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WATERBIRDS IN THE PANHANDLE OF THE OKAVANGO DELTA: DRY SEASON COUNTS OVER TWO SEVEN-YEAR PERIODS

Grzegorz Kopij[a] and Mark Paxton[b]

[a] Department of Integrated Environmental Science, University of Namibia, Ogongo Campus, Namibia;
[b] Shamvura Camp, Rundu, Namibia. Email: mw.paxton@gmail.com
* Corresponding author. Email: gkopij@unam.na

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Abstract. We counted waterbirds along a fixed route in the panhandle of the Okavango River in Mahango Game Reserve in the dry season during two seven-year periods (1991–1997 and 2000–2006). Palearctic migrants represented by 11 species in 1991–1997 and nine species in 2000–2006 together composed only a small percentage of all birds recorded in both periods. The two most numerous foraging guilds were birds foraging in shallow water and those foraging in deep water. The former guild was more numerous in 2000–2006, while the latter guild was more numerous in 1991–1997. The proportion of other foraging guilds varied little between the two periods. The most numerous diet guild was piscivores, they were more numerous in 1991–1997 than in 2000–2006. If the total numbers of birds of each particular species in the years 1991–1997 were pooled and compared with those for the years 2000–2006, then highly significant changes in their numbers between these periods could be seen for 53 out of 93 waterbird species. Over the timespan 1991–2006, 12 species significantly increased in numbers while one species, the Cattle Egret, declined; seven other species showed no significant changes in abundance. The increase can be linked to the volume of water flowing through the river. While during the years 1991–1997 the total volume measured at Mohembo was 45.9 km^3 (SD = 1.43), during the years 2000–2006 the volume was 60.9 km^3 (SD = 1.41). Diversity was very similar during the two periods (1991–1997: S = 1.4; 2000–2006: S = 1.3), with no difference in evenness. The striking feature is that species diversity and abundance of birds was far greater than any records from other southern African rivers to date.

INTRODUCTION

Freshwater ecosystems comprise an atypical habitat, in that they do not cover one large area in a particular zoogeographical region like other biomes, but are scattered within the biomes. Unlike other biomes they have also well-marked, almost linear limits. They play a very important role by distributing and retaining water in each biome, especially in those which have distinctive and prolonged dry seasons. For example, in the savanna biome in north-eastern Namibia and northern Botswana the dry season usually lasts eight months. The Okavango River flowing through this region therefore plays a crucial role in this long season for all forms of life (Barnard 1998; Mendelsohn and El Obeid 2003, 2004). Despite its huge role in the ecosystem, no part of this river in Namibia has been proclaimed to date as a Ramsar site and only a small section is formally protected within the Mahango Game Reserve.

Waterbirds are associated with wetlands, lakes, ponds, rivers and other freshwater ecosystems as their main foraging and/or nesting habitats. The group includes numerous members of orders such as the Anseriformes, Ciconiiformes, Gruiformes and Charadriiformes, and several smaller families, e.g. Podicepidae, Phalacrocoracidae, Alcedidae, and Accipitridae. The Okavango River constitutes a very important habitat for hundreds of species belonging to these groups, and therefore plays a crucial role in their conservation (Bethune 1991).

In comparison with terrestrial habitats, tropical freshwater ecosystems are regarded as more stable habitats over the year (one of the most important ecological factors, water, is not a limiting factor there). The same could be expected in regard to the bird fauna associated with such ecosystems, but waterbirds are known to be highly mobile seasonally (Cumming et al. 2012). However, too little is known about waterbird communities in tropical ecosystems, especially in the arid areas, to make any predictions concerning population changes (Cumming et al. 2012).

The aim of this study was 1) to compare the species composition, diversity, abundance and dominance of waterbird species in two seven-year periods with a different water regime in the river; 2) to study changes in the main ecological guilds of waterbirds in these two periods; 3) to investigate population trends of the more common waterbird species over 16 years; 4) to compare the waterbird assemblage with those in other African rivers; and 5) to evaluate the site for nature conservation, especially as a potential Ramsar site (http://www.ramsar.org/sites).

Study area

The study was conducted in the panhandle of the Okavango River located in Mahango Game Reserve (18˚12'S, 24˚41'E) in the Kavango East region, NE Namibia. The main channel surveyed was 50–200 m wide and ca. 28 km long, in a river valley 2–6 km wide. The main river channel has sandbanks and numerous vegetated islands. It forms wetlands connected to the main channel by many small channels. The banks are covered with tall grasses Poaceae and sedges Juncidae, primarily *Phragmites australis* reeds and papyrus *Cyperus papyrus*. The marshes are often several hundred meters in width (Figure 1 and 2). There are also extensive floodplains in the valley (Bethune 1991; Cumming et al. 2012). The riparian forest further afield is composed mainly of *Garicinia, Sclerocarya, Diospyros, Acacia, Grewia, Pterocarpus, Ricinodendron, Ziziphus, Baikiaea, Baphia, Phoenix,* and *Adansonia*. Bethune (1991) provided a check-list of 869 plant species from 88 recorded in the Kavango Valley.

The Okavango River is unique on a global scale. It collects all its water in a drainage basin of ca. 112000 km^2 in Angola, then flows ca. 500 km with no further influx, forming a sort of linear oasis on the border of Namibia and Angola, and enters Botswana where it finally disperses its water into a 'sea' of sand forming a unique inland delta.

Figure 1. Okavango River valley with a floodplain.

Figure 2. Riparian forest in Okavango River valley.

The mean annual rainfall in the study area is 550–600 mm, with ca. 80% between December and March (Mendelsohn and el Obeid 2003, 2004). Annual rainfall varies substantially from year to year, but local rainfall contributes little to water levels in the river. The annual cycle of flood is the most prominent feature of the Okavango River. It influences the nutrient content in the water and consequently all forms of life in the river and its whole valley. The total volume of water passing in Mukwe varies greatly (from 5607 million m^3 to ca. 15354 million m^3) from year to year (Mendelsohn and el Obeid 2003, 2004). The highest river flow is in January–March, the lowest in September–October. The water level is the lowest in the river in November, the highest in April (3–4 m difference, sometimes up to 6 m). The long-term average (1948–1998) is 9594 million m^3. Compared to April (end of rainy season), the water volume carried in October (end of dry season) is much lower. However, the flows are much more stable in the dry than in the rainy season.

MATERIALS AND METHODS

All waterbird species were counted; we did not count passerines such as reed warblers. The following groups were distinguished: grebes (Podicipedidae), cormorants (Phalacrocoracidae), pelicans (Pelecanidae), herons and egrets (Ardeidae), storks (Ciconiidae), ibises and spoonbills (Threskiornithidae), Hamerkop (Scopidae), ducks and geese (Anatidae), cranes (Gruidae), rallids (Rallidae), waders (Charadriiformes), kingfishers (Alcedidae) and raptors (Accipitridae) associated with wetlands (*Circus* spp., *Pandion haliaetus, Haliaeetus vocifer*).

Counts were conducted in the dry season in two seven-years periods (1991–1997 and 2000–2006). The periods differed with the annual water discharge as well as with annual precipitation (Mendelsohn and el Obeid 2004; Bauer, Grumbicht, and Kinzelbach 2006; Mendelsohn et al. 2009). Each count was conducted during a whole day, usually under windless and cloudless weather.

We surveyed both the main river channel and the small secondary channels from a motor boat. All inundated areas outside the main river channel were surveyed on foot. The same route was followed each year. Counts were conducted by a team of 2–5 persons using binoculars (10 × 50). All birds seen and heard were identified to species level and counted. The following parameters were used to describe waterbird assemblages:

1) N – number of individuals recorded,

2) %N – dominance expressed as the percentage of a given species relative to the total number of all individuals of all species recorded.

The seasonal difference in the total number of a particular species for the years 1991–1997 and 2000–2006 was tested with the Chi-square test. Species for which the expected value was lower than 5 were excluded from this analysis. Seasonal differences in the number of particular species in each year over the period 1991–2006 were tested with Wilcoxon's test for matched pairs, when the number of matched pairs whose differences were not zero was at least 6. Regression analysis was applied to test the population trends over the years 1991–2006. This analysis was performed only for the more common species. For each species overall dominance was also calculated separately for the years 1991–1997 and 2000–2006.

Dominance is expressed as the percentage of the total number of individuals of a given species recorded in the whole period 1991–1997 and 2001–2006 in relation to the total number of all individuals of all species recorded over the same period. A dominant species is defined as the one comprising 5% or more of all individuals of all species recorded, while subdominant species comprised 2–4.99%.

The following guilds were distinguished:

1) Foraging: OW – outside wetlands, SV – in short vegetation (including grass) and mud, EV – in emergent vegetation (including reed, rush and lilies), SW – in shallow water, DW – in or over deep water, A – aerial feeders.
2) Diet: F – piscivorous, V – vegetarian, I – insectivorous, P – carnivorous, VI – vegetarian and insectivorous, PI – carnivorous and insectivorous, O – omnivorous.
3) Migration: R – resident (present throughout the year), RN – resident during breeding, otherwise nomad, PM – resident during the breeding season, partial migrant after breeding, N – nomad, IA – intra-Africa migrant, P – Palearctic migrant.
4) Nesting: NB – near the bank; W – on water surface, G – on the ground; EV – emergent vegetation; H – in tree holes; TS – in trees or shrubs.

The following indices were used to characterize the diversity and evenness of the communities:

1) Shannon's diversity index:
$H' = -\sum p_i \log p_i$,

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

2) Simpson's diversity index:
$D = ((\sum n(n-1))/N(N-1)$,

where n is the total number of breeding pairs belonging to a given species, N is the total number of breeding pairs of all species.

3) Pielou's evenness index:
$J' = (-\sum p_i \log p_i)/\log S$,

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 the variation between species in a community, the higher the J'.

4) Community dominance index:
$DI = (n_1 + n_2)/N$,

where n_1, n_2 is the number of pairs of two most abundant species, N is the total number of pairs of all species.

5) Sörensen's coefficient:
$I = 2C/A+B$,

where A is the number of bird species in 1991–1997, B is the number of bird species in 2000–2006, C is the number of bird species common to both periods.

An index of abundance was calculated as the proportion of the number of pairs of a given species in relation to the numbers of the most common species. The systematics and nomenclature of bird species follow Hockey, Dean, and Ryan (2005). All common (English) and scientific (Latin) names of birds are listed in Appendix 1.

RESULTS

In total, 93 waterbird species were recorded, 77 in 1991–1997 and 78 in 2000–2006 (Appendix 1). This difference was not statistically significant (Chi-square test: $x^2 = 0.006$; $p > 0.05$). The total number of individuals recorded was unexpectedly much lower in 1991–1997 (N = 4953) than in 2000–2006 (N = 17226) (Chi-square test: $x^2 = 64558$; $p < 0.01$). This difference however was biased by a few species, such as African Skimmer, White-faced Duck, Spur-winged Goose, and Collared Pratincole, which were by far more common in 2000–2006 than in 1991–1997 (Appendix 1). Sörensen's similarity index between 1991–1997 and 2000–2006 was S = 0.78 (Table 1).

In 1991–1997 seasons, the group of dominants was composed of four species: Reed Cormorant, African Darter, Cattle Egret, and Red-billed Teal. Together they comprised 45.7% of all waterbirds recorded. In 2000–2006, the contribution of dominant species was higher (65.4%) than in the previous period and was composed of seven species: Reed Cormorant, African Darter, Squacco Heron, African Openbill, White-faced Duck, Spur-winged Goose, and African Skimmer. The Reed Cormorant and African Darter were, therefore, the only dominant species in both 1991–1997 and 2000–2006. The number of subdominant species was the same (N = 8) in both periods compared and their proportions were also similar, i.e. 25.0% in 1991–1997 and 21.3% in 2000–2006. The Community Dominance Index was much the same in 1991–1997 and 2000–2006 (Table 1).

Simpson's Diversity Index was almost identical in

1991–1997 and 2000–2006, while Shannon's Diversity Index was slightly higher in 1991–1997 (S = 1.4) than in 2000–2006 (S = 1.3). Also, Pielou's Evenness Index was similar in both periods compared (Table 1).

Palearctic migrants constituted 11 species in 1991–1997 and nine species in 2000–2006, with only a small percentage of all individual birds recorded in both periods. The intra-African migrants represented by four species in both periods were twice as numerous in 2000–2006 as in 1991–1997. Residents were more numerous in 2000–2006 than in 1991–1997, while the reverse was true in the case of the partial migrants.

The two most numerous foraging guilds were birds foraging in shallow water and those foraging in deep water. The former guild was more numerous in 2000–2006 than in 1991–1997, while the latter guild was more numerous in 1991–1997 than in 2000–2006. The proportion of other foraging guilds differed little between those two periods (Figure 3A).

The most numerous diet guild was the piscivores, which were more numerous in 1991–1997 than in 2000–2006. Herbivores and species with a mixed plant/invertebrate diet were more numerous in 2000–2006 than in 1991–1997. Other guilds had similar proportions in both periods (Figure 3B).

The birds resident during the breeding season and otherwise nomad, as well as partial and Palearctic migrants were more common in 1991–1997 than in 2000–2006, while the reverse was true for guilds such as residents throughout the year, nomads and intra-African migrants (Figure 3C).

In 1991–1997, most breeding birds were grouped in the guild of emergent water vegetation nesters; in 2000–2006, most birds fell into the nesting guild of trees and shrubs nesters. The guild of the ground-nesting birds was equally common in 1991–1997 and 2000–2006. Other nesting guilds comprised only a small proportion of the total in both periods (Figure 3D).

If the total numbers of birds of particular species in the years 1991–1997 were pooled and compared with those

Table 1. Parameters and indices characterizing waterbird assemblages in 1991–1997 and 2000–2006.

Parameter	1991–1997	2000–2006
Number of species	77	78
Number of individuals	4953	17226
Number of dominant species	4	7
Cumulative dominance (%)	45.7	65.4
Number of subdominant species	8	8
Cumulative subdominance (%)	25.0	21.3
Simpson's Diversity Index (D)	0.92	0.90
Shannon's Diversity Index (H')	1.41	1.29
Pielou's Evenness Index (J')	0.75	0.68
Community Dominance Index (DI)	0.34	0.30

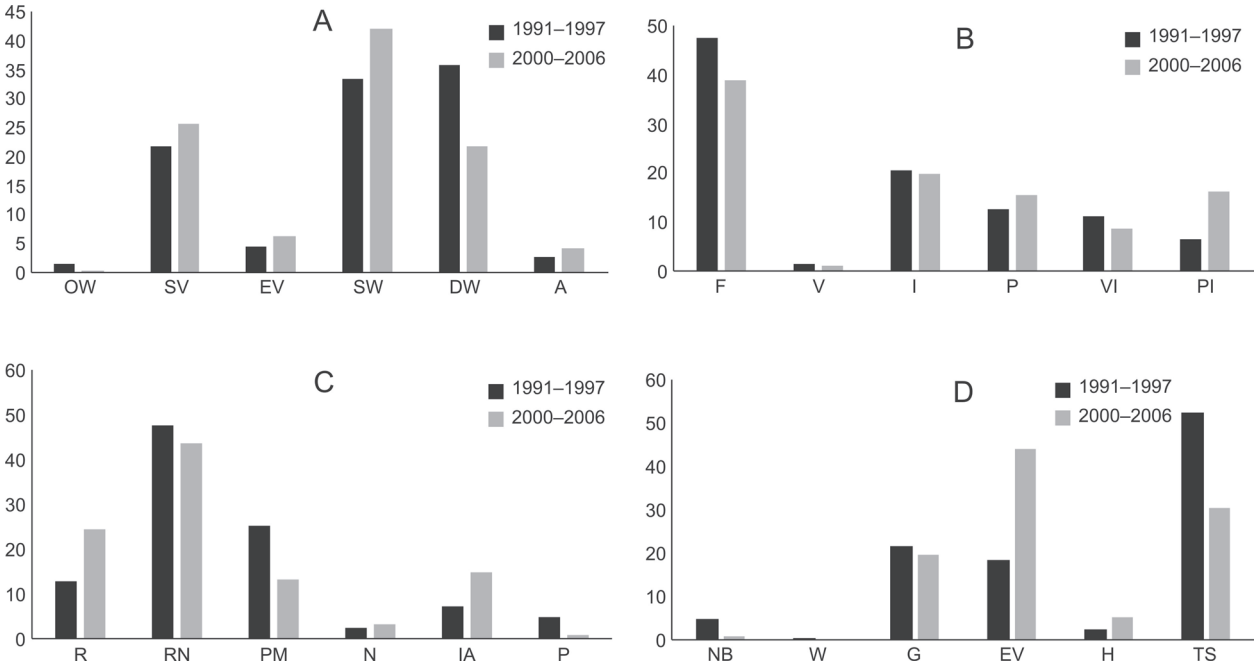

Figure 3. Interannual changes in the proportion of ecological guilds of waterbirds in the Okavango River in the Mahango Game Reserve: A. Foraging: OW – outside wetlands, SV– in short vegetation (including grass) and mud, EV – in emergent vegetation (including reed, rush and lilies), SW – in shallow water, DW– in or over deep water, A – aerial feeders; B. Diet: F – frugivorous, V – vegetarian, I – insectivorous, P – carnivorous, VI – vegetarian and insectivorous, PI – carnivorous and insectivorous; C. Migration: R – resident (present throughout the year), RN – resident during breeding, otherwise nomad, LM – resident during the breeding season, partial migrant after breeding, N – nomad, AM – intra-Africa migrant, P – Palearctic migrant; D. Nesting: NB – near the bank, W – on water surface, G – on the ground, EV – in emergent vegetation, H – in tree holes, TS – in trees or shrubs.

for the years 2000–2006, then highly significant changes in their numbers between these periods could be seen for 53 out of 93 waterbird species (Appendix 1).

During the years 1991–2006, 12 species significantly increased in numbers: Goliath Heron, Little Egret, Squacco Heron, Green-backed Heron, Black Crake, African Jacana, African Skimmer, Whiskered Tern, Long-toed Lapwing, White-faced Duck, Spur-winged Goose, and African Fish Eagle (Figure 4). Only one species, the Cattle Egret, significantly declined, and numbers of seven species (Reed Cormorant, African Darter, Grey Heron, Blacksmith Lapwing, Wattled Lapwing, and Collared Pratincole) have not changed significantly over the years 1991–2006 (Figure 4).

DISCUSSION

A strong increase in the numbers of most waterbird species in Mahango during the years 1991–2006 can be linked to the volume of water flowing through the river. While during the years 1991–1997 the total volume measured at Mohembo was 45.9 km^3 (SD = 1.43), during the years 2000–2006 the volume was 60.9 km^3 (SD = 1.41) (Mendelsohn et al. 2009). During the years 1991–1997 there was a steady decrease in this volume, while in the 2000–2006 there was a steady increase (Figure 5). A clear positive relationship was also recorded between the water volume and the number of waterbird species recorded in each year.

During the years 1991–2006, a decline in the numbers of 11 waterbird species was recorded, namely Fulvous Duck, Red-billed Teal, Purple Heron, Rufous-bellied Heron, Black-crowned Night Heron, Baillon's Crake, Lesser Jacana, Marabou Stork, Great White Pelican, Wood Sandpiper, and Ruff. At the Orange River mouth, where counts were conducted during the years 1980–2001, 11 of 57 waterbird species showed a decline in abundance (Anderson et al. 2003). However, only the Ruff was recorded as declining both at the Orange River mouth and in Mahango. Its decline can be linked with a parallel one in its breeding range over the same period (Zöckler 2002). These differences between the Orange River mouth and Mahango may indicate that different factors influenced these declines. In the Orange River mouth, deterioration of a muddy habitat was regarded as the main reason for declines (Anderson et al. 2003). In Mahango, these declines could have been caused by several factors, such as deteriorating food resources, increased interspecific competition and predation, local movements due to the creation of other foraging ground (e.g. inundated shallow sites around pans and river banks) and deteriorating feeding conditions in their natal places from where they had emigrated to Mahango (e.g. in the larger heronries in Okavango Delta or further afield).

Contrary to expectations, there was a higher proportion of birds foraging in shallow water in 2000–2006 (42.1%) than in 1991–1997 (33.4%), while for birds foraging in deep water, the reverse situation was recorded (2000–2006: 21.7%, 1991–1997: 35.9%). It appears from this that birds foraging in deep water, such as cormorants and darters, prefer to forage in rivers with lower water levels, possibly because in rivers with higher water levels turbidity may handicap the pursuit of fish. On the other hand, species such as herons and egrets, which prefer shallow water as foraging places, may exploit inundated shallow sites outside the main river channel, which form when water levels are high. So, as a result the proportion of piscivorous birds was higher in 1991–1997 (47.5%), when the water level was lower, than in 2000–2006 (39.0%), when the water level in the river was higher.

The proportion of Palearctic migrants was much higher in 1991–1997 (4.8%) than in 2000–2006 (0.6%). Most of this group were waders which prefer muddy river margins. Such habitat is more available when the water level in the river is high. Thus sandpipers (*Tringa/Actitis/Calidris*) were more numerous in 2000–2006 than in 1991–1997 (82 versus 55 individuals from seven species). However, a total of 161 Ruffs were recorded in 1991–1997, and only 17 in 2000–2006. This change may reflect a decline in their breeding range in Europe (Zöckler 2002).

The proportion of intra-African migrants and residents was almost twice as large in 2000–2006 as in 1991–1997, while this was reversed for the partial migrants. These changes suggest that birds are more sedentary when the water level is higher. High water level in the river may create more stable feeding conditions for breeding birds, which need food resources from the same site for a longer period in relation to breeding (nest building, egg incubation, chick rearing).

There was a much higher proportion of birds nesting in emergent vegetation in 2000–2006 than in 1991–1997 (43.8% vs. 18.4%), while the proportion on birds nesting in trees and shrubs was lower in 2000–2006 than in 1991–1997 (30.4% vs. 52.6%). Emergent vegetation, occupying sites mainly outside the main river channel, provide a better cover when the water level in the river is high. When the water level is low, the emergent vegetation zone becomes more accessible for predators, and birds may avoid nesting there.

The following waterbird species have shown similar population trends in Mahango (in the years 1991–2007; this study) and in Namibia as a whole (in the years 1991–2008; Kolberg 2001a, b, 2011a, b, c, d, 2012a, b, c, d, 2013a, b, c, d): 1) population increase: Goliath Heron, Squacco Heron, Green-backed Heron, African Sacred

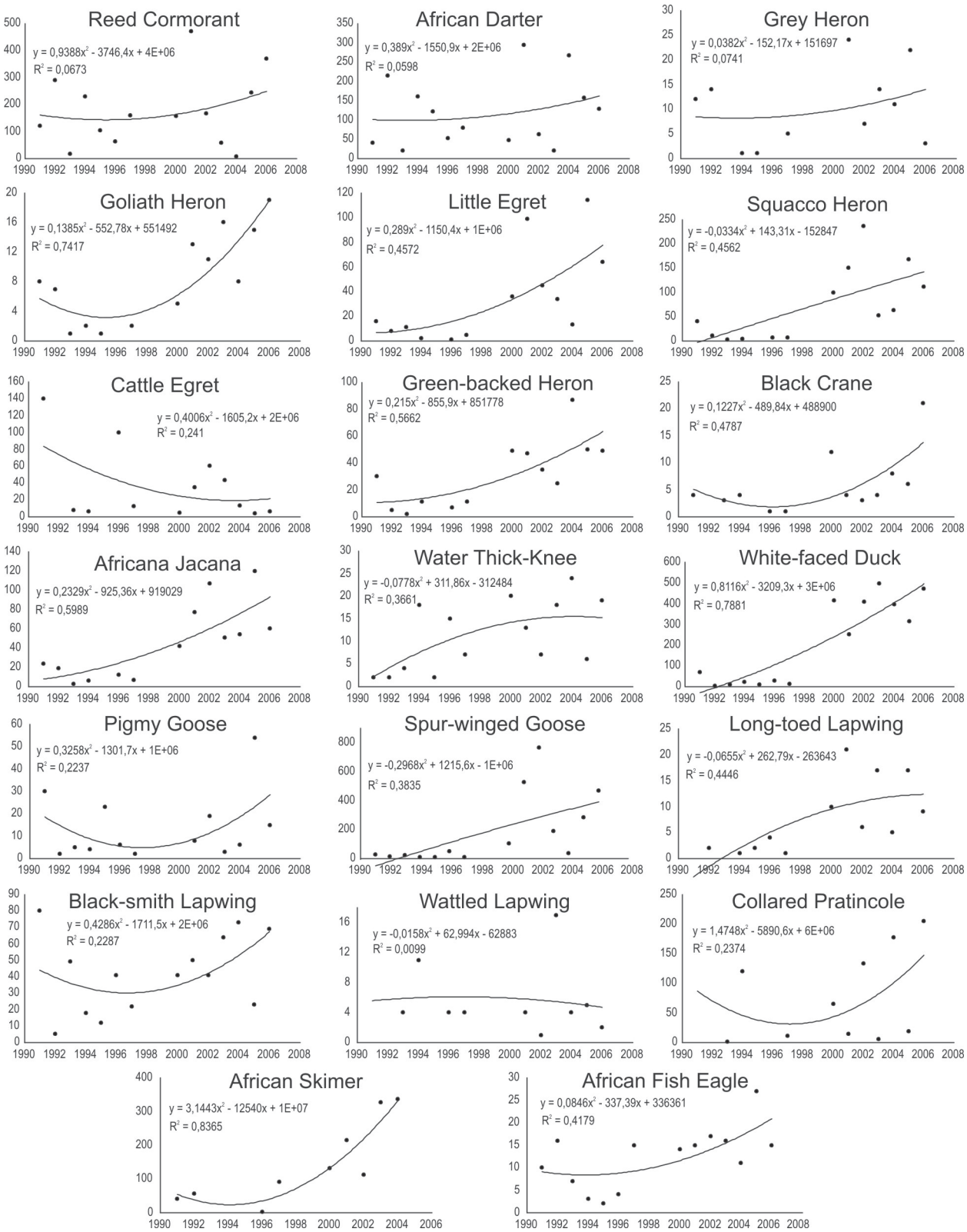

Figure 4. Interannual changes in the number of individuals (vertical axis) of particular waterbird species in the Okavango River in the Mahango Game Reserve: A: Reed Cormorant, B: African Darter, C: Grey Heron, D: Goliath Heron, E: Little Egret, F: Squacco Heron, G: Cattle Egret, H: Green-backed Heron, I: Black Crake, J: African Jacana, K: Water Thick-knee, L: White-faced Duck, M: Pygmy Goose, N: Spur-winged Goose, O: Long-toed Lapwing, P: Black-smith Lapwing, R: Wattled Lapwing, S: Collared Pratincole, T: African Skimer, U: African Fish Eagle.

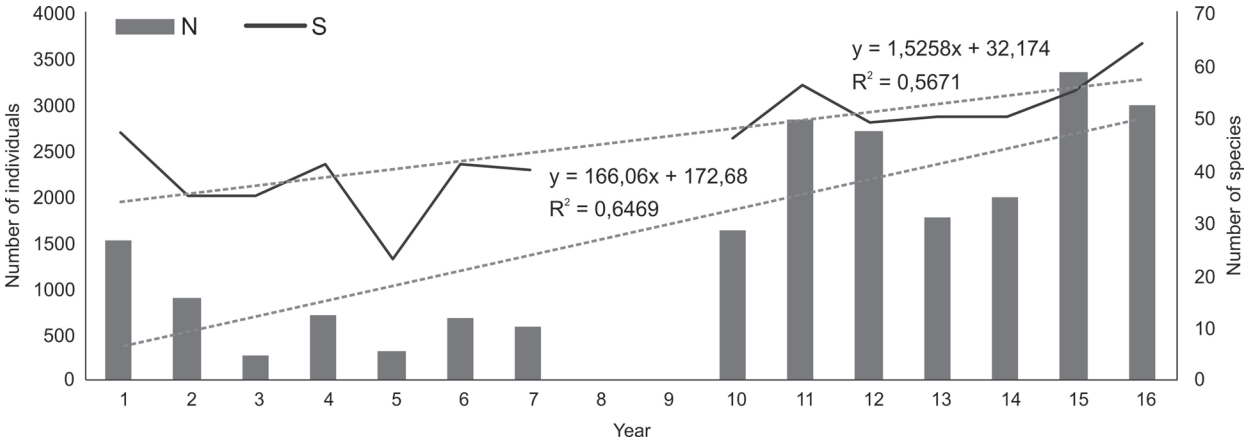

Figure 5. Annual changes in the number of waterbird species (S) and individuals (N) in relation to the water volume in the Okavango River in the Mahango Game Reserve: 1 = year 1990, 2 = year 1991 and so on.

Ibis, White-faced Duck, Spur-winged Goose, Egyptian Goose, Black Crake, African Jacana, Black-winged Stilt, Common Greenshank, and White-fronted Plover; 2) population decrease: Purple Heron and Fulvous Duck; 3) population stability: Wattled Crane, Comb Duck, and Common Sandpiper. On the other hand, the Cattle Egret, Red-billed Teal, and Ruff were in decline in Mahango, but apparently increased in Namibia generally. Species such as the Great Egret, Yellow-billed Egret, Little Egret, Little Bittern, Yellow-billed Stork, and African Openbill increased in numbers in Mahango, but their populations were considered stable in Namibia (Appendix 1). It is, however, unlikely that the survey of Namibian wetlands and water bodies were sufficient enough. Sites selected for sampling could influence dramatically these data, especially in regard to species which breed colonially, and consequently also forage in large flocks (e.g. African Openbill or ardeids).

Although rivers play an important role in most southern African ecosystems (Simmons and Allan 2002), quantitative data on waterbirds associated with the rivers (excluding estuaries, e.g. Anderson et al. 2003) are scanty (Table 2). Kopij has conducted extensive surveys of birds associated with the rivers of the Orange River/Senque drainage basin in the Lesotho highlands (Kopij 2013a, c), foothills, lowlands, and in the Senque Valley (Kopij 2013b, c). Allan and Jenkins (1993) and Simmons and Allan (2002) also provided valuable quantitative data on waterbirds of the lower Orange River on the Namibian/South African border. Counts of birds associated with rivers in the subtropical parts of southern Africa are limited to short stretches of the Komati (7.5 km) and Usuthu Rivers (18 km) in the lowveld of Swaziland (Allan and Davies 1999; Monadjem 2000) and Chobe River (46 km) on Namibia/Botswana border (Herremans 1999). A few other studies simply list the species recorded in a given stretch of a river, without any quantitative data, e.g. the Save River in Mozambique (Storer and Dalquest 1967; Allan, Davies, and Parker 2000), the Kunene River on Namibian/Angolan border (Damasius and Marais 1999), and the Okavango River (Winterbottom 1966).

Along the lower Orange River only 20 waterbird species were recorded, with the African Darter, White-breasted Cormorant, Reed Cormorant, Grey Heron, Goliath Heron, Egyptian Goose, and Pied Kingfisher as dominant species (71.3%) (Allan and Jenkins 1993; Simmons and Allan 2002). The rivers in the lowlands, the Senque

Table 2. Waterbird surveys of some southern African rivers.

River name and country	Length [km] surveyed	Number of species	Individuals per 10 km	Source
Kavango, Namibia; 1991–1997	28	77	1769	this study
2000–2006	28	78	6150	this study
Chobe, Botswana; dry season	46	36	378	Herremans 1999
wet season	46	27	399	Herremans 1999
Komati, Swaziland	62	19	92	Allan and Davies 1999
Usutho, Swaziland	18	21	43	Monadjem 2000
Lower Orange, Namibia/RSA	160	20	44	Allan and Jenkins 1993
	50	16	26	Simmons and Allan 2002
Upper Orange/Senque, Lesotho	131	15	19	Allan 1999
Malibamatsu + tributaries, Lesotho	214	11	18	Kopij 2013ac
Makhaleng/Caledon, Lesotho	76	10	10	Kopij 2013bc

Valley and the foothills in Lesotho have a rather poor waterbird fauna. In 75.5 km of river surveyed during the years 1997–2002, only 10 resident (including two swallow species) and two Palearctic migrant waterbird species were recorded (Kopij 2013b, c). The rivers are even poorer in that regard in the Lesotho highlands, where on 155 km surveyed, just three Palearctic waterbird species were recorded (Kopij 2013a). On the Komati River (17 km strech) only 11 waterbird species were recorded (Allan and Davies 1999), and on the Usutu River (18 km stretch) 21 waterbird species, including swallows and five Palearctic migrants (Monadjem 2000). The group of most common species included Cape Wagtail, Green-backed Heron, Water Dikkop, Pied Kingfisher, Wire-tailed Swallow, and Common Sandpiper. On the Chobe Riber, 37 waterbird species were recorded both in wet and dry seasons (Herremans 1999), while on the middle Save River (a stretch of ca. 120 km), 60 waterbird species were recorded by four independent expeditions in 1963–1998 (Allan, Davies, and Parker 2000). In our study area, the number of waterbirds recorded was 88. This shows that the waterbird fauna of the Kavango River is much richer than in any other rivers in southern Africa surveyed to date.

Figure 6. Yellow-billed Storks.

Figure 7. African Fish Eagle.

The study area potentially plays an important role in the protection of waterbird species threatened in Namibia (Simmons, Brown, and Williams 2015). In 1991–1997, 28 such species contributed 22.8%; while in 2000–2006, 24 species contributed 25.3% of all individuals. In total, 31 threatened waterbird species were recorded over the period 1991–2006 (Table 3; Figures 6, 7). The most numerous species (with at least 1% of the total number of birds in Namibia) from this group were African Skimmer (11.2% in 2000–2006), Openbill Stork (5.5% in 1991–1997), Collared Pratincole (3.6% in 2000–2006), Fulvous Duck (2.4% in 1991–1997), Black Heron (2.1% in 2000–2006), African Pygmy Goose (1.5% in 1991–1997), and African Fish Eagle (1.2% in 1991–1997). Most of the threatened species were breeding residents in the study area, with the African Skimmer the most numerous (Table 3). At least six of them have breeding populations larger than 5% of the Namibian total, viz. Slaty Egret (10%), Black Heron (44%), Wattled Crane (20%), Long-toed Lapwing (16%), African Skimmer (40%), and African Fish Eagle (5%) (Table 3).

Since 1986, the section of the river valley which comprised this study area, as well as about 244 km^2 of grassland (62%) and shrubland (38%) on its left bank have been protected as the Mahango Game Reserve. The area is protected not only for its rich waterbird fauna, but also for ungulates, carnivores and other mammals. Among 99 mammal species recorded so far in this reserve three are threatened species, viz. African Hunting Dog *Lycaon pictus*, African Elephant *Loxodonta africana,* and Spotted-necked Otter *Lutra maculicollis*. There are also 200 Hippos *Hippopotamus amphibius*, 300 Elephants *Loxodonta africana*, 500 Buffalos *Syncerus caffer*, and numerous antelopes (Mendelsohn and el Obeid 2004).

In order to classify a wetland as a Ramsar site, one of the two specific criteria based on waterbirds have to be met. The wetland in consideration should regularly support more than 20000 waterbirds (Criterion 5) or/and it should regularly support at least 1% of the individuals in a population of one species or subspecies of waterbirds (Criterion 6) (http://www.ramsar.org/sites). This study has shown that the Okavango River in the Mahango Game Reserve support more than 1% of the global population of the African Skimmer. According to Hockey (2005), the global population of this species is ca. 10000 individuals, i.e. less than 5000 breeding pairs. The Okavango River in Mahango Game Reserve support regularly ca. 200 pairs, i.e. about 4% of the global population (about half of the southern African population).

There are also other factors which firmly confirm its status as a nature reserve. It supports 31 waterbird species listed in the Namibian Red Data Book (Simmons, Brown, and Williams 2015). Three of them are globally threatened (Wattled Crane: VU, Slaty Egret:

Table 3. Estimated maximum number of breeding pairs of waterbird species during the years 2000–2006. Species threatened (Simmons, Brown, and Williams 2015) in Namibia are indicated in bold.

Species	Mah.	Nam.
Little Grebe	2	
Reed Cormorant	100?	
African Darter	45	
Grey Heron	24	
Black-headed Heron	5	
Goliath Heron	19	<500
Purple Heron	6	<500
Great Egret	35?	
Slaty Egret	15	<150
Black Heron	44?	100
Yellow-billed Egret	12	
Little Egret	50?	
Cattle Egret	40?	
Squacco Heron	110?	
Green-backed Heron	50	
Rufous-bellied Heron	6	600
Black-crowned Night Heron	26?	
White-backed Heron	3	<250
Dwarf Bittern	1	<500
Little Bittern	8	<500
Yellow-billed Stork	15	
African Openbill	240?	
Marabou Stork	2	450
Saddlebilled Stork	2	<100
Sacred Ibis	50?	
Glossy Ibis	1	
African Spoonbill	4?	
Hamerkop	6	
Wattled Crane	2	10
Fulvous Duck	1	<500
White-faced Duck	250?	
White-backed Duck	2	1000
Spur-winged Goose	330?	
Knob-billed Duck	4	
Egyptian Goose	5	
Pygmy Goose	27	1000
Yellow-billed Duck	1?	<500
Red-billed Teal	8	
Hottentot Teal	2	

Species	Mah.	Nam.
Maccoa Duck	1?	1500
African Rail	10	
African Crake	3	
Black Crake	21	
Baillon's Crake	2	
Common Moorhen	5	
Lesser Moorhen	8	
Allen's Gallinule	15	
Purple Swamphen	1	
Red-knobbed Coot	1	
African Finfoot	1	50
Lesser Jacana	10	
African Jacana	60	
Painted Snipe	4	
Ethiopian Snipe	1	
Black-winged Stilt	5	
Spotted Thick-knee	1	
Water Thick-knee	30	
Black-winged Pratincole	30?	
Rock Pratincole	2	<500
Long-toed Lapwing	16	100
Blacksmith Lapwing	100	
White-crowned Lapwing	3	
Crowned Lapwing	11	
Wattled Lapwing	15	
White-fronted Plover	4	
Kittlit's Plover	5	
Three-banded Plover	5	
Grey-headed Gull	1	
Whiskered Tern	2	
White-winged Tern	2	
African Skimmer	240	600
African Fish Eagle	14	275
African Marsh Harrier	4	300
Marsh Owl	1	
Pel's Fishing Owl	1	60
Pied Kingfisher	68	
Giant Kingfisher	5	
Malachite Kingfisher	30	

Notes: Numbers for Namibia according to Simmons, Brown, and Williams 2015.

VU, African Skimmer: NT). In addition, there are three mammal, one amphibian and two fish species from the current Southern African Red Data Books. The river acts as a linear oasis for a number of bird and mammal species, which would otherwise not have been present in the Kalahari Woodland which borders the river. It is a wintering area for 11 Palearctic migrants, four intra-African migrants and a number of nomadic or semi-nomadic species. It supports more than 1% of the global population of two globally threatened species: the African Skimmer (2.4–4.8%) and the Slaty Egret (1%).

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Appendix 1. Namibian waterbirds (number of individuals), Mahango, dry season. Population trends in Namibia according to Kolberg (2001ab, 2011abcd, 2012abcd, 2013abcd). Species threatened in Namibia are indicated in bold (after Simmons et al. 2015). Explanations for the guilds: A. Foraging: OW – foraging outside wetlands, SV – short vegetation (including grass) and mud, EV – emergent vegetation (including reed, rush and lilies), SW – shallow water, DW– in or over deep water, A – aerial feeders; B. Diet: F – piscivorous, V – vegetarian, I – insectivorous, P – carnivorous, VI – vegetarian and insectivorous, PI – carnivorous and insectivorous, O – omnivorous; C. Migration: R – resident (present throughout the year), RN – resident during breeding, otherwise nomad, PM – resident during breeding season, partial migrant after breeding, N – nomad, IA – intra-Africa migrant, P – Palearctic migrant; D. Nesting: NB – near the bank; W – on water surface, G – on the ground; EV – emergent vegetation; H – in tree holes; TS – in trees or shrubs.

Species	Guilds				1991–1997		2000–2006		Change	Chi-square		Popul. trends	
	A	B	C	D	N	D(%)	N	D(%)	%	X^2	*p*	Mah.	Nam.
Little Grebe *Tachybaptus ruficollis*	SW	VI	PM	W	10	0.20	4	0.02	40	2.5			↑
Black-necked Grebe *Podiceps nigricollis*	DW	F	N	W	0	0.00	1	0.01	*				↑
White-breasted Cormorant *Phalacrocorax lucidus*	DW	F	RN	TS	48	0.97	0	0.00	+	300.0	**		
Reed Cormorant *Phalacrocorax africanus*	DW	F	RN	TS	983	19.85	1476	8.57	150	797.0	**		↓
African Darter *Anhinga rufa*	DW	F	PM	TS	688	13.89	977	5.67	142	546.5	**		↑
Great White Pelican *Pelecanus onocrotalus*	SW	F	N	G	30	0.61	1	0.01	3	89.6	**	↓↓	↔
Pink-backed Pelican *Pelecanus rufescens*	SW	F	N	TS	8	0.16	0	0.00	+				
Grey Heron *Ardea cinerea*	SW	F	R	TS	33	0.67	81	0.47	245	29.5	**	↑	↔
Black-headed Heron *Ardea melanocephala*	OW	F	R	TS	8	0.16	7	0.04	88	0.9			↑?
Goliath Heron *Ardea goliath*	SW	F	R	G	21	0.42	87	0.51	414	44.8	**	↑	↑?
Purple Heron *Ardea purpurea*	SW	F	R	EV	19	0.38	11	0.06	58	4.9		↓	↓?
Great Egret *Egretta alba*	SW	F	RN	T	48	0.97	300	1.74	625	207.7	**	↑↑	↔
Slaty Egret *Egretta vinaceigula*	SW	F	PM	EV	24	0.48	32	0.19	133	4.7		↔	
Black Heron *Egretta ardesiaca*	SW	F	PM	EV	77	1.55	356	2.07	462	223.0	**	↑	
Yellow-billed Egret *Egretta intermedia*	SW	F	PM	TS	2	0.04	30	0.17	1500	21.0	**	↑↑	↔?
Little Egret *Egretta garzetta*	SW	F	RN	TS	43	0.87	405	2.35	942	316.6	**	↑↑	↔
Cattle Egret *Bubulcus ibis*	SV	VI	RN	TS	266	5.37	166	0.96	62	418.6	**	↓	↑
Squacco Heron *Ardeola ralloides*	SW	VI	R	EV	71	1.43	880	5.11	1239	737.6	**	↑↑	↑
Green-backed Heron *Butorides striata*	EV	VI	R	EV	66	1.33	342	1.99	518	223.4	**	↑↑	↑?
Rufous-bellied Heron *Ardeola rufiventris*	EV	VI	PM	EV	40	0.81	16	0.09	40	48.6	**	↓	
Black-crowned Night-Heron *Nycticorax nycticorax*	SW	VI	RN	TS	15	0.30	4	0.02	27	8.1	**	↓	↔?
White-backed Night-Heron *Gorsachius leuconotus*	OW	VI	R	TS	6	0.12	8	0.05	133	2.0			
Dwarf Bittern *Ixobrychus sturmii*	OW	VI	IA	EV	35	0.71	0	0.00	+	146.2	**		
Little Bittern *Ixobrychus minutus*	OW	VI	R	EV	3	0.06	16	0.09	533	8.9	**	↑↑	↔?

Species	Guilds				1991–1997		2000–2006		Change	Chi-square		Popul. trends	
	A	B	C	D	N	D(%)	N	D(%)	%	X^2	*p*	Mah.	Nam.
Yellow-billed Stork *Mycteria ibis*	SW	V	RN	TS	5	0.10	158	0.92	3160	138.0	**	↑↑	↔?
African Openbill *Anastomus lamelligerus*	SW	I	RN	TS	125	2.52	873	5.07	698	646.6	**	↑↑	↔?
White Stork *Ciconia ciconia*	OW	I	P	–	1	0.02	0	0.00	+				
Abdim's Stork *Ciconia abdimii*	OW	I	V	–	1	0.02	0	0.00	+				
Wooly-necked Stork *Ciconia episcopus*	SW	I	RN	TS	13	0.26	0	0.00	+	14.2	**		
Marabou Stork *Leptoptilos crumeniferus*	OW	P	RN	TS	22	0.44	7	0.04	32	17.1	**	↓	↔?
Saddlebilled Stork *Ephippiorhynchus senegalensis*	SW	F	RN	TS	9	0.18	19	0.11	211	3.5		↑	↔?
African Sacred Ibis *Threskiornis aethiopicus*	SV	I	RN	TS	66	1.33	474	2.75	718	348.5	**	↑	↑
Hadeda Ibis *Bostrychia hagedash*	SV	I	R	TS	6	0.12	0	0.00	+				
Glossy Ibis *Plegadis falcinellus*	SV	I	RN	EV	0	0.00	1	0.01	*				↔?
African Spoonbill *Platalea alba*	SW	F	RN	TS	56	1.13	112	0.65	200	40.9	**	↑	↔?
Hamarkop *Scopus umbretta*	SW	V	R	TS	66	1.33	43	0.25	65	62.6	**		↓?
Fulvous Duck *Dendrocygna bicolor*	SW	PI	RN	EV	120	2.42	4	0.02	3	1570.0	**	↓↓	↓?
White-faced Duck *Dendrocygna viduata*	SW	PI	RN	EV	155	3.13	2751	15.97	1775	2446.5	**	↑↑	↑?
Spur-winged Goose *Plectropterus gambensis*	SV	V	R	EV	130	2.62	2369	13.75	1822	2111.3	**	↑↑	↑?
Comb Duck *Sarkidornis melanotos*	SW	V	PM	H	45	0.91	54	0.31	120	17.7	**	↔	↔?
Egyptian Goose *Alopochen aegyptiaca*	SV	V	PM	TS	30	0.61	47	0.27	157	10.4	**	↑	↑
African Pygmy Goose *Nettapus auritus*	SW	V	R	H	72	1.45	105	0.61	146	40.1	**		
Yellow-billed Duck *Anas undulata*	SW	PI	RN	EV	4	0.08	0	0.00	+				
Red-billed Teal *Anas erythrorhyncha*	SW	V	RN	G	326	6.58	67	0.39	21	2097.2	**	↓↓	↑?
Hottentot Teal *Anas hottentota*	SW	PI	R	EV	0	0.00	4	0.02	*				↔?
Wattled Crane *Bugeranus carunculatus*	SW	O	R	G	28	0.57	35	0.20	125	6.5	*	↔	↔?
African Rail *Rallus caerulescens*	EV	I	R	EV	0	0.00	12	0.07	*	12.0	**		
African Crake *Crecopsis egregia*	EV	I	IA	EV	0	0.00	3	0.02	*				
Black Crake *Amaurornis flavirostra*	EV	I	R	EV	13	0.26	58	0.34	446	28.9	**	↑	↑
Baillon's Crake *Porzana pusilla*	EV	I	R	EV	4	0.08	1	0.01	25		**	↓	
Common Moorhen *Gallinula chloropus*	SW	O	PM	EV	12	0.24	11	0.06	92	0.0		↔	↑↑
Lesser Moorhen *Gallinula angulata*	EV	O	IA	EV	0	0.00	2	0.01	*				↔?
Allen's Gallinule *Porphyrio alleni*	EV	O	IA	EV	0	0.00	1	0.01	*				
African Purple Swamphen *Porphyrio madagascarensis*	EV	O	R	EV	8	0.16	0	0.00	+				↑?
Red-knobbed Coot *Fulica cristata*	SW	V	PM	EV	20	0.40	0	0.00	+	38.7	**		↔?
African Finfoot *Podica senegalensis*	SW	I	R	EV	6	0.12	0	0.00	+				
Lesser Jacana *Microparra capensis*	EV	I	RN	EV	8	0.16	3	0.02	38	2.7		↓	
African Jacana *Actophilornis africanus*	EV	I	N	EV	71	1.43	511	2.97	720	376.8	**	↑	↑↑
Greater Painted-Snipe *Rostratula benghalensis*	SV	I	N	EV	0	0.00	16	0.09	*	14.3	**		
African Snipe *Gallinago nigripennis*	SV	I	RN	EV	0	0.00	1	0.01	*				
Black-winged Stilt *Himantopus himantopus*	SV	I	RN	G	4	0.08	36	0.21	900	22.7	**	↑	↑
Spotted Thick-knee *Burhinus capensis*	SV	I	R	G	0	0.00	1	0.01	*				
Water Thick-knee *Burhinus vermiculatus*	SV	I	PM	G	50	1.01	107	0.62	214	39.4	**	↑	↔?

Species	Guilds				1991–1997		2000–2006		Change	Chi-square		Popul. trends	
	A	B	C	D	N	D(%)	N	D(%)	%	X^2	*p*	Mah.	Nam.
Collared Pratincole *Glareola pratincola*	A	I	IA	G	132	2.67	618	3.59	468	397.8	**	↑	
Rock Pratincole *Glareola nuchalis*	A	I	IA	G	4	0.08	0	0.00	+				
Common Whimbrel *Numenius phaeopus*	SV	I	P	–	1	0.02	0	0.00	+				↔?
Common Sandpiper *Actitis hypoleucos*	SV	I	P	–	19	0.38	24	0.14	126	2.1		↔	↔?
Marsh Sandpiper *Tringa stagnatilis*	SV	I	P	–	6	0.12	3	0.02	50				↔?
Common Greenshank *Tringa nebularia*	SV	I	P	–	6	0.12	40	0.23	667	22.9	**	↑	↑
Green Sandpiper *Tringa ochropus*	SV	I	P	–	6	0.12	0	0.00	+				
Wood Sanpiper *Tringa glareola*	SV	I	P	–	18	0.36	10	0.06	56	4.5	*	↓	↔?
Little Stint *Calidris minuta*	SV	I	P	–	0	0.00	6	0.03	*				↓↓
Curlew Sandpiper *Calidris ferruginea*	SV	I	P	–	1	0.02	3	0.02	300				↔?
Ruff *Philomachus pugnax*	SV	I	P	–	161	3.25	17	0.10	11	1480.6	**	↓↓	↔?
Long-toed Lapwing *Vanellus crassirostris*	SV	I	PM	EV	10	0.20	85	0.49	850	58.0	**	↑↑	
Blacksmith Lapwing *Vanellus armatus*	SV	I	PM	G	227	4.58	361	2.10	159	172.1	**		↔?
Crowned Lapwing *Vanellus coronatus*	SV	I	PM	G	17	0.34	42	0.24	247	12.0	**	↑	↔?
Wattled Lapwing *Vanellus senegallus*	SV	I	PM	G	23	0.46	33	0.19	143	4.9	*	↑	↔?
White-fronted Plover *Charadrius marginatus*	SV	I	PM	G	5	0.10	31	0.18	620	16.9	**	↑↑	↑↑
Kittlitz's Plover *Charadrius pecuarius*	SV	I	N	G	0	0.00	12	0.07	*	12.0	**		↔
Three-banded Plover *Charadrius tricollaris*	SV	I	PM	G	17	0.34	12	0.07	71	2.1			↔
Grey-headed Gull *Larus cirrocephalus*	OW	VI	PM	W	3	0.06	2	0.01	67				
Whiskered Tern *Chlidonias hybrida*	SW	F	RN	W	6	0.12	20	0.12	333	7.3	**	↑	↔?
White-winged Tern *Chlidonias leucopterus*	SV	F	P	–	10	0.20	1	0.01	10	6.5	*		↔?
African Skimmer *Rhynchops flavirostris*	SW	F	IA	G	187	3.78	1932	11.22	1033	1582.1	**	↑↑	
Osprey *Pandion haliaetus*	DW	F	P	–	2	0.04	2	0.01	100				
African Fish Eagle *Haliaeetus vocifer*	DW	F	R	TS	57	1.15	115	0.67	202	42.4	**	↑	
African Marsh Harrier *Circus ranivorus*	EV	P	PM	EV	14	0.28	17	0.10	121	0.4		↔	
Western Marsh-Harrier *Circus aeruginosus*	OW	P	P	–	1	0.02	0	0.00	+				
Marsh Owl *Asio capensis*	OW	P	R	G	0	0.00	1	0.01	*				
Pied Kingfisher *Ceryle rudis*	DW	F	RN	H	0	0.00	604	3.51	*	592.5	**		
Giant Kingfisher *Megaceryle maxima*	DW	F	PM	H	0	0.00	25	0.15	*	20.8	**		
Malachite Kingfisher *Alcedo cristata*	DW	F	PM	H	0	0.00	124	0.72	*	114.1	**		