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The Okavango Delta's waterbirds – Trends and threatening processes

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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, and its transboundary nature, 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 in three countries to ensure natural flooding regimes, alongside the conservation of neighbouring wetlands.

1. 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

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and Cultural Organization) World Heritage Site. It supports eight large herbivore families, many more antelope species, and 444 species of birds (UNESCO, 2014; Hancock and 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 and 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 et al., 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 because the lack of suitable indicator species is a great impediment to their efficient monitoring (Landres et al., 1988; Carignan and 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, 2018). Census counts and studies of waterbirds exist (Douthwaite, 1979; Fraser, 1971; Tyler and Bishop, 1998; Dodman and 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; Kopij and 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 as they congregate in large numbers, and are valued by the public (Green and Elmberg, 2014), providing an increasingly important source of data for citizen-science analyses (Bonney et al., 2014; Callaghan and Gawlik, 2015).

Citizen science data can increasingly track long term temporal trends at broader geographic scales than most scientific sampling (Dickinson et al., 2010). When linked to remotely sensed data, they provide valuable insights into ecosystem status where there is

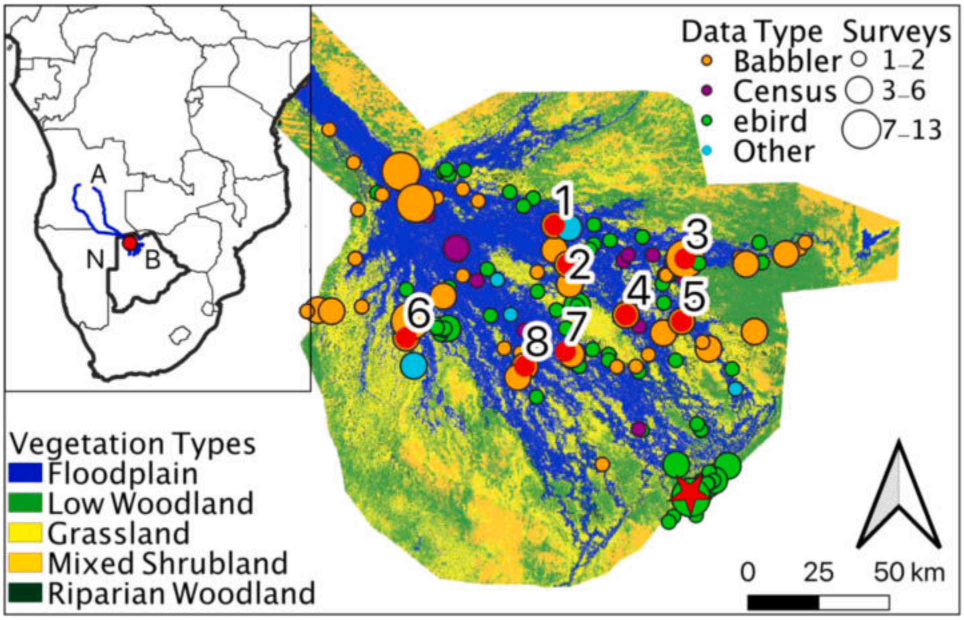

Fig. 1. The Okavango Delta (red dot on lower half of southern Africa inset), in north-western Botswana (B), near the town of Maun (star), where citizen science data were collated from 4 grouped sources 1970–2019 (numbers of surveys shown with different sized circles), receives flows from the Cubango (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). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

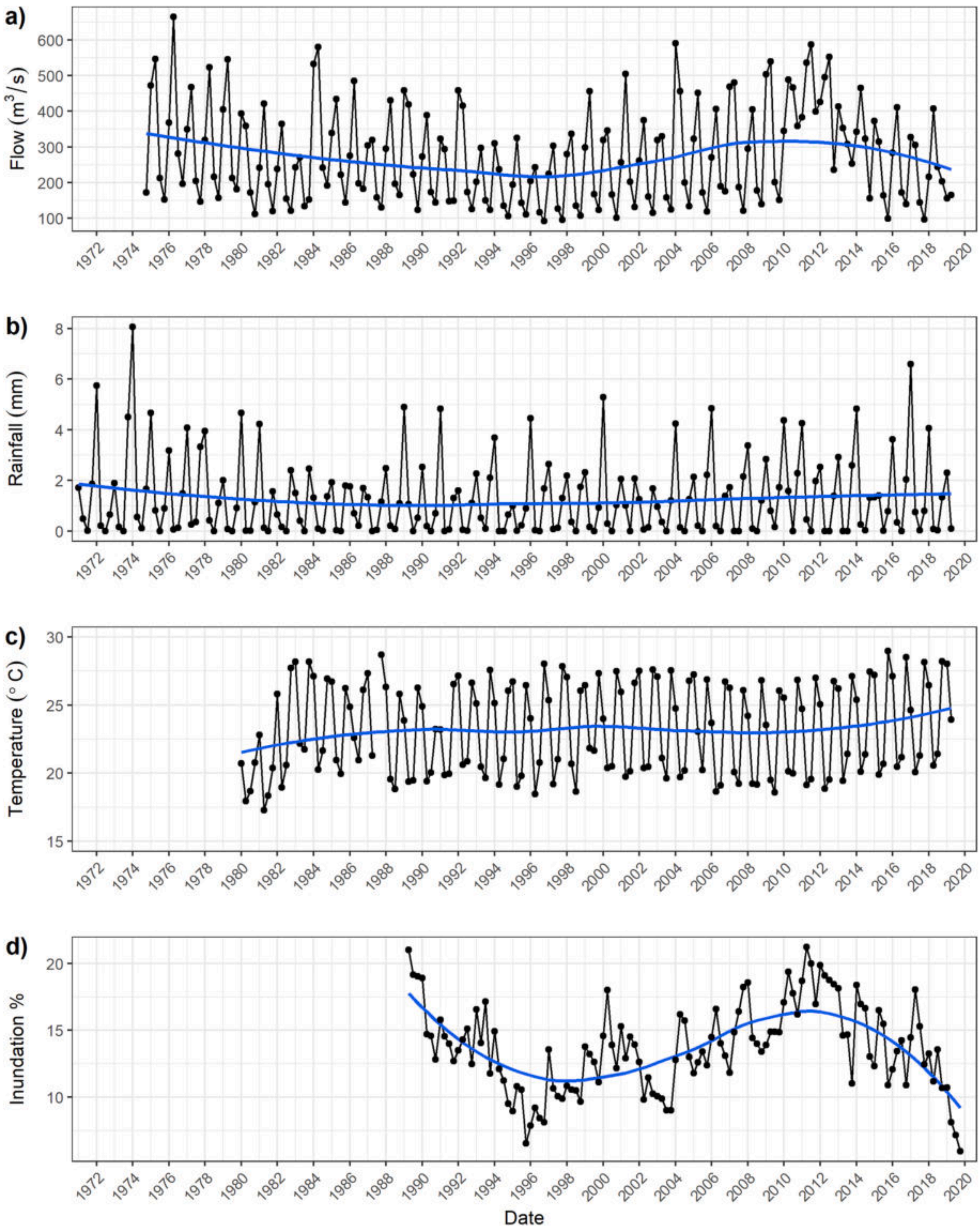

Fig. 2. Quarterly measurements and a loess smooth (blue line) of a) river flow (gauges Appendix A, 1974–2020); b) rainfall (gauges Appendix A) (1970–2019); c) ambient temperature (gauges Appendix A)(1980–2019) and d) percent of mapped inundated area at the Okavango Delta from 1989 to 2020 (n = 127). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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 et al., 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 and 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 and Nordin, 2004; Darkoh and Mbaiwa, 2014). The Okavango River starts as the Cuito and Cubango Rivers in Angola and passes through Namibia before reaching Botswana (Fig. 1), and so threatening processes in all of the three countries are able to affect the downstream Okavango Delta. Reduction of flows due to upstream water extraction and damming (Pinheiro et al., 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 local people, 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 and Stanford, 2002; Smardon, 2009; Uddin et al., 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 and 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.

2. Material and methods

2.1. 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. 1). The Okavango River starts after the confluence of the rivers, crossing Namibia and entering northern Botswana, where it inundates the Okavango Delta (Fig. 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).

2.2. 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. 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 A) (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 B). We also collated daily rainfall data from six gauges across the Okavango Delta (Maun airport, Disaneng, Guma, Nxaraga, Sexaxa and Xakanare) (Appendix A) (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. 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).

We used Google Earth Engine (https://earthengine.google.com/) to calculate area inundated across the Okavango Delta floodplain (~53,000 km^2, the Delta boundary as delineated in the flood imagery, Appendix A) (Gorelick et al., 2017), from Landsat-5, 7 and 8 images (Inman and 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 (30 m) 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 and Lyons, 2020). Classification accuracy was within 92–98%, dependant on the testing method (see Inman and 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 A). 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 and Grothendieck, 2005), in the R programming environment (R Core Team, 2019) (Fig. 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 et al., 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 and Cumming, 2016).

2.3. 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 C for species' names), from eight sources: African Waterbird Census (AWC) (Dodman and 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 and Herremans, 1994, 1996; Herremans et al., 2002; Hancock et al., 2003), personal communications from two sources (Mueller 2012; Hancock 2018) and personal observations (Fig. 1, Table 1). These citizen science surveys listed abundance of all species observed at a particular time of the year, and their location (Fig. 1). We focussed on the waterbird species that breed colonially because these are established as effective indicators of wetland ecosystem health and condition in relation to river flows (Frederick et al., 2009; Henry and Cumming, 2016). We also included two crane species, given that wattled cranes are vulnerable. We did not assemble data on other waterbirds. 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 (personal communications and published literature), 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

Table 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. 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 the eastern channels) which were largely repeated in each year of the survey, and includes transect counts, and point counts.	56 (2011–2017, 6)	36
eBird (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. 1), with observations ranging from stationary 5 min surveys to travelling surveys of 240 min over 5 km. 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 and Herremans, 1994; Herremans, 1996; Herremans et al., 2002; Hancock et al., 2003)	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
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

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. 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 C). 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.

2.4. 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 often highly correlated with its corresponding variable (eg. mean discharge and mean discharge with a lag of 12 months). We kept both lags due to their potential ecological importance to the model, and 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 1) as a random variable, comprising four broad groups (eBird, AWC, Babbler and remaining types grouped into an 'other' category, Table 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 D). We assessed model fit using the corrected Akaike's Information Criterion (AICc) (Burnham and Anderson, 2004), 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 C). 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 $\alpha < 0.05$.

2.5. Waterbird breeding colonies

We also investigated associations between locations of waterbird colony breeding sites (Fig. 1) and vegetation communities and flooding frequency (1970–2019). Colony data were compiled from the collated data set from a range of citizen science surveys (Table 1), comprising 682 observations across eight colonies (Fig. 1). We used existing vegetation classifications, derived from remotely sensed data (pixel size 400 m^2) across 31,607 km^2 of the Delta (Inman, 2020), which covered all colonies. The five vegetation classes included floodplain (9103 km^2), grassland (9186 km^2), low woodland (7671 km^2), mixed shrubland (3009 km^2) and riparian woodland (2638 km^2), (Fig. 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 and Flake, 1985; Bryan and 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 10 km distances (Q1: 0% flooded, Q2: 0.01–1.6%, Q3: 1.6–22.8%, Q4: 22.81–100%, Appendix A). 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).

3. 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. 2). Three-monthly mean inundation percent declined (1989–2019, X2(1, N = 73) = 0.451, p = 0.055). There were clear seasonal patterns (Fig. 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 1) in the Okavango Delta (Appendix C). Split into foraging guilds, most species were shallow water feeders (n = 22), terrestrial feeders (n = 7), followed by short vegetation or mud (n = 3), emergent vegetation including reeds and lilies (n = 2), and deep water (n = 3)

(Appendix C). 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 C). Detection of species across the Delta varied over time, reflecting survey methods and frequency (Fig. 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 1), including rare and vulnerable species (lesser flamingo, slaty egret, wattled crane, woolly-necked stork) (Fig. 3). There was no African Waterbird Census in 2018 and 2019 and these years had no recordings of these vulnerable species (Fig. 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 (eeBird, 2019)(Fig. 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. 2).

Survey methods varied in their effectiveness in detecting waterbird species (Fig. 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) ($p < 0.001$) and quarterly ambient temperatures ($p < 0.001$), negatively with lagged inundation percent (12-month) ($p = 0.055$) and year ($p < 0.001$)(Fig. 5). This was on the basis of seven averaged models within 2 ΔAICc of the best fit model (Appendix D), providing relative importance of each variable in Appendix E. Waterbird abundance declined at a rate of 2.7% per year since 1990 (Fig. 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

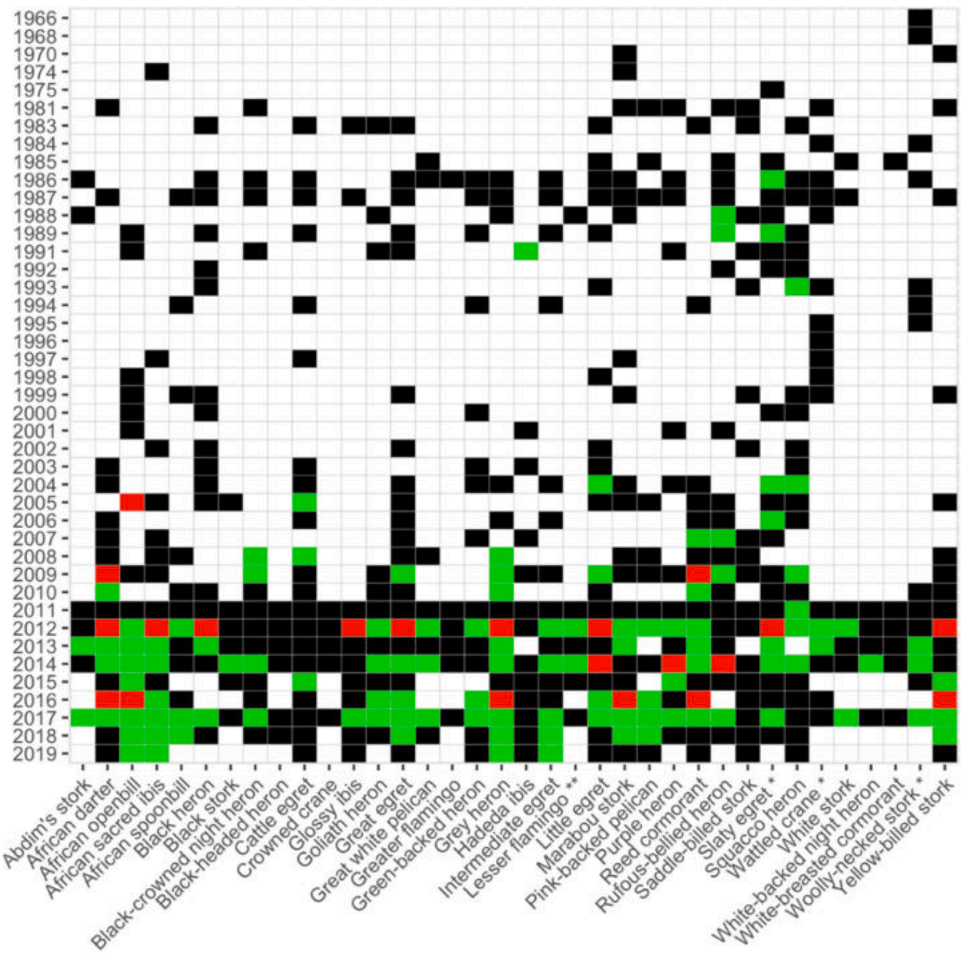

Fig. 3. Presence of the 36 waterbird species recorded in one (black), two (green) or three or more (red) of the five survey groups (AWC, BLB, eBird, Drone, Other) in the Okavango Delta (1970–2019), identifying vulnerable (*) and near threatened (**) species (Appendix C). Years with no data were omitted. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

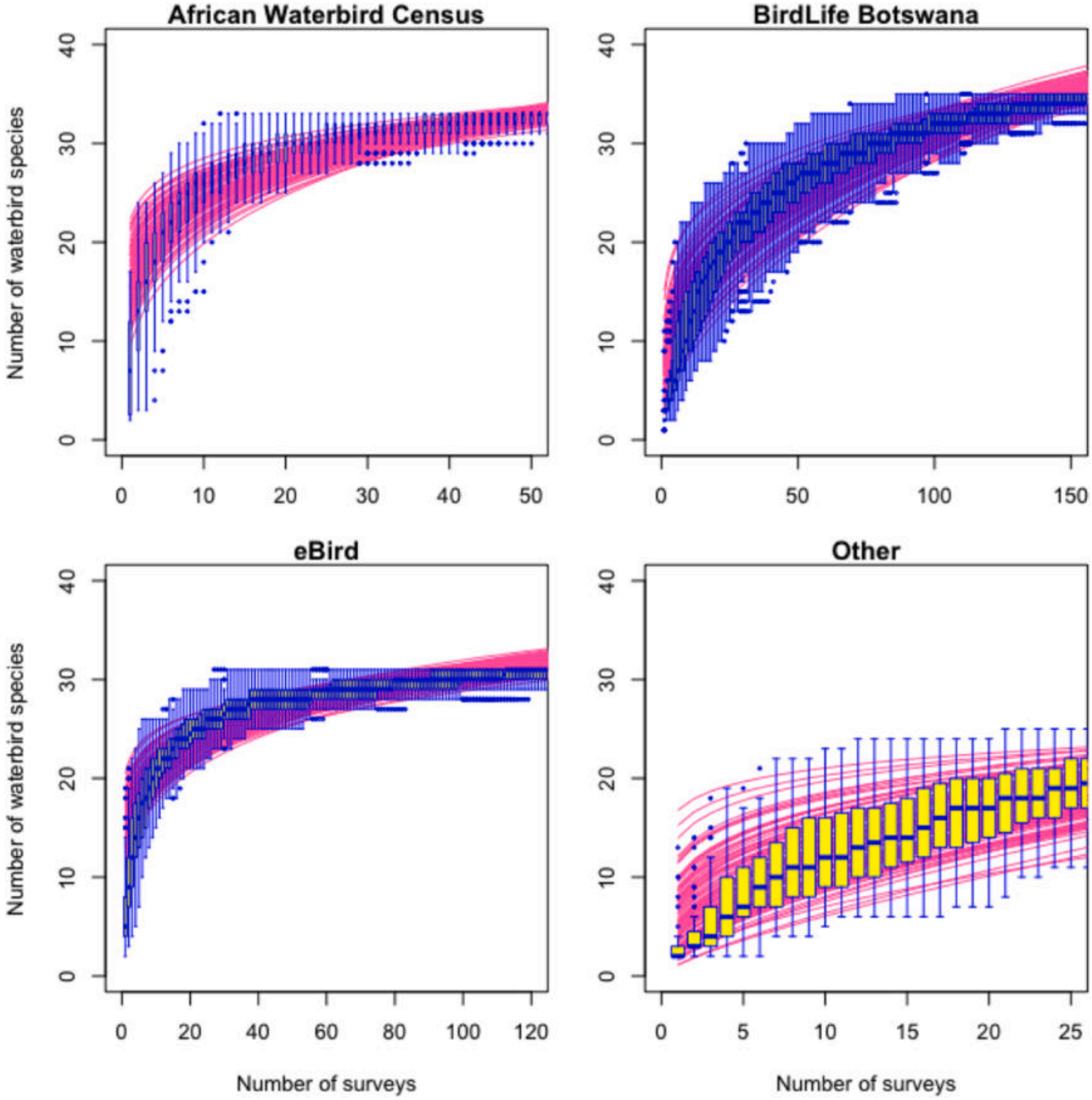

Fig. 4. Rarefaction curves for numbers of waterbird species accumulated with increasing numbers of surveys for the four survey groups (drone data excluded given few years), 1970–2019.

increased (1.1%) (Table 2). Mean abundance of ten of the 15 species were significantly associated with environmental variables, after accounting for annual trends (Table 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 decreased. Further, mean abundance of little egrets and rufous-belled 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.

3.1. Colonial waterbird breeding sites

Of the eight colonial breeding sites in the Okavango Delta (Fig. 1), the Kanana colony supported the highest abundance of breeding waterbirds, despite the low number of observations compared to other colonies (Table 3). Species' richness was high at Xini, Xakanaxa and Xobega, compared to other colonies (Table 3, Appendix F).

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 10 km) 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 to 8.19 (Fig. 6a). All colonies had relatively high proportions of

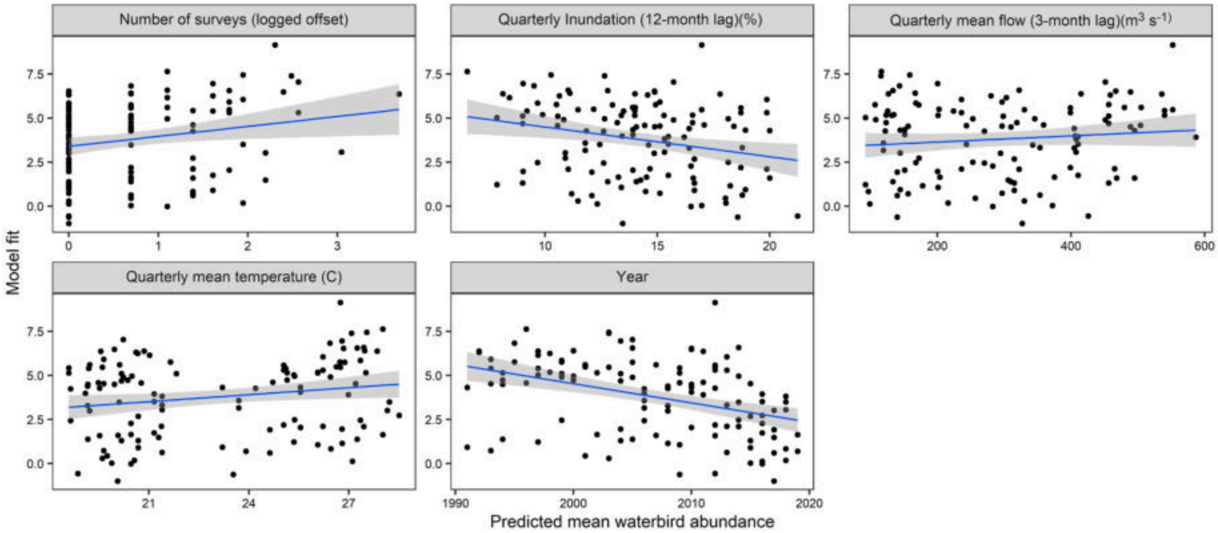

Fig. 5. Predicted mean waterbird abundance across the Okavango Delta (1990–2019), in relation to model fit of the final averaged model from seven plausible models showing the five significant predictors, with the blue line representing the linear smoother and its 95% confidence interval (grey shading). 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. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 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. 1).

Species (n observations)	Model # (ΔAIC)[a]	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

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

floodplain and riparian woodland (1, 5 and 10 km), compared to the other areas in the Delta (Fig. 6a, Appendix G and H). 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. 6b). Ratios were higher in the inundation than vegetation selection, perhaps suggesting inundation is a more important driver of colony location.

4. 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 et al., 2007; McCulloch et al., 2017) and World Heritage Site (UNESCO, 2014), effective management is essential (The Ramsar Convention Secretariat, 2014; BirdLife International, 2021a, 2021b; Kingsford et al., 2021). Despite plans to monitor (Mfundisi, 2008), there is little consistent and

Table 3
Eight main waterbird breeding colonies within the Okavango Delta (Fig. 1), identified from citizen science data (Table 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 ± 266.07 [5–669]	11.46 ± 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 ± 1793.5 [80–5031]	8.39 ± 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 ± 354.37 [1–760]	13.5 ± 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 ± 1791.23 [2–4411]	9.02 ± 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, Reed Cormorant, Rufous-bellied Heron, Saddle-billed Stork, Slaty Egret, Squacco Heron, Wattled Crane)	99	10
Xho	413.08 ± 414.68 [1–810]	3.67 ± 2.46 [1–6]	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

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, 2021b). In the absence of rigorous monitoring data, we used available citizen science data (Table 1, Fig. 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, identifying major threats in need of management. In particular, further upstream development of water resources reducing inflows and inundation extent and frequency, exacerbated under climate change scenarios (Andersson et al., 2006; Darkoh and Mbaiwa, 2014). Waterbirds could be useful ecological indicators of such hydrological change and ecosystem 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 et al., 2017). Total waterbird abundance was positively related to Okavango River flow at a 3-month lag, likely as birds respond to ecosystem changes in prey availability (Frederick et al., 2009). A negative response in abundance to a 12-month lag in inundation is more difficult to interpret, but may relate to a positive response in vegetation growth (which could take up to 12 months to occur), obscuring waterbirds and reducing counts. In addition to declines in total abundance over time, 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. 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 and Mbaiwa, 2014). Due to the small scale at which this study was conducted we cannot be sure species' declines reflect declines in the total population, or if birds are instead using wetlands elsewhere (Thomas et al., 2015). However, African waterbird declines, alongside degradation of African wetlands make it likely that population declines may be occurring at a broader scale than the Okavango Delta (Jogo and 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 and Seavy, 2003), possibly contributing to population declines of waterbird species. Declines in the squacco heron occurred 1970–2000 across its range in both Africa and Europe

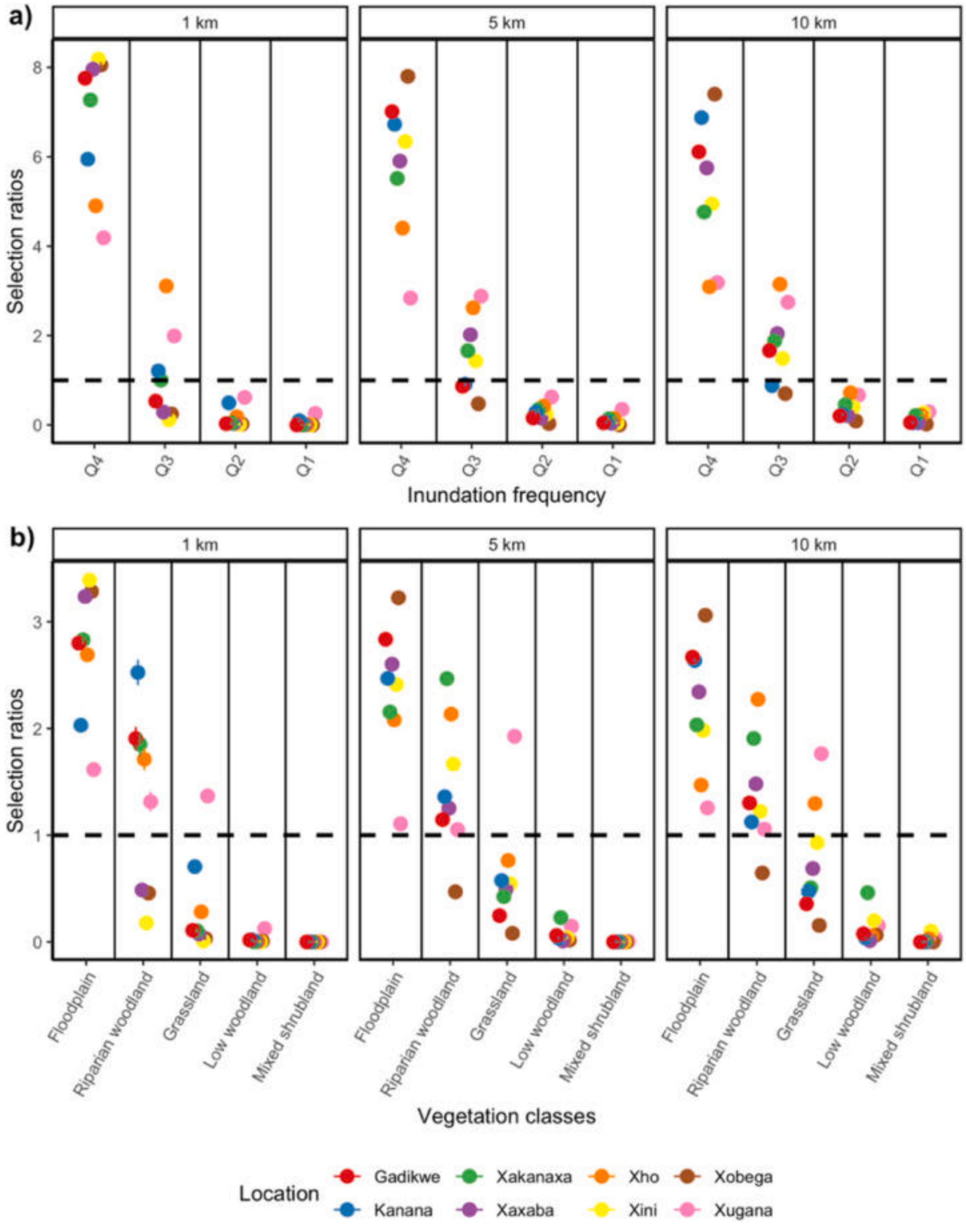

Fig. 6. Habitat selection ratios (Manly selection ratios) for the eight key waterbird colonies in the Okavango Delta, in relation to a) frequency of quartiles of flooding (Q1: 0% flooded, Q2: 0.01–1.6%, Q3: 1.6–22.8%, Q4: 22.81–100%) and b) five vegetation types (floodplain, riparian woodland, grassland, low woodland and mixed shrubland), within three areas of the colonies (1, 5 and 10 km).

(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 in Zambia (Collar and 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 and Kibuule, 2017; Thabethe and 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 et al., 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 3, Fig. 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 and Herremans, 1994; Bowker and Downs, 2012; Monadjem et al., 2012). The breeding of marabou stork at these colonies, particularly Kanana (Table 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 B) (Hancock et al., 2007; Motsumi et al., 2007; BirdLife International, 2020a, 2020b, 2021a, 2021b). Slaty egret and wattled crane were recorded at seven of the eight breeding colonies (Table 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, 2018). 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 et al., 2000; Tockner and 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 et al., 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. 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). 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. Records of local knowledge and change over time from the many villages across the Okavango Delta would be an important data source to expand on the trends we have identified. To date, there have been many community-based initiatives to address threats to the Delta, including the gazetting of controlled hunting areas as community photographic areas, and the training of locals as bird guides, supplying an income that offsets the lack of hunting. This encouragement of local involvement in avian conservation is another important monitoring source that would substantially increase the spatial complexity of bird observations across the Delta. Community based natural resource management options, such as these, which consider the stakeholders across all involved countries (Angola, Namibia, Botswana) will likely be the only effective way to reduce long term pressures on this natural system (Mbaiwa and Stronza, 2010; Kingsford and Watson, 2011).

Species' accumulation curves indicated the African waterbird census recorded the greatest numbers of species with the least number of surveys, indicating 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. This dataset would benefit from an assessment to determine whether it is capturing the temporal and spatial variation it is aiming to explore as has been done with similar datasets in South Africa (Thomas et al., 2015), which would only further increase its usefulness. 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 (Nicolaides, 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 et al., 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. 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.

5. Conclusions

The Okavango Delta is a system of great biological importance, which also faces many threats. Its transboundary nature means its conservation is dependant on three countries who are heavily reliant on it for freshwater and other ecosystem services. The relation between waterbird breeding and abundance and inundation suggest declining trends in inundation may be responsible for the observed waterbird declines. These trends require continued monitoring, both with the encouraged use of citizen scientists and systematic scientific study. The Okavango Deltas long term conservation will be highly dependant on the cooperation of the involved countries and their commitment to protect its natural flooding regimes, and the use of waterbirds as environmental indicators will be a useful tool for its efficient monitoring.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Waterbird count data is provided publically on FigShare 10.6084/m9.figshare.16401072

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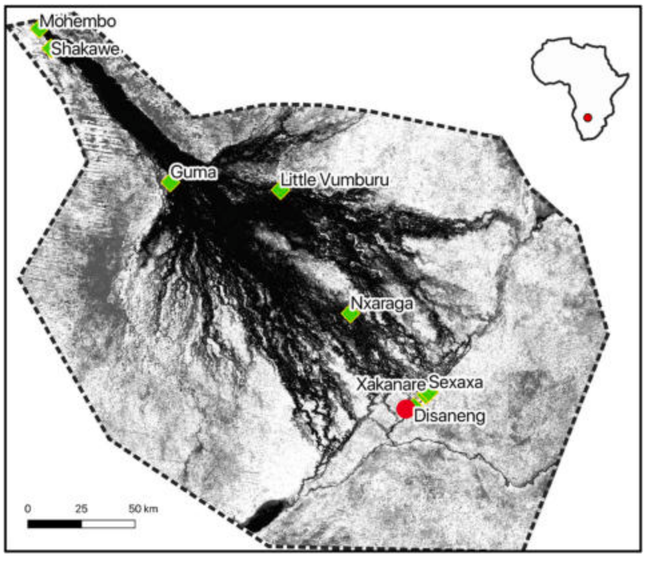
Appendix A. Gauges from where water level and flow, rain and temperature data were collected can be seen in green on the mean inundation raster (1984–2019), with Maun town marked in red, located within southern Africa (inset)



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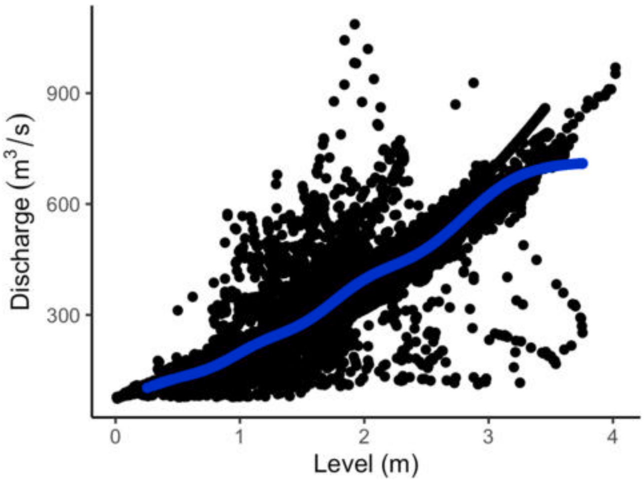
Appendix B. Missing flow values were filled using the gam model relationship between flow and level, with the missing values predicted into the final flow dataset (blue)



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Appendix C. 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 ± SD

Common Name	Species	Functional Group	Foraging Group	Conservation Status	Count
Abdim's stork	*Ciconia abdimii*	Terrestrial invertivore	0	LC	6 (4.04 ± 21.08)
African darter[a]	*Anhinga rufa*	Aquatic carnivore	4	LC	31 (10.66 ± 23.48)
African openbill[a]	*Anastomus lamelligerus*	Aquatic invertivore	3	LC	39 (173.41 ± 510.87)
African sacred ibis[a]	*Threskiornis aethiopicus*	Aquatic carnivore	1	LC	18 (5.44 ± 13.99)
African spoonbill	*Platalea alba*	Aquatic carnivore	3	LC	12 (5.55 ± 24.87)
Black heron	*Egretta ardesiaca*	Aquatic carnivore	3	LC	34 (25.73 ± 59.91)
Black stork	*Ciconia nigra*	Aquatic carnivore	3	LC	2 (0.06 ± 0.24)
Black-crowned night heron	*Nycticorax nycticorax*	Aquatic carnivore	3	LC	18 (6.3 ± 15.71)
Black-headed heron	*Ardea melanocephala*	Terrestrial carnivore	0	LC	4 (0.25 ± 0.84)
Cattle egret[a]	*Bubulcus ibis*	Terrestrial carnivore	0	LC	47 (126.7 ± 462.03)
Crowned crane	*Balearica regulorum*	Aquatic omnivore	3	LC	1 (0 ± 0)
Glossy ibis	*Plegadis falcinellus*	Aquatic invertivore	1	LC	16 (6.12 ± 23.55)
Goliath heron	*Ardea goliath*	Aquatic carnivore	3	LC	7 (1.19 ± 4.65)
Great egret[a]	*Ardea alba*	Aquatic carnivore	3	LC	36 (35.8 ± 125.01)
Great white pelican	*Pelecanus onocrotalus*	Aquatic carnivore	3	LC	17 (10.11 ± 28.45)
Greater flamingo	*Phoenicopterus roseus*	Aquatic invertivore	3	LC	2 (0.02 ± 0.14)
Green-backed heron[a]	*Butorides striata*	Aquatic carnivore	2	LC	9 (2.76 ± 10.05)
Grey heron[a]	*Ardea cinerea*	Aquatic carnivore	3	LC	20 (4.07 ± 9.16)
Hadeda ibis	*Bostrychia hagedash*	Aquatic invertivore	1	LC	8 (2.13 ± 2.51)
Intermediate egret (Yellow-billed egret)	*Egretta intermedia*	Aquatic carnivore	3	LC	23 (16.78 ± 79.02)
Lesser flamingo	*Phoenicopterus minor*	Aquatic invertivore	3	NT	4 (10.54 ± 42.49)
Little egret[a]	*Egretta garzetta*	Aquatic carnivore	3	LC	38 (37.58 ± 184.73)
Marabou stork[a]	*Leptoptilos crumenifer*	Terrestrial carnivore	0	LC	26 (47.34 ± 156.02)
Pink-backed pelican	*Pelecanus rufescens*	Aquatic carnivore	3	LC	15 (25.17 ± 71.36)
Purple heron	*Ardea purpurea*	Aquatic carnivore	3	LC	14 (3.3 ± 11.32)
Reed cormorant[a]	*Microcarbo africanus*	Aquatic carnivore	4	LC	34 (30.38 ± 202.32)

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(*continued*)

Common Name	Species	Functional Group	Foraging Group	Conservation Status	Count
Rufous-bellied heron[a]	*Ardeola rufiventris*	Aquatic carnivore	2	LC	24 (9.51 ± 22.48)
Saddle-billed stork[a]	*Ephippiorhynchus senegalensis*	Aquatic carnivore	3	LC	10 (2.46 ± 4.17)
Slaty egret[a]	*Egretta vinaceigula*	Aquatic carnivore	3	VU	32 (29.07 ± 97.25)
Squacco heron[a]	*Ardeola ralloides*	Aquatic carnivore	3	LC	43 (68.71 ± 181.16)
Wattled crane	*Grus carunculatus*	Aquatic omnivore	3	VU	36 (53.31 ± 151.08)
White stork	*Ciconia ciconia*	Terrestrial carnivore	0	LC	6 (4.37 ± 27.22)
White-backed night heron	*Gorsachius leuconotus*	Aquatic carnivore	2	LC	3 (0.1 ± 0.59)
White-breasted cormorant	*Phalacrocorax lucidus*	Aquatic carnivore	4	LC	3 (0.08 ± 0.34)
Woolly-necked stork	*Ciconia episcopus*	Aquatic carnivore	3	VU	16 (37.2 ± 120.65)
Yellow-billed stork[a]	*Mycteria ibis*	Aquatic carnivore	3	LC	25 (20.95 ± 73.17)

[a] The 15 species included in the species-specific modelling.

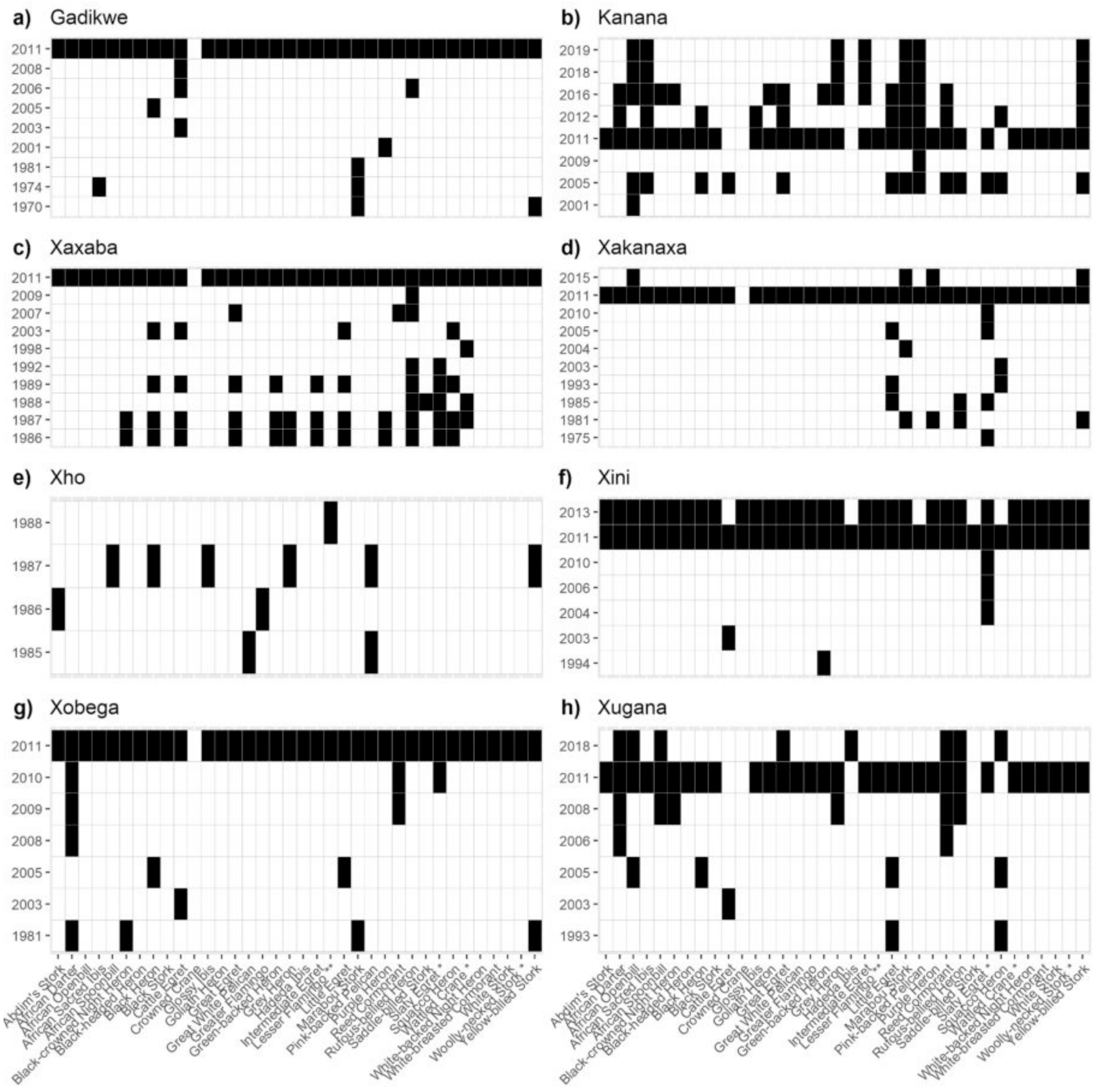
Appendix D. Seven best fit models were used in the model averaging process with their log likelihood, Akaike information criterion (AICc), the difference between the models AICc and the best fit model AICc (ΔAIC) and the importance of each model (weight)

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 E. Results of the fixed variables selected in the final conditional averaged model of seven models with ΔAIC <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 F. Species present at each of the key colonial waterbird breeding sites, when surveyed in the Okavango Delta from 1970 to 2019, with the Kanana colony including drone counts from 2018 and 2019



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Appendix G. Model results (selection ratio, χ2, 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
	LowWoodland	0.02, 107985, < 0.001	0.06, 699730, < 0.001	0.08, 2136278, < 0.001

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Location	Vegetation Type	1 km Buffer	5 km Buffer	10 km Buffer
	Grassland	0.11, 17280, < 0.001	0.25, 141421, < 0.001	0.36, 295800, < 0.001
	Mixed Shrubland	0, Inf, < 0.001	0, Inf, < 0.001	0, Inf, < 0.001
	Riparian Woodland	1.91, 320, < 0.001	1.15, 322, < 0.001	1.3, 4943, < 0.001
Kanana	Floodplain	2.03, 2901, < 0.001	2.47, 175492, < 0.001	2.64, 984444, < 0.001
	LowWoodland	0.02, 93046, < 0.001	0.04, 1259177, < 0.001	0.04, 4687558, < 0.001
	Grassland	0.71, 353, < 0.001	0.57, 21539, < 0.001	0.47, 157337, < 0.001
	MixedShrubland	0, Inf, < 0.001	0, 35124735, < 0.001	0, 562455469, < 0.001
	Riparian Woodland	2.52, 726, < 0.001	1.36, 1688, < 0.001	1.12, 939, < 0.001
Xakanaxa	Floodplain	2.83, 15097, < 0.001	2.15, 93993, < 0.001	2.03, 292061, < 0.001
	Low Woodland	0, 709649, < 0.001	0.23, 130870, < 0.001	0.46, 133429, < 0.001
	Grassland	0.1, 18092, < 0.001	0.43, 50578, < 0.001	0.51, 128682, < 0.001
	Mixed Shrubland	0, Inf, < 0.001	0, Inf, < 0.001	0, 41385981, < 0.001
	Riparian Woodland	1.85, 289, < 0.001	2.47, 17101, < 0.001	1.91, 31994, < 0.001
Xaxaba	Floodplain	3.24, 57431, < 0.001	2.6, 229454, < 0.001	2.34, 548114, < 0.001
	Low Woodland	0, 392776, < 0.001	0.01, 5196485, < 0.001	0.01, 16302774, < 0.001
	Grassland	0.07, 27167, < 0.001	0.49, 34752, < 0.001	0.69, 40560, < 0.001
	Mixed Shrubland	0, Inf, < 0.001	0, Inf, < 0.001	0, Inf, < 0.001
	Riparian Woodland	0.49, 356, < 0.001	1.25, 893, < 0.001	1.48, 11141, < 0.001
Xho	Floodplain	2.69, 11032, < 0.001	2.08, 80792, < 0.001	1.47, 59903, < 0.001
	Low Woodland	0, 392676, < 0.001	0.02, 2429133, < 0.001	0.05, 3302331, < 0.001
	Grassland	0.28, 4557, < 0.001	0.76, 5407, < 0.001	1.3, 24889, < 0.001
	Mixed Shrubland	0, Inf, < 0.001	0, Inf, < 0.001	0.03, 2474746, < 0.001
	Riparian Woodland	1.71, 216, < 0.001	2.13, 11446, < 0.001	2.27, 54871, < 0.001
Xini	Floodplain	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	0.18, 2422, < 0.001	1.67, 4858, < 0.001	1.22, 2851, < 0.001
Xobega	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
	Riparian Woodland	0.46, 420, < 0.001	0.47, 9813, < 0.001	0.65, 12910, < 0.001
Xugana	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 H. Model results (Selection ratio, χ2, 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

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Location	Flooding Frequency %	1 km Buffer	5 km Buffer	10 km Buffer
	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

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