

Structure of breeding bird assemblages in the city of Windhoek, Namibia

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Abstract

Structure of breeding bird assemblages in the city of Windhoek, Namibia. The line transect method was employed to count birds in four urbanized habitats in the city of Windhoek, Namibia. Most counts were conducted during July–October, in 2012–2014. Twelve transects with a total length of c. 86 km were located in places representing major urban habitats: residential areas (city centre, suburbs in lowland, suburbs in highland, and city periphery), sport fields, and a modern industry area. In total, 80 bird species (excluding Palearctic visitors) were recorded. For all species, I calculated linear population densities and dominance. Six species were classified as dominant: house sparrow, red-eyed bulbul, Southern masked weaver, laughing dove, wattled starling and white-backed mousebird. Their cumulative numerical abundance comprised 54.2% of all the breeding species. The group of dominant species varied markedly among transects. Granivores were the most important feeding guild, comprising more than half of all birds in Windhoek. Frugivores (26%) were more numerous than insectivores (19%). Birds nesting in trees and/or in shrubs comprised two thirds of all birds. Surprisingly, few differences in the structure of feeding and nesting guilds were recorded among the four urban habitats. Windhoek avifauna is similar in dominance structure to avifauna in other southern African cities and towns, where sparrows, doves/pigeons, bulbuls and mousebirds dominate, and with granivores being the main feeding guild. Species richness declines and bird abundance increases along urban gradient (towards the city centre).

Key words: Urban ecology, Population densities, Avian communities

Resumen

Estructura de los conjuntos de aves reproductoras en la ciudad de Windhoek, Namibia. Se empleó el método del transecto lineal para contar aves en cuatro hábitats urbanizados de la ciudad de Windhoek (Namibia). La mayoría de los recuentos se realizaron entre julio y octubre, en el periodo 2012–2014. Se seleccionaron 12 transectos con una longitud total de 86 km aproximadamente en lugares que representaban los principales hábitats urbanos: zonas residenciales (centro de la ciudad, suburbios en tierras bajas, suburbios en tierras altas y periferia de la ciudad), campos de deporte y una moderna zona industrial. En total se registraron 80 especies de aves (excluidos los visitantes paleárticos). Se calcularon las densidades de población lineales y la dominancia de todas las especies. Seis especies se clasificaron como dominantes: gorrión común, bulbul de ojos rojos, tejedor enmascarado

meridional, paloma reidora, estornino pinto y pájaro ratón dorsiblanco. Su abundancia numérica acumulada comprende el 54,2% de todas las especies reproductoras. El grupo de especies dominantes varió notablemente entre los distintos transectos. Los granívoros fueron el gremio alimentario más importante, con más de la mitad de todas las aves de Windhoek. Los frugívoros (26%) resultaron más numerosos que los insectívoros (19%). Las aves que anidan en árboles y/o arbustos representaron dos terceras partes del total de aves. Sorprendentemente, se registraron pocas diferencias en la estructura de los gremios de alimentación y nidificación entre los cuatro hábitats urbanos. La avifauna de Windhoek presenta una estructura de dominancia similar a la de otras ciudades y pueblos del sur de África, donde dominan los gorriones, las palomas, los bulbules y los pájaros ratones, siendo los granívoros el principal gremio de alimentación. A lo largo del gradiente urbano, la riqueza de especies disminuye y la abundancia de aves aumenta hacia el centro de la ciudad.

Palabras clave: Ecología urbana, Densidades de población, Comunidades de aves

Resum

Estructura dels conjunts d'ocells reproductors a la ciutat de Windhoek, Namíbia. Es va utilitzar el mètode del transecte lineal per comptar ocells en quatre hàbitats urbanitzats de la ciutat de Windhoek (Namíbia). La majoria dels recomptes es van fer entre juliol i octubre, en el període 2012–2014. Es van seleccionar 12 transectes amb una longitud total de 86 km aproximadament en llocs que representaven els principals hàbitats urbans: zones residencials (centre de la ciutat, suburbis en terres baixes, suburbis en terres altes i perifèria de la ciutat), camps d'esport i una moderna zona industrial. En total es van registrar 80 espècies d'ocells (excloent-ne els visitants paleàrtics). Es van calcular les densitats de població lineals i la dominància de totes les espècies. Sis espècies es van classificar com a dominants: pardal comú, bulbul d'ulls vermells, teixidor emmascarat meridional, colom rialler, estornell comú i ocell ratolí dorsiblanco. L'abundància numérica acumulada d'aquestes espècies comprèn el 54,2% de totes les espècies reproductores. El grup d'espècies dominants va variar notablement entre els diferents transectes. Els granívors van ser el gremi alimentari més important, amb més de la meitat de tots els ocells de Windhoek. Els frugívors (26%) van ser més nombrosos que els insectívors (19%). Els ocells que nien en arbres i/o arbustos van representar dues terceres parts del total d'ocells. Sorprenentment, es van registrar poques diferències en l'estructura dels gremis d'alimentació i nidificació entre els quatre hàbitats urbans. L'avifauna de Windhoek presenta una estructura de dominància similar a la d'altres ciutats i pobles del sud d'Àfrica, on dominen els pardals, els coloms, els bulbuls i els ocells ratolins. Els granívors són el principal gremi d'alimentació. Al llarg del gradient urbà, la riquesa d'espècies disminueix i l'abundància d'ocells augmenta cap al centre de la ciutat.

Paraules clau: Ecologia urbana, Densitats de població, Comunitats d'ocells

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Introduction

Urbanization is a major force affecting the planet's biodiversity. It often leads to biotic homogenization of global avifauna and reduction of species richness (Lepczyk et al., 2017). Since most people live today in cities, many of them have contact with nature in the cities. Therefore, the simplest and efficient way to engage people in nature conservation is through citizen science and urban ecology. As a result, biodiversity conservation in urban environments is today of global focus (Murzluff, 2001a; White et al., 2005). Among the attractive components of the natural world and of the urbanized environment specifically, are birds. Not surprisingly, the structure of bird communities is today intensively studied subjects in urban ecology (e.g. Marzluff et al., 2001a, 2001b, 2001c; Kalcey and Rheinwald, 2005; Chace and Walsh, 2006; Dunn and Weston, 2008; Magle et al., 2012; Luniak, 2013, 2017; Lepczyk et al., 2017; Murgui and Hedblom, 2017).

Most studies on urban ecology and ornithology were conducted in the temperate zone. In 20th century only two out of 100 studies on birds in urban areas were conducted in Africa. At the beginning of 21st century, urban ornithology made a remarkable mile step: 1,021 articles were published in a single decade (2006–2015), but only 22 of them were from Africa (Marzluff, 2016). Urbanization–wildlife dynamics may, however, differ geographically. There is therefore an urgent need to conduct such studies in regions with much higher species diversity than in temperate zones. In the tropical regions of the world, such studies often lack vital information on the population densities and dominance of particular species composing communities. Methods applied in such studies do not allow generation of such information (e.g. Lancaster and Rees, 1979; MacGregor–Fors and Schondube, 2011; Coetzee et al., 2018), but it may be crucial for conservationists to know not only how numerous a species is in particular habitats, but also how its population density varies over years and what factors affect the changes. This is especially important in quickly changing environments, such as suburbs and farmlands.

In particular, little is known about avian assemblages in such highly transformed habitats in Africa (Hockey et al., 2005; Dunn and Weston, 2008; Marzluff et al., 2001a; Magle et al., 2012; Luniak, 2013, 2017; Fidino and Magle, 2017; Lepczyk et al., 2017), with the exception of Namibia. Recently, quantitative studies on avian assemblages were conducted in several towns in the northern part of this country, namely in Outapi (Kopij, 2019b), Onguadiva (Kopij, 2021d), Tsumeb (Kopij, 2021c), Grootfontein (Kopij, 2021b), Rundu (Kopij, 2021b) and Katima Mulilo (Kopij, 2016, 2019c, 2020). Similar studies were also conducted in two Namibian coastal towns: Swakopmund (Kopij, 2018a) and Hentjes Bay (Kopij, 2022). The major findings of these studies are that these urbanized habitats are dominated by granivores birds such as indigenous *Streptopelia* doves and the exotic house sparrow, but not the feral pigeon, dominant in urban habitats in other part of the world (Lepczyk et al., 2017). Corvids, canaries, tits, swallows, and kestrels, so well–adapted to urban environments in other parts of the world (Kalcey and Rheinwald, 2005; Lepczyk et al., 2017), were scarce or absent in these towns.

In the present study, I aimed to quantify assemblages in selected urban habitats in the capital of Namibia, where no studies on avian assemblages have been conducted to date. Specifically, I assessed species richness, species diversity, population densities and dominance of species in urban, suburban and peri–urban habitats in order to determine how urbanization affects these parameters under urbanized subtropical arid conditions.

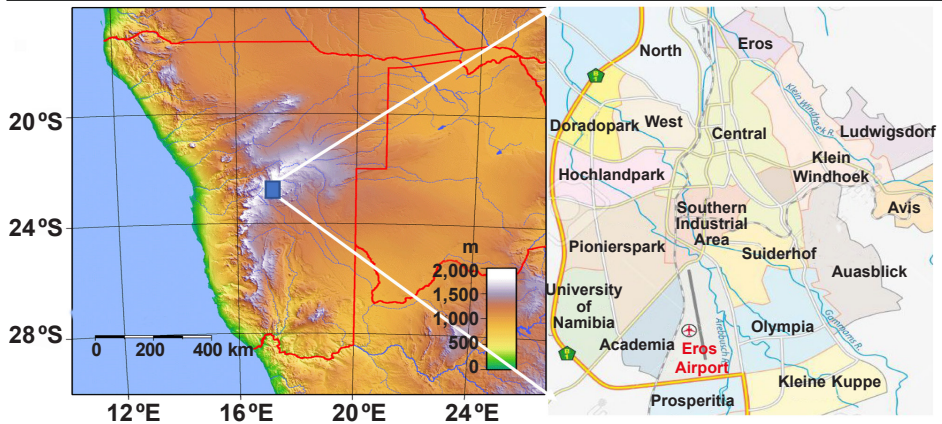


Fig. 1. Location of the study plots.

Fig. 1. Localización de las áreas de estudio.

Material and methods

Study area

The study area was located in the Namibian capital, Windhoek, on the plateau of the Kho-mas Highland (fig. 1), at c. 1,700 m a.s.l. The city was founded in 1840. The population grew by four times from 1971 to 2020 (www.macrotrends.net). Windhoek is surrounded by rocky mountainous areas covered with Highland Shrubland, a sort of Acacia tree-and-shrub savanna (Mendelsohn et al., 2009). This natural vegetation is, however, largely transformed or removed altogether in the city and replaced by exotic trees (mainly acacias, with some jacarandas, gums, cypresses, etc.) and shrubs and herbs (often dense and luxuriant on private properties). There are remnants of natural vegetation along water courses (i.e., the Arebbusch with Gammams, and Kleinwindhoek Rivers, and their tributaries) and on higher and steeper hills (e.g. Aloe Trail, Botanic Garden; fig. 2).

Windhoek has a semi-desert (steppe) climate; over 300 sunny days per year. The coldest month is July, with an average temperature of 15.0°C, while the hottest month is December, with an average temperature 25.1°C. Precipitation is mostly during the summer and minimal during the winter (fig. 3). The average annual precipitation is 367.4 mm, with lows of 106.7 mm in the 2018/19 rainy season, and 97 mm in 1929/30 (Werner and Yokany, 2019).

Methods

Using the transect method (Sutherland, 1996; Bibby et al., 2012) birds were counted while walking along streets, slowly at a mean speed of 30 minutes per 1 km. Most counts were conducted during July–October, in 2012–2014 (table 1), mainly in the morning and under calm, sunny weather conditions.

A total of 12 transects were designed to count birds (table 1). The transects were clumped into six habitat groups, based on their distance from the city centre, the density of built-up areas, and main services offered. The 'centre' includes the oldest and densely built-up areas (more than 75% of the area covered with buildings) in and around the downtown



Fig. 2. Views of habitat characteristics in the study area in the city of Windhoek.

Fig. 2. Vistas de las características del hábitat en el área de estudio en la ciudad de Windhoek.

area, mainly with shopping and public and administration services. The suburban lowlands situated 0–2 km from the city centre comprise mainly a residential area with houses and gardens on a flat terrain (51–75% of the area covered with buildings). The suburban highlands (1–3 km from the city centre) are also residential areas (same building coverage as in lowland suburban habitat) but located on a hilly terrain. The periphery includes loosely built-up area (26–50% covered with buildings), with residential areas and un-built shrubby and grassy places, situated 3–5 km from the centre. Sport fields (1.5–2.5 km from the centre)

Table 1. Transects and time expenditure: Ac, avian communities; Place, city district; Dates, dates of counts on transect.

Tabla 1. Transectos y tiempo dedicado: Ac, comunidades de aves; Place, distrito de la ciudad; Dates, fechas en las que se realizaron conteos en los transectos.

Ac	Place	Dates	Minutes	Km
Centre				
b	Central	26/06/2011, 30/10/2012, 03/07/2013	290	9.7
l	Suiderhof	29/08/2011, 05/07/2013, 12/08/2013, 14/08/2013, 08/10/2013, 11/10/2013	525	17.5
Suburban lowland				
e	Hochlandpark	30/10/2012	65	2.2
f	West	20/08/2013, 21/08/2013	185	6.2
i	Pionierspark	02/07/2013	210	7.0
Suburban highland				
a	Eros	26/06/2011, 30/10/2012, 27/08/2014	325	10.8
h	Klein Windhoek	29/10/2012	190	6.3
Periphery				
g	Academia	09/10/2013	160	5.3
j	Olympia	29/08/2011, 30/10/2012, 08/10/2013, 11/10/2013	285	9.5
c	Kleine Kuppe	31/10/2012	125	4.2
Sport fields				
k	Olympia	29/08/2011, 12/08/2013, 11/10/2013	185	6.2
Industry area				
d	Prosperita	31/10/2012	30	1.0
Total			2,575	85.8

are areas with sport objects and a few buildings (< 25% covered by buildings), large places covered with mowed grass, and some clumps of shrubby vegetation. The industrial area, 3–4 km from the city, includes mainly densely built-up areas (> 75% of the area covered with buildings), mainly with light industry structures (fig. 1).

Statistical analysis

Dominance is expressed as the percentage of the total number of pairs of a given species in relation to the total number of all pairs of all species recorded. Dominant species are defined as comprising 5% and more of all breeding pairs of all species recorded, while subdominant species comprise 2–4.9%. The cumulative dominance is defined as the sum of dominance value of all dominant species.

The community dominance index was calculated as follows:

$$DI = (n_1 + n_2) / N$$

where n_1 , n_2 are the number of pairs of the two most abundant species, and N is the total number of pairs of all species (Krebs, 2009).

The following guilds were distinguished: diet (G, granivorous; I, insectivorous; F, frugivorous; N, nectarivorous; V, vegetarian; C, carnivorous); nesting (TS, in trees or shrubs; H, in holes; B, in/on buildings; V, herbaceous vegetation).

The following indices were used to characterize the diversity and evenness of the communities (Krebs, 2009):

Shannon's diversity index:

$$H' = -\sum p_i \ln p_i$$

where: p_i is the proportion of breeding pairs belonging to the i th species.

Pielou's evenness index:

$$J' = (-\sum p_i \ln p_i) / \ln S$$

where p_i is the proportion of breeding pairs belonging to the i th species; S is the total number of species. J' varies between 0 and 1. The less variation between species in a community, the higher J' is.

Similarity between avian communities was investigated using Sørensen's coefficient:

$$I = 2C / A + B$$

where A is the number of bird species in one habitat; B is the number of bird species in another habitat, and C is the number of bird species common to both habitats.

Systematics and nomenclature of bird species follow Hockey et al. (2005), updated by Chittenden et al. (2016). Scientific names of birds recorded on transects are listed in appendix 1; others are given in the traditional way, when mentioned for the first time in the text.

Results

In total, 80 bird species (excluding Palearctic visitors) were recorded (fig. 4, appendix 1). Six species were classified as dominant: house sparrow (13.0%), red-eyed bulbul (10.5%), southern masked weaver (10.3%), laughing dove (9.0%), white-backed mousebird (6.4%) and wattled starling (5.0%) (table 2, appendix 1). Together they comprised 54.2% of all the breeding species. However, in particular places, the dominant species were different. Only the house sparrow was recorded as a dominant species in all 12 places. Five species, the southern masked weaver, laughing dove, red-eyed bulbul, white-backed mousebird, and little swift, were recorded in at least 50% of these places. Twelve other species were dominant in less than 50% of places (table 3). Cumulative dominance was high everywhere, varying from 61.7% to 86.7%, while the dominance index varied from 21 to 50, with a mean of 0.24 (tables 2–5).

Another ten species are classified as subdominant: little swift, African palm swift, chestnut-vented tit-babbler, white-browed sparrow-weaver, feral pigeon, black-throated canary, red-billed quelea, blue waxbill, Egyptian goose and black-chested prinia. They comprised together 33.0% of all breeding birds (table 2).

However, although Egyptian goose, red-billed quelea and wattled starling are classified as African breeding residents, they did not breed in the city (only overwinter in large numbers).

Among Palearctic visitors, the following species were recorded: red-footed kestrel *Falco vespertinus*, European bee-eater *Merops apiaster*, and willow warbler *Phylloscopus trochilus*. However, only a single example of each of these species was recorded.

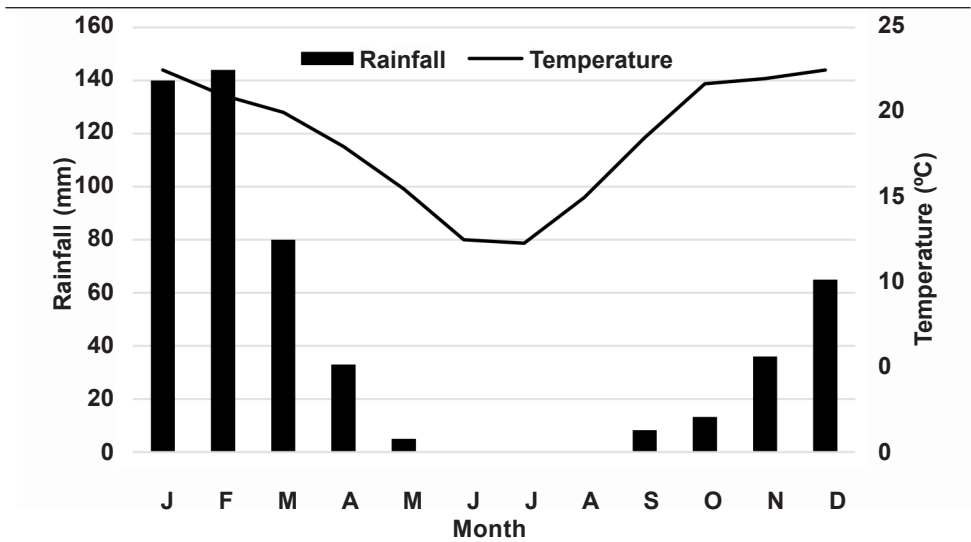


Fig. 3. Climatogram for Windhoek (based on <https://pl.climate-data.org/afryka/namibia/khomas-region/windhuk-834>).

Fig. 3. Climograma de Windhoek (basado en <https://pl.climate-data.org/afryka/namibia/khomas-region/windhuk-834>).

Shannon's diversity index varied from 2.0 to 3.1 in a particular place and was 3.2 overall, while Pielou's Evenness Index varied from 0.75 to 0.85 (table 4).

Proportions between related species were as follows: laughing dove:Cape turtle dove: 0.99:0.01 (n = 467 breeding pairs of both species); rock dove:speckled pigeon: 0.97:0.03 (n = 528); white-backed mousebird:red-faced mousebird: 0.94:0.06 (n = 351); house sparrow: Southern grey-headed sparrow: 0.99:0.01 (n = 671); black-throated canary:yellow canary: 0.93:0.07 (n = 163).

Granivores were the main feeding guild, comprising more than half of all birds in Windhoek. Frugivores (26%) were more numerous than insectivores (19%). Other guilds (carnivores 0.2%, nectarivores 0.6%, vegetarians 2.4%) constituted the remainder (fig. 5A). Birds nesting in trees and/or in shrubs comprised 66% of all birds, 25% on buildings, 5% in low herbs and grasses, and only 1.7% on the ground and 1.6% in holes (fig. 5B). Surprisingly, little difference was recorded between the four urban habitats in the structure of feeding and nesting guilds. Specifically, proportions of main feeding guilds, viz. granivorous, insectivorous, and frugivorous were similar in all these habitats (fig. 6A). This is also applicable to the main nesting guilds (fig. 6B).

Discussion

The number of breeding bird species recorded in urbanized habitats in Windhoek (n = 80) is high compared with other towns in the northern Namibia: Outapi, Ongaudiva, Tsumeb, Grootfontein, Rundo (Kopij, 2019b, 2021b, 2021c, 2021d), but much lower than in Katima Mulilo (Kopij, 2016, 2019c, 2020). Avian species richness and species abundance in urbanized habitats is dependent on the size of compared towns, the location of the study areas



Fig. 4. Lilac-breasted roller right above and Cape glossy starling left above, white-backed mousebirds below.

Fig. 4. En la parte superior, carraca lila a la derecha y estornino pinto del Cabo a la izquierda. En la parte inferior, pájaro ratón dorsiblanco.

within the town (Jokimäki and Kaisanlahti–Jokimäki, 2003), the length of the study period (Ferenc et al., 2014), vegetation cover, human activities, and cat and dog abundance. The abundance of most common bird species is related to infrastructure features (electric cables, lighting rods, building heights), while the abundance of less common bird species is related to habitat structure and urban-related hazards (MacGregor–Fors and Schondube, 2011). Therefore, in two southern African cities, Bloemfontein and Maseru, similar in size to Windhoek, and with similar vegetation diversity and structure, the number of breeding bird species was similar (i.e., 78 and 73 respectively) to that in Windhoek (Kopij, 2001, 2015). The higher number of bird species recorded in Katima Mulilo (despite its smaller size) than in these cities is related to rank vegetation cover. The species richness in Windhoek ($n = 80$) is similar or even higher than that recorded in urbanized areas in the tropical forests in South America, e.g., in San Juan, Puerto Rico ($n = 60$; Wolff et al., 2018), La Paz, Bolivia ($n = 57$; Villegas and Garitano–Zavala, 2010); and south-east Asia, e.g., Calcutta, India ($n = 48$; Sengupta et al., 2014); Singapore ($n = 80$; Lim and Sodhi, 2004). This is unexpected, as species richness in tropical forests of South America and south-east Asia is much higher than that in open grasslands or semi-open savannas of Africa. Urban habitats tend to favour granivores, aerial insectivores and ground-foraging insectivores (Chace and Walsh, 2006). These feeding guilds are probably less representative in forests than in grasslands and

Table 2. Results of breeding bird counts on 12 transects located in the city of Windhoek: N, total number of breeding pairs recorded on all 12 transects; %F, frequency of occurrence in places; Den, linear density (mean number of pairs per 1 km of transect; values from all 12 transects pooled); x, average linear density per one transect (an average from mean values of each transect); D, dominance (percentage of pairs of a given species in relation to the total number of pairs of all species); SD, standard deviation; Var., variance; Min., minimal linear density in any of the 12 places; Max., maximal linear density in any of the 12 places.

Tabla 2. Resultados de los recuentos de aves reproductoras en 12 transectos situados en la ciudad de Windhoek: N, número total de parejas reproductoras registradas en los 12 transectos; %F, frecuencia de aparición en los distintos emplazamientos; Den, densidad lineal (número medio de parejas por 1 km de transecto; valores de los 12 transectos agrupados); x, densidad lineal media por transecto (promedio a partir de los valores medios de cada transecto); D, dominancia (porcentaje de parejas de una especie determinada en relación con el número total de parejas de todas las especies); SD, desviación estándar; Var., varianza; Min., densidad lineal mínima en cualquiera de los 12 emplazamientos; Máx., densidad lineal máxima en cualquiera de los 12 emplazamientos.

Species name	Frequency		Linear density (pairs/1 km)				Dominance (in 12 transects)				
	N	%F	Den	x	SD	Var.	D	SD	Var.	Min.	Max.
Acacia pied barbet	34	75	0.40	0.35	0.24	0.06	0.66	0.24	0.06	0.00	0.70
African grey hornbill	5	33	0.06	0.05	0.10	0.01	0.10	0.10	0.01	0.00	0.30
African hoopoe	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
African palm swift	208	83	2.42	2.08	1.72	2.95	4.05	1.72	2.95	0.00	5.90
African pipit	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20
African reed warbler	9	42	0.10	0.09	0.12	0.01	0.18	0.12	0.01	0.00	0.30
Ashy tit	2	17	0.02	0.03	0.06	0.00	0.04	0.06	0.00	0.00	0.20
Black-chested prinia	105	100	1.22	1.36	0.85	0.72	2.04	0.85	0.72	0.20	3.10
Black-faced waxbill	9	50	0.10	0.08	0.09	0.01	0.18	0.09	0.01	0.00	0.20
Blacksmith lapwing	4	25	0.05	0.03	0.05	0.00	0.08	0.05	0.00	0.00	0.10
Black-throated canary	152	100	1.77	2.25	1.46	2.14	2.96	1.46	2.14	0.40	6.00
Blue waxbill	135	100	1.57	1.51	0.94	0.88	2.63	0.94	0.88	0.20	2.90
Bokmakierie	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Bradfield's hornbill	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20
Bradfield's swift	12	25	0.14	0.10	0.26	0.07	0.23	0.26	0.07	0.00	0.90
Brown-crowned tchagra	3	25	0.03	0.03	0.05	0.00	0.06	0.05	0.00	0.00	0.10
Cape glossy starling	25	75	0.29	0.26	0.24	0.06	0.49	0.24	0.06	0.00	0.60
Cape penduline-tit	4	33	0.05	0.04	0.07	0.00	0.08	0.07	0.00	0.00	0.20
Cape turtle dove	7	42	0.08	0.09	0.14	0.02	0.14	0.14	0.02	0.00	0.40
Cape wagtail	22	75	0.26	0.29	0.28	0.08	0.43	0.28	0.08	0.00	0.90
Cardinal woodpecker	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20
Chestnut-vented tit-babbler	199	92	2.32	2.03	1.01	1.02	3.87	1.01	1.02	0.00	3.30
Common scimitarbill	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Common waxbill	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Crimson-breasted shrike	12	75	0.14	0.13	0.10	0.01	0.23	0.10	0.01	0.00	0.30
Damara red-billed hornbill	3	8	0.03	0.02	0.06	0.00	0.06	0.06	0.00	0.00	0.20
Diederik cuckoo	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Dusky sunbird	11	42	0.13	0.11	0.14	0.02	0.21	0.14	0.02	0.00	0.40
Egyptian goose	123	42	1.43	1.35	2.07	4.29	2.39	2.07	4.29	0.00	5.70
Familiar chat	16	58	0.19	0.15	0.20	0.04	0.31	0.20	0.04	0.00	0.70
Feral pigeon	212	58	2.47	1.53	2.27	5.13	4.13	2.27	5.13	0.00	7.40
Fork-tailed drongo	2	17	0.02	0.03	0.06	0.00	0.04	0.06	0.00	0.00	0.20
Gabar goshawk	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Greater striped swallow	4	33	0.05	0.12	0.29	0.08	0.08	0.29	0.08	0.00	1.00
Green-winged pytilia	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20
Grey go-away-bird	58	75	0.68	0.53	0.51	0.26	1.13	0.51	0.26	0.00	1.70
Groundscraper thrush	2	17	0.02	0.03	0.06	0.00	0.04	0.06	0.00	0.00	0.20
hamerkop	3	25	0.03	0.07	0.15	0.02	0.06	0.15	0.02	0.00	0.50
Helmeted Guineafowl	52	58	0.61	0.60	0.85	0.72	1.01	0.85	0.72	0.00	2.30
House sparrow	669	100	7.79	8.83	5.34	28.5	13.02	5.34	28.53	2.30	19.40
Kalahari scrub robin	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Karoo thrush	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Laughing dove	460	100	5.36	4.82	2.21	4.89	8.95	2.21	4.89	1.90	7.70
Lilac-breasted roller	2	17	0.02	0.03	0.06	0.00	0.04	0.06	0.00	0.00	0.20
Little swift	227	92	2.64	3.28	3.14	9.85	4.42	3.14	9.85	0.00	9.70
Long-billed crombec	7	42	0.08	0.07	0.10	0.01	0.14	0.10	0.01	0.00	0.30
Marico flycatcher	10	42	0.12	0.09	0.12	0.02	0.19	0.12	0.02	0.00	0.30
Marico sunbird	2	17	0.02	0.02	0.04	0.00	0.04	0.04	0.00	0.00	0.10
Namaqua dove	3	25	0.03	0.07	0.15	0.02	0.06	0.15	0.02	0.00	0.50
Pale-chanting goshawk	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Pale-winged starling	35	67	0.41	0.40	0.43	0.18	0.68	0.43	0.18	0.00	1.20
Pearl-spotted owlet	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Pink-billed lark	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20
Pirit batis	15	50	0.17	0.14	0.23	0.05	0.29	0.23	0.05	0.00	0.80
Rattling cisticola	20	75	0.23	0.37	0.45	0.20	0.39	0.45	0.20	0.00	1.40
Red-billed firefinch	5	17	0.06	0.04	0.12	0.01	0.10	0.12	0.01	0.00	0.40
Red-billed quelea	131	25	1.53	0.78	1.84	3.39	2.55	1.84	3.39	0.00	6.30
Red-billed spurfowl	6	42	0.07	0.08	0.15	0.02	0.12	0.15	0.02	0.00	0.50
Red-eyed bulbul	541	92	6.30	5.53	3.34	11.1	10.53	3.34	11.14	0.00	10.60
Red-faced mousebird	22	75	0.26	0.25	0.25	0.06	0.43	0.25	0.06	0.00	0.90
Red-headed finch	23	75	0.27	0.29	0.45	0.20	0.45	0.45	0.20	0.00	1.50
Rock kestrel	3	17	0.03	0.03	0.06	0.00	0.06	0.06	0.00	0.00	0.20
Rock martin	59	92	0.69	0.94	1.02	1.05	1.15	1.02	1.05	0.00	4.00
Rosy-faced lovebird	24	58	0.28	0.25	0.34	0.11	0.47	0.34	0.11	0.00	1.00
Scaly-feathered finch	20	67	0.23	0.26	0.35	0.12	0.39	0.35	0.12	0.00	1.00
Scarlet-chested sunbird	19	50	0.22	0.15	0.20	0.04	0.37	0.20	0.04	0.00	0.60
Short-toed rock thrush	3	25	0.03	0.03	0.07	0.00	0.06	0.07	0.00	0.00	0.20
South grey-headed sparrow	2	8	0.02	0.01	0.03	0.00	0.04	0.03	0.00	0.00	0.10
Southern fiscal	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
Southern masked weaver	527	100	6.14	6.00	3.26	10.6	10.25	3.26	10.60	1.10	11.70
Southern red bishop	30	8	0.35	0.36	1.24	1.54	0.58	1.24	1.54	0.00	4.30
Speckled pigeon	16	58	0.19	0.18	0.20	0.04	0.31	0.20	0.04	0.00	0.50
Swallow-tailed bee-eater	4	25	0.05	0.03	0.05	0.00	0.08	0.05	0.00	0.00	0.10
Wattled starling	257	50	2.99	2.56	5.51	30.4	5.00	5.51	30.40	0.00	18.90
White-backed mousebird	329	100	3.83	3.60	2.16	4.65	6.40	2.16	4.65	1.00	7.90
White-bellied sunbird	1	8	0.01	0.01	0.03	0.00	0.02	0.03	0.00	0.00	0.10
White-brow sparrow-weaver	202	92	2.35	2.12	1.10	1.21	3.93	1.10	1.21	0.00	3.90
White-tailed shrike	4	17	0.05	0.03	0.09	0.01	0.08	0.09	0.01	0.00	0.30
Yellow canary	11	58	0.13	0.13	0.12	0.01	0.21	0.12	0.01	0.00	0.30
Yellow-bellied eremomela	1	8	0.01	0.02	0.06	0.00	0.02	0.06	0.00	0.00	0.20

Table 3. Dominance of bird species in four residential areas located at different distances from the city centre. Dominant species are in bold. Species with a dominance lower of 0.5% in all habitats are excluded from this analysis.

Tabla 3. Dominancia de especies de aves en cuatro zonas residenciales situadas a diferente distancia del centro de la ciudad. Las especies dominantes aparecen en negrita. Se excluyen del análisis las especies con dominancia inferior al 0,5% en todos los hábitats.

Species name	Centre		Suburb. L		Suburb. H		Periphery	
	N	%	N	%	N	%	N	%
Acacia pied barbet	10	0.6	6	0.5	9	1.0	6	0.5
African palm swift	104	6.7	35	3.0	38	4.4	27	2.1
Black-chested prinia	24	1.5	26	2.3	4	0.5	40	3.1
Black-throated canary	26	1.7	31	2.7	37	4.3	39	3.0
Blue waxbill	25	1.6	17	1.5	49	5.7	34	2.6
Cape glossy starling	9	0.6	5	0.4	2	0.2	6	0.5
Cape wagtail	6	0.4	7	0.6	2	0.2	6	0.5
Chestnut-vented tit-babbler	61	3.9	33	2.9	41	4.7	53	4.1
Dusky sunbird	3	0.2	2	0.2	5	0.6	0	0.0
Egyptian goose	14	0.9	40	3.5	0	0.0	60	4.6
Familiar chat	5	0.3	6	0.5	3	0.3	1	0.1
Feral pigeon	166	10.7	31	2.7	7	0.8	8	0.6
Grey go-away-bird	14	0.9	6	0.5	16	1.9	18	1.4
Helmeted guineafowl	28	1.8	17	1.5	5	0.6	2	0.2
House sparrow	172	11.0	228	19.8	73	8.4	170	13.2
Laughing dove	122	7.8	82	7.1	114	13.2	120	9.3
Little swift	27	1.7	72	6.3	58	6.7	41	3.2
Pale-winged starling	6	0.4	1	0.1	11	1.3	14	1.1
Pirrit batis	4	0.3	1	0.1	6	0.7	3	0.2
Rattling cisticola	3	0.2	8	0.7	3	0.3	5	0.4
Red-billed quelea	111	7.1	0	0.0	0	0.0	20	1.5
Red-eyed bulbul	153	9.8	148	12.9	99	11.5	111	8.6
Red-faced mousebird	9	0.6	5	0.4	6	0.7	1	0.1
Red-headed finch	2	0.1	10	0.9	3	0.3	7	0.5
Rock martin	12	0.8	9	0.8	13	1.5	16	1.2
Rosy-faced lovebird	11	0.7	4	0.3	5	0.6	4	0.3
Scaly-feathered finch	3	0.2	3	0.3	3	0.3	10	0.8
Scarlet-chested sunbird	10	0.6	2	0.2	5	0.6	2	0.2
Southern masked weaver	121	7.8	97	8.4	106	12.3	185	14.3
Speckled pigeon	2	0.1	3	0.3	6	0.7	2	0.2
Wattled starling	122	7.8	18	1.6	0	0.0	110	8.5
White-backed mousebird	73	4.7	102	8.9	69	8.0	66	5.1
White-brow sparrow-weaver	51	3.3	43	3.7	36	4.2	57	4.4

savannas. It has been shown that in temperate zone forest species are less-adaptable to urban habitats than species associated with 'open' habitats (Marzluff et al., 2001b; Murgui and Hedblom, 2017). The same may be true in tropical zones. Bellocq et al. (2017) have demonstrated that urbanization in South America has a stronger negative affect on avian species richness in tropical than in temperate or arid regions.

It has been shown that in urban areas avian species richness is usually low and dominated by a few native and/or exotic species (Chace and Walsh, 2006; Villegas and Garitano-Zavala, 2010; Reis et al., 2012; Rodrigues et al., 2018; Wolff et al., 2018; Escobar-Ibañez et al.,

Table 4. Main parameters of avian communities in Windhoek: Suburb. L, suburban lowland; Suburb. H, suburban highland; Ind., industry area; Sport, sport fields.

Tabla 4. Principales parámetros de las comunidades de aves en Windhoek: Suburb. L, zona baja suburbana; Suburb. H, zona alta suburbana; Ind, zona industrial; Sport, campos de deporte.

Parameter	Centre		Suburb. L			Suburb. H		Periphery			Ind. Sport		Total
	b	l	e	f	i	a	h	c	g	j	d	k	
Number of species	35	52	19	30	42	40	34	26	33	50	11	39	80
Number of breeding pairs	225	1,332	126	487	536	545	319	190	422	679	38	240	5,139
Shannon diversity index	2.87	2.96	2.43	2.56	2.90	2.89	2.80	2.63	2.63	2.93	2.01	3.08	3.11
Pielou's evenness index	0.81	0.75	0.83	0.75	0.78	0.78	0.79	0.81	0.75	0.75	0.83	0.85	0.71
Dominance	70.6	71.0	72.9	67.1	72.4	67.3	79.2	67.9	68.7	64.2	86.7	61.7	54.2
Dominance index	0.28	0.22	0.40	0.38	0.26	0.24	0.29	0.37	0.38	0.27	0.50	0.21	0.24

2020). Five dominant species were distinguished in Bloemfontein: Cape sparrow (28.5%), speckled pigeon (19.7%), little swift (10.2%), laughing dove (6.6 %) and Cape turtle dove (6.2 %); and four species in Maseru (n = 1,862 pairs of all species): speckled pigeon (9.9%), and Cape turtle dove (9.0%), common fiscal (8.5%), and laughing dove (7.4%). Of these, only the laughing dove was recorded as dominant in Windhoek. Remarkably, none of the dominant species in the three cities compared was an exotic species, except for the house sparrow. Bird species living in urban areas are often classified as urban avoiders, urban adapters, or urban exploiters (Marzluff, 2016; Lepczyk et al., 2017). Urban avoiders seem to allocate more energy to reproduction than urban adopters and exploiters. Urban adopters are usually sedentary, granivores or omnivores, and generalists in habitat choice. On the other hand, urban avoiders are usually migratory, insectivorous, and forest specialists in habitat selection (stenobionts). Urban exploiters are often ecologically flexible generalists (eubionts) associated with 'open' habitats (Chace and Walsh, 2006; Marzluff, 2016; Abilhaa and Amorin, 2017; Lepczyk et al., 2017). The dominant species recorded in Windhoek can all be classified as urban exploiters; most urban adopters can be found in the group of subdominants. The urban avoiders will be those with dominance lower than 1%. However, a more definite classification can be done by comparing the dominance value of each species in urban and the surrounding exurban habitats.

In studies by Bloemfontein and Maseru, the proportion between laughing and Cape turtle doves were fairly equal, i.e., in Bloemfontein: 0.51:0.49 (n = 661); in Maseru: 0.55:0.45 (n = 304 pairs of both species), but in Windhoek the proportion was totally different: 0.99:0.01

Table 5. The dominance and frequency of occurrence (in 12 transects) of dominant species: Nt, Number of transects where the species was dominant; Np, overall number of pairs and dominance in all transects.

Tabla 5. Dominancia y frecuencia de aparición (en 12 transectos) de las especies dominantes: Nt, Número de transectos donde la especie fue dominante; Np, número total de parejas y dominancia en todos los transectos.

Species	Nt		Np	
	N	%	N	%
House sparrow	12	100	669	7.8
Southern masked weaver	11	92	527	6.1
Laughing dove	10	83	460	5.4
Red-eyed bulbul	8	67	541	6.3
White-backed mousebird	8	67	329	3.8
Little swift	6	50	227	2.6
Black-throated canary	4	33	152	1.8
Egyptian goose	3	25	123	1.4
White-brow sparrow-weaver	3	25	202	2.4
African palm swift	3	25	208	2.4
Feral pigeon	2	17	212	2.5
Blue waxbill	2	17	135	1.6
Wattled starling	2	17	257	3.0
Chestnut-vented tit-babbler	2	17	199	2.3
Helmeted Guineafowl	1	8	52	0.6
Southern red bishop	1	8	30	0.4
Red-billed quelea	1	8	131	1.5
Black-chested prinia	1	8	105	1.2

(n = 467). House sparrow dominance was 2.9% in Maseru, and 4.4% in Bloemfontein, but it was much higher (13.0%) in Windhoek. The Southern masked weaver was subdominant both in Bloemfontein and Maseru, but it was a dominant species in Windhoek (table 5). The predominance of the exotic house sparrow in southern African urban areas appears to increase with the increase of aridity, while the opposite trend characterizes the indigenous Cape turtle dove. The laughing dove predominance in most southern African urbanized areas does not appear to follow this gradient.

Urbanization can result in increasing numbers of exotic species and decreasing richness of native species (Garaffa et al., 2009; Ibañez-Alamo et al., 2017). However, in Windhoek, this can be true in regard to vascular plants, but is not evident in regard to avifauna. In Africa, 65 exotic species were recorded in urban habitats (Lepczyk et al., 2017). However, out of 80 bird species recorded in Windhoek, only two, namely the house sparrow and feral pigeon, were exotic. Furthermore, contrary to expectation, the house sparrow is more abundant on the periphery of the city than in the city centre. On the other hand, the feral pigeon, another common exotic species, is far more abundant in the city centre than in the periphery (table 3). A similar situation prevails in other Namibian towns (Kopij, 2016, 2019b, 2019c, 2020, 2021b, 2021c, 2021d).

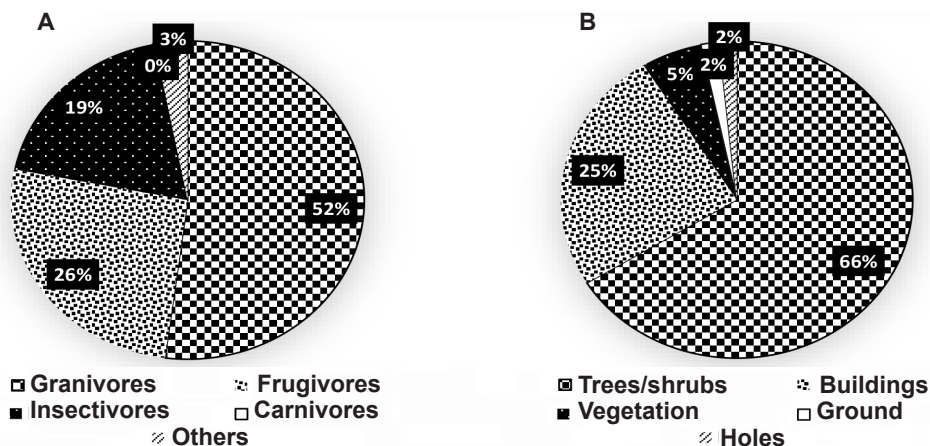


Fig. 5. Feeding (A) and nesting (B) guilds of birds in the urbanized habitats of Windhoek.

Fig. 5. Gremios de alimentación (A) y nidificación (B) de aves en los hábitats urbanizados de Windhoek.

In most Namibian towns where avian assemblages were quantified, the density of the laughing dove was high, with no (or very few) Cape turtle doves recorded (Kopij, 2014a, 2016, 2018a, 2019c, 2020, 2021a, 2021b, 2021c, 2021d). In towns situated in north–eastern Namibia, such as Grootfontein, Rundu and Katima Mulilo, the Cape turtle dove is, however, a common breeding resident (Kopij, 2016, 2019c, 2020, 2021b) as it is in all towns and cities investigated hitherto in South Africa, Lesotho and Botswana (Kopij, 1994, 1996, 2000, 2001, 2004, 2006, 2009, 2011, 2015, 2018b; Parker, 2012). Its absence in towns located on the Namibian coast is understandable as it is very rare also in the areas surrounding the towns (G. Kopij, pers. observ.). However, around Bloemfontein, Windhoek, and all towns in north–central Namibia, Cape turtle doves are common residents (Kopij, 2013, 2014b, 2019d) and yet they are absent or rare in the very towns. However, those towns are suitable for the nesting habitats of this species, offering abundant food and low predation pressure. Also, the years from foundation of the Namibian towns is similar to those in South Africa, Lesotho or Botswana.

In southern Africa cities and towns, 1–3 species of sparrows dominate avian communities. If the invasive house sparrow is well–established, usually the indigenous southern grey–headed sparrow disappears as it has in Bloemfontein (Kopij, 2001, 2015), Bethlehem (Kopij, 1997), Windhoek and all the towns in northern Namibia (Kopij, 2014a, 2019a, 2021d). However, in Lesotho, especially in towns located in the highlands of the Maloti, the southern grey–headed sparrows co–exist with the house sparrows (Kopij, 2011). Nevertheless, the Cape sparrow appears to be better adapted to co–exist with the house sparrow. Whenever the latter is well–established and a common resident, the previous is also common, as it is in South Africa, Lesotho and in Namibian coastal towns (Kopij, 1994, 1996, 2000, 2009, 2011, 2018a, 2022; Kopij and Esterhuizen, 1994). In Windhoek and most other Namibian towns, the Cape sparrow does not occur in the surrounding areas (G. Kopij, pers. observ.), so it is also absent in the towns.

The southern masked weaver, one of the three *Pycnonotus* bulbul species, 1–2 mousebird (Coliidae) species and 1–2 starling (Sturnidae) species are classified in Windhoek, as in most southern African cities and towns, as dominant or subdominant (Kopij, 1994, 1996,

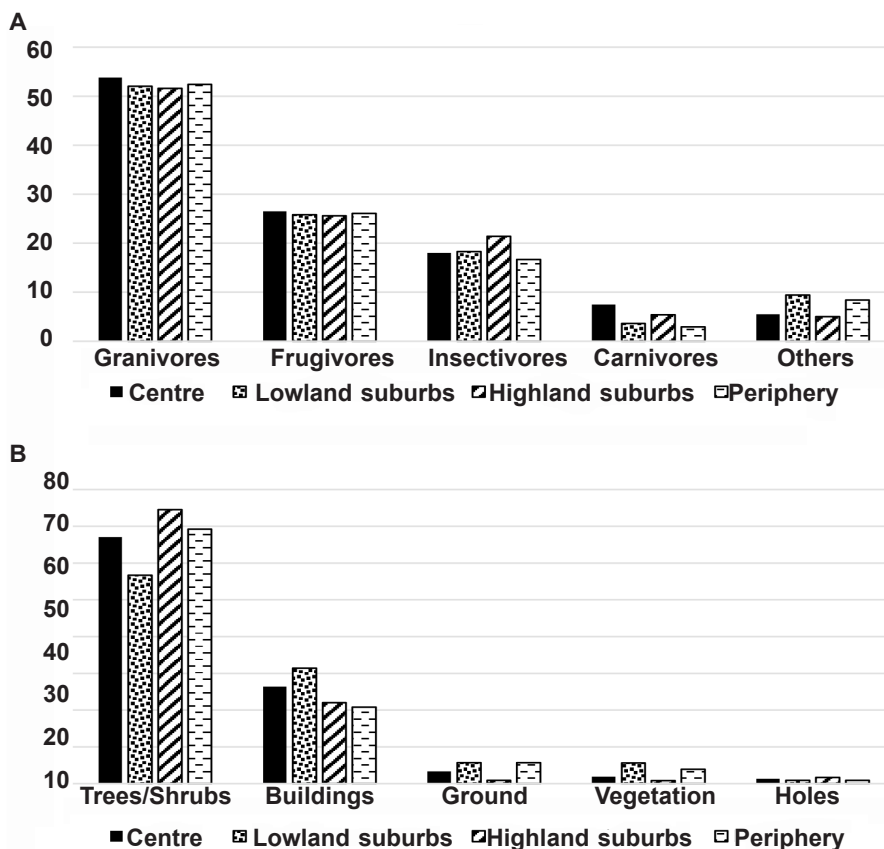


Fig. 6. Proportions of feeding (A) and nesting (B) guilds in four urban habitats in Windhoek.

Fig. 6. Proporción de gremios de alimentación (A) y nidificación (B) en cuatro hábitats urbanos de Windhoek.

1997, 1999, 2000, 2001, 2004, 2006, 2009, 2011, 2014a, 2015, 2016, 2018a, 2018b, 2019a, 2019b, 2019c, 2019d, 2020, 2021a, 2021b, 2021c, 2021d, 2022; Craig et al., 2021). Swifts and pigeons are also in the group of dominant species in many southern African cities and towns, but they usually concentrate in densely built-up city centres. If counts are conducted mainly outside the city centre, as in this study, their numbers may be underestimated. Throughout the world, avian assemblages tend to be relatively uniform across urbanized environments (Ferenc et al., 2014).

It should be noted that in most cities and larger towns, there are some 'unique' dominant species, e.g. common waxbill in Namibian coastal towns (Kopij, 2018a, 2022), rosy-faced lovebird in Grootfontein and Hentjes Bay (Kopij, 2021b, 2022), African palm swift in north-central Namibia (Kopij, 2019b), Indian myna in Bethlehem (Kopij, 1997), common fiscal in Morija (Kopij, 2006) Cape canary in Drakensberg/Maloti (Kopij, 2011) or red-eyed dove in Ladybrand (Kopij, 2009). The swallow-tailed bee-eater and pale-winged starling can be regarded as unique species in Windhoek.

Granivore, omnivore, and cavity–nesters show the strongest association with urbanized environments in temperate zones, while frugivores and nectarivores also predominate in urban environments in the tropical zone (Chace and Walsh, 2007; Lepczyk et al., 2017). In most cities and towns in southern Africa, including Windhoek, granivores are by far the most numerous feeding guild. Insectivores are usually the second most numerous. In Windhoek, frugivores are, however, more numerous than insectivores, probably due to the abundance of trees and shrubs yielding fruits. The hole–nesting birds are, on the other hand, a much less numerous nesting guild in Windhoek than in other towns and cities. This is probably because large trees are rather scarce in Windhoek. Birds nesting in low herbaceous vegetation and on the ground were rare in all habitats due, first, to high human pressure and second, to the high numbers of dogs and cats which can easily prey on ground–nesting birds (fig. 5). In Calcutta, India, the proportion of granivores was higher in urban areas, while carnivores and insectivores were virtually absent (Sengupta et al., 2014).

Avian species richness decreases and its biomass increases as urbanization increases (Chace and Walsh, 2006; Villegas and Garitano–Zavala, 2010; Reis et al., 2012, Vázquez Plass and Wunderle, 2013; Sengupta et al., 2014; Marzluff, 2016). Generalists increase and specialists decrease with the growth of urbanization (Marzluff, 2016). In Windhoek, no clinal variation was recorded for species richness, diversity, or dominance indices (table 4, fig. 5). These indicators are often related to the presence of patches of natural or semi–natural vegetation (Wolff et al., 2018). These patches are distributed regularly all over the urban, suburban and peripheral habitats (gardens, water courses and rocky hills covered with natural vegetation) in Windhoek, and may obscure the pattern of changes along the urbanization gradient. The pattern can be clearly seen only in the abundance of a few of the most common species, such as the feral pigeon, little swift, white–backed mousebird and southern masked weaver (table 3).

The regular distribution of patches of remnant natural vegetation plays an important role in retaining the relatively high species richness and diversity all over the city of Windhoek. Both this natural vegetation and planted garden vegetation may provide suitable nesting sites, shelter, food (frugivore and nectarivore species) and water for birds. It is therefore highly advisable to promote gardening, and conserve remnants of natural vegetation along water courses, rocky hills, and the peripheries of sport fields, schools, churchyards, and similar.

In conclusion, Windhoek avifauna is similar in dominance structure to avifauna in other southern African cities and towns where sparrows, doves/pigeons, bulbuls and mousebirds dominate, and granivores are by far the most numerous feeding guild. The difference lies mainly in the composition of insectivorous guilds and species breeding in low population densities.

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