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Trends in savannah waterbirds: protected area effect and influence of global threats on differing guilds

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Understanding species threats is underpinned by information on their population trends. We investigated the contribution of population drivers associated with 86 waterbird species' trends at a local scale, Hwange National Park (HNP) and a national scale (Zimbabwe). We used logistic regression models to test whether waterbird population trends differed across migration types, seasons, species traits (guild, weight, index of diet variety, social foraging and breeding systems), scale of use by humans (whether the waterbird species utilisation is documented at local or international scale) and susceptibility to hunting and diseases. In HNP during the wet season, waterbird population trends were mostly stable or increasing. During the dry season, larger species were more likely to be recorded, more so for those threatened by hunting, compared with the species limited by diseases. Colonial resident waterbirds had more increasing population trends in HNP in comparison to the solitary ones. At the Zimbabwean scale, records for 35% of species decreased during the wet season, and the declines were more pronounced in large birds. During the dry season, species threatened by habitat disturbances were more likely to decrease. Habitat disturbances and/or use of waterbirds at the international scale are more associated with declining trends than ecological and life history traits. We have shown that HNP, a protected area with mostly a pan wetland-system is supporting growing waterbird populations despite the species facing global negative population trends.

Tendances des oiseaux d'eau de la savane: effet des aires protégées et influence des menaces mondiales sur les différentes guildes.

La compréhension des menaces pesant sur les espèces repose sur des informations sur les tendances des populations. Nous avons étudié la contribution des facteurs de population associés aux tendances de 86 espèces d'oiseaux d'eau à l'échelle locale (parc national de Hwange (PNH) et à l'échelle nationale (Zimbabwe). Nous avons utilisé des modèles de régression logistique pour tester si les tendances des populations d'oiseaux d'eau variaient selon les types de migration et les saisons. Les caractéristiques des espèces (guilde, poids, indice de variété alimentaire, systèmes de recherche de nourriture et de reproduction), l'échelle d'utilisation par les humains (si l'utilisation des espèces d'oiseaux d'eau est documentée à l'échelle locale ou internationale) et la sensibilité à la chasse et aux maladies. Pendant la saison des pluies, les tendances des populations d'oiseaux d'eau étaient pour la plupart stables ou en augmentation. Pendant la saison sèche, les espèces plus grandes étaient plus susceptibles d'augmenter en nombre, surtout pour celles menacées par la chasse que pour les espèces limitées par les maladies. Les oiseaux aquatiques sédentaires coloniaux avaient des tendances de population plus élevées dans la PNH par rapport aux oiseaux solitaires. A l'échelle zimbabwéenne, 35% des espèces diminuaient pendant la saison des pluies et les déclins étaient les plus prononcés chez les grands oiseaux. Pendant la saison sèche, les espèces menacées par des perturbations de l'habitat étaient plus susceptibles de diminuer. Les perturbations de l'habitat et/ou l'utilisation d'oiseaux d'eau à l'échelle internationale sont davantage associées à des tendances à la baisse qu'à des caractéristiques écologiques et biologiques. Nous avons montré que la PNH, une zone protégée avec principalement un système de zones humides basses, soutient les populations d'oiseaux d'eau en croissance malgré les espèces confrontées à des tendances démographiques mondiales négatives.

Keywords: habitat change, Hwange National Park, life history traits, population trends

Supplementary material: available at https://doi.org/10.2989/00306525.2020.1722972

Introduction

The southern Africa wetland system supports a variety of waterbird species within protected areas (PAs), as well as in large and small-scale agricultural lands. In the inland wetland systems, dams, weirs, rivers and small

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endorheic, often ephemeral depressions known as pans (Goudie 1991) attract large populations of waterbirds to breed and winter particularly during the rainy season (Godfrey 1992). There are signs in southern Africa that the destruction of inland wetland areas is placing waterbirds under intense and unsustainable pressure (Allanson et al. 2012), with more declining species' trends than increasing being observed (Kirby et al. 2008). However, these inland systems remain understudied, and analysing waterbird trends in them is therefore critical to understand processes limiting the waterbird populations (Lehikoinen et al. 2013). An understanding of the causes of such trends may help conservationists to mitigate future threats to these waterbirds.

Various threats to waterbirds are documented, including agricultural mediated land use changes and diseases (Haq et al. 2018), deteriorating feeding and breeding habitats (Kirby et al. 2008), infrastructural developments (Allanson et al. 2012) and harvesting (Paillisson et al. 2002, Pöysä et al. 2013). The level at which such threats influence waterbird dynamics might vary. For example the influence of subsistence hunting, egg collection and noise in human settlements could be greater at local, compared with regional scales (Ramachandran et al. 2017). Local feeding conditions may affect the various waterbird feeding guilds differently, for example, Kasahara and Koyama (2010) observed that most of the water-surface foraging waterfowl were declining, but it was different for species of divers in Japan. Although local habitat alterations, such as sewage treatment sites may result in skewed communities dominated by amphibian feeding waterbird species, such as storks, egrets and herons (Hamilton et al. 2005), other studies show that the resultant waterbird communities in such habitats can be broad (Orłowski 2013).

Some studies provide evidence that population trends are not random with respect to life-history traits and ecological traits. Barshep et al. (2017) found that brood size, type of chick development and mating system were related to population trends of resident and migrant species in South Africa. Although chick rearing in colonial nesting waterbirds may be more successful, compared with solitary nesters (McNeil et al. 1993), they can be more vulnerable to disease outbreaks (Kushlan 1993). Species that migrate long distances may also be prone to more global threats, compared with short distance migrants (Barshep et al. 2017).

Although several scientists have explored the role of large wetland systems in waterbird conservation (Owino et al. 2001; Remisiewicz and Avni 2011), very little is known on the contribution of the inland pan systems to waterbird conservation status in southern Africa (Mundava et al. 2012). This is particularly true for pans maintained through artificial pumping of water, a common management strategy in PAs of southern Africa. Some naturally forming pan systems in inland southern Africa have become Important Bird Areas (IBAs) that contribute to many waterbird species' breeding success and increase waterbird diversity (Childes and Mundy 2001). Assessing the outcomes of conservation efforts is crucial, hence the necessity to assess whether designated IBAs are having positive outcomes on waterbird population trends. Here, we used a 25-year dataset of waterbird counts that were conducted in specific water bodies in Zimbabwe, including the extensive pan system of Hwange National Park (HNP), which is a designated IBA. We aimed at testing whether HNP is still retaining its capacity as a waterbird production 'factory' (Godfrey 1992). We also test for the relative contribution of documented life-history traits, ecological characteristics and threats to waterbirds (at local and global scales) in determining trends of waterbirds in such savannah pan systems.

Understanding waterbird dynamics in IBAs in comparison to the national level (here Zimbabwe) should guide conservation efforts. Given that the severity of drivers influencing waterbird population trends could be exerted at various scales (Kirby et al. 2008), comparing trends at any two levels should provide useful information on threats and processes for conservationists, as well as managers. Investigating the trends and status of waterbirds at a national level will also contribute to assessment of Zimbabwe's bird diversity and wetland conservation status. Our general hypothesis was that the HNP pan system would continue to be 'a duck factory', as portrayed in Godfrey (1992), compared with water bodies (mostly dams) elsewhere in the country. More specifically, we predicted that waterbird trends in Zimbabwe during the wet season, when the proportions of migrant species are high, would reflect global pressure more than local ones as highlighted in Dalby et al. (2014). Resident species' trends were predicted to decline faster when they are susceptible to habitat change and disturbances (as was the case in Haq et al. 2018), compared with the migrants. Waterbirds with broader diet niches (generalists) may respond at slower rates to habitat change and disturbance, because of their increased resilience to perturbations (Martínez-Abraín et al. 2016), compared with guilds with narrower diet niches (such as wildfowl). Species consumed by people are predicted to respond more to local uses and hunting, as argued by Freese (1997), compared with those not used.

Materials and methods

Study area

Zimbabwe is a 390 757 km^2 land-locked country that has an estimated 1.3% of its area covered as wetlands (Environmental Management Agency 2012). Its wetlands include dambos, floodplains, riparian systems, pans and artificial impoundments (Matiza and Crafter 1994). Zimbabwe receives its rainfall mainly between November to April (usually the cropping season) and annual amounts decrease from east to west with the eastern highlands receiving approximately 1 050 mm, whereas the dry western and southern parts receive less than 500 mm (Mamombe et al. 2017). According to the Parks and Wildlife Act of Zimbabwe, approximately 13% of Zimbabwean land is under PAs, and Hwange National Park (HNP) is the largest PA (14 651 km^2). HNP receives approximately 600 mm per year of rainfall and is characterised by well-drained Kalahari sands in the south and shallow basalt clay in the north. Hwange NP includes a system of approximately 23 000 mostly shallow seasonal pans (Godfrey 1992) that are part of wider system of pans in southern Africa (Goudie and Wells 1995). Some of the pans in HNP have boreholes powered by diesel, solar pumps or wind to supply water to wildlife during the dry season. There are also dams (artificial impoundments) illustrated in Figure 1.

Species' ecological characteristics, life history traits and phylogenetic data

We reviewed various studies to document characteristics and life history traits for waterbird species that have been recorded in Zimbabwe. We categorised species according to their mating system, level of social nesting, whether or not it breeds throughout the year, level of social foraging, migration type (Supplementary Table S1). Where species are documented as having different breeding times within the southern region (Ndlovu et al. 2017), we considered the patterns of the majority of the population, as documented in (Hockey et al. 2005). We also categorised the species into three functional guilds, as described below in this paragraph (Supplementary Table S2). We determined a species' index of diet variety by counting the number of taxa it consumed from literature. We reviewed species' averages for clutch size, incubation period (days), fledging time (days), generation length (years) and body mass (grams). We also searched literature to find whether or not each species was under immediate threat of habitat change, habitat disturbance, hunting and diseases. We made a case-by-case simplification of the known functional guilds of waterbirds by considering the components of their diet and behaviour, while foraging; a method modified from Liordos (2010). Eventually, we had three broad categories of waterbirds: wildfowl (largely feeding on vegetation matter and very small invertebrates, while on the surface swimming or close to the water), waders (those that utilise mostly the shores foraging on crustaceans and small invertebrates, while walking and probing), and herons, ibis, storks, egrets and other piscivores (HISE), including members from the herons, ibises, storks, egrets and other piscivores that rely on large invertebrates, amphibians and fish). We also downloaded the phylogenetic data for the set of our waterbird species from http://birdtree.org/subsets/ and used *TreeAnnotator* (Bouckaert et al. 2014) to determine our consensus phylogenetic tree. We determined each species' global trend by reviewing its status according to the BirdLife International website at www.datazone.birdlife.org/species, the same information is also found on the International Union for Conservation of Nature (IUCN) website.

Waterbird counts and rainfall records at the local scale

We used waterbird counts in HNP that were coordinated by Wetlands International and BirdLife Zimbabwe between 1992 and 2017. These waterbird counts were conducted during the January to February period (wet season) and in July (dry season) each year. The waterbirds were counted by teams that had between three and six people, using binoculars (magnification of 8 × 40 mm or better) and telescopes. BirdLife Zimbabwe assisted in ensuring that each team had at least two experienced observers to minimise errors in species identification and counting of the waterbirds. Total counts were conducted on the pans in HNP. However, particular sections were sampled consistently each time during the counts for the Detema, Inyantue, Leasha and Mandavu Dams (Figure 1). Counting was done in the morning hours (between 06:00 and 10:30) and late afternoon (between 15:00 and 18:00), when waterbirds were actively feeding and hence were more likely to be overserved. Information included in these data was the date, site name, species name and associated numbers.

We gathered rainfall data from all the gauging station inside HNP. We then averaged the accumulated rainfall (across the gauging stations) received between the onset of rains the preceding year to February (for the wet season); and from the onset of rains the preceding year up to July (for the dry season). The dry season rainfall record was therefore a close proxy of the total rainfall received in the park for the cropping season.

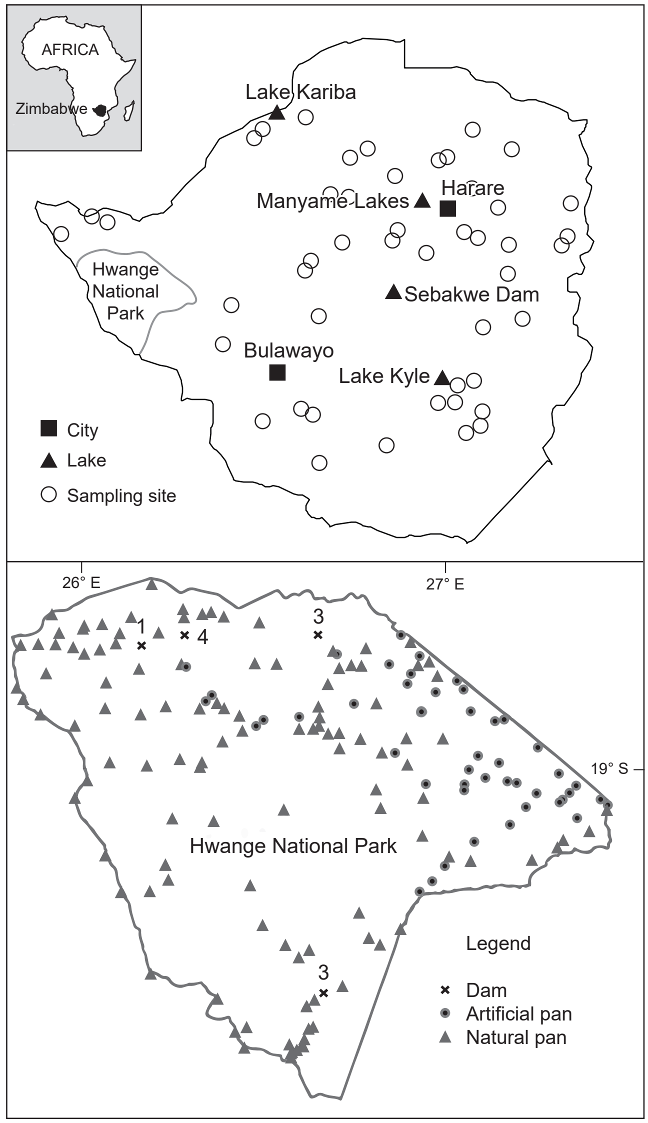

Figure 1: The sites that were used for waterbirds population trends analysis in Zimbabwe (between 1992 and 2017) and the pans inside Hwange National park. Dams demarcated by 1 to 4 are Detema, Inyantue, Leasha and Mandavu, respectively

Waterbird counts and rainfall records at the Zimbabwean scale

Like in the HNP, we also used data from the Zimbabwe national waterbird counts coordinated by Wetlands International and BirdLife Zimbabwe between 1992 and 2017 (for the wet and dry seasons during similar time of the day). These counts were conducted on lakes, river sections, dams and impoundments of various sizes that are presented in Figure 1 and the GPS positions listed in Supplementary Table S3. For large dams and lakes, waterbird counts were mostly done on the shores and its vicinity, because individuals farther into the water bodies were likely to be missed. These large waterbodies had fixed sections where total counts were conducted. For example, the Mteri Dam in Masvingo had seven sections where waterbird counts were done. We used sites where waterbird counts were done consistently across the study period. We believe these data are usable for the intended analysis, because we have participated in the counting teams since 2006 and an analysis was previously used to determine factors behind waterbird trends on artificial lakes in Zimbabwe (Mundava et al. 2012).

Because not all the sites we used had rain gauges with consistent data covering our study period, we resorted to using monthly rainfall averages, as provided on the World Bank website (http://sdwebx.worldbank.org/climateportal/index.cfm). Similar to HNP, we then calculated the accumulated rainfall received between the onset of rains the preceding year to February (for the wet season); and from the onset of rains the preceding year up to July (for the dry season).

Analysis

Determination of trends

We are aware that rainfall has a strong influence on waterbirds abundance. Accordingly, we performed Generalised Additive Models (GAMs) in which we modelled trends for species abundance as a smooth, non-linear function of time, and we used rainfall as a covariate. The GAMs were therefore used to determine trends in abundance for each species for the wet and dry season, and at park and national scales (HNP and Zimbabwe, respectively). We checked the significance of time on the smoothed trend of species abundance in the GAM output ($p < 0.05$) and visually inspected its associated plots. We categorised trends as 'increasing' if time was significant and the predicted values (including the confidence interval) changed from negative to positive across the 25-year period (i.e. crossing the $y = 0$ line once, as illustrated in Appendix Figure 1A and 1B). Our 'stable' category included instances when time was not significant, i.e. predicted trends followed the $y = 0$ line, or when they were cyclic (i.e. crossing the $y = 0$ several times, Appendix Figure 1C and 1D, respectively). We categorised trends with significant ($p < 0.05$) or marginally significant effect ($p < 0.1$) of time that were increasing yet the confidence interval of the predictions largely covered the $y = 0$ line as 'insignificantly increasing' (Appendix Figure 1E), whereas those declining in like fashion as 'insignificantly decreasing' (Appendix Figure 1F). The 'decreasing' category included trends with significant effect of time and the predicted values of population trend (and associated confidence intervals) changing from positive to negative (Appendix Figure 1G and 1H).

Indices from life history traits

In order to reduce the variables in our analysis, we performed two multiple component analyses (MCAs). The first MCA had traits related to species breeding and biology (mating system, nest grouping, whether or not it breeds throughout the year, clutch size, incubation period, fledging period, generation length, body mass and diet guild). The second MCA included threats to the species (habitat change, habitat disturbance, hunting and diseases). We used the dudi-hillsmith procedure for the MCAs, which made it possible to combine both categorical and continuous variables (Thioulouse et al. 2018) through the *ade4* package (Dray et al. 2007). We then inspected the axis of each MCA output, and interpreted the main components represented by these MCAs and renamed the axis accordingly, as presented in Supplementary Tables S4 and S5. For example, the HabChan.Dist variable represented species that were mostly documented to be affected by habitat disturbances (high values) versus those affected by habitat change (low values), as illustrated in Supplementary Table S5. We retained the renamed axis values for each species and included them in our global dataset. In order to illustrate the relative influence of species' anthropogenic uses at various scales in the PCAs, we employed their scale of use by humans (local or international), because we had information from people in and around HNP (Uchiyama and Radin 2009) and elsewhere from literature. We standardised the renamed PCA variables, so that the lowest value was zero, to facilitate easy interpretation of results, and we log-transformed species body mass.

Models

We tested for association between species' temporal population trends at national and park level (for the wet and dry season counts) and those between population trends and functional guilds across the waterbird migration status using Fisher`s exact tests. Our set of independent variables were species feeding guild, global trend, use level, Colonial-Solitary, Hunting-Diseases, Small-Large Parties, index of diet variety, and the interaction of these variables with body mass. Because we targeted to explore the drivers that are associated with species decline, we recategorised the species' temporal population trend modalities 'stable', 'insignificant decrease', 'insignificant increase' and 'increasing' as 'Not decreasing'. We tested for the strength of phylogenetic relationships when we built models relating species trends to our set of independent variables using the Phylogenetic generalised least squares (PGLS) (Veltri et al. 2011). For all PGLS models lambda was close to zero (<0.001), which implied very weak influence of species' phylogeny relatedness on the waterbird trends. We therefore resorted to using standard logistic regressions. We modelled the probability of a species to decrease (versus not decreasing) for resident and migrant waterbirds at the Zimbabwe scale for the two seasons (wet and dry) given our set of independent variables using binomial logistic regressions. However, at the HNP level, there were few species with decreasing population trends in the wet and dry seasons (one and five, respectively) and would not allow for any statistical modelling of the probability of decreasing. We therefore used logistic regressions to model the probability of increasing versus stable (here the ‘stable’ modality also included those with ‘insignificant increase’ and ‘insignificant decrease’). For each case, we selected the best model, based on the Akaike Information Criterion (AIC) using the stepwise algorithms through the stepAIC function in the *MASS* package (Woodhouse 2001). All analyses were done with the R statistical package (R Development Core Team 2017).

Results

For the period under study, 132 waterbird species were recorded in Zimbabwe. After removing the ‘rare’ species and those with annual averages below three, we present population trends for 86 species consisting of 23 wildfowl species, 24 waders and 39 HISE (Supplementary Table S2). From these 86 species, 50% of them are used for food, medicine, arts and pets by people at local scales; and 67% (n = 58) have solitary nesting systems. Overall, the population trends across the three waterbird guilds in HNP pans showed upward trends, whereas those in water bodies in the rest of Zimbabwe had downward trends across the study period (Figure 2). During the wet season in HNP, the Cape Teal *Anas capensis* was the only species with a significantly decreasing population trend in HNP, whereas 62.3% (n = 33) had stable and 35.8% (n = 19) were significantly increasing. However, on the Zimbabwean scale, 34.9% (n = 30) had significantly decreasing population trends; 58.1% (n = 50) were stable and only 7% (n = 6) were significantly increasing. In our data, 63% of species with a BirdLife International declining status were also significantly declining in Zimbabwe in both the wet and dry seasons.

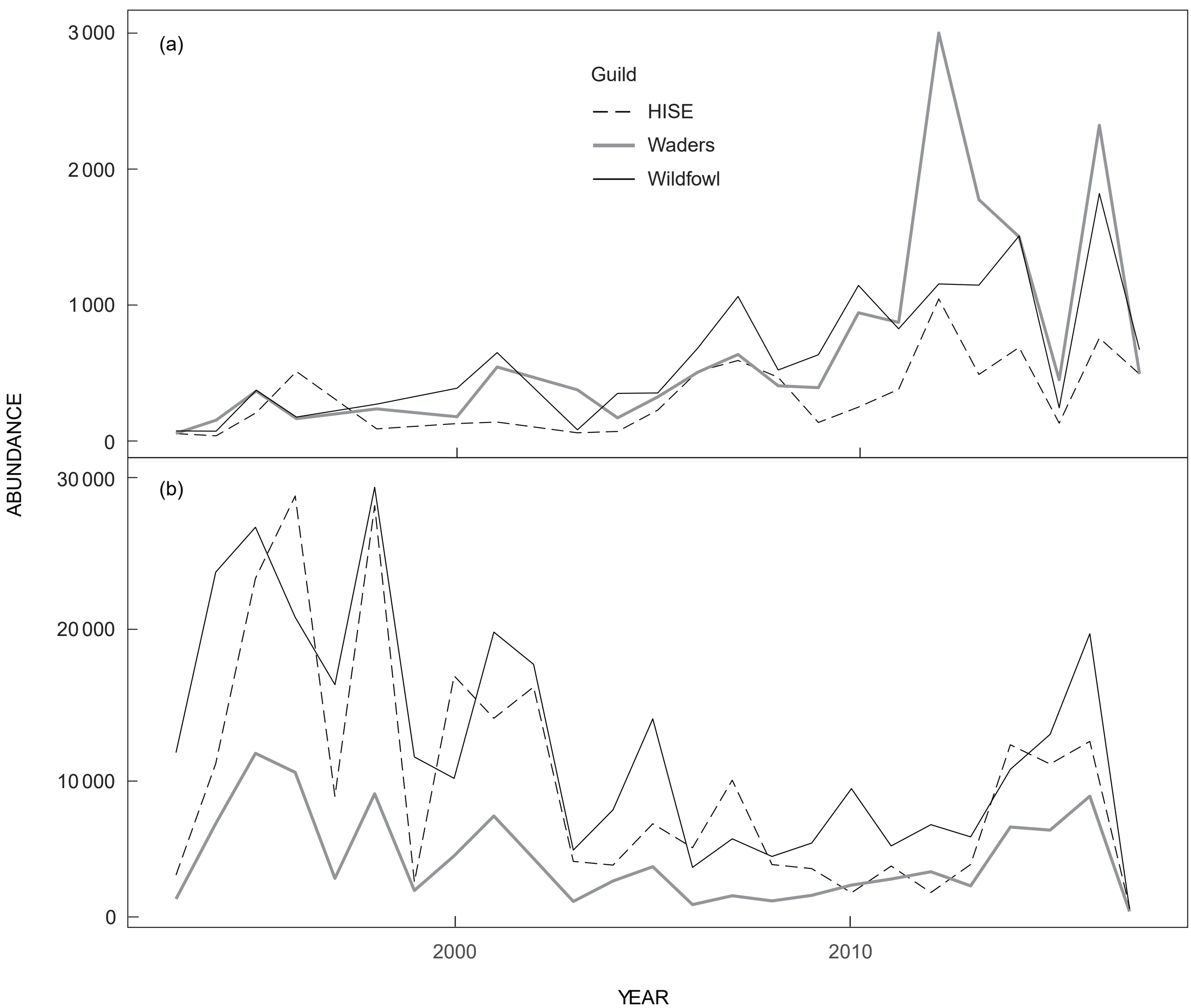

Figure 2: The trends of total numbers of waterbirds counted in each guild (abundance) at the (a) Hwange National Park and (b) Zimbabwe scale per year between 1992 and 2017. HISE = herons, ibis, storks, egrets and other piscivores

Waterbird population trends across migration types and feeding guilds

The distribution of waterbird species across migration status and functional guilds is presented in Table 1. We found no association in population trends between HNP and Zimbabwe in both the wet and dry season ($p > 0.05$ in all cases). There was also no association between migration types and population trends in HNP for both the wet and seasons; and at the Zimbabwean scale during the dry season ($p > 0.05$ in all cases). However, at the Zimbabwean scale, the wet season waterbird population trends were significantly associated with migration type (Fisher's exact test, $p = 0.022$); with greater proportions of the Afrotropical (60%) and resident (63%) species having stable status than the Palearctic migrants (33%). There was also no significant association between population trends and functional guilds for HNP and Zimbabwe across seasons.

Determinants of trends across scales, season and migration status

HNP scale

For the resident waterbirds during the wet season, the probability for species to have increasing population trends were higher on average for heavier species and those with local uses when, compared with those with mostly international uses (Figure 3; Table 2). A striking exception is that lighter waterbirds that are used mostly internationally have higher probability of having increasing population trends in HNP. On average, the probability for species to have increasing population trends decreased with increasing documented levels of threats by habitat disturbances. The probability of a species to have increasing population trends was higher for waterbirds with colonial nesting system, compared with the solitary ones. The probability of having increasing population trends decreased with increasing species body mass for the migratory species.

For residents during the dry season, species that are more susceptible to hunting have greater chances of having increasing population trends, compared with those more susceptible to diseases (Table 2). The heavier species that are more susceptible to habitat disturbances have higher probabilities of having increasing population trends, compared with the lighter ones.

Zimbabwean scale

For resident species during the wet season, HISE and wildfowl species had higher probabilities of population declines when, compared with waders. In addition, the species with uses documented at the international scale were more likely to have decreasing population trends when, compared with those only used at local scales. For species that are susceptible to threats by hunting, smaller species had greater likelihoods of population declines than larger ones (Figure 4). However, the species that are more susceptible to diseases had similar average probabilities across the range of body mass, although for those species that are more susceptible to habitat disturbance, smaller

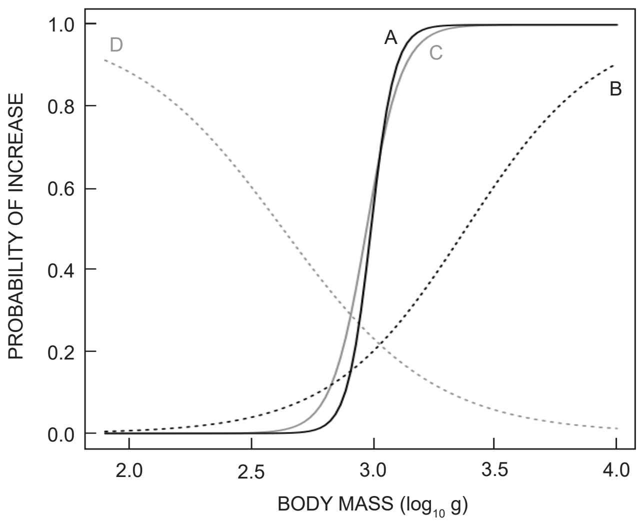

Figure 3: The predicted probability of increasing population trends, as opposed to stable trends, for waterbirds species in HNP using wet season data from 1992 to 2017. The full black line (a) is the predicted probability curve for species mostly used locally in Zimbabwe that also have high susceptibility to habitat disturbances. The dotted black line (b) is for species mostly used internationally (on the flyway or region) and with high susceptibility to habitat disturbances. The full grey line (c) is the predicted probability curve for species mostly used locally in Zimbabwe that have low susceptibility to habitat disturbances. The dotted grey line (d) is for species mostly used internationally and with low susceptibility to habitat disturbances. Refer to Table 2 for model coefficient values. Parameters for other variables were fixed at their median value

Table 1: The trends for waterbird species in HNP and Zimbabwe during the wet and dry seasons across migration types and functional guilds. HISE represent herons, ibis, storks, egrets and other piscivores

Scale	Season	Trend	Migration type			Functional guild		
			Afrotropical	Palaearctic	Resident	HISE	Waders	Wildfowl
HNP	Wet	Increasing	6	3	10	5	8	6
		Stable	6	7	20	17	9	7
	Dry	Increasing	1	0	11	8	2	2
		Stable	8	3	10	6	8	7
Zimbabwe	Wet	Decreasing	4	8	18	16	9	5
		Not decreasing	16	4	36	24	15	17
	Dry	Decreasing	5	0	14	10	2	7
		Not decreasing	12	9	36	26	18	13

Table 2: Variables selected in logistic regressions and the magnitude of their influence on waterbird population trends in HNP (probability of increasing) and in Zimbabwe (probability of decreasing) across the seasons. HNP = Hwange National Park; SE = standard error; 'HabChan. Dist' = gradient of those without threats from habitat change to those with habitat disturbance

Status	Season	Candidate variable	HNP trends			Zimbabwe trends		
			Variable estimate	SE	*p* value	Variable estimate	SE	*p* value
Resident	Wet	Intercept	40.1	19.7	0.042	5.0	7.5	0.50
		HabChan.Dist	−37.7	18.2	0.038	−7.8	5.9	0.188
		Colonial-Solitary	0.8	0.5	0.091	–	–	–
		Log(Body mass)	−15.1	7.2	0.036	−2.7	2.7	0.31
		Use level (Local)	−49.6	22.7	0.029	−2.6	1.1	0.016
		Hunting-Diseases	2.6	1.4	0.078	10.7	5.2	0.039
		log(Body mass) × HabChan.Dist	12.5	6.1	0.04	3.8	2.1	0.076
		log(Body mass) × Use level (Local)	17.1	7.8	0.029	–	–	–
		log(Body mass) × Hunting-Diseases	–	–		−4.1	1.9	
		Global trend (Not Declining)	–	–		2.4	1.1	0.036
		Guild:Waders	–	–		−2.5	1.4	0.071
		Guild:Wildfowl	–	–		0.9	1.2	0.462
	Dry	Intercept	24.1	14.5	0.096	2.5	0.9	
		HabChan.Dist	−22.5	14.0	0.109	−1.5	0.8	
		log(Body mass)	−7.9	5.2	0.133	–	–	
		Hunting-Diseases	−3.1	1.7	0.069	–	–	
		log(Body mass) × HabChan.Dist	8.2	5.3	0.12	–	–	
Migrants	Wet	Intercept	4.5	2.7		8.5	6.5	0.19
		Log (Body mass)	−2.3	1.3		−5.0	2.8	0.077
		Hunting-Diseases	–	–		6.3	3.8	0.102
		Guild:Waders	–	–		−1.8	1.6	0.25
		Guild:Wildfowl	–	–		−12.5	5.5	0.023
		Colonial-Solitary	–	–		−3.8	2.7	0.157
		log(Body mass) × Colonial-Solitary	–	–		2.7	1.3	0.041
		log(Body mass) × Hunting-Diseases	–	–		−3.2	1.8	0.066

ones seem more likely to have decreasing trends. For resident species during the dry season, species likelihood of population declines significantly increased with increasing susceptibility to threats from habitat disturbance.

Migrant waders and HISE species during the wet season had greater probabilities of having decreasing population trends, compared with wildfowl. The likelihood of a species having decreasing population trends decreased with increasing species body mass, more so for solitary nesters than colonial ones. For species that are mostly threatened by diseases, larger birds had mildly higher probabilities of decreasing when, compared with smaller ones.

Discussion

Most traits, except body mass, do not significantly account for the observed trends at both HNP and Zimbabwean scales. Although we had predicted that the wet season Zimbabwean waterbird trends would be reflective of global pressures more than local ones, our results suggest that species with smaller body mass had steeper declining population trends at the Zimbabwean scale and larger species had more increasing trends in HNP. Body mass is known to be a strong correlate of many life history traits, such as clutch size, fledging period (Blumstein 2006, Végvári et al. 2015), and growth is slower for large species (Harvey 1997). The importance of body mass may explain why most of our models only retained this variable, even after minimising covariations between variables in our analyses. Body mass in wildfowl species can also have direct implications on species' susceptibility to hunting, with larger ones more likely to be targeted (Freese 1997, Uchiyama and Radin 2009). Our results show that in HNP, wildfowl population trends increase during the wet season (where no hunting is allowed in the PA), but the trends of the most abundant species elsewhere in Zimbabwe (the majority of records outside PAs) are declining i.e. where humans can access them or prime habitat can be altered.

In line with our main hypothesis that HNP remains a 'duck factory', our results show that conditions inside HNP are still attractive to waterbirds, because most population trends are increasing, whereas decreasing elsewhere in Zimbabwe. Hence, despite the wetland habitat shifts in HNP associated with pumping and increasing drought frequency (Chamaillé-Jammes et al. 2007), waterbird species' trends suggest that this PA is still holding its capacity as a waterbird breeding area (Godfrey 1992). Although our study did not focus on site fidelity by migrating waterbirds (Yohannes et al. 2007), the increasing trends of both Afrotropical and Palaearctic migrants suggest that HNP is an attractive site for them, compared with most wetlands elsewhere in Zimbabwe. Having illustrated the importance of HNP to favourable waterbird populations, conservationists are urged to continue monitoring the waterbird trends and ensure that the local conditions in this protected area do not deteriorate. Of interest will be the management of pumping at pans where large mammals and megaherbivores are currently causing vegetation

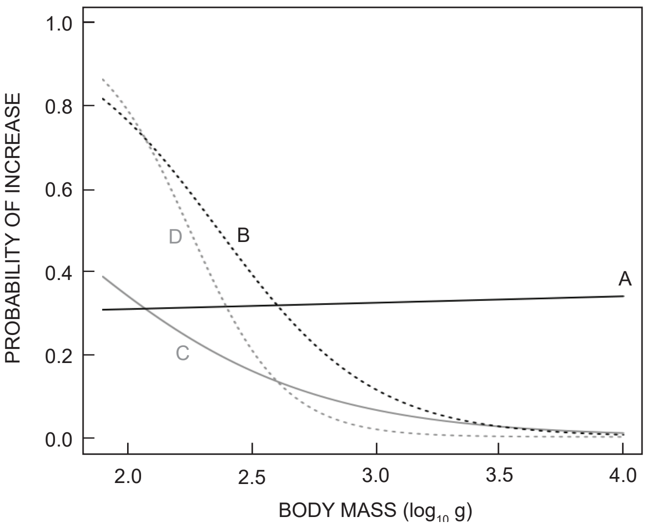

Figure 4: The predicted probability of decreasing population trends (as opposed to not decreasing) for waterbirds species in Zimbabwe using data from 1992 to 2017, as a function of their susceptibility to threats of habitat disturbance, hunting and diseases. The full black line (a) is the curve for species with high susceptibility to habitat disturbance and diseases, but with low susceptibility to hunting. The dotted black line (b) is for species with high susceptibility to habitat disturbance and hunting, but low susceptibility to diseases. The full grey line (c) is the curve for species with low susceptibility to habitat disturbance and hunting, but high susceptibility to diseases. The dotted grey line (d) is for species with low susceptibility to habitat disturbances and diseases, but highly susceptible to hunting. The curves for HISE and waders will be similar, but with different intercepts. Parameters for other variables were fixed at their median value. The level of use was fixed at 'International'. Refer to Table 2 for model coefficient values

damage around them (Chamaillé-Jammes et al. 2009, 2016). This vegetation damage may escalate to thresholds that can negatively affect waterbird nesting (Raeside et al. 2007) and consequently influence trends, but we have no indication that this is the case currently. It is worth noting that the only species, Cape Teal *Anas capensis,* that has a decreasing population trend during the wet season is a dry season breeder (June) in the area (Cumming et al. 2016), and could be affected by high concentration of large herbivores around pans. Indeed, most wildfowl usually nest close to the water (Jungers et al. 2015). It may also be the case for two species Hottentot Teal *Anas hottentota,* and White-backed Duck *Thalassornis leuconotus* that have breeding periods that extends into the dry season, because they both have non-significant decreasing trends (Supplementary Table S2). The low densities of large mammals during the wet season certainly minimise trampling risk for summer breeding species.

Colonial resident waterbirds had more increasing population trends in HNP in comparison to the solitary ones. This suggests that for these resident species, conditions for colonial breeding are still favourable inside HNP (e.g. protection from hunting and disturbances by humans) when, compared with most areas elsewhere. Baker et al. (2015) highlighted the importance of trees in or around wetlands for successful breeding of colonial waterbirds, and habitat change induced by high large mammal pressure do not seem to affect them, although it is known that most members of HISE (the most common colonial waterbirds), can nest some distance away from the water edge (Zanchetta et al. 2016). A finer study may be required to identify species or functional guilds that may be more susceptible to modifications around pans (including the solitary ones) and those that would benefit the most. Complementary studies focusing on the nesting of waterbirds around pans and far away are also required, especially for the late rain season or dry season breeders.

Our results show that the probability of decreasing was high for HISE and wildfowl species during the wet season, compared with waders at the Zimbabwean scale. The HISE guild has mostly carnivorous species feeding on items, such as amphibians, wetland insects and fish. These prey items have been declining in some of the wetlands in Zimbabwe (Ramirez 2006; Kyndt et al. 2016; World Economic Forum 2016), as a result of overexploitation, human disturbances and reduction in wetlands (Environmental Management Agency 2012; Mutisi and Nhamo 2015). Wildfowl are fairly well used by people in Zimbabwe (Uchiyama and Radin 2009), but also susceptible to wetland changes. In addition, in line with our prediction on possible trends of waterbirds that are eaten locally, the small species that are susceptible to hunting have greater probabilities of declining at the Zimbabwean scale. However, the increasing population trends of hunting-prone waterbird species in HNP could be indicative of the high levels of protection inside this IBA (Childes and Mundy 2001). We think that the land use changes and associated disturbances occurring in wetlands across Zimbabwe are the also contributing to the general decreasing trends of the waterbirds, being amplified by challenges in managing wetland resources for agriculture in semiarid climates (Scoones and Cousins 1994).

Our data have shown that 63% of species designated as having declining trends by the IUCN also have decreasing trends at the Zimbabwean scale during the wet season. This is in line with our expectation that during the wet season in Zimbabwe, waterbird trends would reflect global pressure more than local ones. Our findings indeed suggest that the trends at the Zimbabwean scale are indicative of processes occurring on the flyway, particularly for the migratory species (Kirby et al. 2008). We have also shown that for a given body mass, the likelihood of decreasing population trends were higher for species used at international scales, compared with those used at local scales. The constraints faced by species used at international scales could be multifaceted, and therefore the signature of such pressures could be greater when, compared with those used on local scales. For example Hancock et al. (2010) illustrate that storks can be used for medicine in central Africa, but they can also be used in arts or even food elsewhere (Green and Elmberg 2014). Contrary to our prediction that waterbird guilds with broader diet niches respond at slower rates to habitat change and disturbance when, compared with guilds with narrower diet niches, we did not find any significant relationship between waterbird diet spectrum and population trends.

In conclusion, our study has revealed that waterbird population trends in HNP are mostly stable or increasing, whereas those at the Zimbabwean scale are decreasing. Most of the pressures for birds are large scale ones: the international uses of waterbirds and habitat disturbances. This suggests that threats to waterbirds are major determinants of trends rather than most of their ecological and life history traits. We advocate for the continual monitoring of local and national trends, as well as vegetation around pans in the face of increasing large mammal densities. Such analysis could be conducted for all PAs in the southern African region to reveal trends at larger scales, and mostly help in shaping new wetland conservation policies.

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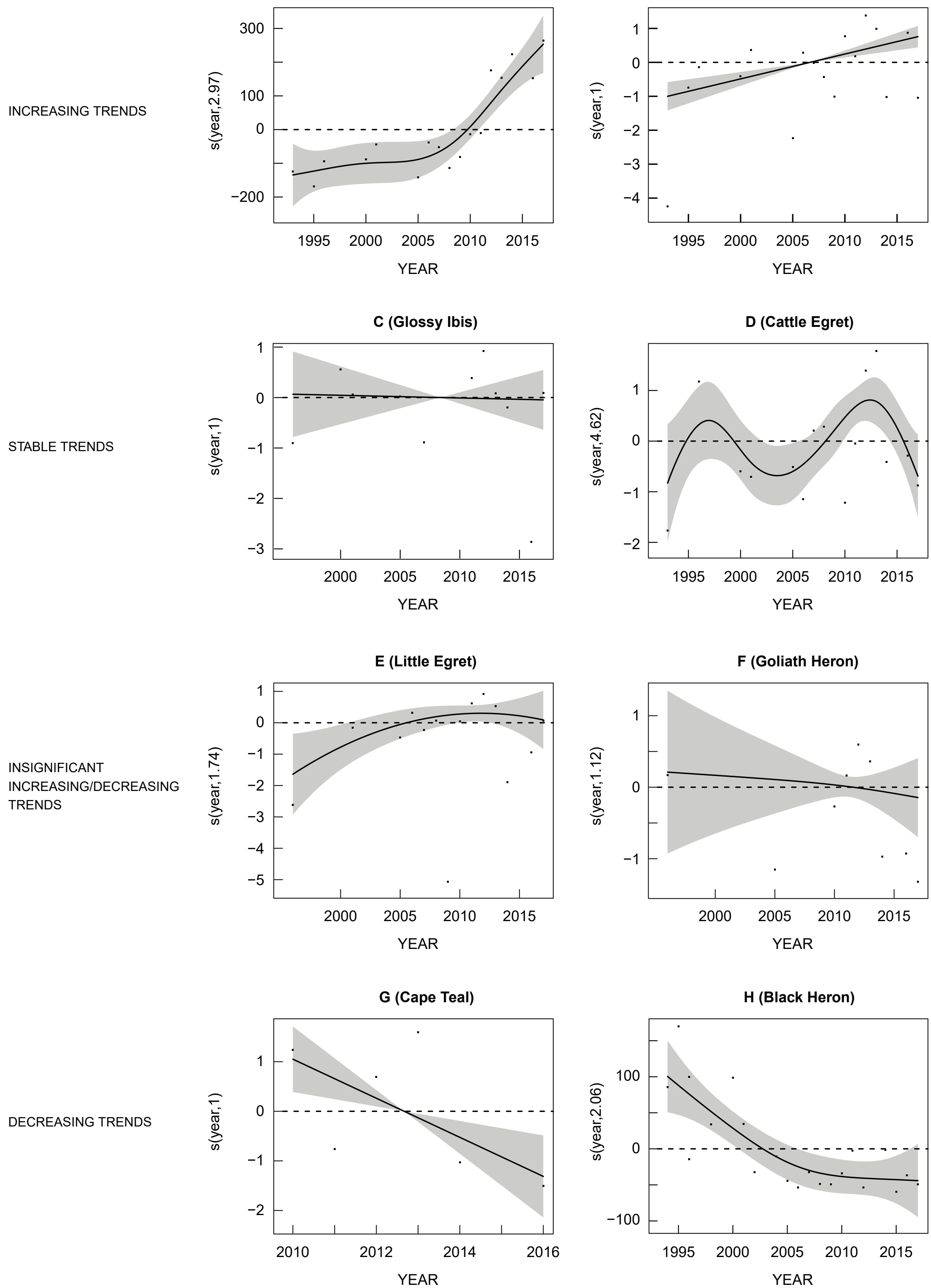
Appendix



Appendix Figure 1: Examples of plots from Generalised Additive Models that were used to categorise waterbird population trends. The plots were constructed from the January waterbird counts, plots A to G were drawn from the HNP data and plot H from the Zimbabwean dataset