International Journal of Biodiversity and Conservation Vol. 1(5) pp. 177-186 September, 2009
Available online http://www.academicjournals.org/ijbc

Full Length Research Paper

Modeling habitat suitability for Grey Crowned-cranes (*Balearica regulorum gibbericeps*) throughout Uganda

Jared A. Stabach[1*], Nadine Laporte[1] and William Olupot[2]

[1]The Woods Hole Research Center, 149 Woods Hole Road, Falmouth, MA 02540 USA.
[2]Wildlife Conservation Society, Plot 802, Mitala, Kiwafu Road, Kansanga, P.O. Box 7487, Kampala, Uganda.

Accepted 12th August, 2009

Grey Crowned-cranes occur throughout the mixed wetland-grassland habitats of Eastern and Southern Africa. Due primarily to loss of habitat, however, the species is in swift decline over much of its historic range. We present a prediction of habitat suitability throughout Uganda using a Maxent modeling approach, combining presence-only field data collected over the last few decades (1970 - 2006) with remote sensing and climate derived variables. We ran six feature type models, with the Auto feature type model having the best fit to the data (AUC = 0.912). Our results provide detailed information regarding the characteristics of habitats used and highlight specific areas of high habitat suitability for the species. While wetlands were certainly important in the prediction (9.2% contribution), other variables (namely temperature seasonality) were more important within the model (19.5%). Areas of high habitat suitability (defined as > 0.6 probability of presence) accounted for only a small amount of the total area throughout the country (5.8 - 6.9%), and were mainly found in the Southwestern corner of the country and along the Albert Nile River. These data provide a statistical basis for extrapolating into areas that have not been surveyed and provide valuable information for the future conservation of the species.

Key words: *Balearica regulorum gibbericeps*, East Africa, Grey Crowned-crane, habitat suitability, maxent, modeling, Uganda.

INTRODUCTION

Grey Crowned-cranes (*Balearica regulorum*) belong to the family Gruidae and are found throughout the mixed wetland-grassland habitats of Eastern and Southern Africa (Walkinshaw, 1964; Meine and Archibald, 1996). They are non-migratory, yet make local and seasonal movements (Pomeroy, 1980, 1987) and are most abundant in Uganda, Kenya and Tanzania (Meine and Archibald, 1996). Their conservation status is currently listed as vulnerable with an estimated population of approximately 47,000 – 59,000 animals (Bird Life International, 2009). However, due primarily to loss of habitat (Meine and Archibald, 1996; Olupot et al., in press), populations are in swift decline (Beilfuss et al., 2007).

In Uganda, home of the subspecies *Balearica regulorum gibbericeps* and where the species is recognized as the national bird, current populations may be as low as 13,000 birds - a potential decline of more than 60% of the population since 1985 (Beilfuss et al., 2007). Of even greater concern is the low breeding success. Muheebwa-Muhoozi (2001) reported a decline in breeding success of 0.42 birds fledged per clutch over a 25-year period (1974/1975 - 1999/2000). If this trend continues, there will be no successful breeding pairs within the country in the second half of this century.

Understanding a species' fundamental niche (Hutchinson, 1957) and the threats to its survival are essential aspects for the future conservation of the species. Past research (Carswell et al., 2005) provided anecdotal information about the habitats where cranes are likely to be found and a map of the occurrence localities received from the National Biodiversity Data Bank at the Makerere University Institute of Environment and Natural Resources. Olupot and Plumptre (2006) conducted a nationwide study to determine the distribution of Grey Crowned-crane breeding sites throughout Uganda. This study provided insight into the many different types of wetland habitat that cranes use as

*Corresponding author: E-mail: jstabach@whrc.org. Tel.: 508.540.9900 x137. Fax: 508.540.9700.

breeding ground and identified 13 districts throughout Uganda with evidence of breeding (Olupot and Plumptre, 2006). Neither study, however, provided information about the habitat quality where cranes were sighted, nor do they provide any information related to habitat quality in areas that were not surveyed.

Our goal in this study was to use these data to provide a country-wide habitat suitability analysis of Grey Crowned-cranes throughout Uganda based on a statistical modeling approach. We utilize the program Maxent (Maximum Entropy), which refers to a machine learning algorithm used for characterizing probability distributions from incomplete information (Phillips et al., 2006). The algorithm has been shown to perform well when compared against other modeling techniques (Elith et al., 2005; Gibson et al., 2007; Pearson et al., 2007; Hernandez et al., 2008) and has been used to success-fully model suitable habitat for various species in other research (Phillips et al., 2006; Ward, 2006; Gibson et al., 2007; Pearson et al., 2007; Hernandez et al., 2008).

Uganda contains an extensive network of wetlands and swamps, among the largest (per unit area) in Africa, which has important implications for conservation and management since cranes most often use wetland edges for nesting (Olupot and Plumptre, 2006). The country is also predominantly (38%) covered by cropland (Bartholomé and Belward, 2005), which often results in conflict with humans since many of these agricultural lands border wetlands and are often used as nesting and foraging sites (Olupot and Plumptre, 2006). While Uganda is one of the most biodiversity-rich countries in Africa (Plumptre et al., 2007), it also harbors one of the highest human population densities (128 per km^2 (2007); USDS, 2008). As such, providing accurate information about the extent of suitable habitat and the variables that may be important for driving crane site selection, are critically important for future conservation efforts.

MATERIALS AND METHODS

Species occurrence data

Species occurrence consisted of point data collected during a nation-wide civilian participatory program by W. Olupot and colleagues (Olupot et al., in press) and from records kept by the Makerere University Institute of Environment and Natural Resources (MUIENR, unpublished data). In total, 456 data points of Grey Crowned-crane breeding/foraging sites were collected throughout the time period 1970 - 2006 (Figure 1). However, the majority of data points (61%) were collected over a 10-year period (1980 - 1990) by MUIENR and are based on opportunistic road sightings.

Environmental variables

To model habitat suitability, twenty-four (24) spatially explicit variables (Table 1) were selected for their potential importance, based on our knowledge and from published sources of what would likely have relevance in relation to the species (Walkinshaw, 1964; Pomeroy, 1980, 1987; Meine and Archibald, 1996; Olupot et al., in press). These variables included both biotic and abiotic variables, such as woody biomass, elevation, landcover, soil, wetlands, and a series of layers (19) related to temperature and precipitation (e.g., Precipitation of Warmest Quarter). These nineteen 'bioclimatic variables', as they are referred to in the text, were extracted from the WorldClim dataset and represent mean conditions for the period 1950 - 2000 (Hijmans et al., 2005).

Projections, grid cell size and alignment, and spatial extent were manipulated to ensure consistency across all data layers using Arc/Info Workstation 9.3 (Environmental Systems Research Institute, Redlands, CA, USA). All files were projected to Albers Equal Area Conic (WGS84 datum) with a grid cell size of 1-km. Bilinear interpolation was used as the resampling method for all variables except for landcover and soil (since these data are categorical variables). In these two cases, nearest neighbor resampling was used.

The wetlands dataset, however, consisted of numerous small polygon segments which therefore could not be directly converted to a 1-km grid cell without underestimating the amount of wetlands throughout the country. Consequently, this dataset was first converted to a 25-m grid cell, with all cells being re-coded to either a '0' (non-wetland) or a '1' (wetland). These data were then summarized within the 1-km grid, providing an assessment of the percentage of wetland within each cell ranging from 0 to 1600 (0 - 100% wetland).

Habitat suitability modeling

Maxent is a general-purpose algorithm for estimating a target probability distribution by finding the probability distribution of maximum entropy (i.e, closest to uniform) (Phillips et al., 2006). The algorithm was chosen for use in this study because it (1) has performed well when compared with other novel methods (Elith et al., 2006; Gibson et al., 2007; Pearson et al., 2007; Hernandez et al., 2008), (2) does not require absence data, and (3) allows for the incorporation of categorical information (that is, landcover). All analyses were conducted using Maxent version 3.2.1, available at http://www.cs.princeton.edu/~schapire/maxent/ (Phillips et al. 2004, 2006).

After first splitting the species occurrence data into two separate partitions (75% for training, 25% for testing), we ran six (6) Maxent models using feature types commonly used for comparison (Phillips et al., 2004, Phillips and Dudik, 2008) with the above mentioned environmental variables (Table 1) to provide an initial assessment of variable contribution. Feature types are algorithm parameters that utilize the available set of environmental variables to constrain the probability distribution that is being computed. The feature types used were Auto features (Auto), Linear features (L), Linear Quadratic features (LQ), Linear Quadratic Product features (LQP), Threshold features (T), and Hinge feature (H). Description for each of the feature type models can be found in Phillips et al. (2006) and Phillips and Dudik (2004). The Auto feature type allows the set of features used to depend on the number of presence records for the species being modeled using general empirically-derived rules. In all instances, a regularization parameter of 1.0 was used to avoid overfitting the test data, the maximum number of iterations was set at 500 (or until the convergence threshold fell below 10^{-5}), and a jackknife procedure was used to assess variable importance.

Each of the feature type models was then re-run a second time, after selecting only those variables that contributed at least 2% to the initial model result (signified in Table 1). This methodology reduced the total numbers of variables used in the analysis to a maximum of sixteen (dependent on the feature type used), with six variables being common to all models.

Model evaluation

To assess model performance, we used Receiver Operating

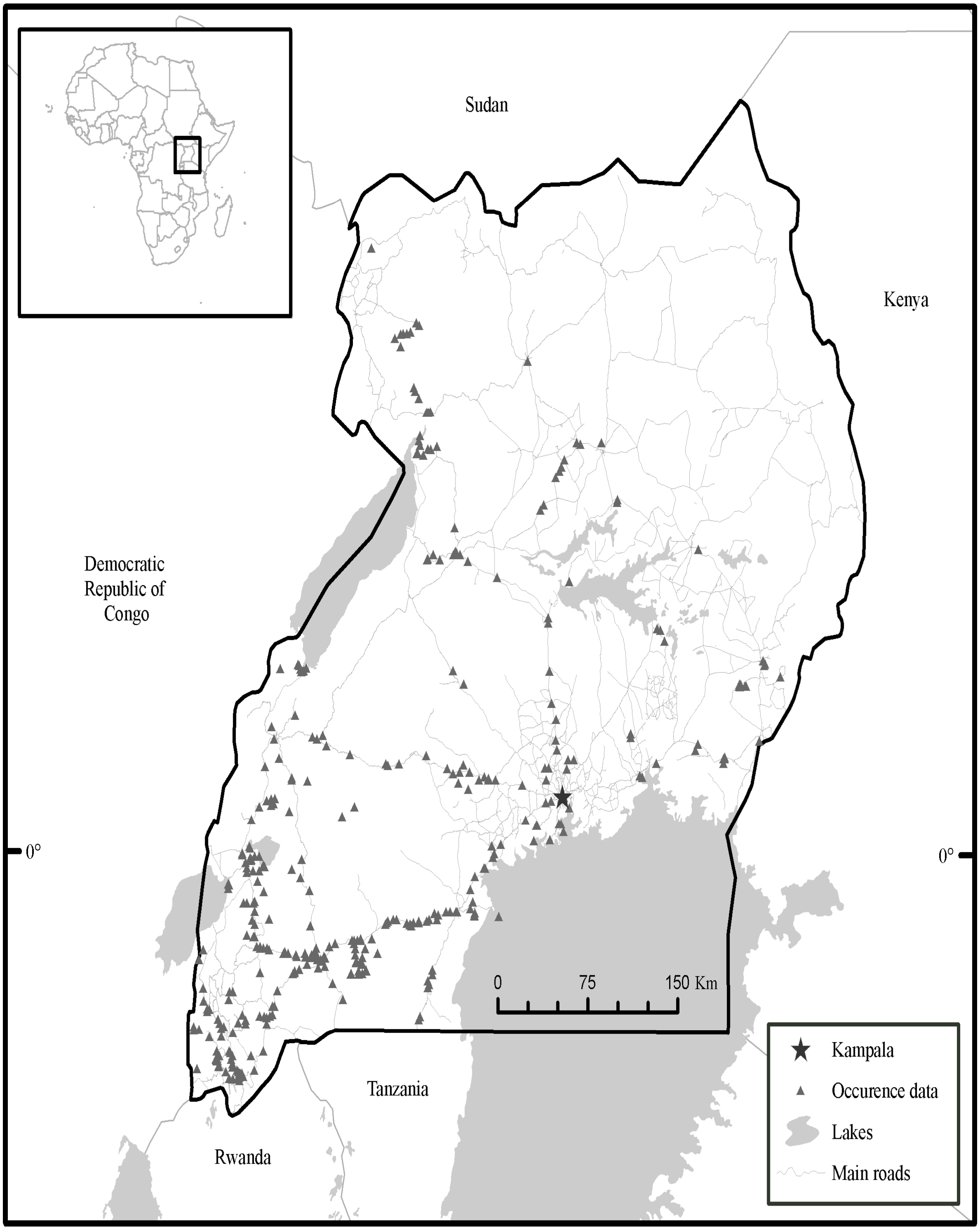

Figure 1. Map of Uganda showing Grey Crowned-crane (*B. r. gibbericeps*) occurrence data. Data provided by the Makerere University Institute of Environment and Natural Resources (Unpublished data) and from records collected by Olupot et al. (2006).

Characteristic (ROC) curves. For more information on ROC curves, see Phillips et al. (2004). The main advantage of ROC analysis is that the area under the ROC curve (AUC) provides a single measure of model performance, independent of any choice of threshold (Phillips et al., 2006). For each run, we calculated the AUC, which is the probability that the classifier orders a random

Table 1. Twenty-four variables used in analysis. Letters (a,b,c,d,e,f) listed after the variable names denote the feature type model with which the variable was used (Auto features (a), Linear features (b), Linear Quadratic features (c), Linear Quadratic Product features (d), Thresdhold features (e), Hinge features (f))

Variable Name	Description	Reference
Bio-Clim 1[d]	Annual Mean Temperature	Hijmans et al. 2005
Bio-Clim 2[d]	Mean Diurnal Range (Mean of Monthly (Max Temp - Min Temp))	Hijmans et al. 2005
Bio-Clim 3[a,e]	Isothermality (Mean Diurnal Range/Temperature Annual Range)	Hijmans et al. 2005
Bio-Clim 4[a,b,c,d,e,f]	Temperature Seasonality (Standard Deviation)	Hijmans et al. 2005
Bio-Clim 5	Maximum Temperature of Warmest Month	Hijmans et al. 2005
Bio-Clim 6[a,b,c,d,f]	Minimum Temperature of Coldest Month	Hijmans et al. 2005
Bio-Clim 7[a,b,c,d]	Temperature Annual Range	Hijmans et al. 2005
Bio-Clim 8	Mean Temperature of Wettest Quarter	Hijmans et al. 2005
Bio-Clim 9[a,d,e]	Mean Temperature of Driest Quarter	Hijmans et al. 2005
Bio-Clim 10	Mean Temperature of Warmest Quarter	Hijmans et al. 2005
Bio-Clim 11[d]	Mean Temperature of Coldest Quarter	Hijmans et al. 2005
Bio-Clim 12[a,e]	Annual Precipitation	Hijmans et al. 2005
Bio-Clim 13[a,e,f]	Precipitation of Wettest Month	Hijmans et al. 2005
Bio-Clim 14[d]	Precipitation of Driest Month	Hijmans et al. 2005
Bio-Clim 15[a,b,c,d,e,f]	Precipitation Seasonality (Coefficient of Variation)	Hijmans et al. 2005
Bio-Clim 16[d,f]	Precipitation of Wettest Quarter	Hijmans et al. 2005
Bio-Clim 17[d]	Precipitation of Driest Quarter	Hijmans et al. 2005
Bio-Clim 18[a,e,f]	Precipitation of Warmest Quarter	Hijmans et al. 2005
Bio-Clim 19[a,b,c,d,e,f]	Precipitation of Coldest Quarter	Hijmans et al. 2005
Biomass	Aboveground Woody Biomass (2000)	Baccini et al. 2008
Elevation[a,b,c,d,e,f]	Elevation	USGS 2004
Landcover[a,b,c,d,e,f]	Landcover (GLC2000)	Bartholomé E. and Belward A.S 2005
Soil[a,b,d,e,f]	Soil	Makerere University Insitute for Environment and Natural Resources
Wetland[a,b,c,d,e,f]	Wetlands	Uganda Wetlands Inspection

positive and random negative point correctly (Phillips et al., 2004). A perfect classifier therefore has an AUC of 1, although the maximum AUC is less than one because of the use of presence-only data (Wiley et al., 2003; Phillips et al., 2004). Generally, AUC values greater than 0.7 are considered to be potentially significant, while scores of 0.5 imply a predictive discrimination that is no better than random (Elith et al., 2006).

To provide an assessment between the different feature type models, we generated 1000 random points throughout the study area and extracted the probability value from each of the six model results. The nonparametric Kruskal-Wallis multi-comparison, *H*, test (Kruskal and Wallis, 1952) was then used to examine if the extracted values differed and a Behrens-Fisher test was used to identify inequalities (Zar, 1999). All statistical analyses were conducted using the statistical package ‘R’ (R Development Core Team, 2009).

RESULTS

Statistics from each of the six Maxent feature type models are summarized in Table 2. AUC values for all models are > 0.85, implying a potentially significant result. The model results suggest that the best method for predicting crane habitat suitability was the Auto (a) feature set (AUC = 0.912), although admittedly only marginally better than the other models. Visualizations for each model are provided in Figure 2, highlighting for the most part (with the exception of the low habitat suitability area in the Southern section of Uganda in feature type models T, H, and Auto), that model outputs are visually very similar. The Kruskal-Wallis comparison test, however, indicates a significant difference between models ($\chi^2 = 39.9032$, $p < 0.0001$). Further analysis (Behrens-Fisher test) shows that this inequality lies with the Linear (L) and Linear Quadratic (LQ) feature type models (L-Auto: $p < 0.05$, LQ-Auto: $p < 0.0001$, L-LQP: $p < 0.05$, LQ-LQP: $p < 0.0001$, LQ-H: $p < 0.05$). After removing these two feature types, no significant difference was found between models ($\chi^2 = 7.6552$, $p > 0.05$).

Areas of high habitat suitability in each of the models (considered to be areas with > 0.6 probability of presence) account for only a small portion of the country (5.8 - 6.9% depending on model, Table 2), with the Linear (L) and Linear Quadratic (LQ) feature type models indicating the largest area of suitable habitat. This was an arbitrary

Table 2. Summary statistics for the six Maxent habitat suitability models. Variable combinations for each model provided in Table 1.

Feature Type Model	AUC	Suitable Habitat (km^2)* and % of country
Auto (Auto)	0.912	13,931 (5.8%)
Linear (L)	0.861	15,899 (6.6%)
Linear Quadratic (LQ)	0.854	16,619 (6.9%)
Linear Quadratic Product (LQP)	0.880	14,125 (5.8%)
Threshold (T)	0.909	14,540 (6.0%)
Hinge (H)	0.886	14,851 (6.1%)

*Suitable habitat defined as areas with ≥ 0.6 probability of presence

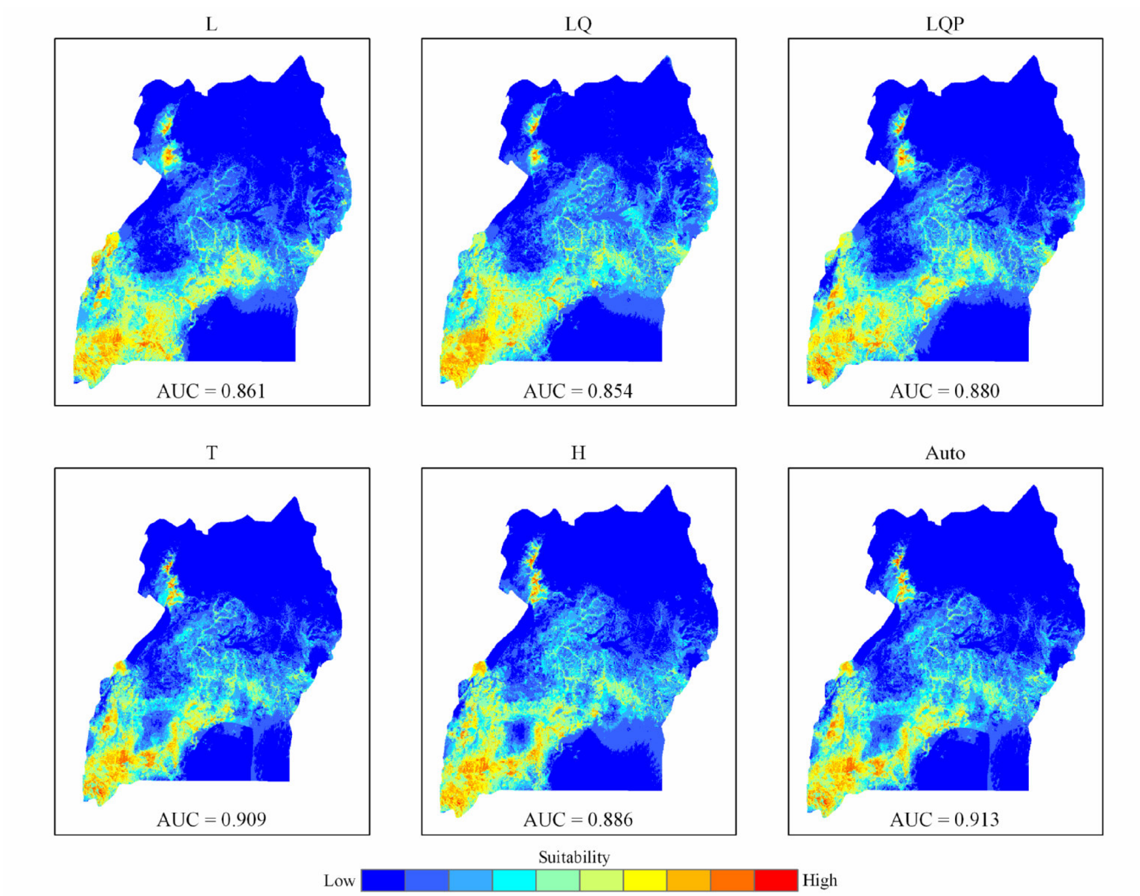

Figure 2. Maxent feature type models. The predictions analyzed are: Linear (L); Linear and Quadratic (LQ); Linear, Quadratic, and Product (LQP); Threshold (T); Hinge (H); and Auto (Auto). Model performance value (AUC) provided.

threshold to estimate the area of 'good' habitat and provided a means of comparison between models. Six of the variables were common to each model and found to contribute at least 2% to the model result. These variables were: 'Temperature Seasonality (Bio-Clim 4)', 'Precipitation Seasonality (Bio-Clim 15)', 'Precipitation of Coldest Quarter (Bio-Clim 19)', 'Elevation', 'Landcover', and 'Wetlands' (Table 1).

Best model fit

The Auto feature type model (Figure 3) was selected as the best predictive model due to having the highest model performance value (Table 2) and its more conservative estimate of high habitat suitability (13,931 km^2, 5.8%; Table 2). For this reason, the remainder of the results apply only to this feature type model.

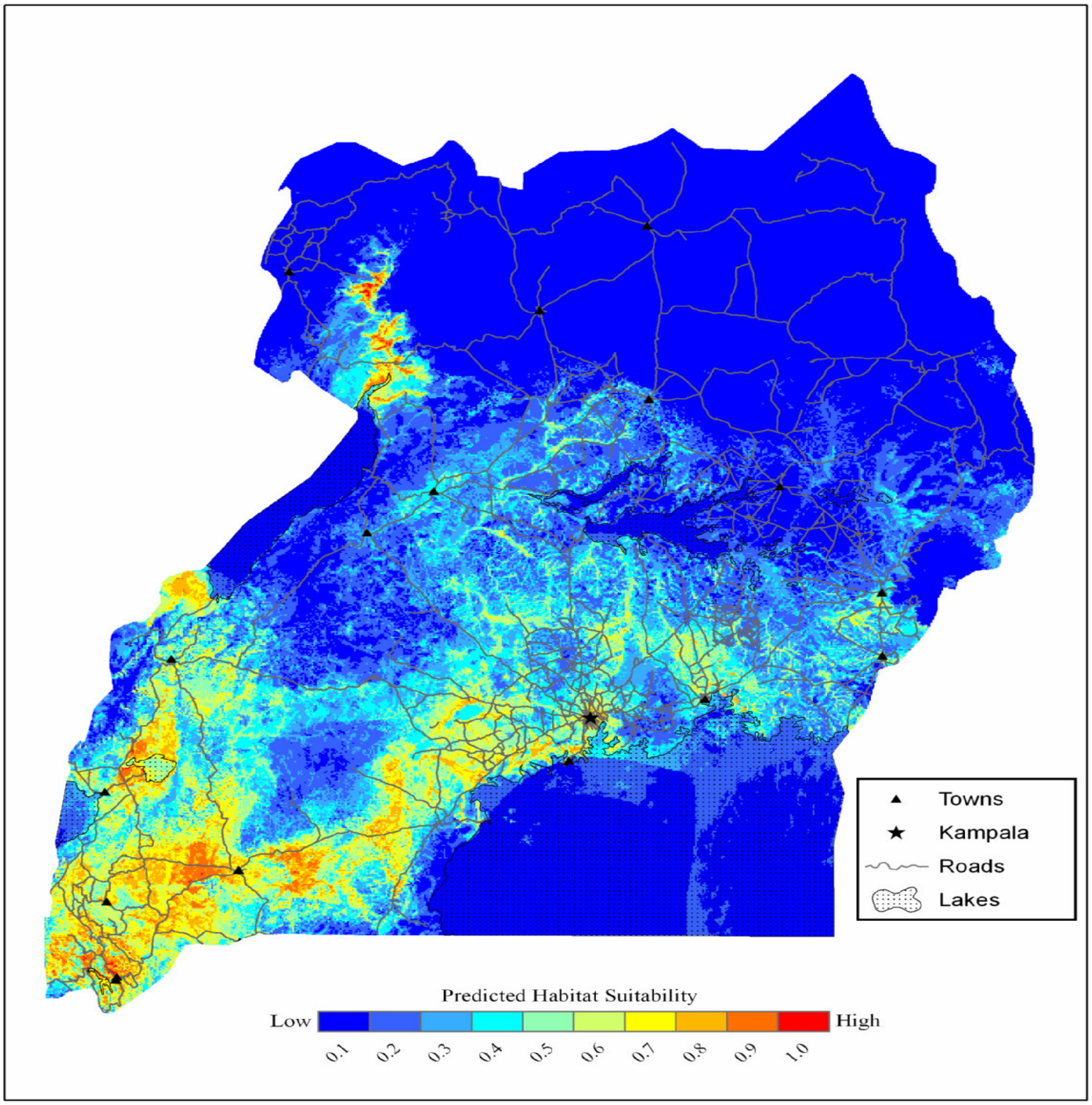

Figure 3. Auto feature type model showing predicted habitat suitability with warmer colors representative of higher suitability. Roads, Lakes, and major cities/capital provided for reference.

The most important explanatory variable was 'Temperature Seasonality (Bio-Clim 4)', with 'Precipitation of Warmest Quarter (Bio-Clim 18)' and 'Precipitation Seasonality (Bio-Clim 15)' collectively contributing 43% to the model output (Table 3). 'Wetlands' and 'Landcover' also proved to be important variables in the prediction, but with smaller individual contributions (9.2% and 7.3%, respectively). In total, nine variables (including those variables mentioned above plus 'Mean Temperature of Driest Quarter (Bio-Clim 9)', 'Precipitation of Coldest Quarter (Bio-Clim 19)', 'Precipitation of Wettest Month (Bio-Clim 13)', and 'Elevation' contributed 86% to the model output (Table 3). The response curve for 'Temperature Seasonality (Bio-Clim 4)' shows a bi-modal distribution, with the highest probability of crane presence related to areas having both the highest and lowest values of temperature seasonality throughout the country (Figure 4). These areas appear in the Southwestern part of the country (lowest temperature seasonality) and the area just North of Lake Albert/Murchison Falls National Park along the Albert Nile (highest temperature seasonality). This variable was evaluated as having the most useful information by itself, based on the jackknife test to assess variable importance.

The only other variables with bi-modal distributions were 'Isothermality (Bio-Clim 3)' and 'Temperature

Table 3. Analysis of variable contribution for the Best model fit result (Auto feature type).

Variable Name	Description	% Contribution
Bio-Clim 4	Temperature Seasonality (Standard Deviation)	19.5
Bio-Clim 18	Precipitation of Warmest Quarter	12.4
Bio-Clim 15	Precipitation Seasonality (Coefficient of Variation)	10.8
Wetland	Wetlands	9.2
Bio-Clim 9	Mean Temperature of Driest Quarter	7.5
Landcover	Landcover (GLC2000)	7.3
Bio-Clim 19	Precipitation of Coldest Quarter	6.9
Bio-Clim 13	Precipitation of Wettest Month	6.6
Elevation	Elevation	6.1
Bio-Clim 3	Isothermality (Mean Diurnal Range/Temperature Annual Range)	3.5
Soil	Soil	3.3
Bio-Clim 12	Annual Precipitation	3.1
Bio-Clim 6	Minimum Temperature of Coldest Month	2.9
Bio-Clim 7	Temperature Annual Range	0.8

Annual Range (Bio-Clim 7)', with the highest and lowest values overlapping the same geographic areas as described above for 'Temperature Seasonality (Bio-Clim-4)'. For 'Isothermality (Bio-Clim 3)', however, the high and low values are opposite to those of 'Temperature Seasonality (Bio-Clim 4)' (that is, the lowest isothermality appears in the Southwestern portion of the country and highest being along the Albert Nile).

The response curves for 'Precipitation of Warmest Quarter (Bio-Clim 18)' and 'Precipitation of Coldest Quarter (Bio-Clim 19)' show that highest predicted suitability are in areas of low to medium precipitation (200 – 400 mm during the warmest quarter, <300-mm during the coldest quarter). Medium 'Precipitation Seasonality (Bio-Clim 15")' also leads to higher probability of presence. Not surprisingly, predicted habitat suitability increases with an increase in the amount of wetlands and decreases sharply when elevation exceeds 2200-m (Figure 4). However, these results are not without exception. For instance, the Lake Kyoga area in the center of the country has the highest proportion of wetland habitat and yet, the habitat suitability of this area is quite low.

Analysis of the landcover indicates that cranes were most often found in "Regularly Flooded Shrub and/or Herbaceous Cover" (7), "Artificial Surfaces" (12), "Broadleaved Deciduous Closed Canopy Tree Cover" (2) and "Cultivated/ Managed Areas" (8). Response curves for all variables can be found in Figure 4.

DISCUSSION

Our results suggest that the Southwestern portion of Uganda contains the highest amount of suitable habitat for Grey Crowned-cranes throughout the country. This region lies roughly along the equator and thus, as the bioclimatic variables illustrate, experiences low temperature seasonality with moderate but sustained precipitation. The other region that contains high habitat suitability lies just North of Lake Albert along the Albert Nile River. This area has a higher mean annual temperature than areas in the Southwest, but receives a similar amount of precipitation. It is therefore likely that the increased precipitation and close proximity to a year-round water source provides ample food resource opportunities even though the temperature is warmer than further to the south.

All other areas in the North have extremely low habitat suitability with most areas being mapped as completely unsuitable. This area is seemingly too dry, having the lowest annual precipitation throughout the country and as a result, is covered by mostly open shrub/tree cover (15 - 40% tree cover; Bartholomé and Belward, 2005). Earlier observations from this area (pre-1970), however, suggest that Grey Crowned-cranes may have occurred in some of these areas. It is unclear if the current absence of cranes in this area is a result of changes in climate, or due to regional disturbances that may have occurred from the civil unrest in the area over the past 20 years.

Depending on the type and intensity of disturbance, disturbances can either have a positive or negative effect on cranes. For example, the burning of seasonally inundated wetlands (as commonly occurs in the Northern part of the country) may destroy nesting habitat. Wetland cultivation, however, may (in some cases) provide crops that offer both a food source and shelter from predators for cranes (Olupot and Plumptre, 2006). While the type and intensity of disturbance were not specified in this study, they could be important variables to consider in future research.

Three of the models (Auto, H, and T) depict an area along the equator and West of Lake Victoria that has very low habitat suitability, an unexpected result considering the high habitat suitability in neighboring areas. A

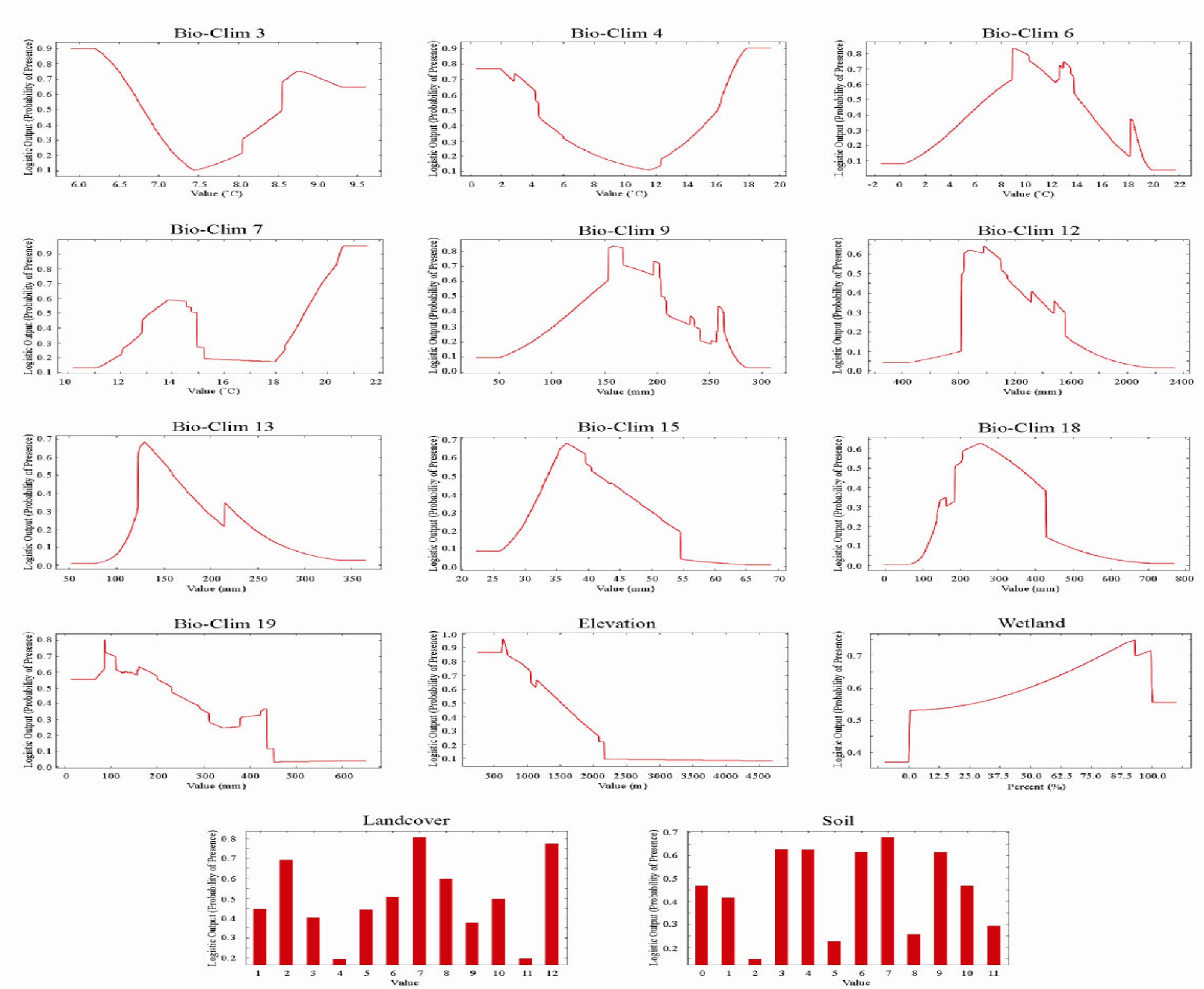

Figure 4. Response Curves for the Auto feature type model. Values for landcover (Bartholomé and Belward, 2005) are: (1) Tree cover, broadleaved, evergreen; (2) Tree cover, broadleaved, deciduous, closed; (3) Tree cover, broadleaved, deciduous, open; (4) Mosaic: tree cover/other natural vegetation; (5) Shrub cover, closed-open, deciduous; (6) Herbaceous cover, closed-open; (7) Sparse herbaceous or sparse shrub cover; (8) Regularly flooded shrub and/or herbaceous cover; (9) Cultivated and managed areas; (10) Mosaic: cropland/tree cover/other natural vegetation; (11) Mosaic: cropland/shrub or grass cover; (12) Water bodies; and (13) Artificial surfaces and associated areas. Values for soil (Makerere University Institute of Environment and Natural Resources, unpublished data) are: (1) Clays; (2) Sandy clay; (3) Clay loam; (4) Poorly drained soils; (5) Water; (6) Sandy clay loam; (7) Loamy sand; (8) Sandy loam; (9) Loam; (10) Sand; (11) Unclassified.

detailed evaluation of the bioclimatic variables indicates that this area has lower annual precipitation than neighboring areas (comparable to the annual precipitation in the Northeast section of the country) and is also characterized by mainly sparse shrub cover (Bartholomé and Belward, 2005). As the gradient of precipitation changes, so too does the landcover throughout the area, resulting in higher habitat suitability.

Based on the landcover, cranes were most likely to be found in “regularly flooded shrub and/or herbaceous cover”. This was an anticipated result, as this type of habitat would likely provide a plentiful food supply year-round. The same would hold true with regard to “Cultivated/managed areas”, although this would be dependent on the type of crop being managed. The two landcover categories “Broadleaved deciduous closed canopy tree cover” and “Artificial surfaces”, however, were unexpected. We believe these two categories to be results of sampling bias as cranes are more likely to be seen near settled areas and related to inaccuracies in the landcover classification which was completed on a regional scale at 1-km resolution. Such inaccuracies are common when relating presence locations with categorical information. We did run our analysis using an alternative landcover classification (Africover; Alinovi et al., 2000).

However, no significant differences were found between the model results. The landcover types from this classification that most explained the crane presence locations were (1) "Urban areas", (2) "Aquatic agriculture", (3) "Rainfed herbaceous crops", (4) "Tree and shrub savannah", and (5) "Irrigated and post-flooding herbaceous crops". Again, the category "Urban areas" highlights issues associated with the sampling design, but may also imply that cranes have grown adapted to a human disturbed landscape.

Particular areas throughout the country are very remote with difficult access. This could be the reason that the area around Lake Kyoga (center of country) is considered to be of low habitat suitability even though it contains some of the largest wetland complexes to be found in the country. This area is covered by reeds and other asso-ciated vegetation that make field sampling extremely difficult. Other areas throughout the country may have the opposite bias, as field sampling may have been facilitated by the terrain (ability to see longer distances) and/or by degradation of wetland habitat (allowing for increased accessibility). We also recognize that our evaluation of each model was derived from withheld data. While these data are likely to have the same biases as the training data, they were deemed the best validation dataset to use. Therefore, additional research is necessary to verify areas with little to no field sampling and provide a second and independent dataset for testing.

Our results also highlight the interactive effects of variables for predicting habitat suitability. For instance, while wetlands are certainly vitally important for crane nesting and foraging habitat, wetlands alone do not provide an accurate picture of habitat suitability (as exemplified by the Lake Kyoga area) and models run without this parameter were not significantly different than when the parameter was included. A traditional des-cription of suitable crane breeding habitat is shallow, flooded grass savannahs with scattered trees. This description is consistent with many of the wetlands to the east and mid-west of the country. Cranes do not occur in papyrus swamps abundantly found in the central and southwestern portions of Uganda. However, our results show that the Southwestern portion of Uganda contains the highest habitat suitability throughout the country. It is possible that as papyrus swamps become degraded, they become more suitable for cranes and as grass swamps with scattered trees become similarly degraded, they become less suitable.

We were encouraged by the similarity of our results between models. Although the Linear and Linear Quadratic feature type models were shown to be statistically different than all other models (and indicated the largest area of suitable habitat), the general trend was similar: highest habitat suitability was concentrated in the Southern part of the country with a small area of suitable habitat in the Northwest corner around the Albert Nile. The difference between the models can be explained by the fact that the Linear and Linear Quadratic feature type models were less conservative and over-estimated the total amount of suitable habitat throughout the country (at least 1,000 km^2 more suitable habitat than any of the other models).

The Maxent output provides quantitative information about the suitability of habitat throughout Uganda on a pixel by pixel basis, extrapolating into areas that were under-sampled or not sampled at all on a statistical basis. As such, the result is an easy-to-interpret map that can be imported into other programs (e.g. ArcGIS) and further analyzed and is far better than shaded outline maps of species distri-butions that are commonly found in standard field guides (Phillips et al., 2006). Maxent also provides detailed information about the variables along with their impor-tance in relation to the contribution to the model, which may have important implications for the conservation of the species. The Auto feature type model was selected as the model of choice because it had the highest AUC value, although admittedly only marginally better than any of the other models.

It is important to note that while our results illustrate the current extent of suitable habitat throughout Uganda, some of the variables may not accurately depict current conditions (e.g., the bioclimate variables represent mean values for the time period 1950 - 2000). And, as swamp reclamation is currently ongoing in Uganda, conditions related to crane habitat may be rapidly changing. Additionally, our model does not capture the ease (or difficulty) of sighting cranes in different areas, crane hunting intensity, or the levels of harassment which potentially influence crane distributions. If reliable datasets of current conditions and threats to the species can be identified, these data can be incorporated into Maxent to improve results. Additionally, if future scenarios related to changing climatic conditions and/or land-use practices can be developed, the presence localities from this study can be 'projected' onto these scenarios to provide detailed information about changing conditions that may affect Grey Crowned-crane populations.

Lastly, Uganda has 10 national parks that cover a total land area of 12,172 km^2, protecting a number of different habitat types (from montane rainforests to grassland savannahs) and species. However, only 1,469 km^2 (12%) of the total habitat that we have identified as highly suitable (13,931 km^2) for cranes are found within these protected area limits; the majority of which (784 km^2, 54%) are located within the boundaries of Queen Elizabeth National Park. These results highlight the inadequacies of current protected areas in regard to formal protection for Grey Crowned-cranes, but also provide information to guide future management plans if these populations are to remain viable in a dynamically changing landscape.

Conclusion

This study provides the first detailed map of Grey Crowned-crane habitat suitability throughout Uganda. The Maxent modeled result provides an easy-to-interpret output that can be incorporated into conservation management plans and could similarly be carried out in other countries throughout the region should datasets of presence be available. In particular, we draw attention to some of the main variables that may contribute to crane site selection and highlight the fact that Uganda plays a crucial role in the long-term survival of crane populations throughout east Africa. While future research could improve the models in terms of calibration and validation, these data provide important information towards the future conservation of the species.

ACKNOWLEDGEMENTS

This research was supported by the NASA Application Program – Integrating Earth Science Enterprise Results into Project Areas Decision Support for the Albertine Rift (grant #NNS06AA06A). Many thanks go to D. Pomeroy, Director of the MUIENR databank/WCS-Uganda, for providing coordinates of crane flock and nest sightings and to A. Baccini, G. Fiske, C. Stickler, and W. Walker for advice regarding the manuscript.

REFERENCES

Alinovi L, Di Gregorio A, Latham J (2000). The FAO AFRICOVER – Eastern Africa Project. Land Cover assessment based on Remote Sensing. General description. http://www.africover.org/documents .htm.

Baccini A, Laporte N, Goetz SJ, Sun M, Dong H (2008). A first map of tropical Africa's above-ground biomass derived from satellite imagery. Environ. Res. Letters 3: 045011. doi:10.1088/1748-9326/3/4/045011.

Bartholomé E , Belward AS (2005). GLC2000: A new approach to global land cover mapping from Earth observation data. Int. J. Remote Sensing, 26(9): 1959-1977.

Beilfuss RD, Dodman T, Urban E (2007). The status of cranes in Africa in 2005. Ostrich, 78(2): 175-184.

BirdLife International (2009). Species factsheet: *Balearica regulorum*. Downloaded from http://www.birdlife.org.

Carswell M, Pomeroy D, Reynolds J, Tushabe H (2005). The bird atlas of Uganda. British Ornithologist Union, London.

Elith J, Graham CH, Anderson RP, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton J, Townsend Peterson A, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, and Zimmermann NE (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography, 29: 129-151.

Gibson L, Barrett B, Burbidge A (2007). Dealing with uncertain absences in habitat modeling: a case study of a rare ground-dwelling parrot. Divers. Distribut., 13(6): 704-713.

Hernandez PA, Franke I, Herzog SK, Pacheco V, Paniagua L, Quintana HL, Soto A, Swenson JJ, Tovar C, Valqui TH, Vargas J, Young BE (2008). Predicting species distributions in poorly-studied landscapes. Biodivers. Conserv., 17: 1353-1366.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, and Jarvis A (2005). Very high resolution interpolated climate surfaces for global land areas. Available at http://www.worldclim.org. Cited 24 March 2009. Int. J. of Climatol., 25: 1965-1978.

Hutchinson GE (1957). Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22: 415-427.

Kruskal WH and Wallis WA (1952). Use of ranks in one-criterion analysis of variance. J. of the Am. Statist. Assoc., 47: 583-621.

Meine CD , Archibald GW (1996). The cranes - status survey and conservation action plan. Gland, Switzerland, and Cambridge, U.K. Int. Union for Conserv. of Nature and Natural Res.

Muheebwa-Muhoozi J (2001). The status of the Grey Crowned Crane, *Balearica regulorum* in Uganda, with special reference to breeding. Ostrich Suppl., 15: 122-125.

Olupot W, Mugabe H, Plumptre AJ (in press). Species conservation on human-dominated landscapes: the case of crowned-crane breeding and distribution outside protected areas in Uganda. Afr. J. Ecol. (in press).

Olupot W, Plumptre AJ (2006). The status of Crowned-Cranes in Uganda: A national assessment of breeding, population distribution, and threats. Unpublished Wildlife Conservation Society report.

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr., 34: 102-117.

Phillips SJ, Dudik M, and Schapire RE (2004). A maximum entropy approach to species distribution modeling. In: Proceed. of the 21st Int. Conf. on Machine Learning, ACM Press, New York, pp: 655-662.

Phillips SJ, Anderson RP, Schapire RE (2006). Maximum entropy modeling of species geographic distributions. Ecol. Modeling, 190: 231-259.

Phillips SJ, Dudik M (2008). Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography, 31: 161-175.

Plumptre AJ, Davenport TRB, Behangana M, Kityo R, Eilu G, Ssegawa P, Ewango C, Meirte D, Kahindo C, Herremans M, Kerbis Peterhans J, Pilgrim J, Wilson M, Languy M, and Moyer D (2007). The Biodiversity of the Albertine Rift. Biol. Conserv., 134: 178-194.

Pomeroy D (1980). Aspects of the ecology of Crowned Cranes *Balearica regulorum* in Uganda. Scopus, 4: 29-35.

Pomeroy D (1987). The ecology and status of Crowned Cranes in East Africa. In: Archibald GW and Pasquier RF (eds) Proceedings of the 1983 International Crane Workshop. International Crane Foundation, Wisconsin, USA. pp. 323-330.

R Development Core Team (2009). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-9000051-07-0, http://www.R-project.org.

United States Department of State (USDS) (2008). United States Department of State background notes. http://www.state.gov/r/pa/ei/bgn/2963.htm.

Walkinshaw LH (1964). The African crowned cranes. Wilson Bull. 76(4): 355-377.

Ward DF (2006). Modelling the potential geographic distribution of invasive ant species in New Zealand. Biol. Invasions 9(6): 723-735.

Wiley EO, McNyset KM, Peterson AT, Robins CR, Stewart AM (2003). Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. Oceanography 16: 120-127.

Zar JH (1999). Biostatistical analysis. 4th ed. Upper Saddle River, NJ Prentice Hall.