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POPULATION DEVELOPMENT OF THREE SYMPATRIC DOVE SPECIES IN AFRICAN ACACIA SAVANNA FOLLOWING A DROUGHT

Grzegorz Kopij

Department of Vertebrate Ecology, Wrocław University of Environmental & Life Sciences, ul. Kozuchowska 5b, 51–631 Wroclaw, Poland
Email: gregorius.kopijus@gmail.com
https://orcid.org/0000-0001-7614-1983

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Abstract. The breeding densities of three dove species: Laughing Dove *Spilopelia senegalensis*, Ring-necked Dove *Streptopelia capicola*, and Mourning Collared Dove *Streptopelia decipiens* were studied by means of the territory mapping method in 400 ha of acacia savanna in northern Namibia. About half of the study area comprised cultivated fields, orchards, sport fields and human settlements. The study was conducted in February–June 2020, after a prolonged drought in 2017–2019. During the drought, most doves vacated their territories and ceased to breed, but breeding populations recovered rapidly. The overall population density of all species was the highest in February/March (30.3 pairs / 100 ha), intermediate in April (27.8), and lowest in May/June (23.5). Population densities were higher in the man-modified than in natural savanna. While the population densities in natural savanna significantly increased with the advance of the dry season, in man-modified savanna the densities decreased slightly.

INTRODUCTION

Among the 37 columbid species occurring in Africa, 10 are representatives of the genus *Streptopelia* and one species belongs to the resurrected genus *Spilopelia*, closely-related to *Streptopelia* and only recently separated from this genus (Urban et al. 1986; Baptista et al. 1997; Johnson et al. 2001; Gill et al. 2023). Beside the Laughing Dove *Spilopelia senegalensis,* three *Streptopelia* species occur in southern Africa: the Ring-necked Dove *S. capicola*, the Red-eyed Dove *S. semitorquata* and the Mourning Collared Dove *S. decipiens* (Hockey et al. 2005; SABAP2 2023). Both the Laughing Dove and Ring-necked Dove occur commonly all over this subcontinent. The Red-eyed Dove is largely restricted to the eastern, more humid, part of southern Africa; in the west it is mainly found in riverine woodland along major rivers. The Mourning Collared Dove occurs in Kaokoland, NW Namibia, Okavango valley and delta, Zambezi region, NE Namibia, Zambezi and Limpopo valleys and in Mpumalanga province, South Africa (SABAP2 2023). In Namibia the two latter species are restricted to the north, while the two former are common all over the country (Rowan 1983; Urban et al. 1986; Hockey et al. 2005; SABAP2 2023).

The Laughing Dove and Ring-necked Dove are among the most ubiquitous and abundant bird species in most natural (Kopij 2010, 2012, 2013a, b, c; Monadjem 2002; Steyn and Maina 2014), agricultural (Kopij 1998a, 2001b, 2018c, 2019b, 2021a; Underhill et al. 1999) and urbanised (Kopij 1997b, 1999, 2001a, 2015, 2019c; Kopij and Esterhuizen 1994; Engelbrecht 2002; Parker 2014) habitats in southern Africa. In grasslands and savanna biomes, they are usually classified as dominant, often comprising more than 5% of all birds in avian communities (Dean 1980; Kopij 1997a, 1998b, 2002b, 2006, 2010, 2012, 2013a,b, c, 2021a; Monadjem 2002; Parker 2014). Their main diet consists of grass seeds, which are superabundant in these biomes in a normal year (Kopij et al. 1999; Adang et al. 2008). However, under drought conditions, this food becomes scarce and population densities of breeding doves are drastically reduced.

All four dove species are easily identified in the field both visually and by their typical cooing calls, which make them convenient objects for ecological surveys. They often breed in sympatry, especially the Laughing Dove with the Ring-necked Dove (Kopij 1998b). In more humid regions of southern Africa, the Red-eyed Dove and Mourning Collared Dove may also breed alongside the Laughing Dove and Ring-necked Dove (e.g. Kopij 2018b, 2019c, 2020a, b). Despite a wide distribution of these dove species, there is a lack of reliable and precise population estimates (large representative study plots with the breeding pair as a census unit, applying the territory mapping method) of their breeding

densities in various habitat types in all biomes of Africa (Rowan 1986; Urban et al. 1986; Baptista et al. 1997; Hockey et al. 2005; Benghedier et al. 2020).

The aim of the study is to: 1) estimate population densities of three sympatric dove species (Laughing Dove, Ring-necked Dove, and Mourning Collared Dove) under savanna conditions, 2) study the speed of recovery of dove populations after a prolonged drought, 3) identify any microhabitat preferences of particular dove species, and 4) compare population densities of these three dove species from other sites in southern Africa.

METHODS

Study area

The study area was located on the UNAM Ogongo campus, Omusati Region, N Namibia. It is situated in the BIOTA Observatory 'Ogongo' within the Cuvelai Drainage System, c. 50 km NW of Oshakati, Outapi district, Omusati region, north-central Namibia (17.7S, 15.31E). This observatory was designated in the early 2000s as the final observatory of the BIOTA Transect and Biodiversity Observatories in southern Africa. This transect starts in Cape Town, runs through Oranjemund, Karios, Nabaos, Windhoek, Okahandja, Sonop, Mutompo, and ends in Ogongo (Jurgens et al. 2010; Schmiedel and Jurgens 2010; Hoffmann et al. 2010).

The Cuvelai Drainage System, where the study area is situated, is a unique ecosystem comprising a network of water canals (oshanas), mopane and acacia savannas (Mendelsohn et al. 2000, 2009; Mendelsohn and Weber 2011). The study area is, however, devoid of these canals, and the natural vegetation comprises acacia savanna composed mainly of *Acacia erioloba, A. nilotica, A. fleckii, A. mellifera, Albizia anthelmintica, Dichrostachys cinerea, Colophospermum mopane, Combretum* spp., *Commiphora* spp., *Grewia* spp., *Ficus sycomorus, Boscia albitrunca, Terminalia sericea, Zyzyphus mucronata*, and *Hyphaene petersiana* (Kangombe 2007) (Figure 1). There is only a small section of mopane savanna (composed almost entirely of young *Colophospermum mopane* shrubs) in the north-eastern corner of the study area. Both savannas are utilized for grazing cattle, sheep, and goats.

The total study area covered 400 ha. About half was converted into cultivated fields, orchards, sport fields and human settlements (Figure 1). The proportion of

Figure 1. Habitats in the study area: upper left: built-up area; upper right: marula tree in disturbed savanna; lower left: orchards and disturbed savanna; lower right: natural savanna.

Table 1. Population densities of the Laughing Dove in different micro-habitats in a Namibian acacia savanna. N = number of breeding pairs; p/100 ha = pairs per 100 ha.

Micro-habitat	Size [ha]	Feb.–March		April		May–June		Average	
		N	p/100ha	N	p/100ha	N	p/100ha	N	p/100ha
Natural savanna	278	69.5	25.0	61.5	22.1	47	16.9	59.2	21.3
Man-modified savanna	52	13.5	26.0	18.5	35.6	19	36.5	17.0	32.7
Disturbed savanna	10	6	60.0	6	60.0	7	70.0	6.3	63.0
Arable fields	30	1.5	5.0	5	16.7	5	16.7	3.8	12.7
Orchards	10	4.5	45.0	6	60.0	5.5	55.0	7.2	72.0
Sports field	2	1.5	75.0	1.5	75.0	1.5	75.0	1.5	75.0
Built-up areas	70	23	32.9	19	27.1	17	24.3	19.7	28.1
Total	400	106	26.9	99	24.8	83	20.8	96.0	24.0

Table 2. Population densities of the Ring-necked Dove in different micro-habitats in a Namibian acacia savanna. N = number of breeding pairs; p/100 ha = pairs per 100 ha.

Micro-habitat	Size [ha]	Feb.–March		April		May–June		Average	
		N	p/100ha	N	p/100ha	N	p/100ha	N	p/100ha
Natural savanna	278	6.5	2.3	5	1.8	3	1.1	4.8	1.7
Man-modified savanna	52	4.5	8.7	2	3.8	3	5.8	3.2	6.1
Disturbed savanna	10	2.5	25.0	1	10.0	1	10.0	1.5	15.0
Arable fields	30	1	3.3	1	3.3	1.5	5.0	1.2	4.0
Orchards	10	1	10.0	0	0.0	0.5	5.0	0.5	5.0
Sports field	2	0	0.0	0	0.0	0	0.0	0.0	0.0
Built-up areas	70	1	1.4	1	1.4	1	1.4	1.0	1.4
Total	400	12	3.0	8	2.0	7	1.8	9.0	2.3

Table 3. Population densities of the Mourning Collared Dove in different micro-habitats in a Namibian acacia savanna. N = number of breeding pairs; p/100 ha = pairs per 100 ha.

Micro-habitat	Size [ha]	Feb.–March		April		May–June		Average	
		N	p/100ha	N	p/100ha	N	p/100ha	N	p/100ha
Natural savanna	278	3	1.1	3.5	1.3	2	0.7	2.8	1.0
Man-modified savanna	52	0	0.0	0.5	1.0	0	0.0	0.2	0.4
Disturbed savanna	10	0	0.0	0.5	5.0	0	0.0	0.2	2.0
Arable fields	30	0	0.0	0	0.0	0	0.0	0.0	0.0
Orchards	10	0	0.0	0	0.0	0	0.0	0.0	0.0
Sports field	2	0	0.0	0	0.0	0	0.0	0.0	0.0
Built-up areas	70	0	0.0	0	0.0	1	1.4	0.3	0.4
Total	400	3	0.8	4	1.0	4	1.0	3.7	0.9

land use is shown in Tables 1–3. There are also numerous exotic trees planted in and around the human settlements, such as *Kigelia africana, Moringa oleifera, Melia azedarach, Dodonaea viscosa, Eucalyptus camelduensis* (Figure 1). There are several permanent water bodies with standing water, and the area borders on an artificial water canal to the north and an extensive oshana (natural grassy depression filled with water in the rainy season) to the east.

Ogongo has semi-arid climate. The summers are sweltering and partly cloudy; the winters are short, comfortable, and clear (Mendelsohn et al. 2000; Mendelsohn and Weber 2011). In Onguediva, located in the middle of the Cuvelai Drainage System, the rainfall during the years 2017–2020, with a long-term average, is shown in Figure 2.

Field procedure

Surveys were conducted in three different seasons of 2020, namely: the rainy season (February–March), an intermediate period (April), and the dry season (May–June). A territory mapping method (Sutherland 1996; Bibby et al. 2012) was used to assess the population densities of the three selected dove species. Four surveys of the whole area were conducted in each season. Each survey consisted of 4–5 counts conducted on different days in a portion of the study area, so as to cover the whole study area. In total, 57 mornings were spent counting (17 in February–March, 19 in April, and 18 in May–June). Only cooing birds showing other territorial or breeding behaviour were plotted on the map. Caution was taken not to register the same individuals by noting all dove movements in the field and by paying special attention to simultaneously cooing birds.

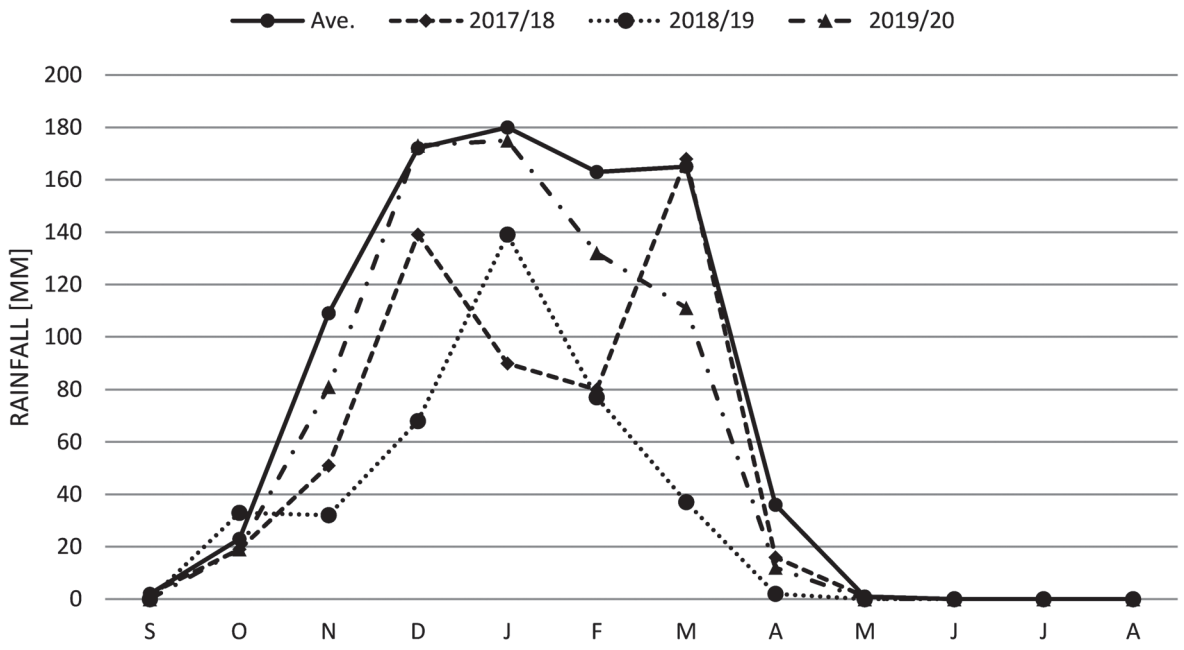

Figure 2. Rainfall in Onguadiva in 2017–2020, with a long-term average.

Statistical analysis

At least two records in a clump were required to confirm an occupied territory (Bibby et al. 2012). An occupied territory was equal to a breeding pair. The number of breeding pairs were counted in the whole study area (400 ha), and in particular microhabitats distinguished in this area (Tables 1–3). Territories which covered two microhabitats were counted as 0.5 pairs for one micro-habitat, and 0.5 pairs for the other microhabitat. Population density was expressed as the number of breeding pairs per 100 ha of a given microhabitat, using the following formula: D = (N × 100)/S, where D – population density, N – number of breeding pairs in a given microhabitat, S – surface area of this microhabitat in ha. Differences in the number of breeding pairs of a given dove species in a particular microhabitat in three breeding seasons (February/March, April, May/June) were tested with the Chi-squared test.

RESULTS

All three dove species were recorded as breeding in the study area in all survey periods (Tables 1–3; Figures 3–5). The overall population density of doves was the highest in February/March (30.3 pairs / 100 ha), intermediate in April (27.8), and the lowest in May/June (23.5). However, the difference is not statistically significant ($x^2 = 3.43$, $p > 0.05$). This pattern was followed by both the Laughing Dove and the Ring-necked Dove, while the population of the Mourning Collared Dove remained more constant (Tables 1–3).

The Laughing Dove reached higher population densities than the other species, both in natural savanna, modified savanna and in built-up areas. The overall population density of the Laughing Dove was of an order of magnitude higher than that of the Ring-necked Dove. The population density of the Mourning Collared Dove was three times lower than that of the Ring-necked Dove (Tables 1–3).

The Laughing Dove breeding density in natural savanna was significantly higher ($x^2 = 7.23$, $p < 0.01$) in the wet (25.0) than in the dry season (16.9). The Ring-necked Dove breeding density was also higher in the wet (3.0) than in the dry season (1.8), but this difference was not statistically significant ($x^2 = 1.32$, $p > 0.05$). No difference was recorded for the Mourning Collared Dove (Tables 1–3).

While the population density of the Laughing Dove in natural savanna significantly increased with the advance of the dry season, in man-modified savanna and built-up areas it slightly decreased ($x^2 = 0.90$, $p > 0.05$; $x^2 = 0.93$, $p > 0.05$, respectively). In the two other dove species, no differences in the population densities between the man-modified savanna and built-up area were recorded (Tables 1–3).

The population density of the Laughing Dove was higher in man-modified savanna (32.7) and built-up area (28.1) than in natural savanna (21.3). The population density of the Ring-necked Dove was also much higher in man-modified savanna (6.1) than in natural savanna (1.7), but it was also much higher in man-modified savanna than in built-up areas (1.4) (Tables 1–3).

Laughing Doves avoided places with short shrubby vegetation, preferring larger acacias and palm trees and proximity to water. The Ring-necked Dove did show a

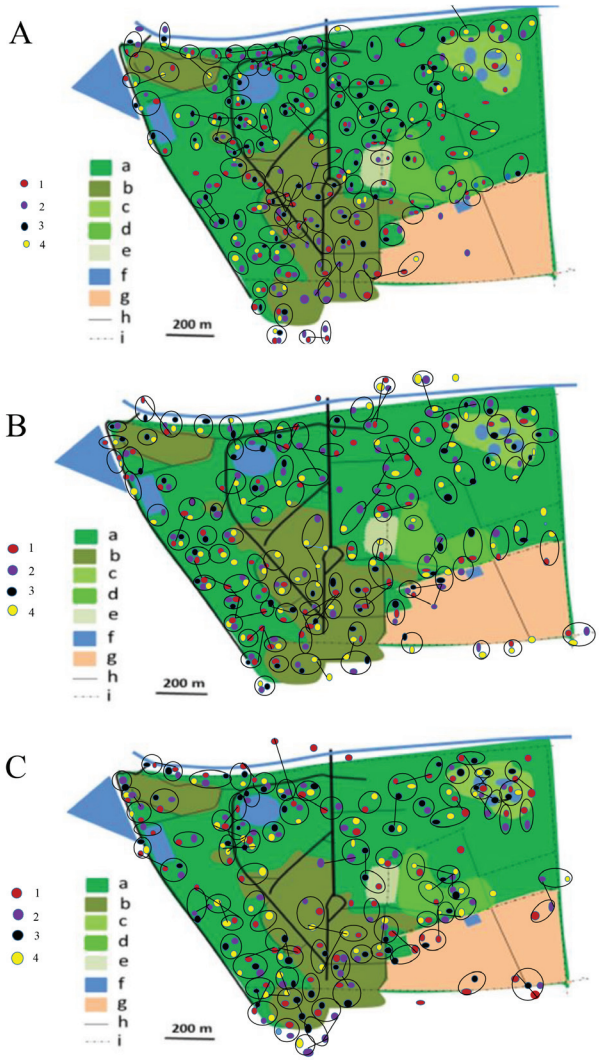

Figure 3. Distribution of occupied territories of the Laughing Dove at Ogongo area in 2020. Explanations: A – February–March, B – April, C – May–June. Habitats (land uses): a – acacia savanna, b – built-up area, c – disturbed acacia savanna, d – orchard, e – sport field, f – water bodies, g – arable ground, h – roads, i – fences. 1, 2, 3, 4 – records of birds during survey 1, 2, 3, or 4. Encircled are occupied territories.

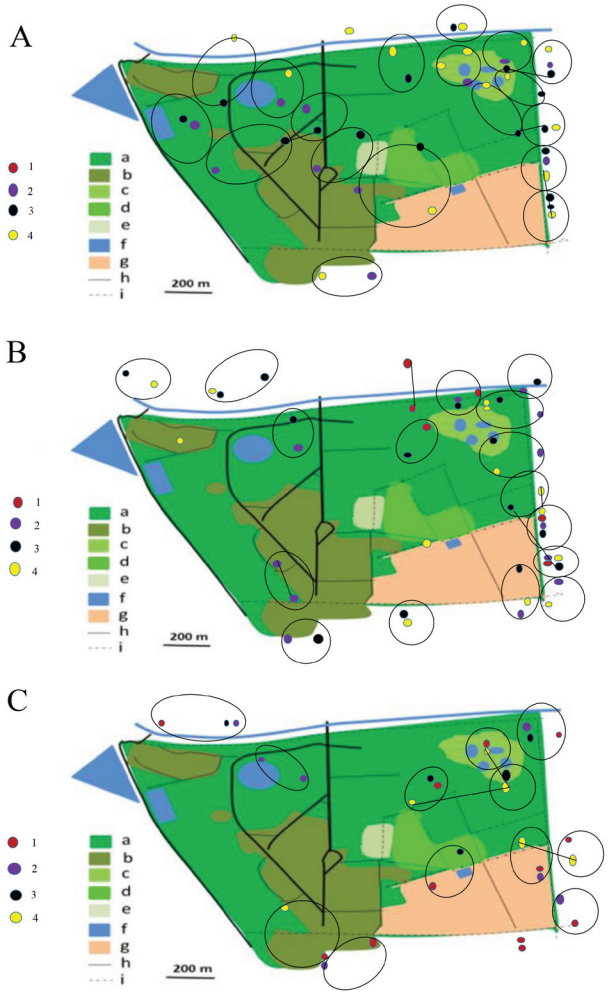

Figure 4. Distribution of occupied territories of the Ring-necked Dove at Ogongo area in 2020. For explanations see Figure 3.

preference for water bodies. Most territories were established in places where territory densities of the Laughing Doves were lower, e.g. on the eastern border and in the north-western corner of the study area. The Mourning Collared Dove showed the highest preference to water bodies. All established territories were in proximity to water bodies, not shifting over the whole study period (February–June) (Figures 3–5).

DISCUSSION

Both the Laughing Dove and Ring-necked Dove occur commonly all over southern Africa. The Red-eyed Dove is found mainly in the eastern, more humid, part of southern Africa. In Namibia it is restricted to Caprivi Strip, Okavango River valley and Kunene River valley (SABAP2 2023). The Mourning Collared Dove occurs in Kaokoland, NW Namibia, Okavango valley and delta, Zambezi region, NE Namibia, Zambezi, and Limpopo valleys and in Mpumalanga province, South Africa. The two latter species occur in higher densities in acacia and wooded river valleys (Kopij 2002a, 2019b). The Laughing Dove is ubiquitous, most numerous in savanna with palms (where palms occur), often in drier habitats and avoiding densely wooded areas. The Ring-necked Dove is associated mainly with savanna, and is characteristic of more humid habitats, but like the previous species avoids forest (Rowan 1983; Baptista et al. 1997). In this study, the two species did not differ in special preferences for any micro-habitats recognized (natural savanna, disturbed savanna, arable fields, orchards, built-up areas).

In this study, breeding population density was estimated by means of the territory mapping method (Sutherland 1996; Bibby et al. 2012). Since these dove species are very vocal in the breeding season (Rowan 1983; Kopij

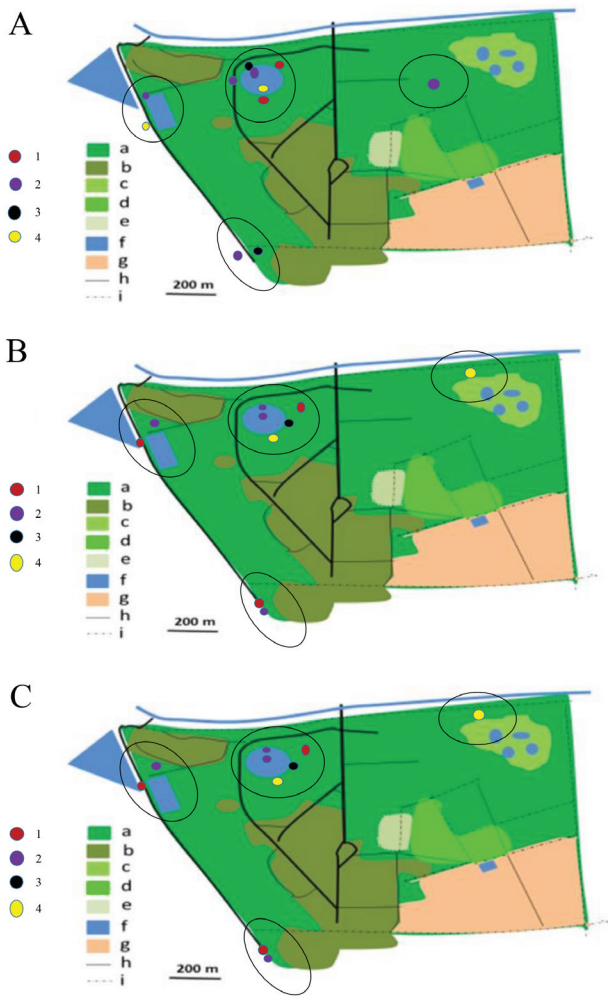

Figure 5. Distribution of occupied territories of the Mourning Collared Dove at Ogongo area in 2020. For explanations see Figure 3.

2003; Hockey at al. 2005), they are easily detected in the field. Four surveys were therefore sufficient to detect their territories. This method produces precise and unbiased estimates. I have used it elsewhere in southern Africa to estimate dove population densities in man-modified habitats. Since the studies were conducted by one researcher, the results can be compared with some confidence (Table 4). The population densities of all three dove species investigated were in most places much higher than in Ogongo, the highest in well-treed suburbs, and the lowest in a city centre void of trees (Bloemfontein) and in a town (Outapi) dominated by non-breeding Pied Crows *Corvus albus* (due to the presence of many huge baobabs in this area) (Table 4).

According to Rowan (1983), whenever such doves breed sympatricaly, the Laughing Dove and Ring-necked Dove always outnumber other species. Katima Mulilo town in the far north-eastern part of Namibia was exceptional in this regard as the Ring-necked Dove bred there at a density lower than the Red-eyed Dove and even lower than the Mourning Collared Dove did (Table 4).

A high site tenacity (philopatry) has been confirmed in the Ring-necked Dove (Dean 1980; Baptista et al. 1997) and Laughing Dove (Baillon and Benvenuti 1990). In the present study, most territories of all three dove species were in the same sites over at least five months, i.e. over 2–3 broods (Figures 3–5). This suggests that high site tenacity over one reproductive season, perhaps even over several years, may be characteristic not only of the Ring-necked Dove, but also of other dove species.

The Laughing Dove is often regarded as an indicator of disturbed habitats. It is therefore one of the most

Table 4. Population densities of doves in man-modified habitats in southern Africa (all results based on the territory mapping method). LD – Laughing Dove, RnD – Ring-necked Dove, ReD – Red-eyed Dove, MD – Mourning Collared Dove.

Country	Habitat	Pairs/100 ha				Source
		LD	RnD	ReD	MD	
Man-modified desert						
Namibia	Swakopmund, suburbs, shrubs; 415 ha	47.0	–	–	–	Kopij 2018a
Namibia	Hentje's Bay, suburbs, palms; 345 ha	73.0	–	–	–	Kopij 2022
Namibia	Walvis Bay, suburbs, palms; 260 ha	59.6	–	–	–	Kopij, in press
Man-modified grassland						
South Africa	Bloemfontein, city centre; 123 ha	14.6	8.9	0.8	–	Kopij 1996
South Africa	Bloemfontein, wooded suburbs; 55 ha	88.2	67.3	1.8	–	Kopij 1994
Lesotho	Roma, wooded suburbs; 82 ha	120	61.0	2.3	–	Kopij 2001b
Man-modified savanna						
Namibia	Outapi, suburbs, baobabs; 130 ha	10.0	–	–	–	Kopij 2019a
Namibia	Onguadiva, suburbs, marulas; 100 ha	84.0	–	–	–	Kopij 2021b
Namibia	Katima Mulilo, suburbs, parkland; 214ha	57.0	5.6	4.0	13.6	Kopij 2019c
Man-modified woodland						
Botswana	Kasane, suburb/rural, woodland; 160 ha	30.0	18.0	4.0	4.0	Kopij 2018b
Namibia	Katima Mulilo, suburbs, woodland; 133 ha	64.4	18.9	22.9	7.1	Kopij 2020b
Namibia	Katima Mulilo, town centre; 85 ha	73.0	4.0	6.0	20.0	Kopij 2020a

numerous breeding birds in urban habitats and well-treed farmlands. In Bloemfontein, where all bird species were quantified, it reached a density of 34 pairs / 100 ha (Kopij 2015).

In many places in southern Africa, the Laughing Dove and the Ring-necked Dove are the commonest dove species; they often nest at the same site, even in the same tree, and their territories may overlap to a large extent. Nevertheless, in most places, where the two species breed sympatricaly, one species is numerically dominant. The factors governing this association are complex and largely still unknown (Rowan 1983).

In the Western Cape province, around Cape Town, the Laughing Dove tends to be the commonest in urban environments, while the Ring-necked Dove is the commonest in a rural environment (Rowan 1983). In many areas of this province, there has been a steady replacement of the Ring-necked Dove by the Laughing Dove, as urbanization (density of human habitations) has increased (Rowan 1983). In a drier north-west province of South Africa, in the Karoo biome and beyond, the Laughing Dove is strongly associated with disturbed areas (farmsteads, artificial dams, heterogeneous vegetation), while the Ring-necked Dove is associated with tall trees and open terrain, i.e. typical savanna, and occurs at a low density generally (Lee et al. 2018, 2021; Lee and Wright 2020). In Bloemfontein, both species are equally common. The overall population density of the Laughing Dove in the city is 34.0 pairs per 100 ha, while that of the Ring-necked Dove is 32.1 pairs per 100 ha (Kopij 2015). Also in the Roma area, Lesotho, both species were found to be equally numerous (Kopij 2001). However, in a grassy area (230 ha) on the periphery of Bloemfontein, both species nested at much lower densities (3.5 pairs/100 ha vs. 1.8 pairs/100 ha, respectively) (Kopij and Esterhuizen 1994).

There was a drought in Namibia from 2016 to 2019. The amount of rain in the 2017/18 wet season was especially low, so that grasses in most places did not sprout. Most doves of both species ceased to breed in the study area. They formed flocks looking for supplementary food other than the grass and herb seeds, which normally comprise the staple food (Urban et al. 1986; Baptista et al. 1997; Kopij et al. 1999; Hockey et al. 2005). They were, for example, often seen on the campus feeding on eucalyptus seeds (Kopij 2022). The populations recovered very fast. While only a few pairs bred in August–September, in the following months they increased rapidly, reaching relatively high population densities by February-March. This was probably because the birds remained in the area during the drought, formed flocks instead of breeding pairs, and fed mainly on seeds from trees and shrubs instead of grass and herbs.

It appears that in urbanized habitats throughout southern Africa, the Laughing Dove outnumbers other dove species. However, the second most numerous dove may be any other species. In more natural areas, like savanna or woodland, the situation is different in different regions (perhaps depending on humidity). For instance, the Ring-necked Dove often dominates in savanna biomes in Namibia (Kopij 2013b, d) and Swaziland (Monadjem 2002) and in the grassland biome of Lesotho (Kopij 2010, 2012, 2013c). The Laughing Dove dominates in arid habits (Kopij 2018a, 2022). The Red-eyed Dove and Mourning Collared Dove are most common in some riparian forests (Baptista et al. 1997; Kopij 2002a, b, 2020b).

In normal years, all three dove species studied in Ogongo breed throughout the year, as in other parts of southern Africa (Rowan 1983). In years with prolonged droughts, most of them cease to breed. However, after droughts, they recover rapidly, saturating the environment within a year. Such a great potential may contribute to their high success in colonizing various savanna and arid habitats. A much smaller Laughing Dove numerically dominates over other dove species in all distinguished microhabitats within the modified African acacia savanna.

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