ABSTRACT

DETERMINING DRIVERS FOR WILDEBEEST (CONNOCHAETES TAURINUS) DISTRIBUTION IN THE MASAI MARA NATIONAL RESERVE AND SURROUNDING GROUP RANCHES

by Meghan Marie Sheehan

A current assessment of wildebeest (*Connochaetes taurinus*) distribution throughout the Masai Mara National Reserve (MMNR) and adjoining group ranches has not been investigated for over 15 years. This information is greatly needed to protect populations of wildebeest and their ranges. MaxEnt, a statistical model, was used to evaluate influential factors for wildebeest distribution and predict suitable habitats throughout the northern extent of the Serengeti National Park, the MMNR, and adjoining group ranches. There were thirty five abiotic and biotic variables used to create two distribution models in MaxEnt across the study area for two different time periods. Both models performed well with training AUCs >0.80. Precipitation seasonality, isothermality, and distances to lodges were the greatest contributing variables to wildebeest distribution in the November model. Kauth-Thomas wetness, annual temperature range, and distances to camps were significant factors for wildebeest distribution in the June model. Predictive maps from the June 2010 model revealed higher concentrations of predicted habitat suitability in areas historically impacted by the expansion of mechanized farming practices. It is recommended that the MMNR collaborate with local group ranch conservancies to secure seasonal dispersal sites for wildebeest and impose land use policies in unprotected areas. Results from MaxEnt also revealed that bioclimatic variables and soil and plant moisture are significant contributors to wildebeest distributions. The MMNR should evaluate the potential effects imposed by climate change to wildebeest distributions and populations.
DETERMINING DRIVERS FOR WILDEBEEEST (CONNOCHAETES TAURINUS)
DISTRIBUTION IN THE MASAI MARA NATIONAL RESERVE AND
SURROUNDING GROUP RANCHES

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This Thesis titled

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Introduction

1.1 Threats to Global Ungulate Populations

Documented declines of global ungulate populations emphasize a need to investigate potential consequences of anthropogenic activities and environmental influences on ungulate ranges and habitats. From their circumpolar ranges in the Arctic to protected boundaries of Kruger National Park in South Africa, the western United States, and foothills of Mongolia, global populations of ungulates have been declining at an alarming rate for the past quarter century (Bolger et al., 2008; Vors & Boyce, 2009). Much of this decline has been attributed to anthropogenic influences on the landscape and biological responses to climate change (Vors & Boyce, 2009). This raises further questions regarding consequences of fluctuating populations and its effect on ecosystem processes (Bolger et al., 2008).

Ungulate populations are often cited as ecosystem engineers for their role in shaping surrounding landscapes (McNaughton & Georgiadis, 1986). Through the process of facilitation, ungulate grazing enhances forage quality for other grazing mammals by their influence on grass productivity (McNaughton, 1976). Thus, threats, declines, and even eradication of large ungulate populations impart potential negative effects on other grazing herbivore populations and plant productivity within the shared ecosystem. In addition to environmental implications, declines in ungulate populations also impart negative consequences to socioeconomic benefits of surrounding native populations by means of hunting, animal husbandry, and tourism (Vors & Boyce, 2009; Estes and East, Unpublished).

Competition with Homo sapiens for resources and occupiable land remains the current greatest threat to populations of large ungulate communities and their habitats (Estes and East, Unpublished). Habitat fragmentation and loss of migratory passageways have been attributed to extensive anthropogenic activities within ungulate ranges. Land cover and land use change (Sawyer et al., 2013; Ogutu et al., 2011), encroachment of agro pastoral activity onto grazing lands (Estes & East, 2009 Unpublished), deterrents within migratory routes such as fences, roads, and power lines (Sawyer et al., 2013), mineral extraction, forestry, and petroleum infrastructure (Vors & Boyce, 2009) have all been cited as major influences on ungulate ranges and population dynamics. Biophysical threats such as climate change are known to influence
migratory ungulate populations by imposing potential threats to food supply with changing rainfall patterns (Robinson et al., 2009) and erratic and unpredictable weather events (Vors & Boyce, 2009). Subsequently, such anthropogenic and environmental factors lead to population interferences, collapse in populations, alterations in migratory behavior (Schaefer et al., 2008) and rerouting of migratory pathways (Sawyer et al., 2013).

1.2 Conservation Challenges
There are several challenges to initiating conservation practices within protective lands for migratory groups of ungulate populations. Bolger et al. (2008) state that very few protective lands have been established worldwide that encompass entire boundaries of migratory passageways and ungulate activity. Even in protected areas such as the Serengeti-Mara Ecosystem (SME) where protected boundaries are established by the extent of wildebeest, zebra, and Thomson’s gazelle migration and activity (Bell, 1971), protection of wildlife populations throughout the ecosystem are still comprised. Within the Kenyan portion of the SME, severe declines in protected areas of the Masai Mara National Reserve (MMNR) have been observed for resident wildebeest (*Connochaetes taurinus hecki* (Neumann)) populations for the past 40 years. Since initial aerial surveys were conducted in the MMNR and adjoining group ranches in the 1970s, resident wildebeest populations have been declining at an annual rate of 8.4% (Ottichilo et al., 2001). Currently, 20,000 resident wildebeest occupy the MMNR and inner group ranches (Mara Eco-Unit), a drastic reduction from their prior populations estimates of nearly 100,000 wildebeest in the 1980s (Ottichilo, 2000). In addition to a marked reduction in resident populations, migratory ungulate populations which frequent the MMNR during the dry season have also declined (Sinclair et al., 2007).

Conservation initiatives and policies are implemented and executed within the MMNR to protect wildlife populations through anti-poaching initiatives and land use restrictions (Ogutu et al., 2011; Homewood et al., 2001), but such restrictions are not recognized within adjoining group ranches. Land use such as pastoralism, wildlife conservation, tourism, subsistence maize cultivation, and commercial wheat cultivation are thought to contribute to losses of seasonal migratory pathways and dispersal regions for resident populations (Ogutu et al., 2011). These
differences in policy initiatives and land use practices have led many to believe that it is anthropogenic activities and subsequent biological responses outside of reserve boundaries that have caused massive declines in both migratory and resident populations of wildebeest for the past 40 years (Ottichilo et al., 2001; Estes & East, 2009 Unpublished; Homewood et al., 2001). As human populations continue to increase rapidly within Kenya (Boone & Coughenor, 2001), the Narok district (Homewood et al., 2001), and surrounding MMNR buffer zones (Homewood et al., 2001), wildebeest populations continue to compete with anthropogenic activities for mobility within and around the MMNR and access to resources.

1.3 Drivers for Conservation: A Case for Wildebeest of the MMNR and Applications of Species Distribution Modeling

It is imperative to continue to monitor wildebeest populations within and around the MMNR to ensure and maintain steady populations. Wildebeest are a crucial species to the MMNR for their important role as ecosystem facilitators for other grazing herbivores and also for their contribution to tourism in particular and biodiversity in general. The annual migration of Serengeti wildebeest, zebras, and Thomson’s gazelles into the MMNR, attracts many tourists to the region (Akama, 2002), where visitors expect to witness the largest and most diverse mammal migration in the world (Bedelian, 2014). The MMNR contributes $20 million (USD) annually, approximately 8% of total revenue, to the tourism economy of Kenya (Zeppel, 2006). Revenue from tourism not only contributes to county government and workers within the reserve, but also supplements secondary incomes for neighboring pastoralist communities around the reserve through tourist-related services and activities (Homewood et al., 2001).

The Serengeti-Mara Ecosystem and the great wildebeest migration has been extensively studied, however, relationships between wildebeest distributions and their habitats throughout the Mara Eco-Unit have not been assessed for the past 15 years. Protection for wildebeest populations and their habitats requires ongoing and consistent attention. Current information is needed to ensure adequate conservation practices for managing wildebeest populations both inside protected areas and ranges outside of the reserve. Species distribution models (SDMs) can provide insight regarding spatial characteristics of a species and factors influencing their
distributions within a particular habitat (Elith & Leathwick, 2009). SDMs have been implemented to determine factors influencing distributions, highlight key areas for conservation, and project future distributions for threatened ungulate populations (Hu & Jiang, 2011; García-Marmolejo et al., 2013). This research utilizes SDMs to highlight current key areas and assess influential drivers for wildebeest distribution. This project aims to provide pertinent information needed to conserve threatened wildebeest habitats and populations throughout northern areas of the SME. The objectives of this project are to assess factors influencing wildebeest distribution and predict current suitable habitat for wildebeest throughout the MMNR and adjoining group ranches.

Literature Review

2.1 History of the MMNR and Inner Group Ranches

The MMNR was established as a national reserve in the late 1940s. In 1961, local Narok County councils took hold of park management from central government authorities (Honey, 2009). Since then, the reserve has become the most visited tourist attraction throughout East Africa, with approximately 50% of all incoming tourists to Kenya visiting the reserve (Honey, 2009). The reserve is unfenced and animals move in and out of the reserve, frequenting unprotected areas of the greater Masai Mara Ecosystem (MME) (Mundia & Murayama, 2009). Most of these wildlife dispersals occur and extend throughout the adjoining group ranches surrounding the MMNR. Historically, these lands have been preserved as communal lands for local Maasai (Honey, 2009). Under pressure of expanding population growth throughout Southern Kenya however, these areas have been transferred into privately owned land parcels (Honey, 2009). Besides restrictions on hunting, private owners of these land parcels are not governed by the same land use restrictions established within the MMNR. Private occupants are free to practice herding, small-scale farming, mechanized commercial farming, and wildlife tourism enterprises (Homewood et al., 2001). It is the subdivision, private land use practices, fragmenting and expansion of Maasai homesteads (Lamprey & Ried, 2004) that many have speculated to influence wildlife distributions within dispersal areas outside of the reserve.
2.2 Areas of Concern: Threats to Wildebeest Populations and Ranges within Adjoining Group Ranches

Since the establishment of the group ranches in 1968, surges in human populations in these areas have transformed surrounding landscapes of the MMNR. Many of these changes have been attributed to subsequent expansions of local human settlements (Lamprey & Reid, 2004) and mechanized farming practices (Mundia & Murayama, 2009; Serneels & Lambin, 2001; Ottichilo et al., 2001). In the early 1970s, the conversion of group ranch rangelands into areas primarily used for agricultural began with the transfer and partitioning of group ranch lands to local Maasai populations. Traditionally pastoralist, many newly awarded Maasai landholders found leasing their land for commercial farming opportunities more economically advantageous (Serneels & Lambin, 2001).

These practices became well established by 1984 (Serneels & Lambin, 2001) and widespread farming expansion began to transform surrounding group ranch rangelands into agriculture. The MME experienced a 10.3% increase in agricultural land cover from 1975 to 2007, resulting in an increase from 15,540 to 147,490 ha of farmland, respectively (Mundia & Murayama, 2009). Further, areas within the Loita Plains, an area historically utilized by wildebeest for grazing, breeding, and calving (Ottichilo et al., 2001), experienced rapid land use change during 1975 to 1995. Where 4,875 to 47,600 ha of the plains were converted to agriculture (Homewood et al., 2001).

Impacts on wildebeest populations and distributions from land use change are well documented and highlight enduring areas of concern for wildebeest throughout the group ranches. Ottichilo et al. (2001) found that agricultural expansion, primarily of wheat crops, within the northern and central regions of the Loita Plains (Figure 1) had the greatest impact on the continual decline of resident wildebeest densities and populations (8.4% population decline per annum from 1977 to 1997). Similarly, since peak estimates of Kenyan wildebeest populations in the late 1970s, decreases in vegetation cover resulting from both small and large-scale agricultural activities in the Loita Plains have resulted in a 77.3% decline in total resident populations from 137,740 wildebeest in 1978 to 31,300 in 1994 (Serneels & Lambin, 2001).
Impediments to historical wet seasonal ranges from agricultural expansions raise further concerns for wildebeest. Loss of access to prior ranges has resulted in the displacement of wildebeest populations to south-eastern portions of the Loita Plains and areas closer to the

Figure 1: Approximate Locations of Farmland as of 2007 Throughout Surrounding Group Ranches of the MMNR
Areas of farmland were modified from Mundia & Murayama (2009) where they determined farmland locations from land cover/use classification from remotely sensed data. Expansion of farming practices in Lemek, Olkiriaine, and Ol Kinyie (apart of northern and central portions of the Loita Plains) since the 1970’s are known to impact population dynamics, densities, and distributions of wildebeest populations. Areas highlighted in red show locations that have experienced greatest decreases in resident wildebeest densities since 1977. Wildebeest density information was adapted from Serneels & Lambin (2001).

MMNR (Serneels & Lambin, 2001). Wildebeest face greater competition for grazeable land from expanding human settlements and farming in these regions. This is evident in Koyake, an inner group ranch of the MMNR, where a growing number of wildebeest, believed to be displaced from the Loita Plains, are found (Lamprey & Reid, 2004). Throughout the wet season, Koyake supports approximately 2,000 resident wildebeest and as many as 18,100 Serengeti wildebeest.
during migratory occupation (Lamprey & Reid, 2004). As these numbers are predicted to increase due to continued displacement from agricultural areas, wildebeest face further competition for resources with an expanding human population (4.4% per annum since 1983) in Koyake (Lamprey & Reid, 2004). It is known that increases in housing density in these regions negatively impact wildlife populations. Lamprey & Reid (2004) estimate that as the construction of housing units increase in Koyake to support human population growth, wildlife populations in Koyake will see a permanent reduction, up to 40% of the current population.

2.3 Movement and Distribution of Resident and Migratory Wildebeest Populations in the Mara Eco-Unit

Approximately 20,000 resident wildebeest (Connochaetes taurinus hecki (Neumann)) and 300,000-750,000 migratory Serengeti wildebeest (Connochaetes taurinus mearnsi (Burchell)) from Tanzania occupy the Kenyan side of the SME throughout the year (Serneels & Lambin, 2001). Resident wildebeest are non-migratory, with their movements remaining local to the MMNR and surrounding group ranches (Ottichilo et al., 2001). From January to May, resident wildebeest populations occupy portions of the Loita Plains as their primary wet seasonal range for calving and grazing (Serneels & Lambin, 2001). In June, these populations move into portions of the Siana Plains for short grassland grazing. With the arrival of the dry season, resident wildebeest join migrant Serengeti wildebeest heading north from their prior wet seasonal ranges in the Serengeti National Park (SNP). From August to October, both populations concentrate in the MMNR, “spilling out” into inner group ranches of Lemek, Koyake, Ol Kinyie, and Siana (Figure 2) (Broten & Said, 1995; Ottichilo et al., 2000; Serneels & Lambin, 2001). In November, Serengeti wildebeest head back south to the SNP and Ngorongoro regions for wet season occupation.
Large-scale movements, population dynamics, and mortality rates of both migratory and resident populations into the Mara Eco-Unit throughout the dry season are believed to be driven by selective foraging strategies to meet nutrient demands during seasonal food shortages (Wilmshurst et al., 1999; Sinclair, 1979; Mduma et al., 1999). Rainfall, as a proxy for new vegetation growth, abundant plant productivity, and availability of high quality, nutrient dense grasses influence movements and distributions of wildebeest during the dry season as they try to meet adequate nutrient demands. Ottichilo (2000) found a strong correlation between dry season movements of migrant wildebeest into the Mara Eco-Unit (Figure 2) and plant productivity as indicated by NDVI. Boone et al. (2006) hypothesized that rainfall and plant productivity are the

**Figure 2: Historical Movement Patterns of Both Migratory and Resident Populations of Wildebeest throughout the Serengeti-Mara Ecosystem (SME).** Timing for movements for both populations throughout the SME is approximate and based upon historical records. Migratory wildebeest from Tanzania and resident Kenyan populations utilize the MMNR and Mara Eco-Unit throughout the dry season. With the arrival of the wet season, migrant populations head south to the Serengeti National Park. Resident populations return to their wet season ranges in the Loita Plains. Modified from Serneels & Lambin (2001). Dotted areas indicate locations of the Loita Hills.
greatest predictors for wildebeest movement throughout the Mara Eco-Unit in the dry season. Holdo et al., (2009) also support that plant productivity provides a framework for explaining large-scale wildebeest movement in the dry season. They further hypothesize that the interactions between small-scale grazing choices and the availability of high quality, nutrient appropriate grasses might better explain such seasonal movement patterns.

2.4 Species Distribution Modeling and MaxEnt
A fundamental tenant of biogeographical research is to understand why a particular species occurs throughout a certain geographic space. SDMs are mathematical tools that enable researchers to quantify and explain such relationships (Guisan & Thuller, 2005; Elith & Leathwick, 2009). SDMs utilize records containing either presence or presence/absence data for a species of interest and environmental data to predict distributions throughout a study region (Segurando & Araujo, 2004). Different types of SDMs are typically selected for their ability to successfully evaluate either presence only data (genetic algorithm for the rule-set prediction (GARP); MaxEnt) or presence/absence data (generalize additive models (GAM), generalized linear models (GLM), and artificial neural networks (ANN)) (Marmion et al., 2009). SDMs have been executed in a wide range of ecological inquiry to evaluate questions pertaining to species richness, epidemiological interactions, projecting future distributions, assessing rare species occurrence, and evolutionary programming (Miller, 2010).

The statistical program MaxEnt is a SDM that uses machine learning and a maximum entropy approach to examine spatial relationships and make predictions. MaxEnt uses algorithms to recognize patterns from values sampled from extracted background points to species presence records to establish distribution probabilities with remarkable accuracy (Bhattacharya, 2013; Merow et al., 2013). MaxEnt was chosen for this analysis due to the expansive geographic extent of the study region, for its effectiveness in predicting suitable habitats, and for its success in assessing drivers for spatial distributions of other ungulate species (Garcia-Marmolejo et al., 2013; Hu & Jiang, 2011; Hu & Jiang, 2012).
Data and Methods

3.1 Study Area

The study area (Figure 3) encompasses the extent of data points that have been collected via aerial survey by the Kenya Wildlife Service (KWS). Most of these data points extend beyond the MMNR into adjoining group ranches and The Northern Serengeti ecological unit of the Serengeti National Park (SNP). The MMNR is located in Narok District, Kenya and spans an area of 1,672 km² within the northernmost extent of the Serengeti-Mara Ecosystem (SME).

Figure 3: Study Area. The study region encompasses the extent of data collected from the Kenya Wildlife Service (KWS) for wildebeest for November 2005, November 2007, and June 2010. The MMNR and SNP are protected areas; private land use practices are restricted. Surrounding group ranches of the MMNR are not governed by similar land use restrictions. Many believe it is land use practices in the surrounding group ranches that have been influencing wildlife distributions and populations outside of the reserve.
Heavily influenced by the Inter-Tropical Convergence Zone, rainfall in the area follows a bimodal distribution with seasonal intermittent short rains in October to December and long rains in March to May (Brown & Cocheme, 1973; Ottichilo, 2000). The wet season occurs from November to June and the dry season exists from July to October (Lamprey & Reid, 2004). Eastern portions of the MME receive approximately 600mm of rainfall annually. Rainfall gradually increases to 1000mm of rainfall in western areas with the influence of Lake Victoria (Norton-Griffiths et al., 1975; Ottichilo et al., 2001). Primary vegetation cover within the MMNR is comprised of themeda grasslands, open grass plains, and savanna woodlands (Ottichiolo et al., 2001; Ogutu et al., 2008). Dwarf-shrubland and Acacia drepanolobium grasslands are found throughout the Loita Plains while Croton shrubland, grasslands, and a variety of woody species dominate the Siana Plains (Ottichiolo et al., 2001).

3.2 Data for MaxEnt Models
There were 35 abiotic and biotic used to create wildebeest distribution models in MaxEnt. Among these variables, topographic and climatic information, vegetation types, and human impact factors were used to build two initial MaxEnt models. These variables were determined to present potentially significant drivers for wildebeest movement and distribution established from prior research and literature. Variables codes and their respective descriptions and sources are found in Table 1.
3.2.1 Wildebeest Occurrence Data

Aerial survey data were obtained from the Kenya Wildlife Service (KWS) for November 2005, November 2007, and June 2010. Survey data are collected by the KWS via low flying aircrafts.
These aircrafts maintain a speed of approximately 128.75 km/hour during collection of wildlife distribution data at approximately 100m above ground. Flight transects are planned to be 1-2 km apart in a west-east or south-north orientation based upon weather conditions and terrain. Crew members count and record animals occurring within 500m from either side of the aircraft. Due to better visibility, only large herbivores populations are recorded. Population estimates and geographic locations are recorded with GPS receivers and compiled as x,y coordinate data. Summaries of each dataset for wildebeest counts can be found in Table 2.

### 3.2.2 Climate Data

There were 19 bioclimatic variables considered as environmental predictors of wildebeest distribution. The bioclimatic variables were obtained from WorldClim Version 1 (worldclim.org). WorldClim offers high resolution (1km) global climate surfaces of aggregated precipitation and temperature data collected from 1950-2000 (Hijmans et al., 2005). These datasets have been widely used in species distribution analysis for assessing impacts of climate on species and their environment (Booth et al., 2014). WorldClim variables used in each model and their respective definitions are shown in Table 1.

### Table 2: Data Collected for Wildebeest at Observance Points.

*Includes both resident and migratory populations. Data collected before migrant wildebeest returned to SNP. **Resident populations only. Data collected while residents are still occupying seasonal ranges.

<table>
<thead>
<tr>
<th>Date</th>
<th>Total Points Collected</th>
<th>Wildebeest (MIN)</th>
<th>Wildebeest (MAX)</th>
<th>Wildebeest (MEAN)</th>
<th>Wildebeest (TOTAL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>November 2005</td>
<td>129</td>
<td>3</td>
<td>7,000</td>
<td>1,170.80</td>
<td>151,033 *</td>
</tr>
<tr>
<td>November 2007</td>
<td>470</td>
<td>1</td>
<td>9,000</td>
<td>278.84</td>
<td>131,053 *</td>
</tr>
<tr>
<td>June 2010</td>
<td>276</td>
<td>1</td>
<td>600</td>
<td>68.16</td>
<td>18,111 **</td>
</tr>
</tbody>
</table>
Figure 4: Wildebeest Occurrence Points Collected from the KWS. Aerial survey data are collected via low flying aircrafts. Survey data contain geographic coordinate information and estimates of total wildebeest counted by crew members. Geographic coordinates collected from aerial surveys were used as sample files in MaxEnt.

3.2.3 Satellite Data

Landsat TM and ETM+ images for the study area were obtained from USGS Earth Explorer (earthexplorer.usgs.gov), converted to reflectance, and corrected for atmospheric effects using ENVI v5.0.3. These images were then clipped to the respective study region and projected. (Table 3). Next, Mean Normalized Difference Vegetation Index (NDVI) images were calculated from each image and NDVI images were then layerstacked. This allowed for the calculation of mean NDVI and standard deviation of NDVI for the study area. NDVI provides an estimate of vegetation biomass and establishes phenological vegetation arrangements across landscapes.
NDVI has become an important component in ecological research for examining animal interactions with their environment and population dynamics with respect to vegetation distributions (Pettorelli et al., 2005).

<table>
<thead>
<tr>
<th>November Model</th>
<th>Date</th>
<th>ID</th>
<th>Cloud Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>ETM+ L1G</td>
<td>27 January 2000</td>
<td>LE71690612000027EDC00</td>
<td>0</td>
</tr>
<tr>
<td>ETM+ L1G</td>
<td>14 February 2001</td>
<td>LE71690612001045SGS01</td>
<td>5</td>
</tr>
<tr>
<td>ETM+ L1G</td>
<td>01 February 2002</td>
<td>LE71690612002032SGS00</td>
<td>2</td>
</tr>
<tr>
<td>ETM+ L1G</td>
<td>19 January 2003</td>
<td>LE71690612003019SGS00</td>
<td>6</td>
</tr>
<tr>
<td>TM L1T</td>
<td>27 November 2009</td>
<td>LT51690612009331MLK00</td>
<td>5</td>
</tr>
<tr>
<td>TM L1T</td>
<td>30 January 2010</td>
<td>LT51690612010030MLK00</td>
<td>0</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>June Model</th>
<th>Date</th>
<th>ID</th>
<th>Cloud Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TM L1T</td>
<td>01 June 2008</td>
<td>LT51690612008153MLK00</td>
<td>16</td>
</tr>
<tr>
<td>TM L1T</td>
<td>06 July 2009</td>
<td>LT51690612009187MLK00</td>
<td>18</td>
</tr>
<tr>
<td>TM L1T</td>
<td>12 July 2011</td>
<td>LT51690612011193MLK01</td>
<td>2</td>
</tr>
<tr>
<td>OLI_TIRS_L1T</td>
<td>01 July 2013</td>
<td>LC81690612013182LGN00</td>
<td>5</td>
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<tr>
<td>OLI_TIRS_L1T</td>
<td>02 June 2014</td>
<td>LC81690612014153LGN00</td>
<td>1</td>
</tr>
</tbody>
</table>

In addition to NDVI, a Kauth-Thomas transformation was applied to June and November images in order to compute KT Brightness (KTB), KT Greenness (KTG), and KT Wetness (KTW) images. These transformations offer a more in-depth assessment of vegetation characteristics in relation to ecological phenomena (Crist & Cicone, 1984). A digital elevation model (DEM) was obtained from METI/NASA’s ASTER Global Digital Elevation Model (METI NASA, 2009). Slope and aspect were derived from the DEM in ArcGIS 10.2. Data pertaining to land cover type was obtained from GlobeLand30 (globallandcover.com). The GlobeLand30 is a global land cover product. The GlobeLand30 product was created utilizing images obtained from Landsat ETM+, Landsat TM, and China Environmental Disaster Alleviation Satellite (HJ-1) satellites. GlobeLand30 contains 10 land cover types at a 30m
resolution (globallandcover.com). All final data layers derived from satellite images were imported into ArcGIS 10.2, projected to UTM Zone 36S, and resampled to a 1km resolution.

3.2.4 Other Data

Geographic Information Systems (GIS) data for the MMNR pertaining to locations of lodges, gates, villages, camps, roads, and rivers were obtained from Serengetidata.org for this analysis (Figure 5). The Serengeti Data site is a collaborative website between Tanzania National Parks, Tanzania Wildlife Research Institute, and the Frankfurt Zoological Society. Their GIS data have been collected for Serengeti, Masai Mara, and Ngorongoro regions. Lodges, gates, villages, camps, and roads were deemed anthropogenic indicators as they show human influence and modification to the natural landscape. Lamprey & Reid (2004) found that areas with greater rates of housing density in Koyake had a greater negative impact on populations of surrounding wildlife. Although GIS data pertaining to housing density were not available for this project, locations of lodges, gates, villages, and camps served as a proxy for this measure. Further, Sawyer et al. (2013) found that areas with greater infrastructure intensity from roads and powerlines were more likely to interfere with migratory behavior of ungulates. GIS data were projected to UTM Zone 36S and clipped to the study region. For each of these datasets ArcGIS 10.2 was used to calculate the Euclidean distance from each feature across a 1km by 1km spatial resolution grid. Cattle density was also used in each model. Due to competition for grazing land, potential increases in livestock densities are thought to impact wildlife distribution of herbivores within the MMNR and surrounding group ranches (Lamprey & Reid, 2004). Aerial survey counts from the KWS for November 2005, November 2007, and June 2010 were used to create density grids of cattle for each year. Kernel densities for each dataset were created in ArcGIS 10.2 at 1km resolutions.
3.3 Preparing Data for MaxEnt Modeling

Anniversary survey data for November 2005 and November 2007 show approximate locations of both migratory and resident wildebeest during the early onset of the wet season. These data were combined into a single dataset using ArcGIS 10.2. It is important to ensure spatial independence of geographic occurrence points of species data before executing an SDM (Elith & Leathwick, 2009). ‘Moran’s I’ Tool was executed in ArcGIS 10.2 and spatially auto correlated points were removed from each dataset containing geographic wildebeest locations. These final locations were used as species’ input data for November and June MaxEnt models. Areas within a study
region that are sampled more often than other regions create a sample selection bias and are known to greatly influence presence-only models (Elith et al., 2011). A bias grid was created in ArcGIS 10.2. Flight paths showing locations of the aircraft during aerial survey sampling for each dataset were provided by the KWS. Using these path lines, an inverse distance grid was created at a 1km resolution. Areas closer to the paths received a higher grid value to indicate a higher level of sampling effort in those areas. Distances further away from the paths received a lower grid value to indicate less sampling intensity. Highly correlated variables are known to impact the interpretability of contributions of variables to the final model (Philips, 2005; Baldwin, 2009). All variable layers were sampled at wildebeest location points in ArcGIS 10.2. Cross correlation of each variable was assessed in IBM SPSS Statistics 21. Variable relationships exhibiting Pearson’s correlations $r > |0.80|$ were removed from their respective model. After removal of highly correlated variables, trial models were run for the November and June models using MaxEnt. version 3.3.3k ([www.cs.princeton.edu/~schapire/maxent](http://www.cs.princeton.edu/~schapire/maxent)). Final models for each dataset were then run following criteria set forth by Evangelista et al. (2009) and York et al. (2011). Results from the initial trial runs were used to determine variables contributing $<1\%$ to the models. These variables were then removed from the final models. Summaries of final input variables used in each model can be found in Table 4. All models were run with the following parameters: random test percentage = 25 ($25\%$ of the presence data were allocated as the training data to evaluate model performance.); maximum number of background points = 10,000; Maximum iterations = 5000. Regularization multipliers were then tested from 1-30 to produce smoother response variable curves and account for any overfitting of the models. A regularization multiplier of 10 was used for both November and June models. Each model was run with all features engaged.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>November Combined 2005 &amp; 2007</td>
<td>BIO₂, BIO₁₃, TKB, VegMap, Rivers, BIO₃, BIO₁₅, Lodges, STDNDVI</td>
</tr>
<tr>
<td>June 2010</td>
<td>BIO₃, BIO₇, KTB, Camps, Rivers, BIO₅, BIO₁₉, Roads, Villages, MeanNDVI, KTW, Roads, Villages, StdNDVI</td>
</tr>
</tbody>
</table>
(linear, quadratic, product, threshold, and hinge). 15 replicate models were run and averages from these models were used to interpret final results.

Results

4.1 Model Performance and Evaluation

The validation of a MaxEnt model is based on the area under curve (AUC) of the receiver operating characteristic curve (ROC) (Phillips et al., 2006). The ROC in MaxEnt reveals how well the data perform at predicting absences (Fielding & Bell, 1997; Baldwin, 2009). If designated by the user, AUCs are provided for both training and testing data. The closer the testing value is to the training ROC value is an indication of the model’s performance at predicting presences contained in the test samples (Phillips, 2005). AUC values closer to 0.5 indicate that the model performed slightly better than random in prediction (Baldwin, 2009). AUCs >0.9 indicates very good performance, AUCs between 0.7-0.9 show good performance, and AUCs <0.7 do not provide any relevant information (Baldwin, 2009). Both models showed good performance. The training AUC for the November model was 0.849 and 0.883 for the June 2010 model. Table 5 provides summaries for training and test AUC values for each model averaged from their 15 replicate runs.

<table>
<thead>
<tr>
<th>Model</th>
<th>Training AUC</th>
<th>Test AUC</th>
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<tbody>
<tr>
<td>November</td>
<td>0.849</td>
<td>0.848</td>
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<tr>
<td>June</td>
<td>0.883</td>
<td>0.874</td>
</tr>
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4.2 Evaluating Variable Contributions to Wildebeest Distributions

MaxEnt determines the relative importance (contribution percentage) of a variable by calculating the amount of training gain the variable imposes on the model (Phillips, 2005). Variables that contribute to the greatest gain thus, have a greater contribution to the model. A Jackknife test evaluates these gains three ways for a variable. First, the Jackknife test evaluates how the variable contributed to gain with all other variables included, when only the variable is used in the model, and when the variable is excluded from the model. Permutation importance is determined from the final MaxEnt model by randomly permutating attributes of a variable
against training data (Phillips, 2005). The final percentage is a normalized value that measures the loss in training AUC when the variable is removed from the model. Thus, a larger permutation percentage shows a greater dependence of the model on the variable (Phillips, 2005).

For the November model, precipitation seasonality (BIO\textsubscript{15}), had the greatest contribution percentage to the model (52.4%). Isothermality (BIO\textsubscript{3}) and distances to lodges also contributed greatly to the November model (19.5% and 14.8%, respectively). For the June 2010 model, Kauth-Thomas wetness (KTW) had the greatest contribution percentage to the model (35.2%). Temperature annual range (BIO\textsubscript{7}) and distances to camps also showed significant contributions to the June model (25.5% and 10.7%, respectively). Summaries of each variable and their respective contributions to the models can be found in Table 6.

<table>
<thead>
<tr>
<th>Table 6: Summaries for Contribution Percentages, Permutation Importance, and Training AUC Gains for Variables Used in Each Model</th>
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</thead>
<tbody>
<tr>
<td><strong>Model</strong></td>
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<td>November</td>
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4.3 Response Curves of the Predictor Values Contributing >10% to the Model

MaxEnt produces response curves to show the effect a particular variable has on the probability of a species’ occurrence (Baldwin, 2009). For response curves, the y-axis shows probability of a species’ presence and the x-axis shows the variable’s range of values. Response curves contributing >10% to each model are presented in Figure 6 and Figure 7.

**November Model**

Response curves produced by MaxEnt for the November model (Figure 6) showed that probability of wildebeest presences gradually decreased as percentages of precipitation seasonality (BIO15) increased. The response curve indicates that these decreases begin when precipitation seasonality is >38%. The response curve for Isothermality (BIO3) shows that wildebeest presences gradually increase as percentages of isothermality also increase. Wildebeest presence probability begins to increase around 79% isothermality. Probabilities for wildebeest presence were greatest at distances approximately 20km away from lodges. These probabilities gradually decreased at distances >20km away from lodges.

![Response Curves](image)

*Figure 6: Response Curves of Variables Contributing >10% to the MaxEnt November Model*
**June Model**

Response curves for the June model showed decreases in probability of wildebeest presence when values of KT Wetness increased from -0.21 to 0.05. Highest probabilities were found where KT Wetness values were < -0.25. The response curves for temperature annual range (BIO7) indicated that probabilities of wildebeest increased between temperatures of 14.5º C and 17.5º C. Probability of wildebeest presence increased with increasing distances from camps from 0 to 40km. These probabilities sharply declined at approximately 40km.

### 4.4 Predictive Maps

The predictive maps produced from each MaxEnt model show a suitability gradient of probability of occurrence on a scale of 0 to 1. Values closer to 1 (deep red) show a higher probability of occurrence and values closer to 0 (green) have a lower probability.

**November Model**

The predictive map (Figure 8) produced from the November MaxEnt model shows predicted habitat suitability for both migratory and resident wildebeest populations during November months of the wet season for 2005 and 2007. Higher
concentrations of higher wildebeest probabilities are found in western regions of the SNP, MMNR, Koyake, Lemek, and OCO group ranches.

![Predicted Habitat Suitability November 2005 & 2007](image)

**Figure 8: Probabilistic Predictive Map of Wildebeest for November MaxEnt Model**

**June Model**

The predictive map (Figure 9) from the June 2010 MaxEnt model depicts predicted habitat suitability for resident wildebeest populations during their occupation of the inner group ranches during the onset of the dry season. Highest concentrations of predicted habitat are found predominantly throughout the Ol Kinyie group ranch. Areas of higher predicted habitat suitability are also present in southwestern Olkiriaine, western Maji Moto, northern Siana, the
eastern border of Koyake, and western regions of OCO. Predicted habitat is low or absent in protected areas of SNP and the MMNR for June 2010.

**Predicted Habitat Suitability**  
*June 2010*

![Predicted Habitat Map](image)

**Figure 9:** Probabilistic Predictive Map of Wildebeest for June MaxEnt Model

**Discussion**

5.1 Significance of Predictor Variables on Wildebeest Distribution

*Bioclimatic Variables*

Significant predictor variables from November and June MaxEnt models offers insight to the influences of bioclimatic variables to wildebeest distribution during different times of the year. Precipitation seasonality (BIO15) was the greatest contributing predictor variable to the November model (52.4%). Response curves for precipitation seasonality also showed that
wildebeest presences gradually declined as percentages of rainfall variability increased (Figure 6). Precipitation seasonality is a ratio of the standard deviation of total monthly rainfall to the average of total monthly rainfall where higher percentages reveal greater variability in rainfall (O’Donnell & Ignizio, 2012). The importance of precipitation seasonality to wildebeest distribution in the November model might emphasize the importance of consistent and predictable rainfall patterns on wildebeest distributions during the onset of the wet season.

Rainfall has been hypothesized to affect ungulate distributions due its impact on habitats, vegetation growth, vegetation quality, and accumulation of surface water (Ogutu et al., 2008). Rainfall variability, independent of changes in total precipitation, has been shown to affect carbon cycling processes and community plant structures within grassland ecosystems (Knapp et al., 2002). Such changes hold implications for grazing ungulates. Wildebeest are characterized as hypergrazers, where the vast majority of their dietary intake is comprised of C4 grasses (Cerling & Harris, 1999). Variable or altered rainfall patterns could potentially impact nutrient content and productivity of these grasses and ultimately, impact dietary needs of grazing ungulates due to effects on isotopic compositions of C4 grasses and soil water availability (Fay et al., 2003). With a continued increase in global unpredictable weather events influenced by climate change, examining wildebeest distribution in response to rainfall variability deserves further attention and investigation.

Isothermality (BIO3) is a ratio of mean diurnal temperature range to temperature annual range (O’Donnell & Ignizio, 2012). Larger percentages in isothermality indicate smaller differences in day to night temperatures in relation to the differences in annual (summer to winter) temperatures (O’Donnell & Ignizio, 2012). Isothermality was the second greatest contributing predictor variable to the November model (19.5%). Predicted wildebeest presence showed that wildebeest occurrence steadily increased as percentages of isothermality also increased. This suggests that wildebeest prefer areas with more stable day-to-night and seasonal temperature ranges. Annual temperature range (BIO7) was the only significant contributing bioclimatic variable to the June model (25.5%). Annual temperature range is the difference between the maximum temperature of the warmest month and the coldest temperature of the coldest month (O’Donnell & Ignizio, 2012). Higher values of annual temperature range indicate
more extreme temperature differences between maximum temperatures of the warmest month and colder temperatures of the coldest month (O’Donnell & Ignizio, 2012). Response curves for annual temperature range show that wildebeest presence steadily increased between annual temperature ranges of 14.5º and 17.5º C where they then decreased after 17.5 º C.

**Anthropogenic Indicators**
Distances to lodges and distances to camps contributed 14.8% to the November model and 10.7% to the June model, respectively. Response curves for the November MaxEnt model show that probabilities of wildebeest presence increase at distances of approximately 0-22km and gradually declines after distances of 22km. For June response curves, wildebeest probabilities increase at distances from approximately 0-40km and sharply decline after 40km. These distances might correspond to features in the group ranches such as fences or farms that might inhibit wildebeest movement in the northern Loita Plains. Data pertaining to fences and other obstructions or barriers to wildebeest movement were not available however, this relationship deserve further investigation.

**Vegetation Indices**
Kauth-Thomas Wetness (KTW), a measure of soil and plant moisture, was the greatest contributing variable to the June 2010 model. Response curves for the June 2010 model indicate that wildebeest probabilities were highest between KTW values of -0.25 to -0.22. Wildebeest probabilities then gradually declined as values of KTW increased. Smaller values of KTW are associated with lower moisture content of soils and plants. The greater predicted responses from wildebeest in the June MaxEnt model between these ranges might suggest optimal ranges of moisture associated with vegetation types or grasses preferred by wildebeest during this time of the year.
5.2 Predicted Habitat Suitability

**November Model**

The predictive map produced for the November MaxEnt model shows the extent of predicted habitat suitability for both migratory and resident wildebeest populations during this time of the year. The November map reveals that areas of predicted suitable habitat cover an expansive range throughout the study region and are located both within protected boundaries of the SNP and MMNR and are also present in unprotected areas in the group ranches. High concentrations of predicted suitable habitat are observed in unprotected regions in Koyake, Lemek, and OCO group ranches.

**June Model**

The predictive map produced from the June 2010 MaxEnt model revealed suitable habitat for resident wildebeest populations throughout the group ranches during the onset of the dry season. Higher probabilities for resident populations were found in Ol Kinyie and the surrounding group ranches of Koyake, Lemek, and OCO. Areas of higher predicted habitat suitability were shown to be within close proximity to farming areas in the Loita Plains known to negatively impact resident wildebeest populations (Figure 1).

**Conclusion**

**6.1 Conclusion**

MaxEnt modeling can be used to identify variables that influence a species’ distribution and predict suitable habitat across their ranges for past, present, and future scenarios. This information is useful for conservation planning and management and also has potential applications for assessing distributions of other species of the MMNR. Results from both MaxEnt models provide a fairly recent assessment of influential drivers for wildebeest distributions across the study region for different times of the year. Response curves suggest that wildebeest prefer less variation in rainfall patterns and more stable day-to-night and seasonal temperature ranges during the onset of the wet season. Response curves from the June MaxEnt model indicate that wildebeest prefer specific ranges in soil and plant moisture and annual ranges.
in temperature between 14.5° and 17.5° C during the onset of the dry season. Climate change is an increasing threat to East African ecosystems and presents new and ongoing challenges for wildlife conservation. Climate change could influence how wildebeest respond to their environment and may disrupt their distributions throughout the MMNR and surrounding regions. Utilizing MaxEnt in further research could be useful to project future climate scenarios and assess potential impacts from climate change on wildebeest distributions and areas of suitable habitat.

Predictive maps produced from both MaxEnt models reveal that suitable habitats for both migratory and resident wildebeest populations occur across extensive ranges of the study region throughout the year. These areas extend across both protective boundaries of the SNP and MMNR and throughout unprotected regions within the group ranches. Further, results from MaxEnt show that driving abiotic and biotic factors for wildebeest distribution also fluctuate throughout the year. These variations present challenges to identifying key conservation areas and wildebeest habitats. Using MaxEnt with monthly aerial survey datasets could be used to provide a more thorough understanding of how suitable habitats and influential factors for wildebeest distribution change throughout the year.

6.2 Limitations
Aerial survey data for wildlife populations only offers a snapshot of the relationship between spatial dynamics of a species and characteristics of their habitat. These datasets lack temporal components, descriptive information pertaining to physiological (gender, age, and so forth.) attributes, and activity of the species at the time of the survey. The absence of more descriptive information limits the types of inferences and the significance of the results generated by modeling. Cross examining the results of this analysis with telemetry data containing temporal or other attributes, could offer further explanations for how wildebeest are utilizing their environment.
6.3 Recommendations

Results from this project indicate that bioclimatic variables such as temperature and precipitation as well as levels of soil and plant moisture are important drivers for wildebeest distribution during different times of the year. Climate change and incidences of extreme weather events could impact how wildebeest respond to changes in these variables, their environment, and may influence wildebeest distribution throughout the MMNR and surrounding regions. According to the Intergovernmental Panel on Climate Change (IPCC), many regions in Africa could experience temperature increases from 0.2º to 0.5º C per decade in coming years. These rising temperatures may lead to an increase in the intensity and frequency of major weather events such as droughts, floods, and tropical storms (IPCC, 2001). Precipitation is also estimated to increase, anywhere from 15-20% during wet seasons and decrease 5-10% in dry seasons. Warming sea surface temperatures are also believed to increase the frequency of droughts in equatorial and subtropical regions of East Africa (Funk et al., 2005). Successful conservation initiatives to protect wildebeest populations in light of climate change depend on the preparedness of the MMNR to respond to changing climate conditions. It is recommended that the MMNR monitor seasonal wildebeest distributions and their responses to bioclimatic variables throughout different times of the year. The MMNR should collect up-to-date temperature and precipitation data for the region to be used in SDMs, utilize telemetry methods and interpret telemetry data, map distributions, and project future climate scenarios and their impacts on wildebeest distributions.

Land use practices and the expansion of agriculture in the Loita Plains continues to present persistent threats to wildlife populations and their seasonal ranges (Ogutu et al., 2011). With current land use trends in the group ranches, the future of the MMNR and their capability of conserving wildebeest populations in unprotected seasonal dispersal regions is uncertain. The combined efforts of the MMNR and private land owners of the group ranches are needed to implement land use regulations and restrictions necessary to protect threatened wildlife populations. In recent years, eight wildlife conservancies have been established by ‘ecotourism operators’ throughout the group ranches (Bedelian, 2014). These conservancies are community oriented and offer economic incentives to private land owners that utilize their land to conserve
critical dispersal areas frequented by wildlife (Bedelian, 2014). The MMNR should work with conservancies to implement land use planning and policies in the group ranches that ensures adequate protection for wildebeest. These policies should strive to also promote livelihoods of local Maasai land owners and accommodate expanding farming practices needed to support growing human populations in these areas.
References


