii* (Rutaceae), *Trema micrantha* (Ulmaceae), *Trichilia havanensis* (Meliaceae), *Citharexylum donnell-smithii* (Verbenaceae), *Sapium glandulosum, Croton draco, C. niveus* (Euphorbiaceae), *Rubus rosifolius* (Rosaceae), *Psidium guajava* (Myrtaceae), and *Musa x paradisiaca* (Musaceae). We observed individuals consuming seed of *Montanoa hibiscifolia*, *Bidens pilosa* (Asteraceae), and *Achyranthes aspera* (Amaranthaceae). Additionally, we observed adults eating small crickets and katydids

(Tettigoniidae), cockroaches (Blattodea), snails (Mollusca), and both larval and adult stages of moths (Lepidoptera). Stomach contents of the individuals deposited at MZUCR showed that 71% of adults and 60% of juveniles contained arthropods (e.g., beetles), 43% of adults and 20% of juveniles contained fruit, and 57% of adults and 20% of juveniles contained seeds.

Discussion

The densities that we report for Cabanis's Ground Sparrow are similar to those reported for Canyon Towhee *Melozone fusca*, which reaches densities of 0.08–0.33 mature individuals/ha (Johnson and Haight 2020). However, they are lower compared to those reported for Abert's towhee *Melozone aberti*, in which density varies from 0.75 to 1.37 mature individuals/ha (Tweit and Finch 2020). Considering that these species are congeners, live in similar habitats (ground and dense understory of shrubs), share habits regarding territorial and pair bond behavior, have similar diets (ground-dwelling invertebrates and seeds), and are similar in size (based on tarsus and bill morphology), we expect that they require territories of similar size to survive and therefore should occur in similar densities (Sandoval et al. 2014; Johnson and Haight 2020; Tweit and Finch 2020). The habitat quality (e.g., resource abundance) may be the factor driving differences in densities observed in these two species, because Abert's Towhee was studied in large areas of well-developed understory whereas Cabanis's Ground Sparrow occurs along an urban-rural gradient with isolated patches of thickets (Lefebvre and Poulin 1996; Hart et al. 2011; Tweit and Finch 2020; Muñoz et al. 2021). The relationship between habitat quality and bird densities has been found in Wilson's Warbler and Black-throated Blue Warbler *Setophaga caerulescens*, which occur in higher densities in their highest quality habitat (Holmes et al. 1996; Ruiz-Sánchez et al. 2017).

Considering that Cabanis's Ground Sparrow is territorial, it is possible that we would have obtained different data on territory size if we had used playback. However, for a closely related species, White-crowned Sparrow *Zonotrichia leucophrys*, the territory sizes obtained using observations and playback stimulus were closely correlated (Patterson and Petrinovich 1978). The territory size of Cabanis's Ground Sparrow was larger than that of other congeners, including White-eared Ground Sparrow which has a territory size of 0.18 ± 0.03 ha (Juárez et al. 2020). Cabanis's and White-eared Ground Sparrows occur sympatrically, inhabit the same habitat, and overlap territories across much of their ranges in the Costa Rican Central Valley (Sandoval et al. 2013, 2017; Sandoval 2020). Thus, differences in habitats may not explain the differences in territory size between these two species. It is also known that a bird's size correlates positively with its territory size (Schoener 1968; Alcock 2016). Cabanis's Ground Sparrow is smaller than White-eared Ground Sparrow (Sandoval and Mennill 2013); nonetheless, Cabanis's Ground Sparrow has larger territories than the socially dominant White-eared Ground Sparrow (Sandoval et al. 2013). It is well established that resource availability, especially of food and nesting places, plays an important role in determining territory size because individuals inhabiting poor-quality environments need to protect larger areas to secure all necessary resources to survive and reproduce (Alcock 2016; Ruiz-Sánchez et al. 2017). If Cabanis's Ground Sparrow has more specific requirements than White-eared Ground Sparrow, such as smaller seeds, because they have a smaller beak than White-eared Ground Sparrow, and if its main food resources (seeds and arthropods) are becoming scarcer across urban landscapes, this may explain the differences in territory size between these two congeners. Additional support for the relevance of resource availability for determining territory size in Cabanis's Ground Sparrow is present in our results because the territories are larger in the highly urbanized sites, where resources may be scarcer. Further support for the resource availability hypothesis is provided by a White-eared Ground Sparrow study which detected a similar pattern, i.e., larger territories in urban than in rural sites (Juárez et al. 2020). However, a detailed study to evaluate the differences in the availability of specific resources used by these two syntopic ground sparrows along an urban gradient is still necessary.

There is little information published on the breeding biology of Cabanis's Ground Sparrow, except for nest description, egg measurements, and clutch size from a single nest (Cherrie 1892). All nests that we found were located above the ground; however, there is a record of a nest located directly on the ground in the base of sugarcane stalks (Cherrie 1892). Previous measurements of one nest and the materials used to build it are similar to the nests we describe here (Cherrie 1892). Previous measurements of two eggs are larger, 23.0 ± 0.1 mm by 16.6 ± 0.3 mm (Cherrie 1892), compared to our measurements, for a combined average of egg size of 22.7 ± 0.4 by 16.4 ± 0.3 mm. Our report of clutch size is in line with what was previously known, suggesting that this species has a smaller clutch size than the closely related White-eared Ground Sparrow (Cherrie 1892; Sandoval and Mennill 2012). This species has the longest known breeding season of all *Melozone* species, lasting up to 10 months, while the breeding season of most congeners lasts between 4 and 7 months (Rising 2011). There is only one previous publication about plumage development and molt in Cabanis's Ground Sparrow. According to Cherrie (1892), Cabanis's Ground Sparrow obtains an adult-like plumage by the end of the "first molt", i.e., by the end of the preformative molt, which is consistent with what we present

here. Birds with a totally developed formative plumage are similar to birds in basic plumage (Fig. 5). This ground sparrow begins its preformative molt as early as 10 days after leaving the nest, and they may require about 3 months to complete the preformative molt (Cherrie 1892), which is consistent with the timing and duration of the preformative molt in other Passerellidae (Howell et al. 2003; Pyle 1997). The development of juvenile and formative plumages suggests that this species exhibits a complex basic strategy molt (Howell et al. 2003). Likewise, Canyon Towhee, Abert's Towhee, and California Towhee *Melozone crissalis* all follow the complex basic strategy (Pyle 1997). Adult Cabanis's Ground Sparrows appear similar year-round, suggesting the occurrence of a single molt each year for adults, which is consistent with the complex basic strategy. Nevertheless, we do not have the data to exclude the occurrence of a prealternate molt. The closest relative of Cabanis's Ground Sparrow, White-faced Ground Sparrow *Melozone biarcuata*, may have a prealternate molt (Howell et al. 2003; Pyle 1997; Sandoval et al. 2017). In White-faced Ground Sparrow, a replacement of crown, back, and face feathers occurs in late February and early March (Dickey and van Rossem 1938), which would correspond to a prealternate molt following all the standard guidelines to classify molts and name the corresponding plumages (Howell et al. 2003; Pyle 1997; Johnson and Wolfe 2017). After breeding, molt is the second most important event during a life cycle of any resident bird (Howell et al. 2003; Johnson and Wolfe 2017). Considering the inextricable relation between molt and food availability (Howell et al. 2003), the molt strategies followed by birds restricted to urban environments need to be better understood.

The diet of this species includes several types of fruits; some of the tree species that produce fruits are scarce or are removed from cities because they are larger (e.g., *Ficus* spp., or *T. micranta*) or do not produce flowers (e.g., *Sapium glandulosum*, *Croton draco*, *C. niveus*) compared with more commonly used tree species in cities (Biamonte et al. 2011; Sandoval et al. 2019). Additionally, coffee farmers are removing trees or changing pruning techniques to increase sunlight exposure and reduce American leaf spot and coffee rust diseases caused by the fungi *Mycena citricolor* and *Hemileia vastatrix*, respectively (Avelino et al. 2004, 2007; Meylan et al. 2017). All these practices reduce fruit availability for birds. Arthropods are also an important part of the diet of this ground sparrow, and inside cities, these are decreasing, as well as inside the coffee plantations, due to the use of pest control substances (Perfecto et al. 1996; McIntyre 2000; Kekkonen 2017).

In this study, we estimated the global population of mature individuals of Cabanis's Ground Sparrow to be between 2942 and 11,769, which is well below the current IUCN estimate of 20,000–49,000 mature individuals (BirdLife International 2020). Until as recent as August 2020, its population trend was defined as increasing (BirdLife International 2020). However, two independent studies suggest that this species is declining (Stiles 1990; Biamonte et al. 2011). At the Universidad de Costa Rica and its surroundings, until 1968, this ground sparrow was abundant but during a 20-year period, it became uncommon (Stiles 1990). A study carried out during 2004–2009 with the same approach to classify abundance as Stiles (1990) found Cabanis's Ground Sparrow to be scarce (Biamonte et al. 2011). Finally, Cabanis's Ground Sparrow nests are parasitized by Bronzed Cowbird (Sealy et al. 1997). In the early 1980s, when the species was still fairly common, Cabanis's Ground Sparrow was one of the main hosts for the cowbird in the Central Valley (Stiles 1990; Sealy et al. 1997). By the late 1980s, Rufous-collared Sparrow *Zonotrichia capensis*, an abundant species of the Central Valley, was the main host for the cowbird there (Stiles 1990; Sealy et al. 1997; Biamonte et al. 2011). Even though Cabanis's Ground Sparrow is now scarce, our data suggest that it is still used as a host regularly by the cowbird; 16% of the nests studied were parasitized by Bronzed Cowbird. Considering our results regarding population size, consistent habitat loss as reported for a period of 30 years due to urbanization, population trend, and extent of occurrence as given by the IUCN (Biamonte et al. 2011; Martínez 2014; BirdLife International 2020), we recommend a re-evaluation of its IUCN status. The Costa Rican government lists the Cabanis's Ground Sparrow as Critically Endangered (SINAC 2017).

In conclusion, we observed similar densities of Cabanis's Ground Sparrow compared to those reported for other congeners. However, we found that this species has larger territories than a sympatric congener (Juárez et al. 2020). The breeding season for this species spans 10 months with a peak in the middle of the year. Nests are less variable than those reported for other congeners (Sandoval and Mennill 2012). Our results on territory size, population density, and natural history provide important information for the protection of a range-restricted species, Cabanis's Ground Sparrow, an endemic species found in urban areas. Even in highly urbanized environments, this species is restricted to scrubby habitats like coffee and other agricultural plantations, early successional vegetation, and secondary forest. These habitats are an irreplaceable trophic substrate for other birds, mammals, and arthropods specialized or restricted to these environments in the Costa Rican Central Valley (Sandoval et al. 2019; Juárez et al. 2020; Muñoz et al. 2021). Given our population estimate, extent of occurrence, population trend, and consistent 2–3% annual habitat loss over a period of 30 years due to urbanization (Stiles 1990; Biamonte et al. 2011; Martínez 2014; BirdLife International 2020; Muñoz et al. 2021), we believe a careful re-evaluation of the species' IUCN status is required. To save Cabanis's Ground Sparrow from extinction, we recommend taking into consideration

this species' habitats in future urban development, improving the connectivity of natural habitats, and implementing a program for payment of environmental services to landholders to protect scrubby habitats throughout its limited range, the Costa Rican Central Valley.

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Author contribution Luis Sandoval originally formulated the main idea. María de la Paz Angulo Irola, Ernesto M. Carman, and Luis Sandoval conducted the field work. Luis Sandoval maintained the database. Roselvy Juárez and Luis Sandoval carried out the data analysis. Roselvy Juárez wrote the manuscript with advice from Luis Sandoval. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability The datasets used for this publication are available from the corresponding author upon reasonable request.

Code availability Not applicable

Declarations

Ethics approval This study did not require us to handle animals. All applicable national and institutional guidelines for observation and photo documentation of animals were followed. This research was conducted under the permit number B9-123, licensed by Vicerrectoria de Investigación, Universidad de Costa Rica.

Consent to participate Not applicable

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Conflict of interest The authors declare no competing interests.

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