

Birds as indicators of change in the freshwater ecosystems of Botswana

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Francis, Roxane

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School of Biological Earth and Environmental Sciences

Faculty of Science
University of New South Wales

Birds as indicators of change in the freshwater ecosystems of Botswana



Roxane Francis

Supervisors: Richard T Kingsford, Katherine J Brandis

Co-supervisors: Keith Leggett, Mike Murray-Hudson

A thesis submitted in fulfillment of the requirements for the degree of Doctor of Philosophy.

April 14, 2021

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Thesis Title and Abstract

Declarations

Inclusion of Publications
Statement

Corrected Thesis and
Responses

Thesis Title

Birds as indicators of change in the freshwater ecosystems of Botswana

Thesis Abstract

Freshwater ecosystems support highly biodiverse plant and animal populations and provide crucial ecosystem services to human communities. Despite this importance, these systems are being degraded faster than terrestrial or marine environments, resulting in large global declines in freshwater biodiversity. To track such environmental change, birds are often used as indicator species. I focused on tracking changes in significant waterbird breeding colonies, rivers and internationally listed wetlands in Botswana facing a wide range of threats. I identified that riparian bird communities along the Chobe River were more biodiverse in sites with the presence of large herbivores, highlighting the direct and indirect relationships between these seemingly unconnected taxa. Using a drone, I explored the relationships between waterbird breeding and river levels and inundation. Drone imagery on the Chobe River provided comprehensive data on the reproductive success, size and composition of the Kasane waterbird breeding colony, which were linked to river levels and inundation, while citizen science collected abundance data helped identify a threshold river level to support large waterbird breeding colonies. This underlined the importance of river flows for waterbird populations and the potential for the breeding of waterbirds to inform river management. Similarly in the Okavango Delta, citizen science data highlighted positive relationships between waterbird abundance and river flows, but there were indications of long-term declines in waterbird abundances. River flows were again important for waterbird breeding, with key waterbird breeding colonies located in areas experiencing moderate to high flood frequencies. I also developed a semi-automated counting technique for investigating colony sizes with a drone, negating the need to physically enter a colony or manually count imagery, saving time in image processing and ensuring researcher safety. Finally, I investigated the potential effects of foraging at landfill on the marabou stork. Plastics formed a significant proportion of marabou regurgitant while trace metal concentrations in feathers were higher than in naturally foraging populations, indicating potential deleterious impacts. My work highlighted the value of riparian bird communities, predominantly waterbirds, as indicators of change, reflecting herbivore population structures, land use alterations and changes in freshwater flows and inundation.

Thesis Title and Abstract

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Preface

This thesis is a culmination of published or currently in review papers, and as such formatting may differ across chapters, and references and appendices follow each chapter. I have reduced white space in this thesis, with the interest of reducing paper wastage when printing. Please note that chapters 2-6 use the collective term of ‘we’, acknowledging the work as a team to reach publication stage.

This work comes as a result of 10 months living in Botswana where I conducted all data collection myself. All chapters were conceptualized largely by myself with the help of co-

authors. Analyses, and writing was done by myself, with assistance and input from co-authors, particularly in the editing stages, and I generated all figures and maps in this thesis.

Spending so long in another country is no easy feat, and comes with endless visa, permitting and financial challenges. For many months we were uncertain as to whether returning to Botswana was possible in 2019 due to government permitting restrictions, and when these issues were resolved, I returned to the country within 5 days of having received the news. As a result, with circumstances totally out of our control, my second field season was cut short. Despite these difficulties, I am proud to present this culmination of four years hard work.

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Abstract

Freshwater ecosystems support highly biodiverse plant and animal populations and provide crucial ecosystem services to human communities. Despite this importance, these systems are being degraded faster than terrestrial or marine environments, resulting in large global declines in freshwater biodiversity. To track such environmental change, birds are often used as indicator species. I focused on tracking changes in significant waterbird breeding colonies, rivers and internationally listed wetlands in Botswana facing a wide range of threats. I identified that riparian bird communities along the Chobe River were more biodiverse in sites with the presence of large herbivores, highlighting the direct and indirect relationships between these seemingly unconnected taxa. Using a drone, I explored the relationships between waterbird breeding and river levels and inundation. Drone imagery on the Chobe River provided comprehensive data on the reproductive success, size and composition of the Kasane waterbird breeding colony, which were linked to river levels and inundation, while citizen science collected abundance data helped identify a threshold river level to support large waterbird breeding colonies. This underlined the importance of river flows for waterbird populations and the potential for the breeding of waterbirds to inform river management. Similarly in the Okavango Delta, citizen science data highlighted positive relationships between waterbird abundance and river flows, but there were indications of long-term declines in waterbird abundances. River flows were again important for waterbird breeding, with key waterbird breeding colonies located in areas experiencing moderate to high flood frequencies. I also developed a semi-automated counting technique for investigating colony sizes with a drone, negating the need to physically enter a colony or manually count imagery, saving time in image processing and ensuring researcher safety. Finally, I investigated the potential effects of foraging at landfill on the marabou

stork. Plastics formed a significant proportion of marabou regurgitant while trace metal concentrations in feathers were higher than in naturally foraging populations, indicating potential deleterious impacts. My work highlighted the value of riparian bird communities, predominantly waterbirds, as indicators of change, reflecting herbivore population structures, land use alterations and changes in freshwater flows and inundation.

Chapter 1. Introduction

The world's freshwater ecosystems support over 10% of all known species, despite covering only 1% of the world's surface area (Mittermeier et al. 2010, Dijkstra et al. 2014), with their annual ecosystem services valued at over US \$4 trillion (Darwall et al. 2018). This importance to human communities is a driver for conservation, while water resource development for agriculture, industry and communities drives degradation (Darwall et al. 2018, Albert et al. 2020). As a result, three-quarters of the world's inland wetlands are already lost (Darwall et al. 2018), with loss accelerating in the 20th and 21st centuries (Davidson 2014). As such, there are higher rates of decline in freshwater biodiversity than terrestrial or marine ecosystems (Dijkstra et al. 2014), with a third of all freshwater species at risk of extinction (Collen et al. 2014), covering megafauna to invertebrates (Strayer 2006, He et al. 2019).

The role of biodiversity in maintaining air, soil and water quality, and supporting the world's food, fuel and fibre markets is critical, and its loss often affects humanity's poorest the most (Mace et al. 2018). Biodiversity declines would therefore be felt strongly in Africa, where conservation efforts, knowledge and outcomes vary considerably among countries (Thiollay 2007, Jenkins et al. 2010, Wotton et al. 2017). Understanding the nature of these trends and effects on ecosystems and their services is challenging, particularly as there is often little

data, relatively poor understanding of cause and effect relationships and lacking identified indicator species (De Cáceres et al. 2010).

The use of indicator species can be contentious in science, given different definitions (Heink and Kowarik 2010). I defined an ‘indicator’ as a surrogate for evaluating environmental conditions (Heink and Kowarik 2010). Indicator species can be useful when other assessment options are unavailable, particularly when linked to landscape ecology (Landres et al. 1988). Further, efficacy of indicator species can improve when many species, representing various taxa and life histories, are included in monitoring, cognisant that indicator species may not adequately track or reflect true ecological change (Carignan and Villard 2002).

In freshwater ecosystems, waterbirds can be useful indicator organisms, both to evaluate current environmental conditions and track ecosystem change, given their dependencies on river ecosystems. Their distribution, abundance, and breeding often reflects variations in flow and flooding regimes (Kingsford and Auld 2005, Desgranges et al. 2006, Amat and Green 2010, Brandis et al. 2018). Colonially breeding waterbirds (Ciconiiformes, Pelecaniformes and Suliformes such as spoonbills, ibis, egrets, storks, cormorants and herons) often nest over water in large mixed species colonies. Breeding data can be collected relatively quickly because birds often aggregate, during which birds may forage locally or over extensive areas, sometimes up to 30 kms (Siegfried 1971). At other times, waterbirds range over continent-wide scales (Donnelly et al. 2020). As such, waterbirds can potentially track freshwater ecosystem change, reflected in food resources, at a range of spatial scales (Ogden et al. 2014). The study of such colonies can also highlight a range of different threats affecting the long-term viability and population status of individual species. Further, the natural and cultural interest in birds results in significant bird watching efforts (Green and Elmberg 2014), providing historical citizen science datasets on these species. Such data and resultant information is largely fragmented across Africa (Dodman and Diagana 2019), although there

are indications of waterbird declines (Dodman and Diagana 2019, Wetlands International 2020).

Many of my observations were on large wading birds. These large, long-lived birds produce small numbers of offspring that mature late in life (Valuska et al. 2013, Oschadleus et al. 2019). This “slow-fast” lifestyle is typical of species breeding and residing in the tropics (Wiersma et al. 2007): those that invest heavily in their reproduction and favour adult survivorship (Ricklefs 2000). Some of these traits also contribute to their usefulness as indicator species. Favouring adult survivorship means adverse conditions that are not conducive to both young and adult survivorship can result in nest abandonments (Erikstad et al. 1998), a response to the ecosystem that is easily tracked.

Habitat loss and degradation, climate change, and urbanization are driving current declines in waterbird populations (Kirby et al. 2008, Northrup et al. 2019, Wetlands International 2020).

Such threats are widespread across Africa, including within Botswana. Botswana is a landlocked semi-arid country (Batisani and Yarnal 2010) in southern Africa, highly vulnerable to climate change with increasing temperatures and changing seasonal rains (Batisani and Yarnal 2010, Wolski et al. 2012, Darkoh and Mbaiwa 2014). Its current variable habitat and climatic diversity provide for almost 600 avian species (Hancock and Weiersbye 2015), including 71 Palearctic migrant and 67 intra-African migrant species, making Botswana an important stopping point for many global bird species (Hancock and Weiersbye 2015). Its freshwater biodiversity, significant proportions of terrestrial biodiversity and its people, many of whom are subsistence farmers (Motsumi et al. 2012) rely on the ecosystem services of rivers and their floodplains. Systems such as the Chobe River support 359 recorded bird species (11 globally threatened) (Lepage 2020) within Chobe National Park alone, and it is the main watering point for the annual zebra *Equus quagga* migration, the longest large mammal migration in Africa (Naidoo et al. 2016). Another key

area of biodiversity importance is the Okavango Delta (fed by the Okavango River), a UNESCO (United Nations Educational, Scientific and Cultural Organization) World Heritage Site, a Ramsar wetland of international importance and an Important Bird Area (IBA), home to 22 globally threatened birds and 444 unique bird species (The Ramsar Convention Secretariat 2014, UNESCO 2014, Hancock and Weiersbye 2015, McCulloch et al. 2017). These sites also include some of the more important colonial waterbird breeding populations in Southern Africa, supporting marabou stork *Leptoptilos crumenifer*, African openbill *Anastomus lamelligerus* and threatened slaty egret *Egretta vinaceigula* populations (Randall and Herremans 1994, Monadjem 2005, Tyler 2012).

The Global Ecosystem Typology, developed by the International Union for the Conservation of Nature (IUCN) provides a classification, underpinned by theory and application, with conceptual models of all ecosystems including freshwater aquatic ecosystems (Keith et al. 2020). The Okavango and Chobe Rivers are classified as seasonal lowland rivers, and their associated floodplains as seasonal floodplain marshes. They are driven by cyclical, seasonal flow regimes resulting from rainfall (Keith et al. 2013, Keith et al. 2020). They are highly productive with temporal variability promoting functional diversity in their biota, and with a diverse range of food sources they have complex trophic networks, whilst their food chains remain short and heavily controlled by large mobile predators (eg. crocodilians and piscivorous waterbirds) (Keith et al. 2020). They are therefore complex systems consisting of interacting biotic and abiotic drivers and this is reflected by the organisms and processes that respond to these drivers. Currently these two rivers contrast many large rivers of the world by remaining largely free-flowing with their ecosystem processes and dependencies primarily intact (Nilsson and Jansson 1995) but there are increasing pressures on their water resources from upstream (Mbaiwa 2004).

Ecosystems are dynamic, and understanding and tracking the nature of this dynamism is crucial to maintain the viability of dependent ecosystems and their services, particularly when threatened by human impacts. I focused on the efficacy of using waterbirds as indicators of change in the freshwater ecosystems of the Chobe River and Okavango Delta, linking their responses to ecosystem drivers (particularly river flows and flooding), affected by water resource developments and other anthropogenic stressors. I aimed to provide location specific, affordable and reproducible methods to track and address these changes in Botswana, using avian indicators. To do so, I used a range of innovative scientific tools and techniques which allowed me to explore the current state of avian biodiversity in two regions of Botswana, contributing to the understanding of ecological relationships and on-ground conservation of Botswana's birds and ecosystems.

I investigated:

- 1) the relationships between different herbivore populations and distributions of riparian bird communities (Chapter 2);
- 2) the relationships between river levels and breeding in waterbird colonies (Chapters 3-5) and;
- 3) the effects of urbanization on marabou storks (Chapter 6).

I have written each chapter as a stand-alone scientific paper, including their relevant environmental and spatial data, appendices and references. Parts of Chapter 2 were published in the *Journal of Ornithology* (Francis et al. 2020a); Chapter 4 is accepted in *Global Conservation and Ecology*; parts of Chapter 5 were published in the *Journal of Remote Sensing* (Francis et al. 2020b) and; parts of Chapter 6 were published in the *Journal of Urban Ecology* (Francis et al. 2021).

In Chapter 2, I compared the diversity and abundance of riparian bird communities along three sections of the Chobe River floodplain in 2018. Here, river flows are a major driver of

ecosystem processes and biodiversity and there are abundant large herbivores. I therefore related the bird communities, with data collected using ground surveys, to known herbivore abundances, which differed among the three areas due to highly varied large herbivore management strategies. I also tracked changes in riparian bird communities in relation to floodplain inundation using remotely sensed inundation and vegetation maps. I tested the following null hypothesis: there is no difference in riparian bird composition among three sites, differing in herbivore abundance and composition, subjected to temporal changes in flooding of the Chobe River.

In Chapter 3, I tracked the breeding of six colonial waterbird species in the Kasane colony on the Chobe River in 2018 and 2019. I developed methods for the collection of reproductive success data for this inaccessible mixed species breeding colony, causing minimal disturbance. I also explored the relationship between river levels, inundation and local rainfall and historical citizen science abundance data of the six breeding species, as a surrogate for breeding, given the absence of historical breeding data. My aim was to explore the potential for breeding waterbirds to be used as indicators of ecosystem health, particularly in relation to potential changes to the Chobe River as a result of upstream water resource development, including dams and water abstraction. Based on the key drivers of change in this system; river flow and rainfall, which heavily influence the biodiversity including top order predators such as waterbirds which are useful indicator species, I tested the following null hypothesis: there is no relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance, breeding and reproductive success on the Chobe River.

In Chapter 4, I used citizen science data to identify whether there were any long-term declines of waterbird species, and investigated relationships between waterbird abundances and flow, flooding, local rainfall and temperature in the Okavango Delta. I also investigated

relationships between the locations of eight major breeding colonies in the Okavango Delta and their flooding and vegetation patterns, providing information on the drivers of breeding for these colonies and potential implications of the effects of water resource developments in the Okavango River and climate change. As a seasonal floodplain marsh, with river flow and rainfall the key ecosystem drivers, potentially affected by natural and anthropogenic pressures, I tested the following null hypotheses: there is no relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance and there is no decline in waterbird abundance over time in the Okavango Delta.

In Chapter 5, I developed a repeatable, accessible and effective semi-automated method to count aggregations of breeding waterbirds, focusing on one of the colonies in the Okavango Delta. Expense is a common limitation for environmental monitoring and so I used two methods, using mainly open access software, with one method utilising free software. The methods were user friendly and easy to follow, despite the modelling required, with a step by step 'how to' flow diagram, supported by openly shared code and data.

In Chapter 6, I explored the effects of pollution and human waste on the foraging and health of marabou storks feeding at a landfill site, an important consequence of urbanisation in Botswana and other areas in Africa. In particular, I measured concentrations of potentially lethal trace metals in their feathers, conducted stable isotope analyses of their feathers and collected regurgitated waste, exploring possible implications on their populations. Given the value of waterbirds as indicators of not only natural, but also anthropogenic pressures I tested the following null hypothesis: there are no differences in elemental concentrations or stable isotope analyses of marabou stork feathers as distance from landfill sites increases.

Finally in Chapter 7, I reviewed the implications of my research and its contribution to the long-term management of these iconic river systems and their biodiversity. I also further developed the importance and value of using waterbirds as indicators of long-term changes to

freshwater ecosystems and their biodiversity, as well as the importance of understanding the conservation value of these freshwater ecosystems to the biodiversity and human communities of multiple countries. I highlighted areas of future work within Botswana, and reinforce the considerable opportunities to contribute to sustainable management of rivers in Botswana.

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Chapter 2. Quantifying bird diversity at three sites of differing herbivore disturbance

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I led study design, fieldwork, data collection and compilation, analysis and writing.

2.1 Abstract

Large herbivores directly and indirectly influence ecosystem function, positively and negatively affecting diversity of plants and animals, including birds. Such cascading effects are clearly important, particularly given ongoing global declines in large herbivores and many avian communities. We examined relationships between bird diversity (species richness and Shannon-Weiner Index, at a species and functional group level) at three similarly vegetated and flooded sites in northern Botswana. We explored the role that herbivore presence plays in ecosystem functioning considering bird species richness was significantly higher at the site of intermediate presence, followed by the high presence site. At a functional group level, the site of highest presence consistently had the greatest functional group richness. Also, at a functional group level we identified higher species richness and diversity in the two sites where herbivores were present at high levels. This was

particularly pronounced for the avian aquatic carnivores, terrestrial herbivores, and aerial invertivores functional groupings. We explored the role large herbivores may have played in increasing habitat complexity through their browsing and grazing, altering habitat structure, alongside other benefits such as faeces deposition and mutualistic relationships, creating more niches for avian communities. Fencing out large herbivores to reduce their grazing and browsing may therefore reduce bird diversity and, correspondingly, allowing large herbivores to increase in abundance through protected areas may indirectly increase bird diversity, acknowledging over abundance may be detrimental.

2.2 Introduction

Given the current global loss of large herbivores (Ripple et al. 2015), understanding their functional role in ecosystems is critical to tracking long-term ecosystem change and developing effective management strategies. Large herbivores (body mass $\geq 100\text{kg}$) consume and alter vegetation, sometimes increasing (Rutina et al. 2005, Kerley and Landman 2006, Landman and Kerley 2014, Ripple et al. 2015), but also reducing vegetation available to other animals (Landman et al. 2013). They also disperse seeds (Blake et al. 2009), deposit nutrient rich urine and faeces (van der Waal et al. 2011), and decrease predator numbers (Tambling et al. 2013) whilst also providing predators with a food source when they die (Loarie et al. 2013, Clements et al. 2014). Such alterations can cause cascading effects through ecosystems (Owen-Smith 1992), with complex and wide ranging ramifications. In particular, the presence of large herbivores can affect bird community diversity (Ogada et al. 2008, Gregory and van Strien 2010). In Kenya, for example, elephants *Loxodonta africana* thinned the understory through browsing, which consequently decreased akalat abundance (insectivorous tree dwelling birds *Sheppardia sp.*)(Banks et al. 2010). Further, high densities of elephants and giraffe *Giraffa camelopardalis* decreased the diversity of granivorous and insectivorous birds, and when large herbivores were excluded, bird diversity

increased by 30% (Ogada et al. 2008). Large herbivores can have significant impacts on areas near rivers when congregating during migration, particularly in the dry season (Dipotso and Skarpe 2006, Rutina and Moe 2014) as seen in the Okavango Delta where high elephant numbers disrupted and reduced the size of waterbird colonies (Muller 2013). Waterbird breeding colonies are particularly vulnerable because they usually nest close to water, given their breeding cycles are closely tied to flooding regimes (Kingsford and Auld 2005, Desgranges et al. 2006, Arthur et al. 2012, Bino et al. 2014).

Large herbivore effects on ecosystems and human communities are sometimes mitigated by fence exclusion (Hayward and Kerley 2009) and the culling of animals (Gordon et al. 2004). Contrastingly, protected areas can increase large herbivore densities, albeit varying in success (Craigie et al. 2010), with inevitable restrictions on migration and dispersal (Cushman et al. 2010, Naidoo et al. 2012). In Botswana, about 20-30% of the land is considered as protected areas (Index Mundi 2019) and it has possibly the highest density of large herbivores in Africa, including a third of Africa's remaining elephants (Chase et al. 2016, Schlossberg et al. 2019) and high densities of buffalo *Syncerus caffer* (Alexander et al. 2012). Given the country's rich avifauna including nearly 600 bird species (Hancock and Weiersbye 2015), understanding how large herbivores affect avian populations is important, particularly along rivers where large herbivore pressures can be highest (Smit et al. 2007, Ogutu et al. 2014). Further, the many diverse and important ecosystem services provided by birds including pollination and disease control (Şekercioğlu et al. 2004, Şekercioğlu 2006), and their cultural value merits the investigation into the threats to their populations.

We investigated bird diversity in three equally sized survey sites with similar vegetation types, coverage, and flooding regimes, along the Chobe River in northern Botswana. We tested the null hypothesis: there is no difference in riparian bird composition among three sites, differing in herbivore abundance and composition, subjected to temporal changes in

flooding of the Chobe River. Importantly, these three sites had a known differential level of herbivore presence. We relate herbivore presence to the amount of possible environmental disturbance, which we define as processes that temporally disrupt ecosystems, communities or population structures, changing resource availability (Connell 1978). Generally, despite site similarities, we predicted to see differences in species richness and diversity, with both highest at the site with intermediate presence (and therefore disturbance), because intermediate levels of disturbance provide niches for species who prefer minimal and maximum disturbance (Connell 1978, Wilkinson 1999). We predicted waterbird diversity would decrease over time, with decreasing proportions of sites flooded, given their dependence on aquatic habitats. We also predicted that arboreal species would be lowest in diversity at the site with the highest herbivore presence, due to the role of large herbivores in altering canopy cover (Ogada et al. 2008). Finally, oxpecker species were predicted to be most abundant with high herbivore presence, due to their dependency on large herbivores for food (Ndlovu and Combrink 2015).

2.3 Materials and Methods

2.3.1 Study sites

We surveyed avian communities in three equally sized sites (1000m x 500m, separated by at least 500 m, Fig. 2.1), chosen for their similarities in vegetation types, coverage, and flooding regimes. Sites were located on seasonally inundated floodplain along the Chobe River. These sites differed in levels of large herbivore presence, including elephant, buffalo, giraffe, hippopotamus *Hippopotamus amphibius*, zebra *Equus quagga* and greater kudu *Tragelaphus strepsiceros* (Chase 2011, Chase et al. 2015, Chase et al. 2018) (Appendix 2.1). The “Fenced” site, was enclosed in September 2017, and experienced low levels of large herbivore presence, with only the occasional herbivore bypassing the fences giving it a large herbivore density of roughly 0. The “Unfenced” site was an unprotected site experiencing

intermediate herbivore density of 2.2- 4.3 herbivores km⁻², and the “National Park” site had the highest herbivore presence with a density of 5.0-8.8 herbivores km⁻². Herbivore density measures were calculated from 2010, 2014 and 2018 aerial survey data covering our intermediate site (in the Kasane Forest Reserve survey stratum) and our high presence site (covered within the Chobe River survey stratum)(Appendix 2.1)(Chase 2011, Chase et al. 2015, Chase et al. 2018).

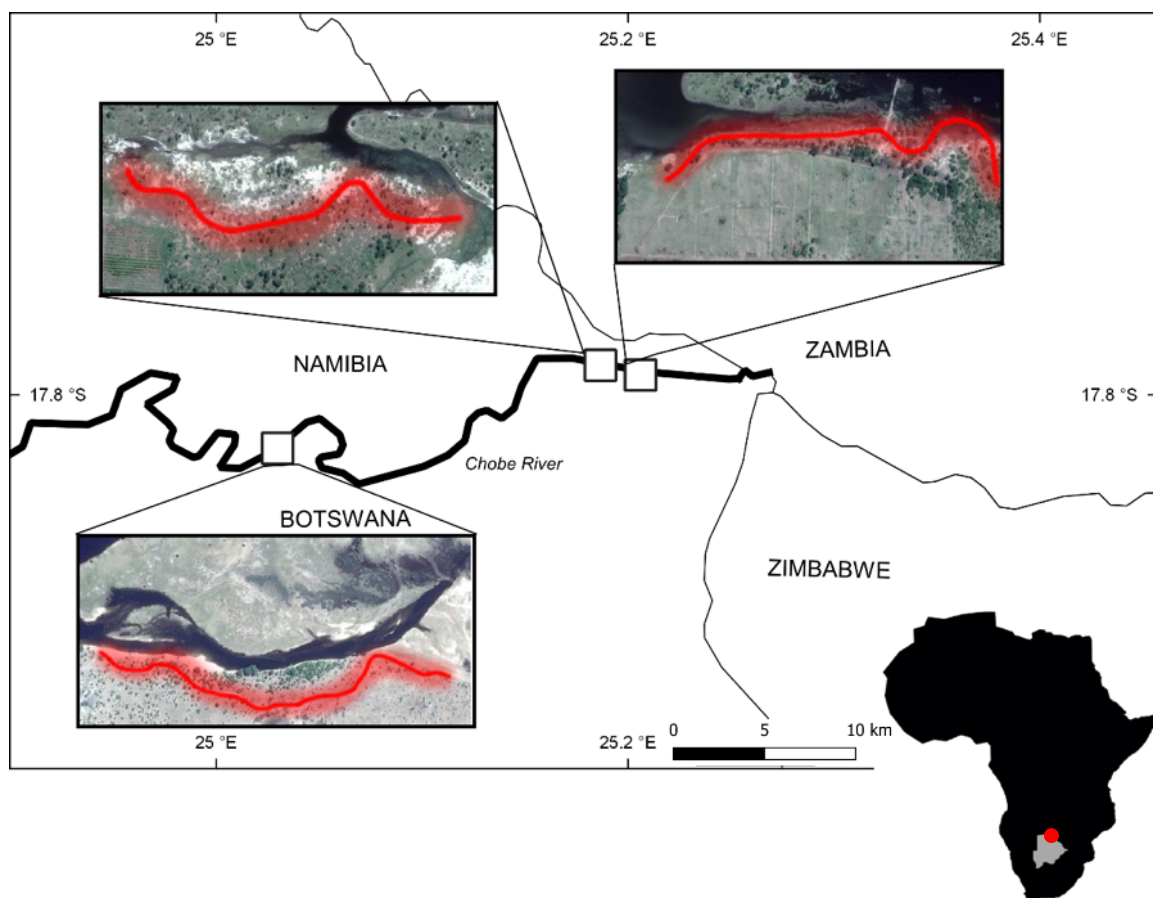


Figure 2.1. Satellite images (Copernicus Sentinel 2018) of our three study sites Fenced (middle), Unfenced (right) and National Park (left, in Chobe National Park), along the Chobe River (north eastern Botswana, red dot), where we surveyed bird diversity, using 1km transect counts (red lines), every week for 10 weeks, 19 June 2018 - 22 August 2018.

2.3.2 Bird surveys

Within each site, we surveyed birds 10 times (weekly over 10 weeks) (Robbins et al. 1989, Hostetler and Knowles-Yanez 2003), 19 June 2018 -22 August 2018, within a 1 km long transect, 30-50m parallel to the river's edge (Fig. 2.1). This distance varied between sites and over time as Chobe River floodwaters receded. Surveys were within two hours of sunrise over 35-45 min for each transect, with the day of the week randomized; we did not survey in inclement weather. Observations were from within the vehicle ($<5 \text{ kmhr}^{-1}$), due to the presence of dangerous animals, using the double observer method (Nichols et al. 2000), where one observer stood through the sunroof, allowing for a wide field of vision, and the second acted as driver and recorder, identifying and counting all birds seen and/or heard up to 50m on each side of the transect. Birds observed as fly-overs were excluded from analyses (Hostler and Martin 2006). Bird nomenclature followed the International Ornithological Congress World Bird List (Gill and Donsker 2019), with functional/dietary guilds following Sundstrom et al. (2012)(Appendix 2.2).

2.3.3 Environmental variables

To track effects of receding flood levels and test for differences in the normalised difference vegetation index (NDVI) among sites, we used Google Earth Engine (Gorelick et al. 2017) and images from the Sentinel-2 satellite (Copernicus Sentinel data 2018). We used the threshold function (Wolski et al. 2017) to calculate percent inundation, filling data gaps with Landsat-8 images (Inman and Lyons 2020) where Sentinel images were of low quality, or did not exist for survey dates (often due to cloud cover, $<10\%$ of data).

The sites (Fenced, Unfenced and Chobe National Park) had similar dominant vegetation types, including Woolly Caper Bush *Capparis tomentosa*, Large Fever-berry Croton *Croton megalobotrys*, Blackthorn Acacia *Senegalia mellifera* and Wild Sage *Pechuel-loeschea leubnitziae*, all seasonally inundated by the Chobe River (peak flows in April-May). To

explore further potential differences in vegetation among sites, we extracted NDVI values at 10m resolution pixels, across sites for images available in September 2018, coinciding with our surveys. NDVI values were classified; values approaching < 0.1 water or barren areas (free of vegetation), and values > 0.1 grass, shrubland or forest (Sentinel Hub 2018). These groups were separated into relative percent coverage by summing the shrub/grassland and forest values, divided by the total pixel number in the images. Vegetation indices were similar during 2018 surveys, with sites dominated by shrubs and grasses across the three sites: the Fenced was 51.21% vegetated (± 0.13), with 2.40% forest; Unfenced was 46.70% vegetated (± 0.50), with 4.12% classified as forest and finally; Chobe National Park was 50.56% vegetated (± 0.24), with 1.33% forest. Given the limited differences in vegetation across the three sites, NDVI was not used in the herbivore presence or flood modelling. We also collected data on three environmental variables during each survey: wind speed, temperature and cloud cover. Plots of environmental variables against avian species richness and diversity highlighted potential relationships with cloud cover and wind speed (Appendix 2.3). However, only wind speed was important in explaining avian species richness and diversity and was included in subsequent modelling, based on the Akaike Information Criterion of the models.

2.3.4 Statistical analyses

We first investigated differences in broad biodiversity metrics for the avian community (i.e., species richness and Shannon-Wiener Diversity Index, referred hereafter as ‘diversity’) among sites (Magurran 2013, Morris et al. 2014). We then analysed community-level differences among sites, using non-metric multidimensional scaling (NMDS), with Bray-Curtis similarity of abundance-weighted matrices. Data were square-root transformed and standardized, according to the Wisconsin double standardization method to satisfy assumptions of normality and homogeneity of variance (Oksanen et al. 2013). We then tested

for statistical differences in community structure among sites using an analysis of similarities (ANOSIM), followed by a similarity percentages procedure (SIMPER) to investigate which species contributed most to differentiation among sites. We used the ‘adonis’ and ‘simper’ functions for analyses, respectively, from the vegan package (Oksanen et al. 2013).

We investigated species-level metrics, with species richness and the Shannon-Wiener Index, as the response variables, using generalized least square models, specifically the ‘glms’ function from the nlme package (Pinheiro et al. 2014). We included temporal autocorrelation in the modelling (week of survey), given likely non-independence of surveys over time; exploratory data analysis revealed some seasonal changes in the bird diversity over our survey period. Wind speed was also included in the models as a covariate. The parametric predictors were changes in percent inundation and site.

Each bird species was then allocated to a functional group (Appendix 2.2), to explore the many diverse ecological functions birds play in the environment (Şekercioğlu 2006). We followed the approach of Sundstrom et al. (2012) incorporating both dietary preference and foraging strategy into the classification. Adult dietary and foraging information used to classify species to functional group were taken from Roberts bird guide 7th edition multimedia version (Chittenden et al. 2007). Where species fell between two groupings, we sought available advice based on location specific dietary and foraging observations (pers comms. Francey, L. 2018). To explore community differences at a functional group level (Sundstrom et al. 2012), we first tested for differences in the number of functional bird groups among sites. We then tested for differences in species richness and Shannon-Wiener Index, within each functional group among sites, using generalized least square models with temporal autocorrelation, with percent inundation and site as predictor variables. An individual model was also run for within each functional bird group over time, to test for changes in the species richness and Shannon-Wiener diversity of that functional group, in

relation to percent inundation and site. The terrestrial carnivores bird functional group was removed from the Shannon-Wiener Index modelling, given White-browed Coucal was the only species.

All analyses were done in the R computing environment (R Core Team 2014), relying on the tidyverse workflow (Wickham 2017) and ggplot2 package (Wickham 2016). Significance of statistical tests was concluded at $\alpha < 0.05$.

2.4 Results

A total of 128 bird species were identified across the three sites (Appendix 2.2), with the highest total species richness in Unfenced (intermediate presence, 96), followed by the National Park (high presence, 78) and Fenced (low presence, 71)(Appendix 2.4). Average species richness differed significantly among sites ($P = 0.02$, $F_{26} = 4.91$, Table 2.1), highest in Unfenced (33.80 ± 6.32), followed by National Park (29.05 ± 4.78) and finally Fenced (23.20 ± 3.93). Total Shannon-Wiener diversity did not differ significantly among sites ($P = 0.07$, $F_{26} = 2.99$, Table 2.1, Appendix 2.4).

Table 2.1. Summary of the species' richness (total and weekly), and Shannon-Wiener diversity for the avian community at each of three sites in northern Botswana (mean $\pm$ SD), surveyed weekly (19 June 2018 - 22 August 2018) and varying in large herbivore presence (low, intermediate and high).

Site	Total Species Richness	Weekly Species Richness	Total Shannon- Wiener Index	Weekly Shannon- Wiener Index
Fenced (low)	71	23.20 (± 3.93)	3.02	2.36 (± 0.25)
Unfenced (intermediate)	96	33.80 (± 6.32)	2.59	2.18 (± 0.25)
National Park (high)	78	29.05 (± 4.78)	2.58	2.07 (± 0.25)

There was a significant difference in avian community composition among the three sites, varying in large herbivore presence, with relatively little overlap in the non-metric dimensional plot ($P= 0.001$, $F_{27}=7.2$, Fig. 2.2). There was a 74% difference between the National Park and the Fenced, the sites with high and low herbivore presence; a 69% difference between Unfenced and Fenced (intermediate and low presence) and; a 51% difference between the National Park and Unfenced (high and intermediate). Differences among sites were mostly explained by variation in the presence and abundance of Ring-necked Doves, accounting for 27-29% of community differences between the low large herbivore presence site Fenced (where they were considerably less abundant) and the two other sites (Unfenced, and National Park). Crowned Lapwings and Red-billed Quelea also explained community level differences among sites (Appendix 2.5), most often observed in sites with herbivore presence. We therefore rejected the null hypothesis in support of the alternative hypothesis: that bird composition differed between the three sites.

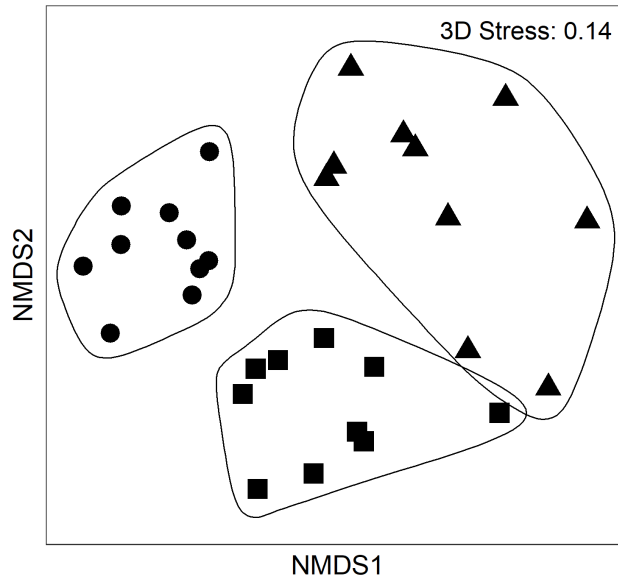


Figure 2.2. Non-metric multidimensional plot showing separation of avian communities among three sites in Botswana varying in large herbivore presence, Fenced (low presence, triangles), Unfenced (intermediate presence, squares) and National Park (high presence, circles) (see Fig. 2.1), where each point represents a unique weekly survey ($N=10$ for each location, 19 June 2018 – 22 August 2018).

In total 15 avian functional groups occurred, and while each site had 14 avian functional groups, the weekly number differed significantly among sites ($F_{26}=3.47$, $P=0.04$, Appendix 2.4); the National Park regularly had the highest number of functional groups, followed by Unfenced and then Fenced (high, intermediate and then low). Within avian functional groups, avian species' richness differed significantly among sites in 11 out of the 15 avian functional groups (Fig. 2.3a). 73% of functional groups were significantly richer in the National Park with aquatic carnivores the richest group ($F_{26}=2.13$, $P=0.04$). Of those that were significantly different in Fenced, 3 out of the 4 groups were significantly less rich (Table 2.2). The only functional group richest at Fenced was the aerial carnivores ($F_{26}=2.25$, $P=0.03$). Average species' richness over the 10 weeks was highest in aquatic carnivores and terrestrial herbivores (5.9 species per group).

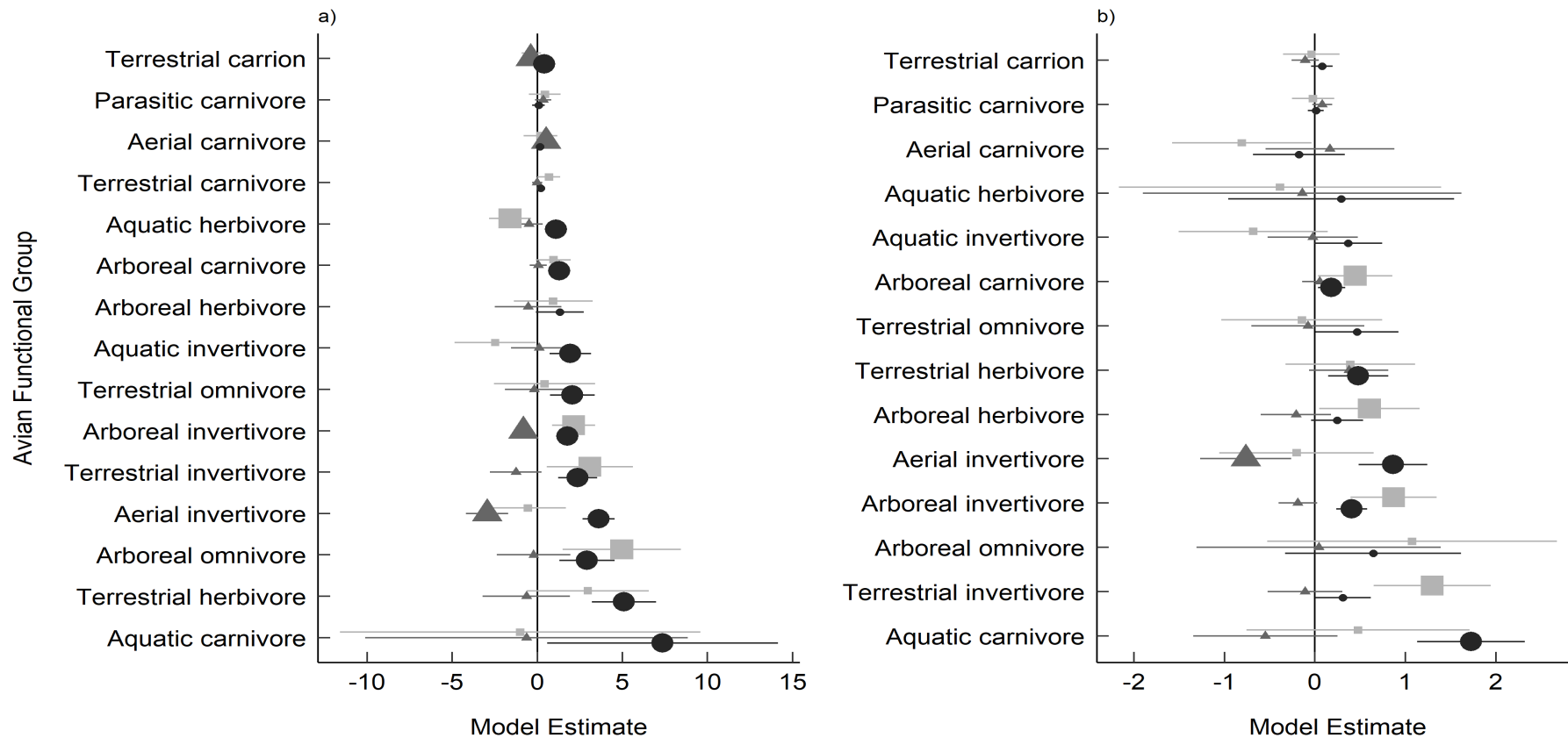


Figure 2.3. Modelled estimates of avian functional groups amongst three sites varying in large herbivore presence (Fenced (low, mid grey triangles), Unfenced (intermediate, light grey squares) and National Park (high, black circles)) measured in species richness (a) and Shannon-Wiener diversity Index (b) in northern Botswana, surveyed weekly (19 June 2018 - 22 August 2018). Statistically significant and insignificant differences marked respectively by large and small symbols, with lines showing the confidence intervals. Symbols <0 and >0 on the x-axis respectively represent negative and positive differences amongst sites.

Table 2.2. Summary of modelled estimates for significant positive and negative responses by avian functional groups for avian species' richness and the Shannon-Wiener Diversity index at three sites varying in large herbivore presence (low, intermediate and high).

Site	Response	Functional Group ^a	Estimate	Standard Error	F Statistic	P Value		
Fenced (low)	Diversity	Aerial invertivore	-0.77	0.26	-2.98	0.01		
	Richness	Aerial carnivore	0.51	0.23	2.25	0.03		
		Aerial invertivore	-2.96	0.63	-4.67	<0.001		
		Arboreal invertivore	-0.82	0.29	-2.79	0.01		
		Terrestrial carrion	-0.41	0.14	-2.88	0.01		
Unfenced (intermediate)	Diversity	Arboreal carnivore	0.45	0.21	2.12	0.04		
		Arboreal herbivore	0.60	0.28	2.13	0.04		
		Arboreal invertivore	0.87	0.24	3.58	0.001		
		Terrestrial invertivore	1.30	0.33	3.93	<0.001		
	Richness	Aquatic herbivore	-1.60	0.63	-2.55	0.02		
		Arboreal invertivore	2.14	0.65	3.30	0.003		
		Arboreal omnivore	4.96	1.77	2.80	0.01		
		Terrestrial invertivore	3.09	1.29	2.40	0.02		
		National Park (high)	Diversity	Aerial invertivore	0.86	0.19	4.44	<0.001
				Aquatic carnivore	1.73	0.30	5.69	<0.001
				Arboreal carnivore	0.18	0.08	2.39	0.02
				Arboreal invertivore	0.41	0.09	4.69	<0.001
Richness	Terrestrial herbivore		0.48	0.17	2.84	0.01		
	Aerial invertivore		3.60	0.49	7.42	<0.001		
	Aquatic carnivore		7.37	3.46	2.13	0.04		
	Aquatic herbivore		1.10	0.31	3.54	0.001		
		Aquatic invertivore	1.95	0.62	3.14	0.004		
		Arboreal carnivore	1.30	0.20	6.44	<0.001		
		Arboreal invertivore	1.77	0.23	7.56	<0.001		
		Arboreal omnivore	2.93	0.83	3.54	0.001		
		Terrestrial carrion	0.41	0.11	3.70	0.001		
		Terrestrial herbivore	5.09	0.96	5.29	<0.001		
		Terrestrial invertivore	2.36	0.59	4.03	<0.001		
		Terrestrial omnivore	2.07	0.67	3.09	0.01		

^aSee Appendix 2.2 for species included.

Also, the Shannon-Wiener Index differed within functional groups among sites for seven avian functional groups (Fig. 2.3b). Six of 14 functional avian groups were most diverse in the National Park or Unfenced (Table 2.2). For the one group showing a significant difference in Fenced, it was significantly lower in diversity. National Park was the only site

with terrestrial carrion feeders (vultures, Appendix 2.2). The most diverse functional groups were the aquatic carnivores (1.46) and arboreal omnivores (1.25).

At Fenced, the functional groups with the highest species' richness and the most diverse were the aquatic carnivores (5, 0.90) and terrestrial herbivores (4.6, 0.91). At Unfenced, the most species' rich group was the terrestrial herbivores (5.9), followed by the arboreal omnivores (4.8). At National Park, the functional groups with the highest species' richness were the aquatic carnivores (5.9) followed by the terrestrial herbivores (4.8).

2.4.1 Flooding responses

At a species level, neither bird species' richness nor the Shannon-Wiener index differed significantly, with changes in the proportion of each site flooded ($F_{27}=2.6$, $P>0.05$). At a functional group level, three groups responded significantly to flooding, when modelling for species' richness; arboreal invertivores showed the strongest response ($F_{27}=4.77$, $P<0.001$, Fig. 2.4a), followed by terrestrial omnivores ($F_{27}=2.08$, $P=0.05$) and finally terrestrial carnivores ($F_{27}=2.62$, $P=0.01$), with species' richness decreasing with less relative area flooded. Diversity within two functional groups decreased significantly with decreased percentage of site flooded (Fig. 2.4b); terrestrial omnivores ($F_{27}=2.31$, $P=0.03$) and arboreal invertivores ($F_{27}=5.28$, $P<0.001$).

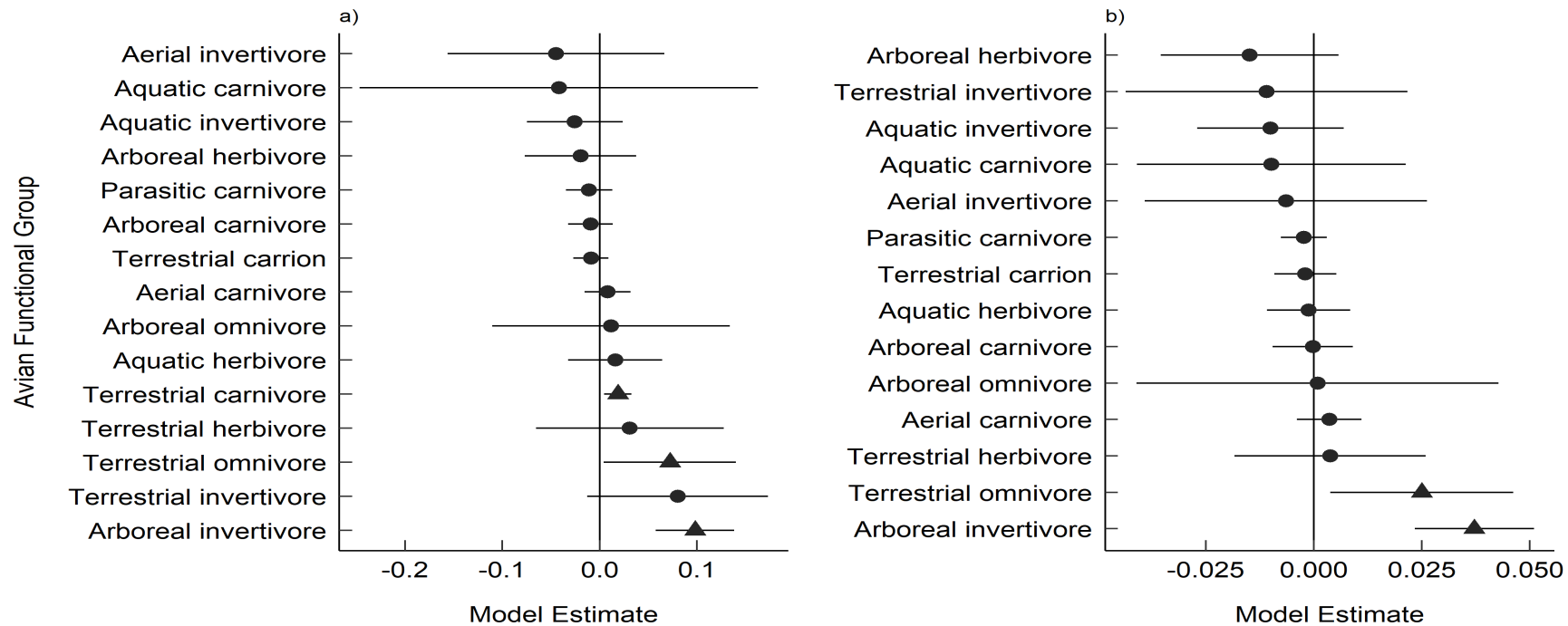


Figure 2.4. Modelled estimates of avian functional groups to changes in flooding (percent inundation) measured in species' richness (a) and Shannon-Wiener diversity Index (b), across the three sites varying presence of large herbivores (Fenced (low), Unfenced (intermediate) and National Park (high)) in northern Botswana, surveyed weekly (19 June 2018 - 22 August 2018). Statistically significant and insignificant responses marked respectively by triangles and circles, with lines showing confidence intervals. Symbols <0 and >0 on the x-axis respectively represent negative and positive responses to inundation.

2.5 Discussion

There is increasing evidence that some animals are functionally important for ecosystems, directly or indirectly driving patterns of diversity and abundance (Sundstrom et al. 2012, Mouillot et al. 2013, Baker et al. 2016, Rolo et al. 2017). The sites of intermediate or high levels of herbivore presence in our study in Botswana were consistently associated with higher avian richness and diversity at species and functional group levels (Fig. 2.3). This is supported by other evidence that large African herbivores are functional drivers of ecosystems (Ogada et al. 2008, Banks et al. 2010), including within Botswana (Herremans 1995).

The higher diversity and richness of 11 avian functional groups at sites with medium or high levels of herbivore presence were likely due to a mix of direct effects and indirect benefits provided by large herbivores. These include variation in vegetation condition, structure, dispersal and germination (Herremans 1995, Campos-Arceiz and Blake 2011, Baker et al. 2016), faeces and urine deposition (van der Waal et al. 2011), and the creation of opportunities for other species including frogs (Nasseri et al. 2011), small herbivorous mammals (Valeix et al. 2011) and birds (Banks et al. 2010), increasing food availability for the avian community.

Avian aquatic carnivores, parasitic carnivores, and terrestrial carrion functional groups likely directly benefitted (Fig. 2.3, Appendix 2.2). The Red and Yellow-billed Oxpeckers, which feed mutualistically on parasites of large herbivores (Ndlovu and Combrink 2015), occurred where there was high herbivore presence. Also, the carrion feeders (e.g. White-backed Vultures) only occurred where there was high herbivore presence, reflecting a common pattern in Africa, where populations are generally higher in protected areas than outside, given the presence of large herbivores and the relative availability of carcasses (Rushworth et al. 2007, Murn et al. 2013). As raptors are more mobile than their non-flying terrestrial

predator counterparts (eg. lions), they can respond faster to population changes in their herbivore prey (Şekercioğlu 2006). It is possible changes in raptor populations occurred between sites, despite the short time frame of exclusion for the Fenced site. Further, large herbivores leave abundant seeds in their dung for avian terrestrial herbivores, such as spurfowl and francolins (Maclean et al. 2011), which may also explain the high abundance of Ring-necked Doves (Campos-Arceiz and Blake 2011, Maclean et al. 2011). Finally, avian aerial invertivores may have directly benefitted from large herbivores which attracted insects, providing an abundant food supply (Møller 1983, Pryke et al. 2016).

There were likely a range of indirect benefits from large herbivore presence, related to vegetation, and we would expect to see differences between sites increase the longer large herbivores are excluded from Fenced. Large herbivores create space in shrub communities, remove grass biomass, and create open patches and areas of bare ground (Onyeausi 1989, Waldram et al. 2008, Kohi 2013), which likely increased feeding opportunities for the terrestrial invertivores, herbivores, and omnivores. This probably favoured babblers (terrestrial omnivores, Appendix 2.2) which forage in and around leaf litter, while the bare ground patches probably favoured the foraging of waxbills and finches in open areas (terrestrial herbivores, Appendix 2.2)(Maclean et al. 2011). Crowned Lapwings, another major driver of community differences (terrestrial invertivores) also prefer open areas, where the grass is kept short, for both foraging and breeding (Maclean et al. 2011). Further, alteration of canopy heights and increased habitat complexity caused by large herbivores (Kohi 2013), provides habitat for a range of nesting birds, lizards and insects (Whitmore et al. 2002, Tews et al. 2004), the prey for arboreal carnivores, invertivores, omnivores and aerial invertivores (such as the weavers, rollers, bee-eaters and martins, Appendix 2.2). Aquatic species such as aquatic carnivores and invertivores may benefit from the stirring of sediment by herbivores disturbing fish, insects and freshwater molluscs (Dinsmore 1973, Wolanski and

Gereta 1999, Bakker et al. 2016), and the passive transport of freshwater invertebrates (Vanschoenwinkel et al. 2011) assisting the foraging of waterbirds such as African spoonbills and African openbills (Maclean et al. 2011). The positive alteration of structural heterogeneity of aquatic vegetation due to grazing and foraging behaviours of hippos (McCarthy et al. 1998, Kanga et al. 2013) likely affected aquatic bird diversity, given dependencies between waterbirds and vegetation (Froneman et al. 2001, Zhou et al. 2020). Hippo grazing may have also attracted other ungulate herbivores (Kanga et al. 2013), compounding the effects of their presence or removal. It is these interactions between many herbivore species of different sizes and feeding and foraging behaviours that are likely contributing to the relationships with bird diversity. We think it unlikely that cattle monocultures would therefore have the same effects on bird diversity, and although we did not test this, livestock grazing has been found to reduce vegetation structural heterogeneity and repels other herbivores (Kanga et al. 2013), limiting the positive indirect effects due to vegetation change, but these effects are highly density dependant (Young et al. 2018). The effects of flooding were not reflected in changes in aquatic functional groups as predicted (Fig. 2.4). Contrastingly, the terrestrial carnivore, terrestrial omnivore and arboreal invertivore groups increased in richness with more flooded area, which could have reflected increased insect populations or seed germination with the flood (Linhoss et al. 2012, Mackay et al. 2012, Pricope 2013).

Our ‘high’ levels of herbivore presence were not likely to exceed natural or historical densities (Chase et al. 2015, Chase et al. 2018, Schlossberg et al. 2019), and although the aerial survey data supports the local knowledge of herbivore presence at the three sites (Francey 2018), we recognise further work should look to elaborate on these patterns with fine-scale herbivore measurements. We acknowledge that we only included three sites, one corresponding to the relative level of presence, but highlighted that sites had similar

vegetation type and coverage, to limit such inherent differences affecting modelling. Clearly, our use of the NDVI index was not sufficient to explore differences in vegetation structure or fine-scale composition. Other factors may also contribute to the differences in bird diversity at the three sites, and future work should look to further replicate these results across a greater number of sites and longer timeframe to capture temporal, climatic and spatial change. One such factor is fire history, a common disturbance factor in African ecosystems (Beckage et al. 2009), which may have affected structure and composition of vegetation, and termitaria which influence bird diversity (Joseph et al. 2011). We do not aim to imply causality between herbivore presence and bird diversity, but rather consider the role herbivores may play in affecting bird diversity when other ecological factors are similar. Importantly, the 10-week time frame of this study is only a small insight into the long-term functioning of these sites. Herbivore exclusion from the Fenced site was only since 2017 and was probably not sufficiently long enough to change woody vegetation, although deposition of faeces, destruction of vegetation and presence of herbivores for parasitic bird species were probably important changes that would occur within this time frame. There may also be differences in bird diversity with season, such as populations of insectivorous birds which vary temporally based on prey availability (Şekercioğlu 2006). One external factor to be considered is human presence, which could also have affected bird species' richness and diversity. However, considering the wealth of information describing the negative effects of human disturbance on bird diversity (Lepczyk et al. 2008, Kang et al. 2015, Vollstädt et al. 2017), we think it unlikely human presence (both on foot and in vehicles) is the major driving factor controlling diversity at these three sites as we would expect to see the opposite pattern; reduced diversity in the site with the most traffic, the National Park. Herbivores have been shown to play an important functional role directly and indirectly altering biotic communities (Waldram et al. 2008, Prugh and Brashares 2012, Parsons et al.

2013, Howland et al. 2014). The high avian diversity in the sites with high herbivore presence in our study probably reflected these dependencies. Declining large herbivore populations through fencing exclusion, habitat loss and degradation and illegal harvesting will likely detrimentally affect species richness or diversity of different bird functional groups. Therefore, future efforts in the conservation of large herbivores and their designated protected areas may also directly contribute to the conservation of bird populations across Africa, particularly if we move away from a single species approach, and implement connected ecosystem management (Schultz et al. 2015).

2.6 Conclusions

Avian species richness was higher in sites with intermediate to high presence of large herbivores, likely due to both the direct effects of herbivores on birds (e.g. a food source to carrion feeders, dung deposition) and indirect effects (altered vegetation structure), however we could not statistically test this relationship. Both species richness and diversity were higher in the sites of intermediate to high herbivore presence at a functional group level, particularly for the avian aquatic carnivores, terrestrial herbivores and aerial invertivores. Future conservation efforts should consider the potential importance of the relationship between birds and large herbivores, with herbivore protected areas therefore likely also benefiting avian diversity.

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2.9 Appendices

Appendix 2.1. Large herbivore aerial survey estimates within the Kasane Forest Reserve survey stratum (encompassing “Unfenced” the intermediate presence site) and within the Chobe River survey stratum (encompassing “National Park” the high presence site), showing the estimated number of herbivores in the area extrapolated from the number of animals seen (Chase 2011, Chase et al. 2015, Chase et al. 2018), with densities given in herbivores km⁻².

Common name	Species	Estimated Number of Herbivores					
		Kasane Forest Reserve			Chobe River		
		July-Oct 2018	July- Oct 2014	Sept- Nov 2010	July- Oct 2018	July-Oct 2014	Sept- Nov 2010
Buffalo	<i>Syncerus caffer</i>	0	4	447	938	2164	2481
Cow	<i>Bos taurus</i>	216	300	0	0	0	0
Eland	<i>Taurotragus oryx</i>	0	0	109	16	27	297
Elephant	<i>Loxodonta africana</i>	607	283	1471	2556	3221	5283
Giraffe	<i>Giraffa camelopardalis</i>	66	29	41	117	104	144
Hippopotamus	<i>Hippopotamus amphibius</i>	0	0	0	197	224	176
Kudu	<i>Tragelaphus strepsiceros</i>	24	0	0	101	126	111
Roan	<i>Hippotragus equinus</i>	0	0	5	69	55	83
Sable	<i>Hippotragus niger</i>	6	695	489	218	574	547
Tsessebe	<i>Damaliscus lunatus</i>	0	0	26	21	22	32
Waterbuck	<i>Kobus ellipsiprymnus</i>	0	0	0	117	148	0
Wildebeest	<i>Connochaetes taurinus</i>	0	0	0	0	0	51
Zebra	<i>Equus quagga</i>	24	12	21	1715	1717	2472
Total		943	1323	2609	6065	8382	11677
Stratum Area (km ²)		423	470	600	1201	1201	1320
Density (Herbivores km ⁻²)		2.2	3.1	4.3	5	7	8.8

Appendix 2.2. All bird species detected on surveys, their scientific name and functional group, with the number of observations for each species, mean count $\pm$ SD, detected across the three sites differing in large herbivore presence; Fenced (low), Unfenced (intermediate) and National Park (high).

Common Name	Species	Functional Group	Site		
			National Park	Fenced	Unfenced
African Darter	<i>Anhinga rufa</i>	Aquatic carnivore	1 (2)	4 (4 $\pm$ 5.35)	4 (3.25 $\pm$ 2.06)
African Fish Eagle	<i>Haliaeetus vocifer</i>	Aquatic carnivore	5 (1.2 $\pm$ 0.45)	6 (1.33 $\pm$ 0.52)	3 (1 $\pm$ 0)
African Golden Oriole	<i>Oriolus auratus</i>	Arboreal omnivore	-	-	1 (1)
African Grey Hornbill	<i>Tockus nasutus</i>	Arboreal omnivore	-	-	1 (1)
African Hoopoe	<i>Upupa africana</i>	Terrestrial carnivore	-	-	1 (2)
African Jacana	<i>Actophilornis africanus</i>	Aquatic invertivore	3 (2 $\pm$ 0)	3 (2 $\pm$ 1)	-
African Marsh Harrier	<i>Circus ranivorus</i>	Aerial carnivore	1 (1)	-	1 (1)
African Mourning Dove	<i>Streptopelia decipiens</i>	Terrestrial herbivore	-	-	1 (1)
African Openbill	<i>Anastomus lamelligerus</i>	Aquatic invertivore	2 (4 $\pm$ 4.24)	-	-
African Palm Swift	<i>Cypsiurus parvus</i>	Aerial invertivore	-	1 (1)	-
African Pied Wagtail	<i>Motacilla aguimp</i>	Terrestrial invertivore	2 (1 $\pm$ 0)	-	2 (1.5 $\pm$ 0.71)
African Sacred Ibis	<i>Threskiornis aethiopicus</i>	Aquatic carnivore	3 (1.33 $\pm$ 0.58)	4 (26.75 $\pm$ 28.78)	2 (2 $\pm$ 1.41)
African Spoonbill	<i>Platalea alba</i>	Aquatic carnivore	1 (2)	2 (3 $\pm$ 1.41)	1 (2)
Arrow-marked Babbler	<i>Turdoides jardineii</i>	Terrestrial omnivore	2 (3 $\pm$ 0)	1 (2)	2 (1.5 $\pm$ 0.71)
Banded Martin	<i>Riparia cincta</i>	Aerial invertivore	9 (5.22 $\pm$ 4.06)	-	1 (2)
Black-backed Puffback	<i>Dryoscopus cubla</i>	Arboreal invertivore	1 (1)	-	7 (1.71 $\pm$ 1.11)
Black-crowned Tchagra	<i>Tchagra senegalus</i>	Terrestrial invertivore	-	-	1 (1)
Black-shouldered Kite	<i>Elanus caeruleus</i>	Aerial carnivore	-	1 (1)	4 (1 $\pm$ 0)
Black-throated Canary	<i>Crithagra atrogularis</i>	Arboreal herbivore	1 (26)	1 (3)	2 (3.5 $\pm$ 0.71)

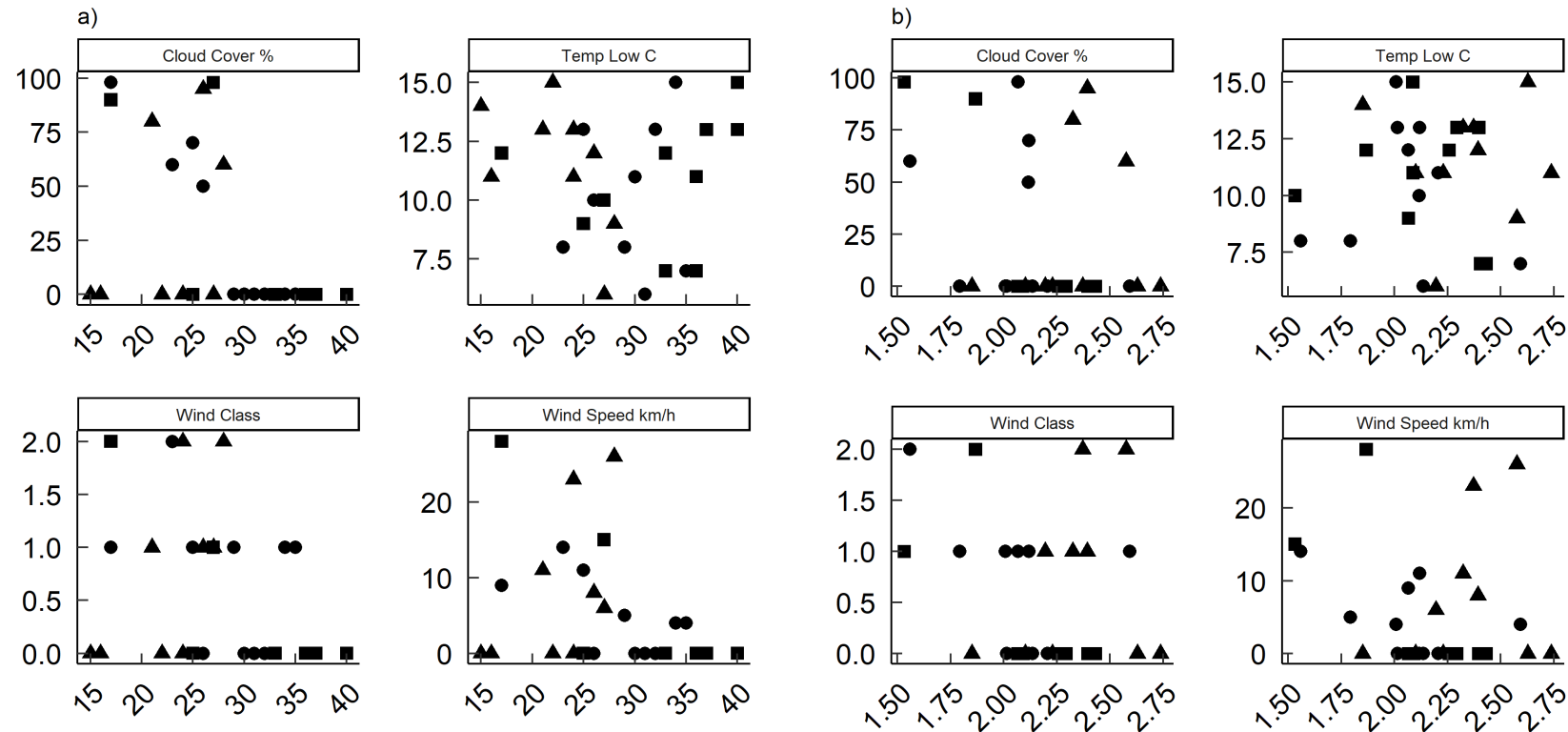
Black-winged Stilt	<i>Himantopus himantopus</i>	Aquatic invertivore	2 (3±1.41)	3 (3±2.65)	1 (3)
Black Heron	<i>Egretta ardesiaca</i>	Aquatic carnivore	-	1 (1)	-
Blacksmith Lapwing	<i>Vanellus armatus</i>	Aquatic invertivore	12 (6±4.16)	22 (5.45±3.66)	16 (3.44±2.19)
Blue Waxbill	<i>Uraeginthus angolensis</i>	Terrestrial herbivore	10 (13.8±15.52)	11 (13.09±19.77)	14 (22.43±20.71)
Bradfield's Hornbill	<i>Tockus bradfieldi</i>	Terrestrial omnivore	2 (2±1.41)	-	-
Brown-crowned Tchagra	<i>Tchagra australis</i>	Terrestrial invertivore	-	-	3 (1.33±0.58)
Brown-hooded Kingfisher	<i>Halcyon albiventris</i>	Arboreal invertivore	1 (1)	-	-
Brown-throated Martin	<i>Riparia paludicola</i>	Aerial invertivore	5 (23.2±28.31)	-	-
Burchell's Starling	<i>Lamprotornis australis</i>	Terrestrial omnivore	-	4 (2.25±1.26)	2 (1±0)
Burnt-necked Eremomela	<i>Eremomela usticolis</i>	Arboreal invertivore	-	-	1 (1)
Cape Turtle Dove	<i>Streptopelia capicola</i>	Terrestrial herbivore	30 (40.27±24.03)	30 (10.47±10.42)	33 (36.79±30.33)
Capped Wheatear	<i>Oenanthe pileata</i>	Terrestrial invertivore	1 (1)	-	-
Common Sandpiper	<i>Actitis hypoleucos</i>	Aquatic invertivore	-	-	1 (1)
Common Waxbill	<i>Estrilda astrild</i>	Terrestrial herbivore	-	-	1 (2)
Coppery-tailed Coucal	<i>Centropus cupreicaudus</i>	Arboreal carnivore	-	4 (1.75±1.5)	3 (1±0)
Crested Francolin	<i>Dendroperdix sephaena</i>	Terrestrial herbivore	1 (2)	-	1 (1)
Crowned Lapwing	<i>Vanellus coronatus</i>	Terrestrial invertivore	17 (15.88±19.43)	2 (3±0)	6 (1.33±0.52)
Dark-capped Bulbul	<i>Pycnonotus tricolor</i>	Arboreal omnivore	5 (2±1.22)	2 (3±1.41)	4 (1.75±0.96)
Egyptian Goose	<i>Alopochen aegyptiaca</i>	Aquatic herbivore	12 (6.08±10.49)	3 (4.33±3.51)	2 (3.5±0.71)
Emerald-spotted Wood Dove	<i>Turtur chalcospilos</i>	Terrestrial herbivore	2 (1.5±0.71)	2 (1±0)	5 (1.8±0.84)
Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	Aerial invertivore	10 (2.3±1.06)	5 (1.4±0.89)	11 (2.09±1.45)
Gabar Goshawk	<i>Micronisus gabar</i>	Aerial carnivore	1 (1)	1 (1)	1 (1)
Giant Kingfisher	<i>Megaceryle maxima</i>	Aquatic carnivore	-	-	1 (1)

Golden-breasted Bunting	<i>Emberiza flaviventris</i>	Terrestrial herbivore	-	-	1 (1)
Great Egret	<i>Ardea alba</i>	Aquatic carnivore	7 (1.86±1.21)	-	4 (1±0)
Greater Blue-eared Starling	<i>Lamprotornis mevesii</i>	Arboreal omnivore	3 (1±0)	2 (1.5±0.71)	4 (2±0.82)
Greater Striped Swallow	<i>Cecropis cucullata</i>	Aerial invertivore	1 (1)	-	-
Green-backed Heron	<i>Butorides striata</i>	Aquatic carnivore	-	-	1 (1)
Green-winged Pytilia	<i>Pytilia melba</i>	Terrestrial herbivore	6 (1.17±0.41)	3 (1.33±0.58)	4 (3.5±4.36)
Green Wood-hoopoe	<i>Phoeniculus purpureus</i>	Arboreal omnivore	-	-	3 (2.67±1.15)
Grey-backed Camaroptera	<i>Camaroptera brevipdata</i>	Arboreal invertivore	9 (1.67±0.71)	5 (2±1.41)	9 (3.56±2.74)
Grey-headed Gull	<i>Chroicocephalus cirrocephalus</i>	Aquatic carnivore	5 (2.4±2.07)	1 (1)	3 (2.33±1.53)
Grey-rumped Swallow	<i>Pseudhirundo griseopyga</i>	Aerial invertivore	8 (8.5±6.8)	-	4 (7±5.72)
Grey Go-away-bird	<i>Corythaixoides concolor</i>	Arboreal herbivore	5 (2.2±1.79)	10 (4.4±2.76)	5 (4.6±3.29)
Grey Heron	<i>Ardea cinerea</i>	Aquatic carnivore	6 (1.67±0.82)	3 (2.67±2.08)	5 (1±0)
Hadedda Ibis	<i>Bostrychia hagedash</i>	Aquatic invertivore	-	1 (2)	1 (3)
Hamerkop	<i>Scopus umbretta</i>	Aquatic carnivore	3 (1.33±0.58)	2 (2.5±2.12)	-
Hartlaub's Babbler	<i>Turdoides hartlaubii</i>	Terrestrial omnivore	-	2 (3.5±0.71)	3 (1±0)
Helmeted Guinea fowl	<i>Numida meleagris</i>	Terrestrial omnivore	2 (12±15.56)	-	-
Jameson's Firefinch	<i>Lagonosticta rhodopareia</i>	Terrestrial herbivore	1 (1)	-	-
Kalahari Scrub Robin	<i>Erythropygia paena</i>	Terrestrial invertivore	-	-	2 (1±0)
Kori Bustard	<i>Ardeotis kori</i>	Terrestrial omnivore	3 (2±0)	-	-
Kurrichane Thrush	<i>Turdus libonyanus</i>	Terrestrial invertivore	2 (1±0)	-	-
Laughing Dove	<i>Spilopelia senegalensis</i>	Terrestrial herbivore	5 (1.4±0.55)	5 (1.4±0.89)	9 (1.33±0.5)
Lesser Masked Weaver	<i>Ploceus intermedius</i>	Arboreal omnivore	3 (8.67±12.42)	2 (9.5±0.71)	13 (8.23±8.02)
Lesser Striped Swallow	<i>Cecropis senegalensis</i>	Aerial invertivore	-	-	1 (2)
Lilac Breasted Roller	<i>Coracias caudatus</i>	Arboreal carnivore	14 (1.79±0.97)	10 (1.5±0.71)	10 (1.7±0.95)
Little Bee-eater	<i>Merops pusillus</i>	Aerial invertivore	3 (2±1)	-	-
Little Egret	<i>Egretta garzetta</i>	Aquatic carnivore	7 (1.29±0.49)	5 (2.4±2.07)	4 (1.75±0.96)

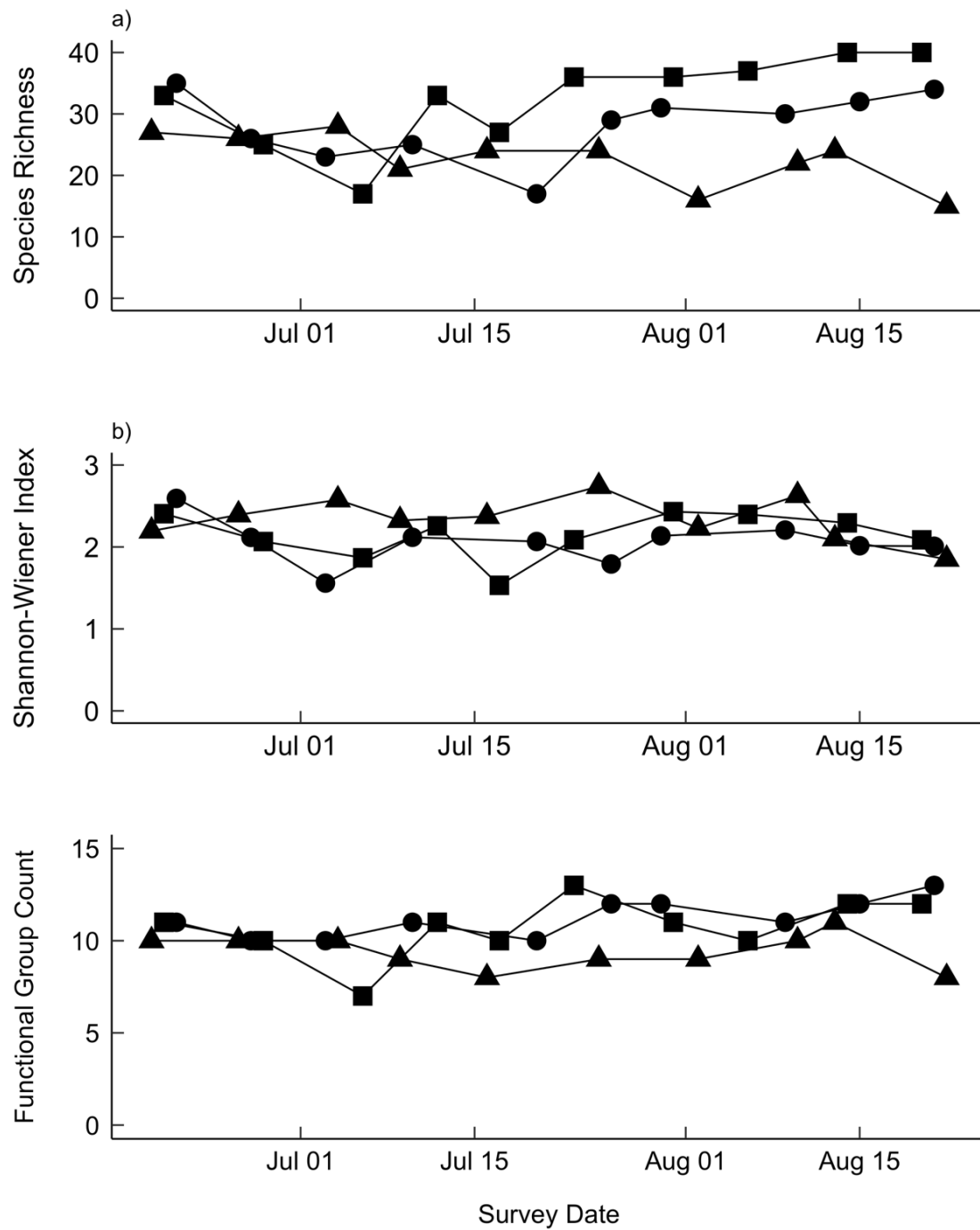
Long-billed Crombec	<i>Sylvietta rufescens</i>	Arboreal invertivore	-	-	3 (1.67±1.15)
Long-tailed Paradise Whydah	<i>Vidua paradisaea</i>	Terrestrial omnivore	-	-	2 (7.5±6.36)
Magpie Shrike	<i>Urolestes melanoleucus</i>	Arboreal omnivore	-	5 (4.8±2.39)	8 (3.62±2)
Marabou Stork	<i>Leptoptilos crumeniferus</i>	Aquatic carnivore	-	13 (13.92±22.27)	-
Marico Flycatcher	<i>Bradornis mariquensis</i>	Terrestrial invertivore	2 (4.5±0.71)	3 (2.33±1.53)	11 (5.64±3.38)
Marico Sunbird	<i>Cinnyris mariquensis</i>	Arboreal omnivore	-	1 (1)	2 (2.5±0.71)
Meyer's Parrot	<i>Poicephalus meyeri</i>	Arboreal herbivore	-	-	2 (1.5±0.71)
Namaqua Dove	<i>Streptopelia decipiens</i>	Terrestrial herbivore	-	1 (1)	2 (1.5±0.71)
Orange- breasted Bushshrike	<i>Chlorophoneus sulfureopectus</i>	Arboreal invertivore	-	-	2 (1.5±0.71)
Pale Chanting Goshawk	<i>Melierax canorus</i>	Aerial carnivore	-	-	1 (1)
Pale Flycatcher	<i>Bradornis pallidus</i>	Arboreal invertivore	-	1 (1)	-
Pied Crow	<i>Corvus albus</i>	Arboreal omnivore	-	9 (3.11±2.32)	10 (1.7±1.57)
Pied Kingfisher	<i>Ceryle rudis</i>	Aquatic carnivore	8 (2.38±1.41)	2 (3.5±3.54)	4 (2.5±1)
Pin-tailed Whydah	<i>Vidua macroura</i>	Terrestrial omnivore	-	1 (5)	2 (7±7.07)
Rattling Cisticola	<i>Cisticola chiniana</i>	Arboreal invertivore	3 (2.33±0.58)	-	4 (3.25±1.5)
Red-billed Buffalo Weaver	<i>Bubalornis niger</i>	Arboreal omnivore	-	2 (1.5±0.71)	-
Red-billed Firefinch	<i>Lagonosticta senegala</i>	Terrestrial omnivore	10 (6±3.77)	6 (4.67±4.68)	11 (8.73±6.44)
Red-billed Oxpecker	<i>Buphagus erythrorhynchus</i>	parasitic carnivore	-	2 (2.5±2.12)	-
Red-billed Quelea	<i>Quelea quelea</i>	Terrestrial omnivore	1 (27)	6 (36.67±30.14)	4 (85.5±143.25)
Red-billed Spurfowl	<i>Pternistis adspersus</i>	Terrestrial herbivore	10 (2.8±1.75)	11 (5.55±3.45)	12 (5.5±4.4)
Red-breasted Swallow	<i>Cecropis daurica</i>	Aerial invertivore	-	1 (4)	1 (1)
Red-eyed Dove	<i>Streptopelia semitorquata</i>	Terrestrial herbivore	5 (1.2±0.45)	1 (1)	2 (3±0)
Red-faced Mousebird	<i>Urocolius indicus</i>	Arboreal herbivore	2 (4.5±4.95)	-	1 (1)
Reed Cormorant	<i>Microcarbo africanus</i>	Aquatic omnivore	2 (19±16.97)	8 (3.12±2.36)	9 (6.89±6.15)

Rock Dove	<i>Columba livia</i>	Terrestrial herbivore	-	1 (8)	-
Scaly-feathered Finch	<i>Sporopipes squamifrons</i>	Terrestrial omnivore	1 (26)	-	-
Senegals Coucal	<i>Centropus senegalensis</i>	Terrestrial carnivore	1 (1)	1 (1)	4 (1±0)
Southern Carmine Bee-eater	<i>Merops nubicoides</i>	Aerial invertivore	-	-	1 (1)
Southern Grey-headed Sparrow	<i>Passer diffusus</i>	Terrestrial omnivore	3 (2±1)	1 (5)	4 (2.75±2.22)
Southern Red-billed Hornbill	<i>Euplectes orix</i>	Terrestrial omnivore	2 (1±0)	5 (2.4±0.89)	9 (3.67±3.32)
Southern Red Bishop	<i>Tockus rufirostris</i>	Arboreal omnivore	-	-	1 (1)
Spectacled Weaver	<i>Ploceus ocularis</i>	Arboreal invertivore	-	-	1 (2)
Spotted Thick-knee	<i>Burhinus capensis</i>	Terrestrial invertivore	1 (1)	3 (1.67±0.58)	2 (1.5±0.71)
Spur-winged Goose	<i>Plectropterus gambensis</i>	Aquatic herbivore	1 (7)	1 (1)	1 (2)
Squacco Heron	<i>Ardeola ralloides</i>	Aquatic carnivore	1 (1)	1 (5)	-
Swainson's Spurfowl	<i>Pternistis swainsonii</i>	Terrestrial herbivore	1 (1)	4 (8±4.24)	8 (5.5±4.07)
Tawny-flanked Prinia	<i>Prinia subflava</i>	Arboreal invertivore	1 (2)	-	4 (2±1.41)
Tawny Eagle	<i>Aquila rapax</i>	Aerial carnivore	-	5 (1±0)	-
Three-banded Courser	<i>Rhinoptilus cinctus</i>	Terrestrial invertivore	-	-	1 (1)
Three-banded Plover	<i>Charadrius tricollaris</i>	Aquatic invertivore	2 (1.5±0.71)	2 (2±0)	-
Tropical Boubou	<i>Laniarius major</i>	Arboreal omnivore	8 (3.5±1.77)	3 (1.33±0.58)	9 (3.89±2.8)
Verreaux's Eagle Owl	<i>Bubo lacteus</i>	Arboreal carnivore	1 (1)	-	-
Village Indigobird	<i>Vidua chalybeata</i>	Terrestrial herbivore	1 (1)	-	-
Water Thick-knee	<i>Burhinus vermiculatus</i>	Aquatic carnivore	3 (1.67±0.58)	-	1 (1)
Western Cattle Egret	<i>Bubulcus ibis</i>	Terrestrial invertivore	-	1 (1)	-
White-backed Vulture	<i>Gyps africanus</i>	Terrestrial carrion	4 (8.25±9.67)	-	-
White-bellied Sunbird	<i>Cinnyris talatala</i>	Arboreal omnivore	1 (1)	12 (5±4.81)	2 (4±1.41)
White-breasted Cormorant	<i>Phalacrocorax lucidus</i>	Aquatic carnivore	-	1 (1)	-

White-browed Coucal	<i>Centropus superciliosus</i>	Terrestrial carnivore	-	-	1 (1)
White-browed Robin-Chat	<i>Cossypha heuglini</i>	Terrestrial invertivore	2 (1.5±0.71)	1 (1)	7 (1.86±1.21)
White-browed Scrub Robin	<i>Erythropygia paena</i>	Terrestrial invertivore	1 (2)	-	8 (2±1.07)
White-browed Sparrow Weaver	<i>Plocepasser mahali</i>	Arboreal omnivore	6 (1.83±0.75)	-	-
White-crowned Lapwing	<i>Vanellus albiceps</i>	Aquatic carnivore	-	1 (1)	1 (1)
White-faced Whistling Duck	<i>Dendrocygna viduata</i>	Aquatic herbivore	-	-	1 (13)
White-fronted Bee-eater	<i>Merops bullockoides</i>	Aerial invertivore	-	1 (1)	-
Wire-tailed Swallow	<i>Hirundo smithii</i>	Aerial invertivore	3 (1.67±0.58)	-	-
Yellow-billed Egret	<i>Egretta intermedia</i>	Aquatic carnivore	3 (1.67±0.58)	2 (1.5±0.71)	2 (1±0)
Yellow-billed Oxpecker	<i>Buphagus africanus</i>	parasitic carnivore	-	2 (2.5±2.12)	1 (4)
Yellow-billed Stork	<i>Mycteria ibis</i>	Aquatic carnivore	5 (2±0.71)	-	1 (1)
Yellow-fronted Canary	<i>Crithagra mozambica</i>	Arboreal herbivore	3 (41.67±17.67)	-	1 (3)



Appendix 2.3. Environmental variables tested against avian species' richness (a) and Shannon-Wiener Diversity (b) at three sites differing in large herbivore presence; low (Fenced, triangles), intermediate (Unfenced, squares) and high (National Park, circles). Wind class was judged by the observers as no wind (0), little wind (1), or quite windy (2).



Appendix 2.4. Weekly changes in species richness (a) and Shannon-Wiener diversity (b) and number of functional groups (c) at three sites in Botswana, (19 June 2018 - 22 August 2018) varying in large herbivore presence: Fenced (low presence, triangles), Unfenced (intermediate presence, square) and National Park (high presence, circles).

Appendix 2.5. Results of the Simper analysis showing the top 10 species contributing to community differences across the three sites differing in large herbivore presence; Fenced (low), Unfenced (intermediate) and National Park (high).

Group: Fenced vs. Unfenced (Low vs. Intermediate)		Av. dissimilarity: 68.5%			
Species	Cumulative %	Average	SD	Ratio	
Ring-necked Dove	29.34	0.20	0.07	2.81	
Red-billed Quelea	40.77	0.08	0.10	0.80	
Blue Waxbill	48.39	0.05	0.04	1.29	
Marabou Stork	53.91	0.04	0.05	0.74	
Lesser Masked Weaver	57.42	0.02	0.02	1.08	
African Sacred Ibis	60.58	0.02	0.04	0.54	
Blacksmith Lapwing	63.40	0.02	0.01	1.39	
Red-billed Firefinch	65.92	0.02	0.01	1.36	
White-bellied Sunbird	68.06	0.01	0.02	0.94	
Marico Flycatcher	70.02	0.01	0.01	1.66	
Group: Unfenced vs. National Park (Intermediate vs. High)		Av. Dissimilarity: 50.6%			
Species	Cumulative %	Average	SD	Ratio	
Ring-necked Dove	15.70	0.08	0.07	1.22	
Crowned Lapwing	25.04	0.05	0.04	1.21	
Red-billed Quelea	33.15	0.04	0.09	0.47	
Blue Waxbill	40.92	0.04	0.03	1.29	
Yellow-fronted Canary	45.25	0.02	0.04	0.60	
Lesser Masked Weaver	49.18	0.02	0.02	1.12	
Brown-throated Martin	53.06	0.02	0.04	0.54	
Reed Cormorant	55.85	0.01	0.02	0.84	
Red-billed Firefinch	58.49	0.01	0.01	1.48	
Egyptian Goose	61.06	0.01	0.02	0.59	
Group: National Park vs. Fenced (High vs. Low)		Av. dissimilarity: 73.5%			
Species	Cumulative %	Average	SD	Ratio	
Ring-necked Dove	27.36	0.20	0.09	2.15	
Crowned Lapwing	35.43	0.06	0.05	1.28	
Red-billed Quelea	42.07	0.05	0.06	0.83	
Marabou Stork	47.14	0.04	0.05	0.75	

Blue Waxbill	52.09	0.04	0.04	0.98
Yellow-fronted Canary	55.69	0.03	0.04	0.60
Brown-throated Martin	58.95	0.02	0.04	0.56
African Sacred Ibis	61.83	0.02	0.04	0.54
Egyptian Goose	64.09	0.02	0.03	0.61
Blacksmith Lapwing	66.31	0.02	0.01	1.33

Chapter 3. Remote sensing techniques track colonial waterbird breeding, a surrogate for river inundation patterns on the Chobe River, Botswana

Francis, R.J., Kingsford, R.T. and Brandis, K.J.

I led study design, methods creation, equipment purchasing, permit applications, fieldwork, data collection and compilation, analysis and writing.

3.1 Abstract

Many of the world's freshwater ecosystems are degrading with increasing water resource developments, necessitating identification of useful indicators that track large scale environmental change. We investigated the effectiveness of waterbird breeding at the Kasane breeding colony as a biotic indicator of river flow and flooding on the Chobe River in Botswana. We counted nests and adult birds, and estimated reproductive success in the breeding colony in 2018 and 2019, using drone surveys. We estimated 4529 birds of six species (African darters *Anhinga rufa*, African openbills *Anastomus lamelligerus*, African spoonbills *Platalea alba*, reed cormorants *Microcarbo africanus*, white-breasted cormorants *Phalacrocorax lucidus* and yellow-billed storks *Mycteria ibis*) on 2861 nests in early August 2018; there were no nests counted in 2019. Reproductive success differed significantly among species, ranging from 81% of eggs fledged for yellow-billed storks to 47% for African openbills and was significantly related to Chobe River level. Given absence of historical colony data, we also investigated relationships between citizen science waterbird counts of the six breeding species on the river (1993-2018), to river flows, flooding and local rainfall. Waterbirds were significantly more abundant at times of lower inundation, and maximum species abundances, likely indicative of breeding, occurred when Chobe River level was >

4.33m. This matched our data: breeding in 2018, when the river level reached 5.09m, and no breeding in 2019, when the river level was 3.23m. Breeding of colonial waterbirds can be a useful indicator for river management because of its dependence on high river level and extensive inundation. It can be tracked using drone surveys, a non-invasive and safe way of estimating reproductive success. Given that river level and flow data are often available for long periods of time, there are opportunities for hindcasting and forecasting effects of climate change and water resource development on aquatic ecosystems.

3.2 Introduction

Freshwater biodiversity is in crisis globally, with an estimated one in three freshwater dependant species threatened with extinction (International Union for Conservation of Nature 2017). One of the greatest causes of this loss is habitat degradation of rivers, lakes and their dependant floodplains through flow modification by dams and water extraction (Vörösmarty et al. 2010, Reid et al. 2019), alongside a range of other threats such as invasive species, contaminants, disease, and climate change (Dudgeon et al. 2006, Reid et al. 2019).

Freshwater ecosystems naturally support high numbers of aquatic and terrestrial biota and provide a range of ecosystem services to human communities, such as freshwater provision and purification (Durance et al. 2016, Jorda-Capdevila et al. 2019). Tracking degradation in freshwater biodiversity and ecosystem services represents a major challenge, particularly given the importance of informing communities and governments about changes at large spatial and long temporal scales. Adding to the complexity, many rivers flow between countries, with effects of water resource developments in one country impacting freshwater biodiversity and ecosystem services thousands of kilometres downstream in another country (Awulachew 2012, Zawahri and Hensengerth 2012, Williams 2020).

It is therefore critical to identify low-cost indicators that effectively track changes in rivers, their floodplains and dependent biota. Indicator species can be defined as a set of species with presence or absence patterns that are correlated functionally with species richness of a larger group or organisms. Useful indicators for rivers and wetlands include dependent aquatic vegetation, native fish species and waterbirds (Amat and Green 2010, Ogden et al. 2014a, Orth et al. 2017, Tsai et al. 2017). Distribution, abundance and reproductive success of waterbirds is highly dependent on rivers and related wetland ecosystems, and they respond to variations in flow and flooding regimes and associated management (Desgranges et al. 2006, Brandis et al. 2011, Lantz et al. 2011, Ogden et al. 2014b, Brandis et al. 2018). Presence and size of breeding colonies of large wading birds (e.g. Ciconiiformes, Pelecaniformes and Suliformes such as spoonbills, ibis and herons) usually reflect ecosystem condition (often extent of flooding), over large temporal and spatial scales (Crozier and Gawlik 2003, Brandis et al. 2011, Brandis et al. 2018) and resulting availability of food resources (Neckles et al. 1990, Frederick and Ogden 2001, Blewett et al. 2017). Several waterbird species breed in colonies, often together, relying on food resources away from the colony (Siegfried 1971, Bryan et al. 2012), providing a measure of ecosystem responses at large scales. Because different species feed on different prey, their successful breeding can reflect different parts of the ecosystem. For example, white ibis *Eudocimus albus* and snowy egret *Egretta thula* breed together in the Florida Everglades but the former feeds on crayfish and the latter on fish (Boyle et al. 2012). Given that flow and flooding regimes are often affected by water resource developments, the close relationships between flow and the breeding of colonial waterbirds means that effects of water management and water resource developments can be assessed (Kushlan and Frohring 1985, Fox et al. 1991, Kushlan 1993, Kingsford and Thomas 1995, Brandis et al. 2018). Identifying the usefulness of waterbirds as indicators requires an understanding of location specific cause and effect relationships,

including flow or flooding thresholds which determine successful recruitment (Brandis et al. 2011, Arthur et al. 2012, Bino et al. 2014). Study into the biological mechanism causing change in indicator species is critical (for eg. waterbird responses due to increased food resources), providing the causal link to ecosystem change (Carignan and Villard 2002). Surveys of breeding waterbirds need to collect accurate data, using repeatable methods, while ensuring limited disturbance. Ground based surveys can cause disturbance, reducing reproductive success through nest abandonment, increased predation and increased chick mortality (Tremblay and Ellison 1979, Götmark and Åhlund 1984, Carney and Sydeman 1999, Blackmer et al. 2004, Carey 2009). Such effects can be minimised by reducing survey time at nests (Carney and Sydeman 1999) and limiting nest visitation (Brandis et al. 2014). Some colonial waterbird breeding sites around the world can be in either remote, difficult to access or even dangerous areas (e.g. African predators such as Nile crocodiles *Crocodylus niloticus* or hippopotamuses *Hippopotamus amphibius*). Drones can overcome some of these problems, inexpensively collecting data on colony size, composition and reproductive success (Koh and Wich 2012, Brody 2017, Ezat et al. 2018). Such drone data for the breeding of colonial waterbirds can be more precise and less variable, compared to traditional methods (Hodgson et al. 2016, Lyons et al. 2018, Lyons et al. 2019, Barr et al. 2020); they also allow for later counting (albeit labour intensive) and error checking, as images are permanently captured. Finally, advances in semi-automated counting techniques (Descamps et al. 2011, McNeill et al. 2011, Chabot and Francis 2016, Francis et al. 2020) significantly reduce processing time for colony counts using drone imagery, addressing a major cost (Callaghan et al. 2018). However, tracking reproductive success over time using drone imagery is not as well developed because of low data resolution (Callaghan et al. 2018).

There are many citizen science based projects around the world which contribute waterbird data. Citizen science can contribute to the temporal monitoring of species, particularly useful

and important in areas where little scientific monitoring is occurring (Chandler et al. 2017).

In Botswana, citizen science monitoring of birds has been occurring on a small scale since 1970, with programs such as the African Waterbird Census contributing significant amounts of data (Dodman and Diagana 2019).

We investigated the effectiveness of using colonial waterbird breeding in tracking hydrological changes over time in a significant multi-species waterbird colony on the Chobe River, Botswana (Fig. 3.1). The Chobe River is largely free flowing, unlike most of the world's rivers (Nilsson et al. 2005, Grill et al. 2019), although there is growing pressure for water resource development in Angola, Namibia and Botswana which share the river and its headwaters (Mbaiwa 2004, Mendelsohn 2019). With little knowledge of minimum flows to maintain biological integrity and protect ecological services in this system (Neubauer et al. 2008), it is essential to ascertain easily identifiable, affordable and responsive indicator species. We tested the efficacy of using waterbird breeding as an indicator of hydrological change (and resultant environmental change) by: 1) counting numbers of nests of six species in a breeding colony on the Chobe River in 2018 and checking the same area in 2019, when there was no breeding; 2) tracking reproductive success of four of the species in this inaccessible multispecies breeding colony in relation to river level, while minimising disturbance and maximising researcher safety; 3) determining the long-term response of waterbirds along the river to river level, inundation and rainfall using citizen science data and; 4) providing river management recommendations to maintain waterbird breeding on the Chobe River. We tested the null hypothesis: there is no relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance, breeding and reproductive success on the Chobe River.

3.3 Methods

3.3.1 Waterbird breeding colony

The Chobe River has highly variable but seasonal flow and flooding patterns, predominantly driven from rainfall in the Angolan highlands, where the Chobe River begins as the Kwando River (Fig. 3.1). The Chobe River meets the Zambezi River (headwaters in Zambia), near the town of Kasane in Botswana (Fig. 3.1) and sometimes high flow in the Zambezi River can reverse the direction of flows in the Chobe River. We measured colony size, reproductive success and nest success of a multispecies waterbird breeding colony in a grove of jackalberry (*Diospyros mespiliformis*) and water berry trees (*Syzygium guineense barotsense*), on an island, surrounded by rapids on the Chobe River, near the town of Kasane in north east Botswana (Fig. 3.1). This same location is regularly used by breeding waterbirds across years.

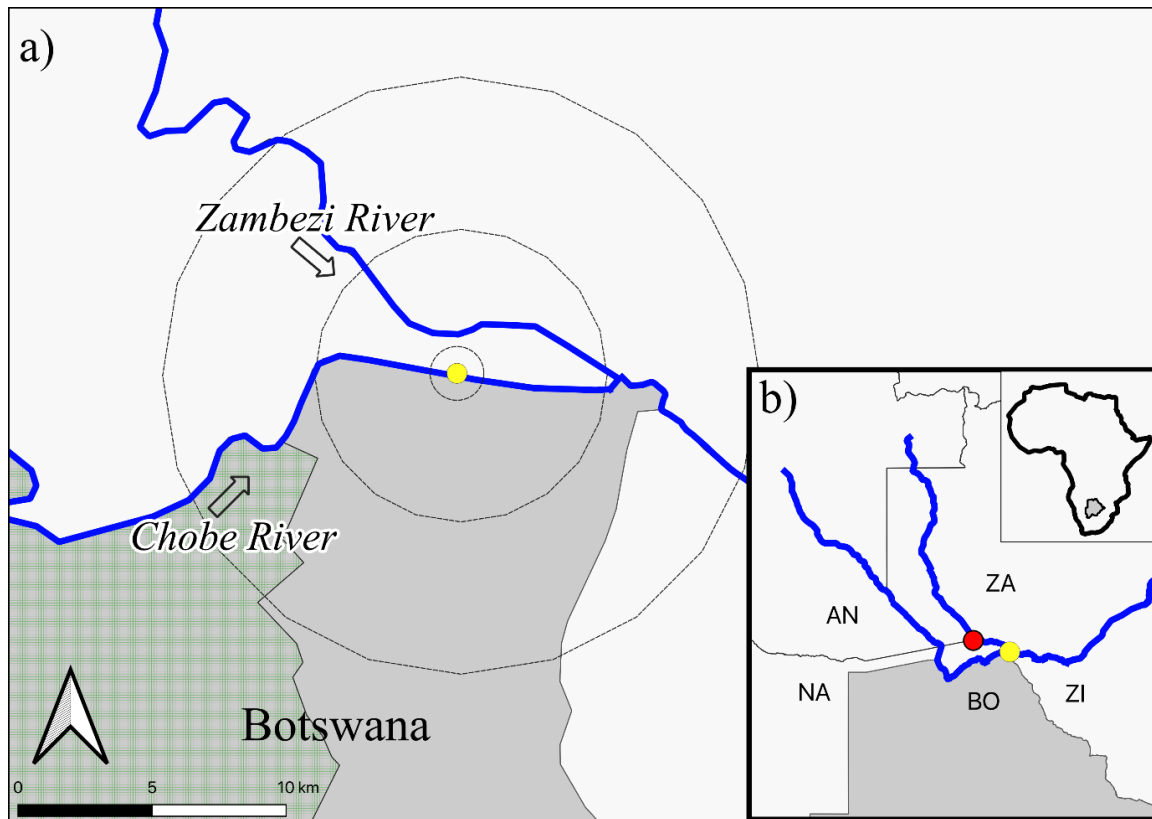


Figure 3.1. Location of the multispecies breeding colony of waterbirds at Kasane (yellow circle) on the Chobe River in Botswana (arrow indicates usual flow direction), dependent on river flows from the Kwando River from rainfall in the Angolan (AN) highlands, passing through Namibia (NA), before reaching Botswana (BO) (inset), showing 1, 5 and 10km buffer inundation zones (dashed lines) around the colony, including Chobe National Park (green), with daily river level data in the Chobe River collected at the colony in Kasane and Katima Mulilo (red circle) on the Zambezi River and daily rainfall data from Kasane.

The waterbird colony in 2018 included six breeding species: African darters *Anhinga rufa*, African openbills *Anastomus lamelligerus*, African spoonbills *Platalea alba*, reed cormorants *Microcarbo africanus*, white-breasted cormorants *Phalacrocorax lucidus* and yellow-billed storks *Mycteria ibis*. We collected drone imagery of the breeding colony, using a DJI Phantom 4 Advanced multi rotor drone, with the standard 20MP camera (5472 x 3648 image size, lens field of view 84° 24mm). We pre-programmed flight transects using Pix4d Capture

application (Pix4D 2014), which created polygons of the breeding colony, allowing flights at a constant speed (about 2ms^{-1}), reducing changes in altitude and drone noise (McEvoy et al. 2016), from 26th May-1st October 2018 (every 7-10 days), and from 20th July – 23rd September 2019 (every 14 days). Transects were flown to produce images with 40% front and side overlap (nadir perspective), taking still images at evenly spaced intervals along the transect. We initially flew a polygon at 120m altitude (above the riverbank), photographing the main breeding section. This allowed assignation of individual tree numbers (~60 trees) for weekly identification, using high resolution low-level images (16 m above the riverbank). We tested different heights in relation to differentiation of nests and their contents, starting at 25m, observing if nesting birds were disturbed. We considered signs of disturbance to include standing and flying from nests. Even at 16m above the river bank, most birds remained undisturbed and, importantly, images were of sufficient resolution to clearly identify breeding stages of most species. Subsequently, we flew at this height twice each week, immediately repeating the survey, doubling our imagery, and improving identification of nests and their young, as breeding adults often shifted their seated position or stood up. As the colony extent increased over time in 2018, transects were added to cover the area, but flown at 18m (to cover the entire area allowing for battery life, ~ 40 additional trees). Finally, adults and nests were counted in a large low density (>50% less nests) section of the colony at 45m, an insufficient resolution to track reproductive success (>100 trees) but allowing the whole colony to be counted (~40 ha), using drone imagery. Transects flown at 16m altitude above the riverbank had a resolution of $\sim 4.4\text{mm pixel}^{-1}$; 18m $\sim 4.9\text{mm pixel}^{-1}$; and 45m $\sim 12.3\text{mm pixel}^{-1}$. We flew a total of 20 surveys in 2018 (31st May – 1st October) and the same area in 2019 with five surveys to check for breeding (20th July – 23rd September, totalling > 80 hours). The frequency of drone flights was lower in 2019, because the birds did not breed.

There were no bird strikes, despite the high density of raptors in the area (eg African fish eagle *Haliaeetus vocifer*, and tawny eagle *Aquila rapax*).

To estimate total number of birds and nests present in the colony in 2018, we manually counted and identified nests from the drone imagery, visually aligning images flown at 16m to ensure overlapping areas were not counted twice and cropping the overlap for images flown at 18 and 45m, before counting. Images were not stitched together to form a mosaic. We calculated weekly bird totals by summing the count of each species on all trees. The total colony count for 2018 was the summed maximum count for each species. We used plumage and size differences, clearly visible in the drone imagery, to differentiate waterbird species and age groupings (Appendix 3.1).

Our measure of reproductive success was calculated as the number of young that leave the nest / total number of eggs (Murray Jr 2000), tracking nests until fledging. Nest success was calculated as the proportion of nests with at least one egg that produced at least one fledgling, accounting for ‘nest-day’ or the number of observation days per nest (see pg. 459 Mayfield (1975)), a measure independent of clutch size. Age at fledgling used for each species can be found in Appendix 3.1. To calculate reproductive and nest success indices from the 16m drone imagery in 2018, we first separated photos, based on the unique ID of the tree captured, marking them using Photoscape X (Mooii Tech 2019). We then randomly selected 61 African darter, 26 African openbill, 47 African spoonbill and 33 yellow-billed stork nests, and assigned them an identification number and tracked each nest through time. This included recording eggs (where possible), chicks, juveniles and fledglings, based on visual changes in plumage (Appendix 3.1) and known fledgling ages (Maclean et al. 2011). We recorded when sightings were partially obscured (e.g. by a parent bird), restricting total nest coverage. We did not track reproductive or nest success in reed cormorants or white-bellied cormorants because respectively, nest contents were not easily visible in the drone imagery

and we did not see them fledge. We followed 167 nests for the four species in each drone survey; only 11% of nests had egg sightings not obscured by a parent bird. For the reproductive success calculations which require clutch sizes we adjusted counts from the standard in-situ observers' method (Erwin and Custer 1982), backward filling to estimate actual clutch size at the time of survey. We applied a correction to avoid an inflated reproductive success value which assumed all eggs fledged. If the backwards filled egg number fell below average published clutch size data (Maclean et al. 2011) (African darter, African spoonbill, yellow-billed stork), or our clutch size data (African openbill), we increased the estimate to the average number (Table 3.1, Fig. 3.2, Appendix 3.2). We used our clutch size data for the African openbills only, given we had more clutch sizes recorded than reported elsewhere (Maclean et al. 2011). The total number of nests used to calculate reproductive success differed among species. We tracked 61 African darter nests (37% of total nests counted), with 60 requiring backfilling; 26 African openbills nests (1% total nests), with 9 requiring backfilling; 47 (24% of total nests) African spoonbill nests, with 44 requiring backfilling; and 33 yellow-billed stork nests (20% of total nests), with 26 requiring backfilling. To solidify reproductive success calculations, we cross-checked visual age assignments (Appendix 3.1) against the number of days young were in the drone imagery. We found that visual aging closely aligned with growth stages previously reported, using nestling age in days as a criterion to determine fledging (Hockey et al. 2005, Maclean et al. 2011).

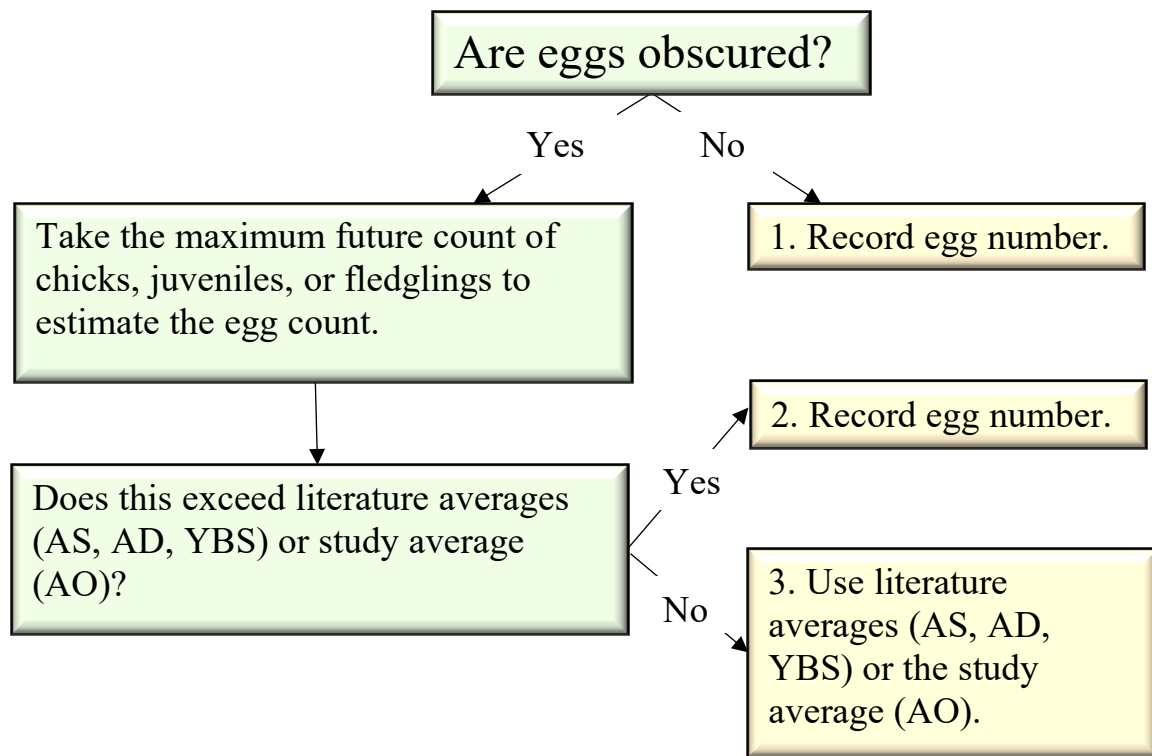


Figure 3.2. Three-step decision tree used for identifying egg counts where parents obscured nest contents, for African openbills (AO), African spoonbills (AS), African darters (AD), yellow-billed storks (YBS) and during the 2018 monitoring of the Kasane breeding colony on the Chobe River.

3.3.2 Waterbird abundances of six breeding species on the Chobe River

There were no historical data on numbers of nests in the Kasane breeding colony, despite regular breeding. We therefore used abundances of the six breeding species along the Chobe River, as a surrogate of breeding, assuming large abundances of these species probably indicated breeding. We collated waterbird counts (1993-2018) from grey literature sources, including the African Waterbird Census (n=204, Dodman and Diagana 2019), personal communications (n=19) and observations in ‘The Babbler’ published by Birdlife Botswana (n=6, BirdLife Botswana 2019). For each record, we recorded the number of observers as a measure of survey effort and date for each observation. We included observations along the Chobe River front from the Kasane colony to the Western edge of Chobe National Park. The

African waterbird census included transect counts and point counts largely conducted in January, February or July by a team of two to four people. Other citizen science data used were largely point counts conducted by an individual or two people with most counts conducted between July to January. Many of the AWC counts were also recorded in The Babbler, which we excluded to avoid duplication.

3.3.3 River levels, inundation and local rainfall

We collected daily river level data at station 6624 on the Chobe River at Kasane (Fig. 3.1), provided by the Department of Water Affairs Botswana (Department of Water Affairs Botswana 2018). A third of the data were missing (largely between 2002–2006) and so we modelled the relationship between daily river level data from the Zambezi River at Katima Mulilo (Fig. 3.1) and the Chobe River at Kasane for 2000-2019, when there were no missing data (Department of Water Affairs and Forestry Namibia 2019), using a Generalized Additive Model (GAM) (Hastie 2019) (Appendix 3.3), which explained 91% of observed variation ($GCV_{3255} = 0.09$, $P < 0.001$). To track inundation changes proximate (areas within 1, 5 and 10 kms) to the Kasane breeding colony (Fig. 3.1), we used the Google Earth Engine (Gorelick et al. 2017) and Landsat-5, 7 and 8 images (Inman and Lyons 2020) and stacked available imagery across three month intervals (January 1993-December 2019) (Wolski et al. 2017). These areas were assumed to include potential foraging grounds in Chobe National Park where birds were regularly seen foraging, given breeding waterbirds forage at reasonable distances from their colony, even up to 29kms for cattle egrets (Bryan Jr and Coulter 1987, Alonso et al. 1991, Gibbs 1991, Tiller et al. 2005). For each three-month stacked raster, we calculated the proportion of flooded and dry pixels, deriving percent inundation for each area from the colony (Wolski et al. 2017). We removed inundation percentages in January-March higher than the subsequent peak flood (Chobe River peak flooding, April-May), because they probably overestimated inundation due to local rainfall in

the rainy season (Wolski et al. 2017). We filled missing values (e.g. cloudy imagery or overestimations) using interpolation with the function *na.approx()* (2% of all values for 1km, 5% for 5km and 5% for 10km areas from the colony). We also collected local daily rainfall data from the Department of Meteorological Affairs, Kasane for 2001-2018 (Department of Meteorological Affairs 2018). To fill missing daily rainfall data (7%), we modelled the relationship between rainfall at Kasane and Maun airport, 560km to the southwest (Okavango Research Institute 2020), using GAM modelling which explained 77% of observed variation ($GCV_{90} = 144.1$, $P < 0.001$, Appendix 3.4).

3.3.4 Analyses

To explore differences in reproductive success among the four species with data from 2018, we modelled proportion of successes (i.e. total eggs/ number fledged) as the response variable, an offset equal to the total eggs, and nest ID as a random variable, using a binomial family and the *glmmTMB* package (Brooks et al. 2017), ie. *glmmTMB(Fledged/Eggs ~ Species + (1|NestID), data, offset = Eggs, family = binomial(link = "logit"))*. Next, to explore species' specific reproductive success responses to Chobe River level, we separated reproductive success for each species (four separate models) and analysed variation in reproductive success in relation to Chobe River level ie. *Fledged/Eggs ~ ChobeLevel + (1|NestID), data, offset = Eggs, family = binomial(link = "logit")*.

We then examined how year- round abundances of the six breeding waterbird species along the river varied in relation to abiotic variables. Rainfall, river level and inundation data were grouped into 3-month periods (mean). We first tested for correlations among percent inundation percent among the three areas (1km, 5km and 10km from the colony site, Fig. 3.1) surrounding the colony, Kasane rainfall and Chobe River level data. Resultingly, we excluded inundation data in the 5km area, given high correlation with inundation within 10km area (96%); we retained the 10km area, as many of the waterbird bird counts came

from this area within Chobe National Park. We used a glmmTMB model with a negative binomial family (Brooks et al. 2017) to examine the relationship between total waterbird abundance of the six breeding species and Chobe river level, rainfall, inundation, and time of year (southern hemisphere seasons: September-November, December-February, March-May, June-August), using an offset for the number of observers in counts (survey effort) and species as a random variable (1993-2018). Predictor variables were scaled to improve model convergence ie. (*glmmTMB(BirdCount ~ Season + scale(ThreeMonthlyMeanKasaneRain) + scale(InundationBufferOne) + scale(ThreeMonthlyMeanChobeLevel) + scale(BufferTen) + (1|Species) + offset(log(SurveyEffort))*), *data, family = nbinom2*)). We then separately modelled each species using the same approach but removing species as a random variable.

We then investigated a possible breeding threshold effect in river level at the annual scale, by modelling the maximum yearly species' counts for the six species (maximum counts for all breeding species in any one year). This maximum count was probably most indicative of a breeding event. Predictor variables included maximum annual inundation percent within 1km of the colony site, maximum annual Chobe river level and maximum annual rainfall (1993-2018). We had to remove maximum inundation extent within 1km because of its high correlation (85%) with maximum river level. We again used the glmmTMB package with scaled predictor variables, species as a random variable and an offset for number of observers, with a negative binomial family (ie. *glmmTMB(MaxPerSpeciesPerYear ~ scale(MaxChobeLevel) + scale(MaxRainfall) + scale(MaxInunPercentBufferTen) + offset(log(ObserversFilled)) + (1|Species)*), *data family = nbinom1*)).

Our analyses indicated a threshold effect: abundances of breeding waterbirds increased significantly with river levels, as in other breeding colonial waterbirds (Arthur et al. 2012). So, we quantitatively identified this threshold by modelling species and Chobe River levels in

relation to maximum annual abundances of the six breeding species along the river (proxy to breeding), using a classification and regression tree analysis (CART), with no assumptions about distributions (Breiman et al. 1984), with the *rpart* package (Therneau and Atkinson 2019) (ie. *rpart(MaxPerSpeciesPerYear ~ Species + MaxChobeLevel, data)*). We then compared inferred flooding threshold to our actual breeding data for 2018 and 2019 and then then estimated the likely number of breeding events, 1993-2019.

All analyses were performed within the R computing environment (R Core Team 2014), relying on the tidyverse workflow (Wickham 2017) and ggplot2 package (Wickham 2016). Significance of statistical tests was concluded at $\alpha < 0.05$. For all models, we tested for temporal auto correlation using an ACF plot (*acf* function) and checked the QQplot and residual vs predicted values of the glmmTMB using the DHARMa package (Hartig 2020), which upheld assumptions of normality and equal variance. Variation is reported as standard deviation throughout, except when specified otherwise.

3.4 Results

3.4.1 Kasane breeding colony in 2018 and 2019

Breeding colony establishment coincided with peak river level of the Chobe River in April / May of 2018 (~5m), increasing in number of nests over time (Fig. 3.3). By the 30 May 2018, five species, African darters, African spoonbills, reed cormorants, white-breasted cormorants and yellow-billed storks had nests (low numbers) (Fig. 3.3b). African openbills arrived later, arriving on the 12th June 2018, and building the first nests on the 25th June (Fig. 3.3b).

Colonial waterbirds first nested in the water berry trees in the western section of the grove. Different species reached their maximum nest counts over more than a two-month period (Fig. 3.3). Nest counts peaked on 12th June for African darters; 9th July for reed cormorants; the 20th August for African spoonbills; white-breasted cormorants and yellow-billed storks; and the 27th August for African openbills (Fig. 3.3). On completion of the final drone survey

(1st October 2018), there were < 20 nests for African darters, African spoonbills, reed cormorants, and white-breasted cormorants; 60 nests of yellow-billed storks, most with adult sized young, and; 833 nests of African openbills (Fig. 3.3). Two species, African sacred ibis *Threskiornis aethiopicus* and grey herons *Ardea cinerea*, were also occasionally identified in drone imagery, in small numbers (<5 per survey) but did not nest. In 2018, there were 4529 birds, and 2861 nests, representing separate maxima for each species aggregated (Fig. 3.3). The colony expanded easterly as it increased in July and August. Nesting trees (only water berry trees) were initially submerged in deep fast flowing water, but an island emerged as water levels dropped (~ early September), accessible by foot. At the peak of breeding, a tree could support all six breeding species and up to 365 adult birds and 162 nests. All species, except reed cormorants, nested on the outer edges of the trees. Most colonially breeding waterbirds flew west to forage in the shallow waters of the Chobe River floodplain, within Chobe National Park (Fig. 3.1). As water levels dropped some birds foraged around the nesting area, particularly yellow-billed storks.

In 2019 drone surveys (beginning 20th July), there were no nests, with only 15 African sacred ibis, four yellow-billed stork and two African darters in the colony area. African darters and yellow-billed stork (<10 nests per species) had started to breed in early June, but by 20 July 2019 at the time of the first drone surveys, there were no nests remaining.

Weekly reproductive success varied significantly among species ($\chi^2(3, N= 892) = 10.22, p = 0.02$) (Fig. 3.3d). Yellow-billed storks had the highest average reproductive success rate (81%), followed by African darters (67%), African spoonbills (52%) and finally the African openbills (47%). For all species, most losses occurred between the juvenile and fledgling stages (Table 3.1), with no losses between the chick and juvenile stage. Reproductive success increased with decreasing Chobe River level for African darters ($\chi^2(1, N= 244) = 5.73, p = 0.02$), African openbills ($\chi^2(1, N= 145) = 23.11, p < 0.001$), African spoonbills ($\chi^2(1, N=$

209) = 12.50, $p < 0.001$), and yellow-billed storks ($X^2(1, N = 294) = 25.46, p < 0.001$)(Fig. 3.3d).

Table 3.1. *Reproductive success estimates for the four waterbird species breeding at the Kasane colony on the Chobe River for three stages (see Appendix 3.1) and through to fledging (total), surveyed in 2018 (12th June – 1st October), using drone imagery, with sample sizes (number of nests) for each species provided with total numbers of observations of those nests throughout the sampling period.*

Species	Egg-Chick	Chick-Juvenile	Juvenile-Fledgling	Final Reproductive Success	Nest Success	Nests tracked (total observations)
African darter	0.82	1	0.82	0.67	0.85	61 (244)
African openbill	0.59	1	0.79	0.47	0.56	26 (145)
African spoonbill	0.67	1	0.82	0.52	0.92	47 (209)
Yellow-billed stork	0.89	1	0.92	0.81	0.97	33 (294)

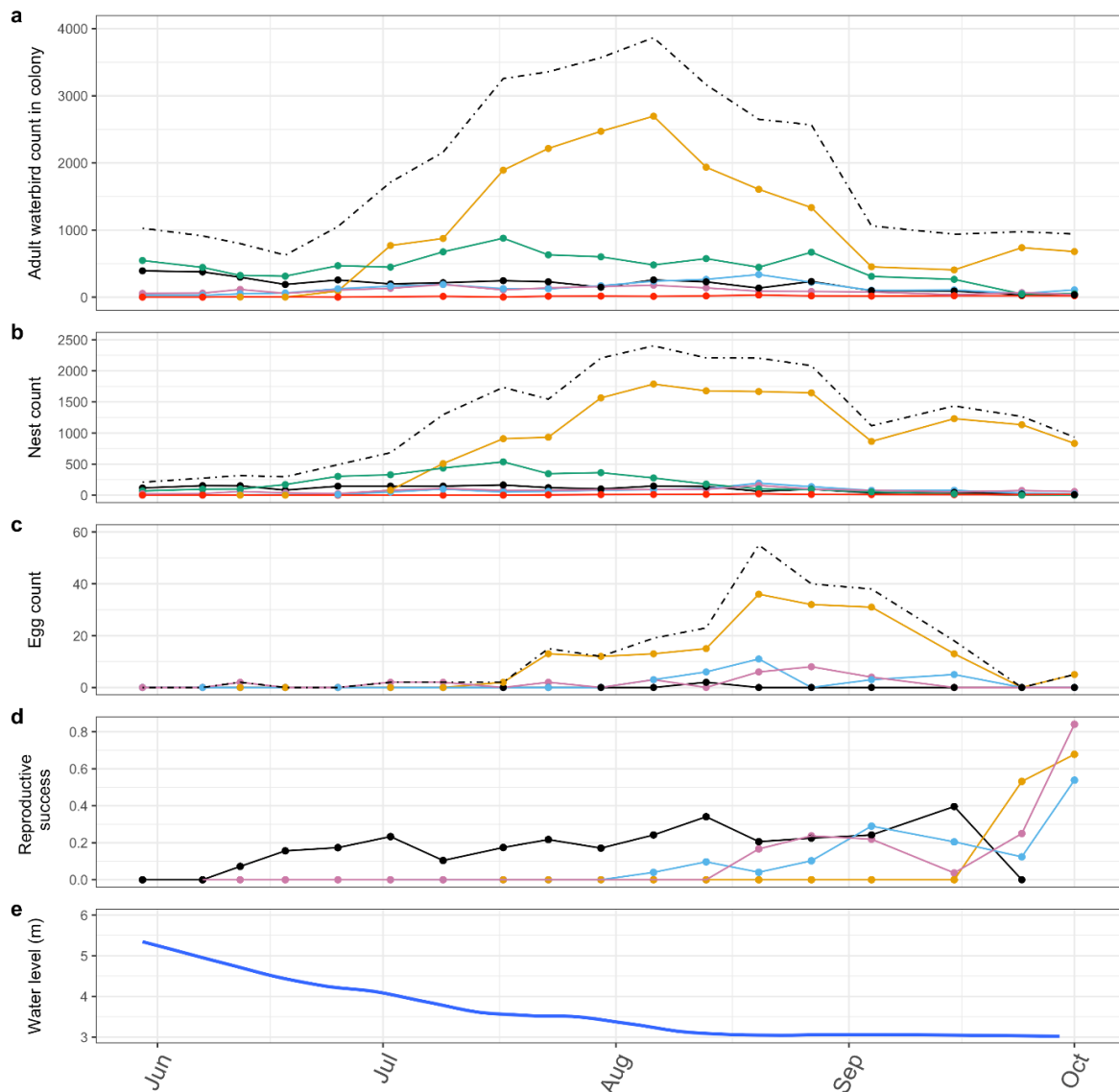


Figure 3.3. Counts of six colonially breeding waterbird species (all species (3866 max), dashed line; African darter (393 max), black line; African openbill (2696 max), orange line; African spoonbill (max 338), blue line; reed cormorant (max 879), green line; white-breasted cormorant (max 33), red line; yellow-billed stork (max 190), purple line) in the Kasane colony on the Chobe River in northern Botswana (30 May-01 Oct, 2018) using drone imagery, including (a) adults, (b) nests, (c) egg counts and (d) reproductive success (percent of eggs fledged) in relation to (e) river level.

3.4.2 Abundance of the six colonially breeding waterbird species along the Chobe River in relation to flooding, river levels and rainfall

River level, flooding and rainfall were all highly seasonal (Fig. 3.4), corresponding to high flows in the middle of the year, causing increased flooding, with local rainfall mostly late in the year. Chobe River level (1993-2019) ranged from 2.4–6.4 m, with an annual mean of 3.4 ± 1 m and annual maximum averaging 5.2 ± 1 m. Maximum level in 2018 was 5.09 m, compared to only 3.23 m in 2019 which fell below the 26 year average peak flow (Fig. 3.4). Inundation was highest within 1 km of the colony (1993-2019), averaging $29 \pm 5\%$ flooded (max. $35 \pm 40\%$), compared to $13 \pm 10\%$ (max. $27 \pm 10\%$) within 10 km of the Kasane colony (Fig. 3.4). Within 1 km of the Kasane colony site, inundation ranged from 4.2–47% (Fig. 3.4). Inundation was much higher (39%) in 2018 compared to 2019 (27%, Fig. 3.4). Chobe mean monthly rainfall (1993-2018) ranged from 0-394 mm, with a monthly mean of 22 ± 40 mm. Mean monthly rainfall in 2018 was 15.9 ± 28 mm, however the maximum monthly rainfall was high at 97 mm (Fig. 3.4). No rainfall data were available for 2019.

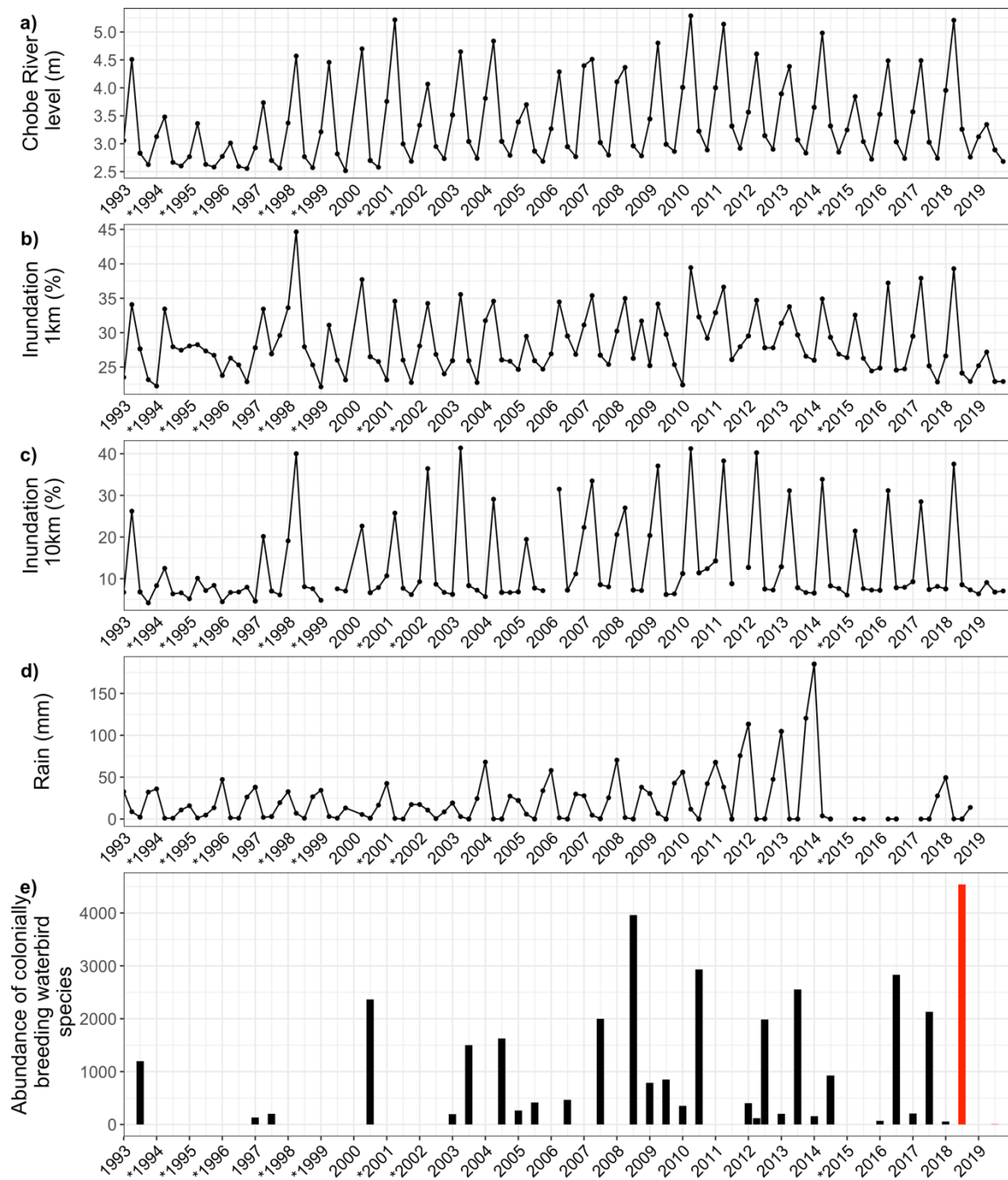


Figure 3.4. Temporal variation (1983-2019) in abiotic variables calculated for every three months; mean percent inundation within a) 1 km and b) 10 km of the colony, c) Chobe River level and d) rainfall and e) total counts (max. of three monthly counts for each species summed) of the six colonially breeding species (African darter, African openbill, African spoonbill, reed cormorant, white-breasted cormorant, yellow-billed stork), counted along the Chobe River by citizen scientists as an indicator of breeding in the Kasane colony, (missing data denoted by *), with maximum species drone counts summed (red).

Waterbird abundances of the six colonially breeding species in the citizen science data counted along the Chobe River varied considerably over time, with maximum counts of 108 African darter, 2150 African openbill, 737 African spoonbill, 2179 reed cormorant, 175 white-breasted cormorant and 518 yellow-billed stork. Total abundance of the six species was highest in 2008 (3960 birds) (Fig. 3.4). The combined species' model suggested abundance was related to time of year ($X^2(2, N= 177) = 29.62, p < 0.001$), and negatively to inundation percent within 1km of the colony site ($X^2(1, N= 177) = 4.01, p = 0.05$). Counts were highest June-August, followed by September-November and then December-February (no bird observations March-May). Species' specific models showed abundance relationships to abiotic variables varied. African darter abundance decreased significantly with rainfall ($X^2(1, N= 29) = 4.13, p = 0.04$). African openbills were significantly more abundant in June-August ($X^2(1, N= 28) = 4.75, p = 0.03$) than at other times of the year, and positively related to percent inundation within 10 km of the colony site ($X^2(1, N= 28) = 3.93, p = 0.05$). Abundance of African spoonbills was significantly negatively related to inundation within 1km of the colony site ($X^2(1, N= 30) = 5.53, p = 0.02$). Abundance of reed cormorants was significantly higher in June-August than other times ($X^2(1, N= 30) = 24.86, p < 0.001$). There were no significant relationships between abiotic variables and abundances of white-breasted cormorants. Abundance of yellow-billed storks was significantly higher September-November, than other times ($X^2(1, N= 31) = 33.18, p < 0.001$), and negatively related to increasing rainfall ($X^2(1, N= 31) = 3.99, p = 0.05$).

Maximum annual abundances of all six colonially breeding waterbird species was significantly positively related to maximum Chobe River level ($X^2(1, N= 121) = 22.78, p < 0.001$) (Fig. 3.4). Large abundances of waterbirds, indicative of a colonial breeding event, were supported at a water level threshold of about 4.33m in the Chobe River (Fig. 3.5). This threshold was particularly apparent for the African openbills, African spoonbills, reed

cormorants and yellow-billed storks (Fig. 3.5). Chobe River level reached a maximum of 5.09 m in 2018, when there was the large breeding event but only 3.23 m in 2019 when there was no successful breeding. This matched the river level breeding threshold of 4.33m as predicted by the citizen science data. The predicted threshold level for largescale breeding of the colonial waterbirds in the Chobe River was reached in 67% of years (1993-2019, n=27), a likely breeding frequency of about 7 in every 10 years, under current conditions.

We were therefore able to reject the null hypothesis in support of the alternative hypothesis: there is a relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance, breeding and reproductive success on the Chobe River.

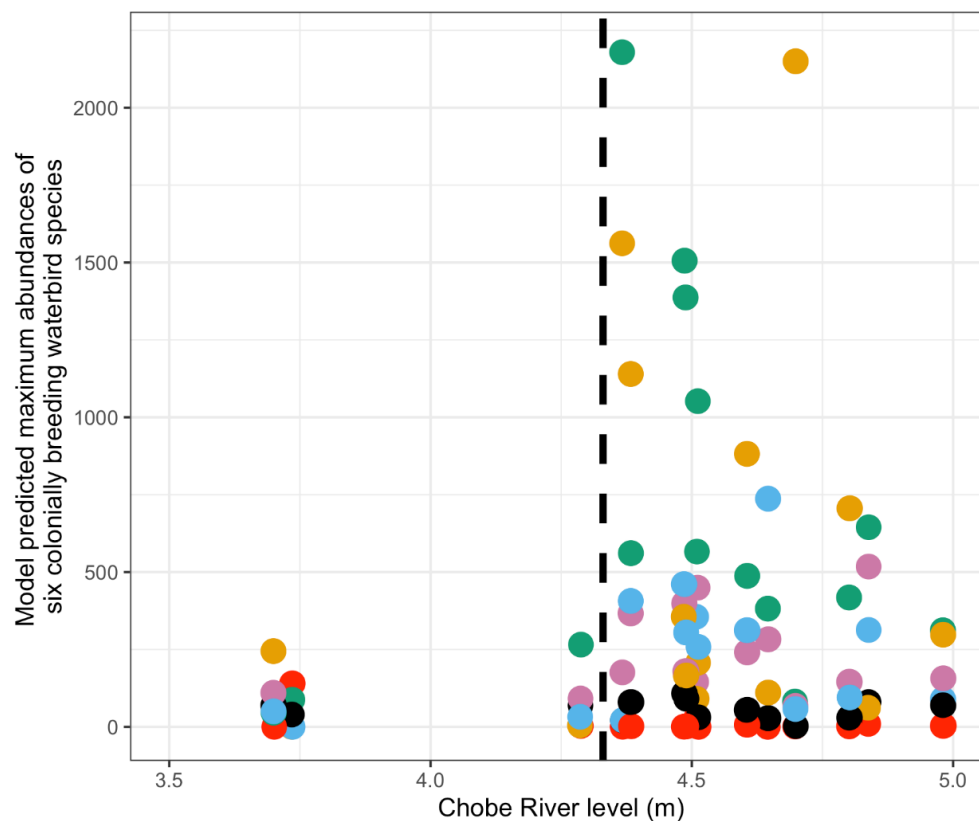


Figure 3.5. Maximum abundances of six breeding waterbird species (African darters (black), African openbills (orange), African spoonbills (blue), reed cormorants (green), white-breasted cormorants (red) and yellow-billed storks (purple)) from citizen science data along the Chobe River in relation to river level (1993-2018) showing the breeding threshold identified using CART analyses (dashed line).

3.5 Discussion

Managing ecosystems for biodiversity is increasingly challenging, but remains necessary for informing natural resource management. River systems are particularly difficult as changes upstream, sometimes thousands of kilometres away, cause large scale degradation and loss of downstream ecosystems. The use of colonially breeding waterbird species as an indicator for such change offers considerable promise, given the relationships between breeding and reproductive success, reflecting changes in ecosystem flow and flooding. On the Chobe River, colonial waterbird breeding was related to river flows, with larger breeding events occurring with larger floods, likely indicative of widespread flooding downstream and increased food resources, as in other colonially breeding waterbird species (Poiani 2006, Arthur et al. 2012). This provides an opportunity to use the breeding of waterbirds to track anthropogenic impacts on this river, such as upstream river development in the form of dams on ecosystem biodiversity. Our drone surveys proved effective in monitoring reproductive success, allowing assessment of changes within and between years and differences among species. Using available hydrological models, it would be possible to use the breeding of colonial waterbirds to hindcast, as we showed, as well as forecast potential water resource developments or other scenarios (e.g. climate change) and their effects on the breeding of colonial waterbirds.

There are increasing numbers of dams, agricultural areas and rising populations across Africa, modifying flow and flooding regimes, land cover and water tables (Mahé et al. 2013). Water resource development is predicted in Angola (African Development Bank 2017), Namibia, Zambia and Botswana, leading to the building of dams and increased water extraction from the Chobe River (and its upstream tributaries). This will reduce flows in the Chobe River and detrimentally affect dependent downstream ecosystems, including the Kasane waterbird breeding colony, as well as wildlife dependent on the Chobe River in

Chobe National Park. Further, climate change impacts are predicted to decrease rainfall by about 10%, reducing river flows by 28-58% across Botswana (De Wit and Stankiewicz 2006).

Waterbird breeding could be used to estimate environmental impacts of any proposed dams or water extraction or other long-term changes on ecosystems. Our modelling showed the Kasane colony is located in an area of high inundation with low inundation variability (relative to the broader landscape within the 10km buffer), ensuring the colony experiences sufficient flooding to support breeding, which was also strongly linked to river levels, as with other breeding colonies (Kingsford and Auld 2005, Connor and Gabor 2006). Water resource development impacts on this colony and its birds could be forecasted, using hydrological models which predict annual river level changes in the Chobe River, using our identified threshold for breeding (Fig. 3.5). Further understanding of the relationships between breeding and hydrology at this colony requires effective measures of breeding and reproductive success, which can be regularly conducted into the future.

We found drone surveys to be particularly useful in collecting detailed information on breeding waterbirds and their reproductive success, and is a method that can be easily repeated. A great advantage is their ability to collect good data from a distance, keeping people safe from potentially dangerous systems such as the Kasane colony's fast-moving turbulent water, crocodiles and hipopotamuses. Drone survey data differed in its effectiveness, with drone surveys more effectively surveying some breeding waterbird species than others. For example, yellow-billed storks were one of the easiest species to survey due to their size, and their nest location in the canopy, with parents often standing to shade chicks providing a clear view of nest contents. Species such as reed cormorants which nested below the canopy were often obscured, making estimates of reproductive success impossible although counts of nests could be done (Fig. 3.3). Advances in camera resolution

may improve monitoring of such species. Such problems also plague traditional ground surveys, given the difficulties of observing nests from below. Our aerial drone surveys also effectively tracked movements between nests by juvenile or fledgling birds, including créching, given imagery covered entire trees. Importantly, drones covered an extensive area, likely to improve with enhanced future battery life. Further, processing of drone data will be more efficient with semi-automated drone counting of imagery (Chabot et al. 2018, Francis et al. 2020).

Obscured eggs and chicks meant we had to ‘correct’ drone imagery to estimate actual reproductive success using average clutch size data (Fig. 3.2, Appendix 3.2). If this step was not done, and obscured egg counts used this may result in a lower egg count, overestimating reproductive success. Backwards filling the eggs is more likely to give an accurate reproductive success, albeit slightly underestimated as average published egg number may be higher than the true egg number in the colony, leading to a higher ‘corrected’ loss and a lower reproductive success. The lack of loss documented between the chick to juvenile stage (Table 3.1) can be allocated to the back-filling process: as juveniles were often easier to see in drone imagery (due to size), they had higher counts, which then replaced obscured chick counts, meaning no loss was recorded. Also, chicks were aged when first sighted on the imagery, meaning it is possible that age is underestimated as the drone may not have captured the chicks early after hatching as they sheltered under parents. Nest success provided a measure independent of clutch size, which is particularly useful considering the difficulties of viewing eggs in drone imagery. The inclusion of nest days accounted for the different number of days a certain nest may be monitored, depending on when nesting began: the more time a nest is monitored, the more likely “accidents are to happen” and nests are to fail (Mayfield 1975). This reduced the likelihood of overestimating nest success, but this method lacked the same level of detail as reproductive success. For this reason, we used both indices and there

are data collection options which could improve data quality in further studies. This includes flying at the hottest part of the day when adults stand using their wings to shade the nest, improving visibility of nest contents. Also, frequency of drone surveys could be increased, improving data acquisition (Erwin and Custer 1982). We recommend a low frequency at the beginning of the breeding season, when birds are sensitive to disturbance (personal observation). Importantly, drone surveys are transferrable spatially and temporally, allowing monitoring of differing colonies.

At the most basic level, these rigorous drone survey data highlighted the conservation importance of the Kasane breeding colony. Our count of 3500 African openbills (Fig. 3.3) approaching 1% of the estimated global population (300,000-500,000) (BirdLife International 2018), makes Kasane as important as more well-known waterbird breeding colonies in the Okavango Delta, established as Important Bird Areas (IBAs). Importantly, eggs and chicks of African openbills are being harvested when river levels decline and the colony is accessible by foot, with no formal status as a protected area or IBA. This was probably the main reason for their low reproductive success (Fig. 3.3). We recorded six colonially breeding waterbird species but green-backed herons *Butorides striata* and grey herons *Ardea cinerea* and egret species *Egretta sp.*, have also bred in in small numbers (~5 nests) in other years (pers comm Lyn Francey), further highlighting the diversity and importance of this colony.

African spoonbill abundance significantly increased along the river as flood area receded within 1 km of the colony (Fig. 3.3), probably reflecting concentration of prey (e.g. fish, macroinvertebrates)(Maclean et al. 2011). This process was similarly reflected in increased abundance of yellow-billed storks after the flood (e.g. highest in September-November). Contrastingly, African openbills and reed cormorants were at peak abundance nearer the peak of the flood when there was significant flooding within 10 km of the colony site. Possibly,

this also related to peak abundance in their food resources and ability to capture the food. Although these relationships were not clear in all species, it was clear that large scale breeding in the colony only occurred in flood years when the river was high. The citizen science data, which were used to develop the river level threshold, supported the two years of quantitative data we had for the colony, and provides historical waterbird counts of the colony not recorded elsewhere. Importantly, the use of these data was not intended to explore waterbird population status along the Chobe River, given the small spatial scale of our study and the highly mobile nature of waterbirds. Low counts may reflect this movement, not population reductions.

As well as differences in timing, reproductive success varied among species (Table 3.1), also probably reflecting availability of food resources for their chicks. Yellow-billed storks had the highest reproductive success, higher than reported elsewhere (Parsons 1977, Maclean et al. 2011). They nested high up in the canopy, probably protected from nest harvesting with some evidence for re-laying (Parsons 1977)(Appendix 3.5). Nesting location within a tree could have affected reproductive success of other species as well, with increased height potentially conferring more protection from ground predators and other disturbances. Yellow-billed stork reproductive success increased with increasing availability of shallow pools for foraging (fish, crustaceans and insects (Maclean et al. 2011)), probably at their highest availability in October when chicks were almost mature. This was the same for African spoonbills, as reported elsewhere in southern Africa (Kopij 1997, Maclean et al. 2011). Reproductive success of African darters, like their abundance, peaked earlier, soon after the Chobe River level dropped to about 3.5m, but then declined as determined for a colony in Ghana (Maclean et al. 2011). These deep water feeders may have their highest food availability soon after flows begin to drop and fish are recruiting, before fish are concentrated in shallow pools and more easily predated by shallow foraging birds and other predators such

as crocodiles. The patterns for African openbills were not easily interpretable, even though our reproductive success estimates were similar to others (Maclean et al. 2011). These differences in feeding strategies, timing, and resultant differences in reproductive success probably reflect species specific responses to a changing flooding environment and food availability, varying for different foraging groups (Kingsford et al. 2010). Such differences among species based on their foraging behaviours were similar in the Okavango River, likely reflecting the ‘exploitation hypothesis’ where birds move towards resource-rich patches to exploit high food abundance driven by the flow regime (Cumming et al. 2012).

In conclusion, we showed that the breeding of colonial waterbirds in the Kasane waterbird breeding colony could track hydrological change, and if there are significant declines in flows resulting from water resource developments upstream or climate change or management of water (Brandis et al. 2011, Bino et al. 2014) the colony will suffer. The Kasane colony is supporting high numbers of breeding waterbirds, and should be declared as an IBA, particularly for African openbills. Drones proved to be a highly effective method for surveying this difficult to access and dangerous colony while limiting disturbance to breeding birds, with considerable application around the world. Our study demonstrated that species in waterbird breeding colonies can be useful indicators of not only broad water availability and water resource developments, but requirements of individual species differ and can therefore reflect a range of unique ecosystem functions and processes.

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3.8 Appendices

Appendix 3.1. *Descriptions of the visual cues in drone imagery, used to classify birds into the chick, juvenile, fledgling or adult stages, were informed by brooding data (Maclean et al. 2011). These calculations allowed estimates of reproductive success for four colonially breeding waterbird species in the Kasane colony (May-October 2018).*

Species	Adults	Chick - Juvenile	Juvenile - Fledgling
African darter	Brown plumage under the neck, long sharp bill. Slightly larger than the reed cormorant, but size is not always a useful determinant in drone imagery.	Adult colouring (brownish-blackish feathers) started to replace white down feathering at about 28 days.	Fledglings started venturing from the nest at around 50 days and developing visible flight feathers. At this stage they had almost totally lost the white plumage.
African openbill	Largest birds in the colony, heavy bill. Iridescent plumage.	Loss of fluffy down around 25 – 40 days.	Differentiated by back-dating approximate fledling age at 55 days, as other changes difficult to see.
African spoonbill	All white plumage, pink flat bill and reddish cheeks.	Bill is yellow instead of pink and has formed its distinct spoon shape (~25 days).	Differentiated by back-dating approximate age at 35 days, as other changes difficult to see.
Yellow-billed stork	White plumage with black wing tips, bright yellow bill.	Loss of down feathering, and early growth of flight feathers visible. The black bill started fading (~35 days).	The turning of tail feathers to black and the total yellowing of the bill at approximately 55 days after hatching.

Appendix 3.2.1. Backwards filling for nesting data

Parents often obscured eggs and chicks and so we needed to estimate the number of offspring for these obscured nests, particularly for early imagery when chicks were difficult to see and eggs were being incubated. For example, if there were 3 chicks (juveniles or fledglings) one month after nesting started, there must have been a minimum of 3 eggs. But, between our surveys, one or more eggs, chicks, juveniles or fledglings could have been lost. A simple backwards filling method could underestimate the true numbers of eggs and therefore overestimate reproductive success. To cater for this, we used average known clutch size for the species. If after backwards filling, the egg number fell below average clutch sizes, we increased the number to average clutch size. If actual clutch for this example was lower, then reproductive success could be underestimated. We used published average clutch size data but our own clutch size estimates for the African openbills as we had more of these sightings in our data than elsewhere in the literature (Appendix 2.2).

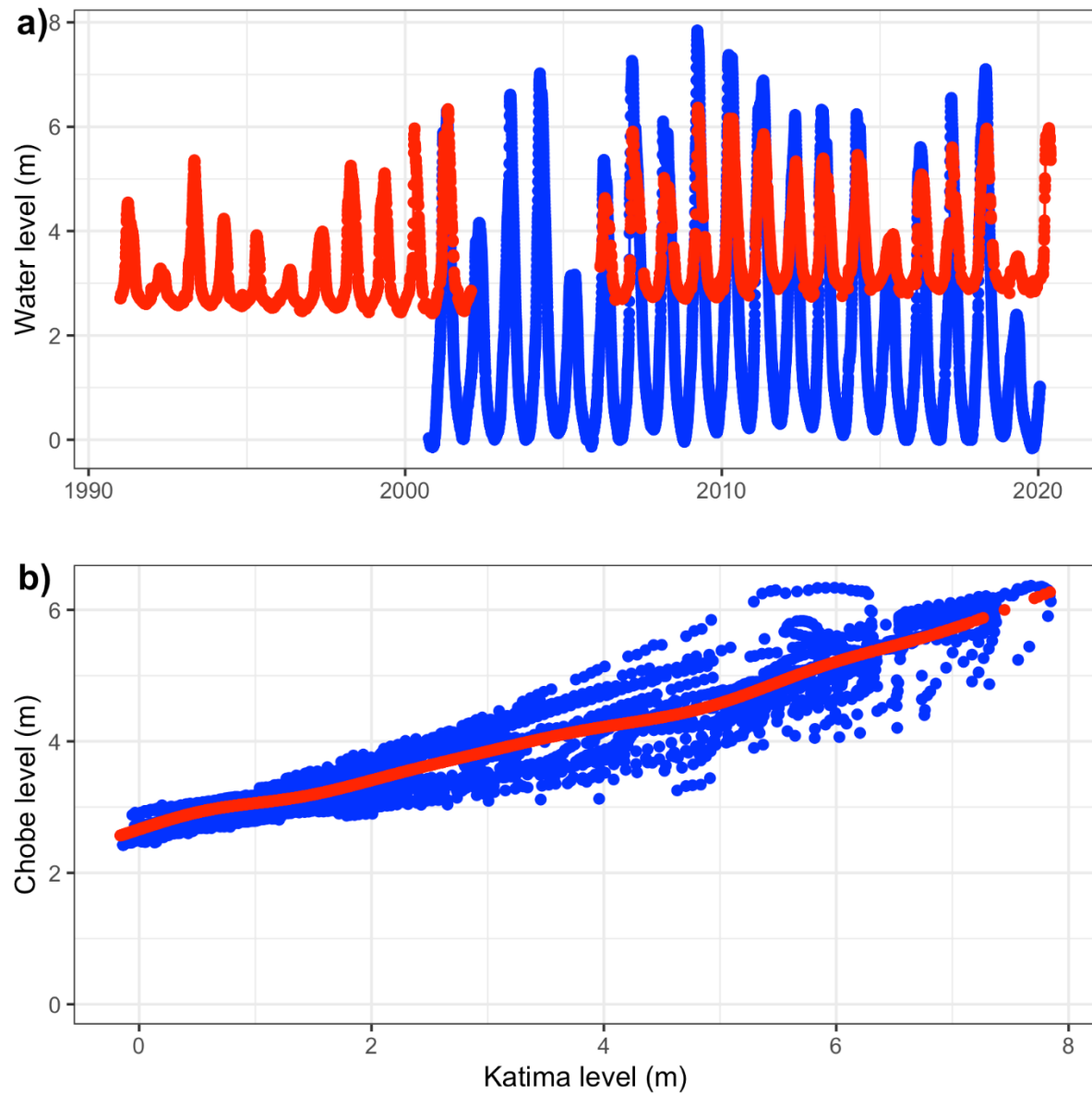
Appendix 3.2.2. Mean egg counts (clutch size) ($\bar{x}$ (n, max)) for six colonially breeding waterbird species recorded in our drone imagery, and the mean ($\bar{x}$ (n)) published clutch size for southern Africa (Maclean et al. 2011).

Species	This Study	MacLean et al (2011)
African darter	NA ²	3.2 (826)
African openbill ¹	3.47 ± 0.82 (68, 4)	3.9 (28)
African spoonbill	2.86 ± 0.38 (7, 3)	2.6 (303)
Reed cormorant	2 (2,1)	
White-breasted cormorant	NA ²	
Yellow-billed stork	1.82 ± 0.60 (11, 2)	2.6 (51)

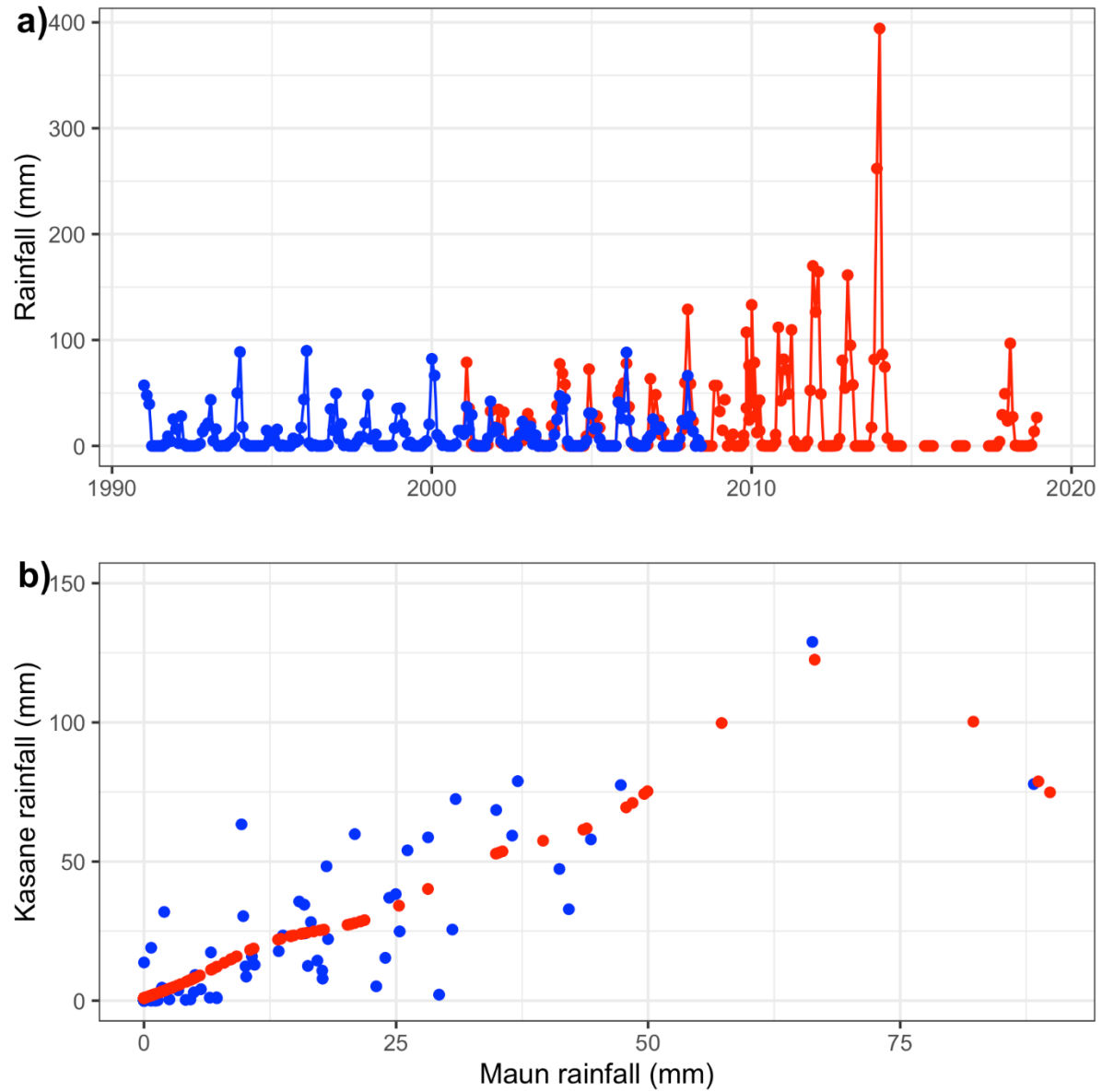
¹Our data from drone imagery were greater than available in the literature and so we used our own clutch size in further reproductive success calculations.

²No egg sightings in the drone imagery.

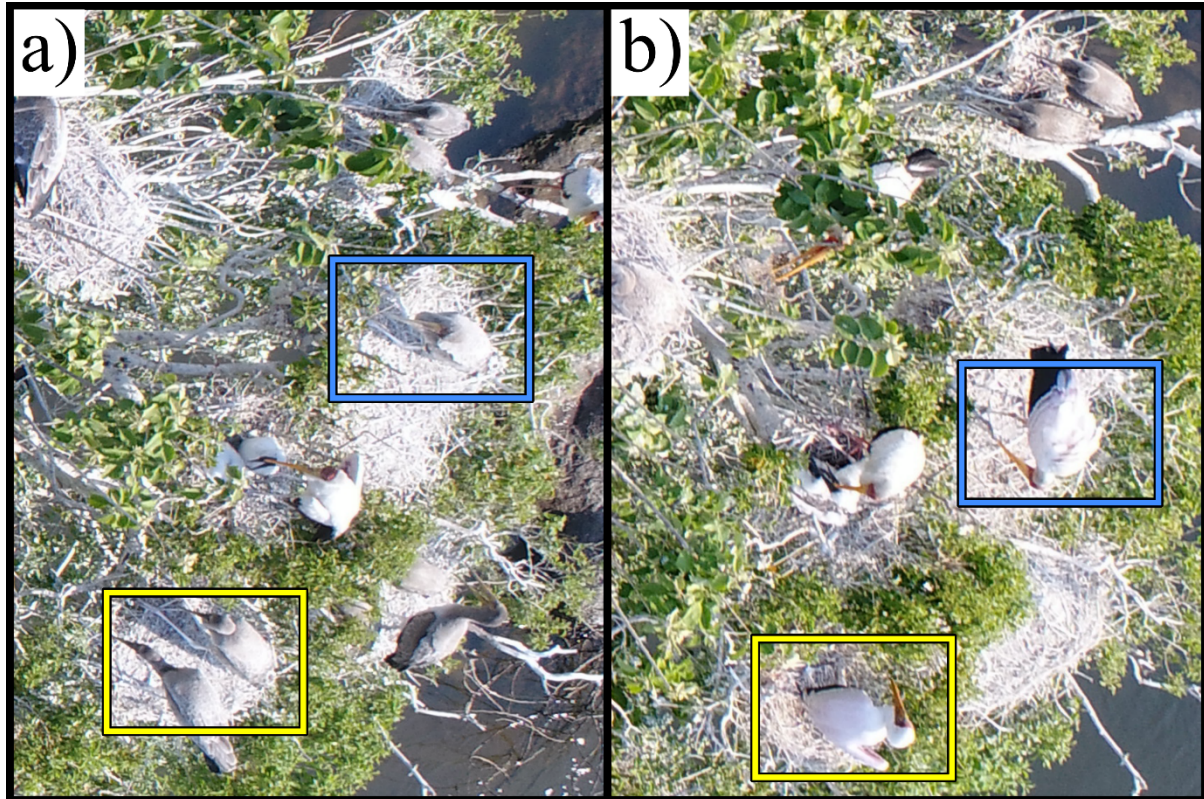
Appendix 3.3. Relationships between a) daily Chobe River level at Kasane (red) and Zambezi River level at Katima Mulilo (blue) and b) the results of gam modelling, filling gaps in data for the Chobe River.



Appendix 3.4. Relationships between a) monthly mean rainfall at Kasane (red) and Maun (blue) and b) results of gam modelling filling gaps in Kasane rainfall data.



Appendix 3.5. Evidence of re-nesting for Yellow-billed storks, where the same nests occupied by chicks and juveniles on the 4th September 2018 (a), were subsequently occupied by adults sitting on eggs on the 15th September 2018 (b).



Chapter 4. The Okavango Delta's waterbirds –trends and dependencies

Francis, R., Bino, G, Inman, V., Brandis, K., Kingsford, R.T.

Parts of this manuscript have been accepted for publication in *Global Conservation and Ecology*. I led study design, methods creation, equipment purchasing, permit applications, fieldwork, data collection and compilation, analysis and writing.

4.1 Abstract

The Okavango Delta is renowned as an extraordinary ecosystem of high biodiversity, listed as both a Ramsar and World Heritage Site, with part protected in the Moremi Game Reserve. This extensive floodplain ecosystem has 444 recorded bird species, with just under a quarter of these waterbirds, including at least 16 breeding and 4 threatened (1 endangered, 3 vulnerable) species. Despite the global importance of this ecosystem, there are surprisingly few long-term assessments of status of the ecosystem or waterbird communities, a key indicator of ecosystem health, with threats such as upstream water extraction, and climate change threatening its outstanding biodiversity. We compiled a comprehensive 53-year dataset comprised of citizen science and other datasets (1970-2019), on 36 waterbird species (Anhingidae, Ardeidae, Ciconiidae, Gruidae, Pelecanidae, Phalacrocoracidae, and Phoenicopteridae), including eight waterbird breeding colonies in the Okavango Delta. We investigated trends in waterbird biodiversity as well as responses to temperature, flow, flooding, and local rainfall. Waterbird breeding colonies were associated with relatively high areas of riparian woodland, and experienced moderate flooding frequencies (> 1 in 5 years). Total abundance of all 36 waterbird

species was positively related to river flows. Despite increased citizen science effort over time, total abundance within the Okavango Delta significantly declined with declining average inundation. Four species led these declines (African darter *Anhinga rufa*, green-backed heron *Butorides striata*, slaty egret *Egretta vinaceigula*, squacco heron *Ardeola ralloides*) and one marabou stork *Leptoptilos crumenifer*, increasing (only sufficient data to analyse 15 species individually). Decreased inundation within the Delta and other internal factors (urbanisation, tourism, vegetation change), as well as external factors (habitat loss elsewhere), are likely driving these declines. Rigorous monitoring of waterbirds, including the eight breeding colonies across the Delta, is needed to explore these changes closely, providing baselines in the case of water resource developments on the rivers supplying the Okavango Delta. Long-term conservation of the magnificent Okavango Delta and its dependent biodiversity, including its waterbirds, is highly reliant on protection of river flows to ensure natural flooding regimes, alongside the conservation of neighbouring wetlands.

4.2 Introduction

The Okavango Delta is an extensive endorheic system of channels, marshes and lagoons fed by the transboundary Okavango River. The Delta is a global biodiversity hotspot, a Ramsar-listed wetland and the 1000th UNESCO (United Nations Educational, Scientific and Cultural Organization) World Heritage Site. It supports eight large herbivore families, many more antelope species, and 444 species of birds (UNESCO 2014, Hancock & Weiersbye 2015) of which 22 are globally threatened. Of the bird species, 104 are waterbirds (Herremans 1999, Lepage 2020), including the vulnerable maccoa duck *Oxyura maccoa*, slaty egret *Egretta vinaceigula* and wattled crane *Bugeranus carunculatus* and near threatened lesser flamingo *Phoeniconaias minor*, with core populations in Botswana. The rivers of the Okavango Delta,

with the Chobe River, have the highest diversity of waterbirds in Botswana, particularly in the dry season, when the Delta's backwaters and floodplains support high densities of waterbirds (Herremans 1999). High diversity and abundance of waterbirds reflects differential responses to temporal and spatial hydrological variation, with community composition of foraging guilds reflecting changing inundation patterns of the Delta (Cumming et al. 2012).

Globally, waterbird populations are in decline (Delany & Scott 2006), with the Palearctic – African region comprising one of the higher proportions of threatened waterbirds: 16% of all species (Kirby et al. 2008). This is primarily due to habitat loss and degradation (Kirby et al. 2008, Northrup et al. 2019, Wetlands International 2020), particularly the modification of rivers, lakes and floodplains to meet human demands, usually overlooking associated ecosystem services (Nilsson et al. 2005, Kingsford, Lemly, & Thompson 2006, Vörösmarty et al. 2010). As a result, wetlands and their biodiversity are in global decline, degrading at a higher rate than marine and terrestrial ecosystems (McLellan et al. 2014). Currently less than one fifth of the world's pre-industrial wetlands remain (Albert et al. 2020). Such dramatic losses have serious consequences not only on biodiversity but also human communities, as freshwater ecosystems provide clean water, food, recreation, and other ecosystem services at an estimated US \$4 trillion annually (Darwall et al. 2018). With rising human populations such threats will only increase alongside the demand of freshwater resources (Arsiso et al. 2017, Darwall et al. 2018, Seeteram et al. 2019).

Tracking changes in the status of expansive internationally important wetland ecosystems is generally poorly implemented around the world (Kingsford et al. 2021) partly because of lack of resources but also lacking suitable indicator species (Landres, Verner, & Thomas 1988, Carignan & Villard 2002, De Cáceres et al. 2010). There are few large-scale analyses of changes to the

Okavango Delta's freshwater flora and fauna, except regular surveys of groups of vertebrates (Chase 2011, Chase et al. 2015, Chase et al. 2018). Census counts and studies of waterbirds exist (Douthwaite 1979, Fraser 1971, Tyler & Bishop 1998, Dodman & Diagana 2007), however these are largely dependent on volunteer availability. With the exception of a few papers, which explore waterbird responses to the hydrological regime of the Okavango Delta (Cumming et al. 2012, Kopyj & Paxton 2019) (1991-2007), there is little published information on the specific responses of waterbirds to flooding in Botswana or links to breeding and reproductive success. Waterbirds are a highly responsive indicator group to long term changes in flow and flooding regimes, given their dependence on fresh water for nearly all aspects of their life history (Desgranges et al. 2006, Frederick et al. 2009, Brandis et al. 2018). They are also easy to detect, congregating in large numbers, and are valued by the public (Green & Elmberg 2014), providing an increasingly important source of data for citizen-science analyses (Bonney et al. 2014, Callaghan & Gawlik 2015).

Citizen science data can increasingly track long term temporal trends at broader geographic scales than most scientific sampling (Dickinson, Zuckerberg, & Bonter 2010). When linked to remotely sensed data, there provide valuable insights into ecosystem status where there is insufficient monitoring (Chandler et al. 2017). Citizen science data are often available from tourism hot spots, where charismatic species attract visitors to a range of biodiversity (Steger, Butt, & Hooten 2017), such as the Okavango Delta (Mbaiwa 2005, 2017). Citizen science groups in Botswana have monitored and documented avian biodiversity since 1970, providing a valuable dataset for conservation analysis (Rhemtulla & Mladenoff 2007, Hoeksema et al. 2011, Gatti et al. 2015).

The Okavango Delta and its biodiversity, including waterbirds, are threatened by poaching and overharvesting, invasive species, fire, tourism, urbanization and water resource development (Alonso & Nordin 2004, Darkoh & Mbaiwa 2014). The Okavango River starts as the Cuito and Cubango Rivers in Angola and passes through Namibia before reaching the Delta in Botswana (Fig. 4.1). Reduction of flows due to upstream water extraction and damming (Pinheiro, Gabaake & Heyns 2003) represents a prescient threat affecting the entire Delta, including its herbivore, bird and fish populations (Mosepele et al. 2009), also impacting on fire frequency (Heinl et al. 2006) and the livelihoods of dependent farmers and tourism operators (Motsumi et al. 2012, Hambira et al. 2013). Further, climate change is projected to reduce seasonal rains and increase temperatures across Botswana (Wolski et al. 2012), reducing mean flows by up to 26% into the Okavango Delta (Andersson et al. 2006). On a continent where 65% of people are already reliant on limited and highly variable water resources (Vörösmarty et al. 2005), and floodplains are disappearing at accelerating rates (Tockner & Stanford 2002, Smardon 2009, Uddin, Asaeda, & Rashid 2014, Dube et al. 2015) identifying temporal ecosystem changes and potential abiotic and biotic indicators is critical to sustain freshwater biodiversity.

We investigated long-term change in the status of the Okavango Delta, using waterbirds as indicators. We used available citizen science data, collected from a range of sources between 1970-2019 for 36 waterbird species (Anhingidae, Ardeidae, Ciconiidae, Gruidae, Pelecanidae, Phalacrocoracidae, and Phoenicopteridae), given the absence of any other data sources. We then used available environmental and remotely sensed data to 1) determine associations with waterbird abundance; 2) explore temporal trends; and 3) identify flooding and vegetation requirements of key waterbird breeding colonies, exploring current trends in waterbird population status within the Delta and providing baselines for their future conservation. We

therefore tested the following null hypotheses: there is no relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance and there is no decline in waterbird abundance over time in the Okavango Delta.

4.3 Methods

4.3.1 Study Area

Water flows into the Okavango Delta from the Angolan highlands, following summer rains feeding into two main tributaries, the Cubango and Cuito Rivers (Fig. 4.1). The Okavango River starts after the confluence of the rivers, crossing Namibia and entering northern Botswana, where it inundates the Okavango Delta (Fig. 4.1). Seasonal variation in flows and flooding is large, ranging from wide fast flowing rivers and inundated floodplains to a system of connected marshes, river channels and other wetlands in the dry season. Flows arrive from the Angolan highlands between May at the top of the Okavango Delta (known as the upper panhandle) and August (lower distributaries, marshes and streams of the southern delta), supplemented by local rainfall in February-March (Bhalotra 1987, Milzow et al. 2009).

4.3.2 Local environmental data

We compiled data on flow, rainfall, and temperature, across the Okavango Delta. Daily river flow (1974-2019) in the Okavango River came from the Mohembo gauge (Fig. 4.1) which had missing data (2.2%, 1974-1991; 16%, 1991–2019, mainly from 2010). To fill these gaps, we modelled associations between daily flow on the Okavango River at Mohembo with average daily water level from six other gauges across the Okavango Delta (Mohembo, Guma, Little Vumburu, Nxaraga, and Xakanare) (Appendix 4.1) (Okavango Research Institute 2020). We used a Generalized Additive Model (GAM), an extension of a Generalized Linear Model with an

optimized smoothing function that allows for the fitting of non-linear data using the ‘mgcv’ package (Wood 2011). We assumed a Gaussian distribution, confirmed using the gam.check function to inspect model residuals (Wood 2011). Much of the variation was explained (83%), allowing filling of missing daily flow for Mohembo ($GCV_{14409} = 4061.8$, $P < 0.001$), (Appendix 4.2). We also collated daily rainfall data from six gauges across the Okavango Delta (Maun airport, Disaneng, Guma, Nxaraga, Sexaxa and Xakanare) (Appendix 4.1) (Okavango Research Institute, 2020). As availability of rainfall data varied in frequency and duration, we calculated the average daily rainfall across all six gauges (Fig. 4.2). Further, we used average daily temperature data from four gauges across the Okavango Delta (Shakawe, Sexaxa and two gauges in Maun) (National Oceanic and Atmosphere Administration, 2020; Okavango Research Institute, 2020).

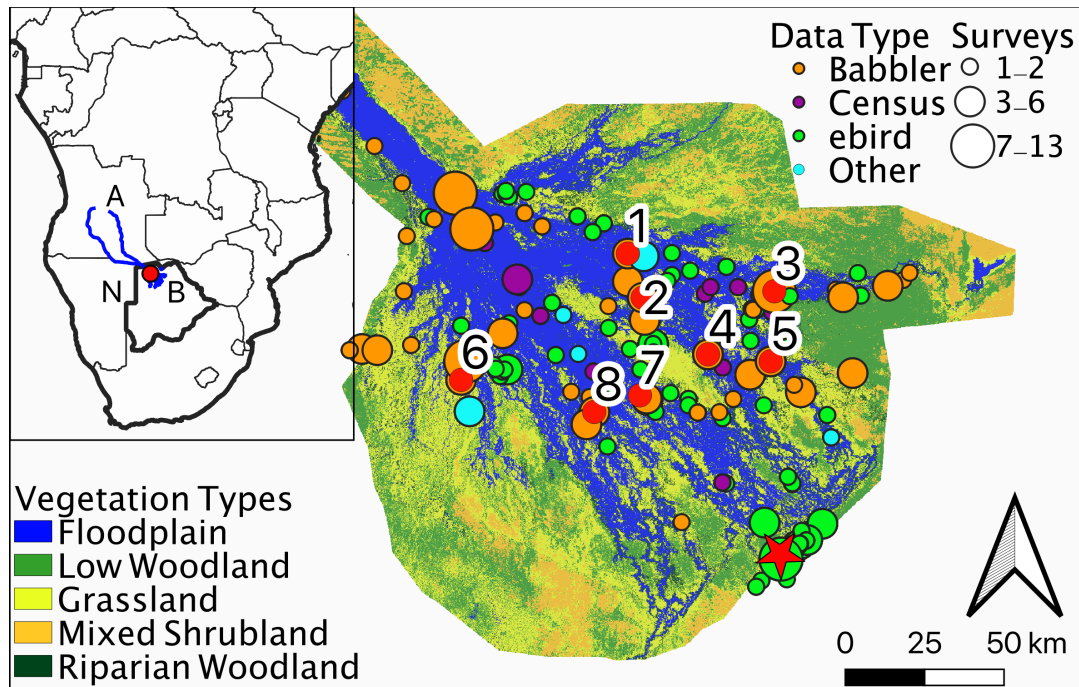


Figure 4.1. The Okavango Delta (red dot on lower half of southern Africa inset), in north-western Botswana (B), near the town of Maun (star), where citizen science data were collated from 4 grouped sources 1970-2019 (numbers of surveys shown with different sized circles), receives flows from the Cubango (western tributary) and Cuito (eastern tributary) Rivers in Angola (A), through Namibia (N), showing the eight key waterbird colonies (1. Xobega, 2. Gadikwe, 3. Xakanaxa, 4. Xini, 5. Xho, 6. Xugana, 7. Xaxaba, 8. Kanana) with five major vegetation classes (Inman 2020).

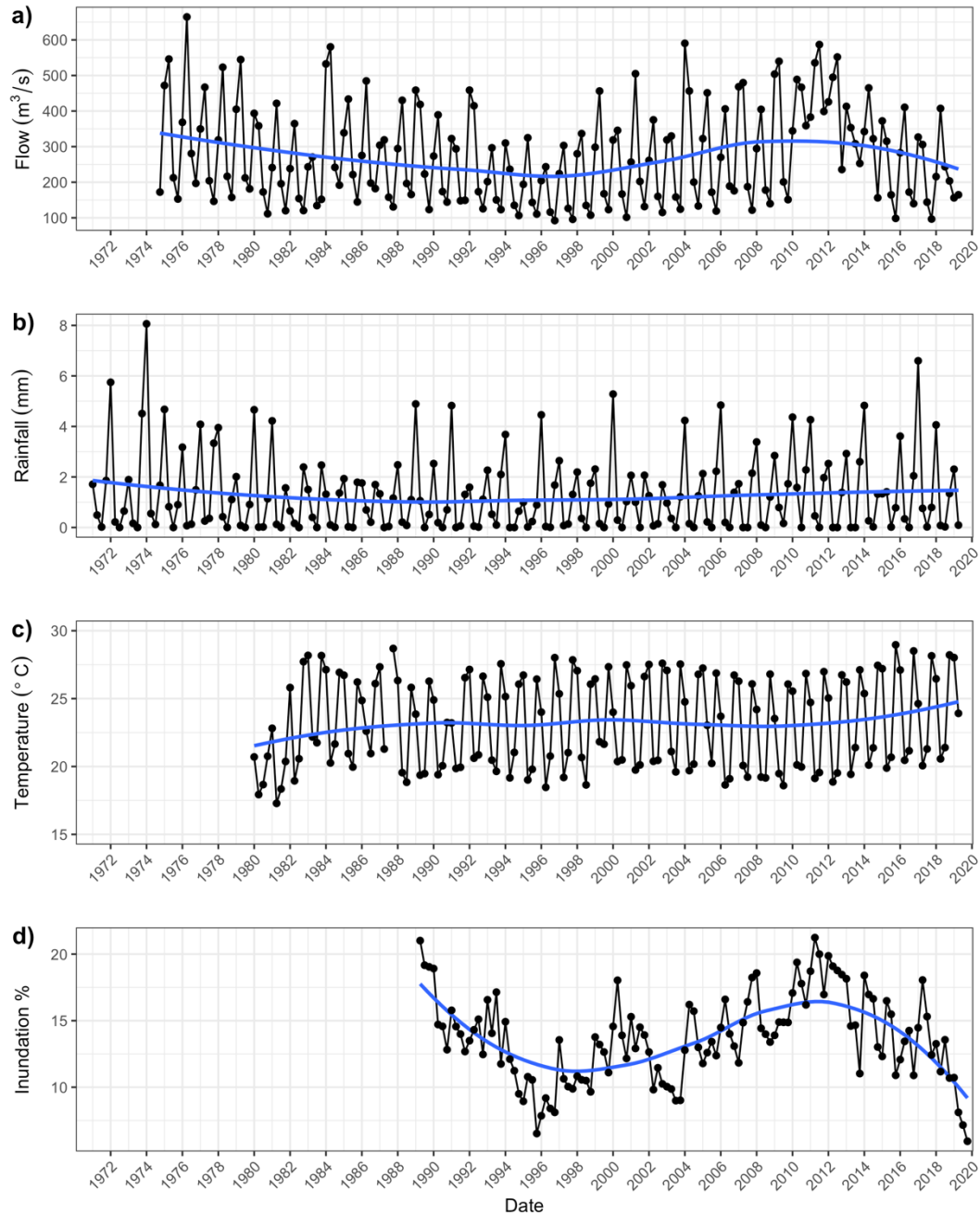


Figure 4.2. Quarterly measurements and a loess smooth (blue line) of a) river flow (gauges Appendix 4.1, 1974-2020); b) rainfall (gauges Appendix 4.1)(1970-2019); c) ambient temperature (gauges Appendix 4.1)(1980-2019) and d) percent of mapped inundated area at the Okavango Delta from 1989 – 2020 ($n=127$).

We used Google Earth Engine (<https://earthengine.google.com/>) to calculate area inundated across the Okavango Delta floodplain (~53,000 km², the Delta boundary as delineated in the flood imagery, Appendix 4.1) (Gorelick et al. 2017), from Landsat-5, 7 and 8 images (Inman & Lyons 2020). We combined available images (2072 images from January 1989 - December 2019), taking the median pixel value, at 3-month intervals (Jan-Mar, Apr-Jun, July-Sep, Oct-Dec which aligned with flooding cycles). Pixels (30m) were then classified as either wet or dry, using a method designed specifically for the Okavango Delta which separated inundated areas from dry land even in areas with emergent aquatic vegetation (Wolski et al. 2017, Inman & Lyons 2020). Classification accuracy was 92-98%, dependant on the testing method (see Inman & Lyons 2020). For each 3-month period, we calculated the percent inundation: the number of ‘wet’ pixels/ total number of pixels within the assigned Okavango Delta boundary (Appendix 4.1). We removed three maps with errors, late in the rainy season (Jan – Mar 1996, 2000, 2017), when there was poor spectral separation between dryland and inundated areas after heavy rainfall (Wolski et al. 2017). We also excluded 10% (10 composite images) of the 3-month stacked images that did not cover the Okavango Delta boundary because of a missing scene (January 1991-December 2019). We replaced missing periods with a linear interpolation of percent inundation, using the function ‘na.approx’ in the ‘Zoo’ package (Zeileis & Grothendieck 2005), in the R programming environment (R Core Team 2019)(Fig. 4.2).

To match the three-month windows of the inundation data, we grouped daily flow (Mohembo), rainfall and temperature into the same three-month windows, by averaging the daily values (Jan-Mar, Apr-Jun, July-Sep, Oct-Dec). We assessed long-term trends in flow, inundation, rainfall, and temperature across the Okavango Delta by modelling the three-month aggregations against year (i.e., four separate models) using a Generalized Linear Model assuming Gaussian errors in

the R package ‘*glmmTMB*’ (Brooks et al. 2017). We checked the QQplot and residual vs predicted values of the *glmmTMB* using the DHARMA package (Hartig 2019), which upheld assumptions of normality and equal variance. None of the four environmental variables were strongly correlated ($r < 65\%$) (Zou, Tuncali, & Silverman 2003). We then calculated a three-, six-, nine- and 12-month lag for each environmental variable, accounting for delayed temporal responses in waterbird communities as the ecosystem responds to changing environmental factors eg. prey productivity (Frederick et al. 2009, Henry & Cumming 2016).

4.3.3 *Waterbird citizen science data*

We collated the most comprehensive citizen science data set available, comprising 3105 temporal waterbird abundance observations of 36 species (1970–2019) in the Okavango Delta (see Appendix 4.3 for species’ names), from eight sources: African Waterbird Census (AWC) (Dodman & Diagana 2019), Birdlife Botswana (BirdLife Botswana 1981-2019), eBird (eBird 2019), drone count data at Kanana colony (Francis et al. 2020), published literature (Utschick and Brandl 1986, Randall & Herremans 1994, Herremans 1996, Herremans et al. 2002, Hancock et al. 2003), personal communications from two sources (Mueller 2012, Hancock 2018) and personal observations (Fig. 4.1, Table 4.1). These citizen science surveys listed abundance of all species observed at a particular time of the year, and their location (Fig. 4.1). We focused on the waterbird species that breed colonially in response to flow and flooding regimes, given they are effective indicators of wetland ecosystem health and condition (Frederick et al. 2009, Henry & Cumming 2016). We also included the vulnerable wattled crane and related crowned crane *Balearica regulorum*. For data visualisation, points without an accurate location were assigned to an area. For example, an observation in “upstream Boro River” was assigned an estimated coordinate, however locations were not included in data analysis. Most surveys were point

surveys and many did not record the extent of the survey or the time spent surveying. We could not assess observer identification accuracy, but much of the data came from expert birders or was reviewed and verified before release (eBird 2019). The 36 species selected were also reasonably discernible birds (as opposed to small, fast moving and similarly coloured woodland species). Without further information, we assumed all surveys were similar as they were ground surveys (mostly point surveys) from within accessible (and often popular) areas of the Okavango Delta, hence many survey locations were repeated (183 locations from 422 unique surveys, Fig. 4.1). A survey was considered unique if it was the only survey at a specific location in that month (as many data observations did not include the full date). We explored species' richness and sampling saturation of the citizen science data groups, using species rarefaction curves. We assigned each waterbird species to a foraging guild (Cumming et al. 2012), and a functional group (Sundstrom et al. 2012), using broad dietary preferences (Maclean et al. 2011) (Appendix 4.3). We followed the approach of Sundstrom et al. (2012) as it incorporated both dietary preferences and foraging style into the classification. Waterbird abundances for each three-month period were the mean of counts of all surveys within the three-month period. We chose to use the mean to reflect the variation in abundance across the entire Okavango Delta, as we had done for the environmental variables.

4.3.4 Waterbird analysis

We investigated relationships between waterbird abundances and the four environmental variables (flow, rainfall, temperature, and inundation), restricting this analysis to 1990-2019 because inundation data were not available prior to this date. First, we explored correlation in the predictor variables, finding the 12-month lag was highly correlated with its corresponding variable (e.g. mean discharge and mean discharge with a lag of 12 months). We kept both lags,

due to their potential ecological importance to the model. No plausible model (within 2 ΔAICc of the best fit model) included correlated variables. We modelled the association of our 3-month measure of waterbird abundance in response to the predictor variables flow, rainfall, temperature and inundation, and their 3-, 6-, and 9 and 12-month lagged variables, using a Generalized Linear Mixed Effect Model (GLMM). We also included year and 3-month period (Jan-Mar, Apr-Jun, July-Sep, Oct-Dec) and data collection type (Table 4.1) as a random variable, comprising four broad groups (eBird, AWC, Babbler and remaining types grouped into an ‘other’ category, Table 4.1). We assumed a negative binomial distribution and used the package ‘*glmmTMB*’ (Brooks et al. 2017), within the R environment (R Core Team, 2019). To improve model convergence and interpretation, we standardized continuous predictor variables by subtracting the mean and dividing by the standard deviation (i.e. Z score) (Schielzeth 2010). We also included an offset variable for survey effort, as the natural log transformed number of surveys conducted during the three-month period. Using the ‘dredge’ and ‘model.avg’ functions from the ‘MuMIn’ package (Barton 2019), we assessed all possible combinations of predictor variables. To limit model overfitting, we limited the number of predictor variables to five and only considered models with data collection type and offset of survey effort ($n=4048$, Appendix 4.4). We assessed model fit using the corrected Akaike’s Information Criterion (AICc) (White & Burnham 1999, Burnham & Anderson 2002), averaging model coefficients over the top seven plausible models, within 2 ΔAICc of the best fit model.

To explore individual species’ responses, we identified 15 waterbird species which we considered had sufficient data for analysis (at least 20 three-monthly observations) (Appendix 4.3). We assessed the association between abundances of each of the 15 species and each environmental variable separately (inundation, flow, rainfall, and temperature and their 3-month

lag, i.e., eight models for each species), given the limited data, including year, data type as a random variable and an offset of the log of survey effort. We carried out all statistical analyses within the R environment (R Core Team 2019), and significance of statistical tests was concluded at $\alpha < 0.05$.

Table 4.1. Descriptions of citizen science data sourced comprehensively from all available sources, comprising 3105 waterbird observations of 36 species and abundances (1970 – 2019) of waterbirds and breeding sites across the Okavango Delta (see Fig. 4.1 for distribution of surveys from each source).

Source	Description	Number of surveys	
		(temporal span, years with observations)	Species
The Babbler (BirdLife Botswana 1981-2019)	Biannual publication released by Botswana’s biggest citizen birding organization. This consisted of mainly point surveys at 57 locations in the Okavango Delta. Generally the same locations were recorded over time, and surveys occurred across most of the delta (including the panhandle), except the southwest.	168 (1970-2016, 30)	34
African Waterbird Census (Dodman and Diagana 2019)	The African Waterbird Census (AWC) is part of the greater African-Eurasian Waterbird Census (AEWC), a citizen-based waterbird count, which is part of the broader International Waterbird Census, covering all of Africa, Europe and large parts of South-West and Central Asia. The AWC covered 35 locations spread across the Okavango Delta (mainly in	56 (2011-2017, 6)	36

the eastern channels) which were largely repeated in each year of the survey, and includes transect counts, and point counts.

eBird (Sullivan et al. 2009, eBird 2019)	eBird is the world's largest biodiversity-related citizen science project, managed by the Cornell Lab of Ornithology, receiving > 100 million bird sightings annually, with historic data uploaded to their database (https://ebird.org/home). eBird data covered 100 locations across the delta (Fig. 4.1), with observations ranging from stationary 5 minute surveys to travelling surveys of 240 minutes over 5km. Many surveys were conducted in the south around the town of Maun.	139 (1991-2019, 23)	30
Drone (Francis et al. 2020)	Drone surveys of the Kanana colony were flown at 20 m, with imagery clipped to prevent overlap and birds identified and counted.	2 (2018-2019, 2)	7
Published literature (Utschick and Brandl 1986, Randall & Herremans 1994, Herremans 1996,	Published data of bird observations conducted across Botswana. Data includes multiple survey types, including aerial surveys. Aerial survey data was only recorded when single observations were given (ie. summaries of entire area counts were not used).	40 (1966 – 1999, 16)	13

Herremans et al.

2002, Hancock et al.

2003)

Personal communications M. Mueller (Mueller 2012)	Travelling counts of breeding waterbirds in the Kanana colony were conducted. The entire colony area was surveyed, with an estimated 10 species recorded breeding.	1 (2016, 1)	12
Personal communications P. Hancock (Hancock 2018)	Collated citizen observations collected over years and stored personally by Pete Hancock. This dataset covered 10 locations within the Okavango Delta and largely consisted of point counts.	24 (2001-2009, 7)	14
Personal observations (Francis 2018)	Point counts at the Xugana breeding colony performed by Roxane Francis. Three species were recorded breeding.	1 (2018, 1)	4

4.3.5 Waterbird breeding colonies

We also investigated associations between locations of waterbird colony breeding sites (Fig. 4.1) and vegetation communities and flooding frequency (1970-2019). Colony data were compiled from collated data set from a range of citizen science surveys (Table 4.1), comprising 682 observations across eight colonies (Fig. 4.1). We used existing vegetation classifications, derived from remotely sensed data (pixel size 400m²) across 31,607 km² of the Delta (Inman 2020), which covered all colonies. The five vegetation classes included floodplain (9103 km²), grassland (9186 km²), low woodland (7671 km²), mixed shrubland (3009 km²) and riparian woodland (2638 km²), (Fig. 4.1). For flooding, we estimated the average long-term (33 years, 1984-2019) inundation frequency within 1, 5, 10 km of the colony location, as breeding waterbirds usually forage near their colony sites, but sometimes up to 29 km away (eg. cattle egrets *Bubulcus ibis*) (Siegfried 1971, Dowd & Flake 1985, Bryan Jr & Coulter 1987, Alonso et al. 1991, Gibbs 1991, Tiller et al. 2005). We then classified inundation frequency into the natural quartiles of inundation, producing a range reflecting the average number of years flooded per pixel within the 1, 5 and 10km distances (Q1: 0% flooded, Q2: 0.01-1.6%, Q3: 1.6 – 22.8%, Q4: 22.81 – 100%, Appendix 4.1). We also calculated areas of each of the five vegetation classes across the Okavango Delta within the 1, 5, and 10 km distances from each colony. We then calculated the Manly selection measures, separately for flooding and vegetation, comparing “used habitat” (ie. proportions of flooding quantiles and vegetation types within the buffer areas) to all available habitat, (ie. proportions of flooding quantiles and vegetation types across the entire delta) (selection ratio: used habitat/available), using the ‘ADEHabitatHS’ package, using a Chi-Square test of the hypothesis that the selection ratios are equal to one (Calenge 2006).

4.4 Results

There were no significant changes over time in the three-monthly mean Okavango River flow at Mohembo (1974-2019, $X^2(1, N=179) = 0.03, p=0.86$), three-monthly mean temperature (1980-2019, $X^2(1, N=158) = 0.13, p=0.13$), or three-monthly mean rainfall (1970-2019, $X^2(1, N=198) = 0.95, p=0.95$), (Fig. 4.2). Three-monthly mean inundation percent declined (1989-2019, $X^2(1, N=73) = 0.451, p=0.055$). There were clear seasonal patterns (Fig. 4.2), coinciding with the flooding in the second half of each year.

Over the past 53 years (1966 – 2019), 36 waterbird species were recorded from citizen science and other surveys (Table 4.1) in the Okavango Delta (Appendix 4.3). Split into foraging guilds, most species were shallow water feeders ($n=22$), terrestrial feeders ($n=7$), followed by birds that feed in short vegetation or mud ($n=3$), emergent vegetation including reeds and lilies ($n=2$), and deep water ($n=3$) (Appendix 4.3). By functional group, most waterbirds were aquatic carnivores ($n=24$), aquatic invertivores ($n=5$), terrestrial carnivores ($n=4$), aquatic omnivores ($n=2$) and terrestrial invertivores ($n=1$) (Appendix 4.3). Detection of species across the Delta varied over time, reflecting survey methods and frequency (Fig. 4.3), with increased detection and number of surveys over time. In the years of the African Waterbird Census (AWC, 2011-2017), there were two more species recorded than in other surveys (Table 4.1), including rare and vulnerable species (lesser flamingo, slaty egret, wattled crane, woolly-necked stork) (Fig. 4.3). There was no African Waterbird Census in 2018 and 2019 and these years had no recordings of these vulnerable species (Fig. 4.3) again, showing the importance of the African Waterbird Census. Common species across the Delta were recorded by multiple different survey types, particularly the yellow-billed stork, little egret and African darter, with an increased frequency of species captured by multiple survey types from 2011, reflective of increased survey frequency and the

introduction of new survey methods such as eBird, beginning in 2002 (eBird 2019)(Fig. 4.4). All of the 36 species in the citizen science data were recorded in 2011, 2012 and 2014, encompassing the years with some of the highest inundation percentages since 1990 (Fig. 4.2).

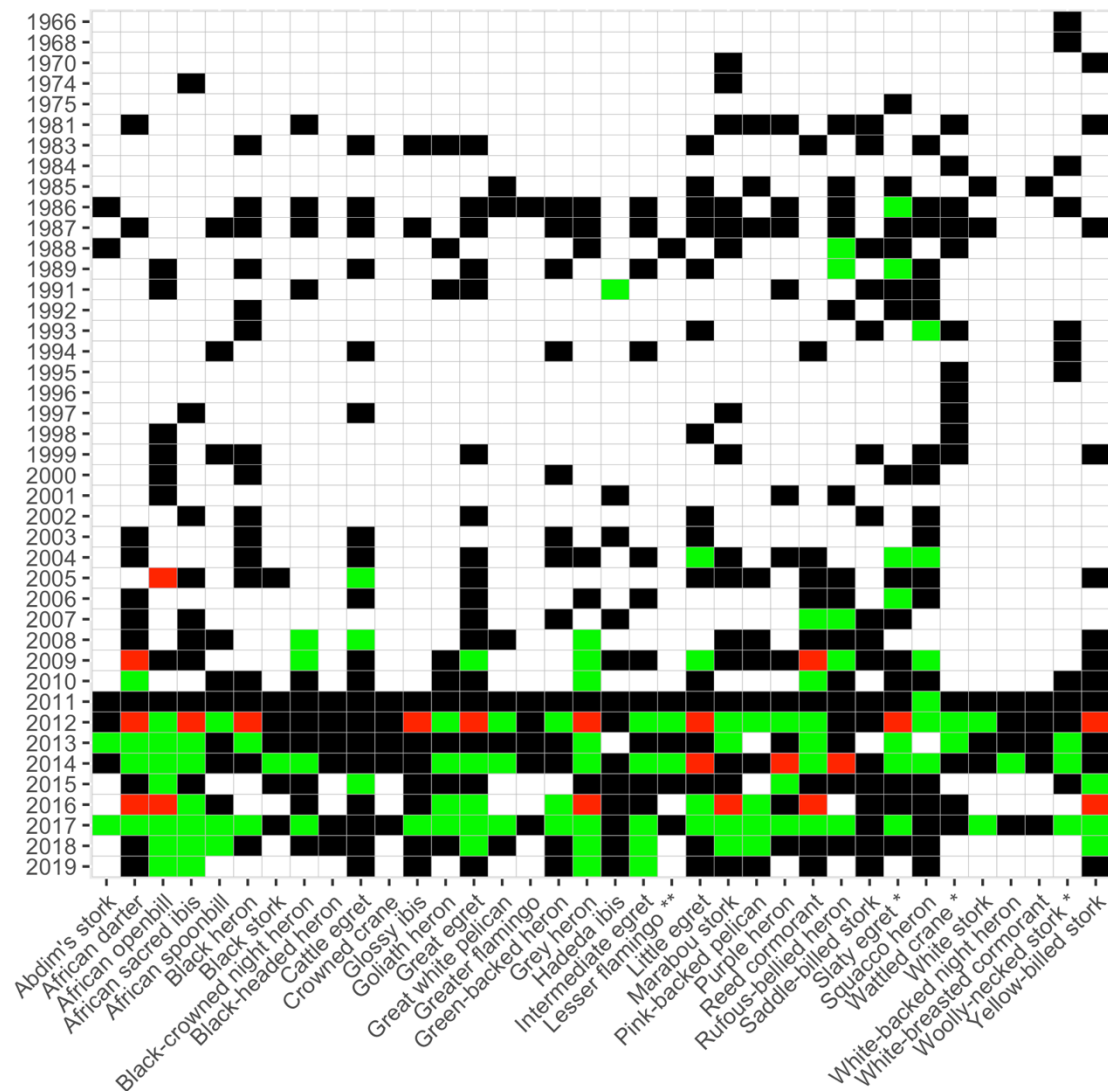


Figure 4.3. Presence of the 36 waterbird species recorded in one (black), two (green) or three or more (red) of the five survey groups (AWC, BLB, eBird, Drone, Other) in the Okavango Delta (1970-2019), identifying vulnerable (*) and near threatened (**) species (Appendix 4.3). Years with no data were omitted.

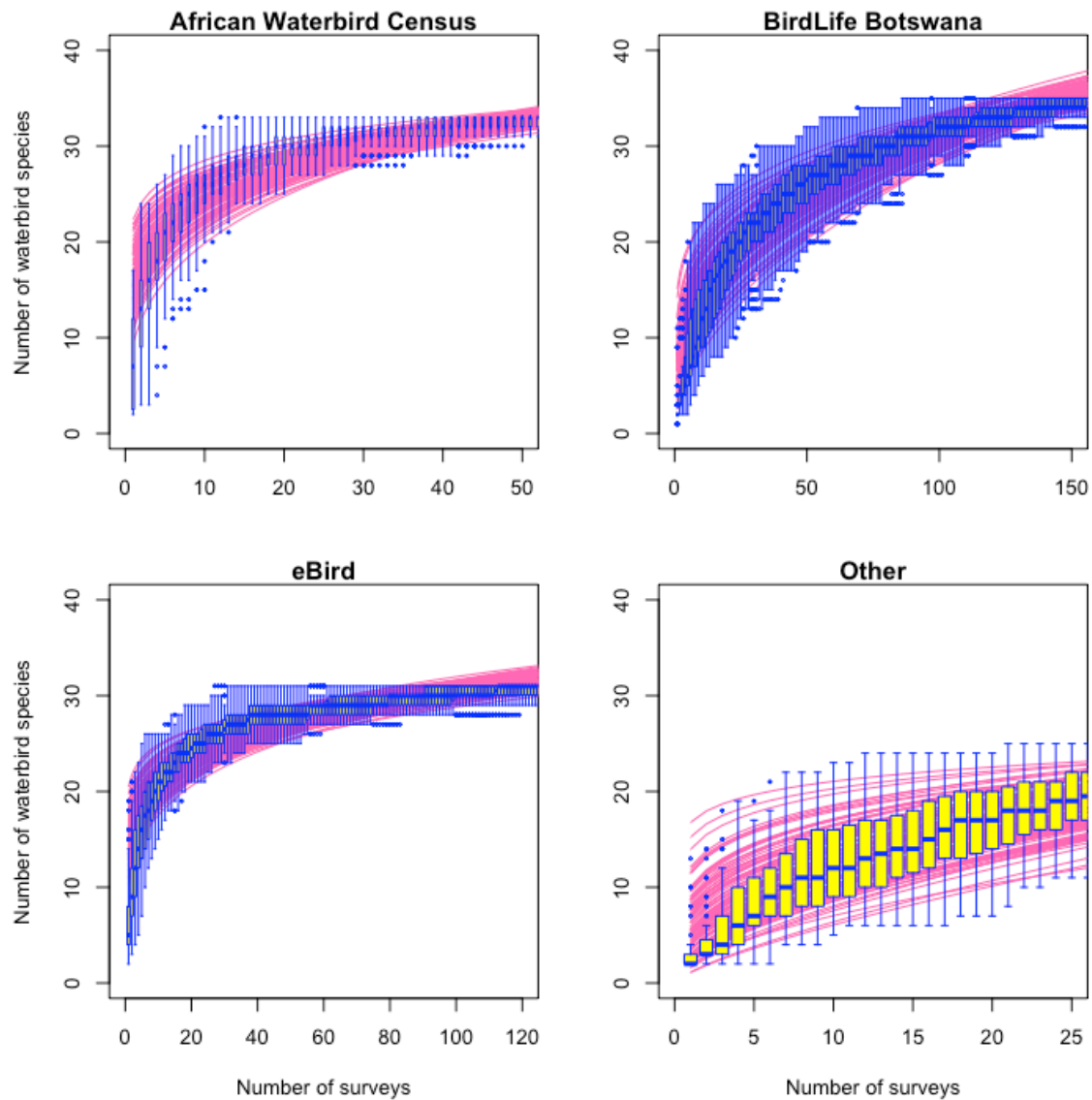


Figure 4.4. Rarefaction curves for numbers of waterbird species accumulated with increasing numbers of surveys for the four survey groups (drone data excluded given few years), 1970-2019.

Survey methods varied in their effectiveness in detecting waterbird species (Fig. 4.4), in relation to the number of surveys. Saturation of species was reached after 19 surveys for AWC (from a total of 56 surveys used), covering the highest number of species (36), 26 surveys for the “other”

survey group covering 19 species (of 66 surveys), ~40 surveys for eBird covering 30 species (of 139 unique surveys), and 100 + unique surveys for Birdlife Botswana surveys recording 34 species (of 168 total surveys). Since 1970, the three most abundant species were the African openbill (representing 25% of total counts), followed by cattle egret (14.7%), and squacco heron (10.4%).

Mean waterbird abundance across the entire Delta was associated positively with lagged quarterly mean flow (3-month) ($p < 0.001$), lagged inundation percent (12-month) ($p = 0.055$) and quarterly ambient temperatures ($p < 0.001$) but negatively with year ($p < 0.001$) (Fig. 4.5). This was on the basis of the averaged seven models within $2 \Delta AICc$ of the best fit model (Appendix 4.4), providing relative importance of each variable (Appendix 4.5). Waterbird abundance declined at a rate of 2.7% per year since 1990 (Fig. 4.5). Of the 15 species with sufficient data to be modelled, five had significant associations with year, of which four had significant negative annual declines (African darter (-8%), green-backed heron (-6%), slaty egret (-9%) and squacco heron (-5%)) while marabou stork increased (1.1%) (Table 4.2). Mean abundance of ten of the 15 species were significantly associated with environmental variables, after accounting for annual trends (Table 4.2). Mean abundances of great egrets and green-backed herons significantly declined with flow, while reed cormorants increased with flow lagged by 3-months. Mean abundance of saddle-billed storks significantly increased with inundation, while squacco herons decreased with inundation. Reed cormorants increased with inundation lagged by 3-months, while rufous bellied herons and slaty egrets increased. Further, mean abundance of little egrets and rufous-bellied herons significantly increased with daily rain and daily rain lagged by 3-months. Finally, mean abundances of marabou storks increased with temperature and African

darters and rufous-bellied herons increased with temperature lagged by three months, while reed cormorants declined.

We were therefore able to reject the null hypotheses in support of the alternatives: there is a relationship between environmental variables (river level, inundation and rainfall) and waterbird abundance and there is a decline in waterbird abundance over time in the Okavango Delta.

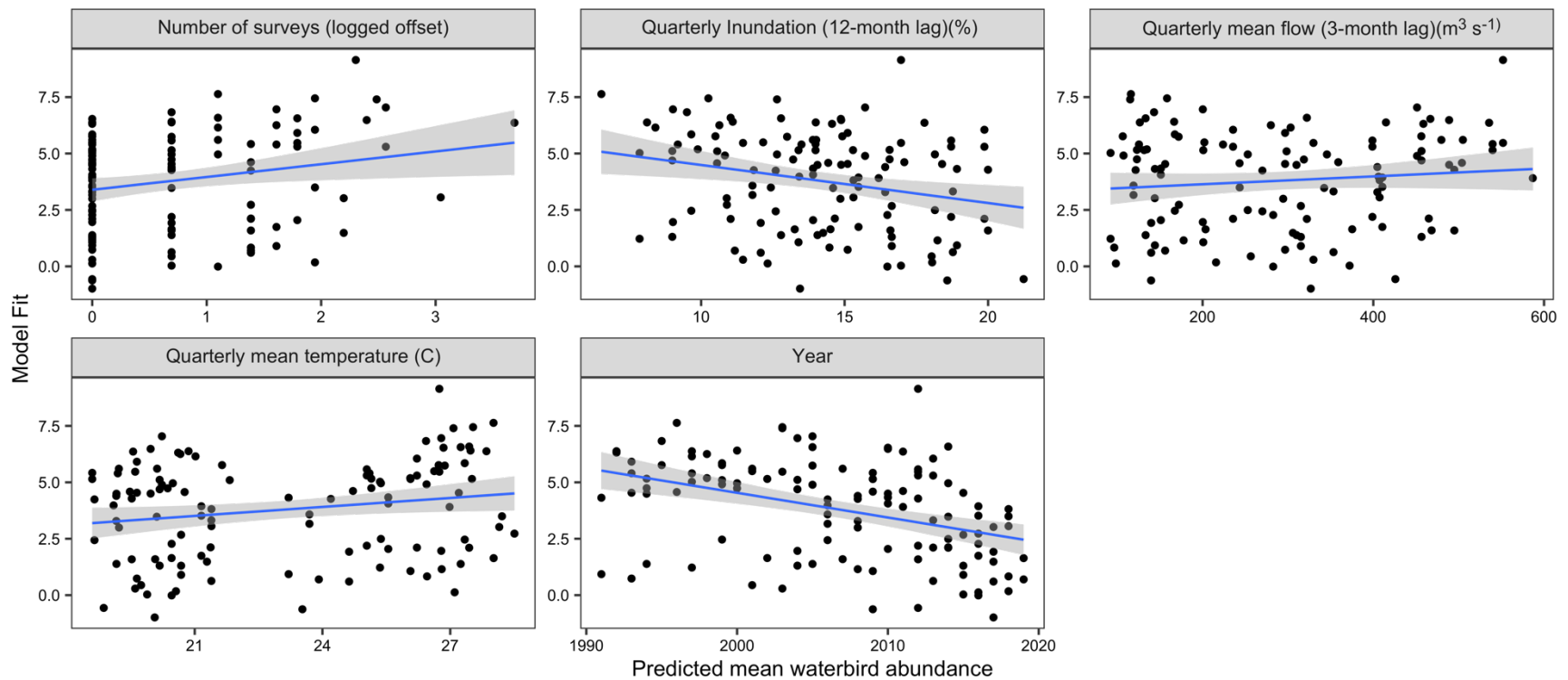


Figure 4.5. Predicted mean waterbird abundance across the Okavango Delta (1990-2019), in relation to model fit of the final averaged model from seven plausible models, showing the five significant predictors, with the blue line representing the linear smoother and its 95% confidence interval (grey shading). The slope of the predictors is dependant on the final averaged value across the seven plausible models, meaning a variable that was consistently highly significant showed a stronger trend.

Table 4.2. Summary of general linear modelling, providing model ΔAIC , where there were significant environmental predictors with their coefficients for abundance of different waterbird species, based on citizen science data (1990-2019, see Fig. 4.1).

Species (n observations)	Model # (ΔAIC) [†]	Predictor	Coefficient	SD	P value
African darter (41)	1 (0)	Year	-0.65	0.22	<0.001
		Quarterly mean temp (3-month lag)	0.51	0.21	0.02
Great egret (39)	1(0)	Quarterly mean flow	-0.59	0.29	0.04
Green-backed heron (21)	1(0)	Year	-1.05	0.28	<0.001
		Quarterly mean flow	-1.12	0.3	<0.001
Little egret (40)	1(0)	Quarterly mean rain	0.74	0.33	0.03
Marabou stork (21)	1(0)	Year	1.15	0.37	<0.001
		Quarterly mean temp	1.88	0.45	<0.001
Reed cormorant (47)	1(0)	Quarterly mean flow (3-month lag)	0.69	0.28	0.03
	2(1.16)	Quarterly mean temp (3-month lag)	-0.63	0.28	0.04
	3(1.35)	Quarterly inundation (3-month lag)	0.67	0.32	0.001
Rufous-bellied heron (22)	1(0)	Quarterly inundation (3-month lag)	-0.94	0.37	0.01
	2 (0.05)	Quarterly mean rain (3-month lag)	0.71	0.30	0.02
	3 (0.29)	Quarterly mean temp (3-month lag)	0.98	0.37	0.01
Saddle-billed stork (21)	1(0)	Quarterly inundation	-0.41	0.20	0.04
Slaty egret (37)	1(0)	Year	-1.42	0.24	<0.001
		Quarterly inundation (3-month lag)	-0.85	0.23	<0.001
Squacco heron (39)	1(0)	Year	-0.61	0.28	0.03
		Quarterly inundation	-0.58	0.22	0.009

[†]Some species had multiple significant predictor variables, and therefore multiple models, which are listed in order of importance based on the ΔAIC between models.

4.4.1 Colonial waterbird breeding sites

Of the eight colonial breeding sites in the Okavango Delta (Fig. 4.1), Kanana site supported the highest abundance of breeding waterbirds, despite the low number of observations compared to other colonies (Table 4.3). Species' richness was high at Xini, Xakanaxa and Xobega, compared to other colonies (Table 4.3, Appendix 4.5).

The colonies were located in areas of the Delta which experienced the most frequent inundation (flooded 22.8-100%), measured at the three distances (1, 5 and 10km) from colonies, indicating a flooding frequency of at least once every five years is necessary for colony establishment with Manly selection ratios ranging from 2.84–8.19 (Fig. 4.6a). All colonies had relatively high proportions of floodplain and riparian woodland (1, 5 and 10km), compared to the other areas in the Delta (Fig. 4.6a, Appendix 4.6 & 4.7). This was reflected in disproportionately more floodplain areas, indicated by the Manly selection ratios (1.11-3.28). Resultingly, colony areas had little mixed shrubland, and disproportionately low areas of grassland and low woodland (Fig. 4.6b). Ratios were higher in the inundation than vegetation selection, perhaps suggesting inundation is a more important driver of colony location.

Table 4.3. Eight main waterbird breeding colonies within the Okavango Delta (Fig. 4.1), identified from citizen science data (Table 4.1), showing waterbird abundance in a given year (mean across annual summed counts, SD, range), number and composition of species in a given year (mean, SD, range), total species recorded, total number of surveys (N), and years of observation (1970-2019).

Colony	Abundance	Species	Total species	N	Years of observations (n)
Gadikwe	486.31 $\pm$ 266.07 [5-669]	11.46 $\pm$ 6.81 [1-16]	19 (African sacred ibis, African spoonbill, black heron, black-crowned night heron, cattle egret, glossy ibis, great egret, great white pelican, hadeda ibis, intermediate egret, little egret, marabou stork, pink-backed pelican, purple heron, reed cormorant, rufous-bellied heron, squacco heron, yellow-billed stork)	35	9
Kanana	1956.1 $\pm$ 1793.5 [80-5031]	8.39 $\pm$ 2.99 [1-12]	22 (African darter, African openbill, African sacred ibis, African spoonbill, black heron, black-crowned night heron, cattle egret, glossy ibis, goliath heron, great egret, green-backed heron, grey heron, intermediate egret, little egret, marabou stork, pink-backed pelican, reed cormorant, rufous-bellied heron, slaty egret, squacco heron, wattled crane, yellow-billed stork)	70	8
Xakanaxa	436.7 $\pm$ 354.37 [1-760]	13.5 $\pm$ 7.66 [1-20]	22 (African darter, African openbill, African sacred ibis, African spoonbill, black heron, black-crowned night heron, glossy ibis, great egret, great white pelican, green-backed heron, hadeda ibis, intermediate egret, little egret, marabou stork, purple heron, reed cormorant, rufous-bellied heron, saddle-billed stork, slaty egret, squacco heron, wattled crane, yellow-billed stork)	56	9
Xaxaba	2443.48 $\pm$ 1791.23 [2-4411]	9.02 $\pm$ 3.72 [1-12]	18 (African Darter, Black Heron, Black-crowned Night Heron, Cattle Egret, Great Egret, Great White Pelican, Green-backed Heron, Grey Heron, Intermediate Egret, Little Egret, Marabou Stork, Purple Heron,	99	10

Xho	413.08 ±414.68 [1-810]	3.67 ±2.46 [1-6]	Reed Cormorant, Rufous-bellied Heron, Saddle-billed Stork, Slaty Egret, Squacco Heron, Wattled Crane) 10 (Abdim's stork, African spoonbill, black heron, glossy ibis, great white pelican, greater flamingo, grey heron, lesser flamingo, pink-backed pelican, yellow-billed stork)	12	4
Xini	44.02 ±17.78 [1-59]	9.16 ±4.31 [1-13]	17 (African darter, African sacred ibis, African spoonbill, black heron, cattle egret, great egret, great white pelican, green-backed heron, intermediate egret, little egret, reed cormorant, saddle-billed stork, slaty egret, squacco heron, wattled crane, woolly-necked stork, yellow-billed stork)	51	7
Xobega	204.62 ±348.49 [10-1377]	6.92 ±4.87 [1-12]	17 (African sacred ibis, black heron, black-crowned night heron, cattle egret, great egret, great white pelican, grey heron, intermediate egret, little egret, marabou stork, pink-backed pelican, reed cormorant, rufous-bellied heron, slaty egret, squacco heron, yellow-billed stork)	26	7
Xugana	300.65 ±395.51 [4-1285]	4.74 ±2.5 [1-8]	15 (African darter, African openbill, African spoonbill, black heron, black-crowned night heron, cattle egret, great egret, great white pelican, grey heron, hadeda ibis, little egret, reed cormorant, rufous-bellied heron, squacco heron, yellow-billed stork)	31	7

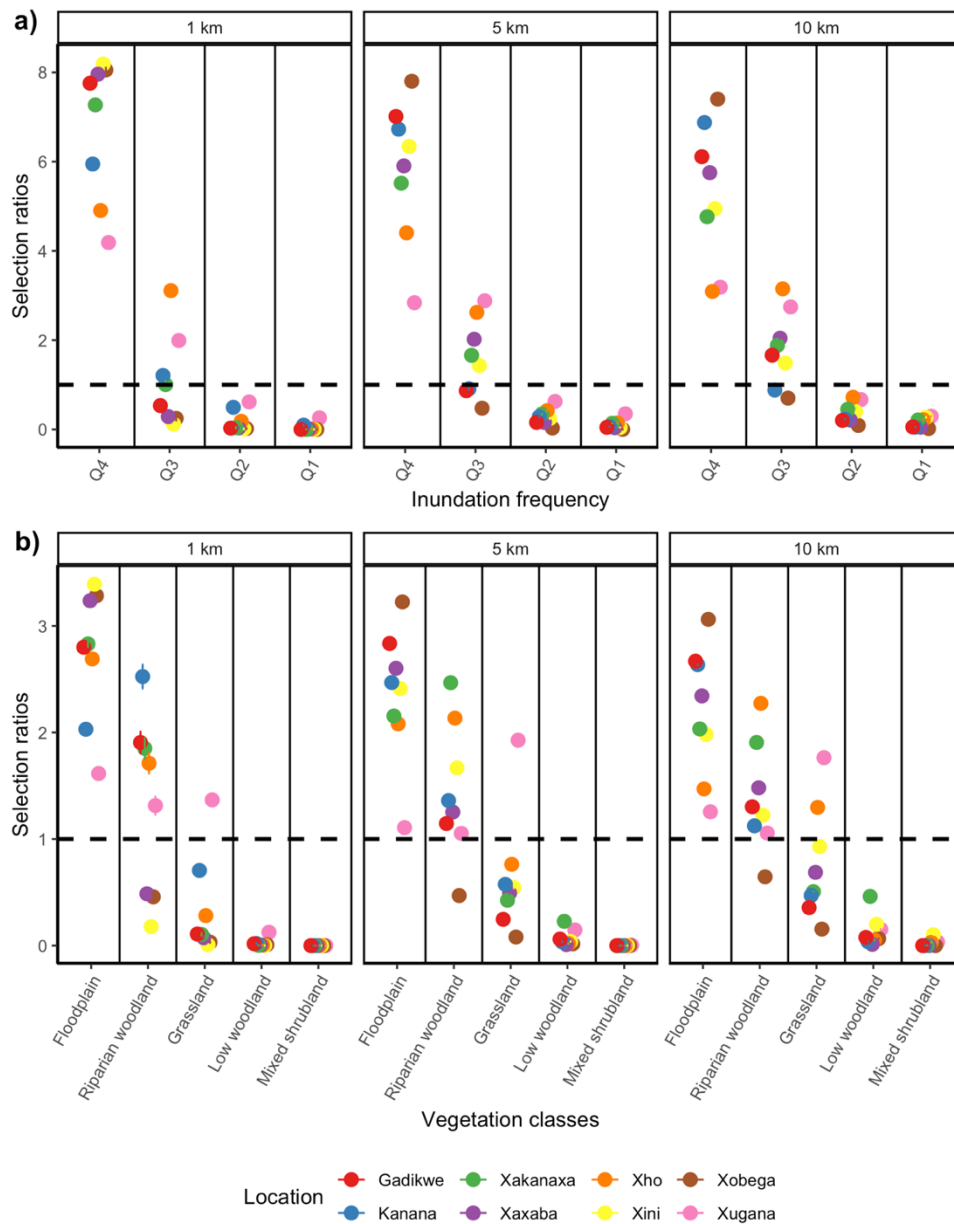


Figure 4.6. Habitat selection ratios (Manly selection ratios) for the eight key waterbird colonies in the Okavango Delta, in relation to a) frequency of quartiles of flooding (Q1: 0% flooded, Q2: 0.01-1.6%, Q3: 1.6 – 22.8%, Q4: 22.81 – 100%) and b) five vegetation types (floodplain, riparian woodland, grassland, low woodland and mixed shrubland), within three areas of the colonies (1, 5 and 10 km).

4.5 Discussion

The Okavango Delta is a large, highly variable wetland fluctuating from periods of widespread flooding to dry floodplain interspersed with perennial lagoons. This makes it a hotspot of biodiversity and of very high conservation importance. It faces many threats, emphasising the importance of ongoing monitoring to track changes over time. As one of the larger Ramsar sites in the world (Department of Environmental Affairs Ministry of Environment, 2006), an important bird area (IBA)(Hancock, Muller, & Tyler 2007, McCulloch, Kootsositse, & Rutina 2017) and World Heritage Site (UNESCO 2014), effective management is essential (The Ramsar Convention Secretariat 2014, BirdLife International 2021b, Kingsford et al. 2021). Despite plans to monitor (Mfundisi 2008), there is little consistent and rigorous tracking of ecological change across the Okavango Delta, including for waterbirds, and in a 2012 assessment the Delta was assessed as ‘high’ threat and ‘unfavourable’ condition (BirdLife International 2021a). In the absence of rigorous monitoring data, we used available citizen science data (Table 4.1, Fig. 4.1), identifying a significant decline in waterbird abundance over the past two decades within the Delta. We also identified a strong link between water flow in the Okavango River and waterbird abundance with critical implications for management under climate change and potential for upstream development of water resources reducing inflows and inundation extent and frequency (Andersson et al. 2006, Darkoh & Mbaiwa 2014). Waterbirds could therefore be useful ecological indicators of potential hydrological change and condition of the Delta.

The Okavango Delta is very biologically diverse and particularly important for waterbirds, supporting globally threatened species, and more than 1% of the biogeographic population for at least 13 bird species (Hancock et al. 2007, McInnes, Ali, & Pritchard 2017). In addition to declines in total abundance, we estimated that a third of species (five), with sufficient data for

analysis, were in decline. Of these the slaty egret is already vulnerable, and heavily dependent on the Okavango Delta for breeding. Abundances of the four declining species associated strongly with flow or inundation, and inundation was found to be significantly declining over time (Fig. 4.2). These waterbird declines are likely therefore attributed to inundation declines, and resulting impacts on vegetation, or increasing disturbance through tourism and urbanisation (Mbaiwa 2003, Darkoh & Mbaiwa 2014). Due to the relatively small spatial scale of my study, species' declines may not reflect population declines, given birds may be using wetlands elsewhere (Thomas et al. 2015). However, waterbirds are declining in Africa, as are their wetland habitats providing evidence for large scale declines (Jogo & Hassan 2010, Orimoloye et al. 2020). At the species level, African darters in South Africa have high levels of organochlorine contaminants in their eggs (higher than other species studied), with eggshell thinning occurring, raising concerns for their reproductive health (Bouwman et al. 2008). Green-backed heron are a common resident of the forests around Kasenda crater lakes in Uganda, however more than half of the lakes are now severely or completely deforested (Pomeroy & Seavy 2003), possibly contributing to population declines of waterbird species. Declines in the squacco heron occurred from 1970-2000 across its range in both Africa and Europe (migrant) (Sanderson et al. 2006). Slaty egrets are likely declining across Namibia, Botswana and Zambia due to habitat disturbance, degradation of breeding areas with increased tourism, and increased frequency of reed bed fires (Hines 1992). Further, the building of a dam on the Kafue River in Zambia probably caused their disappearance from the Blue Lagoon National Park (Collar & Stuart 1985), given their dependence on ephemeral wetlands (Hines 1992). Contrastingly, marabou increased in abundance which may be due to access to urban waste across Africa (Pomeroy & Kibuule 2017, Thabethe & Downs 2018), although the population of marabou in the Delta is one of the few

naturally feeding populations in Botswana (Francis et al. 2021). Perhaps they are also benefiting from increased warm thermals on hot days which enhance foraging efficiency (Monadjem et al. 2012), potentially reflected in the positive association with temperature. More work is required to understand long-term fine scale deleterious changes in the Delta, including vegetation change (Ringrose, Vanderpost, & Matheson 2003), which alongside rigorous monitoring of waterbirds will increase understanding of cause and effect relationships and ecosystem changes in the Delta. Around the world, the establishment, frequency, and distribution of waterbird colonies can successfully track ecosystem change due to their dependencies on flow and inundation for breeding (Frederick et al. 2009, Brandis et al. 2018). In the Okavango Delta, we focused on eight key breeding colonies (Table 4.3, Fig. 4.1), although other small colonies also occur (Hancock et al. 2007). These eight large breeding colonies contribute significantly not only to the Okavango Delta but also the viability of populations for the whole of southern Africa (Child 1972, Randall & Herremans 1994, Bowker & Downs 2012, Monadjem et al. 2012). The breeding of marabou stork at these colonies, particularly Kanana (Table 4.3), make these colonies among the most important sites in southern Africa (Monadjem 2005, Hancock et al. 2007). About 80% of the estimated total global population (2500-3300) of the vulnerable slaty egret and >15% of the global population (~6000) of the vulnerable wattled crane occur in the Delta (Appendix 4.2) (Hancock et al. 2007, Motsumi et al. 2007, BirdLife International, 2020a, 2020b, 2021a). Slaty egret and wattled crane were recorded at seven of the eight breeding colonies (Table 4.3), underlining the importance of the Okavango Delta as a breeding stronghold for these vulnerable species. Further, high numbers of breeding African openbills (max count 3600), reed cormorants (max count 2600), and marabou storks (max count 722) at the Kanana colony were significant. The numbers of African openbills exceeds 1% of the estimated global population (300,000-

500,000), qualifying the area as an Important Bird Area and fulfilling one of its Ramsar criteria (Department of Environmental Affairs Ministry of Environment Wildlife and Tourism 2006, BirdLife International 2018a). These colonies in the Okavango Delta are significant for the Delta and more broadly to waterbird conservation but they are also important as indicators for flow and flooding, requiring ongoing monitoring. Reflecting the importance of flow and flooding regimes, all colonies were in areas of floodplain and riparian woodland, where flooding frequency was high, at least 1 in 5 years. Such results were based on the natural quartiles of flooding frequency which covered a large range in frequency, reflecting the natural breaks in the system. As for other waterbird breeding colonies around the world, changes in vegetation structure, flooding frequency and flooding volume due to upstream water extraction, would inevitably decrease breeding habitat of many dependent waterbird species (Ma et al. 2010).

Ecosystem degradation is increasing, particularly for freshwater ecosystems (Darwall et al. 2018, Albert et al. 2020). There is an urgent need to use available data to try and track changes, inform management and establish baselines (Lemly, Kingsford, & Thompson 2000, Tockner & Stanford 2002, Rood et al. 2005, Brandis et al. 2011). In the absence of rigorously collected temporal and spatial data, we used citizen science data to examine long-term changes in the waterbird community of the Okavango Delta, providing a baseline and some insight into ecosystem changes (Amano, Lamming, & Sutherland 2016, Steger et al. 2017). There are inevitable uncertainties in using citizen science, including variable temporal and spatial effort (Boakes et al. 2010, Courter et al. 2013). In particular we needed to make three assumptions in using our data to track changes over time: similar areas were surveyed; survey effort was comparable over time and; across different survey types. Citizen science observations showed many areas were repeatedly visited over time (Fig. 4.1), probably reflecting observations by tourists. This can

produce spatial bias, but also ensures the same sites were regularly surveyed, the first assumption. Also, much of the tourism in Botswana is led by high-end avitourism, meaning guests are often semi-expert or expert birders making mis-identifications unlikely. As our abundances were averaged across the area of the Delta we also limited the effects of fine scale spatial differences and outliers. There were likely temporal biases in our data, largely as many parts of the Delta became inaccessible during high floods, but these tended to be temporally consistent over time due to the strong seasonality of the Delta. To limit the effects of temporal biases, we averaged our abundance data over 3-month windows, limiting daily and even monthly variations. There were also differences among surveys, with the 2011 African Waterbird Census providing the highest species' richness with the least effort (Fig. 4.4). However, it is unlikely that the level of this bias was sufficient to explain temporal differences, given there was also considerable variation within survey type data (conducted 2011 - 2017). We also accounted for effects of data types by including it as a model variable and used the number of surveys, as a measure of sampling effort, which increased over time. Some of these biases could be further limited or controlled for in the future with improved data collection.

There are increasing improvements in citizen science data collection, including citizen science apps (e.g. eBird), which prompt users to record spatial and temporal variables related to their surveys. To improve the usability of data recorded by Birdlife Botswana, African waterbird census and other observations the noting of these extra variables should be encouraged, in particular exact locations (coordinates), duration of survey, number of observers and distance travelled. Species' accumulation curves indicated the African waterbird census recorded the greatest numbers of species with the least number of surveys, underlining their importance. This is likely due to the purposeful sampling of this data source, rather than the incidental

observations often provided by other survey types. However these data may not adequately capture sufficient temporal and spatial variation of changes in waterbird abundances, which should be assessed as done for similar datasets in South Africa (Thomas et al. 2015). Ideally, more systematic rigorous large scale waterbird counts would be conducted regularly across the Okavango Delta, including aerial surveys (Kingsford et al. 2020), supported by citizen science ground counts. The financial evaluation of avitourism (Nicolaidis 2013, Callaghan et al. 2018) and other ecosystem services could encourage the dedication of funds back into conservation, perceiving the expense of conservation efforts as an investment into the future of biodiversity driven tourism. Other alternatives include the use of drones (particularly over colonies), which have proven useful for obtaining counts of large aggregations of breeding waterbirds at little expense (Afán, Máñez, & Díaz-Delgado 2018, Lyons et al. 2019, Francis et al. 2020).

The Okavango Delta faces many threats, including vegetation loss, urbanisation, tourism development, and reductions to river flows. It is highly dependent on flows from the Cuito, Cubango and Okavango Rivers from Angola, Namibia and Botswana (Fig. 4.1), making it particularly vulnerable to the effects of dams and river regulation. Climate change will likely compound such impacts. Waterbirds are a major biodiversity component of the Okavango Delta and are highly dependant on river flows and subsequent flooding regimes, and as such, they provide an opportunity to track potential long-term changes to the Okavango Delta. Citizen science data currently provides some method of tracking change but this needs to be supported by more rigorous data collection. Monitoring is essential to safe-guard avitourism revenue (which could be converted into conservation efforts), and using waterbirds as indicator species may be a cost-efficient way to track changes over time, inform management and policy and protect the extremely rich and biodiverse Okavango Delta.

4.6 Acknowledgements

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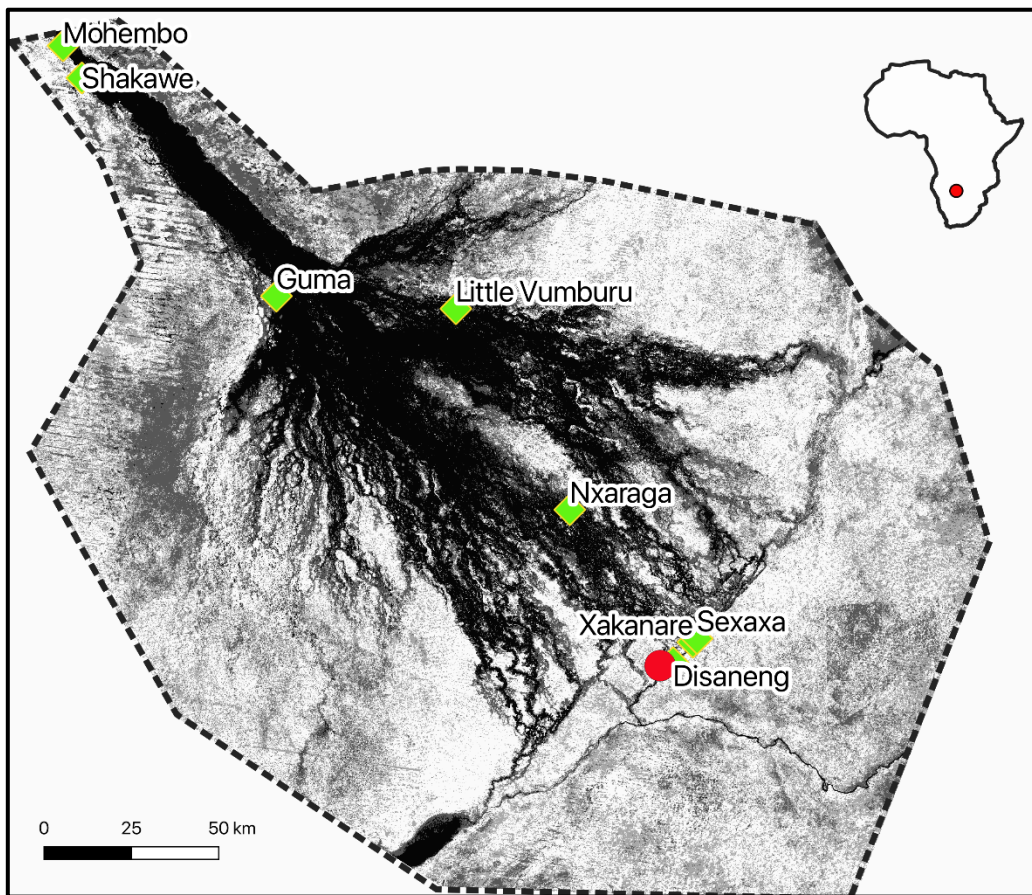
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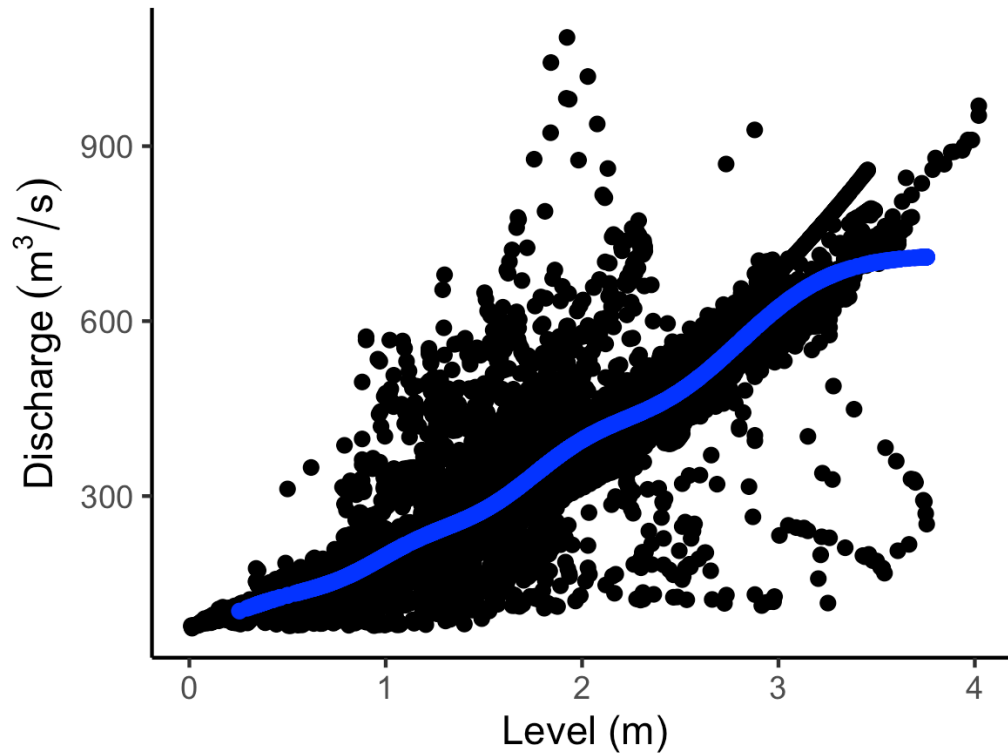
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4.8 Appendices

Appendix 4.1. Gauges from where water level and flow, rain and temperature data were collected can be seen in green on the mean inundation raster (1984-2019), with Maun town marked in red, located within southern Africa (inset).



Appendix 4.2. *Missing flow values were filled using the gam model relationship between flow and level, with the missing values predicted into the final flow dataset (blue).*



Appendix 4.3. Species and their assigned foraging group (Cumming et al. 2012); 1) short vegetation or mud, 2) emergent vegetation including reeds and lilies, 3) shallow water, 4) in or over deep water, alongside their functional group (Sundstrom et al. 2012), with their conservation status according to IUCN (IUCN, 2020) and the number of observations for each species, mean count $\pm$ SD.

Common Name	Species	Functional Group	Foraging Group	Conservation Status	Count
Abdim's stork	<i>Ciconia abdimii</i>	Terrestrial invertivore	0	LC	6 (4.04 $\pm$ 21.08)
African darter [†]	<i>Anhinga rufa</i>	Aquatic carnivore	4	LC	31 (10.66 $\pm$ 23.48)
African openbill [†]	<i>Anastomus lamelligerus</i>	Aquatic invertivore	3	LC	39 (173.41 $\pm$ 510.87)
African sacred ibis [†]	<i>Threskiornis aethiopicus</i>	Aquatic carnivore	1	LC	18 (5.44 $\pm$ 13.99)
African spoonbill	<i>Platalea alba</i>	Aquatic carnivore	3	LC	12 (5.55 $\pm$ 24.87)
Black heron	<i>Egretta ardesiaca</i>	Aquatic carnivore	3	LC	34 (25.73 $\pm$ 59.91)
Black stork	<i>Ciconia nigra</i>	Aquatic carnivore	3	LC	2 (0.06 $\pm$ 0.24)
Black-crowned night heron	<i>Nycticorax nycticorax</i>	Aquatic carnivore	3	LC	18 (6.3 $\pm$ 15.71)
Black-headed heron	<i>Ardea melanocephala</i>	Terrestrial carnivore	0	LC	4 (0.25 $\pm$ 0.84)
Cattle egret [†]	<i>Bubulcus ibis</i>	Terrestrial carnivore	0	LC	47 (126.7 $\pm$ 462.03)
Crowned crane	<i>Balearica regulorum</i>	Aquatic omnivore	3	LC	1 (0 $\pm$ 0)
Glossy ibis	<i>Plegadis falcinellus</i>	Aquatic invertivore	1	LC	16 (6.12 $\pm$ 23.55)
Goliath heron	<i>Ardea goliath</i>	Aquatic carnivore	3	LC	7 (1.19 $\pm$ 4.65)
Great egret [†]	<i>Ardea Alba</i>	Aquatic carnivore	3	LC	36 (35.8 $\pm$ 125.01)
Great white pelican	<i>Pelecanus onocrotalus</i>	Aquatic carnivore	3	LC	17 (10.11 $\pm$ 28.45)

Greater flamingo	<i>Phoenicopterus roseus</i>	Aquatic invertivore	3	LC	2 (0.02±0.14)
Green-backed heron [†]	<i>Butorides striata</i>	Aquatic carnivore	2	LC	9 (2.76±10.05)
Grey heron [†]	<i>Ardea cinerea</i>	Aquatic carnivore	3	LC	20 (4.07±9.16)
Hadedda ibis	<i>Bostrychia hagedash</i>	Aquatic invertivore	1	LC	8 (2.13±2.51)
Intermediate egret (Yellow-billed egret)	<i>Egretta intermedia</i>	Aquatic carnivore	3	LC	23 (16.78±79.02)
Lesser flamingo	<i>Phoenicopterus minor</i>	Aquatic invertivore	3	NT	4 (10.54±42.49)
Little egret [†]	<i>Egretta garzetta</i>	Aquatic carnivore	3	LC	38 (37.58±184.73)
Marabou stork [†]	<i>Leptoptilos crumenifer</i>	Terrestrial carnivore	0	LC	26 (47.34±156.02)
Pink-backed pelican	<i>Pelecanus rufescens</i>	Aquatic carnivore	3	LC	15 (25.17±71.36)
Purple heron	<i>Ardea purpurea</i>	Aquatic carnivore	3	LC	14 (3.3±11.32)
Reed cormorant [†]	<i>Microcarbo africanus</i>	Aquatic carnivore	4	LC	34 (30.38±202.32)
Rufous-bellied heron [†]	<i>Ardeola rufiventris</i>	Aquatic carnivore	2	LC	24 (9.51±22.48)
Saddle-billed stork [†]	<i>Ephippiorhynchus senegalensis</i>	Aquatic carnivore	3	LC	10 (2.46±4.17)
Slaty egret [†]	<i>Egretta vinaceigula</i>	Aquatic carnivore	3	VU	32 (29.07±97.25)
Squacco heron [†]	<i>Ardeola ralloides</i>	Aquatic carnivore	3	LC	43 (68.71±181.16)
Wattled crane	<i>Grus carunculatus</i>	Aquatic omnivore	3	VU	36 (53.31±151.08)
White stork	<i>Ciconia ciconia</i>	Terrestrial carnivore	0	LC	6 (4.37±27.22)
White-backed night heron	<i>Gorsachius leuconotus</i>	Aquatic carnivore	2	LC	3 (0.1±0.59)
White-breasted cormorant	<i>Phalacrocorax lucidus</i>	Aquatic carnivore	4	LC	3 (0.08±0.34)

Woolly-necked stork	<i>Ciconia episcopus</i>	Aquatic carnivore	3	VU	16 (37.2±120.65)
Yellow-billed stork [†]	<i>Mycteria ibis</i>	Aquatic carnivore	3	LC	25 (20.95±73.17)

[†]The 15 species included in the species-specific modelling

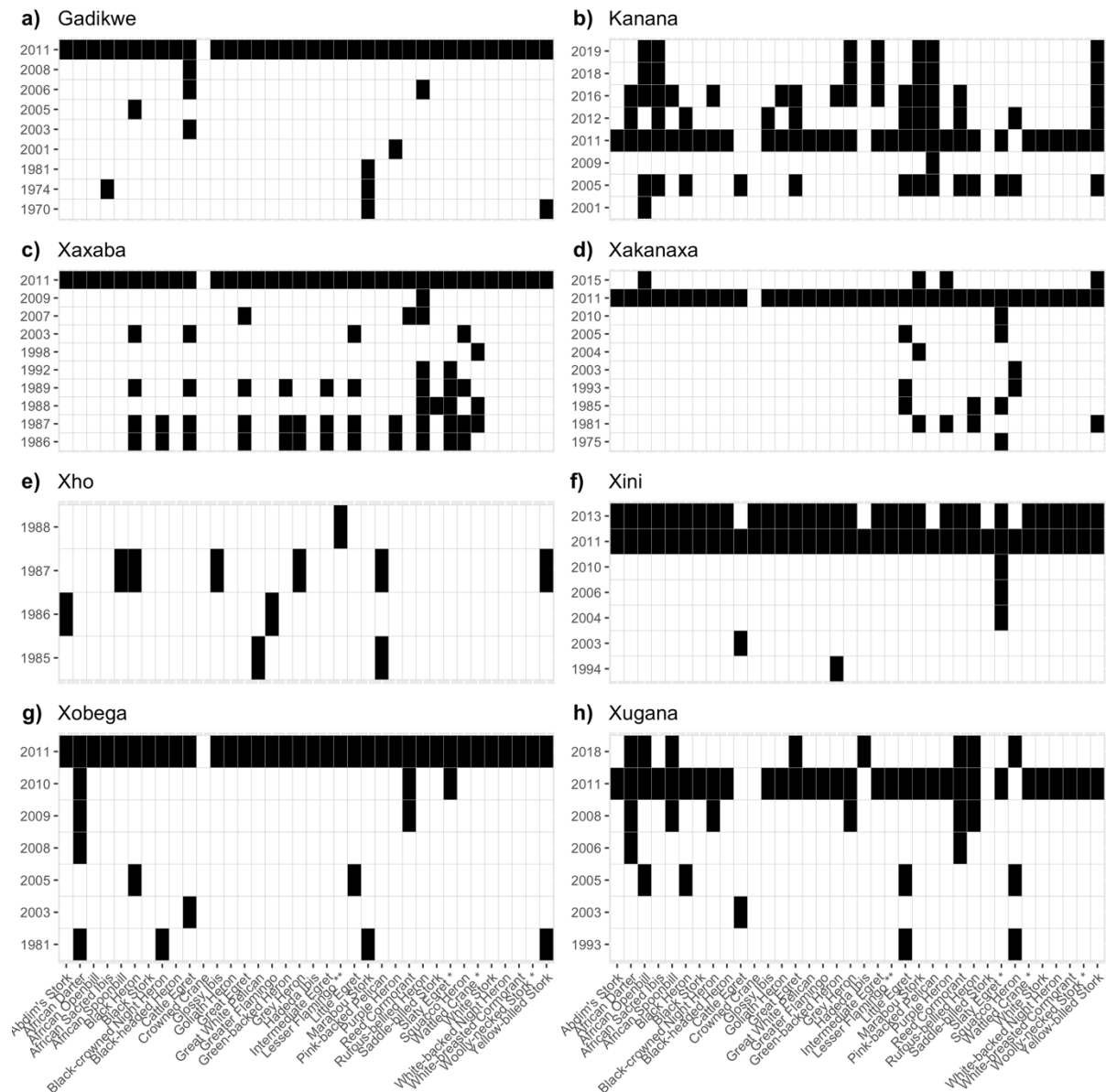
Appendix 4.4. Seven best fit models were used in the model averaging process with their log likelihood, Akaike information criterion (AICc), the difference between the models AICc and the best fit model AICc (ΔAIC) and the importance of each model (weight).

Model	Variables	logLik	AICc	ΔAIC	Weight
1	Quarterly Inundation (12-month lag), Quarterly Mean Flow (3-month lag), Mean Temperature, Year, Survey Effort Offset	-574.40	1163.80	0.00	0.14
2	Quarterly Mean Flow (3-month lag), Quarterly Mean Temp, Quarterly Mean Temp (6-month lag), Year, Survey Effort Offset	-574.91	1164.82	1.02	0.09
3	Quarterly Mean Flow (3-month lag), Quarterly Mean Temp, Year, Survey Effort Offset	-576.20	1165.15	1.35	0.07
4	Quarterly Mean Flow (3-month lag), Quarterly Mean Temp, Quarterly Mean Rain (12-month lag), Year, Survey Effort Offset	-575.14	1165.28	1.48	0.07
5	Quarterly Inundation, Quarterly Mean Flow (3-month lag), Quarterly Mean Temp, Year, Survey Effort Offset	-575.30	1165.60	1.80	0.06
6	Quarterly Inundation (6-month lag), Quarterly Mean Flow (3-month lag), Quarterly Mean Temp, Year, Survey Effort Offset	-575.33	1165.66	1.86	0.06
7	Quarterly Mean Flow (3-month lag), Quarterly Mean Rain, Quarterly Mean Temp, Year, Survey Effort Offset	-575.34	1165.68	1.88	0.06

Appendix 4.5. Results of the fixed variables selected in the final conditional averaged model of seven models with $\Delta AIC < 2$ exploring waterbird abundance responses to environmental variables. The relative importance (RI) of each variable across the seven models is also included.

Model Variables	Estimate	Adjusted SE	RI	z	P value
Intercept	3.15	0.79	NA	3.99	<0.001
Inundation (12-month lag)	-0.33	0.17	0.26	1.92	0.055
Discharge (3-month lag)	1.00	0.22	1	4.5	<0.001
Quarterly Temperature	1.31	0.27	1	4.88	<0.001
Quarterly Rain	-0.25	0.19	0.10	1.32	0.19
Temperature (6-month lag)	0.39	0.24	0.16	1.61	0.11
Rain (12-month lag)	-0.33	0.23	0.13	1.48	0.14
Quarterly Inundation	-0.27	0.20	0.11	1.34	0.18
Inundation (6-month lag)	-0.21	0.16	0.10	1.33	0.18
Year	-0.74	0.19	1	1.82	<0.001

Appendix 4.6. *Species present at each of the key colonial waterbird breeding sites, when surveyed in the Okavango Delta from 1970-2019, with the Kanana colony including drone counts from 2018 and 2019.*



Appendix 4.7. *Model results (selection ratio, χ^2 , P -value) testing variation in breeding colonies in relation to vegetation types, proportional to their availability across the Okavango Delta. “Inf” values occur when there was none of that vegetation within the buffer.*

Location	Vegetation Type	1 km Buffer	5 km Buffer	10 km Buffer
Gadikwe	Floodplain	2.8, 14039, <0.001	2.84, 381429, <0.001	2.67, 1053659, <0.001
		0.02, 107985, <0.001	0.06, 699730, <0.001	0.08, 2136278, <0.001
	LowWoodland	0.11, 17280, <0.001	0.25, 141421, <0.001	0.36, 295800, <0.001
	Grassland	0, Inf, <0.001	0, Inf, <0.001	0, Inf, <0.001
	Mixed Shrubland	1.91, 320, <0.001	1.15, 322, <0.001	1.3, 4943, <0.001
	Riparian Woodland	2.03, 2901, <0.001	2.47, 175492, <0.001	2.64, 984444, <0.001
Kanana	Floodplain	0.02, 93046, <0.001	0.04, 1259177, <0.001	0.04, 4687558, <0.001
		0.71, 353, <0.001	0.57, 21539, <0.001	0.47, 157337, <0.001
	LowWoodland	0, Inf, <0.001	0, 35124735, <0.001	0, 562455469, <0.001
	Grassland	2.52, 726, <0.001	1.36, 1688, <0.001	1.12, 939, <0.001
	MixedShrubland	2.83, 15097, <0.001	2.15, 93993, <0.001	2.03, 292061, <0.001
	Riparian Woodland	0, 709649, <0.001	0.23, 130870, <0.001	0.46, 133429, <0.001
Xakanaxa	Floodplain	0.1, 18092, <0.001	0.43, 50578, <0.001	0.51, 128682, <0.001
		0, Inf, <0.001	0, Inf, <0.001	0, 41385981, <0.001
	Low Woodland	1.85, 289, <0.001	2.47, 17101, <0.001	1.91, 31994, <0.001
	Grassland	3.24, 57431, <0.001	2.6, 229454, <0.001	2.34, 548114, <0.001
	Mixed Shrubland	0, 392776, <0.001	0.01, 5196485, <0.001	0.01, 16302774, <0.001
	Riparian Woodland	0.07, 27167, <0.001	0.49, 34752, <0.001	0.69, 40560, <0.001
Xaxaba	Floodplain	0, Inf, <0.001	0, Inf, <0.001	0, Inf, <0.001
		0.49, 356, <0.001	1.25, 893, <0.001	1.48, 11141, <0.001
	Low Woodland	2.69, 11032, <0.001	2.08, 80792, <0.001	1.47, 59903, <0.001
	Grassland	0, 392676, <0.001	0.02, 2429133, <0.001	0.05, 3302331, <0.001
	Mixed Shrubland	0.28, 4557, <0.001	0.76, 5407, <0.001	1.3, 24889, <0.001
	Riparian Woodland	0, Inf, <0.001	0, Inf, <0.001	0.03, 2474746, <0.001
Xho	Floodplain	1.71, 216, <0.001	2.13, 11446, <0.001	2.27, 54871, <0.001
		3.39, 232615, <0.001	2.41, 156912, <0.001	1.98, 260638, <0.001
	Low Woodland	0, 3558807, <0.001	0.04, 1154322, <0.001	0.2, 639640, <0.001
	Grassland	0.01, 302047, <0.001	0.54, 25821, <0.001	0.93, 1668, <0.001
	Mixed Shrubland	0, Inf, <0.001	0, Inf, <0.001	0.1, 626838, <0.001
	Riparian Woodland			
Xini	Floodplain			
	Low Woodland			
	Grassland			
	Mixed Shrubland			

Xobega	Riparian Woodland	0.18, 2422, <0.001	1.67, 4858, <0.001	1.22, 2851, <0.001
	Floodplain	3.28, 76004, <0.001	3.23, 1353977, <0.001	3.06, 2824558, <0.001
	Low Woodland	0.01, 234282, <0.001	0.02, 2837252, <0.001	0.07, 2569546, <0.001
	Grassland	0.03, 68408, <0.001	0.08, 616148, <0.001	0.15, 1104428, <0.001
	Mixed Shrubland	0, Inf, <0.001	0, Inf, <0.001	0, Inf, <0.001
Xugana	Riparian Woodland	0.46, 420, <0.001	0.47, 9813, <0.001	0.65, 12910, <0.001
	Floodplain	1.61, 1004, <0.001	1.11, 873, <0.001	1.26, 18673, <0.001
	Low Woodland	0.13, 11916, <0.001	0.15, 243206, <0.001	0.15, 924778, <0.001
	Grassland	1.37, 373, <0.001	1.93, 57765, <0.001	1.76, 154427, <0.001
	Mixed Shrubland	0, Inf, <0.001	0, 4858784, <0.001	0.03, 2216533, <0.001
	Riparian Woodland	1.31, 53, <0.001	1.05, 46, <0.001	1.06, 207, <0.001

Appendix 4.8. Model results (Selection ratio, χ^2 , P-value) testing variation in breeding colonies in relation to flooding frequency, proportional to frequencies across the Okavango Delta, based on natural quartiles Q1: 0% flooded, Q2: 0.01-1.6%, Q3: 1.6 – 22.8%, Q4: 22.81 – 100%.

Location	Flooding Frequency %	1 km Buffer	5 km Buffer	10 km Buffer
Gadikwe	0	0, 4254009, <0.001	0.05, 1037252, <0.001	0.05, 3466712, <0.001
	0.01-1.6	0.03, 19713, <0.001	0.16, 68588, <0.001	0.2, 192736, <0.001
	1.6-22.8	0.53, 183, <0.001	0.87, 235, <0.001	1.66, 13919, <0.001
	22.8-100	7.76, 35690, <0.001	7.01, 341345, <0.001	6.11, 672523, <0.001
Kanana	0	0.1, 18461, <0.001	0.06, 778957, <0.001	0.05, 3775356, <0.001
	0.01-1.6	0.5, 333, <0.001	0.28, 28646, <0.001	0.23, 160788, <0.001
	1.6-22.8	1.21, 18, <0.001	0.91, 107, <0.001	0.88, 730, <0.001
	22.8-100	5.95, 6022, <0.001	6.73, 265518, <0.001	6.88, 1205660, <0.001
Xakanaxa	0	0, 4241849, <0.001	0.14, 307613, <0.001	0.21, 690050, <0.001
	0.01-1.6	0.04, 14252, <0.001	0.34, 19874, <0.001	0.45, 42741, <0.001
	1.6-22.8	1, 0, <0.001	1.66, 3450, <0.001	1.88, 22502, <0.001
	22.8-100	7.27, 17786, <0.001	5.52, 114803, <0.001	4.77, 291570, <0.001
Xaxaba	0	0.01, 263302, <0.001	0.04, 1297931, <0.001	0.05, 3917360, <0.001
	0.01-1.6	0.03, 16607, <0.001	0.16, 69029, <0.001	0.21, 185569, <0.001
	1.6-22.8	0.29, 764, <0.001	2.02, 7140, <0.001	2.04, 29639, <0.001
	22.8-100	7.96, 56909, <0.001	5.9, 146653, <0.001	5.75, 532209, <0.001
Xho	0	0.01, 174366, <0.001	0.14, 287062, <0.001	0.22, 665535, <0.001
	0.01-1.6	0.18, 2230, <0.001	0.42, 12694, <0.001	0.72, 7360, <0.001
	1.6-22.8	3.11, 959, <0.001	2.62, 15369, <0.001	3.15, 99005, <0.001
	22.8-100	4.91, 3171, <0.001	4.41, 58587, <0.001	3.09, 94464, <0.001
Xini	0	0, 1420932, <0.001	0.04, 1113907, <0.001	0.27, 481131, <0.001
	0.01-1.6	0.01, 43245, <0.001	0.25, 36068, <0.001	0.4, 57390, <0.001
	1.6-22.8	0.12, 2783, <0.001	1.43, 1643, <0.001	1.49, 8134, <0.001
	22.8-100	8.19, 152330, <0.001	6.34, 197442, <0.001	4.95, 325133, <0.001
Xobega	0	0, 4254009, <0.001	0, 21551057, <0.001	0.02, 9746199, <0.001
	0.01-1.6	0.02, 28372, <0.001	0.03, 452119, <0.001	0.09, 549493, <0.001
	1.6-22.8	0.25, 987, <0.001	0.48, 6435, <0.001	0.7, 5812, <0.001
	22.8-100	8.05, 77497, <0.001	7.8, 975840, <0.001	7.4, 2078628, <0.001
Xugana	0	0.26, 5136, <0.001	0.35, 78337, <0.001	0.3, 419384, <0.001
	0.01-1.6	0.62, 158, <0.001	0.63, 3684, <0.001	0.67, 10972, <0.001
	1.6-22.8	1.99, 273, <0.001	2.88, 19714, <0.001	2.75, 69445, <0.001
	22.8-100	4.19, 2049, <0.001	2.84, 18967, <0.001	3.19, 101909, <0.001

Chapter 5. Counting Mixed Breeding Aggregations of Animal Species

Using Drones: Lessons from Waterbirds on Semi-Automation

Roxane J Francis, Mitchell B Lyons, Richard T Kingsford and Kate J Brandis

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I led study design, methods creation, equipment purchasing, permit applications, fieldwork, data collection and compilation, analysis and writing.

5.1 Abstract

Using drones to count wildlife saves time and resources and allows access to difficult or dangerous areas. We collected drone imagery of breeding waterbirds at colonies in the Okavango Delta (Botswana) and Lowbidgee floodplain (Australia). We developed a semi-automated counting method, using machine learning, and compared effectiveness of freeware and payware in identifying and counting waterbird species (targets) in the Okavango Delta. We tested transferability to the Australian breeding colony. Our detection accuracy (targets), between the training and test data, was 91% for the Okavango Delta colony and 98% for the Lowbidgee floodplain colony. These estimates were within 1%–5%, whether using freeware or payware for the different colonies. Our semi-automated method was 26% quicker, including development, and 500% quicker without development, than manual counting. Drone data of waterbird colonies can be collected quickly, allowing later counting with minimal disturbance. Our semi-automated methods efficiently provided accurate estimates of nesting species of

waterbirds, even with complex backgrounds. This could be used to track breeding waterbird populations around the world, indicators of river and wetland health, with general applicability for monitoring other taxa.

5.2 Introduction

There is an increasing need to estimate aggregations of animals around the world, including turtles, seals and birds [1–6]. Regular monitoring of these concentrations allows decision-makers to not only track changes to these colonies but also long-term environmental changes, given that large aggregations of some species can be used to monitor environmental change (e.g., waterbird breeding colonies) [7,8]. Existing methods to monitor such occurrences include the use of camera traps [9,10], radar [11], aerial surveys [12,13] and in-situ observers [14,15]. Each of these methods has limitations, including expense [9], poor accuracy [16], danger to the researchers [17] or disturbance to wildlife [14].

Drones, or unmanned aerial vehicles (UAVs), can collect considerable data quickly over large areas. They provide advantages over in-situ observations, accessing physically inaccessible or dangerous areas in a relatively small amount of time [18–20]. Drones are also relatively cheap, safe and less disturbing, improving traditional wildlife surveys [3,19,21,22]. They can, however, disturb some animal populations, requiring careful consideration of appropriateness when surveying [23]. As a result of such time and cost savings, drones are increasingly used to monitor bird communities [24–26].

Alongside the increasing availability of large amounts of drone datasets, there is a need for effective and efficient processing methods. There are two broad options: manual counting of images and semi-automated methods. The former can be extremely labour-intensive and consequently expensive, particularly for large aggregations of wildlife [27], further complicated when more than one species is counted. Semi-automated methods, including the counting of animals from photographs (e.g., camera traps) and drone imagery, are increasingly

being developed around the world [28]. These methods reduce the time required to count and process drone images [29], accelerating the data entry stage and encouraging the use of drones as scientific tools for management. Such benefits allow for real-time monitoring and management decisions and could, for example, assist in the targeted delivery of environmental flows for waterbird breeding events [30].

Generally, semi-automated counting methods are most effective for species where there are strong contrasts against the backgrounds, particularly when background colours and shapes are consistent [29]. They can distinguish large single species aggregations on relatively simple backgrounds [31–33], up to sixteen avian species (numbering in the hundreds) on simple single colour backgrounds, such as oceans [34,35], or single species aggregations of hundreds of thousands on complex backgrounds [3].

Development of flexible, repeatable and efficient methods, using open source software, is important in ensuring methods are applicable across a range of datasets [36,37]. Further, there are potential cost implications of processing data, given that some processing software can be expensive (i.e., compulsory licence fees, called ‘payware’ in this paper) and so are often only accessible to large organisations in high-income countries [38]. Open source software, or software with optional licence/donation fees (‘freeware’ in this paper), can overcome such restrictions, providing repeatable processing techniques, which are accessible to all users.

We aimed to develop a semi-automated method for counting large aggregations of mixed species of breeding waterbirds, with highly complex vegetation backgrounds. Specifically, we had four objectives: (1) to develop a transferrable semi-automated counting method with high accuracy (>90%) for counting mixed species of breeding colonies on complex backgrounds, (2) to compare the time using a semi-automated compared to a manual method, (3) to identify whether birds were on (incubating) or off their nests and (4) to ensure methods were

reproducible and accessible by comparing two processing pathways (freeware to payware). Finally, we discussed such an application on other breeding aggregations of wildlife.

5.3 Materials and Methods

5.3.1 Study Areas

We focused on two different waterbird breeding colonies (Figure 5.1): the Kanana colony in the Okavango Delta, Botswana, and the Eulimbah colony in the Lowbidgee floodplain, Australia. The colonies were respectively established in 2018 and 2016 following flooding, in a range of vegetation types (Table 5.1).

Table 5.1. Main waterbird breeding species (targets) in the two waterbird colonies, Kanana colony (Okavango Delta) and Eulimbah colony (Lowbidgee floodplain), counted using semi-automated methods, including their size and colour (important for detection), the dominant vegetation on which they nested (the background) and estimated number of each species in the two colonies.

Colony	Waterbird descriptions			Dominant vegetation
	Species	Colour	Size (cm)	
Kanana	African Openbill <i>Anastomus lamelligerus</i>	Black	82	Gomoti fig <i>Ficus verrucolosa</i>
	African Sacred Ibis <i>Threskiornis aethiopicus</i>	White	77	Papyrus <i>Cyperus papyrus</i>
	Egret sp. <i>Egretta sp</i> ¹	White	64–95	
	Marabou Stork <i>Leptoptilos crumeniferus</i>	Grey	152	
	Pink-backed Pelican <i>Pelecanus rufescens</i>	Grey	128	
	Yellow-billed Stork <i>Mycteria ibis</i>	White	97	
Eulimbah	Australian White Ibis <i>Threskiornis molucca</i>	White	75	Lignum shrubs <i>Duma florulenta</i>
	Straw-necked Ibis <i>Threskiornis spinicollis</i>	Grey	70	Common reed <i>Phragmites australis</i>

¹ Predominantly Yellow-billed Egrets *Egretta intermedia* with some Great Egrets *Ardea alba*.

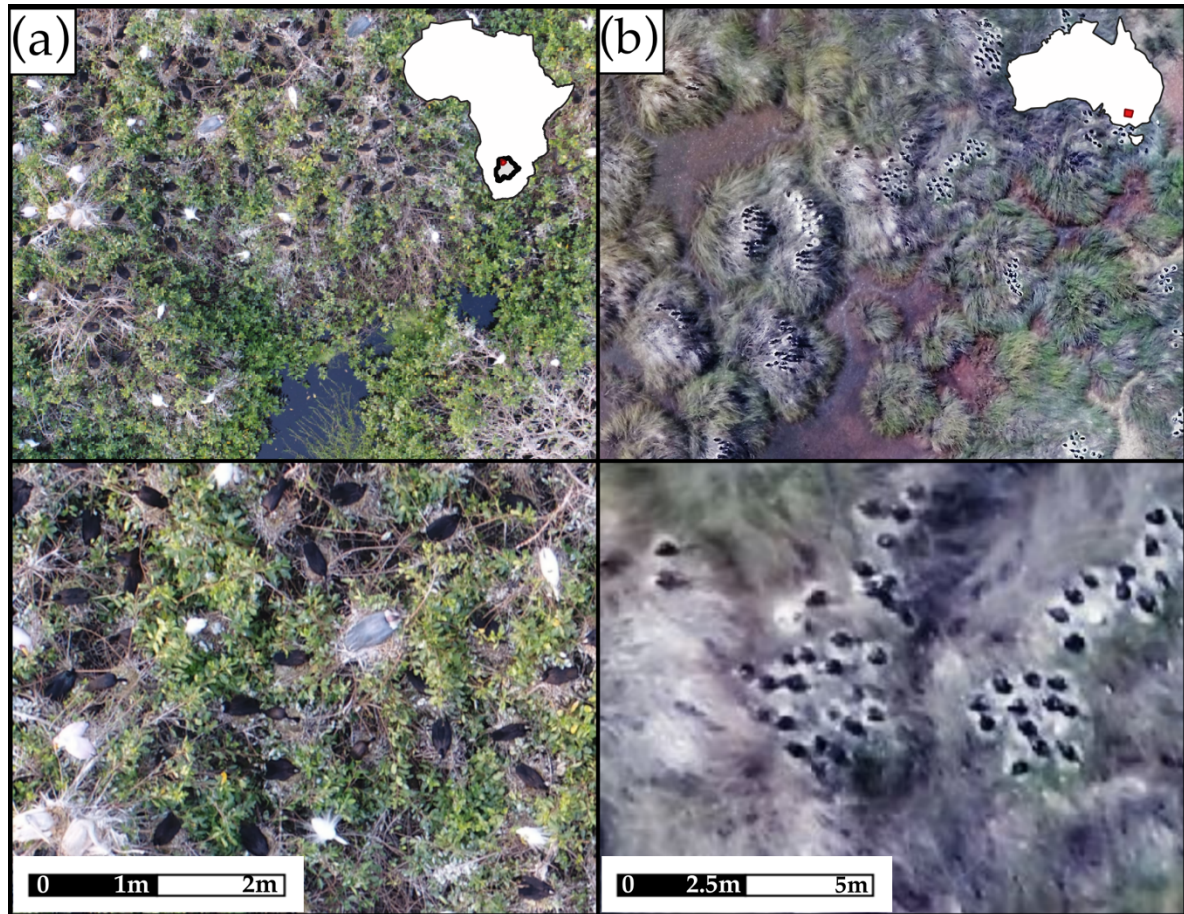


Figure 5.1. Locations' imagery at two resolutions and an example of the segmentation process of the two waterbird colonies: (a) Kanana (Okavango Delta, Botswana) taken using a Phantom 4 Advanced at 20 m, and (b) Eulimbah (Lowbidgee floodplain, Australia) using a Phantom 3 Professional at 100 m.

5.3.2 Image collection and Processing

First, we created polygons surrounding the Kanana colony in September 2018, using Pix4d Capture [39], allowing pre-programming of drone flights and reducing drone noise by adjusting the flight's height and speed [25]. We collected imagery using a DJI Phantom 4 Advanced multi-rotor drone with the stock standard 20 MP camera (5472×3648 image size, lens Field of View (FOV) 84° 24 mm) over the breeding colony (30–40 ha), at a height of 20 m. We flew the drone at the slowest speed ($\sim 2 \text{ ms}^{-1}$), with 20% front and side image overlap, taking still images at evenly spaced intervals, along parallel line transects, with the camera positioned at 90° (nadir perspective). Waterbirds mostly remained on their nests. Resulting photos were

clipped to remove the 20% overlap on each side and placed into a 5×9 grid (Figure 5.2, Step 1), with images aligned within the freeware Photoscape X [40]. We did not orthorectify the images, treating them as joined images (jpegs), in an arbitrary coordinate system, allowing us to provide a freeware processing pathway.

We flew the Eulimbah colony manually in October 2016 at a height of 70 m, launching the drone from a nearby levee bank to reduce disturbance, given that many birds were moving on and off their nests. We collected imagery over the colony (15–20 ha) using a DJI Phantom 3 Professional multi-rotor drone, again with the stock standard camera and an additional neutral density filter (4000×3000 image size, lens FOV 94° 20 mm). We flew at $5\text{--}10\text{ ms}^{-1}$ aiming to acquire imagery with $\sim 70\%$ forward and lateral overlap, along parallel flight lines at 90° [3, 26]. We processed the imagery using the commercial software Pix4DMapper (v4.19, 166 Pix4D SA), with a photogrammetry technique called ‘structure from motion’, which identified points in overlapping images, building a three-dimensional (3D) point cloud reconstruction of the landscape, and finally, generating a digital surface model and an orthorectified image mosaic (Figure 5.2, Step 1). This data was originally collected for another purpose, hence the differing collection methods between colonies, however this allowed us to test the transferability of the following methods.

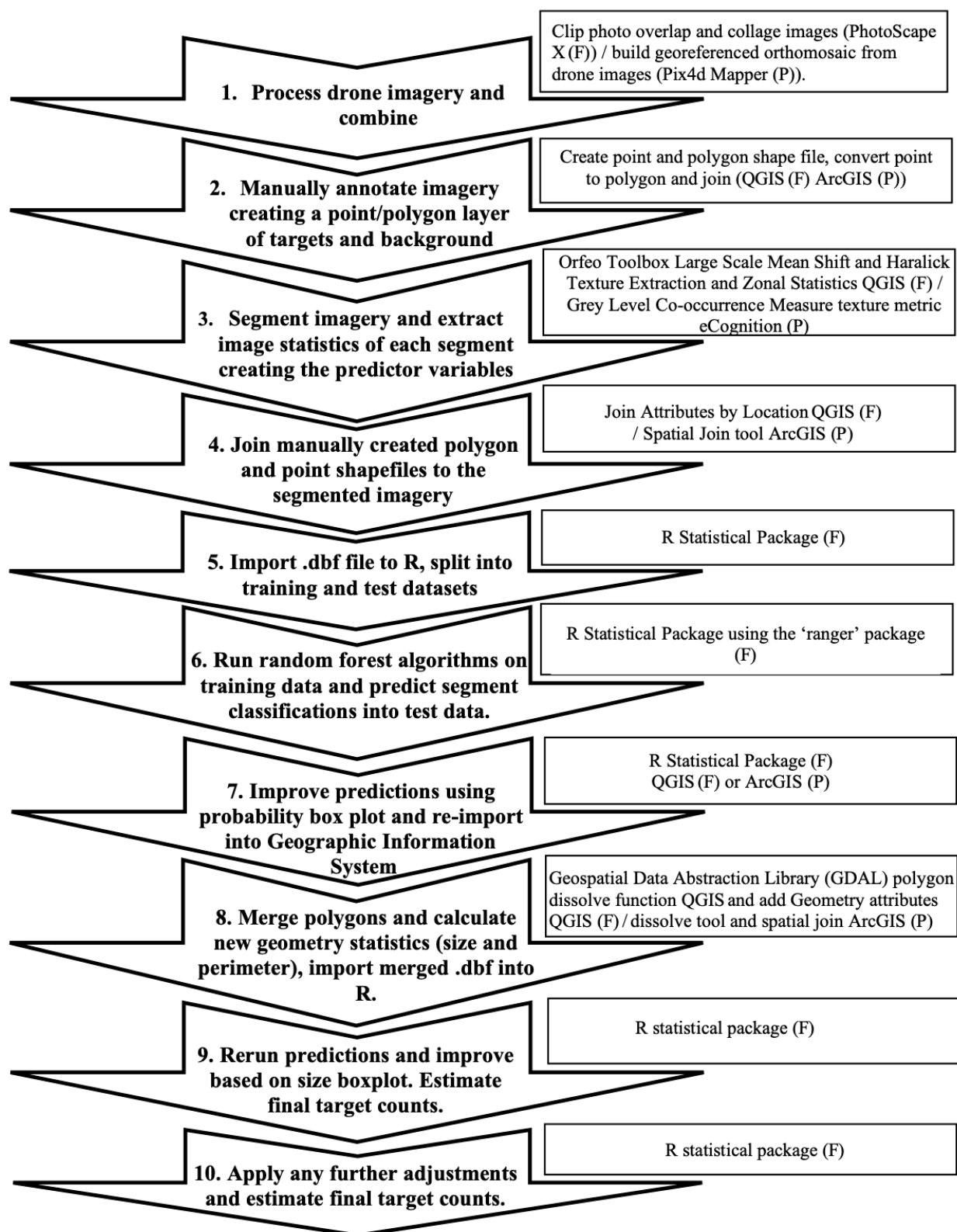


Figure 5.2. The ten steps required to process drone imagery of waterbird colonies using our semi-automated approach, with descriptions of specific software, tool boxes and functions compared (large-scale mean shift (LSMS), freeware (F) and payware (P)).

5.3.3 Semi-Automated Image Analysis

We aimed to develop transferable methods for the two datasets, despite different data collection methods (drone, height), colonies (locations, species) and image processing pathways. We delineated targets (waterbird-related) and backgrounds (surrounding areas in the colony). There were five target species in the Kanana colony (Yellow-billed Storks *Mycteria ibis*, African Openbills *Anastomus lamelligerus*, Marabou Storks *Leptoptilos crumeniferus*, egrets (predominantly Yellow-billed Egrets *Egretta intermedia* and some Great Egrets *Ardea alba* which could not be separated) and Pink-backed Pelicans *Pelecanus onocrotalus*) and two species in the Eulimbah colony (Straw-necked Ibis *Threskiornis spinicollis*, Australian White Ibis *Threskiornis Molucca*). At the Eulimbah colony, we also separately identified whether the two species were on-nests or off-nests (Straw-necked Ibis only), or if the nest had egg/s or was just nest material: in total, five target objects at each colony.

We used a supervised learning approach, given the complexities of the mixed species' aggregations and varied background vegetation. This included an object-based image analysis [41] and a random forest machine learning classifier [3]. The approach had five steps: (1) curation of a training and test dataset (subsets of the entire dataset) for respective modelling and validation, (2) segmentation of the image data (entire dataset) into objects for modelling, with the extraction of colour, texture and morphological features of image objects to use as predictors, (3) fitting of a random forest model to predict different target objects into images across the entire datasets and (4) estimation of target species' numbers in the two colonies.

5.3.4 Training and Test Datasets

Supervised machine learning required a training dataset to develop the algorithm and a test dataset for targets (one for each colony), before estimating target species numbers in the colonies. We therefore manually annotated up to 50 of each target object including birds and nests (annotating both occupied and unoccupied nests in the nest category) on the original

imagery, incorporating a range of different images and areas of the colony (Figure 5.2). We also delineated enough ‘background’ polygons (5-10 in each colony) to include the range of different backgrounds visible (e.g., water, vegetation, bare ground, sand and mud) to train the algorithm, allowing for their specification as non-targets, producing point (targets) and polygon (background) shapefiles (Figure 5.2, Step 2).

5.3.5 Image Object Segmentation and Predictor Variables

For these two (one for each colony) manually selected datasets of targets and backgrounds, we combined object-based segmentation principles, grouping similar attributes (texture, shape, neighbourhood characteristics [42]), with machine learning predictive modelling for semi-automated detection of birds from drone imagery [41,43]. We compared two image segmentation approaches on each image set from the Kanana and Eulimbah colonies: orfeo toolbox in QGIS v3.6.3 (freeware) and eCognition v8 (payware) (Appendix 5.1). We used trial and error for the spatial radius parameters, starting with the defaults and adjusting based on visual determination of appropriate segment size, ensuring effective delineation of individual birds/targets. This resulted in 20 for the Kanana colony and 100 for the Eulimbah colony, reflecting differences in pixel size (smaller pixels and lower height in the Kanana colony) (Figure 5.2, Step 3). Each image segment was attributed with its colour properties (brightness, mean and standard deviation of the blue, green and red photo bands, Figure 5.1), geometric features (e.g., size, ellipse radius, rectangularity, roundness), and textural character (e.g., Gray-Level Co-Occurrence Matrix (GLCM) contrast, entropy), depending on the software used (Figure 5.2, Step 3).

After segmentation, the manually created point and polygon files of targets and background were then intersected with the corresponding segmented image layer (Figure 5.2, Step 4), separately using the freeware and payware. As a result, each target object and/or

background segment was associated with its corresponding suite of predictor variables and exported as database files (.dbf) for import into R for modelling [44].

5.3.6 Machine Learning

We developed our machine learning methods in R on the imagery from the Kanana colony. After importing the two .dbf files into R (freeware and payware files), we split the manually identified datasets into training (80%) and testing (20%) groups, using stratified random sampling focused on background and targets (Figure 5.2, Step 5). We first developed and tested our modelling and classification on these two datasets and then fitted the model to the entire image sets to estimate the total numbers of targets.

On the training dataset, we used the random forest algorithm, a widely used machine learning approach which deals with correlated or redundant predictor data by creating decision trees, where each different split is based on choosing from a random subset of the predictor variables [44]. We fitted separate random forest models to the training dataset of each approach (freeware versus payware), using the ‘ranger’ package on R v3.4.x [45] (Figure 5.2, Step 6). First, our classification tree separated different target and background features. We then fitted a (binomial) regression tree, splitting bird and non-bird targets into 1 and 0 respectively, based on the probability of identification as a bird. The random forest classification and regression used 1000 trees, the square root of the number of predictors as the size of the random subset to choose at each split, and a minimum leaf population of 1 for classification and 5 for regression [44,45]. The final prediction models used the mode of the classification trees and the mean of the predictions for our regression trees.

We then tested our prediction models on the test data (remaining 20%), reporting accuracy (Figure 5.2, Step 6). To improve classification predictions and better separate between the target and background classes, we inspected the data using boxplots and 99% quantile statistics and developed thresholds (Figure 5.2, Step 7). We changed segments that were likely to have

been misclassified, as either bird or background, to the correct class based on the values of the 99% quantile (Figure 5.3). We reported on comparison of these datasets as a standard error matrix-based accuracy assessment and with receiver operating characteristic (ROC) plots (see Appendix 5.2) [46].

The classified database files (.dbf), with target and background probabilities corrected, were reimported into GIS software (using freeware or payware). They were inspected visually, and we noted there were cases where a single target was divided into two segments. We corrected this by merging neighbouring segments, with the same classifications, ensuring that targets were only counted once. We then calculated the new segment area and perimeter and imported the database files (.dbfs) back into R (Figure 5.2, Step 8). We reran the prediction models and created boxplots of the areas identified for each species (Figure 5.4), which allowed us to detect outliers in area across both datasets (freeware or payware), that exceeded thresholds as specified by the 99% quantile and which therefore needed to be reclassified as targets or background (Figure 5.2, Step 9). We replicated the code and GIS steps above and tested transferability of our approach to the Eulimbah colony.

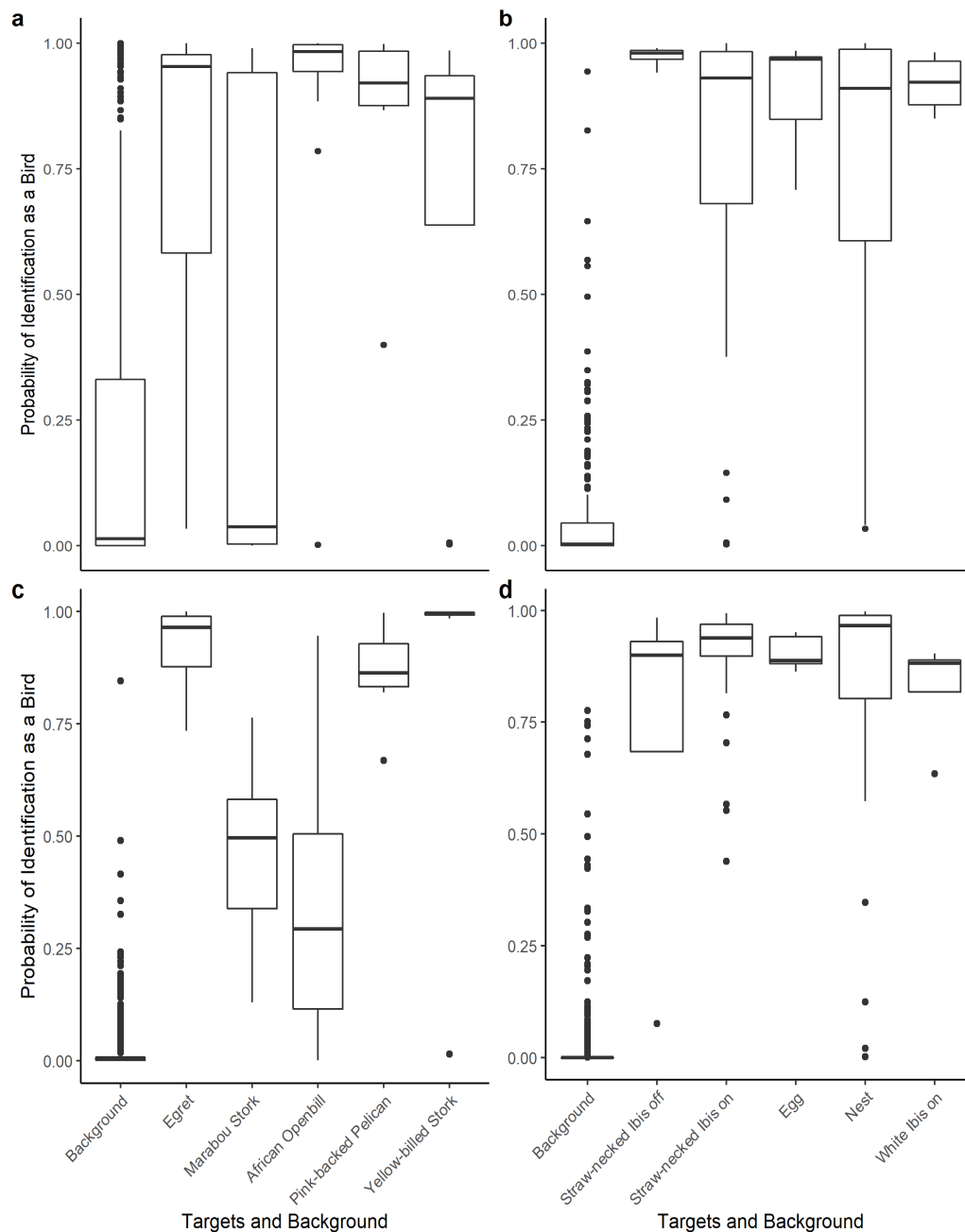


Figure 5.3. The boxplot used to identify classification errors between targets and background using 99% thresholding for the freeware method at (a) the Kanana colony and (b) the Eulimbah colony, and the payware method at (c) Kanana and (d) Eulimbah. At the Eulimbah colony, birds were identified as being either on or off their nests.

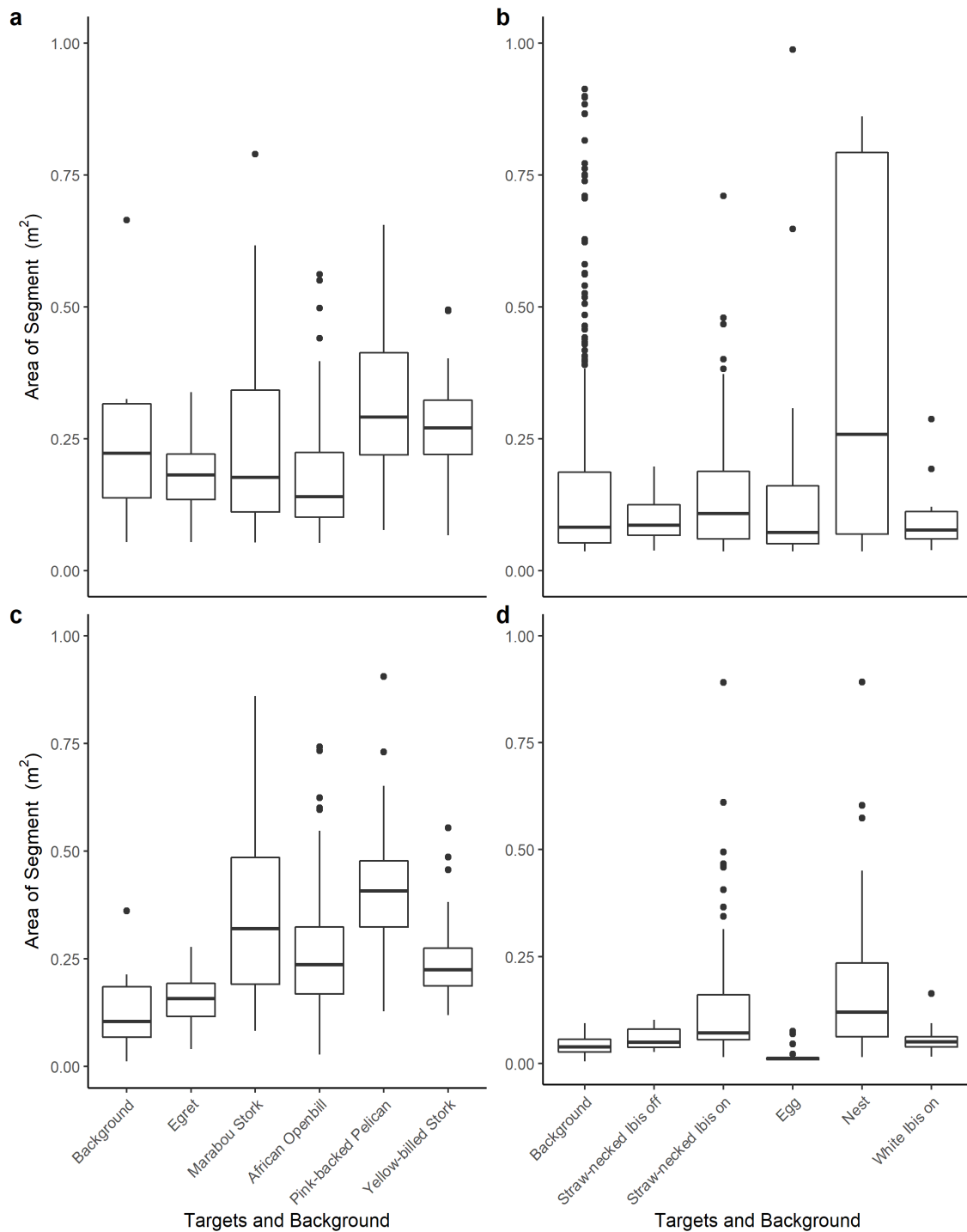


Figure 5.4. The boxplot used to identify classification errors between segment areas of targets and background using 99% thresholding for the freeware method at (a) the Kanana colony and (b) the Eulimbah colony, and the payware method at (c) Kanana and (d) Eulimbah. At the Eulimbah colony, birds were identified as being either on or off their nests.

5.3.7 Estimation of Target Populations

Once classifications were cleaned, we could estimate numbers (i.e., targets) for each species in the Kanana colony, summing the semi-automated classifications, given limited clumping in this colony (Figure 5.2, Step 10). In contrast, birds in the Eulimbah colony often nested closely together, demanding an additional step for estimation of numbers, as our classification inevitably segmented a group of nesting birds as a single target. To estimate individual bird numbers in these clumped targets, we divided all bird classifications by average bird size ($\sim 0.08 \text{ m}^2$ [47]), before summing to estimate numbers of individuals of the two species in the colony (rounded to integer) (Figure 5.2, Step 10). Before estimating the nest count at Eulimbah, we filtered out other targets (e.g., empty nests) which were less than ‘bird size’, to remove noise and misclassifications that could not be birds or nests. To compare semi-automated count estimates across the entire image sets to the ‘true’ count, we also manually counted all birds in both colonies by separating the imagery into grids, annotating birds as a point shapefile and summing grid numbers. We compared these estimates to our semi-automated counts, including the time taken for both counts.

5.4 Results

The Kanana colony consisted of 45 stitched images of 7,181,016 pixels (size $\sim 5.5 \text{ mm}$), covering an area of $\sim 39,500 \text{ m}^2$ while the stitched orthomosaic image for the Eulimbah colony had 41,785,728 pixels (size $\sim 3 \text{ cm}$) extending over an area of $\sim 120,000 \text{ m}^2$. It took 650 and 250 min for respective total manual counts of the Kanana and Eulimbah colonies. In comparison, our semi-automated approach took 480 min for initial development and an additional 60 min to edit the code for the Eulimbah colony. This was a time savings of about 26%, including the development of this method. Excluding this development, we estimated that about 90 min was required to work through the ten steps (Figure 5.2), an estimated time

savings of 250%–700% (not including processing time, given this can occur independently on the computer, and would differ between systems). In the Kanana imagery, we manually counted 4140 birds from five species, while Eulimbah had 3443 birds from two species, including nests totalling 6310 targets (Table 5.2).

Table 5.2. Final target counts for both the Kanana and Eulimbah colonies with calculations of manual versus semi-automated methods.

Colony	Target	Final Counts			Difference %	
		Freeware	Payware	Manual	Freeware	Payware
Kanana	Bird ¹	2128	1797			
	Egret Sp. ²	587	605	578	1.56	4.67
	Marabou Stork	156	102	137	13.87	–25.55
	African Openbill	725	681	2986	–4.45 ³	–17.01 ⁴
	Pink-backed Pelican	154	71	59	161.02	20.34
	Yellow-billed Stork	336	354	380	–11.58	–6.84
	Total targets	4086	3610	4140	–1.30	–12.80
Eulimbah	Bird ¹	N/A	1155			
	Egg	108	287	80	35.00	258.75
	Nest	3458	3390	2787	24.08	21.64
	Straw-necked Ibis on nest	2271	2590	3267	–30.49	–20.72
	Straw-necked Ibis off nest	196	91	136	44.12	–33.09
	White Ibis on nest	111	99	40	177.50	147.50
	Total targets	6144	7612	6310	–2.63	20.63

¹ Originally, background segments which based on their probabilities were reassigned to a general ‘bird’ category, and upon inspection of the error matrix identified as mostly African Openbills. This step was not necessary at Eulimbah using the freeware method.

² Predominantly Yellow-billed Egrets *Egretta intermedia* with some Great Egrets *Ardea alba*.

³ –75.72 before assigning the misclassified background segments from the ‘bird’ category as African Openbills.

⁴ –77.19 before assigning the misclassified background segments from the ‘bird’ category as African Openbills.

Using freeware to estimate numbers of breeding birds of each species in the Kanana and Eulimbah colonies, our initial accuracies were respectively, 88% and 99% (Table 5.3). In the Kanana colony, African Openbills had the lowest detection accuracy, and were likely contributing to the initial low-accuracy measure. Once we applied our probability threshold

method (Figure 5.3) and inspected the error matrix (Table 5.4), we identified that many nesting African Openbills were misclassified as background, because of their dark plumage and its similarity to the background. We corrected this misclassification by delineating background as any area with a probability (bird classification) of <0.3 or >1 , (Figure 5.4a), producing a recalculated accuracy of 99% (Table 5.3). For the Eulimbah colony, it was not necessary to separate birds from backgrounds with the probability threshold method, and we only corrected for area (>0.5 as background, Figure 5.4b), producing a final bird detection accuracy of 98% (Table 5.5). Finally, after these corrections, our estimated counts using freeware were within 2% and 3% of respective manual counts for the Kanana and Eulimbah colonies (Table 5.2).

Table 5.3. Results for the freeware and payware used in the development of semi-automated counting methods for the Kanana and Eulimbah colonies, showing the initial, secondary (after correcting for probabilities) and final model accuracies (after correcting for area).

Kanana Freeware	Initial	Secondary	Final
Target versus Background Accuracy	0.99	0.99	0.91
Between Target Detection Accuracy	0.88	0.88	0.99
Kanana Payware			
Target versus Background Accuracy	0.99	0.99	0.90
Between Target Detection Accuracy	0.57	0.82	0.99
Eulimbah Freeware			
Target versus Background Accuracy	0.98	N/A ¹	0.98
Between Target Detection Accuracy	0.99	N/A	0.98
Eulimbah Payware			
Target versus Background Accuracy	0.99	0.99	0.93
Between Target Detection Accuracy	0.88	0.93	0.98

¹It was not necessary to correct for bird probabilities at Eulimbah using the freeware method, hence the N/A values in the secondary model accuracies.

Table 5.4. Results for the freeware and payware used in development of semi-automated methods for the Kanana colony, showing the secondary error matrix after correcting for probabilities, and the final error matrix after correcting for area, where rows are the test data and columns are the predicted data.

Kanana Freeware							
	Background	Bird	Egret Sp.	Marabou Stork	African Openbill	Pink-backed Pelican	Yellow-billed Stork
Background	3310	14	0	0	0	0	0
Egret Sp. ^a	0	0	11	0	0	0	0
Marabou Stork	0	6	0	5	0	0	0
African Openbill	14	11	0	0	7	0	0
Pink-backed Pelican	0	0	0	0	0	7	0
Yellow-billed Stork	0	1	2	0	0	1	10
	Background	Bird	Egret Sp.	Marabou Stork	African Openbill	Pink-backed Pelican	Yellow-billed Stork
Background	2	10	1	0	0	0	0
Egret Sp. ^a	0	0	50	0	0	0	2
Marabou Stork	0	4	0	49	0	0	0
African Openbill	3	12	0	0	126	0	0
Pink-backed Pelican	1	0	1	0	0	28	0
Yellow-billed Stork	0	0	2	0	0	0	66
Kanana Payware							
	Background	Bird	Egret Sp.	Marabou Stork	African Openbill	Pink-backed Pelican	Yellow-billed Stork
Background	3310	14	0	0	0	0	0
Egret Sp. ^a	0	0	11	0	0	0	0
Marabou Stork	0	6	0	5	0	0	0
African Openbill	14	11	0	0	7	0	0
Pink-backed Pelican	0	0	0	0	0	7	0
Yellow-billed Stork	0	1	2	0	0	1	10
	Background	Bird	Egret Sp.	Marabou Stork	African Openbill	Pink-backed Pelican	Yellow-billed Stork
Background	2	10	1	0	0	0	0
Egret Sp. ^a	0	0	50	0	0	0	2
Marabou Stork	0	4	0	49	0	0	0
African Openbill	3	12	0	0	126	0	0
Pink-backed Pelican	1	0	1	0	0	28	0
Yellow-billed Stork	0	0	2	0	0	0	66

Table 5.5. Results for the freeware and payware used in development of semi-automated methods for the Eulimbah colony, showing the secondary error matrix after correcting for probabilities (not necessary at Eulimbah using the freeware method), and the final error matrix after correcting for area, where rows are the test data and columns are the predicted data.

Eulimbah Freeware							
	Background	Bird ¹	Egg	Nest	Straw-necked Ibis On nest	Straw-necked Ibis Off nest	White Ibis On nest
Background	366	N/A	0	1	0	0	0
Egg	2	N/A	19	3	0	0	0
Nest	2	N/A	0	194	1	0	0
Straw-necked Ibis on nest	4	N/A	0	3	162	0	0
Straw-necked Ibis off nest	0	N/A	0	0	1	21	0
White Ibis on nest	0	N/A	0	1	0	0	19
Eulimbah Payware							
	Background	Bird	Egg	Nest	Straw-necked Ibis On nest	Straw-necked Ibis Off nest	White Ibis On nest
Background	1243	0	0	2	2	0	0
Egg	0	1	3	1	0	0	0
Nest	4	1	0	31	0	0	1
Straw-necked Ibis on nest	1	1	0	2	28	1	0
Straw-necked Ibis off nest	1	1	0	0	0	2	0
White Ibis on nest	0	0	0	0	0	0	4
	Background	Bird	Egg	Nest	Straw-necked Ibis On nest	Straw-necked Ibis Off nest	White Ibis On nest
Background	1	2	0	2	0	0	0
Egg	1	0	22	1	0	0	0
Nest	0	0	0	31	0	0	0
Straw-necked Ibis on nest	3	2	0	0	111	0	0
Straw-necked Ibis off nest	0	3	0	0	0	19	0
White Ibis on nest	0	0	0	1	0	0	19

¹It was not necessary to correct for bird probabilities at Eulimbah using the freeware method, hence the N/A values.

Using payware, our initial bird detection accuracies for the Kanana and Eulimbah colonies respectively, were 57% and 88%. After re-classifying bird and backgrounds, based on the probability boxplot (< 0.1 as background and >0.2 as birds for Kanana and <0.5 as background and >0.5 as birds for Eulimbah), we improved the accuracy to 85% and 93%. We then re-classified using our area threshold (>1 and <0.3 as background for Kanana and <0.01 and >0.8 as background for Eulimbah). This improved respective accuracies to 99% and 99% (Tables 3 and 4). Finally, after these corrections, our estimated counts using payware were within 13% and 21% of respective manual counts for the Kanana and Eulimbah colonies (Table 5.2). Using the freeware method provided a more accurate overall count compared to the total manual counts than using payware (Table 5.2).

The different steps (Figure 5.2) had an associated code within R for freeware and payware, allowing modification and transfer from the Kanana colony where it was developed to the Eulimbah colony. Alteration in the code between colonies is firstly in the correct usage of target object names (which naturally differ based on the species or object being counted, Figure 5.2, Step 5). Secondly, thresholds used to differentiate between and re-classify targets will differ based on the segment statistic used and the target objects' physical attributes (e.g., area or colour, Figure 5.2, Step 9). The major alteration to code required when transferring between freeware and payware is assigning the correct predictor variables to the random forest modelling, based on the output of the image statistics of each segment (Figure 5.2, Step 3). All code/data required are available for download (see Appendix 5.3).

5.5 Discussion

Methods which can rapidly collect data over large areas and process these data quickly are important for understanding systems and in providing timely data analyses to managers and the public. Drones are becoming increasingly powerful tools for the collection of such data on

a range of organisms [26,49,50], given that they can capture imagery over inaccessible and sometimes dangerous areas. This is only half the process: the imagery needs to be analysed to provide estimates of organisms. Manual counting is the traditional approach but, it is slow and laborious and may be prone to error. New and improved methods are required to process images quickly and efficiently. Our semi-automated system of counting breeding waterbirds on nests on highly variable backgrounds was effective and efficient. Importantly, we successfully applied the methodology, developed on one colony with different species in a different environment (on another continent) to another colony. This transferability is particularly useful. Significantly, payware and freeware methods were equally effective and accurate, providing global opportunities where resourcing is limited. Finally, there are opportunities to apply this approach to other organisms, amassing in large aggregations.

Using our approach, waterbird colonies around the world could be quickly and accurately counted using drone data. There are many active research teams, often providing information for management, surveying and estimating sizes of breeding colonies of waterbirds, including colonies in Australia [51], Southern India [52] and Poland [53]. But our methodology is also transferable to other aggregations of species, such as the Valdez elephant seal *Mirounga leonine* colony in Patagonia [54] or macaques *Macaca fuscata* in tourist areas in Japan [55]. Transferability requires some key idiosyncratic steps in image processing, data training and modelling. These include either the initial clipping of overlap in drone imagery or the creation of orthomosaics, then the development of a training model for classifying species (Figure 5.2, Step 2) and finally, testing the model using derived thresholds (Figure 5.2, Step 9), discriminating between animals and backgrounds. Such steps can be applied to drone imagery captured in different environments, making the use of citizen science drone-collected imagery a feasible data source [56].

Every species of waterbird or other organism will differ in different ways from the background, be it in size, colour or a combination of multiple such image statistics. For this reason, we focused on the entire colony, but these methods could be altered to focus on a certain species, which may be of more use to environmental managers. To edit and implement our methodology for any waterbird colony around the world, after initial image processing, the manually annotated dataset must be created to train the model on target species. Subsequently, edits must be made to the R code aligning target names and the image statistics to be used as predictors, which can then be used to estimate thresholds distinguishing species from backgrounds. When focusing on a single species, the misclassifications specific to this species could be explored to adjust and improve species' specific accuracies. Extending to other organisms can take a similar approach, with final modelling dependant on the creation of the initial manually annotated dataset classifying the organisms and background. While each study will have its own requirements for the data, we aimed to develop a methodology that would produce a maximum of 10% disparity between semi-automated and manual counts, which with more time invested, could be further reduced.

Consideration of drone height is an important first step when collecting imagery for use with this method. In general, a lower flight height and a better camera will produce images of a larger pixel size, however this needs to be balanced against disturbance to the species of interest. Furthermore, a lower drone height equates to less area covered in the imagery within the span of one battery, and so the number of available batteries and survey area therefore need to be considered. When surveying a single species that contrasts a relatively simple background, less image detail will be required to differentiate between the target and background. Conversely, the more species to differentiate between, particularly if on a varied background such as the colony at Kanana, the more detail required in the imagery to obtain

accurate estimates. Drone height requirements will therefore be unique to study location, area, species and aims.

The most challenging aspect of our methodology was identifying and dealing with misclassification errors. Ultimately, inaccuracy occurs and needs to be reported. Identifying the source of errors is critical and there are two ways to improve the final estimates: increasing sample sizes of training data and identifying attributes that better discriminate between objects and backgrounds. Increasing sample sizes of training datasets likely improves models. This may be particularly relevant where colonies are repeatedly surveyed (i.e., multiple breeding events over time), as the greater initial time investment in training the model may reduce the time required for following surveys. We only used ~50 individual objects for each species' grouping, which may have reduced the power of our models. For example, for the pink-backed pelicans in the Kanana imagery, we only had 32 training points (as they were relatively rare in the colony) and so increasing sample size in future years or from other sources would probably improve the model and classification. Increased sample sizes are particularly important for discriminating between highly similar target objects, improving the model's discriminatory capacity to identify a unique attribute or set of attributes for each object.

Even with reasonable sample sizes, there may be confusion among species and the background, contributing to errors. For our Kanana colony, the dark plumage of the African Openbills was often confused with dark patches of background, such as water. Also, similarly sized, shaped and coloured egret species could be confused with Yellow-billed Storks, contributing to inaccuracies (Table 5.2). As well as size, there could be other sources of discrimination between targets (e.g., pigmentation means or deviations) which could be incorporated in modelling and identified from boxplots (Figure 5.2, Step 9). Our script can easily be altered, to incorporate such a change. Improvements in image collection such as the use of a multi-spectral sensor (as opposed to the combined standard Red Green Blue sensor

used here) could also improve modelling and separation of backgrounds from birds. Further, software improvements could also improve outcomes. Inevitably, more data, repeated measurements and time invested will improve effectiveness, accuracy and efficiency, in the equally performing freeware and payware software (Table 5.2).

There were considerable time efficiency benefits in using our semi-automated approach. We differentiated among five species in 26% less time than when we used manual counting, with time savings likely to improve with repeated counts due to user experience. Further, such manual counting was probably also prone to some error, as observers tire or inadequately discriminate. We considered the manual count as the ‘true’ count and the most accurate, particularly as our annotations allowed us to revisit the imagery and scour for any birds missed. There was still the possibility that birds and nests were obscured by vegetation in the drone imagery, and therefore were not counted, but these omissions applied to any counting method from imagery. Increasingly, machine learning approaches are improving and becoming more accurate than manual methods in a range of disciplines (e.g., medicine, identification of melanomas [57] and astronomy, identification of chorus elements [58]). There is no reason why our approach, and more broadly, approaches of counting animals using drone imagery and machine learning, will not become increasingly more accurate and more efficient with growing amounts of data, with wide applications. Such savings in time would allow for counts and reports to be rapidly provided to environmental managers, providing information for real-time management decisions, where field data may not be sufficient [30].

Drone imagery can also provide baseline data of environmental importance. Although the Kanana colony is one of the biggest and most frequently used breeding grounds of waterbirds in the Okavango Delta, a United Nations Educational Scientific and Cultural Organization (UNESCO) World Heritage Site, there are few quantitative data on the size or composition of this breeding colony. Another six colonies in the Okavango Delta similarly have little

information. Some of these are difficult and dangerous (crocodiles, hippopotamuses, elephants) to approach on foot and so drones provide an excellent data collection method. The importance of these data could grow when combined with increasing knowledge of the link between flooding and waterbird breeding. Similarly, the Eulimbah colony is one of the only breeding colonies of up to 50,000 breeding pairs in the Lowbidgee floodplain, which also includes other breeding species, such as cormorants, herons and spoonbills. These data are also increasing in their value in determining historical impacts of river regulation and management on major wetlands [59,60], as well as guiding management of flows to improve waterbird breeding and wetland condition [61,62].

The use of drones and the processing of imagery for ecological applications will increase, given their advantages. Processing methods also continue to improve to capitalise on this technology, increasing our understanding and ability to manage complex ecosystems, not only for waterbird colonies but other aggregations of wildlife. Eventually, software informed by training data could be installed on drones, allowing real-time processing and estimation of numbers of birds or other target organisms. Until this happens, the semi-automated methods described here provide considerable promise and opportunity around the world, with the added values of efficiency, free software options and opportunity for improvements in accuracy.

5.6 Conclusions

We developed a semi-automated machine learning counting method, using both freeware and payware, that was transferable between waterbird colonies on different continents. Our detection accuracy (targets), between the training and test data, was 91% for the Okavango Delta colony and 98% for the Lowbidgee floodplain colony. These estimates were within 1%–5%, whether using freeware or payware for the different colonies. Our semi-automated method was 26% quicker, including development, and 500% quicker without development than manual counting. Using drones and semi-automated counting techniques therefore saves time and

resources, whilst allowing access to difficult or dangerous areas. As a result, the use of drones as scientific tools will increase, particularly to survey wildlife aggregations. Importantly, their low cost and the option of using freeware provides research opportunities globally, including where resourcing is limited. We predict that these benefits will only increase as battery life is extended and a greater range of drone software options become available.

5.7 Acknowledgements

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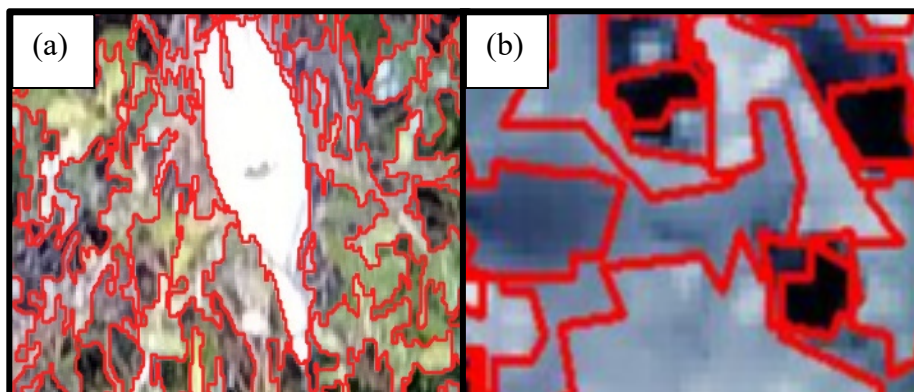
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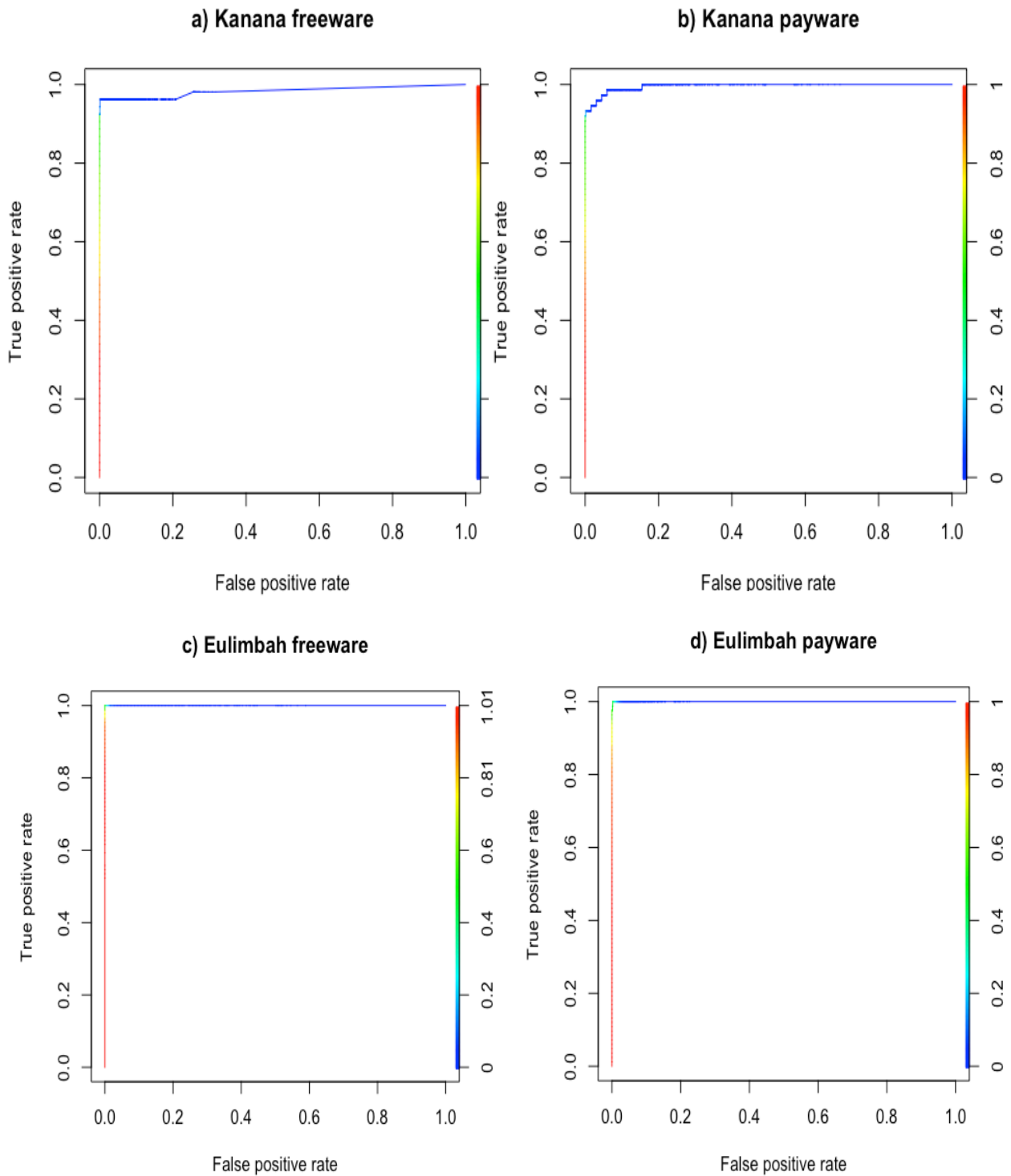
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5.9 Appendices

Appendix 5.1. Examples of the segmentation process, showing the differentiation of background segments and an egret at Kanana ((a), white segment) and Straw-necked Ibis at Eulimbah ((b), black segments).



Appendix 5.2. ROC plots of the background or not initial classifications (before corrections) at the Kanana colony using a) freeware and b) payware, and at the Eulimbah colony using c) freeware and d) payware



Appendix 5.3. Descriptions of datasets with their location and digital object identifier (DOI).

Description	Location	DOI
Eulimbah imagery	https://datadryad.org/stash/dataset/doi:10.5061/dryad.m4r0cn0	10.5061/dryad.m4r0cn0
Kanana imagery, .dbf files for the freeware and payware methods at both the Kanana and Eulimbah colonies.	https://figshare.com/articles/Flight1ImageCombined_jpg/11911314	10.6084/m9.figshare.11911314
R code for the freeware and payware methods at both the Kanana and Eulimbah colonies.	https://github.com/RoxFrancis/Automated-Waterbird-Counts https://doi.org/10.5281/zenodo.3715894	10.5281/zenodo.3715894

Chapter 6. Urban waste no replacement for natural foods – Marabou storks in Botswana

Francis, R.J, Kingsford, R.T., Murray-Hudson, M., and Brandis, K.J.

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I led study design, methods creation, import permit applications, fieldwork, data collection and compilation, lab analyses, data analysis and writing.

6.1 Abstract

We compared diets of marabou storks *Leptoptilos crumenifer* foraging from urban landfills and natural areas in northern Botswana using stable isotope analyses and inductively coupled plasma mass spectrometry (ICP-MS) on moulted feathers. There were significant differences in the diet of marabous foraging from natural areas compared to urban waste sites, reflected by lower $\delta^{13}\text{C}$ and less enriched $\delta^{15}\text{N}$ concentrations in those feeding at landfills, suggesting a shift in trophic niche. Feathers from birds foraging at landfills also had significantly higher concentrations of chromium, lead, nickel, and zinc and lower levels of cadmium and potassium than feathers sampled from natural areas. We also analysed marabou regurgitant (42 kgs, naturally expelled indigestible food resources) from the Kasane landfill site. More than half was plastic, with single regurgitants weighing up to 125g. Urban waste stored in open air landfills is altering some marabou diets, affecting their natural trophic niche,

resulting in the consumption (and regurgitation) of large amounts of plastic, and exposing marabou to potentially chronic levels of trace metals. Despite the marabou's apparent resilience to this behavioural shift, it could have long term effects on the population of the marabou stork, particularly considering Botswana has some of the few regular marabou breeding colonies in southern Africa.

6.2 Introduction

As human populations increase and concentrate in the world's cities (Giles-Corti et al., 2016; Zhang, 2016), direct and indirect interactions with wildlife also increase. Urbanisation effects such as habitat loss and degradation, pollution, disease (Crist, Mora, & Engelman, 2017; Duh, Shandas, Chang, & George, 2008; Laurance, 2010), and human-wildlife conflict (Dickman, 2009; Dunham, Ghiurghi, Cumbi, & Urbano, 2010; Lamarque et al., 2009) are the cause of much of these interactions, which commonly arise between people and bird species (Lambertucci, Shepard, & Wilson, 2015; O'Bryan et al., 2018; Oduntan, Shotuyo, Akinyemi, & Soaga, 2015). Such interactions occur globally, including within urbanising populations of African countries (Thabethe & Downs, 2018).

In low and middle income countries, waste stored in open air landfills is increasing (Yang, Ma, Thompson, & Flower, 2018), attracting many avian species to the abundant food scraps (Ciach & Kruszyk, 2010; de la Casa-Resino, Hernández-Moreno, Castellano, Pérez-López, & Soler, 2014). For example, different stork species feed in landfill sites across Europe, Africa and America (Ciach & Kruszyk, 2010), altering their diet. The ingestion of waste, including plastic and trace metals, as a result of this dietary shift can result in mortality from poisoning (Piper, 2004), decreased egg production and increased hatchling mortality (Abdullah et al., 2015; Lavers, Bond, & Hutton, 2014; Liu et al., 2019; Malik & Zeb, 2009).

The marabou stork *Leptoptilos crumenifer* has frequented human landfill sites for more than six decades (Kahl, 1966). They are widely distributed across Africa (Brown, Urban,

Newman, Woodcock, & Hayman, 1982), naturally feeding on insects, fish, frogs, small mammals, small reptiles, including young crocodiles, birds and carrion (Maclean, Roberts, Newman, & Lockwood, 2011). They can swallow large whole food items, weighing up to 600g (J. Hancock, Kushlan, & Kahl, 2010), which they process in their crop, regurgitating unwanted parts (e.g. bone). When feeding at landfill sites, they use this behaviour to regurgitate unwanted plastic, foil, cardboard, polystyrene and even a knife (J. Hancock et al., 2010). Little is known about the effect of this novel feeding behaviour on individuals or populations, although marabou chicks had slow development near a Kenyan landfill site, where they were fed abattoir scraps and material from the landfill (Kahl, 1966).

Due to the use of regular roosting sites (D. Pomeroy, 1973) the collection of discarded feathers is a simple and non-invasive sampling method. Feathers can provide a dietary signature, reflecting both trophic level and dietary niche information, and trace metal uptake (Furness, Muirhead, & Woodburn, 1986; Markowski et al., 2013; Mizutani, Fukuda, & Kabaya, 1992). Niche and trophic level changes can be detected with isotopic analyses, as the isotopic composition of an animal's tissues reflect its diet (DeNiro & Epstein, 1978, 1981). In feathers in particular, the isotopic composition reflects diet during feather growth (Dauwe, Bervoets, Pinxten, Blust, & Eens, 2003; Hobson & Clark, 1992), with nitrogen isotope ratios undergoing a stepwise enrichment with trophic level (DeNiro & Epstein, 1981), and carbon ratios indicating dietary contributions from differing sources (e.g. freshwater vs. terrestrial plants) (DeNiro & Epstein, 1978). A changing dietary niche in a top predator and scavenger such as the marabou stork could have cascading effects through the ecosystem (Antiqueira, Petchey, & Romero, 2018; Letnic, Koch, Gordon, Crowther, & Dickman, 2009; Reznick, Ghalambor, & Crooks, 2008), opening the niche to other (often invasive) species (González-Moreno, Diez, Richardson, & Vilà, 2015) and affecting interspecies resource partitioning and competition (Córdova-Tapia, Contreras, & Zambrano, 2015; Wang, Huan, YuWei, Lu, &

Guangchun, 2018). Trace metals ingested in dietary items can be detected in feathers, given that metals absorbed through the intestinal tract can be sequestered in feathers (Furness et al., 1986) during feather growth. Therefore, comparison of isotopic ratios and metals in feathers can help differentiate variations in the diets among and within bird populations, reflecting site specific feeding responses (Doucette, Wissel, & Somers, 2011; Hebert et al., 2016; Jackson, Inger, Parnell, & Bearhop, 2011; Mikoni et al., 2017).

This uptake of metals into a birds' feathers means they are useful bioindicators of metal pollution, with total metal concentrations reflecting internal (from food) and external (from the environment) contamination (Goede and De Bruin 1986, Hahn et al. 1993). Using predatory birds can be an effective way to explore biomagnification of certain metals and, depending on the species and their prey, can be used to explore metal accumulation along different food chains (Lodenius and Solonen 2013). This use of birds as bioindicators can be implemented in monitoring programs to track changes over time and across a range of environments (Eens et al. 1999), however the mobility of birds must be accounted for in this design. As such, the role of birds in monitoring or indicating metal pollution contributes to the role they often play as ecosystem health indicators around the world.

In Botswana, the marabou stork can be frequently seen feeding at landfill sites, and to explore the effects of this behaviour we compared isotopic ratios (^{13}C and ^{15}N) and trace metal concentrations (Al, Cd, Cr, Cu, Fe, K, Ni, Mn, Pb and Zn) in feathers collected from a range of urban landfills and natural environments. We predicted that the populations feeding at landfill sites would show a shift in their trophic position and feeding niche, reflected by higher ^{13}C and enriched ^{15}N in their feathers, due to the ingestion of abundant and highly varied sources of terrestrial protein and plants material which differ in isotopic fractionation processes to their natural food. We also predicted trace metal concentrations (ppm) in feathers would reflect proximity to landfill sites due to the uptake of metals with ingestion of

waste via bioaccumulation, as with other bird species (de la Casa-Resino et al., 2014). We therefore tested the null hypothesis: there are no differences in elemental concentrations or stable isotope analyses of marabou stork feathers as distance from landfill sites increases. This dietary shift could have serious consequences on individuals, including mortality (Piper, 2004), affecting Marabou populations in southern Africa.

6.3 Methods

6.3.1 Study Area

We studied marabou populations from eight locations across northern Botswana, comprising urban and natural feeders. Marabou fed at two landfill sites: Maun and Kasane. Maun and Kasane landfill sites contained household, hospital, industrial and mechanical waste, with abattoir waste also present at the Maun landfill. Adjacent to the Kasane landfill (~500m), there was a fenced reserve where marabou roosted nightly, returning daily to feed at the landfill. These three locations comprised the urban feeding marabou populations of our study. Naturally feeding marabou populations also occurred at three locations within Chobe National Park, about 50kms from the nearest landfill (between Ngoma (C3) and Ihaha Campsite (C1), Fig. 6.1), and from two sites within the Okavango Delta, about 80km from the nearest landfill (Chiefs Island (CI) and Kanana breeding colony (KC), Fig. 6.1).

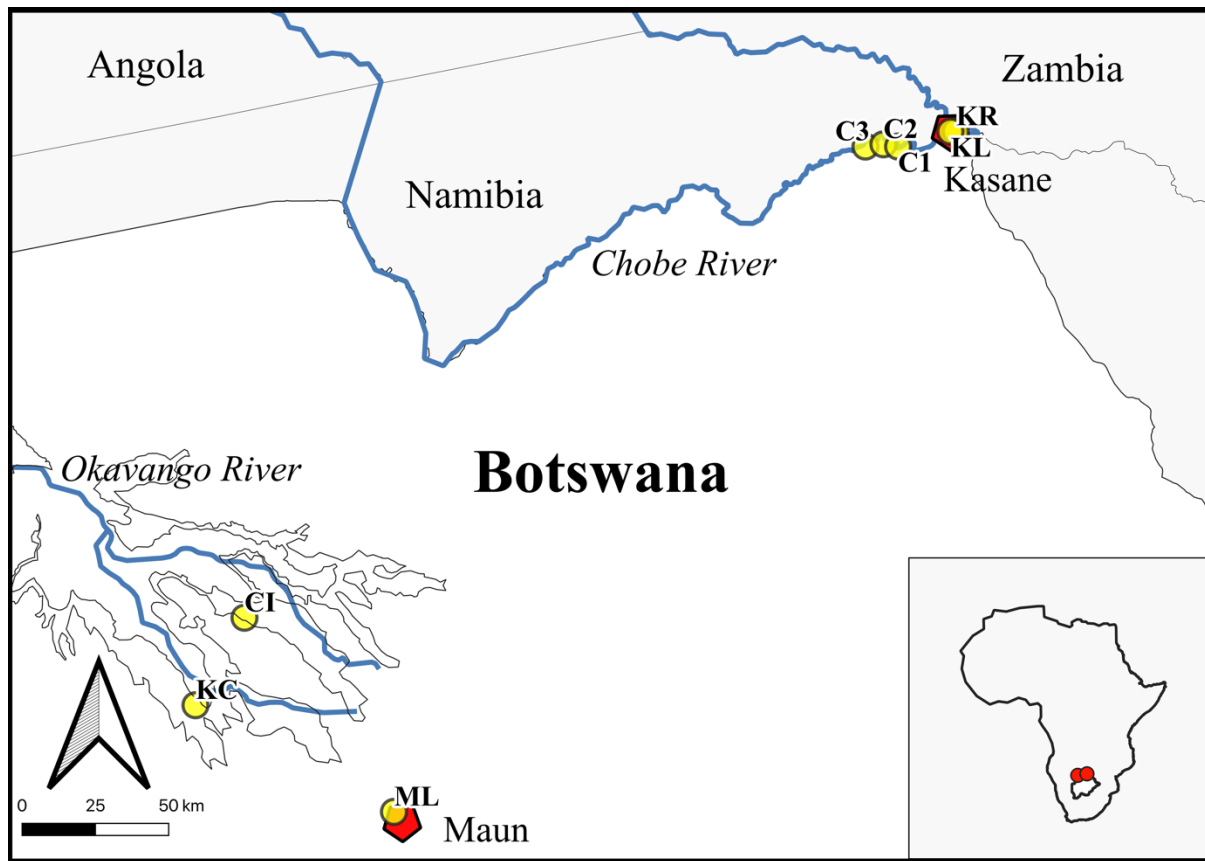


Figure 6.1. Eight locations (yellow circles) where feathers of marabou storks were collected from five natural environments, including the Okavango Delta (Kanana Colony (KC, $n=9$, 22.8582, -19.5429) and Chiefs Island (CI, $n=10$, 23.0064, -19.2746)), and Chobe National Park (C1 ($n=5$, 25.0156, -17.8313), C2 ($n=3$, 24.9666, -17.8249) and C3 ($n=1$, 24.9113, -17.8331)) and two landfill sites (red pentagons, Maun Landfill (ML, $n=10$, 23.4657, -19.8688) and Kasane landfill (KL, $n=2$, 25.1706, -17.7869), which also included the adjacent Kasane Reserve (KR, $n=20$, 25.1884, -17.7853)) at the respective urban communities of Maun and Kasane.

6.3.2 Sampling

We collected 60 discarded marabou feathers from across the eight locations. Marabou feathers were easily identified by their large size and distinct colouring, and were often sampled directly under roosting sites. Feathers were cleaned on site with filtered water, then dried and packaged for later stable isotope and trace metal analyses.

We also collected regurgitate (once every two weeks, 18 June 2018 – 25 August 2018) from

marabou at the site adjacent to the Kasane landfill (KR, Fig. 6.1), where they habitually regurgitated. Regurgitate was sun-dried and weighed with contents sorted by material, colour, size, and brand. We also compared this collection of materials, colours, sizes and brands of major rubbish types to four randomly selected and photographed areas (2m x 2m) of the Kasane landfill site (21st September 2018).

6.3.3 Stable Isotope and Trace Metal ICP-MS Analyses

We removed any remaining surface dirt on feathers with distilled water, followed by vigorous washing in deionized water (RO) and a chloroform methanol solution wash (see methods in Paritte and Kelly (2009)) to remove any surface oils. Feathers were then left to air dry for 24-48 hours. Feathers were identified as either body or flight feathers based on their size, colouration and structure. For stable isotope analyses, feather barbs from the tip of each feather were clipped, placed in tin capsules and weighed (~500 ug). Standards of glutamic acid 40 and glutamic acid 41 were analysed at the beginning, middle and end of each run through the mass spectrometer (Seminoff, Bjorndal, & Bolten, 2007), with their accuracy measured as continuous flow isotope ratio mass spectrometry for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Brenna, Corso, Tobias, & Caimi, 1997). For ICP-MS analyses of trace metals (Aluminium, Cadmium, Chromium, Copper, Iron, Lead, Manganese, Nickel, Potassium and Zinc), a piece ~4x2cm of feather was removed from the top of the vane of each feather, avoiding the centre rachis, sampling about 0.2g (DeNiro & Epstein, 1981). Samples were digested with HNO_3 (open), and then analysed using an inductively coupled plasma mass spectrometer (ICPMS, Perkin Elmer, NexION 300D with universal cell technology). Calibration standards were prepared from commercial stock standard solutions, referenced to certified bovine liver (Altmeyer, Dittmann, Dmowski, Wagner, & Müller, 1991; Cardiel, Taggart, & Mateo, 2011; Kim, Goto, Tanabe, Tanaka, & Tatsukawa, 1998) (Appendix 6.1).

6.3.4 Statistical Analyses

We separately modelled for differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios across sites, varying in distance from the closest landfill (Fig. 6.1). We used a linear modelling approach, with the *glmmTMB* package (Brooks et al., 2017), with fixed predictor variables including collection site (converted to a numerical variable based on the distance from the closest landfill); collection region (Chobe in the East vs the Okavango in the West) and feather type (body vs flight). We included region in the model to account for geological differences which may alter trace metal concentrations naturally present in the environment (Huntsman-Mapila, Kampunzu, Vink, & Ringrose, 2005; Kelepile, Betsi, & Shemang, 2020). For example, the Chobe region largely consists of metarhyolites, metabasalts, siliciclastic and carbonate rock, whereas the Okavango Delta consists largely of granitoids (see Fig.1 Huntsman-Mapila, Kampunzu, Vink, & Ringrose, 2005; Kelepile, Betsi, & Shemang, 2020). We performed a power analysis on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ model results using the *pwr* package (Champely et al., 2018), with both falling above the standard 0.8 threshold indicating our significance testing was valid (Cohen, 1965).

To determine differences in the isotopic niches of the marabou population, we then divided the feathers into three distance divisions. This separated marabou feeding at the landfills in Maun and Kasane (<10 km); in Chobe National Park, where they potentially still visit the Kasane landfill (10-55km) and; those unlikely to be frequently visiting landfills in the Okavango Delta (>55km). We used the R package *SIBER*, which fits ellipses to isotopic data using Bayesian inference to describe and compare isotopic niche based on the standard ellipse areas (SEA) using default settings (Jackson et al., 2011)(also reliant on the *rjags* package (Plummer, 2013)). We also calculated the overlap of the niche area occupied by each group with the package *nicheROVER* (Lysy, Stasko, & Swanson, 2014), which uses the

Monte Carlo method to bootstrap the same number of samples for each group (500), repeated 500 times ($\alpha=0.05$), averaged to provide final percentages.

To model trace metal concentrations in feathers, we used separate glmmTMB models (with a gaussian family), including collection region, distance from landfill sites and feather type as predictor variables. No trace metals fell below the measurement detection limit, and so all were included in the modelling (Appendix 6.1). We used the DHARMA package (Florian Hartig, 2019) to visualise the QQplot and the residual vs predicted values of all glmmTMB models, checking the data satisfied the assumptions of normality and homogeneity of variance. We log transformed Al, Cr, Cu, Fe, K, Ni and Pb concentrations because data were skewed. Finally, we compared trace metal concentrations to suggested avian healthy limits (Abdullah et al., 2015; Malik & Zeb, 2009; Ullah, Hashmi, & Malik, 2014).

6.4 Results

6.4.1 Regurgitate

We collected 42.18 kgs of regurgitant from six ranked rubbish groups: paper and cardboard, soft plastics, bone, aluminium foil, miscellaneous and polystyrene (Table 6.1, Fig. 6.2). Some single regurgitants weighed up to 125g, with single boluses of plastic weighing up to 83g, or paper up to 43g (Fig. 6.2). Ninety-five percent of all soft plastic collected was thin and clear, resembling cling-wrap with minimal coloured plastics. As well, we identified 110 individual items (Appendix 6.2), in 7 major groupings (Table 6.2). While we could not quantify the total amount of rubbish regurgitated fortnightly in our study area (due to its multiple uses and the presence of dangerous animals), the regurgitant was continually deposited, with fresh wet regurgitants present each time the site was visited (Fig. 6.2). In comparison, rubbish at the Kasane landfill consisted of hard plastic soft drink bottles, plastic bags of all colours and a large amount of cardboard and paper (Table 6.1, Appendix 6.2).

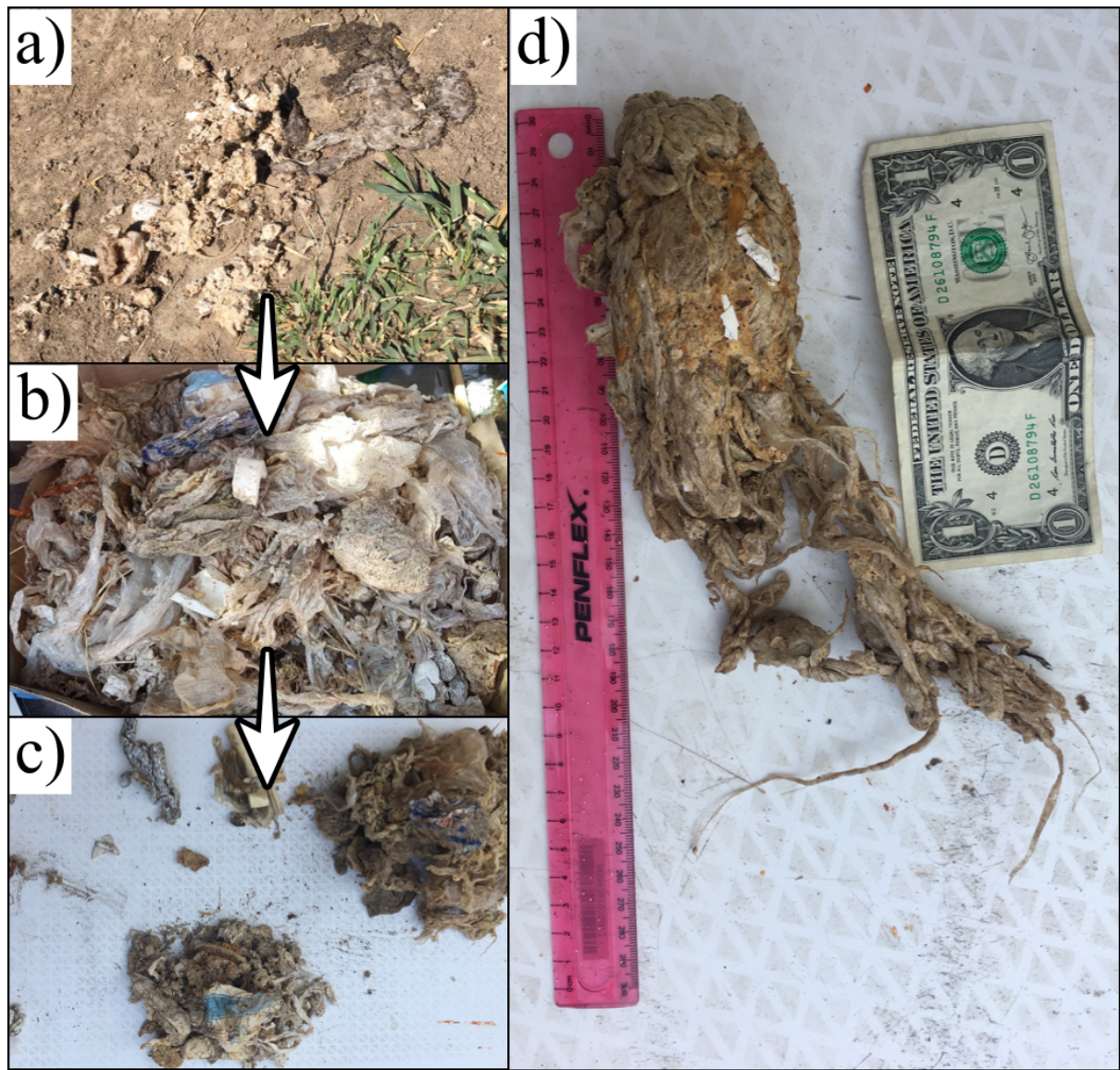


Figure 6.2. Marabou regurgitate was collected from the reserve neighbouring the Kasane landfill site (18 June 2018 – 25 August 2018), with continual fresh depositions of regurgitate during the collection period (a). Regurgitate was collected, compiled (b) and sorted into plastics, paper, bone, aluminium foil and miscellaneous (c). Some regurgitants consisted of many small pieces (a), whilst some were large single boluses (d). A single bolus is displayed next to a United States of America dollar bill for size reference.

Table 6.1. *Relative components of rubbish collected from marabou regurgitations from the Kasane Reserve (18 June 2018 – 25 August 2018, Fig. 6.1) and major rubbish components within the Kasane landfill.*

Material	Example	Regurgitant (kg)	Regurgitant (%)	Landfill (%)
Paper and cardboard	Butter wrapper	10.64	25.23	40
Soft plastics	Cling wrap	22.88	54.25	30
Hard plastics	Plastic bottle tops	0.00	0	20
Foil	Individually wrapped ice cream	0.72	1.7	<5.00
Bone	Beef bone	7.77	18.42	<1.00
Polystyrene	Take away food containers	0.03	0.06	<5.00
Miscellaneous	String	0.05	0.11	10

Table 6.2. *Identifiable items within marabou regurgitate were sorted into their major groupings by type and summarised by the number of occurrences in the total 42kgs of collected marabou regurgitant collected from the Kasane Reserve (18 June 2018 – 25 August 2018, Fig. 6.1). Most often only the packaging remained, assuming the foodstuff had been digested.*

Regurgitant by Type	Example	Occurrences (n)	Occurrences (%)
Dairy	Butter, ice cream, cheese, milk powder	22	20.00
Deli	Food bags, polystyrene food containers, take away containers	7	6.36
Meat	Processed chicken, ham, sausage, salami, devon, polony	48	43.64
Miscellaneous	Spaghetti, string, sock, twine, stockings	8	7.27
Snack Food	Chips, biscuits, coffee, soft drink, lollies	13	11.82
Sanitary Items	Toilet paper, face mask, bandage, make up wipes, wet wipes	9	8.18
Soap	Soap and body wash	3	2.73

6.4.2 Stable Isotope Analyses

There was considerable variation in feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ concentrations in relation to location ($n=59$, Table 6.3). Feather type was not a significant predictor of $\delta^{13}\text{C}$ ($X^2(1, N= 59) = 0.03, p = 0.84$) or $\delta^{15}\text{N}$ ($X^2(1, N= 58) = 0.00, p = 0.98$). Region was not a significant predictor of $\delta^{13}\text{C}$ ($X^2(1, N= 59) = 0.31, p = 0.57$), however it was a significant predictor of $\delta^{15}\text{N}$ ($X^2(1, N= 58) = 7.87, p = 0.005$), more enriched in the Okavango Region than the Chobe Region. We therefore rejected the null hypothesis, and supported the alternative hypothesis: there is a difference in stable isotope analyses of marabou stork feathers as distance from landfill sites increases.

Table 6.3. Mean ($\pm$ SD, n) ratios for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysed in feathers (59) collected across different sites (Fig. 6.1) and their distances from the landfill sites in parentheses with the three SIBER groupings used to explore dietary niche, varying with distance in northern Botswana.

Distance from landfill (km)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Kasane Landfill (0)	-17.72 ($\pm$ 1.81, 2)	9.78 ($\pm$ 0.86, 2)
Maun Landfill (0)	-20.15 ($\pm$ 3.05, 10)	10.24 ($\pm$ 1.15, 10)
Kasane Reserve (0.5)	-19.26 ($\pm$ 2.6, 20)	9.23 ($\pm$ 0.71, 20)
Chobe National Park C1 (49)	-19.72 ($\pm$ 0.88, 6)	10.04 ($\pm$ 1.08, 6)
Chobe National Park C2 (51)	-17.19 ($\pm$ 4.75, 3)	10.42 ($\pm$ 1.57, 3)
Chobe National Park C3 (53)	-17.88 (1)	12.18 (1)
Kanana Colony (78)	-19.77 ($\pm$ 3.27, 7)	11 ($\pm$ 1.02, 7)
Chiefs Island (88)	-15.68 ($\pm$ 1.23, 10)	12.07 ($\pm$ 0.73, 10)
SIBER Landfill Feeders (<10)	-19.44 ($\pm$ 2.71, 32)	9.58 ($\pm$ 0.97, 32)
SIBER Mixed Feeders (10-55)	-18.78 ($\pm$ 2.64, 10)	10.37 ($\pm$ 1.28, 10)
SIBER Natural Feeders (>55)	-17.36 ($\pm$ 3.02, 17)	11.63 ($\pm$ 0.99, 17)

Concentrations of $\delta^{13}\text{C}$ in feathers was significantly less depleted, with distance from the closest landfill ($X^2(1, N= 59) = 7.04, p = 0.008$, Fig. 6.3). Similarly, concentrations of $\delta^{15}\text{N}$ in feathers were significantly more enriched with distance from the closest landfill ($X^2(1, N= 58) = 22.31, p < 0.001$, Fig. 6.3). Differences among feeding preferences were reflected in the

niche width of the groups (Fig. 6.4), with the largest ellipses in the mid-distance group (10.32, 10-55 km), indicating a more varied diet in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ sources. Ellipse size was followed by the furthest distance group (9.95, >55 km), and finally the group closest to a landfill site (8.33, <10km, Table 6.3, Fig. 6.4), indicating the landfill feeders had a smaller range of dietary sources contributing to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in their feathers. Credible confidence intervals of niche width were the largest in the mid-distance group, indicative of individual variation in diet (Appendix 6.3). The final averaged SEA values, developed from posterior probabilities, did not show large differences between groups (unlikely to be significant in a hypothesis testing sense)(Fig. 6.5). There was separation however, amongst feeding groups, with a 74% probability of natural feeders (furthest distance group) feeding within the mixed group's niche (mid-distance), compared to a 50% probability of natural feeders feeding within the landfill niche. Landfill feeders showed an 83% probability of feeding within the niche of the mixed group, but only a 48% chance of niche overlap with the natural feeders. The mixed feeders were more likely to be feeding within the landfill niche (77%) than the natural niche (73%).

6.4.3 Trace Metal Analyses

There were significantly higher concentrations of aluminium, chromium, iron, potassium, manganese, nickel, lead and zinc in flight feathers compared to body feathers (n=60) (Appendix 6.4 & 6.5). Copper was the only metal with significantly higher concentrations in body feathers (Appendix 6.4 & 6.5). Metal concentrations of aluminium, chromium, lead and zinc also decreased with distance from the closest landfill, while potassium and cadmium increased with distance from the landfill site (Appendix 6.5, Fig. 6.6). Although iron and manganese concentrations did not differ with distance to the landfills, they were potentially approaching toxic concentrations. These high concentrations were particularly apparent in the Chobe Region, with the highest mean concentrations in feathers collected from the Kasane

landfill (Appendix 6.5). Cadmium, copper, iron and nickel concentrations in the feathers were significantly higher in the Chobe Region, whilst lead and potassium were higher in the Okavango Delta Region (Appendix 6.6). We therefore rejected the null hypothesis, and supported the alternative hypothesis: there are differences in elemental concentrations of marabou stork feathers as distance from landfill sites increases.

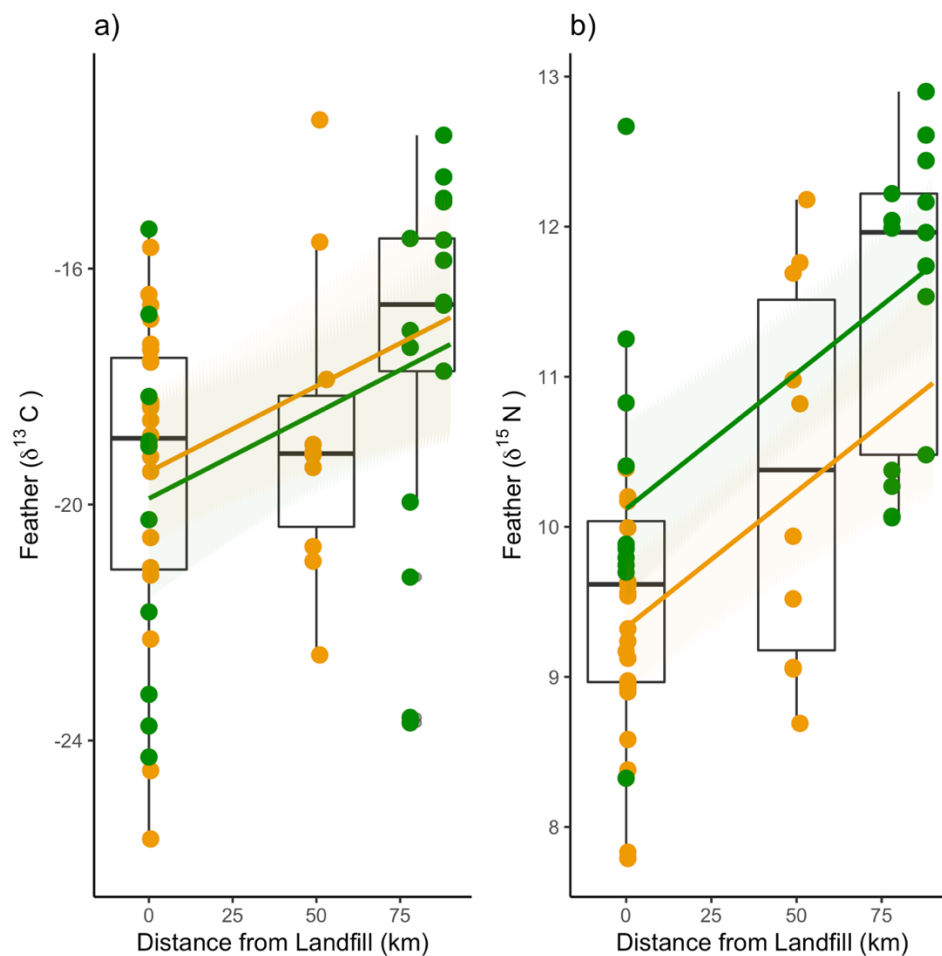


Figure 6.3. Predicted responses of $\delta^{13}\text{C}$ (a) and $\delta^{15}\text{N}$ (b) ratios to distance from the closest landfill site in feathers ($n=59$) collected from eight locations across northern Botswana in the eastern Chobe region (orange) and the western Okavango region (green)(Fig. 6.1), with model 95% confidence interval (coloured bands) where boxplots represent the groupings according to the SIBER models $<10\text{kms}$, $10\text{-}55\text{kms}$ and $>55\text{kms}$ from a landfill.

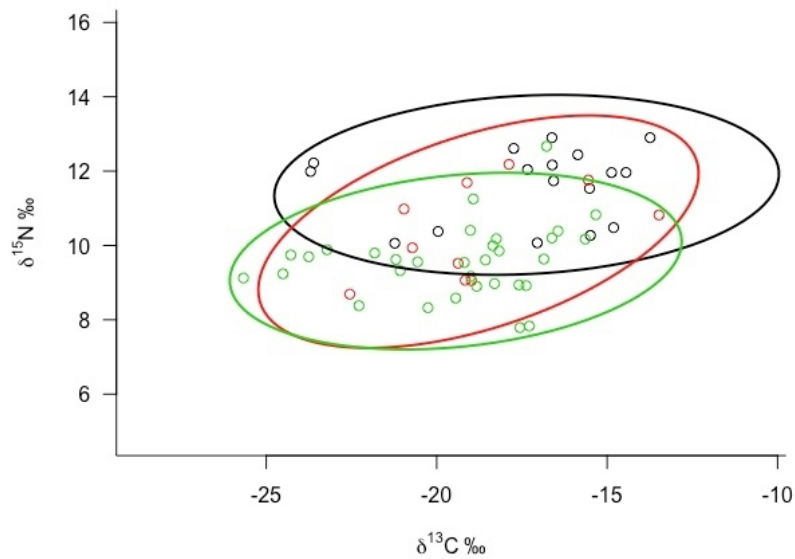


Figure 6.4. Trophic niches developed from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for marabou feathers ($n=59$) collected at differing distances from landfills across northern Botswana; $<10\text{kms}$ (green), $10\text{-}55\text{kms}$ (red) and $>55\text{kms}$ (black), expressed as corrected standard ellipses.

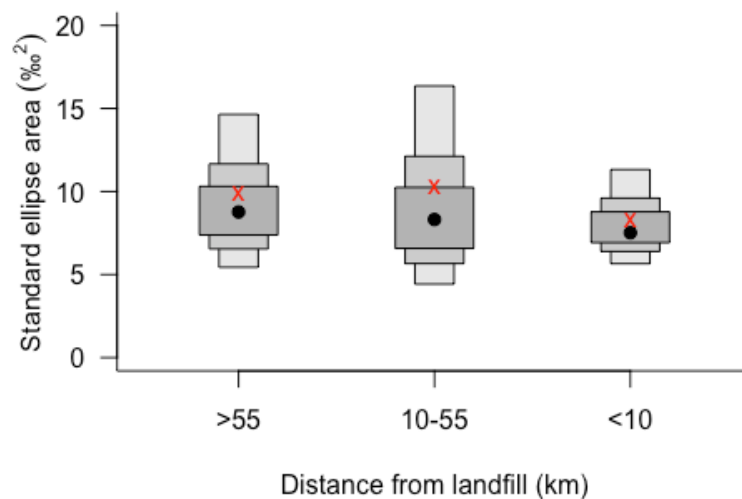


Figure 6.5. Results of Bayesian models exploring the standard ellipse areas developed from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for marabou feathers ($n=59$) collected at differing distances from landfills across northern Botswana; $<10\text{kms}$, $10\text{-}55\text{kms}$ and $>55\text{kms}$.

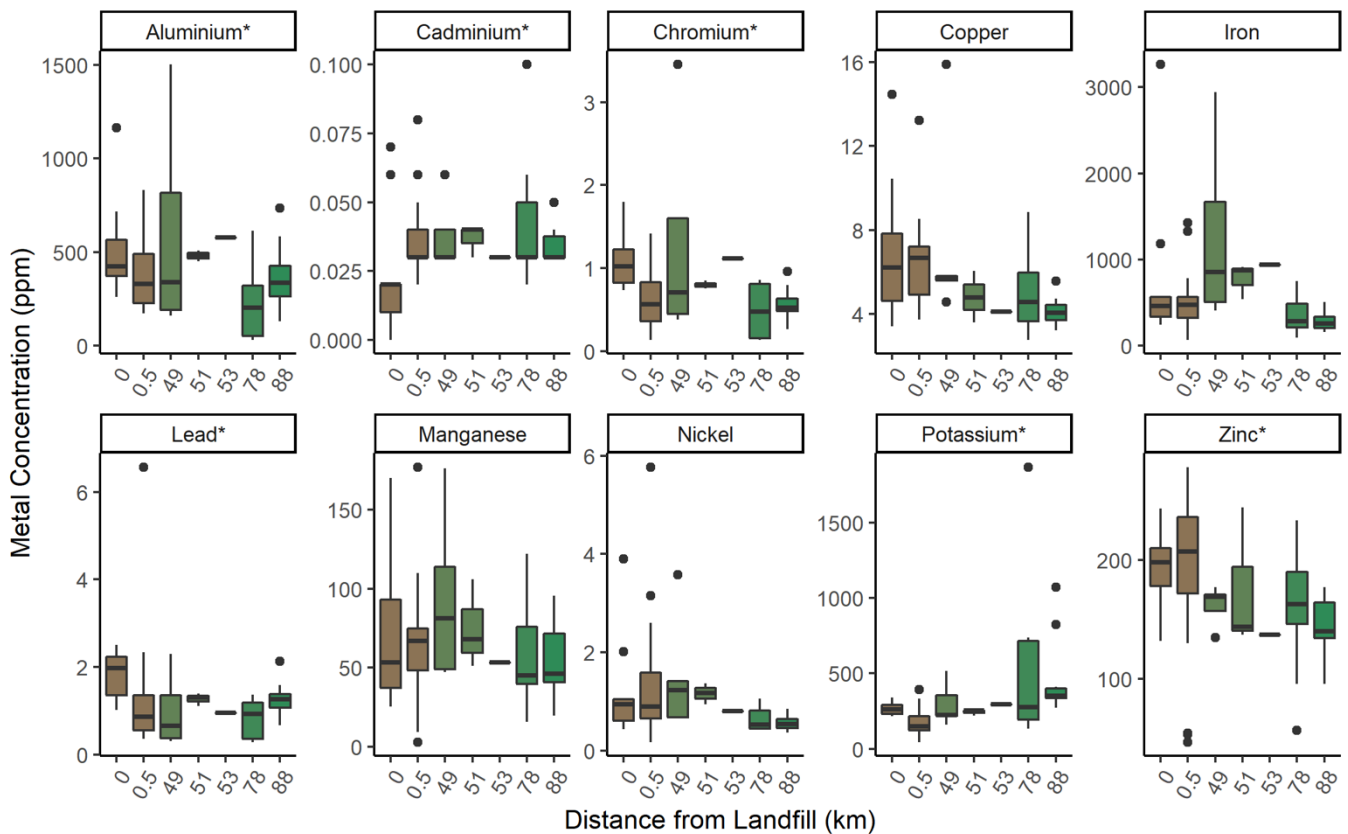


Figure 6.6. Boxplots of trace metal concentrations following ICP-MS analyses showing significant relationships (*) to distance to the nearest landfill in feathers ($n=60$) from eight locations across northern Botswana.

6.5 Discussion

The interactions between urban waste and wildlife are increasing globally, including within many African countries (Cobbinah, Erdiaw-Kwasie, & Amoateng, 2015). Marabou storks exemplify this challenge around landfill sites in northern Botswana. The constant deposition of marabou regurgitant collected in the Kasane Reserve is indicative of this shift in feeding preferences, confirmed by depleted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and reduced feeding niches for those feeding at landfills. Furthermore, individuals feeding at the landfill sites showed significant differences in the trace metal composition of their feathers, with Fe and Mn approaching or exceeding lethal limits.

The remarkable ability of the marabou to regurgitate large chunks of indigestible material (Fig. 6.2) is largely ignored both in scientific literature and general information, with only one reference from 1988 (J. Hancock et al., 2010). Our collection of regurgitant indicated marabous were largely consuming high fat, high protein content foods such as meat and dairy at landfill sites (Table 6.2). Given the range of items at the landfill, and difficulty in finding high protein high fat content foods, marabous clearly selectively sorted through the waste, but still consumed considerable quantities of plastic (Table 6.1). In particular large amounts of cling wrap were present in the regurgitate, likely due to considerable wrapping of pre-prepared meals in local grocers (R. Francis, personal observation), which the marabou then target for their food content. Plastic consumption is often lethal for many species of birds, particularly freshwater (Battisti et al., 2019; Wiemeyer et al., 2017) and marine birds (Lavers et al., 2014; Roman, Schuyler, Hardesty, & Townsend, 2016; Tanaka et al., 2013; Verlis, Campbell, & Wilson, 2013; Wilcox, Van Seville, & Hardesty, 2015), however we only saw two marabou corpses (at the Maun landfill) during this study and so their ability to regurgitate may prevent mortality.

Their altered diet at landfill sites resulted in measurable changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in feathers. The depleted $\delta^{13}\text{C}$ in feathers from landfills (Fig. 6.3) may represent a shift in the types of plant material being consumed, which at landfill sites may comprise of both aquatic and terrestrial C3 plants (including wheat which was found in the form of spaghetti in the regurgitate), C4 plants, and also paper and cardboard. In contrast marabou feeding in natural areas likely feed on mainly aquatic and C4 plants which have higher $\delta^{13}\text{C}$ values, reflected in the slight increase in the $\delta^{13}\text{C}$ (Cerling et al., 1997; Deines, 1980). In contrast to our initial predictions, based on the idea of abundant and varied protein sources with the landfill, urban landfill feeding populations of marabou showed depleted $\delta^{15}\text{N}$ (Fig. 6.3). This likely reflects the human diet, with less variety in protein sources, with the consumption of lower trophic

level animal sources, such as herbivores (e.g. meat from cattle), rather than the natural highly varied diet of the marabou including higher trophic level organisms (fish, birds, rats, even juvenile crocodiles (Hockey et al. 2005)).

Resultingly, the trophic niche of marabous narrowed, although not significantly, with proximity to landfills sites, a typical niche response where food resources are abundant (Wang et al., 2018) (Fig 6.5). The high overlap of the mid-distance group (10-55km) with both the natural and landfill feeders was confirmation that this group were mixed feeders, and indicates they may fly up to 55km to feed at landfill sites. Such foraging information could not be found in published literature for the marabou stork, however the white stork *Ciconia ciconia*, can fly up to 48.2km to reach landfill sites (Gilbert et al., 2016). The smallest trophic niche overlap occurred between birds feeding furthest from and those closest to landfill sites. The decrease in $\delta^{15}\text{N}$ of more than 3‰ (one approximate trophic level) between these two groups indicates a small shift in the feeding trophic position for some individuals (McCutchan Jr, Lewis Jr, Kendall, & McGrath, 2003), which as a scavenger and predator could affect herbivore and mesopredator populations, and increase disease in the environment (O'Bryan et al., 2018).

Higher trace metals (aluminium, chromium, lead and zinc) in feathers of marabous feeding at landfill compared to natural sites, probably indicated ingestion of by-products of batteries, paint, mechanical waste, sewerage and the abundant use of aluminium in human products such as anti-perspirant (Kgosiesele & Zhaohui, 2010; Ullah et al., 2014). Maximum concentration of chromium and lead surpassed the recommended threshold in only one feather (2.8ppm and 4 ppm) and so it is unlikely these trace metals are seriously affecting marabou health (Burger & Gochfeld, 2001; Gochfeld, 2000). Conversely, potassium levels were relatively low and are essential for growth and heart rhythms, with imbalances attributed to the death of broiler chickens (Hopkinson, 1991). Cadmium (a non-essential

trace metal) in feathers was highest closest to natural sites, which may be due to its use in phosphate based fertilisers in agricultural areas (Ali & Khan, 2018), away from urban centres.

Iron and manganese were at surprisingly high levels in marabou feathers from Chobe National Park, which is of concern, given they can cause fatal iron storage disease, anaemia, micromelia, limb twisting, haemorrhage, stunted growth and behavioural disorders (Sheppard & Dierenfeld, 2002). Iron and manganese can originate from uncontrolled waste disposal from the mechanical industry, vehicles, construction materials, diesel fuel burning, untreated traffic waste, industrial effluents, and batteries (Kgosiesele & Zhaohui, 2010; Ullah et al., 2014). Historically manganese was mined in south western Botswana, beginning in 1957, with mines contaminated and abandoned reducing vegetation cover (Abdullah et al., 2015; GIE Ekosse, Fouche, & Mashatola, 2006; Georges Ekosse & Fouche, 2005). In 1997 about 15% of ostrich chicks from a farm in Botswana hatched with limb deformities and elevated serum manganese and zinc levels (Mushi, Binta, Chabo, Isa, & Phuti, 1999). Manganese mining will likely restart in Botswana (Mining Review Africa, 2018), potentially posing an ongoing risk to the wildlife of Botswana.

Trace metal concentrations varied between body and flight feathers, found to also occur in other birds (Pon, Beltrame, Marcovecchio, Favero, & Gandini, 2011). Higher metal concentrations in flight feathers, compared to body feathers, may relate to longer durations for flight feather growth and therefore a greater uptake of metals into the feathers from blood (Dauwe et al., 2003). Also, as periods between moult and moult duration increase with avian body size (Rohwer et al. 2009), this might also explain high metal concentrations in flight feathers (no information specific to marabou feather growth or moult periods was found, but moult is likely annual or bi-annual). While feathers remain a useful tool for the non-invasive analysis of such trace metals, there was limited information on toxicity levels in feathers, and

how these concentrations directly related to blood concentrations. Further, considering the large size of the marabou it is possible toxicity levels differ for this species. Necropsies on the corpses at Maun Landfill and blood collection alongside feather collection would provide insight into such uncertainty, as would further studies into potential differences in behaviour and reproduction of affected individuals. Nonetheless there was a clear relationship between feeding on waste, a shift in trophic niche size and trace metal consumption with proximity to landfill sites.

Other species feed at landfill sites in Botswana: African sacred ibis *Threskiornis aethiopicus*, pied crow *Corvus albus*, banded mongoose *Mungos mungo*, warthog *Phacochoerus africana*, hyena *Crocuta crocuta* and baboon *Papio ursines* (R. Francis, personal observation). Banded mongoose feeding at the landfill site in the Chobe Region of Botswana carry more disease pathogens and are more aggressive than other populations (Flint, Hawley, & Alexander, 2016), and a Ugandan population feeding at urban refuse sites had higher body condition but higher mortality rates in young males than other populations in natural settings (Otalı & Gilchrist, 2004). Many baboons died from an outbreak of bovine tuberculosis from meat in a Kenyan landfill site, changing the culture of the troop for decades (Sapolsky & Share, 2004). Hyenas change their behaviour around landfill sites, potentially increasing predation risk to urban livestock (Kolowski & Holekamp, 2008), including donkeys (Yirga et al., 2012). Urban communities are also affected by the spreading of waste (e.g. sanitary items, Appendix 6.2), potentially carrying disease outside landfill sites (Cook, Rushton, Allan, & Baxter, 2008).

Rubbish at landfill sites is generally buried or covered in Botswana (Suresh & Vijayakumar, 2012), ideally preventing animals feeding, but this is not routine at the Kasane site. Regular burying could reduce marabou and other wildlife foraging at this landfill site. There are other remedial measures available, including exclusion of wildlife from landfill sites through

fencing or netting (Flint et al., 2016), however this is difficult, dangerous to the animals and expensive (Conover, 2001). Recycling also reduces landfill rubbish, a practice increasing in Botswana (Mmereki, 2018), as does reduction of food waste (Newsome & van Eeden, 2017). Considering the few corpses, wide distribution (Brown et al., 1982), and abundance of marabou storks, it is unlikely this behaviour is causing high mortalities despite decades of feeding at landfill sites (J. Hancock et al., 2010), but deserves further investigation, particularly considering the possible negative effects on chick growth (Kahl, 1966). Some populations of the marabou may be higher in urban than natural areas (Derek Pomeroy & Kibuule, 2017), and landfill sites and urban areas provide food for some animals when there is low natural availability (Plaza & Lambertucci, 2017), including other avian species (Meyer-Gleaves & Jones, 2007; Tauler-Ametller, Hernández-Matías, Parés, Pretus, & Real, 2018). This stable food source could therefore also have benefits to marabou body condition or reproduction. Marabou are possibly one of the few species better suited to exploiting this resource, although not totally without consequence.

Landfill sites around urban communities alter the diet of the marabou, changing its natural trophic niche, causing the swallowing and regurgitation of large amounts of waste and exposing the species to trace metal toxicities. The marabou's ability to regurgitate indigestible material probably reduces the effects of rubbish ingestion, but not completely. This is a burgeoning issue as African countries urbanise (Cobbinah et al., 2015), and one requiring close monitoring. There is a need to improve recycling, and reduce and remove human waste to address this impact, considering both the role of landfills in providing a consistent food source to the resilient marabou, but also potentially affecting the health and behaviours of other less resilient species.

6.6 Conclusions

The marabou stork has fed at landfill sites for decades, and despite this behaviour is an abundant and widely distributed species. As Africa increasingly urbanises, more waste will likely be stored in open-air landfills and the costs to marabou storks shifting their feeding from natural to urban areas may also increase. The swallowing and regurgitation of large amounts of plastic and human waste, the alteration of the marabou's natural trophic niche, and the increased exposure to toxic trace metals may affect the future conservation of this species, as for other species which regularly visit landfill sites. Alternatively, like some avian species marabou may continue to benefit from urbanisation and landfills, becoming a success story despite increasing natural habitat loss. We need to understand more about the lethal and sublethal effects of feeding at landfill and the implications for reproductive success to ensure southern African populations of urban marabou persist.

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6.9 Appendices

Appendix 6.1. *Known vs tested levels of trace metals (ppm) using ICP-MS in bovine liver reference material for the first and second run of feathers tested. Method detection limit (MDL) referring to the lowest concentration at which an analyte can be detected in a sample with 99% certainty.*

Bovine Liver	Al	Cd	Cr	Cu	Fe	K	Ni	Mn	Pb	Zn
Reference	N/A	0.097 ±0.00	0.053 ±0.01 4	275.2 ±4.60	197.94 ±0.64	10230 ±640.0	0.0445 ±0.009	10.46 ±0.47	0.0628 ±0.001	181.1 ±1.00
Laboratory 1	1.45	0.095 1	0.051 3	260.4 2 271.1	195.80	Saturated	0.0477	10.13	0.0618	184.0 6
Laboratory 2	2.59	0.10	0.050	0	200.69	10154	0.05	2.59	0.10	0.05
MDL	2.00	0.01	0.01	0.01	2.00	2.00	0.01	2.00	0.01	2.00

Appendix 6.2. Items able to be identified within the Marabou regurgitant (n), sometimes down to brand name, broadly compared to identifiable items in the photos taken at the Kasane Landfill.

Regurgitant	Brand	Kasane Landfill
Absorbant packet from meat (2)		Alcohol bottles
Bacon (2)	Senn Foods	Alcohol packaging
Balloon		Bags of food scraps
Bandage / bandaid		Baking powder
Beans hot atcher	Koo	Black bin bags
Beef cooked	Senn Foods	Cleaning products
Biscuit tennis classic	Bakers	Cordial
Biscuits		Egg cartons
Butter packet (9)	Rama, Spar	Grocery bags
Candy - Mini hot dog	Hapi	Juice
Candy icecream lollipop	Richester	Mattress padding
Candy smoothies super	Beacon	Soft drink
Candy tops – toffee (1)	Lode stone	Water
Cheese (2)	Clover	Yoghurt
Cheese baby bell		
Cheese brie		
Cheese camembert wrapper (4)		
Cheese cheddar (2)	Spar, Parmalat	
Chicken cooked	Notwane, Senn Foods	
Chicken processed (3)	Senn Foods, Choppies	
Chicken raw (3)	Richmark	
Chip packet	Crinkles	
Chord / string		
Cleaning gel lavender soap		
Cleaning new and improved quality freshness		
Coffee sachet (3)	Nescafe	
Condoms		
Deli food container/bag (6)	Spar, Choppies	
Devon	Senn Foods	
Face mask (2)		
Grocery bag	Choppies	
Ham (4)	Senn Foods	
Hot chocolate		
Icecream vanilla (3)	Streets	
Make up wipes (many)		
Meat processed (10)	Parmalat, Senn Foods	
Milk powder infant		

Paper towel	
Pastrami (2)	Senn Foods
Polony mixed (14)	Senn Foods
Salami (2)	Heartlif, Senn Foods
Sanitary pads (multiple)	
Sausage processed (2)	Parmalat
Soap	Protex
Sock	
Soft drink	Fanta
Sorgum stalk	
Spaghetti	
Stockings	
Toilet paper	
Tomato Sauce packet (2)	KFC, Nandos
Twine	
Wet wipes (many)	

Appendix 6.3. *The 95% credible intervals, and their variance, for the standardized ellipse areas (SEA, % σ^2) in the Bayesian modelling using SIBER, developed from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results for the 59 feathers collected across northern Botswana.*

Group (km)	95% Credible Interval	Variability in Intervals
<10	5.49-11.37	5.88
10-55	4.25-16.45	12.20
>55	5.28-14.42	9.13

Appendix 6.4. *Mean ($\pm$ SD, max, n) concentrations (ppm) for trace metals analysed in the 19 body and 41 flight feathers collected across northern Botswana. Significant relationships identified with *.*

Metal	χ^2 , P value	Body	Flight
Aluminium*	10.11, 0.001	279.79 ($\pm$ 112.01, 515, 17)	473.59 ($\pm$ 285.8, 1502, 41)
Cadmium	0.43, 0.51	0.04 ($\pm$ 0.02, 0.1, 8)	0.03 ($\pm$ 0.02, 0.08, 8)
Chromium*	7.09, 0.007	0.57 ($\pm$ 0.3, 1.22, 17)	0.85 ($\pm$ 0.57, 3.45, 33)
Copper*	4.27, 0.04	6.5 ($\pm$ 2.11, 13.22, 19)	5.51 ($\pm$ 2.78, 15.88, 41)
Iron*	16.23, <0.001	318.74 ($\pm$ 141.62, 584, 19)	703.41 ($\pm$ 652.56, 3262, 39)
Lead*	4.13, 0.04	1 ($\pm$ 0.58, 2.43, 19)	1.37 ($\pm$ 1.02, 6.57, 38)
Manganese*	12.63, < 0.001	43.46 ($\pm$ 28.44, 110, 19)	77.13 ($\pm$ 40.1, 177, 41)
Nickel*	12.11, <0.001	0.69 ($\pm$ 0.33, 1.78, 17)	1.26 ($\pm$ 1.11, 5.77, 37)
Potassium*	5.34, 0.02	285.84 ($\pm$ 398.12, 1867, 19)	324.07 ($\pm$ 194.9, 1072, 38)
Zinc*	8.70, 0.003	152.64 ($\pm$ 61.52, 264, 18)	183.95 ($\pm$ 45.52, 278, 35)

Appendix 6.5. Mean ($\pm$ SD, max, n) concentrations (ppm) for aluminium, cadmium, chromium, copper, iron, potassium, manganese, nickel, lead and zinc analysed in the 60 feathers collected across a range of distances from the closest landfill site in northern Botswana. Trace metals that did not significantly differ in concentration between body and flight feathers are pooled. Significant relationships to distance from landfill (X^2 , P value) identified with * and trace metals with potentially lethal concentrations in shaded grey.

Distance From Landfill	Al (6.87, 0.09)		Cd* (14.58, <0.001)	Cr* (4.99, 0.03)		Cu (3.80, 0.05)		Fe (0.8, 0.37)		K* (6.81, 0.009)		Mn (1.29, 0.18)		Ni (2.93, 0.09)		Pb* (7.18, 0.007)		Zn* (8.94, 0.003)	
	Body	Flight		Body	Flight	Body	Flight	Body	Flight	Body	Flight	Body	Flight	Body	Flight	Body	Flight	Body	Flight
Maun Landfill (0)	349.67 ($\pm$ 83.07, 424, 3)	455.67 ($\pm$ 137.81, 716, 6)	0.01 ($\pm$ 0.01, 0.02, 3)	0.94 ($\pm$ 0.25, 1.22, 3)	1.04 ($\pm$ 0.27, 1.48, 5)	5.47 ($\pm$ 0.93, 6.38, 3)	5.59 ($\pm$ 2.08, 8.73, 6)	311.33 ($\pm$ 67.25, 375, 3)	465.17 ($\pm$ 117.53, 570, 6)	246.67 ($\pm$ 36.91, 288, 3)	276 ($\pm$ 46.22, 342, 6)	27.83 ($\pm$ 3.06, 31.3, 3)	78.35 ($\pm$ 43.1, 160, 6)	0.64 ($\pm$ 0.27, 0.94, 3)	0.85 ($\pm$ 0.22, 1.05, 6)	1.86 ($\pm$ 0.73, 2.43, 3)	1.85 ($\pm$ 0.6, 2.5, 6)	191.33 ($\pm$ 17.95, 205, 3)	184.17 ($\pm$ 31.15, 221, 6)
Kasane Landfill (0)	NA	911 ($\pm$ 356.38, 1163, 2)	0.06 ($\pm$ 0.01, 0.07, 2)	NA	1.41 ($\pm$ 0.55, 1.8, 2)	NA	12.45 ($\pm$ 2.84, 14.46, 2)	NA	2224 ($\pm$ 1467.95, 3262, 2)	NA	273.5 ($\pm$ 26.16, 292, 2)	NA	135.5 ($\pm$ 48.79, 170, 2)	NA	2.96 ($\pm$ 1.34, 3.9, 2)	NA	1.5 ($\pm$ 0.04, 1.52, 2)	NA	227 ($\pm$ 22.63, 243, 2)
Kasane Reserve (0.5)	301.9 ($\pm$ 106.7, 515, 9)	466.82 ($\pm$ 224.13, 832, 11)	0.04 ($\pm$ 0.02, 0.08, 6)	0.5 ($\pm$ 0.27, 1.11, 10)	0.8 ($\pm$ 0.39, 1.42, 10)	7.15 ($\pm$ 2.48, 13.22, 10)	5.59 ($\pm$ 1.57, 8.53, 11)	355.9 ($\pm$ 138.88, 565, 10)	694.64 ($\pm$ 381.01, 1429, 11)	124.6 ($\pm$ 42.9, 182, 10)	231.18 ($\pm$ 91.2, 392, 11)	48.16 ($\pm$ 36.15, 110, 10)	78.22 ($\pm$ 38.48, 177, 11)	0.76 ($\pm$ 0.41, 1.78, 10)	1.91 ($\pm$ 1.53, 5.77, 11)	0.74 ($\pm$ 0.37, 1.63, 10)	1.67 ($\pm$ 1.71, 6.57, 11)	143.02 ($\pm$ 71.17, 264, 10)	229.82 ($\pm$ 29.22, 278, 11)
Chobe NP1 (49)	NA	601.2 ($\pm$ 568.09, 1502, 5)	0.04 ($\pm$ 0.01, 0.06, 3)	NA	1.32 ($\pm$ 1.29, 3.45, 5)	NA	7.51 ($\pm$ 4.71, 15.88, 5)	NA	1275.4 ($\pm$ 1054.38, 2941, 5)	NA	295.8 ($\pm$ 141.58, 515, 5)	NA	93.44 ($\pm$ 53.65, 176, 5)	NA	1.51 ($\pm$ 1.21, 3.58, 5)	NA	0.99 ($\pm$ 0.83, 2.29, 5)	NA	161.8 ($\pm$ 16.65, 177, 5)
Chobe NP2 (51)	NA	480 ($\pm$ 28.05, 507, 3)	0.04 ($\pm$ 0.01, 0.04, 2)	NA	0.8 ($\pm$ 0.05, 0.85, 3)	NA	4.8 ($\pm$ 1.23, 6.04, 3)	NA	775.33 ($\pm$ 206.71, 916, 3)	NA	243.33 ($\pm$ 19.35, 255, 3)	NA	75 ($\pm$ 28.13, 106, 3)	NA	1.16 ($\pm$ 0.22, 1.37, 3)	NA	1.27 ($\pm$ 0.14, 1.39, 3)	NA	175 ($\pm$ 59.86, 244, 3)
Chobe NP3 (53)	NA	579 (1)	0.03 (1)	NA	1.12 (1)	NA	4.12 (1)	NA	939 (1)	NA	297 (1)	NA	53.3 (1)	NA	0.8 (1)	NA	0.95 (1)	NA	137 (1)
Kanana Colony (78)	179 ($\pm$ 124.78, 320, 4)	301.6 ($\pm$ 284.94, 615, 5)	0.04 ($\pm$ 0.03, 0.1, 6)	0.52 ($\pm$ 0.37, 0.86, 4)	0.45 ($\pm$ 0.29, 0.81, 5)	6.61 ($\pm$ 1.69, 8.86, 4)	3.62 ($\pm$ 0.69, 4.56, 5)	292.25 ($\pm$ 209.33, 584, 4)	375.4 ($\pm$ 253.93, 750, 5)	704.25 ($\pm$ 788.26, 1867, 4)	403.2 ($\pm$ 298.52, 739, 5)	44.1 ($\pm$ 24.63, 75.8, 4)	71.68 ($\pm$ 43.5, 122, 5)	0.64 ($\pm$ 0.21, 0.91, 4)	0.65 ($\pm$ 0.28, 1.06, 5)	0.94 ($\pm$ 0.48, 1.37, 4)	0.68 ($\pm$ 0.42, 1.2, 5)	155.5 ($\pm$ 72.91, 233, 4)	162.4 ($\pm$ 50.01, 229, 5)
Chiefs Island (88)	266 ($\pm$ 48.08, 300, 2)	399.12 ($\pm$ 191.14, 736, 8)	0.03 ($\pm$ 0.01, 0.05, 3)	0.48 ($\pm$ 0.01, 0.49, 2)	0.6 ($\pm$ 0.21, 0.96, 8)	4.61 ($\pm$ 0.19, 4.74, 2)	3.99 ($\pm$ 0.75, 5.57, 8)	197 ($\pm$ 22.63, 213, 2)	305.12 ($\pm$ 112.08, 508, 8)	314 ($\pm$ 56.57, 354, 2)	502.38 ($\pm$ 283.79, 1072, 8)	42.15 ($\pm$ 1.63, 43.3, 2)	57.1 ($\pm$ 26.95, 95.7, 8)	0.5 ($\pm$ 0.01, 0.51, 2)	0.58 ($\pm$ 0.17, 0.85, 8)	1.15 ($\pm$ 0.17, 1.27, 2)	1.31 ($\pm$ 0.43, 2.13, 8)	137 ($\pm$ 4.24, 140, 2)	146.5 ($\pm$ 27.85, 177, 8)

Appendix 6.6. Mean ($\pm$ SD, max, n) concentrations (ppm) for trace metals analysed in the 60 feathers collected from the Chobe (32) and Okavango Delta (28) regions in northern Botswana. Significant relationships identified with *.

Metal	X^2 , P value	Chobe	Okavango Delta
Aluminium	0.67, 0.41	468.78 ($\pm$ 300.22, 1502, 31)	347.57 ($\pm$ 189.27, 736, 27)
Cadmium*	18.2, <0.001	0.04 ($\pm$ 0.02, 0.08, 7)	0.03 ($\pm$ 0.02, 0.1, 8)
Chromium	0.19, 0.66	0.84 ($\pm$ 0.63, 3.45, 29)	0.68 ($\pm$ 0.34, 1.48, 25)
Copper*	4.09, 0.04	6.69 ($\pm$ 3.02, 15.88, 32)	4.84 ($\pm$ 1.59, 8.86, 28)
Iron*	10.29, 0.001	790.31 ($\pm$ 709.63, 3262, 31)	343.07 ($\pm$ 163.09, 750, 27)
Lead*	6.15, 0.01	1.2 ($\pm$ 1.11, 6.57, 30)	1.31 ($\pm$ 0.63, 2.5, 24)
Manganese	1.18, 0.28	73.7 ($\pm$ 43.55, 177, 31)	58.2 ($\pm$ 34, 160, 28)
Nickel*	7.41, 0.006	1.45 ($\pm$ 1.2, 5.77, 29)	0.66 ($\pm$ 0.22, 1.06, 23)
Potassium*	6.63, 0.01	213.81 ($\pm$ 100.73, 515, 29)	424.14 ($\pm$ 355.71, 1867, 28)
Zinc	0.06, 0.81	183.85 ($\pm$ 59.95, 278, 27)	162.82 ($\pm$ 41.16, 233, 26)

Chapter 7. Discussion

Freshwater ecosystems are complex social-ecological systems, supporting high biodiversity, and human communities. These systems are largely controlled by abiotic variables, particularly rainfall and flow and their often high variability enables a wide range of biota to survive, driving a range of freshwater and terrestrial responses and population dynamics (Kingsford 2006).

Globally, freshwater ecosystems are seriously threatened, largely due to changing climates and flow alteration, including water extraction from rivers and lakes (Craig et al. 2017, Reid et al. 2019). Such changes to flow have caused declines in dependant biodiversity, but also affect the human communities which rely on these freshwater systems for their ecological services (Lemly et al. 2000). Tracking changes in freshwater ecosystem health is essential to conserve biodiversity, protect human populations and their ecosystem services, and inform management decisions about the costs and benefits of proposed developments. Unfortunately, tracking such change can be difficult for freshwater ecosystems because of spatial and temporal complexities: for example, many wetlands are dependent on flows from rivers sometimes thousands of kilometres away, including some that are transboundary rivers. Examples include the Okavango River (supplying the Okavango Delta) and Chobe River of Botswana, both largely free-flowing rivers, beginning in Angola and flowing through Namibia to Botswana. These rivers and the freshwater systems they supply are particularly important for Botswana, supporting high biodiversity, and human communities who are solely dependant on rivers for tourism, fish and other goods and services. Further, the Okavango Delta is a Ramsar-listed wetland, World Heritage Site, Important Bird Area and part is found within the protected Moremi Game Reserve, while the Chobe River supplies Chobe National Park, also an Important Bird Area (Department of Environmental Affairs Ministry of Environment Wildlife and Tourism 2006, Hancock et al. 2007, UNESCO 2014).

In my thesis, I investigated the use of birds as indicators, using them to track broad scale ecosystem change and I explored the connections between avian populations and large herbivores in riparian habitats (Chapter 2). With increasing declines in large herbivores due to poaching across Africa (Somerville 2017), and Botswana (Schlossberg et al. 2019), there may be long-term changes in avian communities which are directly or indirectly dependent on the functional effects of large herbivores. Improvements in understanding of these relationships would benefit from inclusion of an increased number of sites, increasing replication of herbivore densities to help specify the generality of my conclusions and show causality in these relationships.

In Chapters 3 and 4, I used citizen science data, combined with remote sensing techniques such as drone surveys and inundation mapping to explore the relationships between the breeding of waterbirds and river flows and flooding. I modelled these relationships in both the Chobe and Okavango Rivers, identifying species' declines, and breeding requirements. The relationships found between the breeding of waterbirds and Chobe River flows, highlights the usefulness of waterbirds as indicators of ecosystem changes (Chapter 3). The relationships established, particularly around the required threshold to support large waterbird breeding colonies could be used to forecast waterbird success into the future, exploring the impacts large developments on the river could have on waterbird populations in this system (Xia et al. 2016, Kingsford et al. 2017). Further, due to the connections between river flows and overall ecosystem health, waterbirds could be used as indicator species of ecosystem health in the Chobe River region.

I found similar relationships between the waterbirds of the Okavango Delta and Okavango River flows (Chapter 4), further underlining the usefulness of waterbirds as indicators in Botswana. The spatial arrangement of waterbird breeding colonies in the Okavango Delta was also related to the inundation and vegetation requirements for waterbird breeding. This

allows for the use of waterbirds to guide the management of river flows, maintaining a sufficient level to support large waterbird breeding colonies and investigating impacts of upstream developments, as in other parts of the world (Zimmerman et al. 2010, FitzHugh and Vogel 2011, Hecht et al. 2019). Finally, my analyses found significant declines in total waterbird abundance across the delta, including declines in four of 15 species where there were sufficient data. These declines highlight the value of ongoing collection of citizen science data and the need for systematic rigorous monitoring of waterbirds in the Delta, particularly at breeding colonies, supported by methods allowing the collection of detailed and accurate breeding data such as a drone (Chapters 3, 4 & 5).

The use of a drone was a powerful tool for my research, allowing collection of data from breeding colonies in remote and dangerous areas. The quantity of data collected from large colonies of waterbirds meant that processing of drone imagery was extremely time consuming. I improved on current methods by developing a semi-automated counting technique able to count multiple species, using free software (Chapter 5). I also described a novel method for estimating reproductive success indices with a drone (Chapter 3). These methods showed that drone surveys, with subsequent manual or automated counting, could effectively track abundance of breeding birds and breeding success in colonies over time. The shifting of this method to the Google Earth Engine for image processing would allow for larger data sets to be processed in a fraction of the time (Gorelick et al. 2017), compared to my approach using desktop processing. Further advances in drone technology, including the attachment of infrared sensors to standard commercial drones would also improve reproductive success estimates of chick numbers even when under nesting parents based on the known body heat of a single adult, a key drawback affecting my estimates.

Citizen science played an important role in filling gaps in scientific monitoring in areas with relatively limited data collection. Ongoing citizen science programs should be promoted and

more formalised, particularly utilising the capability of applications such as eBird (eBird 2019) which provide local and global reporting capacity. Also, the African Waterbird Census (Dodman and Diagana 2019) was clearly an important contributor to understanding diversity and abundance of waterbirds in the Okavango Delta (Chapter 4) but has now languished because of unavailability of volunteers. Rigorous landscape-scale monitoring data is critically important for the long-term management and sustainability of the Okavango Delta and other important wetlands in Botswana. The dedicated birders of Botswana have contributed much knowledge about their avian populations, and such dedication and passion should be encouraged by governments and organisations, prioritising this type of monitoring. As with citizen science counts in South Africa (Thomas et al. 2015), spatial and temporal analyses of the effectiveness of current citizen science methods, particularly the African Waterbird Census would help improve the quality of the data and resultant analyses, and guide future methods. This is increasingly important given the range of issues affecting avifauna in Africa. For example, there is extensive poisoning of vultures across Botswana, a direct effect of increased poaching (Bradley 2014). An analysis similar to my use of citizen science data in the Okavango Delta, focusing on vultures, could be relatively easily performed to explore the severity of declines. Such analysis is also important for human communities given that, when vulture numbers in India declined, wild dog numbers increased driving increases in human rabies cases (Markandya et al. 2008). Citizen science can provide not only the data to help protect and manage wetlands into the future, but also focus on single species, with the added benefits of increased public engagement.

Community involvement in conservation is extremely important in Botswana, as it is around the world. For example, during my fieldwork on the breeding of colonial waterbirds on the Chobe River (Chapter 3), I discovered African openbill chicks were harvested as bush meat. This killing of chicks is a serious threat to the openbill population and needs to be stopped by

government officials in Kasane. The community can easily access the site and it is adjacent to swimming, recreational and ceremonial areas. Difficulties and resentments will likely arise if regulations to protect the openbills restrict access to this area. Encouraging community valuation of the conservation importance of the area, alongside other uses is critical. Many Batswana rely on the natural world for income and daily needs, meaning that effective long-term conservation requires engagement and commitment from local communities.

I also investigated the effects of pollution on marabou storks (Chapter 6). This species is another colonially nesting waterbird, that often forages in terrestrial habitats. Marabou storks habitually and naturally swallow and regurgitate inedible parts (e.g. bones) of their food, but when foraging at an urban landfill, much of this regurgitant is rubbish. I sorted and quantified regurgitant from the landfill at Chobe and used feathers to investigate the relationships between proximity to the landfill site, metal concentrations and dietary shifts. There were clear pollution signals, with higher levels of chromium, lead, nickel and zinc in feathers of marabou feeding regularly at landfills, alongside a dietary shift reflected by enriched $\delta^{15}\text{N}$ concentrations and lower $\delta^{13}\text{C}$. Further investigations of the relationship between blood and feather samples from the same marabou individuals would help elucidate whether high metal concentrations are also building in blood and potentially exerting chronic effects on the birds, including increasing their mortality. This would allow for increased understanding of the vulnerabilities of the species to pollution, as well as how metal concentrations in feathers relate to blood toxicities. Further, the elevated levels of manganese I detected in all marabou feathers requires investigation given the toxicity of this metal to other species, including humans (Mushi et al. 1999, Avila et al. 2013). Satellite tracking of marabou storks may help identify the source of the manganese in relation to abandoned mine sites, which may require restoration or stabilisation (Ekosse et al. 2006).

Globally, river flows are under threat, and within Africa alone 65% of people are reliant on restricted and highly variable water resources (Vörösmarty et al. 2005). Growing human populations, urbanisation and climate change (amongst others) continue to degrade the natural state of rivers and associated ecosystems (Kummu et al. 2016, Ariso et al. 2017, Seeteram et al. 2019). To explore such changes in Botswana, I focused on birds, primarily waterbirds, investigating the effects of changing herbivore populations, the relationships between abundance and breeding in relation to river flows and flooding, and the effects of other anthropogenic stressors such as urbanisation on bird populations. These analyses showed the value of birds in Botswana as indicators of freshwater ecosystem change. Monitoring of these birds can be used to track environmental change at large spatial and long temporal scales, improved by using a range of data collection tools such as drones and citizen science, coupled with the use of flow and inundation data.

7.1 Conclusions

The freshwater ecosystems of the world are increasingly degrading from a range of threatening processes, including reductions of flows and regulation of rivers, pollution, and climate change. I used birds as indicators of change in the health of freshwater ecosystems by identifying abiotic and biotic drivers of bird communities and their breeding. The avifauna in Botswana is outstanding, reflected in the high biodiversity of the Okavango Delta and Chobe River National Park, and their designation as Important Bird Areas, and the Delta as a World Heritage listed site and Ramsar wetland. Further, the birds of Botswana are fundamental to the global importance of the area for wildlife and tourism. The intrinsic value of the freshwater ecosystems make them a priority for conservation, with birds, particularly waterbirds, offering considerable value as indicators for ecosystem health for large herbivore density, flows, flooding, vegetation and pollution. Improved monitoring can contribute to a greater understanding of the value of these indicators and their effectiveness for predicting

effects of upstream developments on the supply rivers. Collection of these data will continue to rely on citizen science but could be considerably improved with scientific systematic monitoring. Ultimately, the future of these globally important freshwater ecosystems depends on mitigation of a range of threats, including from upstream countries on inflowing rivers. It is critical to provide effective information to inform local and global communities about trajectories of change for these ecosystems, informed by data on avifauna, particularly waterbirds.



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