

## Research Article

**Cite this article:** Phiri CG, Collar NJ, Devenish C, Marsden SJ (2024). Spatio-temporal usage of water sources by Black-cheeked Lovebirds *Agapornis nigrigenis*: implications for conservation planning. *Bird Conservation International*, **34**, e27, 1–9  
<https://doi.org/10.1017/S0959270924000261>

Received: 04 June 2024

Accepted: 19 June 2024

### Keywords:

Arid habitat; Human disturbance; Mopane; Parrots; Seasonal change; South-west Zambia; Water pool

### Corresponding author:

Chaona G. Phiri;

Email: [chaona.g.phiri@stu.mmu.ac.uk](mailto:chaona.g.phiri@stu.mmu.ac.uk)

# Spatio-temporal usage of water sources by Black-cheeked Lovebirds *Agapornis nigrigenis*: implications for conservation planning

Chaona G. Phiri<sup>1</sup> , Nigel J. Collar<sup>2</sup> , Christian Devenish<sup>3</sup>  and Stuart J. Marsden<sup>1</sup> 

<sup>1</sup>Manchester Metropolitan University, Department of Natural Sciences, Faculty of Science and Engineering, Manchester, UK; <sup>2</sup>BirdLife International, Cambridge, UK and <sup>3</sup>Keele University, School of Geography and the Environment, William Smith Building, Newcastle, Staffordshire, UK

## Summary

The Black-cheeked Lovebird *Agapornis nigrigenis* has a highly restricted range in dry south-western Zambia, where its distribution is clumped and localised in association with mopane *Colophospermum mopane* woodland and permanent water pools. Fieldwork and monitoring over 30 months between December 2018 and October 2021 established that the lovebirds' usage of pools for drinking was higher towards the centre of the bird's distribution and influenced by the pools' proximity to mopane woodlands, surrounding tree cover, and level of human activity. Of the four pool types available for use by lovebirds (i.e. mopane, grassland, river, and artificial), mopane and grassland pools were disproportionately susceptible to drying out in the dry season, hence showed greater variation in numbers of visiting birds compared with the other two types. Lovebirds showed a preference for pools with a perimeter of <50 m and tended to avoid those with a perimeter >100 m, consistent with a positive association between pool size and human activity. Convergence between humans and lovebirds in dependence on water resources and mopane woodland points to the need to find ways to overcome potential conflicts. Such ways include creating small, shallow-sided, undisturbed pools in or near mopane woodland, extending water retention in existing mopane pools, and enhancing the capacity of artificial pools to meet the needs of the lovebirds.

## Introduction

The Black-cheeked Lovebird *Agapornis nigrigenis* is endemic to Zambia and is Africa's most localised parrot (Warburton 2003; Warburton and Perrin 2005a). It inhabits the driest region of Zambia, a large plain bisected by seasonal rivers and streams within the country's Southern and Western Provinces, where it is associated with mopane *Colophospermum mopane* woodland, requiring tracts near to permanent water sources and with large trees for nesting and roosting (Dodman 1995a). The species has been classified as "Vulnerable" by the International Union for Conservation of Nature (IUCN) all this century because of a continuing decline in its small population "owing to the gradual desiccation of water bodies within a highly localised range" (BirdLife International 2024). Overall, granivorous birds in southern Africa have been found to be more water dependent than insectivores and omnivores (Smit et al. 2017). Many parrots with diets dominated by herb and grass seeds are obligate drinkers, needing regular water intake to maintain overall homeostatic water balance (Collar 1997; Warburton and Perrin 2005b). With a diet dominated by grass seeds, Black-cheeked Lovebirds need to drink at least twice daily and are therefore heavily dependent on surface water throughout the year, but they are highly cautious drinkers and generally will not visit pools disturbed by humans or livestock (Warburton and Perrin 2003, 2005b, 2005c).

Normal annual rainfall in southern Zambia is 600–900 mm per year but can be as little as 300–450 mm during El Niño periods and as high as 1,200 mm during flooding events (Pierce and Lang 2008; Rembold et al. 2016). There are two distinct seasons within the lovebird's range: a wet season, usually from November to April, reaching a peak between December and February, and a dry season from May to October, the latter causing serious water shortages lasting from June to December (Libanda et al. 2015). Black-cheeked Lovebirds have been recorded using a variety of water sources categorised as: "mopane pools", formed as natural shallow depressions where water collects within the mopane woodland; "river pools" in riverbeds and drainage channels; "grassland pools" in seasonal floodplains, usually adjoining mopane woodland and "artificial pools", any anthropogenic water source such as shallow wells, troughs, dams, and reservoirs close to human settlements and livestock grazing areas (Mzumara et al. 2016; Warburton and Perrin 2005b; CGP 2020, personal observation).

© The Author(s), 2024. Published by Cambridge University Press on behalf of BirdLife International. This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<http://creativecommons.org/licenses/by/4.0>), which permits unrestricted re-use, distribution and reproduction, provided the original article is properly cited.

The absence of Black-cheeked Lovebirds from large portions of otherwise suitable habitat within their range has been found to be directly related to the absence of water (Dodman *et al.* 2000). Moreover, the range itself has been shrinking because of the gradual decline in rainfall in the second half of the last century (Warburton 2003; Warburton and Perrin 2005b). With these insights, we sought to identify the spatial patterns in the distribution of pools, the important predictors of their use by lovebirds, and any significant differences in usage across the four pool categories. An understanding of the factors influencing the lovebirds' spatio-temporal access to water sources is key to the future conservation management of the species.

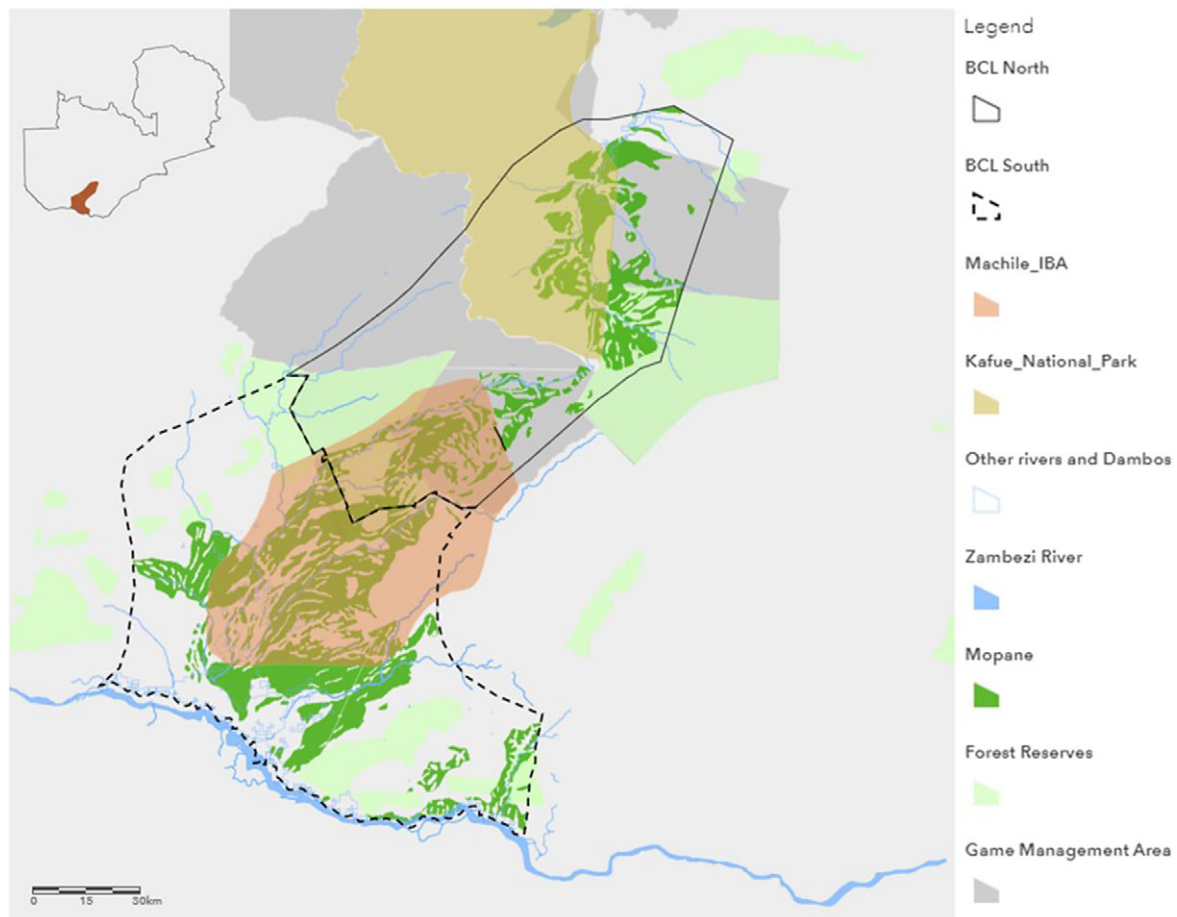
## Methods

### Study area

The Black-cheeked Lovebird (BCL) is known to occur from as far north as the Nanzhila plains in the Kafue National Park (KNP) to Sichili in the west, Ngwezi in the east, and the Zambezi River to the south (Figure 1), with a total range estimated to be around 17,500 km<sup>2</sup> (BirdLife International 2024). The species is reported to exist in two geographically separate subpopulations, as its mopane habitat is bisected by a rocky ridge of miombo (*Brachystegia–Julbernardia*) woodland which has been speculated to form a barrier to lovebird gene exchange (Dodman 1995b; Dodman *et al.* 2000). Although this 45-km barrier (Warburton

2003) has reduced over the past 30 years and now includes scattered patches of fully grown mopane, there is little surface water within it (Warburton and Perrin 2005b; CGP 2022, personal observation). The stands of mopane around the Machile, Sichifulo, Ngwezi, and Nanzhila rivers are considered the species' strongholds (Leonard 2005). All the mopane that hosts the Black-cheeked Lovebird is associated with alluvial clay deposits of an ancient wetland, possibly an earlier course of the Kafue River, thus forming an isolated stand (Bingham 1994; Leonard 2005) and explaining the lovebird's restricted range (Warburton 2003). The southern portion of this range is dominated by seasonal rivers that include the Machile, Sichifulo, Ngwezi, and Simatanga (Dodman 1995b; Warburton 2003), flowing into the Kasaya River, a major tributary of the Zambezi. The north is dominated by the Nanzhila River, a major tributary of the Kafue, fed by its seasonal tributaries (Ashley and Murphy 2012).

Within the species' range there are three designations of protected area and one area of informal conservation status. The KNP is Zambia's largest protected area (Ashley and Murphy 2012; ZAWA 2004), currently under a co-management agreement with the Zambian government and African Parks. Three game management areas (GMAs) serve as buffer zones between the national park and unprotected land, forming prime legal hunting areas (ZAWA 2010). Fifteen forest reserves are intended to conserve the headwaters of major streams and rivers, although these are largely encroached by both settlements and agricultural fields (Shitima 2005). Informal conservation status is bestowed by Machile



**Figure 1.** Range and study area of Black-cheeked Lovebird (BCL) *Agapornis nigrigenis* as documented by BirdLife International (2024).

Important Bird and Biodiversity Area (IBA), notable as a stronghold of the Black-cheeked Lovebird (Leonard 2005). No settlements are present in the national park, but they exist in the park's GMAs (Leonard 2005). The human population within the species' range is estimated to be about 55,000, with the majority being semi-nomadic cattle-herders, fishermen, and small-scale crop farmers (Zambia Vulnerability Assessment Committee 2015). For the purpose of this study, the species' range is divided into a northern and southern region based on area management type, with the north falling within state-protected areas under the Zambian Wildlife Act of 2015 and the south forming predominantly communal or customary owned land.

### Pool location and monitoring

Data were collected over a period of 30 months; pool monitoring was undertaken between December 2018 and December 2020, while searches for other pools continued for an extra six months (May–October 2021) to ensure wider coverage of the species' range and to compensate for fieldwork lost to COVID-19 travel restrictions on CGP between May and December 2020 (pool monitoring by community members – see below – continued in this period). Transects covering multiple habitat types including mopane woodland were undertaken to survey the lovebirds using distance sampling (Buckland et al. 2005). An initial 70 transects were pre-selected in ArcGIS Pro using the Generate Transects Along Lines tool (ESRI 2019).

To locate pools, a combination of methods was used. A desk review collected the coordinates of all the pools used by lovebirds during earlier studies (Warburton 2003). Pools were also located by interviewing local inhabitants, and along transects. Transects were run systematically across the study area from east to west but, to increase the likelihood of finding pools, some transects followed footpaths and streams (Mirzaei and Bonyad 2016). Along transects we constantly attempted to record lovebird presence and numbers at pools. Every pool encountered, whether classified as used or unused by Black-cheeked Lovebirds, was georeferenced, given a project identification number, and categorised as mopane, river, grassland or artificial, following Warburton (2003). Table 1 summarises the number of pools by type, the methods used to locate them, and the number of pools found by each method.

Data were collected on: (i) vegetation type (mopane – dominated by mopane trees; non-mopane – dominated by other species); (ii) tree diameter at breast height (DBH) of the five largest trees (mopane and non-mopane) within 50 m of the pool (DBH

presented here as average basal area in m<sup>2</sup>); (iii) human activities (presence of people or livestock or their tracks) up to 50 m from the pool edge; (iv) distance to mopane (in km, measured as linear distance to the nearest edge of mopane woodlands as defined by the Zambian forests shapefile); (v) distance to the nearest known pool (in km, measured as linear distance to the nearest edge of surface water as defined by the World ESA surface shapefile); (vi) pool condition (water present or not); (vii) pool size gauged as perimeter length (in m) of the polygon around the water's edge, measured using a calibrated rope laid by the designated monitor. Human activity was classified as “no activity evident” or “activity evident” (domestic use and livestock use seen or inferred to be present on each visit). Table 2 shows a full range of parameters considered likely to have an influence on the drinking patterns of Black-cheeked Lovebirds. The distance from each pool to the edge of the species' range as defined by BirdLife International was determined using ArcGIS.

Lovebird usage (presence at/around the pool) and the number of lovebirds observed were also recorded. A pool was classified as used following the confirmation of lovebird presence when the pool was initially located or during the monitoring period. Monitored pools were visited between 24 and 72 times depending on when the pool was initially identified, while those not monitored were visited 2–3 times prior to being classified as used or unused. Of the 64 total pools classified as used, 43 had confirmed lovebird presence 81–100% of the time while the 83 pools classified as unused had no lovebirds on all visits. This strongly suggests that pools used by lovebirds tended to be visited on most days. By extension, it also suggests that it will have been relatively rare for us to have missed lovebirds on the 2–3 visits to pools coded as unused under this study. Figure 2 shows the proportions of lovebirds present (used) and absent (unused) in all the 147 pools included in the analysis in this study.

Local community members living close to the pools were engaged to assist with twice-monthly monitoring of pools across the species' entire range, a task that was too expensive and logistically unfeasible for a single researcher. A total of 147 pools were located (Table 1), of which 53 were monitored from December 2018 to December 2020 by 13 observers who were paid for their services. The monitored pools were selected based on their proximity (within 2 km) to community members willing to be part of the monitoring effort. Based on the Wilcoxon rank sum test, there was no significant difference in pool size ( $w = 2,679$ ;  $P = 0.45$ ) and distance to mopane ( $w = 2,474$ ;  $P = 0.95$ ) between the monitored and unmonitored pools.

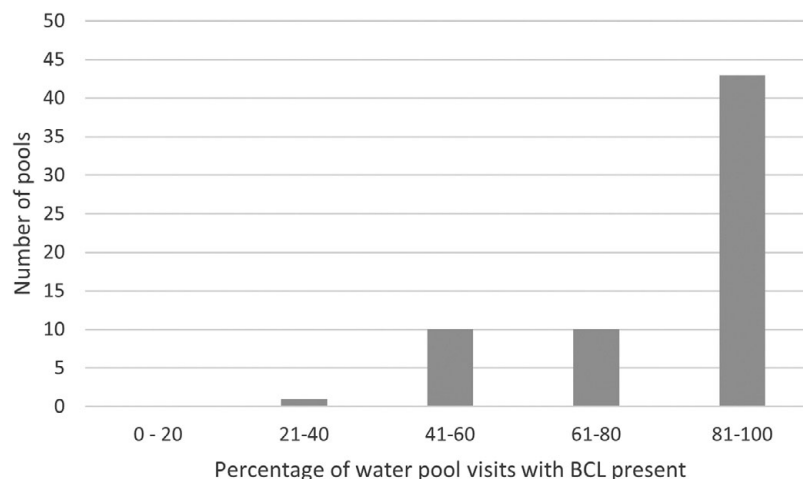
The monitors were trained to make twice-monthly observations at each pool for 10 minutes in either the morning (05h30–10h00) or late afternoon (16h00–18h00), and to record human activity, pool condition, pool size, and the total number of lovebirds present during the monitoring period. This was carried out at both used and unused pools with the same effort. The choice of observation times was based on peak time of lovebird activity at pools observed and documented during the drinking behaviour study by Warburton and Perrin (2005b). Monitors were advised to arrive at a pool 15 minutes earlier than known site-specific lovebird arrival times to record other parameters before sitting quietly at least 50 m from the pool to avoid affecting lovebird behaviour. Weekly telephone contact was maintained with the monitors to remind them of upcoming monitoring visits and to obtain news of any changes at the pools. A total of 1,144 visits were made during the wet season (November–April) and 1,212 in the dry season (May–October) over a period of 54 fortnights from December 2018 to December 2020. Worth noting is a six-month

**Table 1.** Summary of pool numbers by type and in relation to the search methods used

| Pool type  | Method of location |        |                 |        |           |        | Total |
|------------|--------------------|--------|-----------------|--------|-----------|--------|-------|
|            | Previous study     |        | Local knowledge |        | Transects |        |       |
|            | Used               | Unused | Used            | Unused | Used      | Unused |       |
| Artificial | 1                  | 1      | 3               | 2      | 3         | 8      | 18    |
| Mopane     | 5                  | 0      | 5               | 1      | 4         | 3      | 18    |
| Grassland  | 6                  | 1      | 5               | 6      | 5         | 12     | 35    |
| River      | 10                 | 2      | 11              | 13     | 6         | 34     | 76    |
| Totals     | 22                 | 4      | 24              | 22     | 18        | 57     | 147   |
|            | 26                 |        | 46              |        | 75        |        |       |

**Table 2.** Range of pool parameters/predictors likely to influence drinking patterns of the Black-cheeked Lovebird (BCL) *Agapornis nigrigenis*

| Predictor                             | Use in study | Justification  |
|---------------------------------------|--------------|--|
| Water quality (clear/turbid)          | Not used     | Documented not to affect BCL (Warburton and Perrin 2005b)  |
| Water condition (still or running)    | Not used     | Documented not to affect BCL (Mzumara et al. 2016; Warburton and Perrin 2005b)   |
| Pool size (perimeter)                 | Used         | Allied to activity and water condition (Mzumara et al. 2016; Warburton and Perrin 2005b)   |
| Pool depth                            | Used         | Linked to shallow edge at pools (Warburton and Perrin 2005b; Zulfiqar et al. 2023)   |
| Pool cycle (seasonal/permanent)       | Not used     | Linked to pool type – see below (Mzumara et al. 2016; Warburton and Perrin 2005b)  |
| Pool type                             | Used         | Correlated to habitat and pool cycle (Warburton and Perrin 2005b)  |
| Pool condition (water present/absent) | Used         | Linked to pool size above (Mzumara et al. 2016; Warburton and Perrin 2005b)  |
| Activity at pool                      | Used         | Represents measure of disturbance at pools (Mzumara et al. 2016; Ndithia and Perrin 2006; Warburton and Perrin 2005b)                                  |
| Distance to next pool                 | Used         | Related to water availability, and BCL distribution and activity at pools (Ndithia and Perrin 2006; Warburton and Perrin 2005b)                        |
| Tree height around pool               | Not used     | Documented not to affect BCLs (Turshak et al. 2011; Warburton and Perrin 2005b)  |
| Basal area of trees around pool       | Used         | Associated with availability of perching points (Brūmelis et al. 2020)   |
| Distance of trees (perch) to pool     | Used         | Linked to basal area, habitat, and pool type (Mzumara et al. 2016; Warburton and Perrin 2005b)   |
| Overall habitat type around pool      | Used         | Connected to pool type (Warburton and Perrin 2005b)  |
| Distance to mopane                    | Used         | Linked to habitat, distribution of BCLs, and distances travelled to access water (Dodman et al. 2000; Mzumara et al. 2016; Warburton and Perrin 2005a) |
| Distance to settlements               | Not used     | Documented not to significantly affect BCLs (Warburton and Perrin 2006)  |
| Distance to agricultural fields       | Not used     | Documented not to significantly affect BCLs (Warburton and Perrin 2006)  |
| Surrounding temperature               | Not used     | Observation period excluded periods of high daytime temperatures (du Plessis et al. 2012)  |

**Figure 2.** Proportion of pool monitoring visits with Black-cheeked Lovebird *Agapornis nigrigenis* present.

monitoring gap between the first group of pools located in December 2018 and the second group in May–June 2019 as fieldwork could not be undertaken during the peak of the rainy season when most of the study area was inaccessible.

### Data analysis

All analyses were performed using R version 4.1.2 (RStudio Team 2023).

### Distribution of pools

To identify possible patterns in the distribution of used vs unused pools, and to obtain insights on pool availability, a chi-squared test was used to check for an association between the proportion of used and unused pools in the north (protected) and south (communal areas) as well as any variation across the different pool types. Furthermore, a paired t-test was used to detect any significant differences in the mean distance of used vs unused pools from the edge of the species' range.

### Overall patterns of pool usage

To identify the variables most strongly associated with overall pool usage by lovebirds, binomial generalised linear modelling (GLM) (Zhao and Cen 2013) was performed on the complete data set of 147 pools, with presence/absence of lovebirds at pools as the response and predictors selected from candidate covariates in Table 2. All numeric predictors were scaled prior to inclusion in the model, and model selection was based on minimum Akaike information criterion (AIC), adjusted for small sample sizes, on  $\Delta\text{AICc}$  (difference between the AICc of a given model and the lowest AICc model in the set) and on Akaike weight (Burnham and Anderson 2002; Symonds and Moussali 2011). A model was considered to be well supported if it had  $\Delta\text{AICc} < 2$ , and to be strongly supported as the most plausible model in the set if it had a weight ( $w_i$ )  $> 0.03$  (Banner et al. 2017). Additional binomial GLM was undertaken to factor in seasonal variations across the study area with the data set split into wet and dry season.

### Variation in numbers of birds at pools

To test whether the number of birds drinking at a pool varied between morning and afternoon as well as between wet and dry season, a pairwise Wilcoxon rank sum test (Mangiafico 2016) with continuity correction was used to compare the number of drinking birds and monitoring time. Furthermore, Poisson GLM was used to assess the factors influencing the number of birds drinking at each pool during the monitoring period (Zhao and Cen 2013) based on the list of predictors in Table 2. To evaluate the consistency of pool usage, coefficients of variation (CV) were calculated for both seasons across the monitoring period and Spearman's rank correlation (Schober et al. 2018) used to measure the association between the mean number of birds in each season and the season's CV.

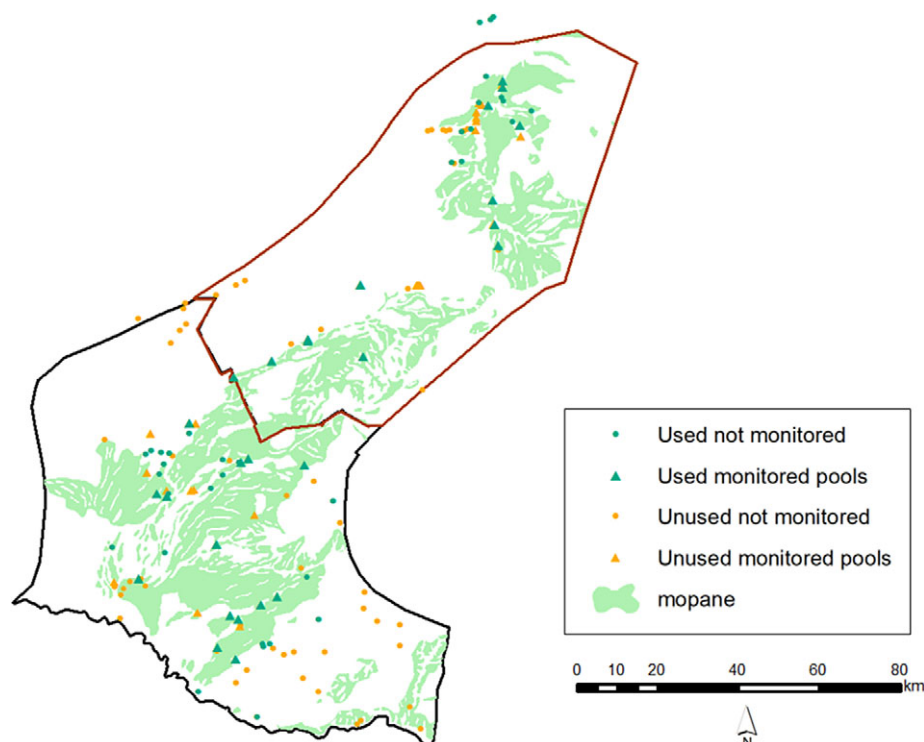
## Results

### Distribution of pools

Of the 147 pools located during the study, 64 (43%) were confirmed to be used by Black-cheeked Lovebirds (Figure 3). Of the 53 monitored pools, 27 were used by lovebirds during the monitoring period, while 14 pools used in the earlier study were found to be no longer available owing to land-use change; all available unused pools from the earlier study remained unused and all available used pools were still used by lovebirds. There was no significant difference ( $\chi^2 = 0.16$ ,  $df = 1$ ,  $P = 0.67$ ) between the proportions of used and unused pools in the northern and southern portions of the species' range. Pools used by lovebirds tended to be closer to the centre of the species' range, as indicated by the significant difference (SD) between the mean distance from the edge of the range of used ( $\bar{x} = 22.56$  km;  $SD = 9.41$ ) vs unused ( $\bar{x} = 15.46$ ;  $SD = 10.9$ ) pools ( $t = -4.13$ ,  $df = 145$ ,  $P < 0.001$ ). Of the 64 used pools, river pools accounted for 41%, grassland 26%, mopane 22%, and artificial 11%.

### Overall patterns of pool usage

There were significant differences in the proportions of pools used across the four pool types ( $\chi^2 = 11.8$ ,  $df = 3$ ,  $P = 0.008$ ) (Table 3). From the GLM results, used pools tended to be close to mopane, have a high basal area of surrounding trees, and lack human activity (Table 4). In the dry season, however, pool usage was influenced by distance to mopane, the basal area of surrounding trees, human activity, distance to nearest pool, and pool size, while pool type was not significant (Table 4). In the wet season, key parameters influencing lovebird usage of pools were almost the same but with pool type replacing human activity.



**Figure 3.** Distribution of pools across the study area; the red border represents the northern region while the black line represents the south.

**Table 3.** Overview of characteristics of used and unused pools

| Category                         | Used (n = 64) | Unused (n = 83) |
|----------------------------------|---------------|-----------------|
| Artificial                       | 7 (39%)       | 11 (61%)        |
| Grassland                        | 17 (49%)      | 18 (54%)        |
| Mopane                           | 14 (78%)      | 4 (22%)         |
| River                            | 26 (34%)      | 50 (66%)        |
| Pool size (m)/SD                 | 50/25.51      | 80/53           |
| Distance to mopane (km)/SD       | 1.15/1.86     | 4.14/6.01       |
| Distance to nearest pool (km)/SD | 5.02/4.84     | 4.68/4.45       |
| Human activity (Y/N)             | 23/41         | 43/40           |
| Basal area (m <sup>2</sup> )/SD  | 1/1.41        | 0.44/0.71       |

### Variation in lovebird numbers at pools

Numbers of birds were influenced only by pool type and were higher where human activity was lower. Pool monitors paid a total of 837 visits to used pools, of which 412 were in the morning. Time of day (morning or afternoon) did not significantly affect the number of birds recorded ( $\chi^2 = 0.75$ ,  $df = 1$ ,  $P = 0.39$ ).

Lovebird numbers at monitored pools varied with pool type and season (wet/dry). The correlation between season and pool type in the dry season ( $r_s = -0.73$ ,  $n = 53$ ,  $P < 0.001$ ) was stronger than that in the wet season ( $r_s = -0.48$ ,  $n = 53$ ,  $P = 0.01$ ), suggesting that pool type has a more substantial and significant impact on the number of birds visiting during the dry season compared with the wet season (an average of 1,920 in the dry season and 2,064 in the wet season). Artificial pools recorded their highest number of lovebirds in May (just after the rains) and October (just before the rains). Mopane pools on the other hand exhibited trends aligning with their documented cycle, with a constant number of birds from January to June and a drop until November as these pools tended to dry out completely after the wet season. Grassland pools hosted their highest numbers in June and March (Figure 4), with their lowest numbers coinciding with the periods of flooding (February) and desiccation (October). The number of birds drinking at river pools was consistent throughout the year, with a slight drop in May and August.

### Discussion

Black-cheeked Lovebirds used only 64 of the 147 pools located in this study, with used pools tending to be located close to the centre of the species' range. A usage rate of 78% for mopane pools is

striking, as it underlines the significance of mopane woodland to the survival of the species (Moura et al. 2017), as well as the need for concerted action to manage such pools for the benefit of the lovebirds. Notable from this and earlier studies is that mopane and grassland pools dry out and become unusable by the lovebirds during the peak of the dry season (Mzumara et al. 2016; Warburton and Perrin 2005b; CGP 2021, personal observation).

Of the 28 confirmed used pools georeferenced as part of a lovebird drinking study in the 2000s (Warburton 2003), only 22 were still used during this study while the six available unused pools remained unused. Such a reduction in the number of pools appears to reflect a reduction in rainfall and land-use change over the last 20 years (Musonda et al. 2021), resulting in several modifications within riverine ecosystems (IPCC 2022). This aligns with evidence across south-western Zambia where reductions in rainfall have been observed since 1978 and are projected to continue past the year 2050 (Libanda and Ngonga 2018; Musonda et al. 2021). Overall, the results of our study provide evidence of additional conditions that need to be met to ensure the long-term survival of Zambia's endemic arid-country parrot.

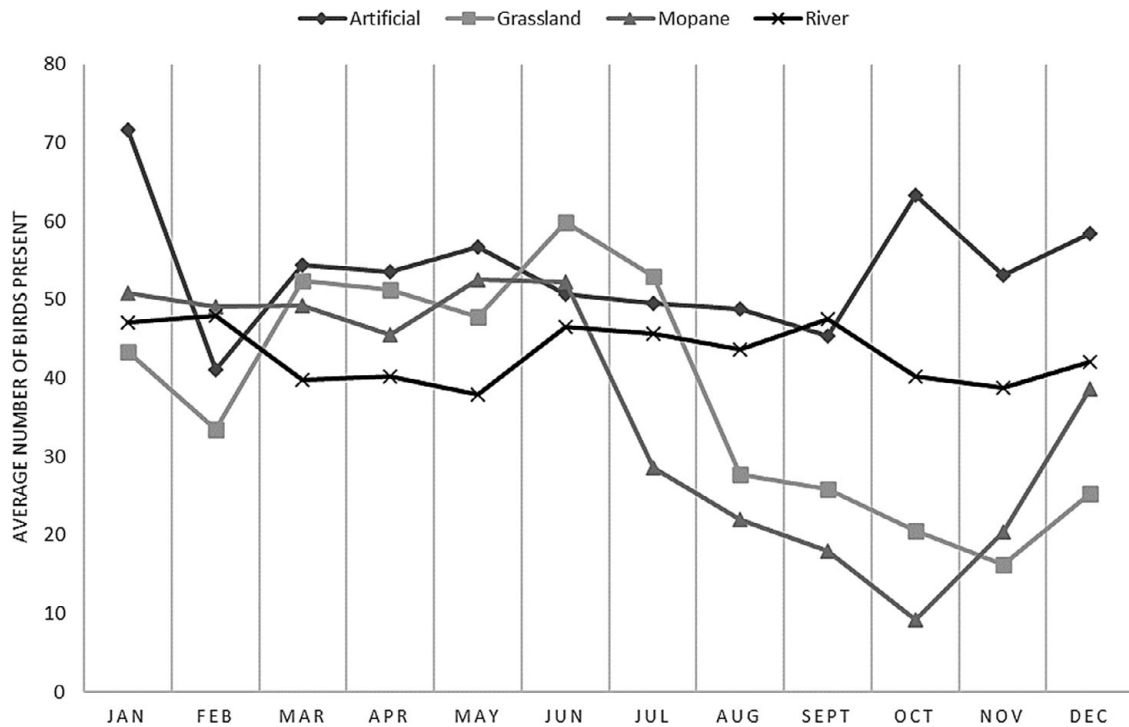
The probability of a pool being used by Black-cheeked Lovebirds increased with greater proximity to mopane, a larger basal area of adjacent trees, and an absence of human activity. Being dependent on mopane for nesting and roosting cavities as well as general cover, the species presumably saves energy and reduces predation risk by foraging and drinking close to mopane (Devereux et al. 2005; Molokwu et al. 2010; Mzumara et al. 2019). Visits to distant and isolated sites by other bird species inhabiting arid areas, for example in the dry season when water is scarce, are only undertaken in large numbers that may lower the individual chances of predation (Devereux et al. 2005; Lima et al. 1990). Variations in numbers drinking at pools probably reflected variations in the lovebird's abundance within its range (Warburton and Perrin 2005b; Phiri et al. in prep.). Arid-habitat species minimise their energetic expenditure to maintain a water balance (Jong 1976; Smit and McKechnie 2015), so using pools close to mopane where the species roosts and nests (Warburton and Perrin 2005a) must prevent large energy outflows (Bryant 1997).

At pools the lovebirds initially gather in nearby bushes or trees before descending collectively to drink (Dodman et al. 2000; Warburton and Perrin 2005b). They avoid pools that lack perches within 20 m of the water's edge (Warburton and Perrin 2005b; CGP 2021, personal observation), and in our study basal area of nearest trees served as a proxy for the quantity of available perches and cover near pools (Brumelis et al. 2020). Nevertheless, although our results confirm the strong association between lovebirds and mopane, some used pools were surrounded not by pure mopane but by mixtures of mopane and other tree species or by other species

**Table 4.** Most supported models from logistic regression for overall and seasonal usage, and numbers of Black-cheeked Lovebirds *Agapornis nigrigenis* using pools from Poisson regression. Figures given are coefficients for each predictor. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; ns = not significant

| Model    | Dependent variable        | Pool type                             | Pool size | Distance to next pool | Distance to mopane | Basal area | Activity |
|----------|---------------------------|---------------------------------------|-----------|-----------------------|--------------------|------------|----------|
| Binomial | Overall usage (n = 147)   | ns                                    | ns        | ns                    | -1.01*             | 3.3**      | -0.93*   |
|          | Dry season (n = 53)       | ns                                    | 1.94***   | -0.69***              | -7.95***           | 1.48***    | -3.55*** |
|          | Wet season (n = 53)       | MP 4.2***                             | 1.82***   | -0.46***              | -2.1*              | 0.33***    | ns       |
| Poisson  | Numbers of birds (n = 53) | AP 3.24***<br>MP 0.36**<br>RP -0.29** | ns        | ns                    | ns                 | ns         | -0.12*   |

AP = artificial pool, MP = mopane pool, RP = river pool (reference level used = artificial pool). No activity present = reference level on human activity



**Figure 4.** Variation in the average number of Black-cheeked Lovebirds *Agapornis nigrigenis* recorded per month across all pool types. The wet season runs from November to May while the dry season is from June to October.

alone, including *Combretum imberbe* and *Diospyros mespiliformis* (Dodman et al. 2000; CGP 2019, personal observation). Overall, fringing vegetation at water points is known to be more critical for small and mid-sized forest birds, whose vulnerability to predation increases when they access drinking sites with too distant or no vegetation (Votto et al. 2022).

Lovebirds are extremely cautious drinkers that avoid drinking from a pool during periods of loud and obvious human activity (Mzumara et al. 2016; Warburton and Perrin 2005b; CGP 2021, personal observation). In the flood months (February–April) water is abundant in most of the shallow wells within villages and livestock enclosures (Lewanika 2003; Thole and Dodman 1997), reducing the need for human activity at natural pools. In the dry season, when smaller pools dry out, most pools, particularly the larger ones, saw an increase in human activity, coinciding with a steady increase in the number of lovebirds visiting river and artificial pools.

Other factors known to influence the numbers of lovebirds using pools include local lovebird abundance, pool physical characteristics, and breeding regime (Mzumara et al. 2016; Warburton and Perrin 2005b, 2005d). In density surface models developed for the species (Phiri et al. in prep), mopane cover was a significant determinant of local abundance, which in turn will likely influence bird usage of pools. Our study also confirms that the physical features of pools play a significant role in determining their usage by lovebirds, aligning with previous findings related to desert birds (Fisher et al. 1972).

Mopane and grassland pools dried out by October, the former refilling after a heavy downpour, the latter refilling according to the flooding regimes of the adjacent river (Naidoo et al. 2020). Consequently, these two pool types showed the most variation in the number of birds across the monitoring period. By contrast river pools, which form in major channels along seasonally dry riverbeds (Warburton and Perrin 2005b) and last until the onset of the rains,

generally hosted a constant number of birds, with a slight increase in the dry season. Similarly, artificial pools recorded the highest number of birds between October and December, when water is extremely scarce in the study area. Greater dependence on artificial pools has been reported previously in the lovebirds' southern rather than in their northern subpopulation (Warburton and Perrin 2000b). The north is dominated by the Nanzhila River and its inundated floodplains (Ashley and Murphy 2012), which have water all year round. In the south, locals dig small dams or maintain dams left after road maintenance activities for their livestock and gardens; we found that nearly 40% of all artificial pools located in the south were used by lovebirds.

River pools and artificial pools evidently play a pivotal role in maintaining lovebird populations throughout the annual cycle. Potential management interventions to improve the long-term survival prospects of the Black-cheeked Lovebird include simply enhancing the capacity of artificial pools to meet the needs of the lovebirds, by ensuring that each pool's characteristics meet the criteria of the best-fitting model. However, the creation of small, shallow-sided, undisturbed pools in or near mopane woodland with larger trees within 50 m must also be considered. This highlights the wider need to review existing best practices of water resource provisioning for wildlife species, to devise interventions that will extend the water retention of mopane pools beyond the wet season. Water provision programmes are prominent in many key biodiversity areas in southern Africa in response to increases in water stress (Selebatso et al. 2018). High-profile sites with such programmes include the Central Kalahari Game Reserve, and Hwange and Kruger National Parks, where diesel engines are used to pump water into pools, evidently promoting the presence and abundance of certain bird species, particularly seedeaters (Abdu et al. 2018; Kamanda et al. 2008). Information from these and similar initiatives can help to identify locations within the mopane woodlands

where pools can be excavated and/or sustained by pumps in the dry season. Additional water sources would benefit other wildlife populations also, by expanding animal distributions and increasing productivity, survival rates, and fitness (Rosenstock et al. 1999). Such interventions, however, need to be carefully planned to ensure compatibility with long-term landscape management and community welfare objectives as well as the natural mosaic of spatio-temporal variability in surface water (Redfern et al. 2005; Smit 2013).

**Acknowledgements.** We thank the Loro Parque Foundation, A. G. Leventis Foundation, and African Bird Club (ABC) for financial support, BirdWatch Zambia for the administrative support to manage the ABC grant, and the Department of National Parks and Wildlife for the research permits. We also thank three referees for their insightful comments on the submitted draft of this paper. Special appreciation goes to the 13 pool monitors in Ngwezi, Machile, Mulanga, and Kafue National Parks, whose commitment and contribution to this work was invaluable. We dedicate this paper to Simaata Mutelo and Brian Zuze, water pool monitors and guardians of the Black-cheeked Lovebirds who passed away before the completion of this study.

**Supplementary material.** The supplementary material for this article can be found at <http://doi.org/10.1017/S0959270924000261>.

## References

- Abdu S., Lee A. and Cunningham, S. (2018). The presence of artificial water points structures an arid-zone avian community over small spatial scales. *Ostrich* **89**, 1–8. <https://doi.org/10.2989/00306525.2018.1509904>
- Ashley N and Murphy I (2012) *The Kafue National Park Zambia*. Totnes: Corporate Brochure Company Publishing.
- Banner K.M. and Higgs M.D. (2017). Considerations for assessing model averaging of regression coefficients. *Ecological Applications* **27**, 78–93. <https://doi.org/10.1002/eap.1419>
- Bingham M (1994) The habitat of the Black-cheeked Lovebird. *Zambian Ornithological Society Unpublished report*.
- BirdLife International (2024). Species Factsheet: *Agapornis nigrigenis*. Available at <https://datazone.birdlife.org/species/factsheet/black-cheeked-lovebird-agapornis-nigrigenis> (accessed 17 April 2024).
- Brümelis G., Dauškane I., Elferts D., Strode L., Krama T. and Krams I. (2020). Estimates of tree canopy closure and basal area as proxies for tree crown volume at a stand scale. *Forests* **11**, 1180. <https://doi.org/10.3390/f11111180>
- Bryant D.M. (1997). Energy expenditure in wild birds. *Proceedings of the Nutrition Society* **56**, 1025–1039. <https://doi.org/10.1079/PNS19970107>
- Buckland S.T., Anderson D.R., Burnham K.P. and Laake J.L. (2005). Distance sampling. In Armitage P. and Colton T. (eds), *Encyclopedia of Biostatistics*. New York: John Wiley. <https://doi.org/10.1002/0470011815.b2a16019>
- Burnham KP and Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second edition. New York, NY: Springer.
- Collar N.J. (1997). Family Psittacidae (parrots). In del Hoyo J., Elliott A. and Sargatal J. (eds), *Handbook of the Birds of the World*, vol. 4. Barcelona: Lynx Edicions, pp. 280–477.
- Devereux C.L., Whittingham M.J., Fernández-Juricic E., Vickery J.A. and Krebs J.R. (2005). Predator detection and avoidance by starlings under differing scenarios of predation risk. *Behavioural Ecology* **17**, 303–309. <https://doi.org/10.1093/beheco/arj032>
- Dodman T. (1995a). Status and distribution of the Black-cheeked Lovebird *Agapornis nigrigenis*. Royal Society for the Protection of Birds unpublished report.
- Dodman T. (1995b). A survey to investigate the status and distribution of the Black-cheeked Lovebird *Agapornis nigrigenis* in south-west Zambia. *Bulletin of the African Bird Club* **2**, 103–105.
- Dodman T., Katanekwa V., Apsinwall D. and Stjernstedt R. (2000). Status and distribution of the Black-cheeked Lovebird *Agapornis nigrigenis* in Zambia. *Ostrich* **71**, 228–234. <https://doi.org/10.1080/00306525.2000.9639919>
- du Plessis K., Martin R., Hockey P.A., Cunningham S.J. and Ridley A.R. (2012). The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology* **18**, 3063–3070. <https://doi.org/10.1111/j.1365-2486.2012.02778.x>
- Environmental Systems Research Institute (ESRI) (2019). ArcGIS Desktop version 10.7. Redlands: ESRI.
- Fisher C.D., Lindgren E. and Dawson W.R. (1972). Desert birds in relation to their ecology and abundance. *The Condor* **74**, 111–136. <https://doi.org/10.2307/1366276>
- Intergovernmental Panel on Climate Change (IPCC) (2022). *Climate Change 2022: Impacts, Adaptations and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press. doi: 10.1017/9781009325844
- Jong A.A.D. (1976). The influence of simulated solar radiation on the metabolic rate of White-crowned Sparrows. *The Condor* **78**, 174–179. <https://doi.org/10.2307/1366852>
- Kamanda M., Ndiweni V., Imbayarwo-Chikosi V.E., Muvengwi J. and Musakwa A. (2008). The impact of tourism on sable antelope (*Hippotragus niger*) vigilance behaviour at artificial waterholes during the dry season in Hwange National Park. *Journal of Sustainable Development in Africa* **10**, 299–314.
- Leonard P. (2005). *Important Bird Areas of Zambia*. Lusaka: Zambian Ornithological Society.
- Lewanika K.M. (2003). The traditional socio-economic systems for monitoring wetlands and wetland natural resources utilization and conservation: the case of the Barotseland, Zambia. In Bernard T., Mosepele K. and Ramberg L. (eds), *Proceedings of the Conference on Environmental Monitoring of Tropical and Subtropical Wetlands*. Maun: Harry Oppenheimer Okavango Research Centre, University of Botswana, pp. 267–277.
- Libanda B. and Ngonga C. (2018). Projection of frequency and intensity of extreme precipitation in Zambia: a CMIP5 study. *Climate Research* **76**, 59–72. <https://doi.org/10.3354/cr01528>
- Libanda B., Nkolola N.B. and Musonda, B. (2015). Rainfall variability over northern Zambia. *Journal of Scientific Research and Reports* **6**, 416–425. <https://doi.org/10.9734/JSRR/2015/16189>
- Lima S.L. and Dill L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**, 619–640. <https://doi.org/10.1139/z90-09>
- Mangiafico S.S. (2016). Summary and analysis of extension program evaluation in R. Version 1.20.05, revised 2023.
- Mirzaei M. and Bonyad A.E. (2016). Comparison of fixed area and distance sampling methods in open forests: case study of Zagros Forest, Iran. *Journal of Forestry Research* **27**, 1121–1126. <https://doi.org/10.1007/s11676-016-0239-9>
- Molokwu M.N., Nilsson J.Å., Ottosson U. and Olsson O. (2010). Effects of season, water and predation risk on patch use by birds on the African savannah. *Oecologia* **164**, 637–645. <https://doi.org/10.1007/s00442-010-1781-3>
- Moura I., Maquia I., Rija A.A., Ribeiro N. and Ribeiro-Barros A.I. (2017). Biodiversity studies in key species from the African mopane and miombo woodlands. In Bitz L. (ed.), *Genetic Diversity*. IntechOpen. <https://doi.org/10.5772/66845>
- Musonda B., Jing Y., Nyasulu M. and Mumo L. (2021). Evaluation of sub-seasonal to seasonal rainfall forecast over Zambia. *Journal of Earth System Science* **130**, 47. <https://doi.org/10.1007/s12040-020-01548-0>
- Mzumara T.I., Martin R.O., Tripathi H., Phiri, C. and Amar, A. (2019). Distribution of a habitat specialist: mopane woodland structure determines occurrence of Near Threatened Lilian's Lovebird *Agapornis lilianae*. *Bird Conservation International* **29**, 413–422. <https://doi.org/10.1017/S0959270918000370>
- Mzumara T.I., Perrin M.R. and Downs C.T. (2016). The drinking habits of the Lilian's lovebird and incidents of poisoning at waterholes. *African Journal of Ecology* **54**, 289–298. <https://doi.org/10.1111/aje.12216>
- Naidoo R., Brennan A., Shapiro A.C., Beytell P., Aschenborn O., Du Preez P. et al. (2020). Mapping and assessing the impact of small-scale ephemeral water sources on wildlife in an African seasonal savannah. *Ecological Applications* **30**, e02203. <https://doi.org/10.1002/eap.2203>
- Ndithia H. and Perrin M.R. (2006). The spatial ecology of the Rosy-faced Lovebird *Agapornis roseicollis* in Namibia. *Ostrich* **77**, 52–57. <https://doi.org/10.2989/00306520609485508>



- Pierce H. and Lang S. (2008). Intense seasonal floods in southern Africa. Earth Observatory. Available at <https://earthobservatory.nasa.gov/images/19501/intense-seasonal-floods-in-southern-africa> (accessed 2 May 2022).
- Redfern J.V., Grant C.C., Gaylard A. and Getz W.M. (2005). Surface water availability and the management of herbivore distributions in an African savanna ecosystem. *Journal of Arid Environments* **63**, 406–424. <https://doi.org/10.1016/j.jaridenv.2005.03.016>
- Rembold F., Kerdiles H., Lemoine G. and Perez-Hoyos A. (2016). Impact of El Niño on agriculture in southern Africa for the 2015/2016 main season. *JRC MARS Bulletin – Global Outlook Series*. European Commission Joint Research Centre. <https://doi.org/10.2788/900042>
- Rosenstock S.S., Ballard W.B. and Devos J.C. (1999). Benefits and impacts of wildlife water developments. *Journal of Range Management* **52**, 302–311. <https://journals.uair.arizona.edu/index.php/jrm/article/viewFile/9421/9033>
- RStudio Team (2023). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Schober P., Boer C. and Schwarte L.A. (2018). Correlation coefficients: appropriate use and interpretation. *Anesthesia & Analgesia* **126**, 1763–1768. <https://doi.org/10.1213/ANE.0000000000002864>
- Selebatso M., Maude G. and Fynn R.W.S. (2018). Assessment of quality of water provided for wildlife in the Central Kalahari Game Reserve, Botswana. *Physics and Chemistry of the Earth, Parts A/B/C* **105**, 191–195. <https://doi.org/10.1016/j.pce.2018.02.012>
- Shitima E.M. (2005). Forest Conservation and People's Livelihoods: Explaining Encroachment on Zambia's Protected Forest Landscapes – The Case of Mwekera National Forest, Kitwe, Copperbelt. Master of Philosophy thesis, Norwegian University of Science and Technology (NTNU), Trondheim. [https://ntnuopen.ntnu.no/ntnu-xmlui/bitstream/handle/11250/264993/125643\\_FULLTEXT01.pdf](https://ntnuopen.ntnu.no/ntnu-xmlui/bitstream/handle/11250/264993/125643_FULLTEXT01.pdf)
- Smit B. and McKechnie A.E. (2015). Water and energy fluxes during summer in an arid-zone passerine bird. *Ibis* **157**, 774–786. <https://doi.org/10.1111/ibi.12284>
- Smit B., Woodborne S., Wolf B. and McKechnie A.E. (2017). Surface water dependency among Kalahari Desert birds. [10.7287/peerj.preprints.3167v1](https://doi.org/10.7287/peerj.preprints.3167v1)
- Smit I. (2013). Systems approach towards surface water distribution in Kruger National Park, South Africa. *Pachyderm* **53**, 91–98. <https://pachydermjournal.org/index.php/pachyderm/article/view/328>
- Symonds MRE and Moussali A (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* **65**, 13–21.
- Thole L.S. and Dodman T. (1997). *Traditional and Modern Approaches to Community Wetland Management in Zambia (Case Study No. 8). Community Involvement in Wetland Management: Lessons from the Field*. Wageningen: Wetlands International.
- Turshak L.G., Mwansat G.S. and Manu S.A. (2011). Effect of habitat structure and altitudinal gradients on avian species. *Zoologist* **9**, 31–37. <https://www.ajol.info/index.php/tzool/article/view/73125>
- Votto S.E., Schlesinger C., Dyer F., Caron V. and Davis J. (2022). The role of fringing vegetation in supporting avian access to arid zone waterholes. *Emu – Austral Ornithology* **122**, 1–15. <https://doi.org/10.1080/01584197.2022.2041441>
- Warburton L. (2003). The Ecology and Conservation Biology of the Black-cheeked Lovebird *Agapornis nigrigenis* in Zambia. PhD thesis, University of Natal, Durban.
- Warburton L. and Perrin M. (2005a). Roosting requirements and behaviour of the Black-cheeked Lovebird *Agapornis nigrigenis* (Sclater 1906) in Zambia. *Tropical Zoology* **18**, 39–48. <https://doi.org/10.1080/03946975.2005.10531213>
- Warburton L. and Perrin M. (2005b). Conservation implications of the drinking habits of Black-cheeked Lovebirds *Agapornis nigrigenis* in Zambia. *Bird Conservation International* **15**, 383–396. <https://doi.org/10.1017/S0959270905000614>
- Warburton L. and Perrin M. (2005c). Foraging behaviour and feeding ecology of the Black-cheeked Lovebird *Agapornis nigrigenis* in Zambia. *Ostrich* **76**, 118–129. <https://doi.org/10.2989/00306520509485484>
- Warburton L. and Perrin M. (2005d). Nest-site characteristics and breeding biology of the Black-cheeked Lovebird *Agapornis nigrigenis* in Zambia. *Ostrich* **76**, 162–174. <https://doi.org/10.2989/00306520509485489>
- Warburton L. and Perrin M. (2006). The Black-cheeked Lovebird (*Agapornis nigrigenis*) as an agricultural pest in Zambia. *Emu – Austral Ornithology* **106**, 321–328. <https://doi.org/10.1071/MU04037>
- Zambia Vulnerability Assessment Committee (2015). *In-depth Vulnerability and Needs Assessment Report*. Lusaka: Zambia Vulnerability Assessment Committee.
- Zambia Wildlife Authority (ZAWA) (2004). *General Management Plan: Kafue National Park, Lusaka, Zambia*. Lusaka: ZAWA.
- Zambia Wildlife Authority (ZAWA) (2010). *General Management Plan: Sichifulo Game Management Area, Lusaka, Zambia*. Lusaka: ZAWA.
- Zhao Y and Cen Y. (2013). Response modelling. In *R and Data Mining*. Amsterdam: Academic Press, pp. 156–177.
- Zulfiqar A., Xue-Ying S., Qing-Ming W., Ahmad T., Zhuo X., Razzaq A. et al. (2023). Distribution of avian ecological groups from different water levels habitats during autumn migration provide way forward to preserve the diversity of birds in reserve. *Pakistan Journal of Zoology*. <https://doi.org/10.17582/journal.pjz/20230403090447>