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Known and potential distributions of the African *Ciconia miscroscelis* and Asian *C. episcopus* Woollyneck Storks

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Abstract Range-wide distribution patterns and environmental requirements of the African *Ciconia microscelis* and Asian *C. episcopus* Woollyneck Storks are poorly understood, which has confounded the ability to develop empirical conservation status assessments for either species. We collated thousands of records for each species to create the first objective distribution maps, and used these data to model environmental suitability at the continental and regional scales in Africa and Asia with the machine-learning program MaxEnt. We found the African Woollyneck to be fairly widespread in southern and East Africa but its distribution in West Africa was fragmented. The Asian Woollyneck had a widespread distribution in south Asia, an isolated population segment in Cambodia and Vietnam, and was sparsely distributed on the southeast Asian islands. Predictions of suitable distributions and responses to climate variables in the MaxEnt models were scale-dependent for both species. Annual and seasonal precipitation were most important in Africa, and the most influential variables differed across Asian models. Field studies testing these findings will bolster the knowledge of ecological requirements, as well as help determine how responses to environmental variation influence population dynamics. While our findings indicate neither species are of immediate conservation concern, there is evidence of population declines and range fragmentation and contractions in some regions. Understanding factors that have caused these changes is especially important in the face of ongoing environmental change on both continents.

Keywords Climate, environmental requirements, land cover, precipitation, temperature.

Introduction

Storks remain a poorly-studied group of waterbirds despite their charismatic appeal. Over thirty years ago Luthin (1987) called this to attention yet still the basic ecology of most species remains unknown. While many African and Asian species have large extents of occurrence, population status and trends and patterns of distribution are often unclear. Inadequate data about these make it difficult to assess species-environment relationships and how individual species are responding to a growing number of threats, thereby presenting a challenge for the development of empirical conservation assessments and strategies (Farashi and Alizadeh-Noughani 2019).

Wetlands are among the most threatened habitats on earth (Junk *et al.* 2013), and as predominantly wetland birds, storks face associated threats,

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including habitat degradation and loss, prey depletion, and climate change. There is growing evidence in Asia, however, that some storks and other waterbirds do well in agricultural landscapes where natural wetlands are maintained primarily for human use within a mosaic of traditional agriculture (Sundar 2006; Kim *et al*. 2008; Masahiro *et al*. 2010; Wood *et al*. 2010; Sundar 2011b; a; Sundar and Kittur 2013; Kamaruddin *et al*. 2017; Koju *et al*. 2019; Ghimire *et al*. in press), yet comparable research from Africa is lacking. Also lacking is information about the ecological requirements of storks and their responses to climate change on both continents. In the Sahel region of West Africa, there is evidence of local extirpations and population declines of several species due to long-term drought related to climate change and anthropogenic landscape alteration (Zwarts *et al*. 2009; Gula *et al*. 2019). The only study to address the threat of climate change for Asian storks was on the Oriental White Stork *Ciconia boyciana*, in which it was found habitat suitability could decline by as much as 80% without conservation action under future climate projections (Zheng *et al*. 2016).

Until recently, the African *Ciconia microscelis* and Asian *C. episcopus* Woollyneck Storks were treated as a single species despite disjunct geographic ranges with no connectivity (Bannerman 1953; del Hoyo *et al*. 2014). The African species occurs throughout sub-Saharan Africa, excluding the dry southwestern subcontinent. The Asian species is found in south and southeast Asia, including the Philippines and Indonesian islands (except Borneo). Within each species' range, patterns of occurrence are not understood except that distribution is fairly patchy, and there is considerable variation in density and flock size with location and season in south Asia (Kittur and Sundar 2020). Both species are described as inhabiting wet grasslands and wetlands, often near open forest (Hancock *et al*. 1992), and Asian Woollynecks also commonly use agricultural areas (Holmes 1977; Sundar 2006; Ghimire *et al*. in press). To date, the only study to provide insight into landscape patterns of woollynecks was in north India, where Asian Woollynecks exhibited scale-dependent patterns with higher abundance in areas with more and larger wetlands (Sundar and Kittur 2013). Migration in Africa has been inferred from influxes of observations and large gatherings (commonly 100 - 300, max. 500 - 1,000; Bulmahn and Bulmahn 1985 in Herremans *et al*. 1996) during the southern wet season (November - May; Benson *et al*. 1971; Irwin 1981; Aspinwall 1987; Herremans *et al*. 1996). However, any aspects of migration beyond seasonal influxes and aggregations are unknown. In Africa, breeding occurs during the respective regional dry season and ends around the onset of the rains, ranging from November - March north of the equator (Brown and Britton 1980; Nikolaus 1987) and August - December south of the equator (Herremans *et al*. 1996; Berruti 1997; Parker 2005). Conversely, breeding in south Asia occurs during the rains from July - October (Hancock *et al*. 1992; Ishtiaq *et al*. 2004; Sundar 2006; Ghimire *et al*. in press). Evidence of seasonal movements or migration in south Asia is now increasing, with some areas witnessing drastic reductions in stork numbers during the rainy season (Mandal *et al*. 2020), and others having fewer storks during the summer (March - June; Sundar 2006; Kittur and Sundar 2020; Roshnath and Greeshma 2020).

Along with poorly-understood distribution patterns, the contrary seasonality of breeding between sister species raises questions about the environmental requirements of the woollyneck storks, especially how similar their niches are to one another. These questions have important conservation implications in the face of the environmental change their wetland and agricultural habitats have and are experiencing. In particular, such information would greatly contribute to the development of conservation assessments and strategies, as the status of the African Woollyneck is uncertain and in need of assessment. Although the Asian Woollyneck has been recently reassessed with a preliminary decision to be downgraded on the IUCN Red List (Sundar 2020), there is still much to learn about population dynamics, distribution, and the environmental processes that influence them. Therefore, we developed maps of known distribution for both species and compared them to the IUCN maps to assess occurrence more precisely. We also modeled potential distribution and environmental relationships to assess determinants of distribution. Our hypothesis was that environmental variables influencing distribution would differ between the two species given the contrasting breeding seasonality, implicit differences in ecology, and variations in human land use on each of the two continents; and that responses to the variables would vary by species.

Methods

Range-wide locality data from eBird (eBird 2020) and the Global Biodiversity Information Facility (GBIF.org 2020) were collated and vetted for both woollyneck species. A variety of additional sources were used for the African Woollyneck, including the West African Bird Database (WABDaB 2020), the National Geographic Okavango Wilderness Project (M. Mills, unpub. data), the West African Ornithological Society's journal Malimbus, the Southern African Bird Atlas Project (SABAP) 1 (Harrison *et al*. 1997), SABAP2 (ongoing effort), and country-specific bird atlases: Benin and Togo (Dowsett-Lemaire and Dowsett 2019), Botswana (Penry 1994), eSwatini (formerly Swaziland; Parker 1994), Ethiopia and Eritrea (Ash and Atkins 2009), Ghana (Dowsett-Lemaire and Dowsett 2014), Kenya (Lewis and Pomeroy 1989), Malawi (Dowsett-Lemaire and Dowsett 2006), Mozambique (central and southern; Parker 1999; 2005), Somalia (Ash and Miskell 1983; 1998), Sudan (including South Sudan; Nikolaus 1987), Tanzania (N. Baker, unpub. data), Uganda (Carswell *et al*. 2005), and Zambia (Dowsett *et al*. 2008). To a lesser extent, records were located by tracing citations from known literature used by Gula *et al*. (2019). Additional records for the Asian Woollyneck were found in the journal Forktail as well as traced through citations therein. Data used for other papers in this issue of *SIS Conservation* were also used for the analyses, especially the following papers: Katuwal *et al*. (2020), Kittur and Sundar (2020), and Win *et al*. (2020). Photographs available on the internet with locational details were also collated by volunteers and data from nearly 1,000 individual records were included for this analysis (see also Sundar 2020). For both species, in cases where records were manually traced in the literature, locations were geo-referenced as precisely as possible given the available descriptions. A detailed list of sources is available upon request. It should also be noted that we were unable to obtain data from International Waterbird Counts, which could increase the extent of occurrence.

Maps of known distribution were developed in QGIS 3.12 (QGIS 2020) at a 0.5° resolution because most African atlases did not provide a higher resolution. The Sudan atlas used a 1° resolution and most of the data compiled for it were historic, thus it was only used for considering historic distribution. Records were categorized as 'historic' if they occurred prior to 1970 and 'recent' from 1970 - 2020. In cases where years of occupied atlas cells were unclear, they were defaulted to the recent period given their more recent compilations. Therefore, it is possible the recent distributions may be an overestimate of modern occurrence in some African countries.

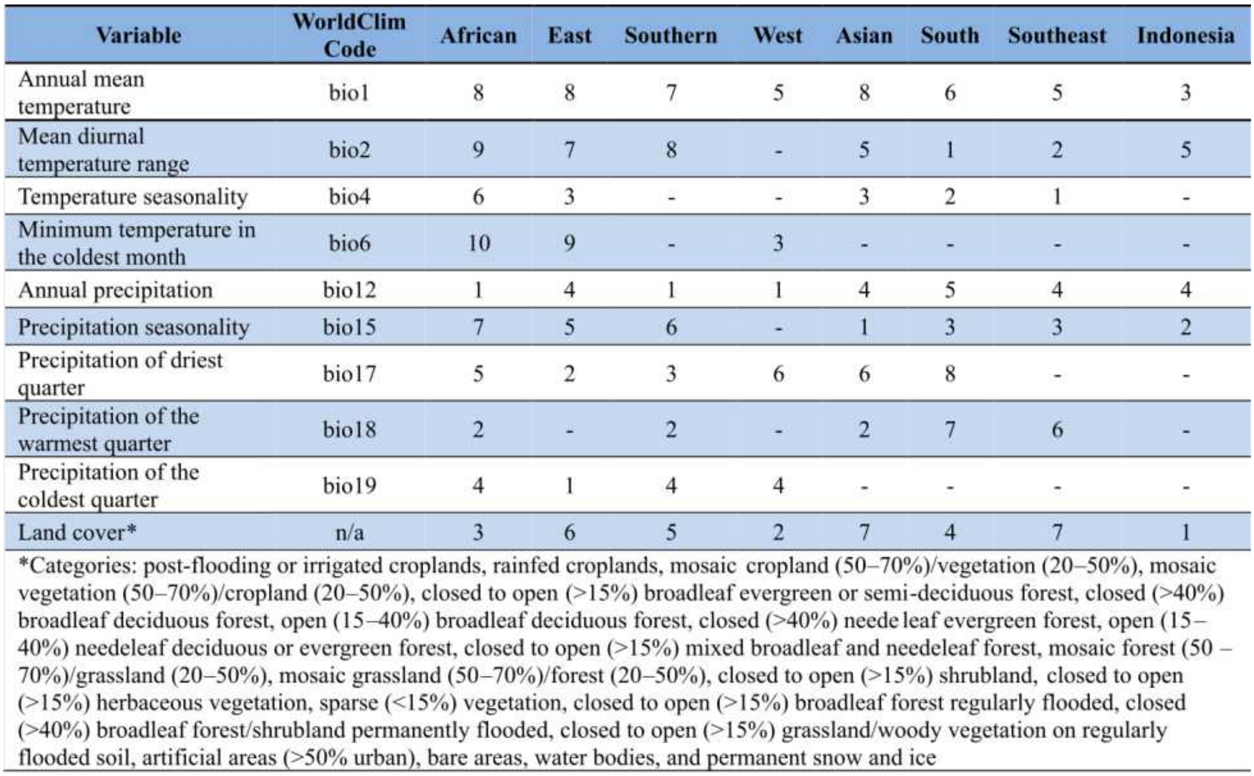
Environmental distribution models were developed at a spatial resolution of 0.67° (10 arcminutes) to account for imprecision in geo-referenced records and because of the large scale of the models. As most atlases provided distributions at resolutions coarser than 0.67°, only geo-referenced point records were used for African modeling. When atlases provided detailed localities in the text, these records were used, however. One exception was SABAP2, which mapped distribution at 0.33° (5 arcminutes), which is smaller than the distribution model resolution. Nearly all data for the Asian Woollyneck were geo-referenced point records aside from several historic ones that were only mapped at the 0.5° resolution due to less precise locality descriptions. Geo-referenced records for both species were filtered to one per 0.67° cell so as to prevent false cross-validation in the model replicate tests (see below). The geographic extent of geo-referenced locality data was buffered by 450 km to define the model extent. Given the lack of information on woollyneck movement, this buffer size was chosen based on the approximate distance between the most outlying record in central Pakistan and the nearest record at the edge of the range in India. This same exercise was not possible in Africa because the patchiness of occurrence made identifying outlying records difficult; therefore, the same buffer was applied to both species. Theoretically, the size of the buffer is meant to characterize the distance a vagrant or dispersing woollyneck could travel and thus habitat in that area would be available to them. For the Asian Woollyneck model, however, the outlying records in Pakistan and China were not buffered because regular occurrence in Pakistan is unclear and the record in China represents vagrancy, so we did not want to overestimate the area available to storks. Additionally, the model extent was cut off at the northern Nepalese border in the Himalayas (elevation ≥ 5,000 m). The highest altitudes recorded for this species have been 3,540 m in Nepal (Ghale and Karmacharya 2018) and 3,790 m in China (Burnham and Wood 2012), so using the edge of the Tibetan Plateau as a cut off for the model provides a reasonable buffer in light of potential unrecorded occurrences.

Distribution of potentially suitable areas was modeled using variables from the WorldClim 2.1 database (Fick and Hijmans 2017) and land cover from the GlobCover project (ESA and UCL 2010; Bontemps *et al*. 2011). The WorldClim variables represent annual trends and extremes in precipitation and temperature while GlobCover provides vegetation cover at a 1 km spatial resolution. For more detailed descriptions of WorldClim variables see the database webpage (WorldClim 2020). To convert the GlobCover layer to the model resolution, the 1 km raster was resampled by the majority of values in a 0.67° cell; the land cover input used herein represents the dominant classification per cell. For each species' independent range, WorldClim (including elevation) variables with Pearson correlation coefficients > 0.75 were eliminated, and only uncorrelated ones were used in the models (Table 1).

A model of suitable continent-wide distribution for each woollyneck was developed using MaxEnt, a statistical machine-learning tool that outperforms similar methods in predicting species distributions (Elith *et al*. 2006; Phillips *et al*. 2006; Elith *et al*. 2010). While many modeling methods require presence-absence data of varying quality (primarily when it comes to true absences), the utility of MaxEnt is in its use of presence-only data to predict potential distributions and estimate non-linear relationships between presence records and a set of environmental variables (Phillips *et al*. 2006; Elith *et al*. 2010). The environmental conditions at the presence locations are considered samples of the realized niche, so the output of a distribution model represents an approximation of the realized niche (Phillips *et al*. 2006). Along with spatial predictions of distribution, MaxEnt generates model-derived response curves that plot bivariate relationships between probability of occurrence (i.e. suitability) and a given environmental variable, with other variables held constant at their means. The MaxEnt algorithm uses the area under the receiver operating curve, known as AUC, as a metric for assessing predictive capacity of models. Essentially, AUC provides the probability that a known presence observation will be selected over a random background observation (Fielding and Bell 1997; Jorge *et al*. 2013). Thus, models that perform better than random will have an AUC that falls between 0.5 and 1.0, with values closer to 1.0 indicating better predictive capacity of the input variables (Fielding and Bell 1997; Phillips and Dudík 2008). Models using population demographics, such as distribution of nesting locations, can further assist in improving the specific needs of each species. For woollynecks, such high resolution data is absent and we restrict analyses in this study to sightings of the species notwithstanding demography.

Fifty replicate models were run for each species and averaged due to the different learning paths the MaxEnt algorithm takes in each run. Running a high number of replicate models has two advantages: (1) it allows averages of AUC and variable contributions to be estimated due to slight variations in the algorithm of each individual model, and (2) it tests each model's predictions against the others using a cross-validation technique, which is beneficial when sample sizes may be small (Phillips 2017). The influence of each variable on distribution was assessed using a jackknife test of AUC, whereby each model was re-tested with one variable removed to determine the subsequent drop in AUC (Elith *et al*. 2010; Farashi and Alizadeh-Noughani 2019). Fifty replicates of three regional models were subsequently developed for each species after the continental models indicated smaller scale variation in environmental relationships. African data were divided into East, Southern, and West, and Asian data were divided into South, Southeast, and Indonesia based on visual clustering of records. Similar to the continental models, variables correlated at the regional scale were removed, resulting in non-identical input variables for each model. Spatial predictions of potential continental and regional distributions are reported, incorporating the cloglog threshold for

Table 1. Uncorrelated environmental variables used in the species-specific environmental distribution models and jackknife test importance ranks. Cells with (-) indicate those variables were eliminated from the model after a correlation test.



Variable	WorldClim Code	African	East	Southern	West	Asian	South	Southeast	Indonesia
Annual mean temperature	bio1	8	8	7	5	8	6	5	3
Mean diurnal temperature range	bio2	9	7	8	-	5	1	2	5
Temperature seasonality	bio4	6	3	-	-	3	2	1	-
Minimum temperature in the coldest month	bio6	10	9	-	3	-	-	-	-
Annual precipitation	bio12	1	4	1	1	4	5	4	4
Precipitation seasonality	bio15	7	5	6	-	1	3	3	2
Precipitation of driest quarter	bio17	5	2	3	6	6	8	-	-
Precipitation of the warmest quarter	bio18	2	-	2	-	2	7	6	-
Precipitation of the coldest quarter	bio19	4	1	4	4	-	-	-	-
Land cover*	n/a	3	6	5	2	7	4	7	1

*Categories: post-flooding or irrigated croplands, rainfed croplands, mosaic cropland (50–70%)/vegetation (20–50%), mosaic vegetation (50–70%)/cropland (20–50%), closed to open (>15%) broadleaf evergreen or semi-deciduous forest, closed (>40%) broadleaf deciduous forest, open (15–40%) broadleaf deciduous forest, closed (>40%) needeleaf evergreen forest, open (15–40%) needeleaf deciduous or evergreen forest, closed to open (>15%) mixed broadleaf and needeleaf forest, mosaic forest (50 – 70%)/grassland (20–50%), mosaic grassland (50–70%)/forest (20–50%), closed to open (>15%) shrubland, closed to open (>15%) herbaceous vegetation, sparse (<15%) vegetation, closed to open (>15%) broadleaf forest regularly flooded, closed (>40%) broadleaf forest/shrubland permanently flooded, closed to open (>15%) grassland/woody vegetation on regularly flooded soil, artificial areas (>50% urban), bare areas, water bodies, and permanent snow and ice maximum test sensitivity plus specificity generated by MaxEnt (De Barros Ferraz *et al*. 2012; Jorge *et al*. 2013; Kebede *et al*. 2014) as a lower end cutoff, below which conditions are likely unsuitable (Phillips 2017). Sensitivity is the probability that a model correctly predicts an observation of a species, and specificity is the probability it correctly predicts an absence (Liu *et al*. 2011). Finally, response curves from respective models are reported and compared qualitatively.

Results

Known distribution

Qualitatively, the map of known distribution of the African Woollyneck matched the extent of occurrence from the IUCN map very closely (Figure 1). However, distribution was sparse outside several southern and East African countries. Recent distribution in West Africa appeared especially fragmented, and most historic records were from central Africa, namely the Democratic Republic of Congo (DRC). The known Asian Woollyneck distribution did not agree as well with the IUCN map (Figure 2). In particular, there were differences in India, Pakistan, Myanmar, Thailand, Indonesia, and the Philippines. The updated range in India extended further east than the IUCN distribution suggests, and the range on Sumatra extended further north. Only four records exist for Pakistan and it is unclear how many of these were vagrants. Porter and Aspinall (2010) considered the species a vagrant in Iran despite the lack of acceptance of one record from the southeast due to lack of details (Khaleghizadeh *et al*. 2011). We could find no further occurrence in Iran, however. No records were found in eastern and far southern Myanmar either. The majority of records from the Philippines were from the historic period, all dating to before 1910. Of the scant records from Thailand that we located, only one observation of three storks in 1995 was during the recent period. Delacour and Greenway (1940) described encountering woollynecks sparingly along the Mekong in Laos, but a precise area was not provided. Nevertheless, a centralized 0.5° cell was mapped as occupied in the general region for visual purposes only because this record represents the only known occurrence of the species from northern Laos. Additionally, a record from the northern Thailand-Laos border also suggests historic presence in the region.

Species distribution models

The average AUCs were 0.80 for the African model (Figure 3) and 0.76 for the Asian model (Figure 4), indicating good predictive capacity for both species. For the African Woollyneck, the

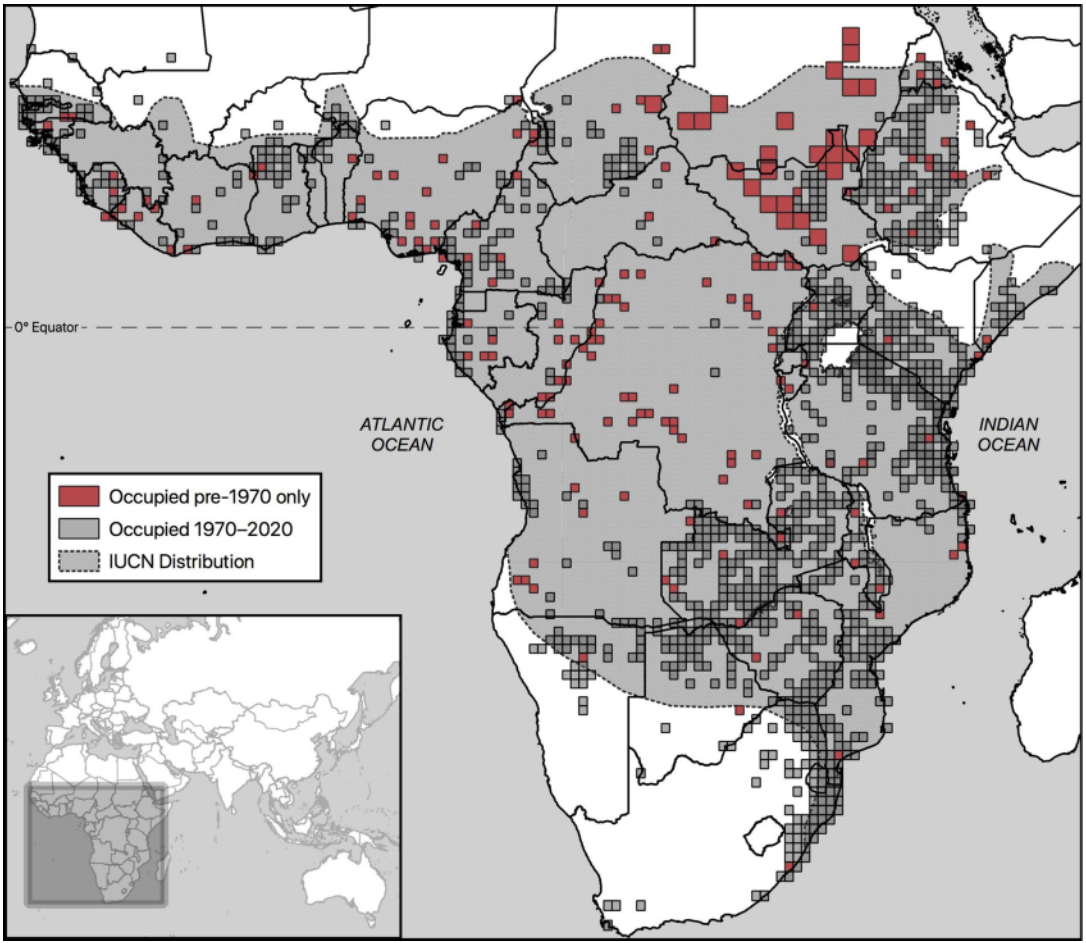


Figure 1. Known records of historic (pre-1970) and recent (1970 – 2020) occurrence of the African Woollyneck with the IUCN distribution map for comparison. The Sudan atlas (Nikolaus 1987) is represented by 1° x 1° cells, which was the highest resolution in which these data were available. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

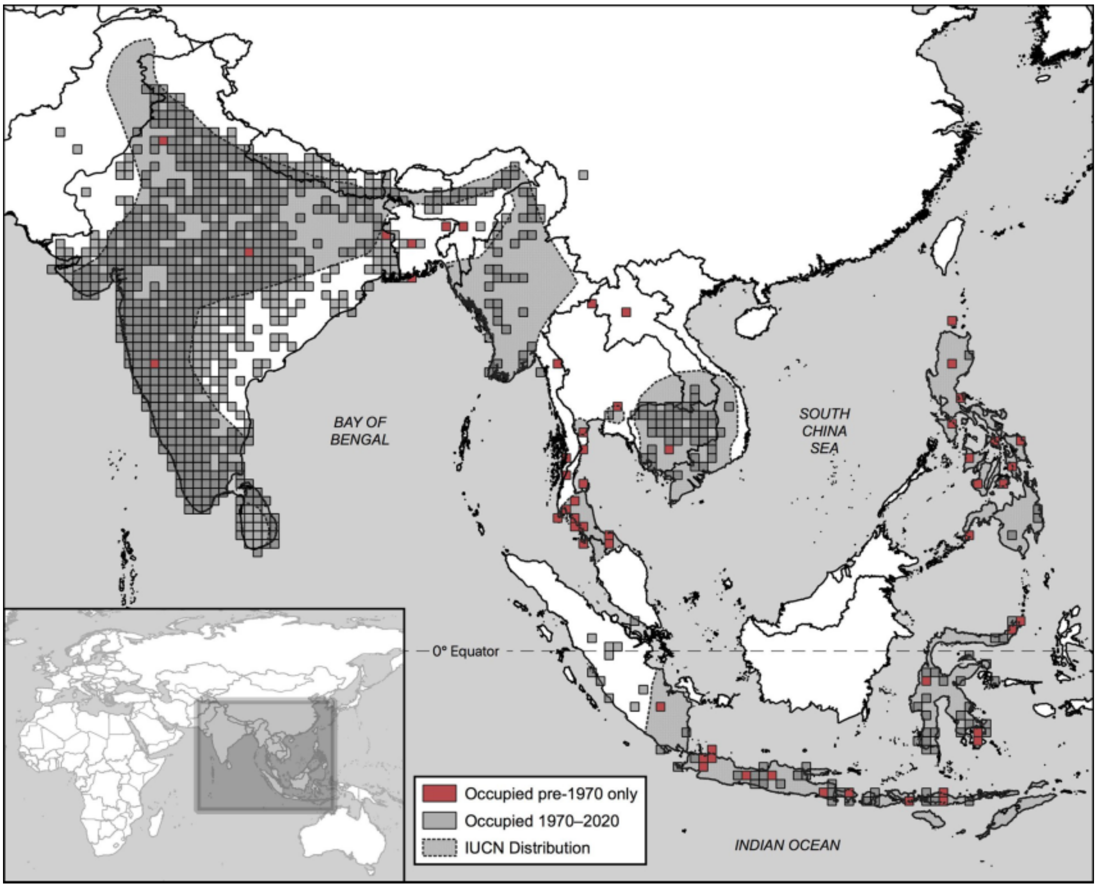


Figure 2. Known records of historic (pre-1970) and recent (1970 – 2020) occurrence of the Asian Woollyneck with the IUCN distribution map for comparison. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

jackknife test showed annual precipitation had the greatest influence on distribution followed by precipitation in the warmest quarter and land cover (Table 1). Precipitation seasonality was the most influential variable in Asia, followed by precipitation in the warmest quarter, temperature seasonality, and annual precipitation. Additionally, the Asian model AUC decreased the most when temperature seasonality was omitted, indicating this variable has the most information not present in others. The models showed contrasting responses to high levels of annual precipitation between the species but similar responses below c. 2,000 mm (Figure 5). Similarly, as precipitation in the warmest quarter increased, the responses of each species diverged. The African species showed an optimal range of precipitation seasonality, which contrasted with the near-logistic response to seasonality in Asia. In Asia there was a lower threshold for precipitation in the driest quarter, and the African model showed an optimal range. Both species had similar responses at high annual mean temperatures, with an apparent threshold at c. 28 - 29° C, but the responses were different at low temperatures, likely reflecting different available conditions on the two continents. Responses to temperature seasonality were generally similar, and there was similarity between the species at higher diurnal temperature ranges. Regarding land cover, the African Woollyneck was positively associated with permanently flooded closed forest/shrubland, regularly flooded grassland with woody vegetation, and urban areas (artificial surfaces) while the Asian Woollyneck was positively associated with urban areas (artificial surfaces) and a mosaic of natural vegetation (50 - 70%) and cropland (20 - 50%).

The African Woollyneck's approximately bimodal response to annual precipitation and the finding that the Asian Woollyneck likely occurs in three disjunct distribution segments led us to develop three smaller scale regional models for each species. The West African regional model (AUC = 0.83) predicted more widespread suitable areas than at the continental scale while in East (AUC = 0.90) and Southern Africa (AUC = 0.85) suitable areas were more limited despite slightly lower cloglog thresholds (Figure 3). Annual precipitation was most important in Southern and West Africa but precipitation in the coldest and driest quarters ranked higher than annual precipitation in East Africa (Table 1). In East and Southern Africa, the jackknife tests also showed AUC decreased the most when annual precipitation was removed, indicating it has the most information not present in other variables. In West Africa, AUC decreased the most when land cover was removed. Land cover played a weaker role in East and Southern Africa, but in West Africa woollynecks responded negatively both to agricultural and closed forest categories. Responses to annual precipitation were similar in East and Southern Africa but the West African model showed a positive relationship well above the optimal range for the other regions (Figure 6). West Africa also showed a negative relationship with precipitation in the dry quarter, which was the opposite of the responses in the other regions. East Africa showed the opposite relationship to precipitation in the coldest quarter compared to the other regions.

The Southeast model (AUC = 0.90) had the highest predictive capacity of the Asian regional models, but the South (AUC = 0.76) and Indonesian (AUC = 0.75) models performed fairly well. The Southeast and Indonesian model predictions contrasted with the continental model in that suitable areas were more widespread at the regional scale (Figure 4). Additionally, suitable areas in Thailand were much more limited in the regional model. The jackknife test for the South Asian model showed temperature seasonality and diurnal temperature range to be of equal importance, followed by precipitation seasonality. The model AUC decreased the most when temperature seasonality was removed. The Southeast model showed temperature seasonality to be the most important variable, ranking significantly higher than others. The model AUC also decreased the most when temperature seasonality was removed. In Indonesia precipitation seasonality and land cover ranked equally as the most important variables, but AUC decreased the most when mean annual temperature was removed. Response to increasing temperature seasonality was negative overall in the South model, while the Southeast model showed optimal ranges of temperature and precipitation seasonality (Figure 7). Response to precipitation seasonality varied greatly between the regional models. The response to land cover in the South model was not very different from the continental model, but in Southeast Asia the highest probability of occurrence was in closed evergreen forests and open broadleaf forests, and to a lesser extent in a mosaic of natural vegetation (50 - 70%) and cropland (20 - 50%). The Indonesian model showed the highest probability of occurrence in rainfed croplands and a mosaic of natural vegetation and cropland.

Discussion

This study is the first to empirically map known distributions, model potentially suitable areas, and

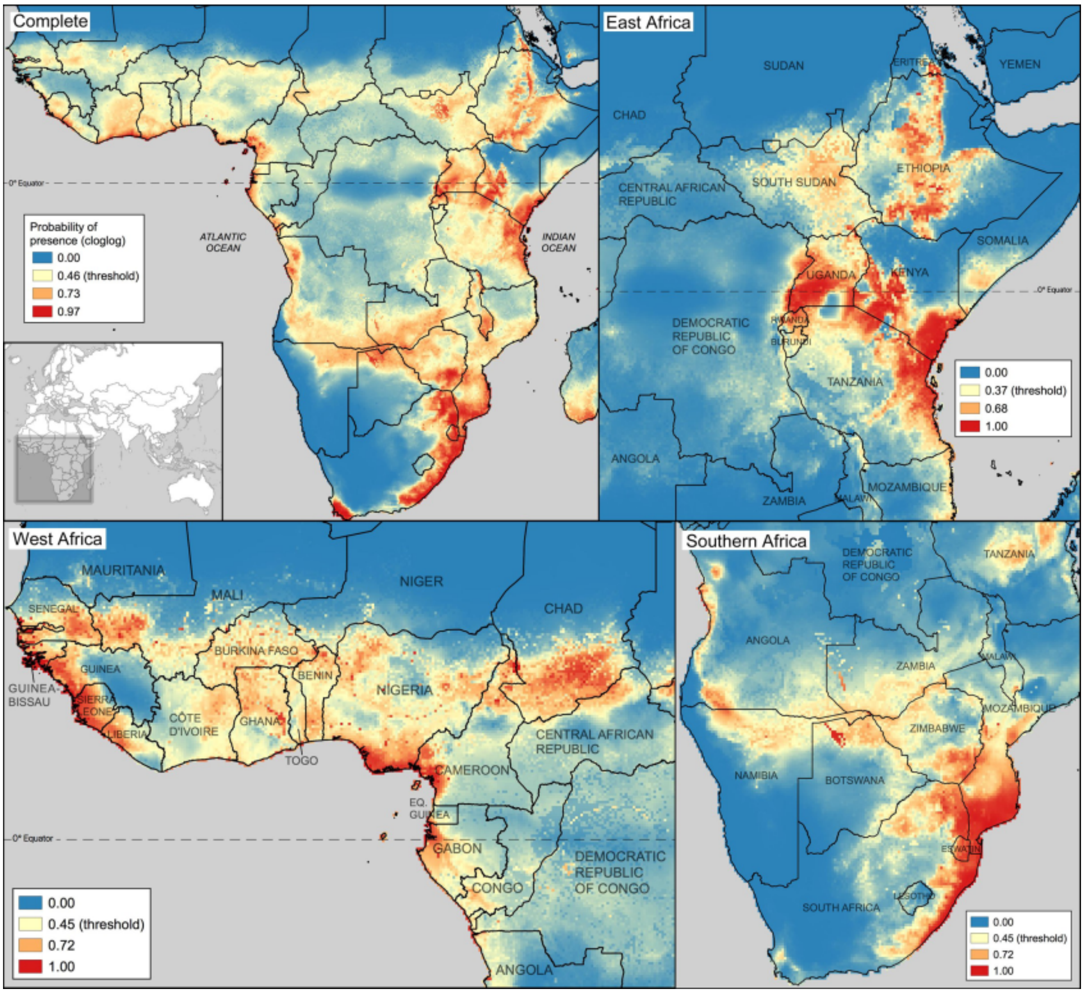


Figure 3. Average suitability predictions from 50 model replicates for the African Woollyneck at the continental and regional scale. Areas with predictions below the cloglog thresholds are likely unsuitable based on the input variables. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

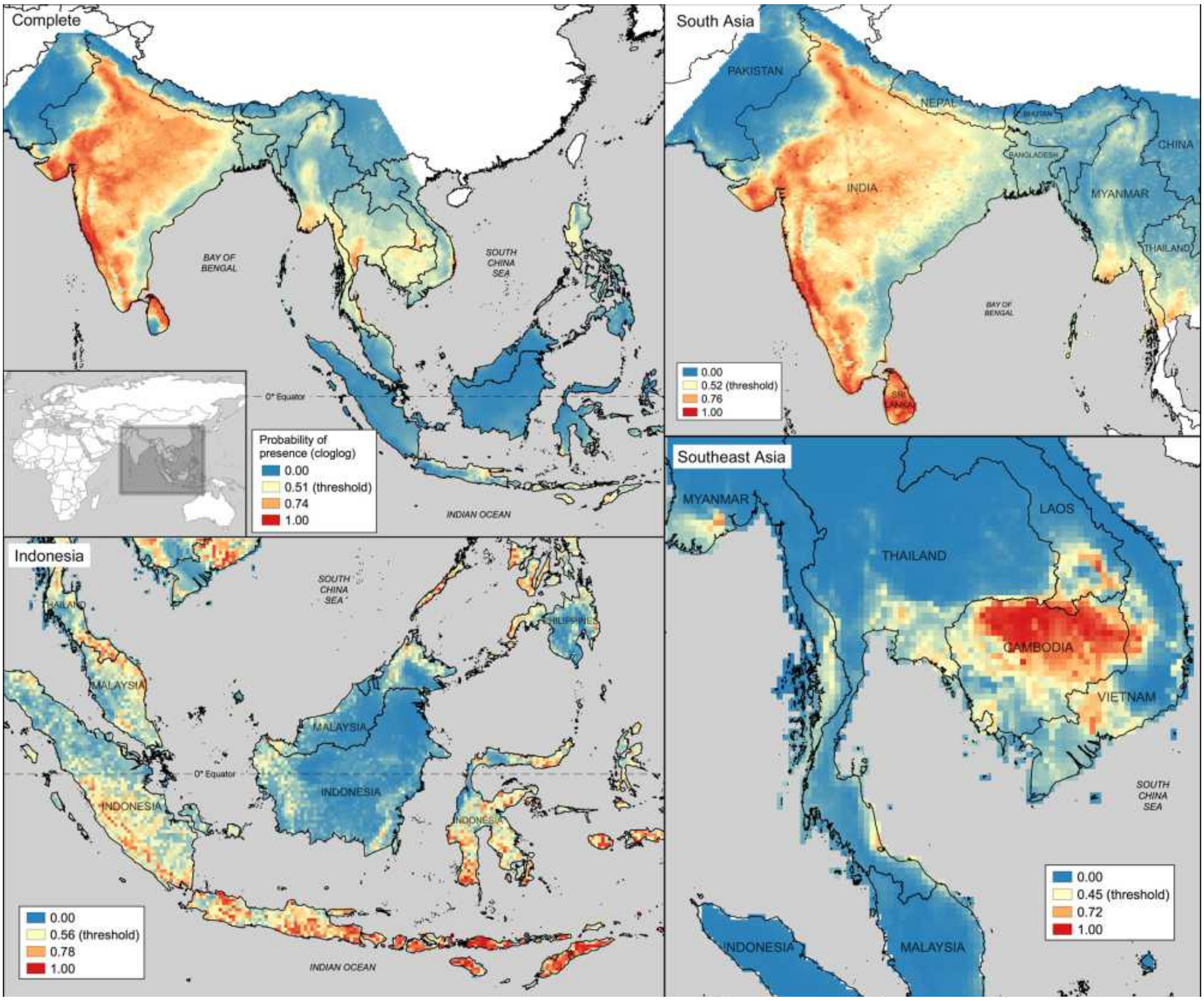


Figure 4. Average suitability predictions from 50 model replicates for the Asian Woollyneck at the continental and regional scale. Areas with predictions below the cloglog thresholds are likely unsuitable based on the input variables. Note: country borders (sourced from www.hub.arcgis.com) are purely for display purposes and do not reflect the authors' particular support for or against existing national claims on international borders.

assess environmental determinants of range-wide distributions of the African and Asian Woollynecks. The development of both continental and regional models has helped characterize what variables are important for each species, which has particularly high value in the face of ongoing and future environmental change. The models also provide for a comparison between sister species on separate continents, although inherent variation in predictor values between the continents is likely responsible for some of the interspecific differences. The predictive capacities of the models indicate there are also other factors that influence distribution not accounted for in the models, and further field studies on woollyneck ecology can help increase this growing area of knowledge. However, one shortcoming is that we did not include any temporal scale to the models, which would be important for both species since they appear to undertake seasonal movements in some regions. Indeed, temporal variation in environmental conditions influences species distributions (Andrew and Fox 2020), and recent research has demonstrated divergence in seasonal climatic niches of some migratory birds, including the White Stork *C. ciconia* (Fandos *et al.* 2020; Ponti *et al.* 2020).

The differences between the continental and regional models highlight that predicting suitable areas for woollynecks is scale dependent. Studies at smaller scales than in this study have found that as model extent increases, model predictive capacity improves (Connor *et al.* 2019; Khosravi *et al.* 2019), which is the opposite of what we found for both stork species. All of the African and one of the Asian regional models were more parsimonious (i.e. higher AUCs and fewer environmental variables) than the respective continental models, suggesting smaller scale environmental variations are important determinants of distribution for woollynecks. However, we did not test varying cell size in conjunction with varying scale, which can influence model accuracy as well (Connor *et al*. 2019). An important caveat of our regional models is that, although they shared some common input variables, the elimination of correlated variables made it so all the models did not have identical combinations of inputs. While this represents an obvious limitation on comparison between models, it was necessary to avoid spurious model outputs using correlated variables. Therefore, this must be kept in mind in light of our interpretations and comparisons of the different models.

Outside its core distribution from Ethiopia to eastern South Africa, the African Woollyneck occurs relatively sparsely despite the extent of suitable conditions predicted elsewhere in the two model scales. There are several possible explanations for the lack of records from such areas: (1) poor ornithological coverage in countries that have experienced civil unrest in recent decades, such as Angola, Côte d'Ivoire, Nigeria, and South Sudan; (2) coverage biased toward protected habitat, especially in West Africa, has prevented woollynecks from being recorded in agricultural areas, which can still provide habitat (W.R.J. Dean, pers. obs.); or (3) there may be biotic factors such as interspecific interactions that exclude them from some areas. Future surveys in such areas will help test the accuracy of the model predictions and these possibilities. The limited number of occupied cells in the DRC exclusively from the historic period is very similar to what was found for the Saddle-billed Stork *Ephippiorhynchus senegalensis* (Gula *et al*. 2019). It is unclear if this reflects decreased coverage in the recent period or real declines in the country, perhaps due to environmental changes in an already-marginal region. The low suitability in each of the regional models for the DRC may indicate conditions have changed since the historic period when occurrence was more widespread. Similar research on the distributions and environmental associations of other sympatric storks may help provided insight about this part of Africa.

The approximately bimodal response of the African Woollyneck to annual precipitation is not intuitive and led us to investigate regional distribution suitability. Most of the continent receives less than 2,000 mm of rain annually except parts of West Africa. And indeed, the division into three regional models demonstrated woollynecks in West Africa are more likely to occur in areas with higher precipitation. This can be attributed to two potentially interacting factors: (1) the greater availability of high rainfall areas in the region, and (2) the inclusion of the much drier southern Sahara Desert along the distribution periphery, where conditions are markedly different from presence records. The response to high rainfall there makes the absence from the DRC all the more curious given the similarity in climatic conditions to West Africa and land cover in other occupied areas. It may be that rapid recent habitat changes, such as the decrease in surface water (Gula *et al*. 2019), reduced more recent occurrence and therefore records available for modeling.

The West African model showed a negative response to increasing precipitation in the driest quarter, which was similar to the warmest quarter at the continental scale. Low seasonal rainfall and

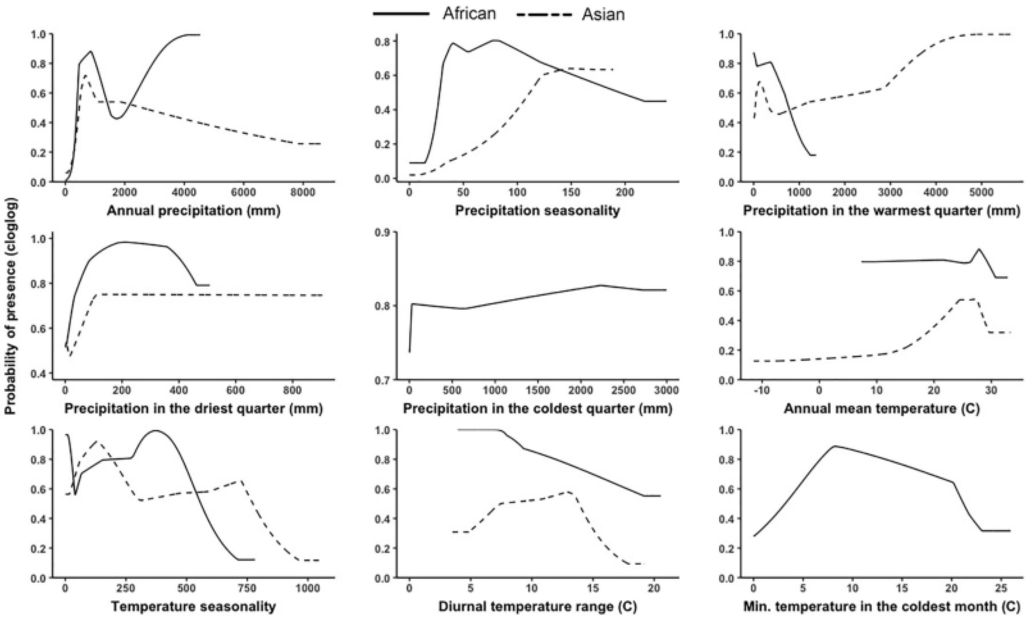


Figure 5. Response curves for both woollyneck species at the continental scale when all other variables are held constant at their means.

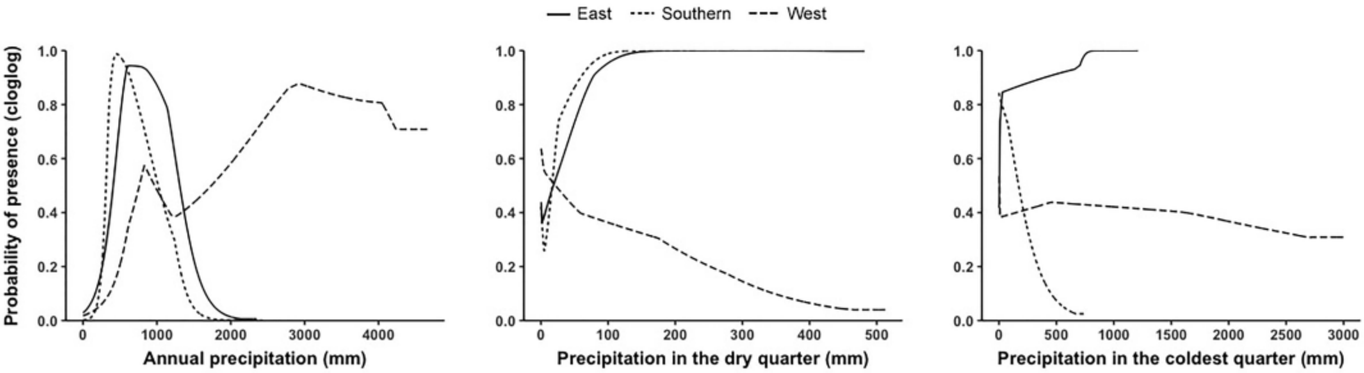


Figure 6. African Woollyneck regional response curves for three important climate variables when all other variables are held constant at their means.

water levels have been shown to be important determinants of reproductive success in the Marabou Stork *Leptoptilos crumeniferus* (Monadjem and Bamford 2009) and the Wood Stork *Mycteria americana* (Kushlan *et al.* 1975; Kushlan 1986), which rely on such conditions for increased and easy access to aquatic prey during the breeding season. Although the dietary habits of woollynecks are poorly known, the observed relationships with seasonal precipitation may be related to foraging in a similar way because breeding occurs during the dry season in most areas (Brown and Britton 1980; Nikolaus 1987; Hancock *et al.* 1992; Parker 2005). The contrast in dry quarter responses of East and Southern with West Africa is probably due to differences in regional precipitation. West Africa naturally experiences higher water levels during the dry season compared to other regions and increased rain would only make foraging more difficult. In East and Southern Africa, on the other hand, water levels are lower during the dry season due to less precipitation in the wet season and higher evaporation during the dry season compared to West Africa. So woollynecks may experience a balance between the need for rain to create foraging habitat yet not too much to make foraging more difficult. If this hypothesis is accurate, these relationships to different quarters of the year may be representative of varying breeding months regionally. Additionally, the optimal range of precipitation seasonality at the continental scale may be responsible for migration, although this needs significantly more study. It may also be that the year-round presence data used in the models do not appropriately incorporate seasonal absences from with certain conditions but testing this requires more precise and a higher quantity of data on migration timing.

The Asian Woollyneck's distribution outside Cambodia, India, Nepal, and Sri Lanka was relatively sparse. It is on the verge of extinction in the Philippines, where it is commonly hunted for food (A. Jensen, pers. comm.). Given the limited suitability in the country, it is possible a combination of environmental change and hunting is responsible for its disappearance in the last century. Curiously, however, models predicted low suitability on the island of Mindanao, where three of the four recent records come from and where a flock of five to six woollynecks have been reported from the Liguasan Marshes (A. Jensen, pers. comm.). Perhaps the species has been pushed to marginal habitat by human persecution, or biotic factors like interspecific interactions may be more important there. Aside from a single occurrence in Thailand during the recent period, the species appears to be functionally extirpated there. In addition, the regional model showed very limited suitable areas where it historically occurred in the country, so it may be that climatic and/or land cover changes and associated human-related activities are responsible for extirpation. The overall historic loss of range in southeast Asia, apparently including interior Laos and Thailand, has likely served to reduce or extinguish population connectivity in the absence of significant long-distance dispersal or movements. What role this lack of connectivity has played in regional adaptations to environmental conditions (Gaston 2003) is beyond the capabilities of the modeling in this study and therefore yet to be described.

In India and Nepal, woollyneck preference for apparently higher quality dry areas in winter and summer (Sundar 2006; Ghimire *et al.* in press), which follows the nesting season (Hancock et al. 1992; Ishtiaq *et al.* 2004; Sundar 2006), may be particularly important for hatch year storks and adults that have spent the monsoons raising chicks.

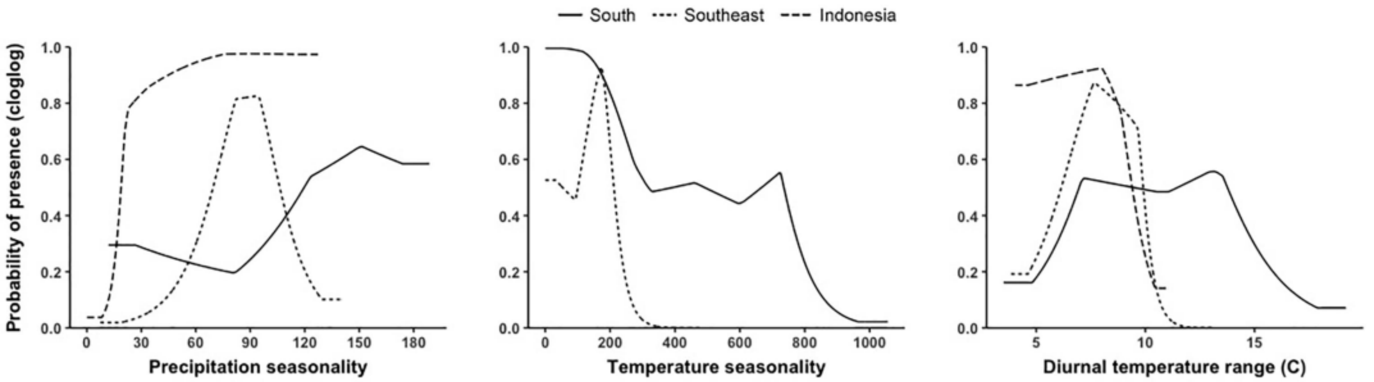


Figure 7. Asian Woollyneck regional response curves for three important climate variables when all other variables are held constant at their means.

They may require periods of reduced precipitation following the monsoons because it helps concentrate prey as water levels drop, thus increasing fitness in a similar way to decreasing seasonal precipitation in parts of Africa. This would explain the importance of precipitation seasonality in the Asian models. This hypothesis is also supported by a camera trap study that found woollyneck use of waterholes in Cambodia during the dry season declined at water depths above 40 cm (Pin *et al*. 2020). Areas with very strong seasonal precipitation would also have reduced tree cover and increased openness, which may be important for woollynecks, especially as irrigation and agriculture-related structures increase in such areas and potentially increase foraging opportunity (Sundar 2006; Katuwal *et al*. 2020; Kittur and Sundar 2020; Win *et al*. 2020). Asian Woollynecks were positively associated with human-altered areas, which agrees with observations in India, Myanmar, and Nepal where many more birds used agricultural areas, and where woollynecks were far more abundant and widespread on agricultural landscapes and outside forested protected areas (Katuwal *et al*. 2020; Kittur and Sundar 2020; Win *et al*. 2020). The positive relationship with precipitation in the warmest quarter could be related to increased stress in late summer as foraging habitat dries leading up to the breeding season. It seems apparent, therefore, that there are seasonal requirements regarding precipitation that have implications for fitness, which also likely explains seasonal variation in group size and habitat use (Sundar 2006; Kittur and Sundar 2020). Yet breeding information for Asian Woollynecks is generally scarce, so the scenario in Nepal and India may not be representative of the whole range. It is less clear why temperature seasonality was so important in the South and Southeast Asian models. While physiological limitations are possible, especially in the Himalayan foothills, it may be that prey such as frogs and insects are dependent on fairly stable temperatures, which would also explain the importance of diurnal temperature range in the same models.

Climate projections for south and southeast Asia predict increased heat stress in the near future, rainfall is predicted to decrease in southeast Asia (mainland and maritime), and there will be increased monsoon variability in south Asia (Tesfaye *et al.* 2017; Amnuaylojaroen and Chanvichit 2019). These changes will have significant consequences for the ecology of woollynecks and have the potential to cause shifts or contractions in distribution in areas that experience extreme climate fluctuations, as has been demonstrated in part of the Oriental White Stork's range (Zheng *et al.* 2016). The already small and sparsely distributed populations in mainland and maritime southeast Asia may be particularly prone to local extirpations in the face of decreased precipitation and changes in seasonality. The response of woollynecks to such changes will also significantly depend on how their prey respond.

Climate models predict decreased rainfall and increased dry spells in southern Africa and some parts of East Africa (Dosio *et al*. 2019; Gaetani *et al*. 2020; Haile *et al*. 2020). In East African countries with predicted increases in rainfall, it is unclear how woollynecks' seasonal reliance on dry conditions may affect distribution. In addition to the environmental changes the Sahel Region of West Africa has already experienced in recent decades (Zwarts *et al*. 2009), an imminent change in the region's climate state is predicted, with marked shifts in precipitation patterns over the next few decades (Gaetani *et al*. 2020). While the current study has shown suitable conditions for woollynecks to be relatively widespread in the region, the fragmented range may contribute to the susceptibility of local extirpations, which has already been found in some other storks in the region due to environmental change (Zwarts *et al*. 2009; Gula *et al*. 2019).

Although some populations of both woollyneck species may experience ecological stress in the near future, there is some evidence from both continents of their plasticity in the wake of environmental changes. In South Africa, African Woollynecks have recently colonized suburban areas, where they have been successful due to man-made wetlands and supplementary feeding at residences (Thabethe and Downs 2018) and landfills (JG, pers. obs.). This ability to use artificial habitats has allowed for an overall 11% range expansion across southern Africa (Okes *et al*. 2008). Asian Woollynecks in India, Myanmar, and Nepal are successful in a mosaic landscape of agriculture and natural wetlands (Sundar 2006; Win *et al*. 2020; Ghimire *et al*. in press). This adaptability appears to be related closely to farmer mindsets that discourage hunting. The Southeast models and data availability pointed to woollyneck occurrence in forested areas that are largely protected reserves. Hunting is far more widespread and intense in southeast Asia, matching with the modeled distributions that suggest agricultural and other human modified areas there are not suitable. However, this study found positive association with a similar mosaic in Indonesia.

Unfortunately, besides data from Kittur and Sundar's (2020) recent study, sufficient data from standardized surveys of woollynecks at scales comparable to our models do not exist for assessing correlations between population metrics (e.g. abundance, density, flock size) and suitability predictions. However, a recent meta-analysis showed a significant positive relationship between abundance and MaxEnt suitability in all cases and that scale of the models did not influence the relationship (Weber *et al*. 2017), which is therefore likely to be the case for woollynecks. Studies on spatial variation in fitness (e.g. across environmental gradients) will answer many questions about smaller scale environmental requirements and the responses of each species to change. These would be especially useful in vulnerable peripheral populations, which may have greater variability in fitness because they experience the limits of environmental tolerances (Sexton *et al*. 2009). Sufficient genetic variation at these edges, however, may also serve to facilitate favorable selection as conditions change outside historic tolerances (Kawecki 2008). In West Africa, this seems unlikely because similar fragmentation occurs with the Saddle-billed Stork (Gula *et al*. 2019) and other African storks (J. Gula, unpub. data), suggesting current and ongoing change may be too rapid for selection to keep up. The region may therefore fit Sexton *et al*.'s (2009) characterization of a range limit where adaptation is prevented by small populations and maladaptive gene flow from core populations with more favorable conditions. Genetics and movement research on woollynecks there would greatly improve the understanding of these dynamics, and a more thorough look into population sizes and trends in southeast Asia may elucidate the scenario there.

Several aspects of the results obtained from MaxEnt modeling appear crucial for conservation planning. In Africa, the strong positive associations with forested areas underscores the importance of current conservation efforts in maintaining populations of Asian Woollynecks. Though as discussed earlier, models indicate suitability in some areas where populations appear to be in decline. In southeast Asia, modeled distributions are also closely related to forested areas overlapping with the protected area network in many countries. This finding matches existing descriptions of the species requiring wetlands inside forested areas with minimal human presence. However, both field observations and outputs of modeled distributions in this study show that large numbers of woollynecks can avail of human-modified landscapes such as agriculture in many locations, but especially Myanmar, Nepal, and India. Woollynecks appear to be an ideal candidate species whose conservation requirements are relatively easy to determine using tools such as MaxEnt but will require field data to explain smaller scale nuances. Our collated data and modeled outputs suggest that neither the African nor the Asian Woollyneck have critical conservation requirements due to being widespread and being able to use areas outside of protected reserves. However, our outputs provide some cause for concern especially in central and West Africa and several southeast Asian countries. Results also signal a strong indication that projected climate change will affect both species, albeit to different extents. We suggest that our work, in combination with emerging new field-based studies, be used to carefully assess the conservation status of woollynecks, and such modeling exercises be urgently considered for similar large waterbirds.

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References

Amnuaylojaroen, T. and P. Chanvichit. 2019. Projection of near-future climate change and agricultural drought in mainland Southeast Asia under RCP8.5. *Climatic Change* 155: 175-193.

Andrew, M. E. and E. Fox. 2020. Modelling species distributions in dynamic landscapes: The importance of the temporal dimension. *Journal of Biogeography* 47: 1510-1529.

Ash, J. and J. Atkins. 2009. *Birds of Ethiopia and Eritrea: an atlas of distribution*. Christopher Helm, London, United Kingdom.

Ash, J. and J. Miskell. 1983. Birds of Somalia, their habitat, status and distribution. *Scopus Special Supplement* 1: 1-97.

Ash, J. and J. Miskell. 1998. *Birds of Somalia*. Pica Press, Sussex, United Kingdom.

Aspinwall, D. R. 1987. Movement analysis charts (MAC), comments on Woolly-necked Stork. *Zambian Ornithological Society Newsletter* 17: 106-112.

Bannerman, D. A. 1953. *The birds of West and Equatorial Africa, vol. 1*. Oliver and Boyd, Edinburgh, United Kingdom.

Benson, C. W., R. K. Brooke, R. J. Dowsett and M. P. S. Irwin. 1971. *The birds of Zambia*. Collins, London, United Kingdom.

Berruti, A. 1997. Woollynecked Stork. Pp. 89-91. In: Harrison, J., D. Allan, L. Underhill, M. Herremans, A. Tree, B. Parker, and C. Brown (eds.). *The atlas of southern African birds, vol. 1*. BirdLife South Africa, Johannesburg, South Africa.

Bontemps, S., P. Defourny, E. Van Bogaert, O. Arino, V. Kalogirou and J. R. Perez. 2011. *GlobCover 2009: Products description and validation report*. European Space Agency and Université Catholique de Louvain.

Brown, L. H. and P. L. Britton. 1980. *The breeding seasons of East African birds*. East Africa Natural History Society, Nairobi, Kenya.

Burnham, J. W. and E. M. Wood. 2012. Woolly-necked Stork *Ciconia episcopus* at Napahai wetland, Yunnan, China. *Forktail* 28: 158-159.

Carswell, M., D. Pomeroy, J. Reynolds and H. Tushabe. 2005. *The bird atlas of Uganda*. British Ornithologists' Club and British Ornithologists' Union, London, United Kingdom.

Connor, T., A. Viña, J. A. Winkler, V. Hull, Y. Tang, A. Shortridge, H. Yang, Z. Zhao, F. Wang, J. Zhang, Z. Zhang, C. Zhou, W. Bai and J. Liu. 2019. Interactive spatial scale effects on species distribution modeling: The case of the giant panda. *Scientific Reports* 9: 14563.

De Barros Ferraz, K. M. P. M., M. F. De Siqueira, E. R. Alexandrino, D. T. A. Da Luz and H. T. Z. Do Couto. 2012. Environmental suitability of a highly fragmented and heterogeneous landscape for forest bird species in south-eastern Brazil. *Environmental Conservation* 39: 316-324.

del Hoyo, J., N. J. Collar, D. A. Christie, A. Elliott and L. D. C. Fishpool. 2014. *HBW and BirdLife International illustrated checklist of the birds of the world, vol. 1: Non-passerines*. Lynx Edicions, Barcelona, Spain.

Delacour, J. and J. C. Greenway. 1940. Liste des oiseaux receuillis dans la province du Haut-Mekong et le royaume de Luang-Prabang. *L'Oiseau et la Revue Francaise d'Ornithologie* 10: 25-59.

Dosio, A., R. G. Jones, C. Jack, C. Lennard, G. Nikulin and B. Hewitson. 2019. What can we know about future precipitation in Africa? Robustness, significance and added value of projections from a large ensemble of regional climate models. *Climate Dynamics* 53: 5833-5858.

Dowsett, R. J., D. R. Aspinwall and F. Dowsett-Lemaire. 2008. *The birds of Zambia: An atlas and handbook*. Tauraco Press, Liège, Belgium.

Dowsett-Lemaire, F. and R. J. Dowsett. 2006. *The birds of Malawi: An atlas and handbook*. Tauraco Press, Liège, Belgium.

Dowsett-Lemaire, F. and R. J. Dowsett. 2014. *The birds of Ghana: An atlas and handbook*. Tauraco Press, Liège, Belgium.

Dowsett-Lemaire, F. and R. J. Dowsett. 2019. *The birds of Benin and Togo: An atlas and handbook*. Tauraco Press, Liège, Belgium.

eBird. 2020. *Basic dataset, version: EBD_relAug-2020*. Cornell Lab of Ornithology, Ithaca, New York, United States of America.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data.

Ecography 29: 129-151.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee and C. J. Yates. 2010. A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions* 17: 43-57.

ESA and UCL. 2010. *GlobCover. European Space Agency and Université Catholique de Louvain*. http://due.esrin.esa.int/page_globcover.php, accessed 30 March 2020.

Fandos, G., S. Rotics, N. Sapir, W. Fiedler, M. Kaatz, M. Wikelski, R. Nathan and D. Zurell. 2020. Seasonal niche tracking of climate emerges at the population level in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences* 287: 20201799.

Farashi, A. and M. Alizadeh-Noughani. 2019. Niche modelling of the potential distribution of the Egyptian Vulture *Neophron percnopterus* during summer and winter in Iran, to identify gaps in protected area coverage. *Bird Conservation International* 29: 423-436.

Fick, S. E. and R. J. Hijmans. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302-4315.

Fielding, A. H. and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38-49.

Gaetani, M., S. Janicot, M. Vrac, A. M. Famien and B. Sultan. 2020. Robust assessment of the time of emergence of precipitation change in West Africa. *Scientific Reports* 10: 1-10.

Gaston, K. J. 2003. *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford, United Kingdom

GBIF.org. 2020. *GBIF occurrence download*. https://doi.org/10.15468/dl.6scxkb, accessed 4 August 2020.

Ghale, T. R. and D. K. Karmacharya. 2018. A new altitudinal record for Asian Woollyneck *Ciconia episcopus* in South Asia. *BirdingASIA* 29: 96-97.

Ghimire, P., N. Pandey, Y. P. Timilsina, B. S. Bist and K. S. G. Sundar. in press. Woolly-necked Stork activity budget in lowland Nepal’s farmlands: The influence of wetlands, seasonal crops and human proximity. *Waterbirds*.

Gula, J., F. Weckerly and K. S. G. Sundar. 2019. The first range-wide assessment of Saddle-billed Stork *Ephippiorhynchus senegalensis* distribution. *Ostrich* 90: 347-357.

Haile, G. G., Q. Tang, S. M. Hosseini-Moghari, X. Liu, T. G. Gebremicael, G. Leng, A. Kebede, X. Xu and X. Yun. 2020. Projected impacts of climate change on drought patterns over East Africa. *Earth's Future* 8: 1-23.

Hancock, J. A., J. A. Kushlan and M. P. Kahl. 1992. *Storks, ibises and spoonbills of the world*. Academic Press, London, United Kingdom.

Harrison, J., D. Allan, L. Underhill, M. Herremans, A. Tree, B. Parker and C. Brown. 1997. *The atlas of southern African birds, vol. 1*. BirdLife South Africa, Johannesburg, South Africa.

Herremans, M., M. Joos-Vandewalle and W. D. Borello. 1996. The status of the Woollynecked Stork *Ciconia episcopus* in Botswana. *Ostrich* 67: 80-83.

Holmes, D. A. 1977. Faunistic notes and further additions to the Sumatran avifauna. *British Ornithologists' Club Bulletin* 97: 68-71.

Ishtiaq, F., A. R. Rahmani, S. Javed and M. C. Coulter. 2004. Nest-site characteristics of Black-necked Stork (*Ephippiorhynchus asiaticus*) and White-necked Stork (*Ciconia episcopus*) in Keoladeo National Park, Bharatpur, India. *Journal of the Bombay Natural History Society* 101: 90-95.

Jorge, M. L. S. P., M. Galetti, M. C. Ribeiro and K. M. P. M. B. Ferraz. 2013. Mammal defaunation as surrogate of trophic cascades in a biodiversity hotspot. *Biological Conservation* 163: 49-57.

Junk, W. J., S. An, C. M. Finlayson, B. Gopal, J. Květ, S. A. Mitchell, W. J. Mitsch and R. D. Robarts. 2013. Current state of knowledge regarding the world’s wetlands and their future under global climate change: a synthesis. *Aquatic Sciences* 75: 151-167.

Kamaruddin, Z., M. Farah Shafawati and M. N. Shukor. 2017. Distribution and habitat selection of the Asian Openbill (*Anastomus oscitans*) in Peninsular Malaysia. *Malayan Nature Journal* 69: 169-181.

Katuwal, H. B., H. S. Baral, H. P. Sharma and R.-C. Quan. 2020. Asian Woollynecks are uncommon on the farmlands of lowland Nepal. *SIS Conservation* 2: xx-xx.

Kawecki, T. J. 2008. Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics* 39: 321-342.

Kebede, F., P. D. Moehlman, A. Bekele and P. H. Evangelista. 2014. Predicting seasonal habitat suitability for the critically endangered African wild ass in the Danakil, Ethiopia. *African Journal of Ecology* 52: 533-542.

Khaleghizadeh, A., D. A. Scott, M. Tohidifar, S. B. Musavi, M. Ghasemi, M. E. Sehhatisabet, A. Ashoori, A. Khani, P. Bakhtiari, H. Amini, C. Roselaar, R. Ayé, M. Ullman, B. Nezami and F. Eskandari. 2011. Rare birds in Iran in 1980–2010. *Podoces* 6: 1-48.

Khosravi, R., M.-R. Hemami and S. A. Cushman. 2019. Multi-scale niche modeling of three sympatric felids of conservation importance in central Iran. *Landscape Ecology* 34: 2451-2467.

Kim, S. K., N. S. Kim, S. Cheong, Y. H. Kim, H. C. Sung and S. R. Park. 2008. A habitat analysis of the historical breeding sites of Oriental White Storks (*Ciconia boyciana*) in Gyeonggi and Chungcheong Provinces, Korea. *Journal of the Korean Geographic Information Society* 11: 125-137.

Kittur, S. and K. S. G. Sundar. 2020. Density, flock size and habitat preference of Woolly-necked Storks *Ciconia episcopus* in agricultural landscapes of south Asia. *SIS Conservation* 2: xx-xx.

Koju, R., B. Maharjan, K. R. Gosai, S. Kittur and K. S. G. Sundar. 2019. Ciconiiformes nesting on trees in cereal-dominated farmlands: Importance of scattered trees for heronries in lowland Nepal. *Waterbirds* 42: 355-453.

Kushlan, J. A. 1986. Responses of wading birds to seasonally fluctuating water levels: Strategies and their limits. *Colonial Waterbirds* 9: 155-162.

Kushlan, J. A., J. C. Ogden and A. L. Higer. 1975. *Relation of water level and fish availability to Wood Stork reproduction in the southern Everglades, Florida*. United States Geological Survey. Tallahassee, Florida, United States of America.

Lewis, A. and D. Pomeroy. 1989. *A bird atlas of Kenya*. A.A. Balkema, Rotterdam, The Netherlands.

Liu, C., M. White and G. Newell. 2011. Measuring and comparing the accuracy of species distribution models with presence–absence data. *Ecography* 34: 232-243.

Luthin, C. S. 1987. Status of and conservation priorities for the world's stork species. *Colonial Waterbirds* 10: 181-202.

Mandal, J., L. M. Abraham and R. Bhaduri. 2020. A note on the temporal and spatial distribution of Asian Woollyneck in Assam, India. *SIS Conservation* 2: xx-xx.

Masahiro, F., L. Sang Don, K. Masayuki and Y. Hoshiko. 2010. Bird use of rice fields in Korea and Japan. *Waterbirds* 33: 8-29.

Monadjem, A. R. A. and A. J. Bamford. 2009. Influence of rainfall on timing and success of reproduction in Marabou Storks *Leptoptilos crumeniferus*. *Ibis* 151: 344-351.

Nikolaus, G. 1987. Distribution atlas of Sudan's birds with notes on habitat and status. *Bonner Zoologische Monographien* 25: 1-322.

Okes, N. C., P. A. R. Hockey and G. S. Cumming. 2008. Habitat use and life history as predictors of bird responses to habitat change. *Conservation Biology* 22: 151-162.

Parker, V. 1994. *Swaziland bird atlas 1985–1991*. Websters, Mbabane, Swaziland.

Parker, V. 1999. *The atlas of the birds of Sul do Save, Southern Mozambique*. Avian Demography Unit and Endangered Wildlife Trust, Cape Town, South Africa.

Parker, V. 2005. *The atlas of the birds of Central Mozambique*. Avian Demography Unit and Endangered Wildlife Trust, Cape Town, South Africa.

Penry, H. 1994. *Bird atlas of Botswana*. University of Natal Press, Pietermaritzburg, South Africa.

Phillips, S. J. 2017. *A brief tutorial on Maxent*. http://biodiversityinformatics.amnh.org/open_source/maxent/, accessed 15 August 2020.

Phillips, S. J., R. P. Anderson and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231-259.

Phillips, S. J. and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31: 161-175.

Pin, C., D. Ngoprasert, T. N. E. Gray, T. Savini, R. Crouthers and G. A. Gale. 2020. Utilization of waterholes by globally threatened species in deciduous dipterocarp forest of the Eastern Plains landscape of Cambodia. *Oryx* 54: 572-582.

Ponti, R., A. Arcones, X. Ferrer and D. R. Vieites. 2020. Seasonal climatic niches diverge in migratory birds. *Ibis* 162: 318-330.

Porter, R. and S. Aspinall. 2010. *Birds of the Middle East*. Christopher Helm, London, United Kingdom.

QGIS. 2020. *QGIS Geographic Information System v. 3.12*. Open Source Geospatial Foundation Project. http://qgis.org, accessed 27 April 2020.

Roshnath, R. and P. Greeshma. 2020. Status of Woolly-necked Storks in Kerala, south-western India. *SIS Conservation* 2: xx-xx.

Sexton, J. P., P. J. McIntyre, A. L. Angert and K. J. Rice. 2009. Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics* 40: 415-436.

Sundar, K. S. G. 2006. Flock size, density and habitat selection of four large waterbirds species in an agricultural landscape in Uttar Pradesh, India: Implications for management. *Waterbirds* 29: 365-374.

Sundar, K. S. G. 2011a. Agricultural intensification, rainfall patterns, and large waterbird breeding success in the extensively cultivated landscape of Uttar Pradesh, India. *Biological Conservation* 144: 3055-3063.

Sundar, K. S. G. 2011b. Farmland foods: Black-necked Stork *Ephippiorhynchus asiaticus* prey items in an agricultural landscape. *Forktail* 27: 98-100.

Sundar, K. S. G. 2020. Special section editorial: Woolly-necked Stork–a species ignored. *SIS Conservation* 2: xx-xx.

Sundar, K. S. G. and S. Kittur. 2013. Can wetlands maintained for human use also help conserve biodiversity? Landscape-scale patterns of bird use of wetlands in an agricultural landscape in north India. *Biological Conservation* 168: 49-56.

Tesfaye, K., P. H. Zaidi, S. Gbegbelegbe, C. Boeber, D. B. Rahut, F. Getaneh, K. Seetharam, O. Erenstein and C. Stirling. 2017. Climate change impacts and potential benefits of heat-tolerant maize in South Asia. *Theoretical and Applied Climatology* 130: 959-970.

Thabethe, V. and C. T. Downs. 2018. Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa. *Urban Ecosystems* 21: 965-973.

WABDaB. 2020. Woolly-necked Stork (*Ciconia episcopus*), West African Bird Database (WABDaB). https://www.wabdab.org/db/species?18319=&d-49653-o=1&pid=viewspecies&pid=viewspecies&d-49653-p=1&d-49653-s=1 - url, accessed 25 March 2020.

Weber, M. M., R. D. Stevens, J. A. F. Diniz-Filho and C. E. V. Grelle. 2017. Is there a correlation between abundance and environmental suitability derived from ecological niche modelling? A meta-analysis. *Ecography* 40: 817-828.

Win, M. S., A. M. Yi, T. S. Myint, K. Khine, H. S. Po, K. S. Non and K. S. G. Sundar. 2020. Comparing abundance and habitat use of Woolly-necked Storks *Ciconia episcopus* inside and outside protected areas in Myanmar. *SIS Conservation* 2: xx-xx.

Wood, C., Y. Qiao, P. Li, P. Ding, B. Lu and Y. Xi. 2010.

Implications of rice agriculture for wild birds in China. *Waterbirds*: *The International Journal of Waterbird Biology* 33: 30-43.

WorldClim. 2020. *Bioclimatic variables*. https://www.worldclim.org/data/bioclim.html, accessed 5 October 2020.

Zheng, H., G. Shen, L. Shang, X. Lv, Q. Wang, N. McLaughlin and X. He. 2016. Efficacy of conservation strategies for endangered oriental white storks (*Ciconia boyciana*) under climate change in Northeast China. *Biological Conservation* 204: 367-377.

Zwarts, L., R. G. Bijlsma, J. van der Kamp and E. Wymenga. 2009. *Living on the edge: Wetlands and birds in a changing Sahel*. KNNV Publishing, Zeist, The Netherlands.