INVESTIGATING THE BIOGEOGRAPHIC NICHE OF BABOON SPECIES IN SOUTHERN KENYA USING GIS

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Investigating the Biogeographic Niche of Baboon Species in Southern Kenya Using GIS

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DECLARATION

This thesis is my original work and has not been presented for a degree in any other University.

Signature: …………………………………… Date: ……………………………….

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This thesis has been submitted for examination with our approval as the university Supervisors.

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DEDICATION

To Salome Nyachae Abuga, for standing with me through this and a lot more...

"If you can fill the unforgiving minute

With sixty seconds' worth of distance run,

Yours is the Earth and everything that's in it,

And—which is more—you'll be a Man, my son!"

Rudyard Kipling.

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LIST OF ABBREVIATIONS/ACRONYMS

AG	Agricultural Land
BU	Savannah Bushes
CRAN	Comprehensive R Archive Network
DN	Digital Number
ESRI	Environmental Systems Research Institute
GIS	Geographic Information Systems
GNSS	Global Navigation Satellite System
GLS	Global Land Survey
GPS	Global Positioning System
GR	Savannah Grassland
IDW	Inverse Distance Weighted
IT	Information Technology
ITCZ	Inter Tropical Convergence Zone
KAPPA	Kappa Index of Agreement
LC	Land-Cover
LOOCV	Leave-One-Out-Cross-Validation
LPI	Local Polynomial Interpolation

LU	Land-Use
LULC	Land-Use/Land-Cover
NASA	National Aeronautics and Space Administration
NIMA	National Imagery and Mapping Agency
RA	Regression Analysis
RBF	Radial Base Functions
RS	Remote Sensing
SE	Spatial Ecology
SRTM	Shuttle Radar Topography Mission
TP	Thiessen Polygons
TSA	Trend Surface Analysis
USA	United States of America
USGS	Unites States Geological Survey
WO	Woodland

OPERATIONAL DEFINITION OF TERMS

Adaptation	A trait that confers an advantage on individuals relative to any other existing alternative exhibited by other individuals within the population, or relative to the ancestral population (Holla & Smith, 2018). Adaptations can be physical traits such as skin color, or density of fur. Adaptations can also be behavioral, where individuals show differences in behavior that are beneficial to fitness compared to other individuals within the population.
Admixture	Admixture occurs when two or more previously isolated populations interbreed.
Allopatry	Species living in isolation from similar species of the same family. The term ‘allopatry’ is often used in biogeography to describe the relationship between organisms whose ranges do not significantly overlap but are immediately adjacent to each other—they do not occur together or only occur within a narrow zone of contact.
Ancestry	An ancestor is a parent from whom one has descended. In genetics, when individuals from different species produce offspring, we refer to ancestry in terms of parental species.
Biogeography	This is the study of the geographical distribution of organisms in geographic space and through geological time (Mast, 2010)
Cognition	The process of acquiring knowledge through thought, experience, and senses. In ecology, a species with good cognitive abilities is one in which individuals are able to learn faster when compared to individuals of a different species.

Dispersal	The movement of an individual or individuals in order to find breeding partners.
Divergence	When a lineage becomes isolated from other members of its species and distinct traits evolve in that lineage, the lineage is said to have diverged from the parental lineage. Morphological divergence occurs when a group forms different physical characteristics from their parental species. Ecological divergence occurs when a group occupies habitat that is markedly different from that of their parental species.
Ecovegetative Zone	Regions characterized by distinct vegetation communities that have formed as a result of shared climate and similar geography.
Evolution	A change in the heritable characteristics of a population over time.
Evolutionary Ecology	The study of how interactions with and within the environment lead to evolution.
GIS	Computer-assisted systems for the acquisition, storage, manipulation, analysis, and display of spatial data (Longley et al., 2005).
Habitat	The habitat of an animal is defined as the environment in which the animal prospers and is able to maintain a healthy population.
Heat stress	Heat stress occurs when the body's means of controlling its internal temperatures start to fail, and as a result body functions are adversely affected.

Hybrid zones	Hybrid zones are regions in which populations of dissimilar parental ancestry meet, mate, and produce hybrids
Hybridization	The interbreeding of individuals from different parental species or species.
Hybrids	Offspring from parents of different species or species ancestry.
Natural Selection	The process that produces evolutionary change when individuals differ in heritable traits that are correlated with differences in Darwinian fitness, which is often measured using lifetime reproductive success.
Range	An area that an animal or group of animals occupy but do not defend, and this is in contrast to a territory, which is defended.
Remote Sensing	Remote Sensing (RS) is the acquisition of information about an object or phenomenon without making physical contact with the object (Lillesand et al., 2015). Here, we refer to satellite RS which entails the acquisition, storage, processing and analysis of satellite images.
Specialization	The adaptation of an animal to a specific environment.
Sympatry	Two closely related species living in the same geographic range.
Thermoregulation	The process of keeping body temperatures within certain boundaries in spite of the temperatures of the surrounding area.

ABSTRACT

Studies on primate distribution and diversity continue to make important contributions to scientific knowledge on species ecology and evolution, and baboons (genus *Papio*) are an ideal model species for biogeographic studies. Whereas the distribution of baboons across Africa has been documented, there isn't enough information on the biogeographic niche of baboon species at the subcontinental scale. Here, Geographic Information Systems were used to investigate the biogeographic niche of anubis baboons, yellow baboons, and their hybrids in southern Kenya. First, a field survey was conducted to ascertain the distribution of baboons in the study area. Next, baboon populations encountered during the field survey were categorized according to their ancestry, i.e. either unadmixed anubis baboon, hybrid, or unadmixed yellow baboon populations. Biogeographic variables representing geography (altitude and distance from the ocean), vegetation, and climate were then estimated for sites where baboons were encountered. Next, using Geographically Weighted Regression Analysis (GWRA) between-species biogeographic niche was assessed, and finally, using Environmental Niche Factorial Analysis (ENFA), within-species biogeographic niche was assessed. The study established that baboon species in southern Kenya (Kanjiado, Makueni and Taita Taveta) were in allopatry, with anubis baboons were found in the north-west, yellow baboons found in the south-east, and hybrids found in between. Between-species niche analysis using GWRA established that there was no significant difference in biogeography between anubis baboons, yellow baboons, and their hybrids whereas within-species niche analysis using ENFA established that each baboon species was highly tolerant to different biogeographic conditions. The results of this study support the designation of anubis and yellow baboons as highly adaptive generalists that are able to survive in different biogeographic conditions.

Keywords: Biogeograpy, GWRA, ENFA, anubis baboons, yellow baboons, hybrids, Geographic Information Systems.

CHAPTER ONE

INTRODUCTION

1.1 Background of the Study

Animals are subjected to competing demands and motivations such as the need to acquire food, find mates, rear offspring, defend limited resources, and avoid predators (Beyer et al., 2010), and fulfill all their needs by balancing activities within their habitat. Traditionally, habitats were defined by describing the ecovegetative zone in which the study species was found. Some species were described as forest dwellers e.g. mountain gorillas (Ganas et al., 2016; Ganas & Robbins, 2005; Robbins et al., 2009), savannah dwellers e.g. savannah baboons (Jolly et al., 1993), or even desert dwellers e.g. desert tortoise (Nussea et al., 2015). Nowadays, in biogeographic studies researchers first identify important biotic or abiotic predictor variables for the study species (vegetation, climate, and soils), and areas where the characteristics of these variables are optimal for the study species are identified as the species' habitat (Hirzel et al., 2002; Beyer et al., 2010; Abade et al., 2014; Fuchs et al., 2018; Preau et al., 2018).

Evolutionary theory teaches that members of a species are often aggregated in favorable habitat (Calenge, 2007; Calenge et al., 2005), and through the process of natural selection evolve in ways that positively influence their performance within this habitat (Hutchinson 1957; Lewontin 1970; Futuyuma & Moreno 1988; Lobo et al., 2010; Liu et al., 2014). Members of the same species found in dissimilar habitat evolve different adaptations over time, diverging from their parental species, and when this divergence is significant enough new species form. In areas where the habitats of two closely related species overlap, interbreeding of individuals from different parental species may produce hybrid offspring (Gabow, 1975; Pinaceae et al., 2017; Ross & Harrison, 2002). Hybridization is an evolutionary mechanism, and the possible consequences are many: parental species may diverge further, they may amalgamate into a new species of hybrid origin, and/or they may continue to hybridize without significant change in their respective compositions (Fredrickson & Hedrick, 2006; Gabow, 1975; Rhymer & Simberloff, 1996; Gese et al., 2015;

Ackermann et al., 2006). Hybrid zones are regions in which hybridization occurs, and are formed by various phenomena. There are reported cases where vegetation change, climate change, and/or human interference with habitats force previously separate populations to merge, thus creating hybrid zones (Brust et al., 2009). In other cases, species have experienced range expansion due to population growth, while others have moved their ranges due to human actions such as forced migration (Rhymer & Simberloff, 1996). Recent hybridization events offer scientists a unique perspective on interactions that may have happened thousands of years ago in natural history (Croucher et al., 2007), and because of this hybridization is an area of interest for researchers in the areas of spatial ecology, evolutionary ecology, evolutionary genetics, and speciation genetics amongst others.

As a model for evolutionary studies, specifically species distribution and hybridization, baboons form a good study system for three reasons (e.g. Ackermann et al., 2006; Fuchs et al., 2018; Hill & Winder, 2019; Chala et al., 2019). First, accounts of baboon systematics generally distinguish six species, all of which are morphologically divergent. This means it is easy to distinguish individual baboons from different parental taxa, a skill that is particularly important when conducting field surveys in areas where the ranges of two baboon species overlap and the researcher is expected to visually distinguish between unadmixed individuals from different parental taxa, and to identify hybrids. The six species are anubis (or “olive baboons”), yellow baboons, Guinea baboons, hamadryas baboons, Kinda baboons, and chacma baboons (Dunn et al., 2013; Stone et al., 2013; Winder, 2014; Fuchs et al., 2018). Whereas anubis, yellow, Guinea, chacma and hamadryas have similar body sizes, Kinda baboons are small bodied when compared to the other taxa (Jolly, 1993). All baboon species are distinguished by differences in their physical appearance (Jolly, 1993; Alberts & Altmann, 2001; Ackermann et al., 2006), and as a result many studies have relied on baboon species morphology to identify and map baboon species distribution, as well as to identify unadmixed and admixed populations. For example, researchers have identified chacma and kinda baboon ranges in Zambia (Jolly et al., 2011), and hamadryas and anubis baboon ranges in Ethiopia (Jolly et al., 1993; Gabow, 1975). In all, 12 boundaries between contiguous species have been reported and studied (Zinner et al., 2013; Boissinot et al., 2014).

Between the boundaries of some species' ranges are zones in which baboon groups show unusual morphology, and these are reasonably interpreted as hybrids (Maples & McKern 1967; Gabow 1975; Jolly et al., 1993; Jolly et al., 2011; Winder, 2015). Hybrids have been observed between anubis and yellow baboons in Amboseli, Kenya (Maples & McKern 1967; Samuels & Altmann 1986; Alberts & Altmann 2001; de Jong & Butynski 2012; Charpentier et al., 2012; Wall et al., 2016), between hamadryas and anubis in Ethiopia (Gabow 1975; Bergman & Beehner, 2003), and between chacma and Kinda baboons in Zambia (Jolly et al., 2011).

Second, there have been numerous short and long-term studies on baboon species distribution and other aspects of baboon ecology in Africa, and as a result many reports and publications on various interest areas that include social and ecological aspects of different baboon populations are available. In Kenya, the Amboseli baboon population has been studied for over 40 years (Alberts. 2019), and published material on baboon distribution and hybridization among other research topics can be found on the Amboseli Baboon Research Project website at https://amboselibaboons.nd.edu. The baboon population in Laikipia, Kenya, has also been studied for over 40 years, and published material on the ongoing research can be found on the Baboons R Us website at http://www.baboonsrus.com. The baboon population in Awash, Ethiopia, has also been studied for numerous years (Gabow, 1975; Bergman & Beehner, 2003).

Finally, despite being geographically and morphologically divergent, there have been numerous reports of baboon species occupying a variety of habitats and it is still unclear if the different baboon species are ecologically divergent (Winder, 2015; Fuchs et al., 2018; Hill & Winder, 2019). This ecological flexibility coupled with the biogeographic spread has made baboons interesting in their own right, and a potential source of analogies for understanding early human evolution (Winder, 2014).

2.2 Problem Statement

Baboons are distributed across Africa, with six species occupying geographically distinct ranges. At the boundaries of some ranges naturally hybrid zones occur. Whereas the ranges of the six baboon species have been well documented, studies investigating baboon species biogeographic niche begun in the last decade. In southern Kenya, the ranges of anubis baboons and yellow baboons have been documented (Maples & McKern 1967; Samuels & Altmann 1986; Alberts & Altmann 2001; de Jong & Butynski 2012; Charpentier et al., 2012; Wall et al., 2016), however the relationship between the observed distribution and biogeography have not been investigated. It is unclear if climate affects baboon distribution in southern Kenya. It is also unclear if vegetation has an influence on baboon species distribution in southern Kenya. As the influence of biogeography on baboon species distribution has not been established, it is unclear if climate change and/or vegetation change, specifically anthropogenic change from natural to agricultural vegetation, has had an influence on baboon distribution. The two baboon species found in southern Kenya, anubis and yellow baboons, hybridize, and it is unclear if current patterns of hybridization were initiated by anthropogenic vegetation changes, natural vegetation changes, climate changes, or other causes. This continued hybridization has had a profound effect on species genetics as has been witnessed in the Amboseli basin (e.g. Alberts & Altmann, 2001; Tung et al., 2008; Tung et al., 2012), and may have a long-term effect on the species diversity in southern Kenya.

1.3 Justification

In recent years, researchers have utilized available datasets to study the biogeographic niche of baboon species at a continental scale (Dunn et al., 2013; Winder, 2015; Fuchs et al., 2018; Hill & Winder, 2019; Chala et al., 2019). Whereas these studies provide much needed insight on baboon species biogeographic niche, the generalization required in creation of continental datasets often means local conditions are not adequately represented (Winder, 2015; Derin & Yilmaz, 2014; Fick & Hijmans, 2017), and because of this it is not clear if the results of these studies will hold for smaller areas such as southern Kenya. Investigations into baboon species distribution within smaller areas such as southern Kenya have also been conducted. However, these studies mainly focused on distribution of baboon species and their hybrids without accounting for the effects of biogeography on the observed distribution patterns as this was not an objective for these studies (e.g. de Jong & Butynski, 2012; Charpentier et al., 2012). Investigating the biogeographical niche of baboon species in southern Kenya using GIS and RS will allow us to understand in much greater detail the correlation between biogeography and baboon species distribution. Specifically, GIS tools will facilitate collection of new data to update existing species distribution data within southern Kenya, and the generation of biogeographical data describing sites where baboon populations are found. This will facilitate the investigation of baboon species biogeographic niche within southern Kenya using GIS-based SDMs, enhancing our knowledge on baboon species biogeographic niche.

1.4 Objectives

1.4.1 The Overall Objective

The overall objective of this study was to investigate biogeographical influences on baboon species distributions in southern Kenya using GIS.

1.4.2 Specific Objectives

1. To determine the distribution of anubis baboons, yellow baboons, and hybrid populations by conducting a field survey within the study area in order to update existing distribution data.
2. To determine influence of land-cover on baboon species distribution.
3. To determine the influence of climate on baboon species distribution.
4. To determine the influence of geography on baboon species distribution.

1.5 Scope and Limitations of the Study

This study focused on characterization of biogeographical variables (land-cover, climate, location, altitude, and distance from the ocean) of baboon habitats within southern Kenya. The study identified sites where baboons ranged within the study area, and categorizing baboon species found within each site as either anubis, yellow, or hybrid. Next, LULC that was important to the study species was generated by classifying satellite imagery. Climatic and geographic data was collated, and finally the influence of these biogeographic variables on baboon species distribution was investigated. The climatic data considered for this study covered an area considerably larger than the study area. Similarly, geographic data (altitude, and distance from the ocean) were available for many baboon populations outside the study area. This presented an opportunity to perform limited analysis outside the study area. It is important to note that both baboon population data and biogeographic data that fell outside the study area were not used for analysis in this work, nor were they used to draw the conclusions of this work.

CHAPTER TWO

LITERATURE REVIEW

2.1 Introduction

Baboons are Old World monkeys, and are the most successful of all the African monkeys (Barrett 2000). Baboons, from the genus Papio, are found all over continental Africa (Boissinot et al., 2014; Zinner et al., 2013). Their range stretches from South Africa through to Egypt, and into the Arab Peninsular (Figure 2.1).

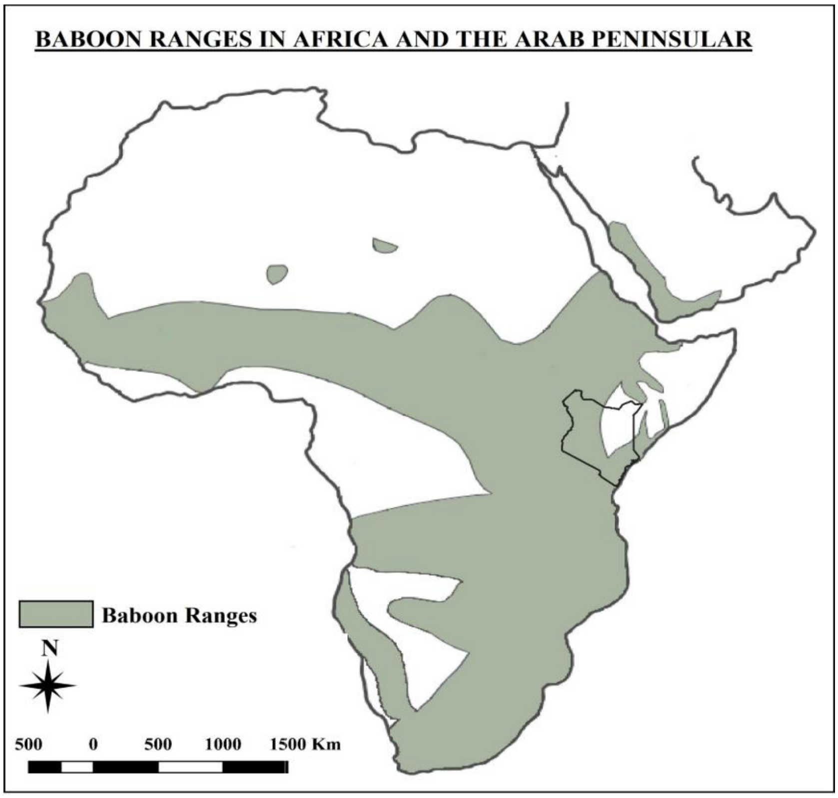


Figure 2.1: The map, adapted from Zinner et al., (2013) shows the range of baboons in Africa and the Arabian Peninsula.

Baboon are classified into six species: *P. ursinus* (chacma baboon), *P. papio* (Guinea baboon), *P. hamadryas* (hamadryas baboon), *P. anubis* (anubis or olive baboon), *P. cynocephalus* (yellow baboon), and *P. kindae* (Kinda baboon) (Zinner et al., 2013). All species have unique morphology making it easy to differentiate between them. Of the six baboon species, anubis, yellow, hamadryas, and Guinea baboons have similar body size. Chacma baboons are the largest whereas kinda baboons are smaller (Rogers et al., 2019). All baboon species live in organized groups with group size ranging from 18 to 120 individuals (Silk et al., 2011; Rogers et al., 2019). These groups show variation in social structure between species. The anubis, yellow, kinda, and chacma baboons live in multi-male, multi-female groups. In this group structure, various females and their offspring live with various males. Females often have a strict hierarchy with one female as the head of the females in the group. The males have a more fluid hierarchy, with the dominant males often being ousted from leadership of the group. On the other hand, Guinea and hamadryas baboons organize themselves in 'one male units', where a single male dominates a small troop of baboons mainly composed of family members (Luong & Galat, 2013; Swedel, 2013), and even when the troop joins up with other troops to form a larger group the 'one male units' remain distinguishable.

Many baboon species' range close to each other. For example, chacma and kinda baboon ranges meet in Zambia (Jolly et al., 2011), and hamadryas and anubis baboon ranges meet in Ethiopia (Jolly et al., 1993; Gabow, 1975). In Kenya the ranges of yellow and anubis baboons meet (Charpentier et al., 2012; Samuels & Altmann, 1986; Tung et al., 2008). In all, there are 12 boundaries between contiguous species (Zinner et al., 2013; Boissinot et al., 2014). It has been reported that the boundaries between neighboring baboon species often lay at the juncture of distinct ecovegetational zones (Jolly et al., 1993), though this observation has never been explicitly quantified. Between the boundaries of some species' ranges are zones in which baboon groups show unusual physical characteristics, and these are reasonably interpreted as hybrids (Maples & McKern 1967; Gabow 1975; Jolly et al., 1993; Jolly et al., 2011; Winder, 2015). Hybrids have been observed between anubis and yellow baboons in Amboseli, Kenya (e.g. Maples & McKern 1967; Samuels & Altmann 1986; Alberts & Altmann 2001; de Jong & Butynski 2009; Charpentier et al., 2012), between hamadryas and anubis in Ethiopia (Bergman & Beehner, 2003), and between chacma and kinda baboons in Zambia (Jolly et al., 2011). Surveys indicated that of the six baboon species found in Africa only two were present in Kenya: anubis baboons and yellow baboons (Maples & McKern, 1967; Charpentier et al., 2012; de Jong & Butynski, 2012; Rauset et al., 2013; Samuels & Altmann, 1986) (Fig 2.2). The anubis baboon has brownish-gray fur, with rings of black and yellowish-brown that give the coat a multi-color appearance from up-close (Charpentier et al., 2012; de Jong & Butynski, 2012). The yellow baboon has yellowish-brown fur that covers their bodies except for their undersides. The inner surfaces of the limbs, cheeks, and patches of fur on either side of the muzzle are lighter in color and sometimes appear white (Alberts & Altmann 2001, de Jong & Butynski 2012). In Kenya anubis baboons have been observed in Kisumu, Laikipia, Gilgil, Naivasha, Nakuru among others, whereas yellow baboons have been observed in Tana River, Mombasa, Manda Islands, Garsen, Garissa among others.

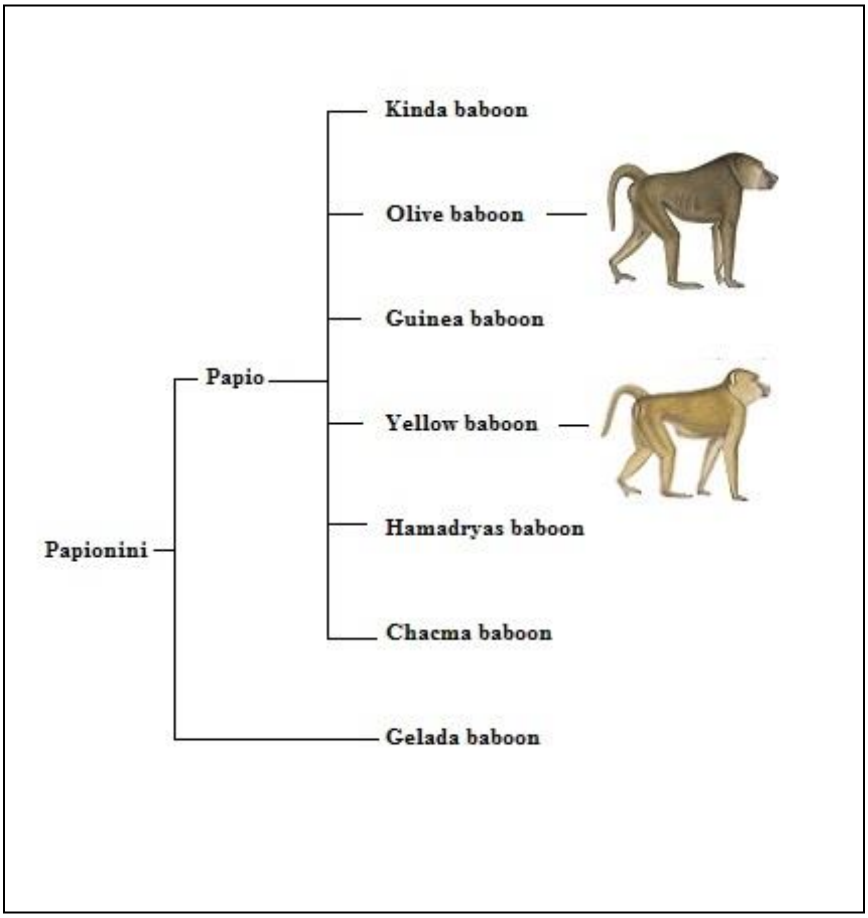


Figure 2.2: The taxonomic classification of Papio with illustrations of anubis and yellow baboons (adapted from Zinner et al., 2013)

Because of the differences in morphology between yellow baboons and anubis baboons, the two species were often hypothesized to be adapted to different biogeographic niche as was often observed in other species. The biogeographic niche of a species can be defined as conceptual space with all the requirements needed for the species to survive (Grinell, 1917; Hutchinson, 1957; Sattler et al., 2007). These resources are provided for in nature from the biogeographic features found in a species habitat, and these include trees and bushes, insects and small rodents, cliffs and caves, rivers and lakes among others. Species adaptations to different habitat often manifest as differences in morphology and/or behavior, and when comparing two or more closely related species, features such as fur color (e.g. dark or light), type of the fur (e.g. thick hairy fur or light fur), overall size (e.g. large or small), and type of feet (e.g. webbed or non-webbed) are examples of traits that are adaptations to niche habitats (Pongracz et al., 2017; Liu et al., 2014). For example, polar bears are adapted to the extremely cold conditions in the Arctic and spend most of their lives out on the sea ice (Liu et al., 2014), whereas the closely related brown bears are adapted to the temperate climate found across America and continental Europe. The polar and brown bear differ fundamentally in their behavior, and physical appearance, reflecting both functional and behavioral adaptations to different habitats (Liu et al., 2014; Pongracz et al., 2017). By examining the dynamics of how these two species of bears are associated with biogeographical factors within their respective ranges, inferences can be made on the habitat demands that influence their distribution (Guisan & Zimmermann, 2000; Beyer et al., 2010), and this quantification of species distribution-biogeographical relationships is the core of GIS ecological modeling (Guisan & Zimmernann, 2000). Just like brown bears and polar bears, anubis baboons and yellow baboons showed clear morphological divergence. It was often suggested that the heavy, dark colored fur of anubis baboons indicated they were more suited to the cool climate of highland areas, and that the light fur of yellow baboons suggested they were more suited to the hot climate of low altitude savannahs (Altmann et al., 2013; Kindgon, 1997; Palombit, 2013). However, unlike brown bears and polar bears, it was unclear if unique physical characteristics of the two baboon species, anubis and yellow, provide an advantage in the respective habitats where the different baboon species are found. Classical ecological models predict that two species that have a similar ecological niche cannot coexist, and one species would competitively exclude the other (Costa et al., 2016), and this assertion raised considerable interest among ecologists studying baboons. Contrary to this, it was suggested that anubis baboons first immigrated into Kenya from the north-western whereas yellow baboons first immigrated into Kenya from the south-east, moving along the Indian Ocean as they immigrated inland. This implied that the observed differences in baboon species biogeographic niche in Kenya, where yellow baboons were found closer to the Indian Ocean and anubis baboons were found further inland, was based solely on natural history and not on ecological specialization (Jolly et al., 1993). The two conflicting views initiated a biogeographic study, focusing on quantifying and qualify the biogeographic niche of the two species in Kenya.

Patterns of vegetation are important ecosystem properties with strong relationships to ecological functions (Gould, 2000, 2016), and variation in vegetation often has an influence on species distribution. For many species the habitat occupied often corresponds to a specific ecovegetative zone, and the range of these species can often be defined by delineating the ecovegetative zone to which the particular species is adapted. Long term or permanent changes in vegetation normally lead to changes in ranging patterns for these species, and may affect the species' population dynamics within the area. The vegetation found within baboon habitat is a vital resource. Trees and plants provide shelter from predation and from the elements, and are also a vital food source. Baboons often sleep in tree canopies, known as sleeping groves (Hausfater & Meade, 1982; Markham, 2012), though in some areas baboon sleep on rocky cliffs (Hamilton, 1982). Baboons have been known to fall prey to lions while foraging during the day (Bosse, 1980), and also fall prey to leopards during the day and also during the night (Akiko, 2015). One of the strategies used by baboons to evade predation is to shelter in trees, specifically on branches that are hard to reach for lions and leopards, which are also good at climbing. Baboons, omnivores with a strong preference for soft-bodied fruits and seeds (Dunbar, 1988; Hill & Dunbar, 2003), have a diverse diet and are able to exploit a wide variety of foods. This flexibility is a necessity in an environment that is highly seasonal and in which the availability of food varies in abundance throughout the year (Alberts et al., 2005; Codron et al., 2006; Hill & Dunbar, 2003; Post, 1982). Baboons often feed on grasses, with leaf blades and seed heads being a staple part of their diet (Alberts et al., 2005). Baboons also feed on root tubers, stem tubers, fruits and seeds (Altmann, 1998), and have also been recorded opportunistically preying on small goats and gazelles. Yellow baboons have been referred to as eclectic omnivores because they have a highly diverse diet, and yet are extremely selective in their foraging (Altmann, 1998). Anubis baboons are also able to make use of highly diverse food sources (Barton et al., 2014). When there are changes in vegetation within baboon habitat, baboons react by altering their diets and/or by expanding their home range to include better habitats (Alberts et al., 2005; Bronikowski& Altmann, 1996), but will generally stay within the same territory.

When studying the biogeographic niche of a species, climate is an important consideration as climate directly affects organisms themselves, or affects their habitat. Climatic variables have a direct influence on vegetation distribution as plants cannot escape hostile climate. Animals on the other hand can respond to climate directly by actively inhabiting regions with favorable climatic, or indirectly by actively inhabiting regions with favorable vegetation that is only found within specific climatic zones (Hirzel & Lay, 2008). For baboons, food and water availability are strongly correlated to climate, and adverse climatic conditions such as drought, extreme hot or cold adversely affect baboons. The beginning of dry seasons in savannah habitats coincides with periods of low plant productivity (Alberts et al., 2005), and animals found in savannahs have to find ways to cope with the scarcity of vegetation and scarcity of surface water. Rainfall, a central component of the hydrological cycle, has a direct and indirect influence on the amount of surface water, often the only source of drinking water in the wild. During prolonged droughts, surface water becomes scarce, negatively affecting thermoregulation. Baboons drink water daily, and are known to travel long distances to search for water during the dry season (Altmann &Altmann, 1970; Bronikowski & Altmann, 1996). Baboons also select sleeping sites to optimize the search for food and water during the dry season (Suire et al., 2021). When plant productivity dropped during the dry season baboon groups normally walked longer distances and spent more time foraging, relying on drought-resistant plants that were more available (Alberts et al., 2005). When conditions improve during the wet season and plant productivity increases, Johnson et al (2015) found that baboon troops covered smaller distances each day in order to look for food.

When the temperatures in an area are far above average (very hot) or far below average (very cold), animals use considerable effort to stabilize their body temperatures , and prolonged exposure to either high or low temperatures often leads to higher stress levels (Gesquiere et al., 2008). In the animal kingdom, responses to adverse conditions brought about by harsh temperatures vary. Some animals become docile and hibernate, others change their ranging patterns, whereas others migrate to different areas. Hill (2006) noted that shade seeking was an important behavioral response to thermal stress, and that baboons often sought out shades when ambient temperatures increased. Hill (2006) also noted that thermoregulatory considerations impacted patterns of habitat choice and day journey routes, with baboons using routes with more shade during hot seasons. Whereas baboons increased their home range during the dry season, it is rare for baboons to systematically migrate to new areas.

The geography of an area inadvertently has direct and indirect influences on habitats found close by, and often has direct and indirect influence on the biogeography. Large geographic features such as lakes and mountains can influence the climate of an area by influencing the rainfall received (Winder, 2014), thereby influencing the vegetation in the surrounding environment. The altitude of an area has a direct influence on temperatures experienced, and this has a direct influence on heat-stress experienced by flora and fauna in an area. The relief of an area may make an area inaccessible to some animals, whereas the lithology may provide shelter for others (Akiko, 2015). Whereas geographic variables often correlate to other variables such as climate and vegatation, they never correspond perfectly and may each have different, partially independent impacts on the animals living in an area. Analysis of the spatial distribution of species is useful in qualifying allopatry or sympatry (Nattier et al., 2012), and ecologists have been particularly interested quantifying baboon species distribution as this has contributed to some of the most important and contentious ideas in ecology and evolutionary biology (Jolly et al., 1993; Zinner et al., 2009).

The definition of biogeography has become more concise over time, and biologically realistic GIS models are now used to explain observed species biogeographic niche (Hill & Winder, 2019; Chala et al., 2019; Pettorelli et al., 2018; Fuchs et al., 2018 Abade et al., 2014; Rood et al., 2010; Brotons et al., 2004; Hirze et al., 2002; Hirzel et al., 2001). The impact of GIS on habitat studies has been immense, with the number of published works increasing each year (Guisan& Zimmermann, 2000; Guisan & Thuiller, 2005; Lobo et al., 2010). Studies on hybridization have also benefited. GIS has been used to study biogeographic niche and hybridization patterns in large house spiders in England and Wales (Croucher et al., 2007), pine trees in the United States (Pinaceae et al., 2017), and viper species in Europe (Martínez-Freiría et al., 2008). Costa et al., (2008) used climate-based GIS models to predict the geographic distribution and range overlap of closely related amphibians and reptiles in Oklahoma, USA, and reported hybridization in some areas where the niche habitat of closely related species overlapped. GIS has also been used to help answer questions on baboon species biogeographic niche in Africa (Frost et al., 2003; Kamilar et al., 2006; Stone et al., 2013; Winder, 2015; Zinner et al., 2011; Zinner et al., 2013).

2.2 Investigating Biogeographic Nich Using Gis

GIS models attempt to summarize complex species distribution patterns with a reduced set of predictor variables (Barry & Elith, 2006), and in Species Distribution Models (SDMs) this involves investigating the relationship between species distribution and biogeographic variables (Barry & Elith, 2006; Rood et al., 2010; Abade et al., 2014; Preau et al., 2018). In common SDMs researchers first obtain species distribution data using various techniques that include physically tracking the study animals and noting down their locations using Global Positioning System (GPS) receivers (Markham &Altmann, 2008), attaching a GPS receiver to one of the study animals (Wimberger et al., 2010; Millard & Blouin-Demers, 2001; Isabel et al., 2018), noting sites where species dung is spotted (Rood et al., 2010), or going through museum records and published reports to obtain archived distribution information (Reutter et al., 2003; Broton et al., 2004; Dunn et al., 2013; Winder, 2015). Second, biogeographical variables are selected, and these are converted into grid data covering the study area (Calenge, 2002). Third, the species distribution data are used as sample points and the values of the biogeographical variables are estimated at these points (Calenge, 2002; Hirzel et al., 2002; Abade et al., 2014; Costa et al., 2016; Preau et al., 2018). A suitable model is then chosen to describe the tabulated relationship between the study species’ distribution and the biogeographical variables.

SDMs can be grouped into two broad categories: Heuristic and Statistical. Heuristic SDMs utilize rules in branched steps to determine the biogeographical niche of the study species. Heuristic models range from very basic single step models to more complex Multi-Criteria Evaluation models. Heuristic SDMs normally utilize input from domain experts, field survey observations, and published literature to determine important biogeographical variables (Crance, 1987). Using methods such as the Delphi (Crance, 1987) or Analytical Hierarchical Process (Nekhay et al., 2009; Store & Kangas, 2001), the selected variables are weighted and then normalized. The variables are then combined using arithmetic overlay analysis in branched steps resulting in a habitat suitability layer. The habitat suitability layer has values ranging from 0 for unsuitable habitat to 1 for suitable habitat (Crance, 1987; Store & Kangas, 2000; Nekhay et al., 2009).

Heuristic SDMs were widely used in the definition of habitats within the United States of America (USA) in the 1980s. The United States Geological Survey (USGS) relied on domain experts to determine what variables were important for species habitats, their limits and interactions (Crance, 1987; Roloff & Kernohan, 1999; Wintle et al., 2005). Using the Delphi method, advice from domain experts was used to generate a large database of habitat models identifying the biogeographical niche for various wildlife species found within the USA. These habitat models can be found on the United States Fisheries and Wildlife Service website at https://www.nwrc.usgs.gov/ wdb/ pub/hsi/ hsiindex.htm. The major advantage of Heuristic SDMs is that habitat models can be quickly produced even where species distribution data are inadequate (Store & Kangas, 2000). Another advantage is that critical information and intricate species-environmental interactions can be easily incorporated (Crance, 1987). The major disadvantage of Heuristic SDMs is that they heavily rely on expert knowledge, knowledge which may not be available for some species, or may be biased. The biggest challenge in developing Heuristic SDMs is determining which variables to include, more so in cases where literature on the interactions between the study species and biogeographical variables is not available (Gusian & Zimmermann, 2000; Calenge et al., 2005).

Statistical SDMs are composed of a random component describing the distribution of the study species, a systematic component composed of biogeographic variables, and a link between the random and systematic components describing how the distribution of the species relates to the biogeographic variables (Wintle et al., 2005; Calenge, 2005). Statistical methods, using various statistical measures, seek to explain the influence of each biogeographic variable on species distribution. Statistical SDMs include models based on linear regression (Gains et al., 1998; Slattery & Alisauskas, 2007; Bittner et al., 2011; Palacio, 2018), environmental envelopes and climate envelopes (Penman et al., 2010; Penman et al., 2010), Principal Component Analysis (PCA) (Calenge, 2005; Abade et al., 2014; Preau et al., 2018), Mahalanobis Analysis (Knick & Dyer, 1997), and Ecological-Niche Factor Analysis (Hirzel et al., 2002; Preau et al., 2018). Multivatiate statistical packages such as *adehabitatHS* (Calenge, 2006) for the statistical software CRAN R (Core Team, 2019) offer a rich variety of analysis tools for modeling, and these include General Linear Models (GLM), Geographically Weighted Regression Analysis (GWRA), Environmental Niche Factorial Analysis (ENFA), and Mahalanobis Distance. Many of these models are based on the framework of the duality diagram (Escoufier 1987), a family of models that can be considered to be extensions of PCA (Dray and Dufour 2007; Calenge et al., 2005; Calenge, 2007). For this study Statistical SDMs were chosen over Heuristic SDMs. This is because many aspects of baboon ecology have not been studied, especially at sites where research camps have never been set up, meaning there were large gaps in information that would be needed if Heuristic SDMs models were to be developed. Here, GWRA and ENFA were used to investigate baboon species biogeographic niche. GWRA was used for between-species biogeographic niche analysis in order to investigate ecological divergance between anubis baboons, yellow baboons, and their hybrids. ENFA was used for within-species niche analysis in order to investigate the biogeographic niche of each baboon species.

GWRA is an extension of ordinary least squares regression that takes non-stationarity into consideration when modeling the local relationships between predictor and dependent variable (Brown et al., 2012; Sheehan et al., 2013). Stationarity implies that the mean, variance, and dependency of location do not change through space whereas non-starionarity implies the mean, variance, and dependence of locaiton change predictably through space. In biogeographic studies non-stationary variables include climate, vegetation, and the physical geography in the study area. Whereas traditional regression techniques such as ordinary least squares (OLS) are often unable to accurately model spatially varying data and may ignore or hide local variations in model coefficients, GWRA has been shown to greatly improve model performance (Brown et al., 2012).

ENFA is a multivariate, presence-only SDM that is able to evaluate habitat-used versus habitat-available. Spatial ecologists often distinguish two categories of SDMs, those that need presence–absence data, and those that only use presence data (Hirzel et al., 2002; Tsoar et al., 2007; Rood et al., 2010). Presence-only SDMs use data that only indicates locations where the target species has been observed (Dettmers & Bart, 1999; Rood et al., 2010), whereas presence–absence SDMs use data that confirms the study species is present in an area whilst also using data that confirms that the study species is totally absent from other areas. For many studies, absence data is particularly difficult to obtain (Hirzel et al., 2002), and this explains the prevalent use of presence-only SDMs in published literature. Often, individuals (or groups of animals) do not range across the whole study area, and for various reasons aggregate in specific areas within a study area. This may be because their adaptations are suited to certain areas within the study area (Liu et al., 2014), because they favor a resource that is not normally distributed within the study area (Abade et al., 2014), or because they are avoiding human disturbance and/or predation (Rood et al., 2010; Isabel et al., 2018). For these reasons, spatial ecologists often differentiate between the habitat-used by study groups and the habitat-available to study groups. ENFA uses three statistics to assess the interactions between individual species distribution and biogeographic variables: Marginality, Specialization, and Tolerance (Hirzel et al., 2002; Calenge 2011; Abade et al., 2014; Pre`au et al., 2018; Rood et al., 2010; Xuezhi et al., 2008; Pettorelli et al., 2008). Marginality indicates a tendency to live in habitats that are different from the biogeographic mean, or how atypical habitat used is when compared to the habitat available (Williams et al., 2009). Low Marginality values indicate the species occupies average habitat when compared to the habitat available in the study area, whereas high Marginality values indicate that the species occupies atypical habitat when compared to the habitat available in the study area. Whereas typically the values of Marginality range from 0 to 1 (e.g. Preau et al., 2018; Hirzel et al., 2002), it should be noted that Marginality can have values higher than 1 (e.g. Ayala et al., 2009; Sattler et al., 2007), and that the Marginality reported largely depends on the reference area chosen as the habitat available (Hirzel et al., 2002). Specialization (S) indicate the levels of 'choosiness' of the study species (S), and indicates the narrowness of the habitat used compared to the habitat available. High specialization means a species occupies very specific habitat whereas low specialization means the species occupies a wider variety of habitat. The inverse of Specialization is Tolerance (Tolerance=1/Specialization), and this indicates a species ability to tolerate different habitats. Whereas values for Specialization can range from one (1) to infinity (∞), the values of Tolerance are limited and range from zero (0) to one (1), and in many cases Tolerance is easier to interpret when compared to Specialization (Costa et al., 2016).

2.3 Critique of Existing Literature

Three approaches have been used to study baboon species distribution. First, much work on baboons focuses on detailing a small number of well-known study groups. For example, a number of baboon groups in the hybrid zone between anubis and hamadryas baboons in Awash National Park, Ethiopia, have been well studied and documented for decades (Nagel, 1973; Gabow, 1975; Philips-Conroy & Jolly, 1986). Gabow (1975) studied hamadryas and anubis baboon populations in Awash National Park, Ethiopia and noted that, despite differences in behavior affecting mating between the different species, the hybrid zone between the two species was stable. Gabow (1975) also noted that the anubis baboons in his study ranged in habitat that was dissimilar to hamadryas habitat, but this did not hinder one species moving into the range of the neighboring species. Philips-Conroy and Jolly (1986) studied the hybrid zone in Awash National Park and noted that the hybrid zone expanded and contracted, and this expansion and contraction was thought to be related to changes in climate witnessed in the national park. Similarly, baboon groups in the Amboseli basin, Kenya, have been studied in detail for decades (Samuels & Altmann, 1986; Alberts & Altmann, 2002; Tung et al., 2008). Samuels and Altmann (1986) reported the first sighting of anubis baboon migration into the Amboseli basin, and also reported on the hybrid zone west of the Amboseli basin. The baboon populations here were again investigated by Alberts and Altmann (2001). Alberts and Altmann (2001) conducted a demographic survey of the Amboseli baboon populations, and reported that there were more hybrid baboons in the predominantly yellow baboon population of the Amboseli basin when compared to previous demographic surveys. Where these studies relied on phenotype to classify baboon populations, newer studies relied on genotype to classify baboon populations. For example, Tung et al (2008), studying the temporal changes in the genotype of the Amboseli baboon population, reported a decrease in the number of unadmixed anubis baboons, but also reported an increase in the number of hybrids between yellow and anubis baboons in the study populations. Whereas all these studies recognize and discuss the importance of biogeography in species distribution, none quantify the relationship between biogeography and baboon species distribution as this was not the focus of these studies. Furthermore, whereas studies on selected baboon groups provide detailed information on the biogeographical niche of study groups, it is often the case that the sites where well-studied groups are found do not encompass the variation seen in the habitat occupied by baboon species (Winder, 2014), and therefore observations based on these study groups cannot be generalized to the larger population.

Second, whenever there were surveys on baboons covering multiple baboon groups within a larger population, the work only focused on the spatial distribution of baboon species (Maples & McKern, 1967; de Jong & Butynski, 2012; Charpentier et al., 2012). Maples and McKern (1967) surveyed baboon populations found in the southern part of Kenya and reported a sharp demarcation between yellow baboons in Amboseli and the nearest population of anubis baboons found in Namanga. These two populations were separated by a 45 km wide dry lake bed. Mapels and McKern (1967) also indicated that yellow and anubis baboon ranges came together at Simba near Sultan Hamud. In a survey of primates in and around the coastal region, de Jong & Butynski (2012) reported sightings of yellow baboons, anubis baboons, and their hybrids. Whereas these studies relied on phenotype to classify baboon populations, Charpentier et al (2012) used genotype to classify baboon populations found in the southern part of Kenya, providing a clearer picture of the spatial distribution of baboon species and their hybridization. These studies provided a wider view of the spatial distribution of baboon species in Kenya. However, they did not investigate the biogeographic variations of the different sites where baboons were found, nor did they investigate the correlation between biogeography and baboon species distribution.

Third, researchers have used datasets covering continental Africa to investigate the biogeographic niche of baboon species (Dunn et al., 2013; Winder, 2015; Fuchs et al., 2018; Hill & Winder, 2019; Chala et al., 2019). Many biogeographic datasets are now available for free (Fick & Hijmans, 2017; Hansen et al., 2003; Hijmans et al., 2005), and researchers have utilized these datasets to study baboon distribution, forming a clearer picture of biogeographic variation at sites where baboons are found across Africa. In order to investigate the contribution of biogeography to baboon species morphology, Dunn et al (2013) studied the skulls baboons collected across Africa. These skulls (N=361) were obtained from museum records. Using specific morphology markers, Dunn et al (2013) used partial regression to establish if a correlation existed between skull morphology and variables representing relief, vegetation and climate. Whereas Dunn et al (2013) reported spatial patterns in the divergence seen in skull morphology, the biogeographic influence on skull morphology was unclear. Similarly, in order to explore the biogeographic niche of baboon species in continental Africa, Winder (2014) selected four sets of data representing the biogeographic conditions within the ranges of the 6 baboon species. The biogeographic data included climatic variables, vegetation data, and physical landscape data that included altitude, terrain roughness, soils and lithology. Winder (2014) used data on baboon species range distribution from the IUCN database (Kingdom et al., 2008). Using GIS, the mean, minimum, and maximum for each continuous variable were calculated for each species range and the data was then analyzed. To explore nominal biogeographic such as lithology and vegetation Winder (2014) used Multiple Correspondence Analysis (MCA) which is comparable to Principal Component Analyses (PCA) for continuous data. Winder (2014) noted that there seemed to be small differences in the biogeographic niche when comparing baboon species, and that all 6 species exhibited characteristics of ecological generalists. Winder (2014) noted that anubis baboon ranges spanned a wide range of conditions for nearly all variables including altitude, temperature, precipitation, vegetation and soil. Similarly, the yellow baboon ranges spanned a wide range of conditions. Results from Winder (2014) suggested that while systematic patterning in the anubis and yellow baboon ranges was less consistent and less visible on continental scale, this was not the same for all species (e.g. Guinea baboons). Fuchs et al (2017) used baboon species distribution data obtained from primary and secondary data (N ranging from 8 to 86 points for each species), and WorldClime data to develop SDMs that covered continental Africa. Fuchs et al (2017) found that baboon species distributions correlated with climatic variables with yellow baboons inhabiting lower latitudes with a cooler mean annual temperature compared to anubis baboons. Fuchs et al (2017) also reported that anubis baboons exhibited more ecologically flexible compared to other baboon species, and this corroborated findings from Winder (2014). As a follow up to work by Fuchs et al (2017), Winder and Hill (2019) explored how each baboon species will be affected by future climate change. Using baboon species distribution data from the Global Biodiversity Information Facility (GBIF, 2017) (N ranging from 54 go 795) and Worldclim data predicting future conditions (Hijmans et al, 2005), Hill and Winder (2019) predicted that yellow baboons will not experience a change in their range, whereas anubis baboons would increase their range when future climate conditions are considered, classifying these two species as resilient species that are able to cope with varied climatic conditions. This was not the same for all species, with chacma, Guinea, and kinda baboons expected to experience a decrease in range when future climatic conditions are considered.

The main critique of studies at a continental scale is that the generalization required in creation of these datasets often means local conditions may not be adequately represented (Winder, 2014; Derin & Yilmaz, 2014), and it is unclear if this issue affected the findings of these studies. Species range data created from continental datasets may include habitat that is avoided by the study species (Winder, 2014), and this may affect results of a study. Similarly, conditions of vegetation and climate at a continental scale may gloss over conditions at a local scale. The question of uncertainty in global spatial datasets is gaining prominence among scientists, and it is now recommended that scientists intricately familiarize themselves with global datasets before using them (Foody & Atkinson, 2002). For example, the IUCN ranges used by Winder (2014) are very general and include areas that would be extremely difficult for baboons to include in their range. Winder (2014) noted that the ranges of some species included areas with average temperatures below 0^0C, and that is was improbable for baboons to include there areas in their day to day activities. Fuchs et al (2017) found that yellow baboons inhabiting areas with cooler mean annual temperature compared to anubis baboons at a continental scale, whereas more intricate observations in Kenya implied that the baboons found in southern Kenya did not follow this pattern (Kingdom, 1997).

While studies at single sites give detailed insight into how baboons interact with their environment in small geographic areas (Alberts & Altmann, 2002), they often do not represent the variation seen in baboon habitats. Studies at a continental scale give a broader but coarser view (Winder, 2015; Fuchs et al., 2018), but the generalization in creating these datasets often means local conditions which may be important to a species are not considered. Whereas studies at this intermediate scale have been conducted Maples & McKern, 1967; de Jong & Butynski, 2012; Charpentier et al., 2012), none of these studies focused on the biogeography of baboon species. There is need for studies that, while maintaining some of the detail that a smaller study would generate, sample multiple sites that are more representative of the variation observed in baboon habitats. This approach would better highlight biogeographic niches occupied by baboon species, and provide an important link between detailed studies covering small areas (Alberts & Altmann, 2002), and larger, continental scale studies (Winder, 2014).

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

The study area, referred to in this text as southern Kenya, was composed of Kajiado, Makueni and Taita-Taveta counties (Figure 3.1). The study area covered approximately 46,368 square kilometers. The Amboseli, Tsavo East, and Tsavo West National Parks are examples of wildlife sanctuaries that were found within this region.

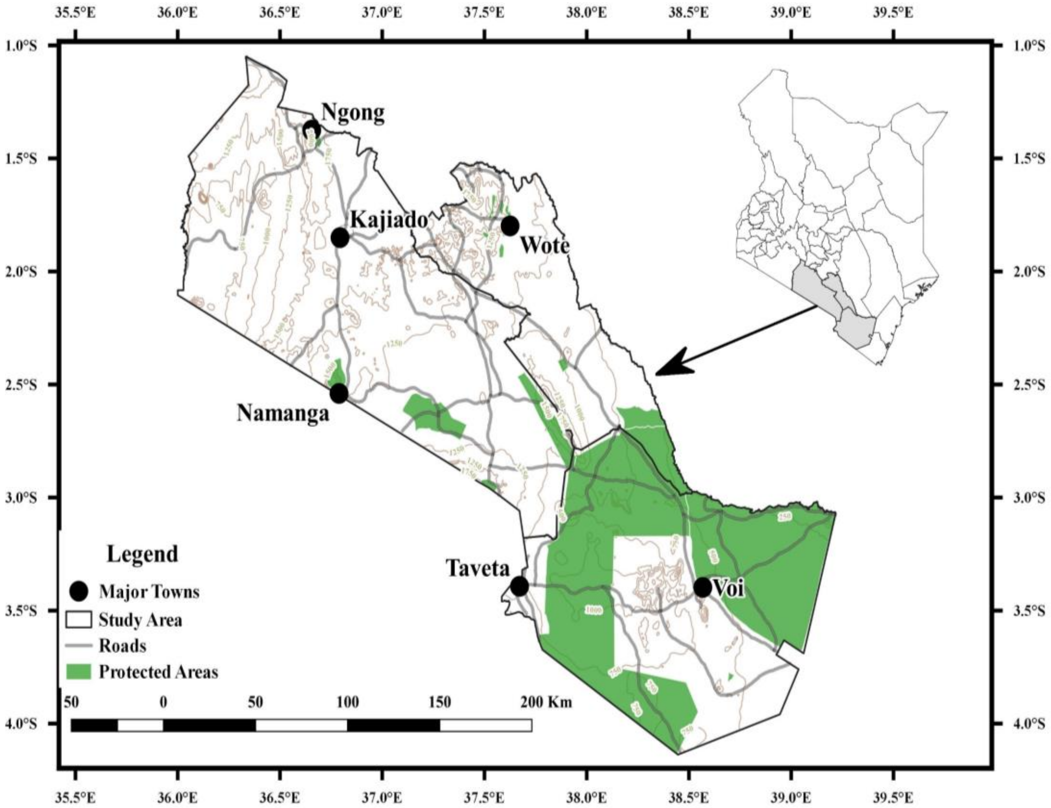


Figure 3.1: A map of the study area, southern Kenya, showing major towns, major roads, and protected areas.

The study area was chosen because it encompasses a well-known hybrid zone between anubis and yellow baboons (Charpentier et al., 2012; Winder, 2015), and because it has a varied geographical outlay. With high altitude areas such as Taita and Ngong Hills, and low altitude areas such as Amboseli and Magadi, it was postulated that there would be areas of varying biogeography where different baboon species ranged.

3.2 Sampling Design and Techniques

Longley et al (2005) described three attributes that distinguish one geographic problem from the next: the geographic area covered by the study, the temporal scale of the study, and the objectives to be met by the study. Numerous scientists have attempted to break down biogeographic relationships with these three attributes in mind in order to identify geographic and temporal scales that would fit their studies. Johnson (1980) recognized four different levels that inform spatial ecologists of the geographic and temporal scale to consider depending on their study question or objectives, and the structure outlined by Johnson (1980) is still used today (Zwolicki et al., 2019; Paolini et al., 2019; Delisle et al., 2019). In First-Level selection studies, the analyst looks at the distribution of an animal within a large area, over a long period of time. An example of a First-Level study is de Jong and Butynski (2012) where the ranges of coastal primate species in Kenya were determined. In Second-Level selection studies, the analyst looks at the distribution of a specific animal or group of animals within their identified range. The study area and time period covered by the study decreases as the level of detail on the study animal and biogeographical variables increase. Examples of Second-Level studies include Fieberg and Kochanny (2005) and Markham et al (2013) where the authors first identify home ranges of the study animals and then compare how animals use shared space within their home ranges. Third-Level selection studies focus on the use of resources within the home range, requiring detailed data on species distribution and biogeographic variables of interest. For example, in order to study baboon responses to thermal stress, Stelzner (1988) first partitioned the home range of selected baboon groups into quadrants, classified each quadrant according to the shade available, and analyzed the behavior of the study group as they moved around their home range in hot and cool weather. The time period considered for such a study is usually even shorter. Fourth-Level selection studies take into consideration micro-biogeographic factors and the choices made when using these resources. Examples include Post (1981) and Bronikowski and Altmann (1996), where the authors detail dietary choices made by individual baboons within their home ranges. Here, the food choices vary from day to day, season to season, and the time period considered for Fourth-Level selection studies tends to be the shortest. A First-Level selection study was best suited for this study as the spatial and temporal resolution best fit the study questions. Specifically, a First-Level selection study that focused on sites baboons had ranged for decades.

Classical statistics often emphasize the importance of randomness in sound sampling design (Longley et al., 2005). However, in nature it is often the case that the phenomena being sampled is disproportionately distributed, and a purely random sample may not represent the distribution of many natural phenomena. This is often overcome by sampling in regular intervals by either following a stratified sample or a stratified random sample. Some phenomena are concentrated along linear features such as roads or rivers, and in such contour sampling is used. Still, some phenomena are concentrated in clustered patterns within the study area, and sampling would then focus around these clusters. This is known as clustered sampling. Animals often congregate near certain resources that provide food, water, or shelter, and thereby follow a clustered pattern. Here, clustered sampling was used. First, a comprehensive literature review was conducted in order to identify traditional sites where baboons had been encountered in literature. Next, a field survey was conducted to establish if baboons were still found in these traditional sites, and to see if new sites that were not reported in the literature could be identified. The baboon populations identified in the field survey were then categorized according to population ancestry. Biogeographic variables, specifically LULU, climate, and geography, were then used to describe the habitats where these baboon populations were found. LULC data was generated, and climatic variables were collated from the WorldClim repository and crossvalidated using climatic data from the Kenya Meteorological Department and the Amboseli Baboon Research Project. Geographic data describing the altitude of the study area was obtained from the Shuttle Radar Topography Mission, and distance from the ocean data was generated within GIS software. Finally, analysis using GWRA and ENFA was conducted to investigate the biogeographic niche of baboon species in southern Kenya (Figure 3.2).

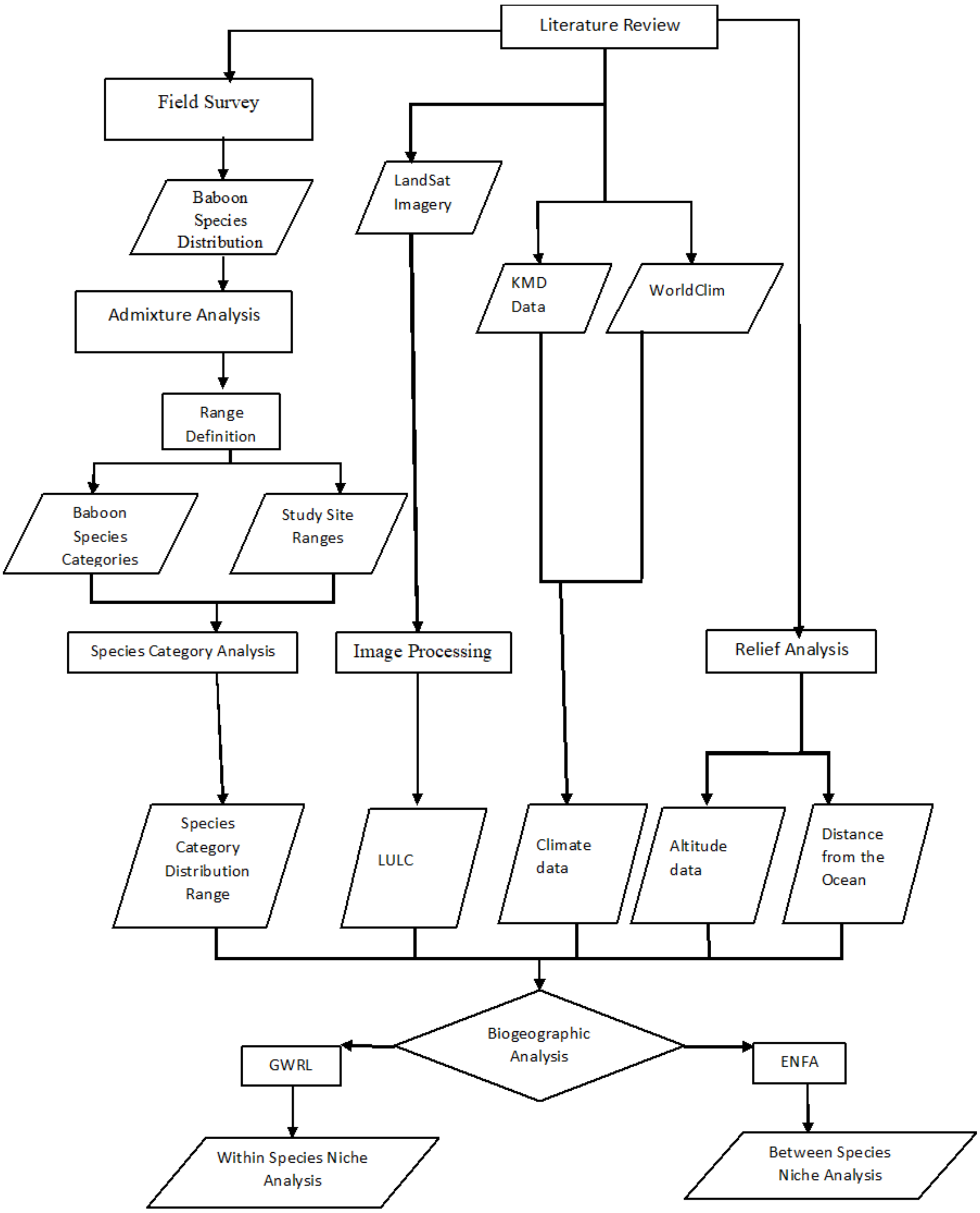


Figure 3.2: A flowchart depicting the research methodology used in the study

3.3 Research Tools

Two Garmin^{T} (USA) GPS receivers (eTrex 10 and eTrex 20) were acquired for field surveys, and used to record the locations of baboons sighted. Both Garmin eTrex 10 and eTrex 20 are rugged GPS receivers capable of a positional accuracy of 3 meters in optimal conditions. A pair of reconditioned Bushnell binoculars donated by the Amboseli Baboon Research Project was used for close-up views of baboon individuals. A field assistant was trained on the use of GPS receivers, the use of binoculars, identification of baboon species, and recording of baboon sightings. A Suzuki Jimny was hired for the field survey. This vehicle has good off-road capabilities making it ideal for field studies. A Dell desktop was loaded with GIS and RS software, statistical analysis software, and word processing software. This desktop was used for data storage, data preparation, and data analysis. Details of the research tools are provided in **Table 3.1**.

Table 3.1: The table gives details on the research tools used in this study.

FIELD SURVEY TOOLS			
		REGISTERED NAME	**SPECIFICATIONS/COMMENTS**
1	Computer	DELL Optiplex 540 Desktop	Intel dual core 3.2GHz processor, 2Gb RAM, 160Gb Hard disk
2	GPS Receiver	Garmin eTrex 1O	GPS receiver with GNASS support for fast positioning and a reliable signal
		Garmin eTrex 20	GPS receiver with GNASS support for fast positioning and a reliable signal
3	Field Vehicle	Suzuki Jimny	1300cc engine, 4 Wheel Drive, Short Chasis field utility vehicle
4	Binocular	Brushnell Powerview	16*50 Magnification, Prism system binocular, coated-lens binoculars
5	GIS Software	ESRI ArcGIS 9.2	Multipurpose GIS software with tools for spatial data creation, spatial analysis, geostatistical analysis, scripting, and digital cartography
		Clark Labs Idrisi Kilimanjaro	Multipurpose Remote Sensing software with tools for image analysis and vegetation mapping
		Google Earth	GIS viewer with tools for exploring digital maps
6	Analysis Software	Microsoft Excel	Mutlipurpose spreadsheet with analysis tools provided through the DataAnalysis Toolkit
		CRAN R	Multipurpose statistical software with various general spatial analysis tools as well as spatial ecology tools
7	Word-processing	Microsoft Word	Multipurpose wordprocesssing software
8	Species Identification Tool	N/A	A Species Identification Tool designed to ease and standardize recording of observations in the field

3.4 Data Collection Procedures

In order to investigate the biogeographic niche of baboon species within southern Kenya, the following datasets were required for analysis: baboon species distribution, LULC, climate, and geography (altitude and distance from the ocean). **A summary of the datasets needed and the sources of the data is provided in Table 3.2.**

Table 3.2: The table summarizes the data needs for the study, and shows the sources of data.

	DATA	SOURCE	COMMENT
1	Baboon Species Distribution	Field Survey	Baboon species distribution data generated from an extensive field survey carried out from 2013 to 2015.
		Charpentier et al., 2012	Genetic analysis data from Charpentier et al (2012).
2	Vegetation Data	Image Classification	Vegetation data generated from classified Landsat imagery from the GLS 2010 collection.
3	Climatic Data	Kenya Meteorological Department	Climatic data from the year 1980 up to 2012 purchased from KMD in Nov 2012.
		Amboseli Baboon Research Project	Climatic data for the Amboseli basin collected by the Amboseli Baboon Research Project covering 1980 to 2012.
		WorldClim	Climatic data depicted by different bioclimatic variables downloaded from the WorldClim repository (Fick & Hijmans, 2017)
4	Geographic Data	SRTM Altitude Data	Altitude data generated by the Shuttle Radar Topography Mission downloaded from the United States Geological Survey website (http://edcsns17.cr.usgs.gov/NewEarthExplorer/).
		Distance from the Ocean	Grid data depicting the distance of a site from the Indian Ocean generated within ArcGIS 9.2.

3.4.1 Baboon Species Distribution

Though surveys on baboon populations in southern Kenya have been conducted before (Charpentier et al. 2012; de Jong & Butynski 2012), it was important to establish if the patterns described in literature depict the current state of baboon species distribution or if there have been notable changes. It was also important to establish if new baboon populations could be identified in the course of the field survey. Lastly, it was also important to establish the ranges of each baboon study population in order to estimate the biogeography within the respective ranges. To establish the current species distribution, a field survey was conducted within our study area. First, using Google Earth, the road network in the study area was identified. Second, locations where baboons had been observed in the literature were noted, and optimal routes to these sites were selected. The field survey was then conducted in intervals from 2013 to 2015 following the road network within Kajiado, then within Taita-Taveta, and finally in Machakos county. During the field survey, locals were questioned to aid in identifying specific spots where baboons were common, and if the baboon populations had been in these area for a long period or if they had recently immigrated. Once baboons were spotted, the locations where they were spotted were recorded on the handheld GPS receivers. Baboons range in groups of between 20~130 individuals (Markham et al., 2012; Raad & Hill, 2019) and have large day ranges (Raad & Hill, 2019), often occupying a significant area while foraging. Baboons are not territorial, and whereas territorial animals do not allow sharing of areas within their home range, numerous baboon groups can share areas within their home range (Slater et al., 2018). Normally, when tracking habituated baboon groups, researchers are advised to take GPS readings from the center of the group once the accuracy of the GPS receiver is 10 meters or below (e.g. see the Amboseli Baboon Research Project data collection protocols online at http://amboselibaboons.nd.edu/). In ecology, habituation is the process where a researcher is repeatedly presented to a group of animals, and eventually the animals do not consider the researcher a threat enabling the researcher to move freely among or near the group of animals (e.g. Holger et al., 2017; Raad & Hill, 2019). It should be noted that none of the researchers in this study were habituated to the baboons encountered in the field, and similar to Johnson et al (2015), GPS readings were taken from a respectful distance (10~20 meters) from baboon groups encountered in order not to startle them. Where possible, the baboon groups were tracked and GPS readings were recorded at one hour intervals for approximately 8 hours each day for 7 days. An average of fifty (N~50) GPS points were taken at each site during the field survey. While advances in animal tracking technology have increased capacity to collect data to support ecological analysis, this has resulted in increasingly autocorrelated species distribution data (Noonan et al., 2019). It is possible to reduce autocorrelation within tracking data, but this is often discouraged. Instead, it is advised that researchers collect as much tracking data as possible and to collect this data after constant time intervals (De Dola et al., 1999).

As baboon groups were being tracked, phenotypic species identification was carried out. Alberts and Altmann (2001), adapting methodology used by Phillips-Conroy et al., (1991), devised a system to categorize a baboon individual as either unadmixed anubis, unadmixed yellow, or hybrid based on phenotype. The characteristics scored by Alberts and Altmann (2001) were coat color, body shape, hair length, head shape, tail length and thickness, tail bend, and muzzle skin. Unadmixed anubis and unadmixed yellow baboons show notable differences in these characteristics, with hybrids exhibiting intermediate characteristics (Alberts & Altmann, 2001). In this study, to categorize a baboon as either unadmixed anubis, hybrid, or unadmixed yellow, only three characteristics were chosen: coat color, body shape, and hair length (Table 3.3). As these three characteristics are very easily distinguished, training an inexperienced researcher to categorize a baboon based on these three characteristics was easy.

Table 3.3: Differentiating between anubis and yellow baboons. The table describes features used to categorize a baboon as either anubis, yellow, or hybrid

APPEARANCE	ANUBIS	HYBRID	YELLOW
COAT COLOR	Olive brown or dark grey	Intermediate	Yellow coat, slightly tinted brown
HAIR LENGTH	Long, thick hair	Intermediate	Short hair
BODY SHAPE	Appears short and bulky with a big chest	Intermediate	Appears tall and slender

An individual baboon was categorized as unadmixed anubis only if it exhibited all three anubis baboon characteristics. Similarly, an individual was categorized as unadmixed yellow only if it exhibited all three yellow baboon characteristics. An individual was categorized as hybrid if it exhibited any characteristic described as intermediate between anubis and yellow. Where multiple baboons were encountered, sampling focused on larger male baboons as these are easier to identify (especially from a distance). It should be noted that male baboons are known to disperse more often than female baboons, and the male demographic is more likely to be mixed (consisting of unadmixed anubis and unadmixed yellow male baboons) when compared to the female demographic of a baboon population. A group consisting of only unadmixed anubis was considered an unadmixed anubis group. Similarly, a group consisting of only unadmixed yellow was considered unadmixed yellow group. A group consisting of a mixture of unadmixed yellow and unadmixed anubis baboons, unadmixed yellow baboons and hybrids, or unadmixed anubis baboons and hybrids was considered a hybrid group. The sighting of a baboon, or group of baboons, combined with proper categorization as either unadmixedanubis, unadmixed yellow, or hybrid constituted a focal sample. To supplement data from the field survey, genotypic data from 11 sites sampled by Charpentier et al (2012) was used. Using data from Charpentier et al. (2012), it was established that there were populations of unadmixed anubis baboons and unadmixed yellow baboons. It was also established that there were admixed populations comprising of anubis-major baboons anubis (>50% anubis ancestry or anubis-major hybrids) and yellow-major baboons (>50% yellow ancestry or yellow-major hybrids).

3.4.2 LULC

LULC data is often obtained by processing satellite imagery from the various earth-imaging systems. Of the numerous earth-imaging systems available, LandSat was the most suitable for this study for three main reasons. First, the spatial, spectral and radiometric resolution of the data facilitate characterization of vegetation at a scale agreeable with the large area covered by the study. Second, LandSat has been in operation for decades, with each successive series is designed with backwards compatibility (Lillesand et al., 2015). Lastly, Landsat imagery has become increasingly available, with some images provided for free. Through numerous Internet portals, LandSat images can be ordered at the cost of packaging and shipment, or downloaded free of charge. Landsat imagery is available for download from the United States Geological Survey (USGS) repositories (http://edcsns17.cr.usgs.gov/NewEarthExplorer/). Satellite images covering southern Kenya were downloaded from the USGS website, specifically from the Global Land Survey (GLS) repository. The GLS project was designed to give scientists a collection of high quality, curated, and preprocessed Landsat imagery. The Landsat data downloaded is part of the GLS 2010 series of Landsat imagery, and was chosen as the images were taken closest to the period during which genetic data from Chapentier et al. (2012) were processed. An informative description of the GLS project can be found at the GLS website https://landsat.usgs.gov/global-land-surveys-gls.

Table 3.4: The table gives details of imagery downloaded from the GLS repository

LANDSAT IMAGE ID	ACQUISITION DATE	WRS	
		PATH	ROW
LE71670622011043ASN00	12-Feb-11	167	62
LE71660632011036ASN00	05-Feb-11	166	63
LE71660632011020ASN00	20-Jan-11	166	63
LE71680612010351ASN00	17-Dec-10	168	61
LE71670632010280ASN00	07-Oct-10	167	63
LT51690612010030MLK00	30-Jan-10	169	61
LE71660622010001ASN00	01-Jan-10	166	62
LE71680622009012ASN00	12-Jan-09	168	62
LE71670612010152ASN00	01-Jun-10	167	61

The satellite imagery was then imported into ArcGIS^T 9.2 (ESRI, USA) and true color composites generated for each image. The study area was then visually inspected by comparing the composite imagery with high resolution imagery from Google Earth^T (Google Inc, USA). Whereas the 30-meter resolution of LandSat imagery was adequate for recognizing medium to large sized features, Google Earth^T gave a more detailed view of the study area and enabled identification of small features such as small ponds, small clusters of trees, bushes, and human settlements in rural areas. The obvious disadvantage of using Google imagery was that changes in land-cover could have occurred between the acquisition dates of the Google imagery (taken between 2010 and 2013) and the Landsat images (taken between 2009 and 2011). Difference in LULC states represented on Google Earth imagery and on Landsat imagery was also a concern. Nevertheless, Google Earth provided a vast amount of detailed information that included the vegetation, small water bodies, roads and settlements, and this made Google Earth a very useful tool for familiarizing oneself with the study area and planning field trips to collect reference data. After considering the geography of the study area and literature published on baboon habitat and behavior (Bronikowsky & Altmann, 1996; Alberts et al., 2005;

Dunbar, 1992; Treves et al., 1998; Hill 2000; Hill & Dunbar, 2003; Markham et al., 2016), seven LULC types were identified as important for the study:

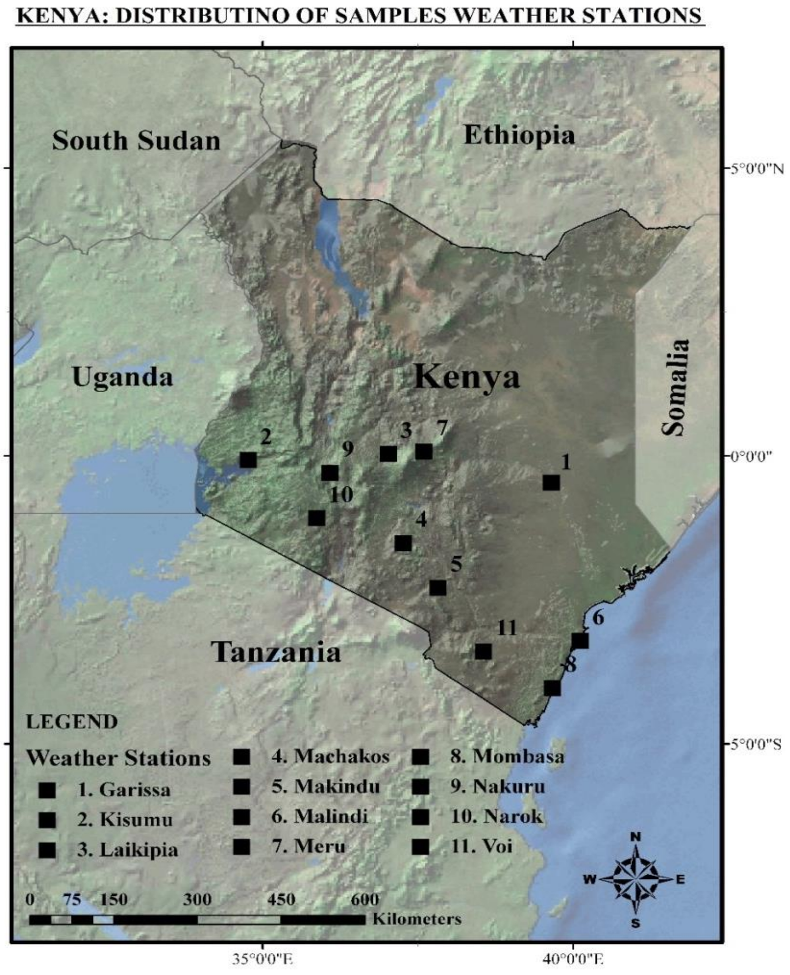
1. Forest: closed stands of trees with at least 80% closed canopy
2. Woodland: open stands of trees with 40-80% canopy cover
3. Bushes: shrub cover of >40% of the landscape
4. Grasslands: open grass cover of >60% of the landscape
5. Bare ground: land devoid of vegetation
6. Swamp land: vegetation immersed in water
7. Agricultural land: land used for crop cultivation

Using the SAMPLE tool in IDRISI Kilimanjaro^{T} (Clark Labs, USA), a vector file containing 600 stratified random points covering the study area was generated. Random sampling or stratified random sampling are favored for their statistical properties (Congalton, 1991; Lillesand et al., 2015), and it is recommended that samples, 10-25 pixels large, numbering 50-100 be collected for each LC type (Congalton, 1991; Lillesand et al., 2015). The file containing the stratified random points was then imported to Google Earth^{T}. Within Google Earth^{T}, 420 points were noted for further investigation based on the clustering of similar vegetation around the points and ease of access. This set was further thinned to a subset of 318 sites that fell in or near homogenous patches of vegetation (20~100 pixels large) based on visual inspection of the LandSat imagery and corresponding Google Earth^{T} images for the same region. The selected points were then imported into ArcGIS. Polygons covering roughly 20 pixels (each pixel covering an area approx. 28 by 28 meters) were drawn around the selected points and the vegetation within each polygon manually assigned. From the 318 sites, 123 sites located in accessible regions were visited in a ground-truthing exercise and reserved for accuracy assessment, the other 195 sites were used as reference data for image classification. In order to generate LULC data for the study area, satellite images acquired for the study were imported into IDRISI Kilimanjaro^{T} (Clark Labs, USA) and individually classified using the ISOCLUST module. ISOCLUST, an unsupervised classification module, is based on an algorithm for data analysis and pattern classification known as ISODATA (e.g. Ball & Hall, 1965; Tou & Gonzalez, 1974; Eastman, 2003). The algorithm accepts a user defined number of spectral classes to be located in the data. The algorithm then arbitrarily locates the mean of each information class and each pixel is assigned to the closest class. After the first classification, the new means of the clusters are calculated and the algorithm then re-assigns the pixels to the closest cluster. The process is repeated until there is no more change in the mean of clusters after successive iterations. By comparing the signatures of each spectral class to the signatures of the reference data, different spectral classes were matched to respective LULC. Spectral classes that did not give useful information were discarded. The retained spectral classes were grouped according to the land-cover types they represented. This procedure allowed classification of ~65% of the study area. The generated data was used to reclassify the images using the maximum likelihood algorithm module in IDRISI, MAXLIKE. The maximum likelihood classifier, a supervised classification algorithm, quantitatively evaluates both the variance and covariance of spectral classes found within a LC class. Assuming a normal distribution, the algorithm then calculates the probability of an unassigned pixel falling within the LULC class (Eastman, 2003). The resulting images were then merged using the Mosaic tool in IDRISI, resulting in LULC data for the year 2010.

To assess the accuracy of the LULC mapping, we compared the resulting assignments to the 123 sites in the ground-truthed data set by first creating polygons (20-100 pixels large) of homogeneous LULC around the 123 sites. The dataset was then imported into IDRISI Kilimanjaro and accuracy assessment was carried out using the module ERRMAT. ERRMAT tabulates the relationship between ground-truthed data and the classified data by creating a confusion matrix, and calculates producer’s accuracy, user’s accuracy, and the overall proportional error or KAPPA.

3.4.3 Climate

Kenya is situated between latitudes 4° N and 4° S, and between longitudes 34° E and 42°E. Kenya shares her borders with Tanzania, South Sudan, Somalia, Ethiopia and Uganda, with the Indian Ocean on the south-eastern edge (Figure 3.3). The country has a sparse network of weather stations, many of which are located in towns along major roads. Kenya lies within the Inter Tropical Convergence Zone (ITCZ), with the main features of annual rainfall and its seasonal variations determined by monsoon weather patterns(Camberlin & Okoola, 2003; Camberlin et al., 2009; Camberlin & Olivier, 2018). Kenya experiences precipitation during the ‘long rains’ (March–May) and during the ‘short rains’ (October–December), with two dry seasons in between (Camberlin & Okoola, 2003; Wango et al., 2018), and these climatic patterns are replicated in the study area, Southern Kenya. Shiklomanov and Nelson (2003) noted that understanding and modeling of ecosystems require accurate, high-resolution temporal and spatial representation of climatic conditions, and this is true for all ecological studies. The climate of an area can impose physiological constraints on plants and animals, affecting their distributions to varying degrees by being too extreme for the study species, or by constraining resources such as food, water, and/or shelter. Climate data, often collected at weather stations, is normally interpolated into grid surfaces in order to estimate climate in areas with no weather stations. Works pioneered by Nix (1986) led to the development of numerous climatic variables known as bioclimatic variables (Booth et al., 2014), and a description is available online at https://www.climond.org/BioclimRegistry.aspx.



3: The location of Kenya in East Africa. The map shows the location of Eastern Africa, and the distribution of weather stations found in and e southern part of the country.

These bioclimatic datasets were generated from spatially interpolated weather station data to enable estimation of climatic conditions at sites where no climatic data is available (Brunsdon et al., 2001; Fick & Hijmans, 2017; Goodale et al., 1998; Goovaerts, 2000; Hijmans et al., 2005; Shiklomanov & Nelson, 2003). Bioclimatic variables were chosen over satellite climatic products (Land Surface Temperature and Land Surface Precipitation) for two reasons. First, bioclimatic variables have been widely adopted and are well understood by spatial-ecologists (Booth et al., 2014; O'Donnell & Ignizio, 2012; Wagner et al., 2018). Second, as recommended by Wango et al (2019), it was important to establish if baboon species distribution is influenced by extreme climatic conditions. Bioclimatic variables capture average as well as extreme monthly and seasonal climatic conditions (e.g. Hutchinson et al. 2009; O'Donnell & Ignizio, 2012), and for this reason bioclimatic variables were the best suited for this study. The bioclimatic variables envisaged by Nix (1986) take a different approach from the traditional ‘long rains versus short rains’ data models commonly used in East Africa (Camberlin & Okoola, 2003; Camberlin et al., 2009; Camberlin & Olivier, 2018). Nix (1986) designed bioclimatic variables that highlight average annual climatic patterns, extreme climatic monthly patterns, as well as extreme climatic seasonal patterns (O’Donnel & Ignizo, 2012) (Table 3.5).

Table 3.5: The table shows the nineteen bioclimatic indices and describes their interpretation in biological studies (see Hijmans et al., 2015; O'Donnell & Ignizio, 2012)

CODE	INDEX	NARRATIVE
BIO1	Annual Mean Temperature	Approximates the total energy inputs for an ecosystem.
BIO2	Mean Diurnal Range	Measures temperature fluctuations.
BIO3	Isothermality	Qunatifies how large the day-to-night temperatures oscillate.
BIO4	Temperature Seasonality	A measure of temperature variation over a year.
BIO5	Max Temperature of Warmest Month	The maximum monthly temperature.
BIO6	Min Temperature of Coldest Month	The minimum monthly temperature.
BIO7	Temperature Annual Range	Measures temperature variation over a year.
BIO8	Mean Temperature of Wettest Quarter	Approximates mean temperatures during the wettest consecutive four months
BIO9	Mean Temperature of Driest Quarter	Mean temperature during the driest consecutive four months.
BIO10	Mean Temperature of Warmest Quarter	Mean temperature during the warmest consecutive four months.
BIO11	Mean Temperature of Coldest Quarter	Mean temperature during the coldest consecutive four months.
BIO12	Annual Precipitation	Annual total precipitation.
BIO13	Precipitation of Wettest Month	Precipitation of the wettest month over the sampled period.
BIO14	Precipitation of Driest Month	Precipitation of the driest month over the sampled period.
BIO15	Precipitation Seasonality	This is a measure of the variation in monthly precipitation totals over the course of the year.
BIO16	Precipitation of Wettest Quarter	Precipitation of the wettest consecutive four months.
BIO17	Precipitation of Driest Quarter	Precipitation of the driest consecutive four months.
BIO18	Precipitation of Warmest Quarter	Precipitation of the warmest consecutive four months.
BIO19	Precipitation of Coldest Quarter	Precipitation of the coldest consecutive four months.

To assess annual climatic patterns, Nix (1986) designed BIO1 (annual mean temperature), BIO2 (mean diurnal range), BIO3 (isothermality), BIO7 (temperature annual range), and BIO12 (annual precipitation). To assess monthly extremes, Nix (1986) designed BIO5 (the maximum temperature of the hottest month), BIO6 (minimum temperature of the coldest month), BIO13 (precipitation of the wettest month), and BIO14 (precipitation of the driest month). To assess seasonal climatic extremes, Nix (1986) designed BIO8 (the mean temperature of the wettest quarter), BIO9 (mean temperature of the driest quarter), BIO10 (mean temperature of the warmest quarter), BIO11 (mean temperature of the coldest quarter), BIO16 (precipitation of the wettest quarter), BIO17 (precipitation of the driest quarter), BIO18 (precipitation of the warmest quarter) and BIO19 (precipitation of the coldest quarter. These seasonal bioclimatic variables are calculated on a quarterly basis, i.e. the coldest three consecutive months, the hottest three consecutive months, the wettest three consecutive months, and the driest three consecutive months (e.g. Hutchinson et al., 2009; O'Donnel & Ignizo, 2012). WorldClim version 2.1 was created by interpolating climatic data for 1970 to 2000 collated from 60,000 weather stations (Fick & Hijmans, 2017). WorldClim version 2.1 has a resolution of 1km^2, and has been shown to accurately depict current average climatic conditions (Wango et al., 2018), and has also been shown to strongly correlate with climate variables derived from satellite imagery (Fick & Hijmans, 2017).

3.4.4 Geography

In this study, the geography of study sites referrers to site's altitude, and the site's distance from the ocean. It was also important to establish if altitude correlated with baboon species distribution. It was also important to establish if the distance from the ocean correlated with baboon species distribution. Yellow baboons were thought to have migrated into the study area as they moved along the Indian Ocean, whereas anubis baboons were thought to have migrated into the study area from the west. Because of this, it was felt that distance from the ocean was an important geographic variable that could be linked to the natural history of baboon species distribution in the study area. Elevation data was estimated from The Shuttle Radar Topography Mission (SRTM) 30m resolution data. SRTM, a joint project of the National Imagery and Mapping Agency (NIMA, USA) and National Aeronautics and Space

Administration (NASA, USA), produced global altitude datasets of 30-meter resolution for public distribution (Lillesand et al., 2015). These datasets are distributed by the United States Geological Survey (USGS) at no cost. To estimate a study site's distance from the ocean, a grid surface indicating the distance of each point within the study area from the Indian Ocean was generated in ESRI's ArcGIS 9.2.

3.5 Processing And Analysis

To investigate the biogeographic niche of baboon species in southern Kenya, GWRA was used to investigate between-species biogeographic niche whereas ENFA was used to investigate within-species niche variability. GWRA was suitable for testing if species distribution correlated with biogeography within the study area, thereby establishing if there was a significant difference between the biogeographic niche of yellow baboons, anubis baboons, and their hybrids. ENFA was used to quantifying the within-species habitat choice, thereby establishing which biogeographic variables are important to each respective species within their distribution ranges in the study area.

3.5.1 Geographic Weighted Regression

Khotari (2004) defined regression analysis as the statistical relationship between a dependent variable Y and an independent variable X. This can be written as:

$$\hat{Y} = \alpha + \beta X$$

Where,

$\hat{Y}$ is the estimated value of Y for a given value of X

α is a constant

β is the rate of change of Y with respect to X.

To find the line of best fit through a set of points using the least-squares method, we solve for α and β. We can say:

$$\sum u_i^2 = \sum x_i^2 - nX^2$$

$\sum v_i^2 = \sum y_i^2 - nY^2$

$\sum u_i v_i = \sum x_i y_i - nX.Y$

Where:

x_i is the value of X at i

y_i is the value of Y at i

X is the mean of variable X

Y is the mean of variable Y

Then $\beta = \sum u_i v_i / \sum u_i^2$ and $\alpha = Y - \beta X$

The Karl Pearson's coefficient of correlation, a measure of the degree of correlation between two variables, and can be defined as follows:

$r = \beta(\sum x_i^2)^{½}/(\sum y_i^2)^{½}$

Positive values of r indicate positive correlation; negative values of r indicate negative correlation. R^2, the square of r, takes values between 0 and 1. When R^2 is equal to 1, there is perfect correlation whereas when R^2 is zero, no correlation exists between two variables.

GWRA is form of regression that allows the relationships between the independent and dependent variables to vary by locality. GWRA takes non-stationary variables into consideration and models the local relationships between these independent variables and the dependent variable. When assessing the biogeography of a species, non-stationary variables often include the geography, vegetation, and climate within the study area. The GWRA model extends the traditional regression framework by allowing parameters to be estimated locally so that the model can be expressed as:

$\hat{Y}_i = \alpha(u_i,v_i) + \beta(u_i,v_i)X$

Where:

$\hat{Y}_i$ is the estimated value of Y for a given value of X at a point i in space

$\alpha(u_i,v_i)$ is a constant at point i in space

$\beta(u_i,v_i)$ is the rate of change of **Y** with respect to **X** at point i i*n space.*

To investigate between-species biogeographic niche, GWRA was undertaken using the package spgwr (Bivand & Danlin Yu, 2020) for the statistical software CRAN R (Core Team, 2020). First, baboon sites were classified using an ordinal scale as follows: unadmixed anubis = 1, anubis-major hybrids = 2, yellow-major hybrids = 3, and unadmixed yellow = 4. Next, similar to Winder (2014), to estimate the biogeography within the range of each baboon population, the mean biogeographic conditions within each population's range was established. To estimate the biogeography within the range of each baboon population, management circles of 10km radius were used. Management circles are often used to estimate biogeographic conditions available to a population (Forsman et al., 2015; Anderson et al., 2005). First, the center of the set of GPS sample points (N~50) for each study site was established. Circles of 10km radius were then drawn around each respective point. Baboons are known to walk up to 10km in search of food and water (Bronikowski & Altmann, 1996), and for this reason circles of radius 10km would provide good estimates of the range available to baboons at each site. The mean for each biogeographic variable representing climate (BioClim variables) and geography (altitude and distance from the ocean) were then estimated within each population's range. The percentage of each LULC class within each population's range was also established. This information was tabulated and then imported into CRAN R for GWRA using the package spgwr.

3.5.2 Ecological Niche Factorial Analysis

The habitat enclosed within the study area, or habitat available (ES), can be defined by a vector space described by n biogeographic variables. Species often use selected areas within the habitat available to them, this is referred to as habitat used (ES^s). By monitoring a population over time, the relocation data can be used to estimate the habitat used with respect to the habitat available. The difference between the mean habitat available (**μES**) and the mean habitat used (**μES^s**) is called Marginality (**M**). The ratio between the standard deviation of the habitat used (**σES^s**) and the standard deviation of the habitat available (**σES**) is called the Specialization (**S**). **S** can be large ($\sim\infty$), so Tolerance (**T**) is defined as **$1/S$**. High **M** indicates that the habitat used greatly deviates from the habitat available. High **S** means that the habitat used is quite narrow when compared to the habitat available, indicating the species is a specialist & uses very specific habitat within the study area (Figure 3.4).

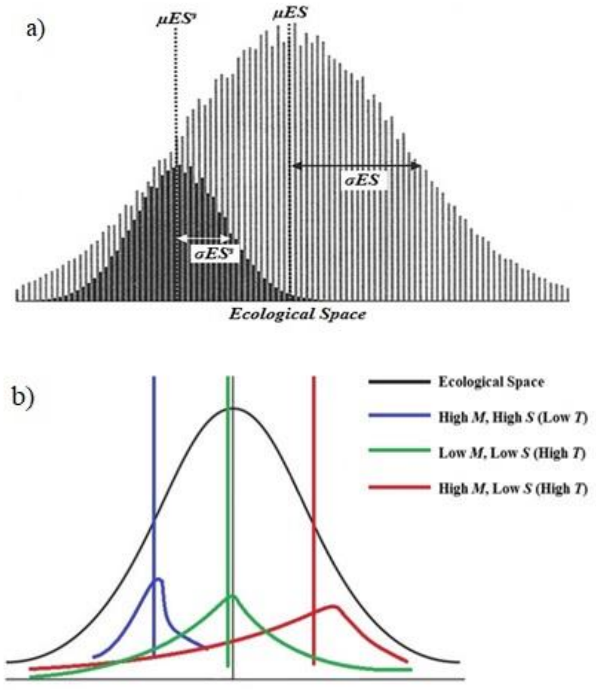


Figure 3.4a) The difference between μES & μES^s is the Marginality (M). The ratio between σES^s & σES is called the Specialization (S) (Adapted from Hirzel et al., 2002). b) The figure indicated different possible outcomes from ENFA analysis.

ENFA starts by extracting values for the biogeographic variables within each species category's range, then performs factorial analysis. Factorial analysis transforms **n** number of ecological variables into **n** number of uncorrelated factors (Hirzel et al., 2002), and subsequent analyses may be restricted to the few important factors. ENFA differs from traditional factorial analysis as the first axis is chosen so as to account for all the Marginality of the species, and the following axes so as to maximize Specialization (Hirzel et al., 2002). ENFA calculates a ‘marginality coefficient’, ***m***, relating the degree of correlation between each biogeographic variable and the Marginality (Abade et al., 2014). High absolute value of a marginality-coefficient indicates that the group of animals favors that particular biogeographic variable, and the more this particular variable contributes to the Marginality (Abade et al., 2014). A negative marginality-coefficient indicates that the group of animals favors lower-than-mean values of a particular biogeographic variable (Hirzel et al., 2002; Pettorelli et al., 2009; Costa et al., 2016). Similarly, ENFA calculates a specialization-coefficient, ***s***, relating the degree of correlation between each environmental variable and the Specialization. High absolute value of a specialization-coefficient indicates that the group of animals is choosy about that particular environmental variable, and the more this particular variable contributes to the global specialization (Abade et al., 2014).

To investigate within-species variability in biogeographic niche, ENFA analysis was conducted using the package *adehabitatHS* (Calenge, 2006) for the statistical software CRAN R (Core Team, 2019). First, the species distribution data was imported into R. Biogeographic variables representing vegetation (percentage canopy cover), climate (BioClim variables), and geography (altitude) were imported into R. ENFA analysis was then carried out and the marginality, specialization, and tolerance established.

CHAPTER FOUR

RESULTS

The overall objective of this study was to investigate the biogeographic niche of yellow baboons and anubis baboons in the study area, southern Kenya. The study area comprised of Kajiado, Machakos & Taita-Taveta counties, and encompassed a well-known anubis-yellow baboon hybrid zone. The study area had variable terrain, and it was proposed that the variable terrain would lead to variable biogeographic conditions at different sites where baboons were found. A field survey using handheld GPS receivers was conducted to determine the distribution of anubis baboons, yellow baboons, and hybrid populations. As surveys had been conducted in the past, the objective of this field survey was to ascertain if baboon populations followed distribution patterns in past reports, and to update existing distribution data in the event new baboon populations were encountered. Once identified, baboon populations were tracked and GPS readings were recorded at one hour intervals. As the research team were not habituated, GPS readings (N ~ 50) were taken from a respectful distance (10~20 meters) from baboons encountered in order not to startle the animals. To estimate the range of each baboon population, the center of the tracking points was determined and management circles of radius 10Km drawn around each center point. Baboons can travel a distance of 10Km when foraging during the dry season, and management circles of radius 10Km covered adequate area for the purpose of estimating the habitat within each population's range. LULC covering the study area was derived by classifying LandSat imagery from the GLS 2010 collection. The percentage cover of each LULC class within the ranges of each baboon population were then determined. Climatic data from the WorldClim online repository were collated and processed, and the average climate experienced by each baboon population was determined. Geographic data representing the distance from the ocean was derived within GIS software, and altitude data was extracted from SRTM data downloaded from the USGS repository. The geography (average altitude and distance from the ocean) of each baboon population was then determined. To investigate between-species niche, baboon populations encountered in the field survey were categorized according to their ancestry using an ordinal scale: 1 =

unadmixed anubis baboon populations, 2 = anubis-leaning hybrid populations, 3 = yellow-leaning hybrid populations, and 4 = unadmixed yellow baboon populations. GWRA was then used to investigate between-species biogeographic niche. GWRA compared the distribution of each species with respect to the selected biogeographic variables, and indicated if there was correlation between biogeography and species distribution. After this, ENFA was used to investigate within-species biogeographic niche. ENFA analyzed the distribution of each baboon species with regards to the biogeography, and indicated if the species was marginal or not. ENFA also indicates if each species was specialized or if it is tolerant to different biogeographic conditions. The field survey established that anubis and yellow baboons were in allopatry, with anubis baboons found in the north-west of the study area, yellow baboons in the south east, and hybrids found in between. GWRA analysis established that baboon category covaried with the distance from the ocean and BIO4, the temperature change over the course of the year. There was no correlation between baboon species and all other biogeographic variables. ENFA established that each baboon category was highly marginal, however all baboon categories showed high tolerance to different biogeographic conditions.

Results of the field survey indicated that baboons were found in sixteen sites within the study area: Kitengella, Ngong, Tuala (Rongai), Kimana, Rombo, Bissil, Magadi, Olorgesaille, Sultan-Hamud, Emali, Kiboko, Namanga, Kibwezi, Oloitokitok, Amboseli, and Taita-Taveta. Of the sixteen sites, the baboon populations in Kitengela and Rongai (Twala) had not been previously cited in scientific literature. Based on the field surveys it was established that populations of unadmixed anubis baboons were found at Kitengela, Ngong, Rongai, Olorgesailie, Magadi, Bissil, and Sultan Hamud. One population of unadmixed yellow baboons was found at Taita-Taveta. Baboon populations in Emali, Namanga, Kiboko, Kibwezi, Oloitoktok, Rombo, and Amboseli were classified as hybrids. Using genotype information from Charpentier et al (2012) the baboon populations were then genotypically classified and categorized using an ordinal scale as follows: unadmixed anubis = 1, anubis-major hybrids = 2, yellow-major hybrids = 3, and unadmixed yellow = 4. Of the sixteen sites, only eleven had accompanying genotype information. These were Bissil, Magadi, Olorgasaile, Sultan Hamud, emali, Kiboko, Namanga, Amboseli, Kibwezi, Oloitokitok and Taita-Taveta (Figure 4.1). Five sites, Kitengela, Ngong, Rongai (Tuala), Kimana, and Rombo had no corresponding genotype data and were not used for analysis.

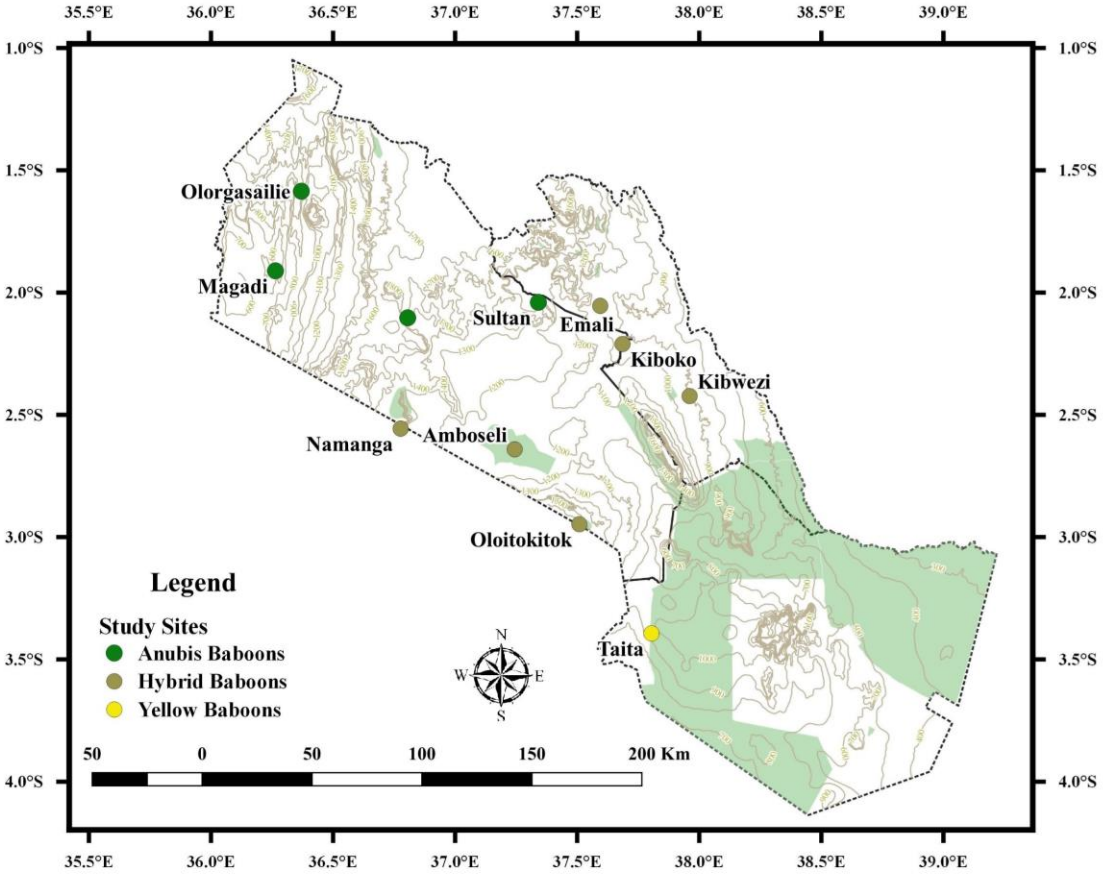


Figure 4.1: A map shows the study sites used analysis.

Results of the satellite image classification showed that woodlands, bushes and grasslands were also well distributed within the study area. Agriculture took up a significant portion of land, with large tracts of agricultural land dedicated to commercial sisal farming. Food crop farming was dominated by small subsistence farms found throughout the study area. Southern Kenya had small pockets of forests and swampy areas. The study area also had barren land, and some of the naturally barren areas were too rocky for any vegetation to grow, whereas others were thought to have soils with very high salt content (Figure 4.2).

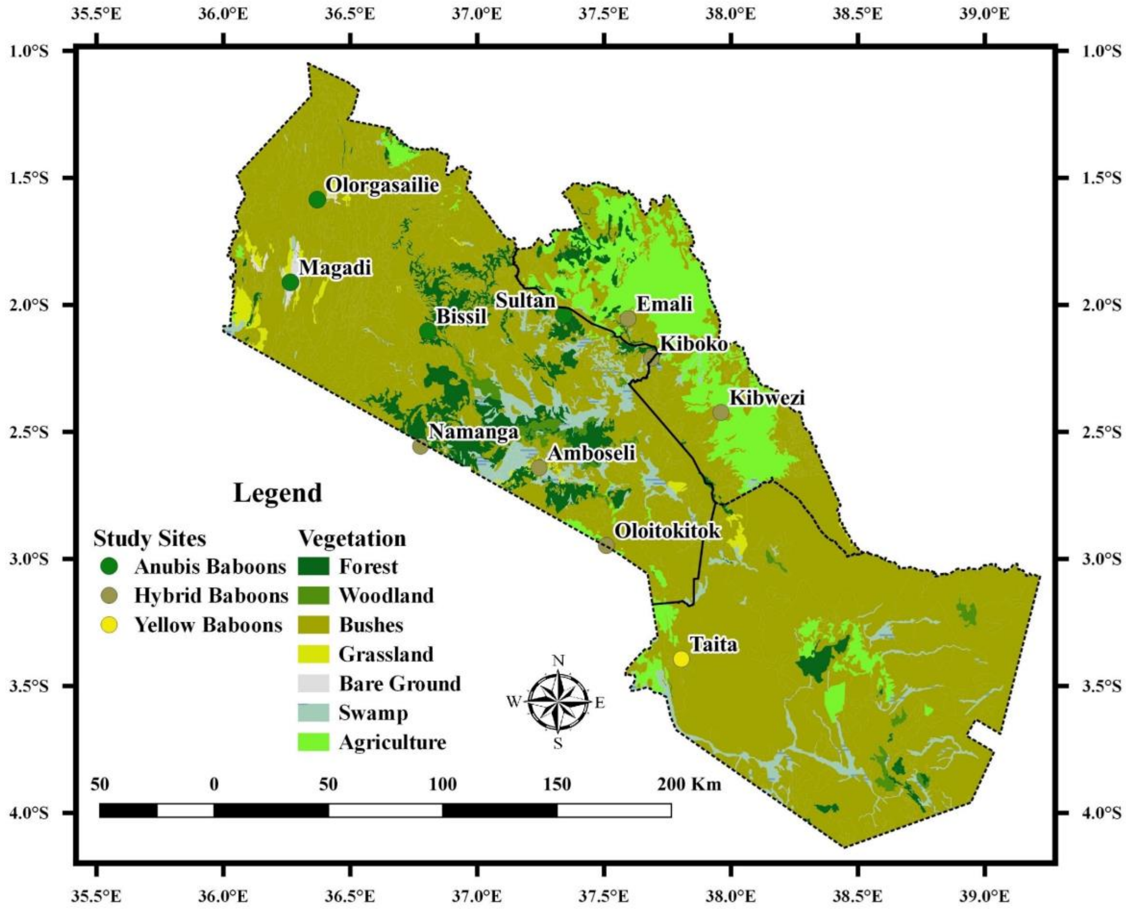


Figure 4.2: LULC map of the study area.

Results from accuracy assessment indicated that producer's accuracy and user's accuracy were high (>70%) for all LULC apart from Bare Ground (Producer's = 65.67%, User's = 61.11%). The Kappa Index of Agreement was 0.68. A closer look at the accuracy matrix indicates that the highest miss-classifications were between bare ground, agricultural land, bushes, and grasslands. It was proposed that the biggest factor influencing the performance of the classification was the farming practices of small scale farmers within the area. Typically, small scale farmers would subdivide their farms by planting bushes and trees at the farm boundaries. This form of fencing was common in many semi-urban areas such as Ngong, Rongai, and Oloitokitok. Before the planting season, the farmers would clear their farms of the previous season's crops and till the land in preparation for a new farming season.

During the planting season, some farmers would grow food crops, but others would not grow any agricultural crop on their land. In farms where no agricultural crops were planted, wild grass and bushes would then grow. In some instances, where wild grasses and bushes had grown, the farmer owners would cut down the wild vegetation and leave the land without any vegetation. In instances where the farmed crop failed, some farmers would also cut down their crop leaving their fields bare. This meant that within land owned by a farming community, the landscape was a mixture of small farms with food crops, small farms with no food crop (bare ground), and small farms with wild bushes and/or grasses. For this reason, the choice to classify an area as either agricultural, bushes, grassland, or bare ground was particularly difficult, and this difficulty is reflected in the poorer classification accuracy for bare ground. However, the Overall Accuracy was 80%, and the classification was accepted based on this (Table 4.1).

Table 4.1: The error matrix table summarizes the results of accuracy assessment. The Accuracy section of the table indicates the producer's accuracy, the user's accuracy, and the Overall Accuracy.

	ERROR MATRIX								**ACCURACY SUMMARY**	
LULC	**AG**	**BA**	**BU**	**FO**	**GR**	**SW**	**WO**	**TOTAL**	**PRODUCER'S**	**USER'S**
AG	187	7	16	0	33	6	10	259	73.91%	72.20%
BA	10	44	5	0	13	0	0	72	65.67%	61.11%
BU	24	4	1023	12	56	6	25	1150	76.63%	88.96%
FO	0	0	13	203	0	0	32	248	76.89%	81.85%
GR	24	12	82	0	844	8	0	970	87.55%	87.01%
SW	8	0	4	7	18	75	12	124	75.76%	60.48%
WO	0	0	192	42	0	4	512	750	86.63%	68.27%
TOTAL	253	67	1335	264	964	99	591	3573	**OVERALL**	**80%**
KEY:	Agriculture= AG, Bare Ground = BA, Bushes = BU, Forest = FO, Grasslands = GR, Swamps = SW, Woodlands = WO									

To investigate the relationship between baboon species distribution and land cover, the percentage cover of each LULC within the respective range for each baboon category were calculated. Results indicated that out of the seven LULC classes, four land cover classes dominated sites where baboons were found: Woodland, Grassland, Bushes, and Agriculture. The sites occupied by baboons showed diversity in LULC composition. For example, among the four major classes of LULC, Bissil had 3% grassland cover whereas Magadi had 48% grassland cover. Magadi had 5% bush cover whereas Bissil had 35% bush cover. Woodland ranged from 6% in Amboseli to 61% in Olorgasailie, whereas Amboseli had 47% bush cover and Kibwezi had only 9% bush cover. Amboseli had 46% grassland cover whereas Oloitokitok had only 0.04% grassland cover. Only these four LULC classes were used for analysis (Figure 4.3).

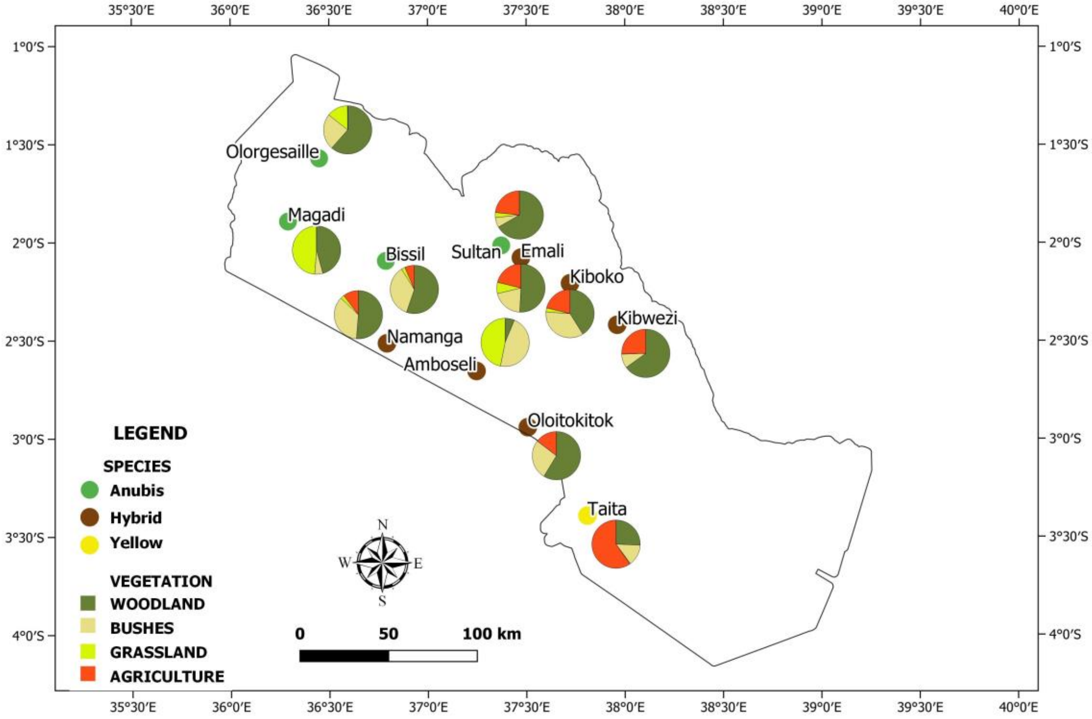


Figure 4.3: A map showing the percentage cover of the four main LULC classes at each study site.

To investigate the relationship between climate patterns and baboon ancestry, Bioclimatic variables from the WorldCilm repository were collated, and the average climatic conditions within each population’s range were estimated. Analysis indicated that the anubis baboon population in Magadi experienced the highest temperatures, scoring high values for BIO1 (263), BIO5 (342), BIO6 (168), BIO8 (258), BIO9 (233), BIO10 (263), BIO11 (233). Analysis indicated that the yellow-major population in Oloitokitok experienced the lowest temperatures, scoring low values for BIO1 (184), BIO5 (250), BIO6 (92), BIO7 (158), BIO8 (177), BIO9 (149), BIO10 (184), BIO11 (149). (Figure 4.4).

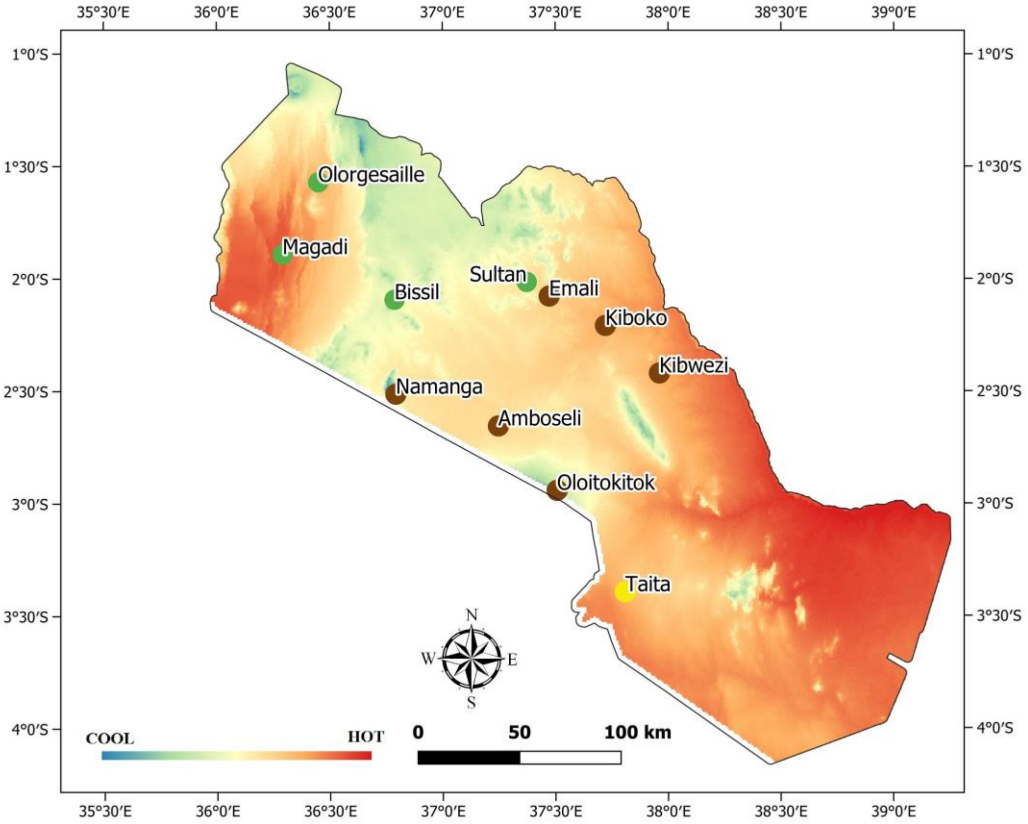


Figure 4.4: The map shows BIO1, the annual mean temperatures, over the study area.

Precipitation within the study area showed great variability between the eleven sites. The anubis populations in Magadi experienced the lowest annual average precipitation (BIO12 =471), the lowest precipitation of the wettest month (BIO12 =471), and the lowest precipitation for the wettest quarter (BIO16 = 237). The hybrid populations in Oloitokitok received the highest average annual precipitation (BIO12 = 941), the highest precipitation for the wettest month (BIO12 = 941), the highest precipitation for the wettest quarter (BIO16 = 469), and the highest precipitation for the warmest quarter (BIO18 = 297). The hybrid populations in Kimana experienced the highest precipitation for the driest month (BIO14 = 9), the highest precipitation for the driest quarter (BIO17 = 36), and the highest precipitation for the coldest quarter (BIO19 = 40). The anubis populations in Bissil experienced the lowest precipitation of the driest quarter (BIO17 = 7), and the lowest precipitation for the warmest quarter (BIO18 = 152) (Figure 4.5).

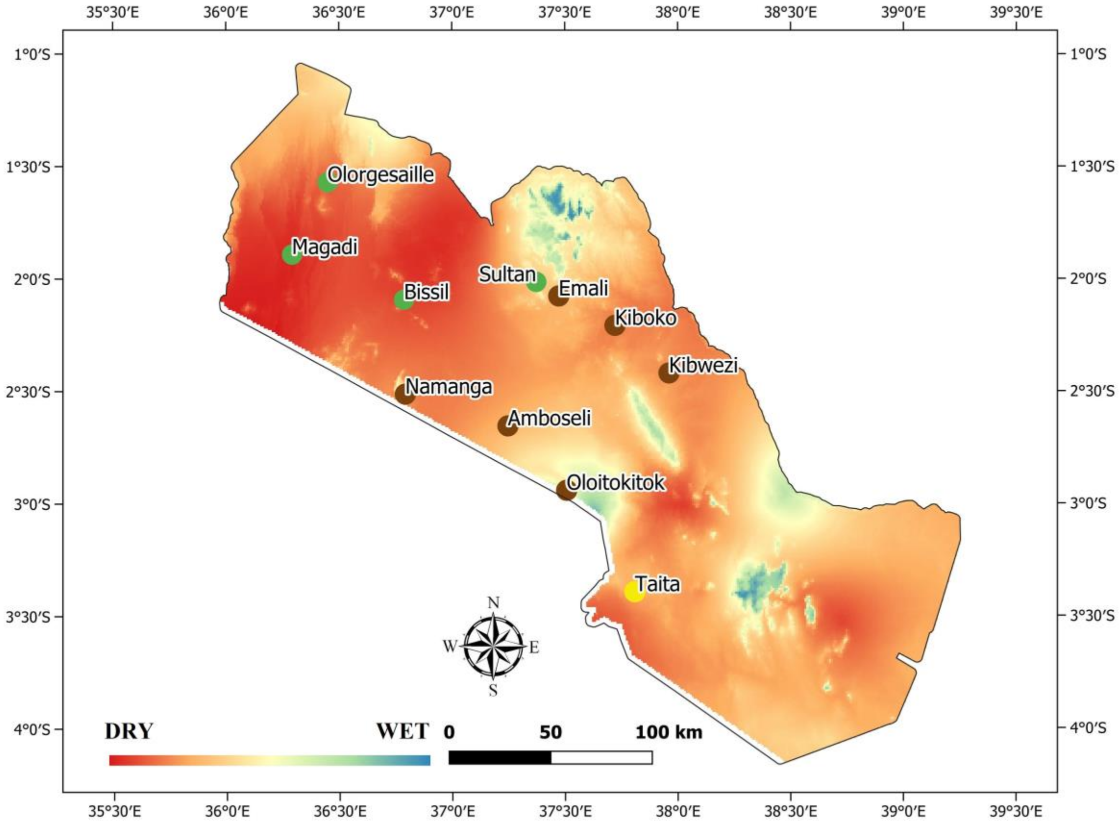


Figure 4.5: The map shows BIO12, the annual precipitation, over the study area.

To investigate the relationship between the geography of our study sites and baboon ancestry, we estimated the average geography (altitude and distance from the ocean) of each study site. The yellow baboon populations in Taita-Taveta were the closest to the Indian Ocean (208Km), whereas the anubis baboon populations in Magadi were the furthest from the Indian Ocean (430Km) (**Figure 4.6**).

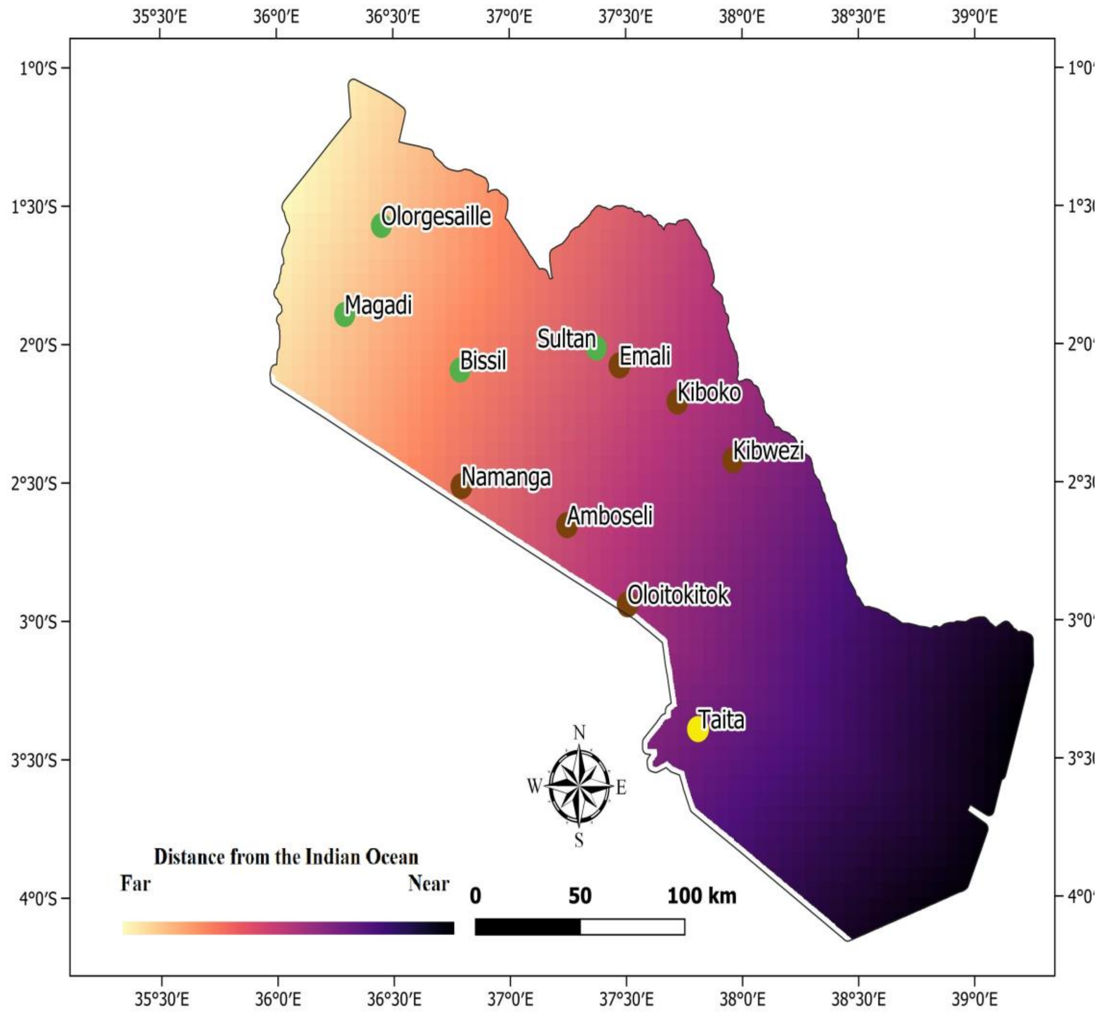


Figure 4.6: The map shows the distance from the Indian Ocean as one moves from south-west to north-east within the study area.

Of the study sites, baboon populations in Magadi were found in the lowest altitude (589m) whereas yellow-major hybrids in Oloitokitok were found in the highest altitude (1705m) (Figure 4.7).

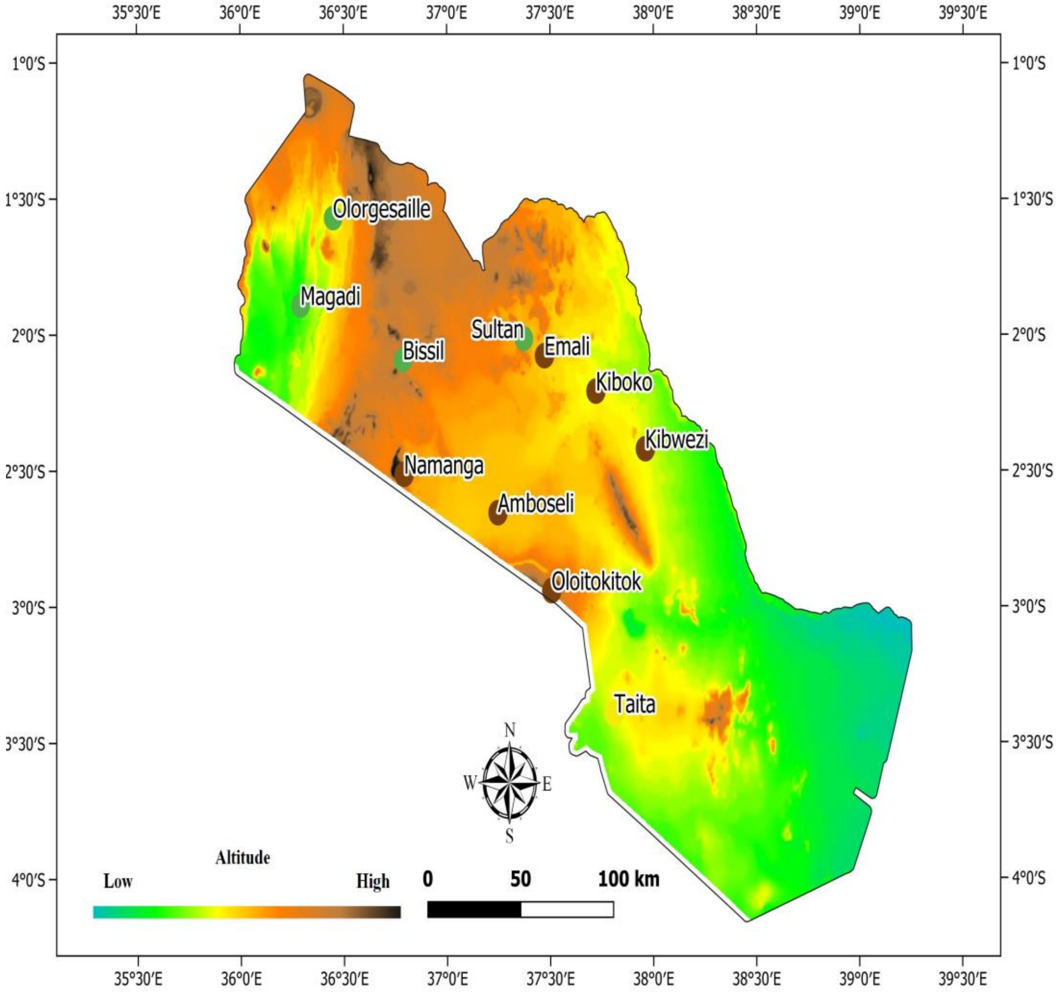


Figure 4.7: The map shows the altitude over the study area.

4.1 Results of Geographically Weighted Regression Analysis

To investigate if there was correlation between LULC proportion and baboon species distribution, we used GWR with baboon species category (1 – 4) as the predictor variable and proportional land cover as the response variable. Analysis indicated that none of the four common LULC types within the home ranges of the study populations were significantly associated with population ancestry assignment. Analysis indicated poor correlation between species category and woodland (R^2 = 0.26, T = -1.76, P = 0.11, N = 11), bushes (R^2 = 0.01, T = 0.34, P = 0.74, N = 11), grassland (R^2 = 0.03, T = -0.53, P = 0.61, N = 11), and agriculture (R^2 = 0.08, T = -0.81, P = 0.44, N = 11), indicating that baboon species distribution within our study area was not associated with LULC. To investigate if there was correlation between climate and baboon species distribution, we used GWRA with baboon species category (1 – 4) as the predictor variable and the bioclimatic variables as the response variable. Our investigation revealed that of the eighteen bioclimatic variables, only three correlations were statistically significant ($P \leq 0.05$). Of these three only one variable showed good correlation ($R^2 > 0.5$) with baboon species category. BIO4 (R^2 = 0.83, T = 6.63, P <0.01, N = 11) showed strong correlation with baboon species category. BIO2 (R^2 = 0.38, T = -2.34, P = 0.04, N = 11) and BIO 16 (R^2 = 0.37, T = 2.32, P = 0.05, N = 11) were statistically significant but showed no correlation with baboon ancestry. BIO4 is a measure of temperature change over the course of the year (standard deviation of monthly averages*100). The larger the value of BIO4, the greater the variability in monthly temperatures. Noting that species distribution wasn't influenced by any other temperature variable, it was difficult to attach a biological interpretation to this result (Table 4.2).

Table 4.2: Correlation analysis between species distribution and bioclimatic variables.

CODE	INDEX	R^2	T	P	N
BIO1	Annual Mean Temperature	0.01	-0.36	0.72	11
BIO2*	Mean Diurnal Range	0.38	-2.34	0.04	11
BIO3	Isothermality	N/A	N/A	N/A	11
BIO4**	Temperature Seasonality	0.83	6.63	0	11
BIO5	Max Temp Warmest Month	0.03	-0.56	0.59	11
BIO6	Min Temp Coldest Month	0.01	-0.35	0.73	11
BIO7	Temperature Annual Range	0.17	-1.37	0.2	11
BIO8	Mean Temp Wettest Quarter	0.04	-0.63	0.54	11
BIO9	Mean Temp Driest Quarter	0.07	-0.82	0.44	11
BIO10	Mean Temp Warmest Quarter	0.01	-0.36	0.72	11
BIO11	Mean Temp Coldest Quarter	0.06	-0.74	0.48	11
BIO12	Annual Precipitation	0.25	1.73	0.12	11
BIO13	Precipitation of Wettest Month	0.29	1.91	0.09	11
BIO14	Precipitation of Driest Month	0.24	1.67	0.13	11
BIO15	Precipitation Seasonality	0.03	0.54	0.6	11
BIO16*	Precipitation of Wettest Quarter	0.37	2.32	0.05	11
BIO17	Precipitation of Driest Quarter	0.2	1.5	0.17	11
BIO18	Precipitation of Warmest Quarter	0.03	-0.48	0.64	11
BIO19	Precipitation of Coldest Quarter	0.14	1.22	0.25	11

To investigate if there was correlation between the geography of baboon ranges and baboon species distribution, we used GWRA with baboon species category (1 – 4) as the predictor variable and proportional land cover as the response variable. The study established that altitude was not correlated to baboon species ancestry (R^2 = 0.0001, T = -0.01, P = 0.99, N = 11). The study also established that the distance from the ocean was correlated to baboon ancestry (R^2 = 0.83, T = -6.58, P = 0.0001, N = 11).

4.2 Results of Environmental Niche Factorial Analysis

To investigate within-species biogeographic niche, ENFA analysis was carried out to establish the marginality, specialization, and tolerance of each species. Results from the ENFA factorial analysis established that there was high Marginality for all baboon categories. Results also established that there was very low Specialization across all categories, indicating that Tolerance for different habitats was high among each baboon category. The first axis of ENFA's factorial analysis explained more than 80% of the variance seen for each baboon category (anubis ~ 93%, anubis-major hybrids ~ 84%, yellow-major hybrids ~ 92%, yellow ~ 91%). This indicated that there was high marginality across all groups. The second axis of ENFA's factorial analysis explained less than 8% of the variance seen for each baboon category (anubis ~ 3%, anubis-major hybrids ~ 7%, yellow-major hybrids ~ 5%, yellow ~ 5%). Because of the low Specialization values, results for the second axis were discarded automatically by the analysis software, R. Similar to Preau et al. (2018), an absolute value of 0.25 was used to determine if each respective category of baboons (anubis, anubis-major hybrids, yellow-major hybrids, and yellow) was marginal for each biogeographic variable.

Analysis indicated that anubis baboons had high Marginality (M=3.99). Looking at the results for marginality coefficient, ***m***, it was noted that anubis baboons were positively marginal for BIO8 (mean temperature of the wettest quarter), BIO9 (mean temperature of the driest quarter), BIO11 (mean temperature of the coldest quarter), and this indicated they inhabited an area with above average conditions measured on these three variables. Anubis baboons were also positively marginal for BIO2 (annual mean diurnal range), indicating that the average monthly variations in temperatures were larger than average. Anubis baboons were positively marginal for BIO19 (precipitation of the coldest quarter), indicating that anubis ranges experienced above average precipitation during the coldest quarter. Anubis-major hybrids also showed high Marginality (M=3.11). Looking at the results for marginality coefficient, ***m***, it was noted anubis-major hybrids were positively marginal for BIO13 (precipitation of the wettest month), BIO15 (precipitation seasonality), BIO17 (precipitation of the driest quarter). Anubis-major hybrids were negatively marginal for BIO14 (precipitation of the driest month).This indicated that anubis-major hybrids ranged in areas with above average precipitation during the wettest month. However, in their range precipitation was below average during the driest month. Yellow-major hybrids showed high Marginality (M=4.33). Looking at the results for marginality coefficient, ***m***, it was noted yellow-major hybrids were positively marginal for BIO12 (annual precipitation), BIO13 (precipitation of the wettest month), BIO14 (precipitation of the driest month), BIO16 (precipitation of the wettest quarter), and BIO17 (precipitation of the driest quarter).This indicated that yellow-major hybrids ranged in areas with above average precipitation. Yellow baboons showed the highest marginality (M=12.85). Looking at the results for marginality coefficient, ***m***, it was noted yellow baboons were positively marginal for BIO14 (precipitation of the driest month), and BIO17 (precipitation of the driest quarter), and Altitude, indicating they inhabited low-altitude areas when compared to the average altitude in the study area (Table 4.3).

Table 4.3: The table shows the results of ENFA

Environmental Variable	**Anubis**	**Anubis-major Hybrids**	**Yellow-major Hybrids**	**Yellow**
BIO1	0.22	0.17	0.03	0.17
BIO2	**0.33**	0.15	-0.06	-0.05
BIO3	0.22	0.09	-0.02	-0.05
BIO4	0.22	0.17	0.03	0.17
BIO5	0.22	0.16	0.02	0.13
BIO6	0.24	0.17	0.02	0.21
BIO7	0.18	0.13	0.02	0.03
BIO8	**0.34**	0.14	-0.02	0.13
BIO9	**0.29**	0.17	-0.03	0.12
BIO10	0.22	0.17	0.03	0.17
BIO11	**0.29**	0.17	-0.02	0.13
BIO12	-0.15	0.11	**0.48**	0.08
BIO13	-0.12	**0.31**	**0.41**	0.09
BIO14	0.14	**-0.42**	**0.46**	**0.60**
BIO15	-0.08	**0.35**	0.15	-0.07
BIO16	-0.12	0.21	**0.48**	0.16
BIO17	0.07	**-0.41**	**0.34**	**0.45**
BIO18	0.21	0.15	0.09	-0.22
BIO19	**0.29**	0.17	-0.03	0.12
Altitude	-0.25	-0.23	-0.06	**-0.29**
Marginality	**3.99**	**3.11**	**4.33**	**12.85**
%Variance Explained	**93%**	**84%**	**92%**	**91%**

CHAPTER FIVE

DISCUSSION

5.1 Amboseli, a Model for Baboon Distribution and Hybridization Studies

The first documented contact between anubis and yellow baboons in Kenya occurred in Amboseli during the 1980s (Samuels & Altmann, 1986), and since then there have been more reports of contact and hybridization in different sites where anubis and yellow baboons are found in Kenya (Charpentier et al., 2012; de Jong & Butynski, 2012). Even so, recent genetic evidence suggests that occurrences of hybridization between anubis and yellow baboons in Amboseli may have occurred over a longer period, and that there had been previous contact between anubis and yellow baboons in this area long before the 1980s (Wall et al., 2016).The Amboseli baboon population is unique because it is among the best studied primate populations in the world (Altmann & Alberts, 2012; Wall et al., 2016), and its recent history is well known. The Amboseli Baboon Research Project has studied the baboon population within the Amboseli basin for decades, with numerous detailed studies conducted on different aspects of baboon biology that include baboon species distribution, ecology and behavior, demography, population genetics, and habitat (see https://amboselibaboons.nd.edu/). Many studies on hybridization in primates and other animals use the Amboseli baboon population as a case study (Charpentier et al., 2012), and the questions raised by reading through the history of hybridization in Amboseli inspired the hypothesis for this study. For this reason, we briefly discuss the Amboseli baboon population.

Amboseli was considered a yellow baboon range in the early 1970s (Mapels & McKern, 1967), but at some point in time the yellow baboon population in Amboseli started receiving immigrant anubis baboons (Samuels & Altmann,1986),and the resulting hybridizations have meant the Amboseli population has been gradually shifting from a yellow baboon population to a hybrid baboon population (Alberts & Altmann, 2001). Observers initially suggested that anubis baboon migration into Amboseli had been initiated by loss of habitat, specifically changes in the vegetation composition of anubis baboon ranges. Samuels and Altmann (1986) reported that the slopes of Mt. Kilimanjaro, where anubis baboons ranged, had seen increased farming activity, with local communities cutting down natural vegetation and using these areas for crop farming. Samuels and Altmann (1986) hypothesized that these changes in vegetation may have forced an anubis baboon range shift, causing anubis baboons to migrate into yellow baboon ranges, though this hypothesis was never tested because the tools and technology to do so at the time were not easily available. An example of similar anthropogenically driven change as was hypothesized by Samuels and Altmann (1986) has been documented in Brazil where human elimination of physical barriers between *C. jacchus* and *C. penicillata*, two marmoset species, has led to formation of a hybrid swarm between them (Malukiewicz et al., 2015).

The migration of anubis baboons into the Amboseli basin was puzzling as morphological differences between anubis and yellow baboons suggest that anubis baboons are more suited to cool and wet areas whereas yellow baboons are suited to hot and dry areas. Amboseli is a low lying savannah that is typically hot and dry throughout the year (Altmann et al., 2002), and the hot-dry habitat in Amboseli contrasts with the cool-wet habitat found at the foothills of Mt. Kilimanjaro where the anubis immigrants were thought to originate from (Samuels & Altmann, 1986). Classic evolutionary theory states that when two populations of a species become separated geographically they may diverge. Divergence often involves adaptation to different habitats, and as the two populations gradually adapt to different habitats they become morphologically and ecologically dissimilar, and as each population evolves traits that make them specialists in their niche habitat quite often these traits are a disadvantage in other dissimilar habitats. In this way divergence acts as an evolutionary mechanism that leads to speciation (Schuler et al., 2016). Areas with habitat that is markedly different from the habitat a species is adapted to can be termed as hostile habitat especially when a species struggles to survive in these habitats, and when hostile habitats are significantly large they form an ecological barrier to the species' dispersal. However, if the ecological barrier between the two neighboring species isn't significant, and if reproductive isolating mechanisms between two species have not yet developed, then members from one species are able to move into the range of a neighboring species, reproduce, and start the formation of a hybrid population (Gabow, 1975; Jolly et al., 1993; Schuler et al., 2016).

The habitats of the Amboseli and the surrounding areas have seen many changes (Alberts et al., 2005; Altmann et al., 2002; Wagenseil & Samimi, 2006), as is common with savannahs around the world. The savannahs of southern Kenya, including Amboseli, are habitats that offer unparalleled foraging opportunities for grazers and browsers such as wildebeest and giraffe (Musiega & Kazadi, 2004), support numerous species of carnivores such as lions and cheetahs, and also support omnivores such as baboons. In addition to wildlife, savannahs are often inhabited by ranching communities such as the Maasai (Blute et al., 2006), and by crop farming communities. One of the challenges savannah communities face is the ever-changing environment, and in southern Kenya shifts in vegetation and climate have been widely reported (Alberts et al., 2005; Altmann, Alberts, & Altmann, 2002; Wagenseil & Samimi, 2006). Human activities and climate change are often cited as contributors to changes seen in savannahs (Lambin & Strahler, 1994; Wagenseil & Samimi, 2006), and in some instances cases habitat degradation caused by wildlife have also been reported (Western & Maitumo, 2004). Overgrazing by ranching communities and irresponsible crop farming practices have been shown to degrade savannahs (Western & Finch, 1986; Western, 1994; Ellis & Galvin, 1994; Copolillo, 2000; Wagenseil & Samimi, 2006), and are thought to be among the major drivers of habiatat change in savannahs all over the world. Reports also indicate that elephants degrade habitats in which they are found, and in some areas elephants are a major cause of vegetation change leading to habitat degredation (Laws, 1970; Cuming et al., 1997; Lombard et al., 2001; Western & Maitumo, 2004; Guldemond & van Aarde, 2007). Rainfall in savannahs is seasonal, and is reported to be increasingly unpredictable whereas the mean temperatures are high and consistently increasing (Altmann et al., 2002), and this has led many to believe that climate change has negatively impacted savannah habitats. For animals living in highly seasonal and ever-changing environments such as savannahs, finding enough food and water determines the success of the species in an area (Alberts et al., 2005). Many animals migrate to greener areas when the conditions in their habitat become hostile, only returning when conditions have improved (Musiega & Kazadi 2004). Of interest to this study was the hypothesized reasons for the migration of anubis baboons from the foothills of Mt. Kilimanjaro to the Amboseli basin. The migration of anubis baboons into the Amboseli basin raised many questions: Were anubis and yellow baboons ecologically dissimilar? Did biogeographical factors influence the distribution of yellow and anubis baboons? Was there an ecological barrier between anubis and yellow baboon ranges, and was this barrier affected by vegetation and/or climate change? Was it possible that anubis baboons were able to tolerate a wide range of habitat? What of yellow and/or hybrid populations, did they show tolerance to different habitats? If there was no ecological barrier between anubis and yellow ranges, would the two species continue to hybridize unabated? If it was possible for anubis baboons from the foothills of Mt. Kilimanjaro to move into the Amboseli basin, was it possible for anubis baboons from other areas to move into the Amboseli basin? As classical ecological theory predicts that two species that have a similar ecological niche cannot coexist, would one baboon species competitively exclude the other? Was it also possible for yellow baboons to migrate from the Amboseli to adjacent areas with dissimilar habitat?

Here, the main objective of the study was to investigate the biogeographic niche of baboon species in order to determine if the distributions of the different species was influenced by biogeography. Within a GIS the habitat of a species can be defined as conceptual space described by biogeographic variables (Grinell 1917; Hutchinson 1957; Sattler et al., 2007), and variation in these variables often has an influence on species distribution. Our study area covered Kajiado, Machakos, and Taita-Taveta counties in Kenya, an area that encompassed a well-known anubis-yellow baboon hybrid zone (Charpentier et al., 2012). The study area has variable terrain, and we postulated that the variable terrain would result in variable biogeographic conditions at different sites where baboons are found, giving us a variety of habitats to compare.

5.2 The Influence of Biogeography on Baboon Species Distribution

During the field survey baboons were encountered in sixteen sites, and of these the baboon populations in Kitengela and Rongai (Twala) had not been previously cited in scientific literature. The Amboseli population was found within the Amboseli basin which encompasses the Amboseli National Park and the surrounding areas.

The Sultan-Hamud, Emali, Kiboko and Kibwezi populaitons were found along the Nairobi-Mombasa highway. The Bissil and Namanga populations were found in towns along the Nairobi-Namanga highway. The Emali, Kimana, and Oloitokitok populations were also found along a major highway. The Kitengela and Twala baboon populations were found in undeveloped and/or under-developed private land, as was the case in other sites such as Magadi and Olorgassailie. However, Magadi and Olorgassailie are found near other features that are of interest to the scientific community, specifically the salt lake found in Magadi and the archaeological sites in Olorgassailie. These geographic and archaeological features have increased the profile of these areas, and this has made them areas of interest to researchers. The Kitengela and Tuala populations are in areas with little scientific interest, and this may be the reason these populations had not been studies in the past. Of the sixteen sites surveyed in this study, eleven had been genetically characterized by Charpeniter et al (2012), and using this genetic data the eleven sites were categorized using an ordinal scale: 1 = unadmixed anubis, 2 = anubis-major hybrids, 3 = yellow-major hybrids , and 4= unadmixed yellow. Whereas many studies have relied on phynotypic classification of baboon populations (Maples & McKern, 1967; Samuels & Altmann, 1986; Alberts & Altmann, 2001; de Jong & Butynski, 2012), genotypic classification provide for more accurate admixture classification, and where available genotypic classification is preferred to phynotypic classification. For this reason, only the eleven baboon populations with accompanying genetic data were used for analysis in this study.

The field survey established that anubis and yellow baboons within the study area were living in allopatry, with anubis baboons found in the north-west of the study area, yellow baboons found in the south-east of the study area, and hybrid baboons were found in between. Anubis baboon populations were found in Olorgesaille, and were also found in Magadi, both within the Rift Valley. As one moved from the north-west to the center of the study area, baboon populations started exhibiting different characteristics from unadmixed anubis baboons, and these were hybrid populations. As one moved further south-east, hybrid baboon populations gave way to yellow baboon populations. This distribution was in agreement with the findings of recent primate surveys in the area (Charpentier et al., 2012; de Jong & Butynski, 2012; Tung et al., 2008). Results of analysis established that baboon species distribution was strongly correlated with the distance of a population from the ocean. This was interpreted as follows: yellow baboons migrated into Kenya along the Indian Ocean, and as they moved along the coast they also moved inland. On the other hand, anubis baboons migrated into Kenya from the west, and have been moving towards the coast as they expand their range. As anubis baboons moved towards the coast their range met with that of the yellow baboon range, and since reproductive isolating mechanisms between two species had not yet developed hybridization occurred. In summary, anubis baboons were found in the north-west of the study area and as one moved to the south-east of the study area, the anubis baboon populations gave way to yellow baboon populations. Incidentally, the altitude of the study area generally decreases as one moves from the north-west towards the south-east. It has been shown that altitude has a strong influence on climate, and as the altitude decreases precipitation decreases as temperatures increase. Observers often noted that baboon species distribution followed the same pattern, and this lead many to speculate that anubis baboons are found in cooler and wetter climate when compared to yellow baboons. However, within the study area there was strong local variation in altitude, and this variation would inevitably influence local trends in climate and vegetation. For example, Olorgasaille and Magadi, both anubis ranges found at the north-western end of the study area had altitudes of 589m and 1007m respectively. Bissil and Sultan Hamud, also anubis ranges, had altitudes of 1635m and 1245m respectively. Emali (Altitude = 927), a hybrid baboon range, was found further inland and yet had lower altitude when compared to Kiboko (Altitude = 898) or Kibwezi (Altitude = 1263m), also hybrid baboon ranges For this reason, this study set out to establish the climate and vegetation baboon populations experienced in their respective ranges in order to quantify and quality the correlation between biogeography and baboon species distribution.

To test the influence of climate on baboon species distribution, the climatic conditions within each range where baboon populations were found was established. The bioclimatic variables developed by Nix (1986) were used to describe the climate of these ranges. Bioclimatic variables highlight the mean annual temperature (BIO1), mean annual precipitation BIO12, the hottest and coldest month (BIO5 and BIO6), hottest and coldest season (BIO10 and BIO11), wettest and driest month (BIO13 and BIO14), and wettest and driest season (BIO16 and BIO17), and this adequately covered average climatic conditions as well as extreme climatic conditions. In a similar study, Wango et al (2019) investigated if climate influenced the distribution of baboon species using climatic variables representing the average seasonal climatic conditions. Wango et al (2019) established the baboon species found near 9 weather stations distributed across Kenya, from Mombasa to Kisumu, and used average minimum temperature, maximum temperature and precipitaion to describe the climate at these sites. The climate was characterized by four distinct seasons, two wet seasons (October to December and March to May) and two dry seasons (January to February and June to September). Wango et al (2019) established that there was correlation between the precipitation of the one wet season (March to May) and baboon species distribution. No other climatic variables correlated with baboon species distribution. Wango et al (2019) noted that the correlation between the wet season (March to May) and baboon species distribution may have been a byproduct of the independent correlation between climate and the distance of a station from the Indian Ocean. To further explore the results reported, Wango et al. (2019) recommended investigating the influence of climate on baboon species distribution using climatic variables such as BioClim that highlight extremes in climate.

Investigations revealed that temperatures experienced by baboon populations strongly correlate with the altitude. Baboon populations found in low lying study sites experienced high average temperatures, whereas baboon populations found in high altitude study sites experienced low average temperatures. It was also established that, within the study area, areas further inland generally experienced higher precipitation. However, local precipitation patterns were very variable, and in many cases considerably deviated from global precipitation patterns. Analysis established that anubis baboons in particular showed large tolerance for different temperatures within the study area. Assessment of the average annual temperatures (BIO1) revealed that anubis baboon populations inhabited hot areas such as Magadi (BIO1 = 263) and Olorgesailie (BIO1 = 241) as well as cool areas such as Bissil (BIO1 = 214) and Sultan Hamud (226). Hybrid baboon populations also showed large tolerance to different temperatures, and some hybrid populations were found in cool areas with others found in hot areas. Hybrid baboon populations were found in cool areas such as Namanga (BIO1 = 194) and Oloitokitok (BIO1 = 184) and in hot areas such as Emali (BIO1 = 231) and Kiboko (BIO1 = 246).Within the study area yellow baboons were found in Taita-Taveta, a relatively hot environment (BIO1 = 243). Assesment of the average annual precipitation (BIO12) revealed that anubis baboon ranged in areas with low precipitation such as Magadi (BIO12 = 471) as well as areas with high precipitation Sultan Hamud (BIO12 = 735). Kibwezi (BIO12 = 632) recorded the lowest precipitation for a hybrid-baboon range whereas Oloitokitok (BIO12 = 941) recorded the highest precipitation for a hybrid-baboon range. Taita-Taveta recorded above average precipitation (BIO12 = 666). Of the climatic variables tested, only BIO4 showed correlation with baboon species distribution. BIO4, the temperature seasonality (the standard deviation of monthly temperature averages), is a measure of temperature change over the course of the year. The larger the value of BIO4 the greater the temperature variability. In interpreting this result, it was first considered that baboon species distribution was not influenced by minimum or maximum temperatures, specificallyBIO1 (annual mean temp), BIO5 (max temp of the warmest month), BIO6 (min temp of the warmest month), BIO7 (temp annual range), BIO8 (mean temp of wettest quarter), BIO9 (mean temp of the driest quarter), BIO10 (mean temp of warmest quarter), and BIO11 (mean temp of the coldest quarter). Majority of these temperature-related variables were strongly correlated to Altitude, whereas BIO4 was strongly correlated to the Distance from the Ocean (Wango et al., 2018). Considering the results of the numerous other statistical tests performed with temperature-related variables, it was difficult to provide a biological interpretation for the correlation between BIO4 and baboon species distribution. In summary, this study established that the climate in different sites where baboon species were found was very variable, and that climate did not have an influence on baboon species distribution within our study area. Studies have shown that climatic variables were poor predictors of baboon species distribution (Stone et al., 2013; Winder, 2014), and the results of this study corroborate these findings.

As Samuels and Altmann (1986) postulated that vegetation changes around Mt. Kilimanjaro had forced anubis baboons to migrate into yellow baboon ranges, Jolly et al (1993)observed that baboon species were found in different ecovegetative zones and that the border between ranges of baboon species often coincided with the border of distinct ecovegetative zones where hybrid zones often formed. As detailed vegetation maps were not available for many of the sites studied, none of these observations were investigated. Later, investigations on baboon species biogeographic niche at a continental scale showed that baboon species distribution was not influenced by vegetation (Winder, 2014). Winder (2014), using vegetation data first developed by White (1983) and later updated by Kindt et al (2011), reported that between species variation in vegetation within baboon species ranges was not significant. Winder (2014) also noted that within-species variation in vegetation was very high. The Vegetation Map of Africa by White (1983) was developed at a scale of 1:5,000,000 i.e 1mm on the map represents 5km in the real world. Whereas this resolution was suitable for studies at a continental scale, the generalizations necessitated when creating this dataset meant local variations in vegetation were not considered. Winder (2014) noted that there was needed to establish the results reported at this scale would hold true for studies done covering smaller geographic areas. For this reason LULC was generated with the objective of determining if vegetation covaried with species distribution within out study area. LandSat imagery from the GLS repository was classified to derive LULC maps, and the results of classification showed that the vegetation in southern Kenya was dominated by savannah vegetation, with agricultural land also covered a significant acreage. The study indicated that southern Kenya did have distinct ecovegetative zones, but that vegetation was not clearly associated with baboon species distribution. Investigation revealed that each study site had a unique vegetation composition, and that each baboon species tolerated a variety of vegetation within their habitat. This was not unique to southern Kenya as similar observations had been made in other areas. Gabow (1975), while studying a hybrid zone between anubis and hamadryas baboons in Ethiopia, noted that the boundary between forests and savannahs in his study area was not a biogeographical barrier between anubis and hamadryas baboon populations. Gabow (1975) observed that anubis baboons, often found in the forests of Awash in Ethiopia, had been found in savannah vegetation where hamadryas baboons are typically found.

It was hypothesized that loss of anubis baboon habitat, more specifically the loss of natural vegetation to agriculture vegetation at the foothills of Mt. Kilimanjaro, led to migration of anubis baboons into yellow baboon ranges (Samuels & Altmann, 1986). However, this study showed that agricultural land formed a significant part of baboon ranges for both species. In Taita-Taveta agricultrual land coverd 59.17% of the yellow baboon population’s range. In Sultan Hamud where anubis baboons were found, agricultural land coverd 23.33% of the baboon population’s range. In Emali, Kiboko, and Kibwezi where hybrid baboons ranged, agricultural land covered over 20% of baboon population ranges. It is now know that baboons add agricultural crops to their diet when it is available (Treves et al., 1998; Hill 2000; Mwangi et al., 2016), and that from a baboon’s perspective maize cobs or grapes are additional food sources. Hill (2000) observed that baboons in Uganda visited farms throughout the year, feeding on different parts of farmed crop. When a crop was nearing harvest, baboons would invest more time feeding on the more nutritious parts of this crop, be it maize or cassavas (Hill, 2000). Mwangi et al. (2016) observed that baboons were responsible for crop raiding and livestock predation, and in many instances were the most notorious crop raiders around Chyulu Hills. Because of the diversity shown by baboons when foraging, and because this study showed that the ranges of both species comprised of natural vegetation as well as agricultural land, it is now felt that land-cover change from natural vegetation to agriculture (food crops in particular) may not have been significant enough to cause large scale range shifts for each of the baboon species as was hypothesized by Samuels and Altmann (1986). In summary, it was established that baboon population ranges had varied vegetation composition, and that vegetation did not influence baboon species distribution.

CHAPTER SIX

CONCLUSION AND RECOMMENDATIONS

6.1 Conclusion

Typically, members of the same species found in different habitats evolve different traits, eventually becoming morphologically and ecologically distinct (e.g. Futuyuma & Moreno 1988), and eventually this divergence leads to the formation of different species. As each respective species develops adaptations that provide advantages in one habitat, these very same adaptations can become a disadvantage in dissimilar habitat. As Jolly et al (1993) stated, specialization, or adaptation to a particular habitat, is a mark of good species, and many biogeographic models are based on the premise that the study species' distribution can be explained or predicted through knowledge and understanding of the species' habitat needs. For many species this is true, and their habitat can be easily matched to their adaptations (e.g. Liu et al., 2014; Ruetter et al., 2003; Penman et al., 2010). Furthermore, long term or permanent changes in habitat normally leads to changes in ranging patterns (e.g. Osko et al., 2005), affecting population dynamics (e.g. Hill & Winder, 2019), and degradation of habitat can force animal populations in affected areas to migrate as they face local extinction. Changes in habitat, population distribution, and population dynamics can be modeled in a in GIS environment (e.g. Penman et al., 2010; DeVries et al., 2011), and this has accelerated the uptake of GIS tools and technology in ecological studies.

The baboons found in southern Kenya, yellow and anubis baboons, have different observable traits, and show clear morphological divergence. However, the migration of anubis baboons into the previously majority yellow baboon ranges in the Amboseli basin in the early 1980s, and the continued hybridization observed in the Amboseli raised important questions. Are anubis and yellow baboons ecologically divergent? If so, which ecological factors could be used to show the ecological separation between the two species? What did the observed anubis baboon migrations mean for the hybrid zone found in the study area? Here, Geographic Information Systems and Remote Sensing were used to first evaluate the distribution of baboons in southern Kenya, then to build quality biogeographic data sets, and finally to investigate the correlation between the biogeographic data and the distribution of the respective baboon species and their hybrids within the study area. The study area was limited to three counties in Kenya (Machakos, Kajiado, and Taita-Taveta). The biogeographic variables were also limited to descriptors of land-cover, climate, and the geography of sites where baboons ranged. GWRA was used to investigate between-species biogeographic niche whereas ENFA was used to investigate within-species biogeographic niche.

The field survey established that baboons were found within sixteen sites in the study area. These were Kitengella, Ngong, Tuala (Rongai), Kimana, Rombo, Bissil, Magadi, Olorgesaille, Sultan-Hamud, Emali, Kiboko, Namanga, Kibwezi, Oloitokitok, Amboseli, and Taita-Taveta. The field survey established that anubis and yellow baboons within the study area were living in allopatry, with anubis baboons found in the north-west of the study area, yellow baboons found in the south-east of the study area, and hybrid baboons found in between. Whereas the altitude of the study area generally increased as one moved from south-east to north-west, there was strong local variation in sites where baboon were found. The distance from the Indian Ocean also increased from south-east to north-west. GWRA analysis established that the distribution of baboon species in the area did not covary with altitude. However, GWRA established that baboon species distribution could be predicted the distance from the Indian Ocean.

To establish the vegetation within baboon population ranges LandSat imagery was classified into seven categories, and the composition of LULC within each baboon population’s range was established. LULC analysis established that four classes dominated sites where baboons were found: Woodland, Grassland, Bushes, and Agriculture. GWRA was then used to investigate if LULC covaried with baboon species distribution. It established that the distribution of baboon species in the area did not covary with vegetation composition, and that each baboon population range had unique LULC composition.

Climatic data from the WorldClime repository was collated and used to investigate if climate covaries with baboon species distribution. The variables used here, known as BioClim, highlight average as well as extreme climatic conditions. To establish the influence of climate on baboon species distribution, the average of each climatic variable at each baboon population's range was established. GWRA was then used to investigate if climate covaried with baboon species distribution. Of the climatic variables tested, only one showed correlation with baboon species distribution. However, the biological relevance of this result could not be established. It was concluded that the distribution of baboon species in the study area did not covary with climate.

One explanation that has been offered for observed species distribution is that historic patterns alone explain baboon species distributions (Jolly et al., 1993). In southern Kenya, it is possible that anubis baboons first immigrated to areas in the north-western part of the study area whereas yellow baboons first immigrated into areas south-east of the study area. The different species then learned how to live in their respective habitats, learning where to source water, how to utilize vegetation available for food in the wet season as well as in the dry season. The different species also learned how to utilize the vegetation and terrain for cover during the night, and to avoid predation. Because of this familiarity with their surroundings, baboon populations rarely migrated into new unfamiliar areas. This, however, does not mean that they couldn't survive in new or different habitats. Baboons have good cognitive skills, and have been shown to learn how to utilize new foraging opportunities presented to them. In conclusion, based on the biogeographic variables tested, this research infers that the geographic separation between the two species in the study area is not maintained due to ecological divergence, rather it is due to historical contingency.

6.2 Recommendations

Resolving the unsettled questions will likely entail insight from complimentary studies, more specifically studies that focus on behavioral adaptations, and that are able to intricately detail differences in behavior between anubis and yellow baboons. This study was limited by two key factors. First, the selection of primate populations to study was non-random. Secondly, the baboon populations were often found in inaccessible areas, on private land, and/or in areas where the local communities were hostile to the primates and researchers. Because of these two reasons, the field survey was limited to protected areas where field research camps had been established, and along established road networks.

To overcome the first limitation it is recommended that complimentary research focuses on documenting the distribution of baboon species by carrying out a wide scale manned or unmanned aerial surveys. This will enable adequate sampling in areas that are inaccessible on foot or by car. To overcome the second limitation, it is recommended that GPS collars are used to provide tracking data used for biogeographic niche analysis. Whereas this study focused on estimating the range of baboon populations using the center of tracking points, high quality GPS collars can be used to provide accurate tracking data on individuals as well as groups of baboons. The major advantage of using GPS collars is that when the study animal moves into areas that are inaccessible to the researcher, data on the movement of the baboon group will still be recorded.

Due to the limitations mentioned above, this and previous studies investigating baboon species biogeographic niche have been First-Level selection studies (e.g. Winder, 2014; Fuchs et al., 2018). Collecting tracking data from collard baboons will enable Second-Level and/or Third-Level selection studies to be undertaken. Second-Level or Third-Level selection studies would give a more intricate view of baboon species biogeographic niche, providing information at a scale that has previously not been studied.

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APPENDICES

Appendix I: List of Publications

Wango, T. L., Musiega, D., Mundia, C. N., Altmann, J., Alberts, S. C., & Tung, J. (2019). Climate and Land Cover Analysis Suggest No Strong Ecological Barriers to Gene Flow in a Natural Baboon Hybrid Zone. International Journal of Primatology. 40(1), 53-70

Wango, T. L, Musiega, D. and Mundia, C. N., (2018) Assessing the Suitability of the WorldClim Dataset for Ecological Studies in Southern Kenya. Journal of Geographic Information System, 10, 643-658. doi: 10.4236/jgis.2018.106033.

APPEARANCE	**ANUBIS**	**HYBRID**	**YELLOW**
COAT COLOR	Olive brown or dark grey	Intermediate	Yellow coat, slightly tinted brown
HAIR LENGTH	Long, thick hair	Intermediate	Short hair
BODY SHAPE	Appears short and bulky with a big chest	Intermediate	Appears tall and slender

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