Quantifying Shoebill (*Balaeniceps rex*) habitat suitability in the Bangweulu Wetlands, Zambia

Honours Thesis

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Abstract

A quantitative analysis of suitable habitat for the Shoebill (*Balaeniceps rex*), a large waterbird confined to African swamps, was conducted by using a combination of aerial photographs and a previously determined habitat suitability model from the Bangweulu Wetlands, Zambia. The Shoebill is considered *Vulnerable* on the IUCN red list, but there are no pre-existing quantitative data on the composition of suitable habitat for this species. Both univariate and multivariate analyses revealed that non-wetland habitats as well as non-vegetated wetland habitats have low suitability compared to vegetated wetland habitats. Notably, reeds correlated significantly and positively with suitability ($r_s = 0.338$, $p < 0.001$). We found little support for the hypothesis that floating vegetation is highly suitable for Shoebills, but the analysis for this habitat may have suffered as a result of confounding factors. The relationship between flooded grassland and suitability was highly variable and was not significant ($r_s = 0.009$, $p = 0.807$). In contrast, dry grassland correlated positively with suitability ($r_s = 0.289$, $p < 0.001$), but its suitability scores were generally much lower than for flooded grassland. Quantitative data on Shoebill habitat suitability will be useful for future Shoebill population surveys, and will improve our ability to make informed decisions regarding its conservation.

Introduction

The Shoebill (*Balaeniceps rex*) is a large (120 - 140 cm), charismatic and little-known bird confined to large African swamps. It has a broad but disjunct distribution from the Sudd in South Sudan, through East and Central Africa, and south to the Bangweulu Wetlands in Zambia. Globally it is classified as *Vulnerable* (BirdLife International 2013a). Its total population is thought to be relatively small, conservatively estimated at 5 000-8 000 individuals (T. Dodman *in litt.* 2002 to Wetlands International 2002), although most population estimates are from the 1980s. In addition, it faces numerous threats, including hunting, capture for the illegal wild bird trade (Baker 1996, Roxburgh et al. 2006), nesting disturbance (Briggs 2007), fires, and, perhaps most notably, habitat modification due to increasing land-use pressure from local people (Roxburgh et al. 2006; Dinesen and Baker 2006). As a result, populations at several sites, including the Bangweulu Wetlands, are believed to be in decline (BirdLife International 2013a). Despite its threatened status, there are important gaps in our knowledge of Shoebill ecology. Besides updating the population estimates, there is also a need for a quantitative analysis of Shoebill habitat preference.

Shoebills occur in permanent wetlands that undergo seasonal flooding and usually comprise various grasses (e.g. *Miscanthidium*) and stands of papyrus (*Cyperus papyrus*) and reeds (e.g. *Phragmites* and *Typha*; Hancock et al. 1992). Shoebill habitat is also characterised by large expanses of floating vegetation, which they use when foraging (Guillet 1979). They avoid very tall and dense stands of vegetation as these restrict access to water and are unsuitable for foraging, and may reduce the birds' ability to take flight (Guillet 1979; Hancock et al. 1992). Presumably for this reason, Vande Weghe (1981; in Hancock et al. 1992) noted that Shoebills generally avoid stands of pure papyrus in the Akagera National Park in Rwanda. Further, Shoebills occur in large numbers in swamps lacking papyrus, such as in the Malagarasi in Tanzania (Dinesen and Baker 2006). Nevertheless, papyrus and tall reeds are important for Shoebills as they provide shelter from predators when the birds are foraging and breeding (Guillet 1979).

Knowledge of the habitat preferences of Shoebills will be important for their conservation. For example, Howard and Aspinall (1984) estimated the Shoebill population size in the Bangweulu Wetlands using an aerial census technique, but only sampled a portion of the total area of the swamps, noting that estimating the population size for the entire area could not be achieved due to a lack of knowledge of the extent of suitable habitat in the non-surveyed areas. The current lack of quantitative data means that it is difficult to evaluate the relative importance of the various vegetation types for Shoebills. Among other things, such data would allow for more efficient and complete aerial censuses of Shoebill populations that take a stratified sampling approach and thus ensure that most or all areas of suitable habitat are covered.

The vast Bangweulu Wetlands in north-eastern Zambia are a Ramsar site and an Important Bird Area (IBA ZM028; Birdlife International 2013b). They harbour a substantial population of Shoebills, although the size of the population is uncertain. Initial estimates based on aerial surveys suggested a population of between 200 and 300 individuals (Howard and Aspinall 1984; Kamweneshe et al. 2003). In a more recent analysis, Roxburgh and Buchanan (2010) provided a conservative population size estimate of 1 296 individuals. Their approach was distinct in that it extrapolated its estimates over a larger area than previous surveys. This was achieved by developing a spatial model of Shoebill habitat suitability for the entire IBA, which allowed the authors to estimate Shoebill numbers for the swamps as a whole, rather than just the survey area. However, the Roxburgh and Buchanan (2010) model is based on satellite imagery data, meaning that it provides information only on the spatial distribution of suitable habitat in the swamps. It does not, however, inform us about the habitat composition of areas classified as either suitable or unsuitable.

In April 2011, surveys of the entire Bangweulu IBA produced a large set of aerial, low-altitude habitat photographs of the swamps (Viljoen 2011). These photographs provided the opportunity to quantitatively assess the suitability of different habitat types for Shoebills based on predictions made by Roxburgh and Buchanan (2010). The objectives of this study are therefore to:

1. Classify and quantify the habitat in the Bangweulu Wetlands based on the 2011 aerial survey photographs

2. Test whether there is a difference in habitats between areas that are suitable and areas that are unsuitable for Shoebills according to the model of Roxburgh and Buchanan (2010)

The Bangweulu Wetlands contain all of the habitat types known to be associated with the presence of Shoebills, including large mats of floating vegetation and vast areas of seasonally inundated grassland (Guillet 1979).Here we predict that wetland habitats (e.g. floating vegetation, papyrus, reeds, etc.) will have higher suitability than non-wetland habitats (e.g. grassland and woodland). More specifically, it is hypothesized that, among wetland habitats, (i) very open, watery habitats will have low suitability, (ii) floating vegetation will be highly suitable , (iii) papyrus will have relatively low to intermediate suitability, although its association with floating vegetation in deeper water may result in higher suitability estimates, and (iv) flooded grassland will have high suitability, but will likely show a high degree of variation in suitability due to the high levels of inter-annual variation in timing and extent of flooding in the swamps, combined with the temporally disjunct nature of the analysis.

Methods

Overview

The study used habitat photographs (n = 1 507) from an aerial survey of the Bangweulu Wetlands conducted in early April 2011 (Viljoen 2011). The photographs were used to classify habitat types in the wetlands. For each photograph the habitat composition was noted, and the percentage cover of each habitat estimated by eye. Also for each photograph, mean suitability for Shoebills was computed based on the suitability model developed by Roxburgh and Buchanan (2010). These variables were compared using both univariate and multivariate statistical approaches. The former assessed correlations between proportion of each habitat and suitability. The latter assessed how suitability varied in relation to different 'habitat mixes' comprising commonly associated habitats.

Study area

The Bangweulu Wetlands in north-eastern Zambia (approximately 11°03′–12°20′ S, 29°37′–30°50′ E) is a 1 284 000 ha area comprising a matrix of grassland, woodland, and seasonally flooded wetland habitats. It is a Ramsar site and an Important Bird Area (IBA ZM028; Birdlife International 2013b), and supports the most southerly known resident breeding population of Shoebills. Water levels vary throughout the year, peaking in late summer (February-March) and being at their lowest around

November, and can also vary hugely between years depending on rainfall. Large areas of permanent wetland are present year-round.

Aerial survey photographs

An aerial survey of the Bangweulu Wetlands, conducted between 20 and 25 April 2011 (Viljoen 2011), produced a total of 2 042 oblique, geo-rectified digital photographs of habitat types in the Bangweulu Wetlands. Of these, 1 507 photographs were suitable for analysis in this study, and were chosen based on their angle and location (see below).

Habitat classification and quantification

Ten different habitat types were defined for the Bangweulu Wetlands, based on observations on the ground and inspection of the photographs. An additional category was created for habitats that were not possible to identify from the aerial photographs (Table 1). Most habitats could be identified with certainty, however, distinguishing between flooded grassland and floating vegetation was challenging. If the vegetation was upright, and if some water could be seen within it, it was identified as flooded grassland. Alternatively, floating vegetation was identified by a lack of upright vegetation and a lack of water between the vegetation.

All habitats were defined in each photograph, and their extent of cover estimated to the nearest five or, more usually, ten percent. The classification and estimations were done by one person (SM) to avoid observer biases. Only photographs directed sideways out of the aircraft were used, as these were fairly consistent in angle (judged by the consistency of the position of the horizon in the photograph; see Figure 1). To account for some of the distortion due to the obliqueness of the photographs, only the bottom half of each photograph was used in the analysis. When photographs were identical or near-identical, i.e. very closely spaced, only one was used in order to avoid pseudo-replication.

Quantifying habitat suitability

For each photograph the mean likelihood of occurrence of Shoebills (habitat suitability) was calculated based on the suitability model presented in Roxburgh and Buchanan (2010). They employed maximum entropy modelling to devise the suitability estimates based on bandwidth data from a Landsat 7 ETM image (spatial resolution of 28.5 m) of the Bangweulu Wetlands, taken on 6 May 2002, and an aerial survey of Shoebills in the swamps conducted in July 2006. The authors also converted suitability into a binary measure, but for this analysis the raw, continuous model output was used.

Table 1: Habitat classification and descriptions

Habitat type	Description
Open water	Flooded areas including rivers and floodplain without any vegetation (excluding waterlilies)
Overgrown water	Open water with emergent vegetation that could not be attributed to any particular vegetation type
Reeds	Reedy vegetation (mainly *Phragmites* spp. and *Typha* spp.)
Papyrus	Papyrus (*Cyperus papyrus*)
Floating vegetation	Mats of vegetation floating on open water
Flooded grassland	Grassy areas with some level of flooding
Grassland	Dry areas covered in grass
Miombo	Miombo woodland (dominated by *Brachystegia* spp.)
Termite mound	Islands of woody vegetation attributable to termite mounds
Settlement	Areas of human habitation

Photographs were taken from the side of the aircraft. The geographical co-ordinates of each photograph represented the position of the aircraft, and thus could not be used to represent the area in the photograph. Consequently, mean suitability was calculated for the area surrounding a point 110 m directly to the east or west of each point for north- and south-running transects, respectively (as photographs were always taken at the right hand side of the aircraft). The appropriate magnitude of the shift was estimated using a trigonometric approach. Assuming each photograph was taken at roughly 110 m above ground level (Viljoen 2011) and at an angle of 60° below horizontal, the central point of each photograph would be roughly 190 m from the aircraft's ground position. However, using the area around this point would include the area above the bottom half of each photograph, which was not considered in the habitat quantification analysis (see above). It was thus necessary to choose a point closer to the aircraft, but not so close that it covered ground that was too close to the aircraft to be in the photograph. Consequently the area surrounding the point at 110 m from the aircraft was used in order to adequately represent the area considered in the habitat analysis of each photograph. Because only east-west shifts were performed, only photographs that were taken on a north or south running line were used.

Figure 1: An example of an aerial photograph of the Bangweulu Wetlands used in the analysis

Mean suitability was calculated for a circular area with a radius of 50 m, at 110 m from the aircraft, which approximated the area considered within each photograph. Over half of each pixel needed to be within the area to be included in the estimation of the mean, and as a result the number of pixels included for each photograph ranged from 8 to 12 (6 498 m^2 to 9 747 m^2).

Statistical analysis

The relationships between habitat proportions and mean suitability were tested using a multiple linear regression analysis. Both the habitat proportion data and mean suitability were arc-sine transformed to better approximate the normal distribution. No interaction terms were included as the aim was to assess the influence of each habitat individually. Model optimization was achieved by successive removal of terms and comparison of resulting Akaike information criterion (AIC) scores. Model validity was assessed through testing for normality of residuals and homoscedasticity by eye.

Relationships between mean suitability and habitat proportions were also tested excluding the zeroes in order to determine the effect of each habitat only when it was present. We used Spearman's rank correlation coefficient to account for non-normally distributed data.

A multivariate approach was used to assess the relationship between commonly associated habitats and suitability. To determine associations between habitats, a detrended correspondence analysis (DCA) was performed on the untransformed, unstandardized habitat proportion matrix, with down-weighting of rare variables. To test the relationship between the DCA axes and mean suitability, the

Table 2: Summary of habitat frequencies and proportions in the set of photographs

Habitat	Frequency	Summed % cover	Mean (SD) % cover
Flooded grassland	678 (45 %)	45225 (30 %)	67 (31)
Grassland	620 (41 %)	39745 (26 %)	64 (29)
Miombo	542 (36 %)	29750 (20 %)	55 (34)
Open water	284 (19 %)	9980 (7 %)	35 (23)
Reeds	254 (17 %)	10250 (7 %)	40 (31)
Papyrus	180 (12 %)	8180 (5 %)	45 (30)
Termite mound	102 (7 %)	1225 (1 %)	12 (6)
Overgrown water	80 (5 %)	3105 (2 %)	39 (26)
Floating vegetation	38 (3 %)	855 (1 %)	23 (15)
Settlement	38 (3 %)	875 (1 %)	23 (20)
Uncertain	22 (1 %)	1510 (1 %)	69 (35)
Total	**1 507**	**150 700**	

method of Bennion et al. (2012) was followed. As there is no reason to assume that the relationship between the ordination space and mean suitability will be linear, a generalized additive model (GAM) using thin-plate splines was used to generate a 2-d function of sample scores on DCA axes one and two. The degree of smoothness in the thin-plate spline was estimated by maximum likelihood. GAMs were also used to separately analyse the effect of each DCA axis on mean suitability, by the same method as above.

All analyses were done using the R statistical language (version 3.0.1; R Development Core Team 2013). Ordinations and response surfaces were produced using functions 'decorana' and 'ordisurf', respectively, in the package 'vegan' (version 2.0-8; Oksanen et al. 2013).

Results

Habitat proportions

The three most frequently occurring habitats were flooded grassland, grassland and miombo, which were present, respectively, in 45%, 41% and 36% of all photographs. These were also the most abundant habitats, making up, when combined, 76% of all habitat cover in the assessed photographs. These habitats also had the highest mean percentage cover when they were present. Termite mound, overgrown water, floating vegetation and settlement were the least abundant habitats, each making up less than 2% of all habitat cover (Table 2).

Table 3: Model coefficients of the linear model of habitat proportions in relation to mean suitability

	Estimate	Std. Error	t value	Pr (>|t|)	
Intercept	0.673	0.01331	50.568	< 2e-16	***
Open water	-0.136	0.02794	-4.85	1.36E-06	***
Reeds	0.223	0.02365	9.437	< 2e-16	***
Overgrown water	-0.236	0.04195	-5.625	2.21E-08	***
Grassland	-0.032	0.01397	-2.275	0.0231	*
Miombo	-0.225	0.01467	-15.342	< 2e-16	***

Significance codes: <0.001 *** ; <0.01 ** ; <0.05 *

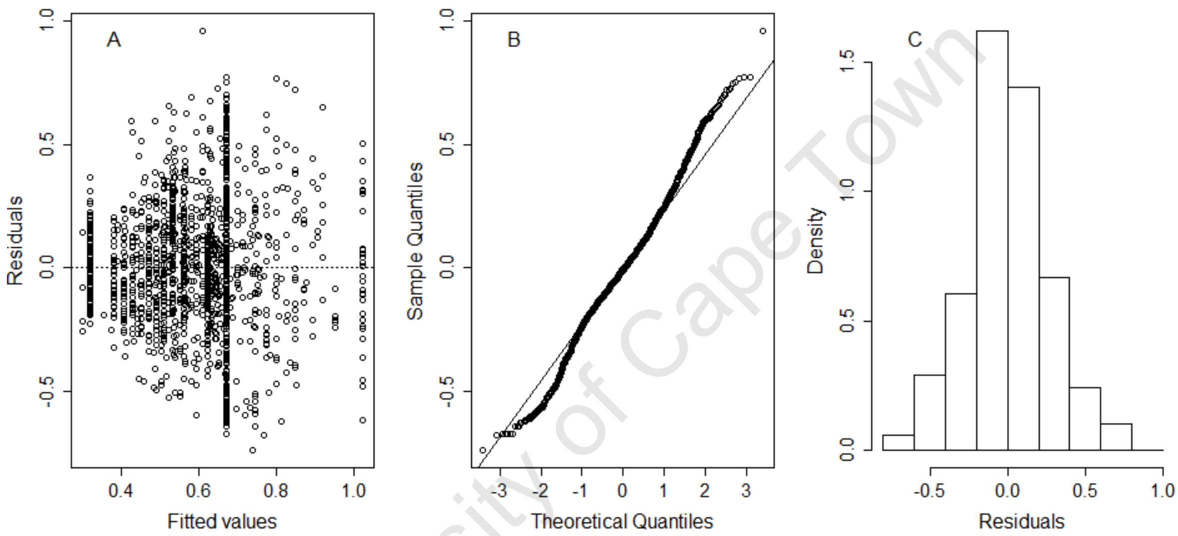

Figure 2: Model validation for the linear model: residuals vs. fitted values (A), QQ plot (B), and histogram of residuals (C)

Univariate analyses

The multiple linear regression outcomes were validated by eye, and showed a normal distribution of residuals and fairly low heteroscedasticity (Figure 2). Mean suitability significantly depended on habitat proportions, although the final model only explained 23% of the variation in mean suitability ($F_{5, 1501}$ = 92.63, p < 0.001, adjusted R^2 = 0.233). The final model included the habitats open water, reeds, overgrown water, grassland and miombo. All habitats were negatively correlated with suitability, except reeds which showed a positive correlation (Table 3).

The results of the non-parametric regression analyses on the non-zero data are presented in Table 4. Proportion of reeds again had a positive effect on mean suitability, while miombo had a negative effect. These habitats showed the strongest correlation with mean suitability (rs = 0.338 and -0.590 respectively). Floating vegetation had the next strongest correlation with suitability, which was near-

Table 4: Correlation tests between habitat proportions and mean suitability using Spearman's rank correlation coefficient (r_s)

Habitat	n	r_s	p-value	
Open water	284	-0.212	<0.001	***
Overgrown water	80	-0.105	0.352	
Reeds	254	0.338	<0.001	***
Flooded grassland	678	0.00939	0.807	
Floating vegetation	38	0.305	0.063	
Papyrus	180	-0.0459	0.541	
Grassland	620	0.289	<0.001	***
Termite mound	102	0.221	0.0257	*
Miombo	542	-0.590	<0.001	***
Settlement	38	0.154	0.357	

Significance codes: <0.001 *** ; <0.01 ** ; <0.05 *

significant (rs = 0.305, p = 0.0630). Flooded grassland showed no correlation with suitability (rs = 0.00939, p = 0.807), whereas grassland was positively correlated with suitability (rs = 0.289, p <0.001). However, the suitability of grassland is generally lower than that of flooded grassland; for example, 27% of photographs with flooded grassland present have a mean suitability of over 60%, compared to just 3.7% of photographs for grassland (Figure 3). Papyrus did not show any correlation with suitability (r_s = -0.0459, p = 0.541).

Multivariate analysis

Three groups of habitat types separated along the first DCA axis: non-vegetated wetland habitats (open water and overgrown water) at low axis 1 values; vegetated wetland habitats (reeds, papyrus and flooded grassland) at intermediate values; and non-wetland habitats (grassland, settlement and miombo) at high values. Vegetated wetland habitats further separated along axis 2, with reeds and papyrus at high values and flooded grassland at low values. Floating vegetation and termite mound were not strongly associated with any habitat type, as indicated by their isolated positions in relation to photographs and other habitats (Figure 4).

The 2-d GAM results indicated a significant relationship between the habitat ordination space and mean suitability (estimated df [edf] = 7.24, F = 53.4, p < 0.001). The model explained 24.7% of the deviance in mean suitability. Mean suitability was non-linearly correlated with the first DCA axis,

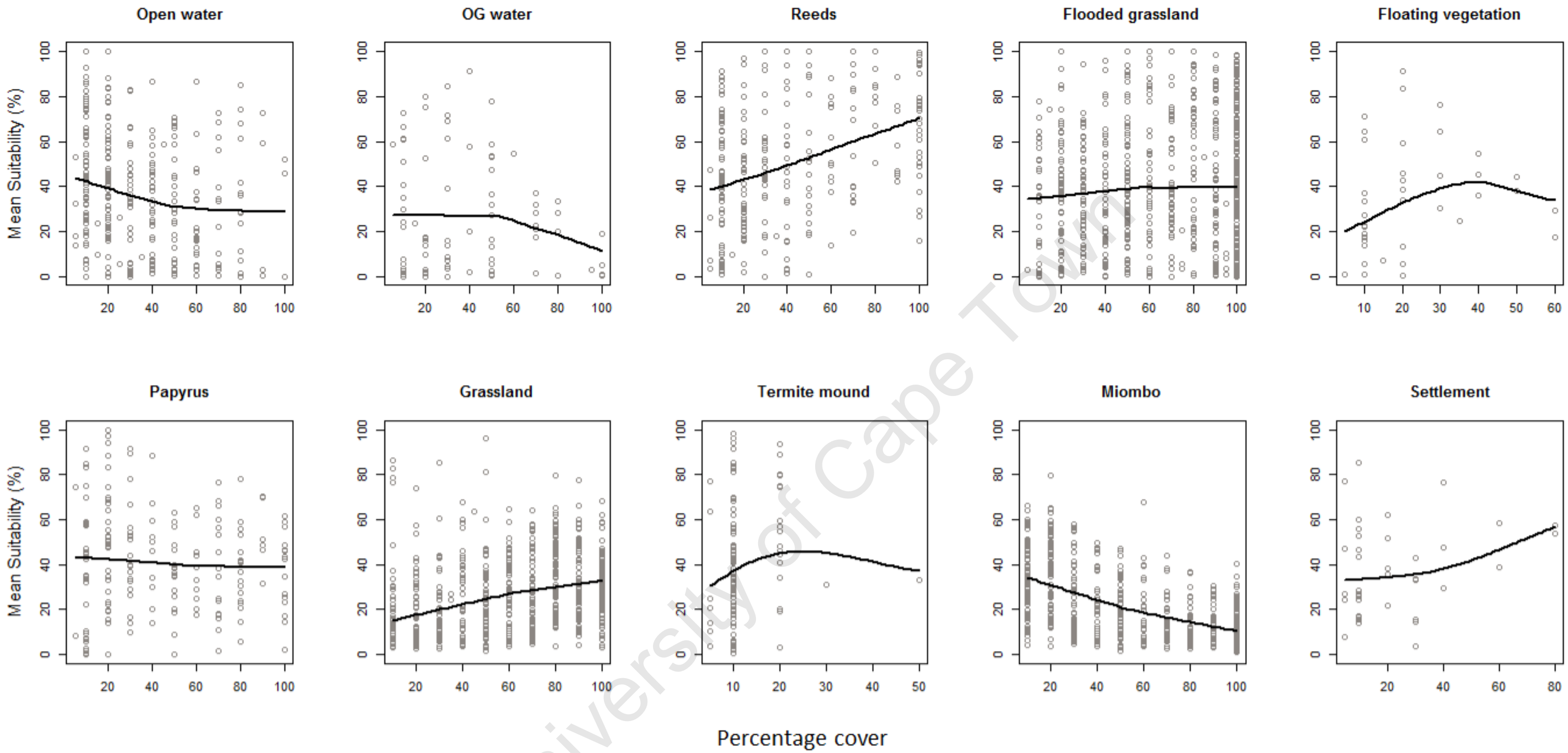

Figure 3: Scatterplots of suitability in relation to cover of each habitat when it was present, with loess fits plotted for each (span = 1, degree = 2). "OG water" = overgrown water

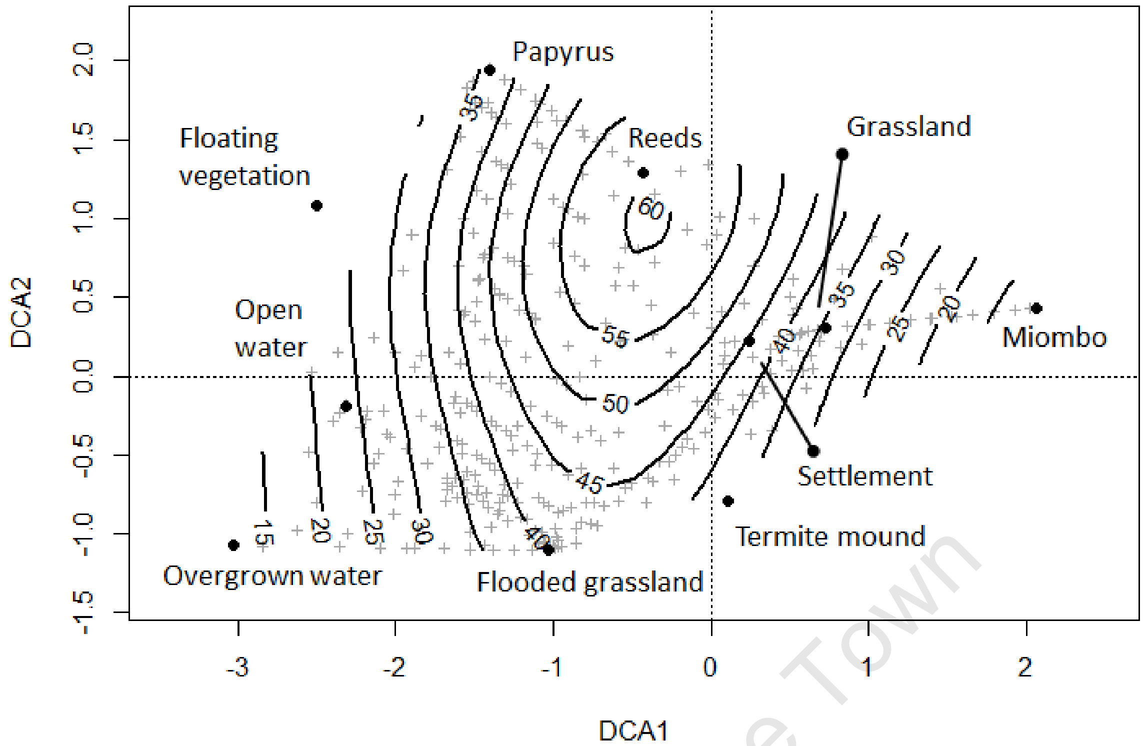

Figure 4: Biplot of the first two DCA axes. Grey crosses are photographs, black dots are habitats (labelled). Contour lines show modelled mean suitability for Shoebills [labels = mean suitability (%); see text for details]

with increasing suitability at intermediate values (i.e. away from both non-vegetated wetland and non-wetland habitats) and reeds having the highest predicted mean suitability (Figure 4). Predicted suitability varied between roughly 15% and 60% along axis 1, in contrast to a 40-60% range along axis 2, suggesting that axis 1 explains more variation in suitability than axis 2.

These results were corroborated by the individual GAMs comparing DCA axes 1 and 2 to mean suitability (Figure 5). Both models suggest significant relationships between the variables (DCA1: edf = 6.66, F = 50.38, $p < 0.001$, adj. $r^2 = 0.233$; DCA2: edf = 7.66, F = 33.87, $p < 0.001$, adj. $r^2 = 0.169$). There is a clear humped relationship between axis 1 and suitability. The relationship for axis 2 is less clear, but shows that the peak in suitability along axis 1 is primarily due to the influence of reeds and – to a lesser extent – papyrus, rather than flooded grassland.

Discussion

We found significant support for the hypothesis that wetland habitats have higher suitability for Shoebills than non-wetland habitats. Furthermore, the analysis was able to distinguish between vegetated and non-vegetated wetland habitats, and showed that vegetated wetland habitats have higher suitability than non-vegetated wetland habitats, which have low general suitability (Figure 4).

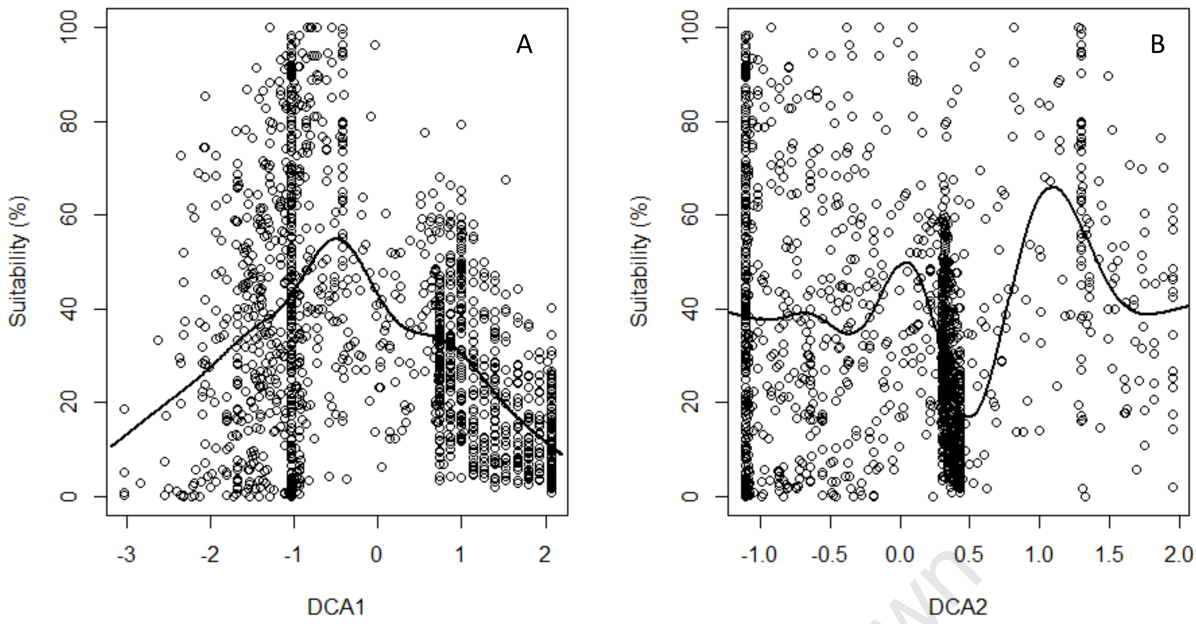

Figure 5: Scatterplots of DCA axes 1 (A) and 2 (B) versus mean suitability, with predicted relationship based the GAM fit (black lines)

These are important findings as they serve to validate the Roxburgh and Buchanan (2010) model at a fundamental level. The model is capable of identifying habitats that are certain to be unsuitable for Shoebills, at both very broad (wetland versus non-wetland) and relatively fine (vegetated versus non-vegetated wetland) scales.

As predicted, papyrus is not associated with high suitability. This is in line with observations that Shoebills are present, and in large numbers, in swamps that lack papyrus (Dinesen and Baker 2006), and that they avoid stands of pure papyrus (Vande Weghe 1981; in Hancock et al. 1992). There is also little evidence that its suitability is higher due to an association with floating vegetation. The reasons for this are uncertain, but may relate to difficulties in identifying floating vegetation (see below).

Little support was found for the hypothesis that floating vegetation is highly suitable habitat for Shoebills, although it does positively correlate near-significantly with suitability when it is present (Table 4). This result is surprising as Shoebills generally forage on top of floating vegetation (Guillet 1979). However, there were a number of potential complicating factors involved that might explain why floating vegetation did not show an effect in our analyses. Foremost is the small sample size. Floating vegetation is difficult to identify with certainty based on aerial photographs. This meant that floating vegetation could only confidently be identified in very few instances (n = 38). Its potential similarity to flooded grassland may have resulted in it being falsely identified as such. However, this also raises the question of whether the Roxburgh and Buchanan (2010) model was capable of distinguishing between these two habitats; addressing this question is beyond the scope of this study.

Flooded grassland was also found to have little association with high suitability. In contrast, dry grassland surprisingly correlated positively with suitability (Table 4). However, when the data including zero values were analysed, grassland showed a significant negative correlation with suitability (Table 3), and furthermore, its suitability has a fairly distinct upper limit at around 60% (Figure 3). In comparison, suitability scores for photographs with flooded grassland present are higher, regularly approaching 100%, despite being variable.

The high degree of variability in suitability for flooded grassland was expected. There are two possible reasons for this. Firstly, as noted above, flooded grassland may have been confused with floating vegetation during the habitat quantification. Given the potential positive correlation between floating vegetation and suitability, this may have led to inflated suitability estimates for flooded grassland. Secondly, there is the issue of temporal variability in flooding levels. Areas of flooded grassland that might have been identified as suitable in the Roxburgh and Buchanan (2010) model, which used an aerial photographs from 2002 and a survey from 2006, may have been dry at the time of the 2011 survey, while the reverse also applies: dry grassland identified by the model as unsuitable may have been flooded in 2011. This might also partially explain why grassland correlated positively with suitability. Unfortunately, data are lacking regarding inter-annual flood level variation in the swamps, and so the similarity between years cannot be assessed. Nevertheless, overall the results suggest that flooded grassland is more suitable for Shoebills than dry grassland. However, the positive correlation for dry grassland is worrying as it suggests that Roxburgh and Buchanan (2010) may have overestimated the extent of suitable habitat in the swamps.

Aside from hypothesis testing, the approach used in this study also has descriptive value. Most notably, there is evidence that reeds are associated with highly suitable habitat for Shoebills (Tables 3 and 4; Figures 3 and 4). The reasons for this are uncertain. Pure stands of reedy vegetation are unlikely to be suitable for Shoebills, which need a relatively solid platform on which to feed (Guillet 1979) and are reported to avoid areas where the vegetation is very dense and exceeds the height of the bird's back (Hanckock et al. 1992). However, the high suitability of reeds might be explained by a number of factors. Firstly, it is often associated with other types of vegetation that are known to be used by Shoebills, mainly floating vegetation and flooded grassland. In addition, reeds are a fixture of permanent swamp, and so their presence is likely to be good a good indicator of swampy habitats preferred by Shoebills. Finally, by providing cover for foraging Shoebills tall reeds could help to optimize foraging success.

There were a number of confounding factors in this study. The most important relate to the dependence of the analysis on the Roxburgh and Buchanan (2010) model. Firstly, there is the possibility that the model's predictions of habitat suitability are inaccurate, particularly at the fine scale of this analysis. Furthermore, the suitability model was built on data taken from different years and at different times of the year to when the photographs used in this study were taken. As noted above, this has important implications for interpretation of the results for habitats that vary with flood levels, notably flooded grassland, which is hypothesized to be highly suitable for Shoebills. To some extent this calls into question the accuracy of the analysis as a whole, as there is uncertainty as to whether the habitats in the photographs represent those that were assessed in the Roxburgh and Buchanan (2010) model. Further uncertainty arises from the way in which areas of the model were chosen to represent areas in the aerial photographs. Variation in angle, focal length and altitude across the set of photographs means that the accuracy of a theoretically determined, fixed area in representing the true area covered by each photograph probably varied greatly. Finally, there may have been some effect of distortion on the accuracy of estimates of habitat proportions due to the obliqueness of photographs, and the accuracy of the habitat quantification may have further suffered from a lack of replication and objectiveness.

Another area of concern is the large human presence within the Bangweulu Wetlands (Roxburgh and Buchanan 2010). Although the effect of the presence of humans on Shoebill behaviour remains unquantified, it is likely that humans compete with Shoebills for both space and food, as the primary human activity within the wetlands is fishing (Roxburgh et al. 2006; Viljoen 2011). If Shoebills are displaced from suitable habitat by humans, this could have implications for the habitat suitability estimates provided by Roxburgh and Buchanan (2010).

Despite the uncertainties, we believe that our approach is adequate, although rough. However, it could be improved by (i) determining empirically the appropriate parameters for estimating the area visible in each photograph, (ii) estimating habitat proportions using a more sophisticated approach to taking distortion into account, and (iii) repeating the habitat quantification for increased robustness, perhaps with a more objective method. Ideally, attempts at repeating the habitat quantification would also be better able to distinguish between floating vegetation and flooded grassland.

This study provides the first quantitative analysis of the composition of suitable habitat for the Shoebill, a relatively little-studied bird of conservation concern. In light of the lack of knowledge of population sizes and trends at various important localities for Shoebills, knowledge of suitable Shoebill habitat will be an important tool in future surveys and monitoring programmes in allowing workers to take a more focused, stratified approach that takes habitat into account. This knowledge will also help inform future conservation decisions. For example, the prioritization of Shoebill conservation areas might be based on the extent of suitable habitat present, particularly when there is uncertainty surrounding population sizes, as is usually the case (BirdLife International 2013a). A large extent of suitable habitat might also indicate the potential for population growth. Furthermore, knowledge of suitable habitat could help in assessing the impact of humans on Shoebills, as the extent to which humans are encroaching on or altering suitable habitat can be determined. The availability of quantitative data on habitat suitability will ultimately enable the formulation of more informed and robust strategies regarding the conservation of Shoebills globally.

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