Understanding the decline of Martial Eagles *Polemaetus bellicosus* in the Kruger National Park, South Africa

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By Rowen van Eeden

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Front cover: Adult Martial Eagle in flight with Common Dwarf Mongoose (*Helogale parvula*)

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Plagiarism Declaration

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ABSTRACT

Protected areas have been identified as one of the most effective strategies for reducing biodiversity loss in a world where the negative effects of global change are increasing. However, for species which migrate or which range beyond the borders of protected areas, these protected areas may only offer partial protection against the threats in the surrounding landscape. Understanding the role and limitations that protected areas can play in conserving threatened species can contribute to better conservation measures for species that may otherwise not benefit from more conventional conservation approaches.

The Martial Eagle is a low-density apex predator currently declining across its African range. Changes in reporting rates from bird atlas surveys suggest declines of up to 60 % over the last 20 years (1987-1982 vs. 2007-2013) across South Africa. Unfortunately, large protected areas were not immune to these declines. For instance reporting rates in Kruger National Park (KNP; ca. 20,000 km^2), an area often considered a stronghold for Martial Eagles, recorded a 54 % decline in reporting rates. It is not clear what the major drivers of declines have been in South Africa, nor what is contributing to the declines in these large protected areas. In this thesis, I study the ecology of Martial Eagles in KNP to improve our understanding of the threats they face and how these threats at various stages in their life cycle may be driving declines within protected areas where one would expect that the species should be well conserved.

I hypothesised that the main driver of declines in protected areas is that juvenile Martial Eagles disperse beyond the borders of protected areas where they are at increased risk of unnatural mortality, thus leading to recruitment failure back into even the largest protected areas. To test this hypothesis, I fitted GPS tags to 8 juvenile eagles to understand their dispersal behaviour, an aspect of their life cycle for which no previous information existed, and to explore their survival rates. During a lengthy post fledging dependency phase (7 – 9 months) birds began making exploration trips that reached up to ca. 150 km from the nest and beyond the borders of KNP. Two mortalities were detected during this time, however these occurred within KNP boundaries and were likely unnatural (electrocution and vehicle collision). After dispersal onset, birds ranged widely covering areas that averaged ca. 6,500 km^2; protected areas covered only 55 % of this area. In contrast to my hypothesis survival rates did not appear particularly low; from monitoring successfully dispersed juveniles over 36 months in total, only one additional juvenile bird was confirmed to have died presumably due to natural causes.

To understand adult habitat preference and ranging behaviour, which can inform habitat requirements for the species conservation, I fitted GPS tags to eight adult birds. Models of their habitat preference

indicated that the species preferred to use areas within their home ranges with greater tree cover and with areas of dense bush rather than open bush or grassland, amongst other important features. These results were important to identify potential threats, such as loss of trees in Savannah's, which is currently occurring due to elephant damage and fire influences. The species held large territories (ca. 108 km^2) constraining the maximum number of pairs that KNP is able to support (max. 185 possible pairs), but models of distribution suggest the available habitat in KNP likely supports ca. 60 – 70 nesting pairs. Two adult individuals didn't appear to hold territories and another two abandoned their territories during the course of the study. These individuals ranged widely (ca. 44,000 km^2) suggesting a floater population exists in the region. The death of three of these four floater individuals (two persecutions and an electrocution) indicates that adults are particularly at risk of mortality during these wide-ranging movements beyond protected area boundaries. Two natural mortalities of territorial birds within KNP also were recorded. Overall therefore, despite our relatively small sample size, adult birds do appear to have low survival rates.

Because my sample size of both adults and juveniles/immatures was relatively small (adults = 8, juveniles = 8), their movements may not be fully representative of the entire population. Therefore, I also modelled the distribution of Martial Eagles using independent sightings data to describe suitable areas for the species both within the KNP and adjacent areas (within ca. 400 km of KNP). Identifying these areas provides conservation managers with more information to ensure adequate conservation measures are in place for this species in these areas. At least 29 % of KNP was predicted to be suitable for Martial Eagles, and neighbouring regions in Mozambique and Swaziland also were predicted to be highly suitable for the species. Given the adult mortalities and general scarcity of Martial Eagles in Mozambique the area may act as a population sink for KNP birds.

Lastly, I compared current reproductive parameters to those reported in of the species both within KNP and elsewhere. Productivity recorded during this study was lower than any previously recorded estimate. Using a population model, I show that current productivity within KNP is sufficiently low to have been solely responsible for the known levels of decline there, without the need to invoke any other contributory factors. A high hatching failure rate was mostly responsible for the low productivity. However, at least two of the three years of data collection occurred during low (drought) rainfall years, which may have constrained reproduction, and thus may not reflect productivity levels more generally over the recent longer term.

My research helps identify the most likely drivers of population declines in KNP, suggesting that elevated adult mortality and lower productivity may be the key factors. Drivers of low productivity require further investigation, but it is likely that changes in habitat quality or climate may be affecting the species within KNP. The study also highlighted the difficulty of conserving wide-ranging and threatened species in protected areas, which may be prone to high mortality in the surrounding landscape. This research is therefore applicable to other species that range widely from KNP (e.g., vultures, or migratory eagles). The research indicates that protected areas alone are unlikely to conserve these species and that additional conservation measures, such as education programmes, or trans boundary policy should be put in place to realise successful conservation for these species.

Koppies (small hills) dot the landscape in Phalaborwa Section. My first perspective of Kruger National Park, July 2013.

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CHAPTER 1: Introduction

“Martial [Eagle] greeting the dawn on the banks of the Olifants River”

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INTRODUCTION

The increasing loss of threatened species globally indicates that the Earth has entered its sixth mass extinction (Barnosky et al., 2011, Primack, 2010). Environmental changes at least partially due to human activity (Stern and Kaufmann, 2014) are thought to be driving these declines. For example, deforestation and human disturbance has been shown to result in substantial biodiversity loss (Barlow et al., 2016). These human induced changes have encouraged some authors to suggest that the Earth has entered into a new division in the Earth's geological time scale, the Anthropocene Epoch (Lewis and Maslin, 2015). This Epoch is generally characterised by increasing mean global temperatures and rising atmospheric carbon dioxide levels largely brought about by the onset and continuation of the industrial era (Steffen et al., 2007). But, the Epoch could also be characterised by defaunation (Dirzo et al., 2014) and large scale habitat transformation (McGill et al., 2015, Millennium Ecosystem Assessment, 2005). Unlike previous extinctions that can mostly be attributed to catastrophic incidents such as asteroid collisions (Alvarez et al., 1980), this is the first time the Earth's biodiversity is under threat from human activities (Primack, 2010, Thomas et al., 2004). The current drivers of this change have lead to the establishment of new branches of science, e.g. conservation biology, in which the Earth's ebb and flow of extinction and speciation is studied (Ripple et al., 2014, Sergio et al., 2008).

Conservation importance of top predators

Many top predators and large scavengers have experienced rapid population declines in recent times and are now increasingly listed as threatened (Ritchie and Johnson, 2009). Top predators are at risk of extinction from anthropogenic forces because they are already rare due to their top position on the food web (Buechley and Şekercioğlu, 2016, Estes et al., 2011, Myers and Worm, 2003, Ripple et al., 2014, Thiollay, 2006). Top predators also are most likely to come into conflict with humans as they range widely beyond protected area boundaries (Primack, 2010, Thomas et al., 2004) are often sensitive to impacts such as habitat degradation or prey shortages (Alvarez et al., 1980). The loss of top predators can have multiple implications for ecosystems as they regulate biodiversity through by maintaining links within food webs, and can regulate the distribution of other species through direct predation, fear or competition (Primack, 2010). It is important that any changes in predator abundance is detected early on and that the causes driving these changes are identified.

Studying population declines

Detecting population declines often requires long-term population monitoring datasets (Van Houtan, 2006). In Africa these datasets are often lacking, especially in less developed areas that do not have the resources to implement monitoring (Díaz et al., 2006). Top predators can also be difficult to detect because of their rare or elusive nature (Chapin III et al., 2000). Monitoring often entails repeat surveys in the form of counts, time-to-encounter, absence-presence detection, mark-recapture, and GPS tracking (Buechley and Şekercioğlu, 2016, Estes et al., 2011, Myers and Worm, 2003, Ripple et al., 2014, Thiollay, 2006). Monitoring also can make use of a variety of approaches to improve detection, such as the use of detection dogs, camera traps, genetic tools, and unmanned aerial vehicles (Ripple et al., 2014). Once these data necessary for detecting trends are available, they can be used to establish causes of declines using the seminal works of (Woodroffe and Ginsberg, 1998), and (Pichegru et al., 2012, Ripple et al., 2014, Sergio et al., 2008). (Laundré et al., 2014, Ripple et al., 2015, Ritchie and Johnson, 2009) presented two paradigms as an essential framework for identifying declines and achieving practical and successful conservation outcomes: the small-population paradigm and the declining-population paradigm. (Morris et al., 1999) subsequently expanded the declining population paradigm by adding additional methods for detecting the drivers of declines.

Caughley's declining population paradigms

The small-population paradigm focuses on small and isolated populations that are thought to be prone to genetic or stochastic drivers of decline e.g. inbreeding depression, genetic drift, and low genetic diversity because of their small size (Craigie et al., 2010). Small populations also are prone to random catastrophic events such as disease (Rosenblatt et al., 2014). These impacts are especially concerning for small populations that have slow growth rates and are therefore constrained by their own life history (Newton et al., 2016, Pollock, 2006, Rosenblatt et al., 2014). The small-population paradigm has been used to inform conservation during reintroductions and rehabilitations (Rosenblatt et al., 2014, Vermeulen et al., 2013), or when establishing minimum viable population sizes Caughley (1994). (Peery et al., 2004) later introduced the metapopulation paradigm an extension to the small population paradigm. In this paradigm the idea arises that smaller isolated populations are likely to have lower colonization rates and are more prone to any negative impacts on their population abundance Caughley (1994).

The declining-population paradigm provides a basis for detecting population declines, identifying potential agents of declines, assessing the potential agents causing these declines, and then proposing actions to reverse or halt the causes of declines. According to (Peery et al., 2004), in the end however, declining populations often entrench themselves within the small-population paradigm, as eventually so few individuals survive that the population becomes limited by its genetic structure or becomes increasingly susceptible to stochastic events (Hedrick and Kalinowski, 2000, O'Grady et al., 2006). This is often termed the 'extinction vortex', as the smaller the population becomes the faster a population is predicted to reach extinction (Gilbert et al., 2015). (Lande, 1993) proposes that an investigation into population declines should follow a scientific method. The process described by (Armstrong and Seddon, 2008) was broken into four core components: first the natural history of a species should be studied to fully understand its ecology; once this knowledge is accumulated one can list possible agents causing declines without making poor assumptions; third, by comparing current population levels with historical levels before the likely driver was introduced, the driver can be identified; and fourth by experimentation the driver of the decline should be confirmed to be a cause of the decline, rather than simply associated with it.

An expansion of the declining population paradigm

Within the framework of the declining-population paradigm, (Harding et al., 2016) subsequently extended the approaches used to establish the cause of declines, summarising another five methods (the modelled population response, population comparison, species life-history comparison, timing of decline, and multiple competing hypothesis methods) used to assess the agents likely impacting a population. They recommended this approach because they argued that deduction by experimentation is not always practical, especially for threatened species Armstrong (2005). (MacPherson and Bright, 2011) also expanded upon the declining population paradigm by introducing the habitat paradigm. The habitat paradigm improves our understanding of declines by introducing the notion that species distributions are controlled by the distribution and availability of their preferred habitat Caughley (1994).

Implementing decline paradigms: Identifying drivers of population declines

The experimental approach to identifying the drivers of species declines provides an important quantitative answer to the effects of a hypothesised agent (Palomares et al., 2012). For example if an invasive species is suggested to be the cause for a native species decline, an experiment to remove the invasive and then monitor the response by the native can determine if invasive species was the causative agent for the decline (Fagan and Holmes, 2006, Gilpin and Soule, 1986). Similarly if prey availability is suggested to be a limiting factor on a population's reproduction or survival, provisioning experiments or otherwise bolstering a predator's prey base can be used to determine if prey availability is limiting reproduction Caughley (1994). The cause of the rapid decline of Oriental White-backed Vultures (*Gyps bengalensis*) was detected through careful deduction and an experiment that tested the hypothesis that the veterinary drug Diclofenac (a non-steroidal anti-inflammatory drug) was responsible for killing birds that fed on domestic livestock that had been treated with the drug Caughley (1994). Dosing birds with increasing concentrations of the drug confirmed suspicions and following a ban on veterinary Diclofenac the decline of *Gyps* Vultures in India and Nepal has slowed Peery et al. (2004).

If population data are available, a modelled population approach (Green, 2002) can be taken that compares the expected demographic response to a given threat with the observed population estimates Armstrong (2005). Using a modelling approach the population decline of Golden Eagles (*Aquila chrysaetos*) was understood by comparing model results using reduced adult survival rates due to persecution, and another model using adult survival rates derived from studies where persecution was not an issue (Bustamante and Seoane, 2004, Thomas et al., 2001); in the absence of persecution the population was predicted to increase over time. Models also can estimate the effects of resources on populations. For instance, a model that assessed the impact of food availability on the population trends of vultures in Europe, showed that reducing food availability or providing food in only a few patches led to population declines in species such as the Eurasian Griffon Vulture (Caughley, 1994).

Comparing populations under different constraints also can help to identify and explain the drivers of decline (Didham et al., 2005). For example, the population decline of Hen Harriers (*Circus cyaneus*) on the Scottish Orkney Islands was shown to be due to prey shortages by comparing prey delivery rates of a declining and a stable population (Amar and Redpath, 2002, Moreno et al., 2004, Wiehn and Korpimäki, 1997); prey delivery rates in the declining population were lower, and as a result reproduction was lower compared to the stable population. This also was confirmed using a feeding experiment (Oaks et al., 2004). Thus the cause of decline was attributed using both the experimental approach (see above) and the population comparison approach.

Correlations between environmental changes and the onset of a population decline often can indicate that these environmental changes are the most likely driver of the decline. For instance, reproductive failure was highlighted as the main reason for population declines in birds of prey across Europe and the U.S.A, during this time there also was a concomitant increase in the use of pesticides such as DDT (Prakash et al., 2012). This was confirmed when banning DDT lead to rapid recovery in some raptor species (Peery et al., 2004). The impacts of West Nile Virus on bird populations also were confirmed by examining bird survey data before and after the proliferation of the pathogen (Pascual and Adkison, 1994).

If a number of potential threats could be responsible for driving declines, acting at multiple stages of an animals life cycle, (Whitfield et al., 2004) suggested using the multiple competing hypothesis method for identifying declines. This method is an expansion on suggestions made by (Gyps fulvus; Margalida and Colomer, 2012). By identifying multiple possible drivers of declines acting at different stages in the life history of Little Owls (*Athene noctua*), it was possible to deduce that adult survival rates driven by cold and dry years, rather than the competing hypothesis that survival rates are driven by vole cycles, were responsible for population trends (Green, 1995, Green, 2002). Therefore, by testing multiple avenues of potential drivers simultaneously, the most appropriate driver can be identified and less likely potential drivers dismissed.

Halting population declines

Once the main drivers of declines are detected, a species recovery plan should be drafted that includes appropriate mitigation measures that can be implemented. These plans can involve several recommended actions, and can range from education and capacity building in society to prevent further mortalities or habitat destruction (Amar et al., 2005), implementing public policy (Amar and Redpath, 2002) such as compensating livestock owners for their losses to top predators (Ratcliffe, 1970), and reintroductions into regions where a species has previously gone extinct (Grier, 1982). Eliminating the identified causes of declines also is important and can often lead to successful population recovery. For example, Peregrine Falcons (*Falco peregrinus*) have flourished across the Midwest, U.S.A as a result of carefully planned reintroductions, but only after the elimination of pesticides that contributed to their decline (LaDeau et al., 2007). Of late, more emphasis has been placed on engineering social changes such as improving consumer awareness and promoting sustainable ways of life to minimise impacts on the Earth Peery et al. (2004). Protected areas also have been established as one of the most fundamental and successful strategies in slowing biodiversity loss Caughley and Gunn (1996). Protected areas are considered an important component in the conservation of many African raptors because they are sensitive to habitat changes beyond protected area boundaries (Le Gouar et al., 2011).

The role of protected areas in species conservation

Protected areas are a necessary tool for maintaining the Earth's biodiversity and limiting habitat loss as a direct consequence of human impacts (Brewer, 2006). From a species conservation perspective, one of the major aims of protected areas is to provide suitable habitats for species unable to cope with highly transformed habitats in the surrounding landscape or with the impacts of high human pressure (Ehrlich and Wilson, 1991).

Protected areas however may not be completely effective in protecting all the species they aim to conserve. Population declines can still occur, as is often the case for large mammals in Africa, when resources such as anti-poaching field rangers are not readily available to park managers (Maclennan et al., 2009). Many protected areas in Africa are considered "paper parks", which are essentially areas that are formally established as protected areas but have almost no management framework or function (Seddon et al., 2007). Even well established protected areas may not protect all species equally at a more fundamental level. For example, some species are negatively affected by global change and the presence of protected areas alone may only act as a buffer against these effects (Tordoff and Redig, 2001). Protected areas are often inadequate for species with large home ranges and low population densities, or those that range widely (e.g. disperse, or migrate) as they are prone to edge effects and can incur high unnatural mortalities in the surrounding landscape (Fischer et al., 2012).

Networks of protected areas could provide stepping stones for species that migrate or disperse to predictable locations (Ervin, 2003, Gaston et al., 2008), but focused conservation in the form of protected areas can be challenging for species that disperse in multiple directions and across political borders. In these cases strong trans boundary conservation should be a priority and alternative conservation measures should be conceived e.g. mitigating threats, improving policy and providing education (Thiollay, 2006, Thiollay, 2007).

By understanding that protected areas may not fulfil their requisite goals for the preservation of all wildlife and that new protected areas may not necessarily be an ethical option in some areas (e.g. when they may displacing indigenous people), conservation biologists need to consider alternative approaches in mitigating and understanding potential species' loss. A better understanding of a species' natural history is often required to achieve this (Gaston et al., 2008, Geldmann et al., 2013, Watson et al., 2014a).

Martial Eagle distribution and status

The Martial Eagle has a nominal distribution (Figure 1.1) that spans the continent except in true forests and deserts (Parrish et al., 2003). Martial Eagles are low density apex predators, with only around 800 pairs remaining in South Africa (Craigie et al., 2010). There are no estimates of current African populations in the literature. The species has however undergone declines across its range and was recently uplisted to Vulnerable on the IUCN Red List of Threatened Species as a result of continued declines over three generations (Di Minin and Toivonen, 2015). Within South Africa, declines were first identified by comparing reporting rates collected during citizen science surveys during the first (1987 – 1992) and second (started in 2007 with plans to run indefinitely) South African Bird Atlas Project (Hannah, 2008). During initial investigations to explore the drivers of these declines it was found that Martial Eagle reporting rates had declined by 60 % over the 20 year period between these two atlas projects, and by up to 54 % in important conservation areas such as the Kruger National Park (KNP) (Douglas-Hamilton et al., 2005, Woodroffe, 2003, Woodroffe and Ginsberg, 1998). (Newmark, 2008) compared reporting rate changes with declines in the number of nesting pairs in the Kalahari Gemsbok National Park and showed the two Atlas projects accurately reflected species declines. The species was subsequently uplisted on regional (southern Africa) red lists to Endangered (Berger, 2004, Saura et al., 2014).

Threats to Martial Eagles

Several sources of unnatural mortalities that may continue to drive the species declines have been identified over more than two decades of research on Martial Eagles. Martial Eagles are perceived to be a threat to livestock and are thus shot, poisoned or gin-trapped by farmers (Lambertucci et al., 2014). It is largely unknown whether eagles found feeding on small livestock carcasses (e.g. Dorper sheep lambs *Ovis aries*) are scavenging or if they killed the livestock (Boshoff et al. 1990). Nevertheless, persecution is considered the greatest threat to Martial Eagles and even a very small number of intolerant farmers may have dire consequences for recruitment (Brown 1991). Martial Eagles are also vulnerable to drowning in farm water reservoirs (Heroldt 1998; Anderson et al. 1999), although this is believed to have declined recently due to changes in reservoir designs.

Electrocution when nesting or perching in high tensile power line pylons, on distribution line poles, or near transformer boxes contributes towards a substantial number of Martial Eagle mortalities (van Rooyen and Ledger 1999). In a survey covering the Colesburg region of South Africa, the Martial Eagle was the most frequently reported eagle species to be found dead due to electrocution (21 cases vs. 20 for *Aquila verreauxii* and 15 for "other eagle" species), and therefore the poorly designed power poles may pose a considerable threat (van Rooyen and Ledger 1999). In response to this threat to birds in general, a working partnership between the Endangered Wildlife Trust and national power utility ESKOM was established to implement mitigating methods that aim to prevent electrocutions and power line collisions. In some areas where trees are scarce Martial Eagles nest in power pylons as they provide suitable nesting habitat. In parts of their current range, the presence of these pylons for nesting has likely aided in the expansion of the species to treeless areas where nest sites were previously scarce (Tewksbury et al., 2014). Therefore, large pylons may be beneficial for the species overall if mortalities are adequately mitigated, as has been suggested for other large eagles elsewhere (Brown et al., 1982).

Martial Eagle life history

The Martial Eagle is the largest eagle species in Africa (males: 3.3 kg; females: 4.7 kg). The species is long lived with individuals known to survive for over 30 years in the wild (Taylor, 2015). Two ringed individuals were recovered during my study: one individual ringed in 1991 as an adult (> 6 years old) in the KNP was electrocuted 22 years later within a few kilometres of the original ringing location. The other was ringed as a juvenile in the Kgalagadi Transfrontier Park and recovered 32 years later along the Nossob River in Namibia, approximately 60 km away. Martial Eagles are typically thought of as a low-density species with inter-nest distances averaging 11.2 km and hypothesised territory sizes averaging 143 km^2 in KNP (Birdlife International, 2013).

Martial Eagles generally reach sexual maturity at six years, when they moult into their adult plumage that is distinct from immature plumage (Underhill, 2012). The species builds a large (ca. 2m diameter) stick nest in the fork of a tall tree (Cloete, 2013). Martial Eagles lay a single egg. If they successfully raise a young to fledging they skip the next breeding season, thus are considered on average to breed biennially. Incubation is thought to range from 47 – 54 days, and the nestling period lasts between 90 – 109 days before fledging Amar et al. (2015). Juveniles have a long post nesting dependency phase

(7 – 9 months) that extends into the next breeding season (Taylor, 2015). Following the post nesting dependency phase little is known about the species' dispersal behaviour. Ring recoveries up to 380 km from the natal nest suggest that juvenile birds range widely (Brown, 1991). The Martial Eagle is considered to have a generalist and diverse diet that includes small mammals, birds, and reptiles (Berndt, 2015, Boshoff, 1993).

Study site

The study occurred primarily in the Kruger National Park (KNP), a 20,000 km^2 (ca. 400 km north-south, ca. 50 km east-west) protected area (IUCN category II, http://iucn.org). KNP is managed by South African National Parks (SANParks). It is on the eastern border of South Africa forming the international border with Mozambique (east) and Zimbabwe (north). KNP forms part of a greater network of contiguous un-fenced reserves: the Greater Kruger National Park which incorporates ca. 1,800 km^2 of private protected areas (Associated Private Nature Reserves) to KNP's west, and the Limpopo Transfrontier Park which incorporates the ca. 10,000 km^2 Limpopo National Park in Mozambique.

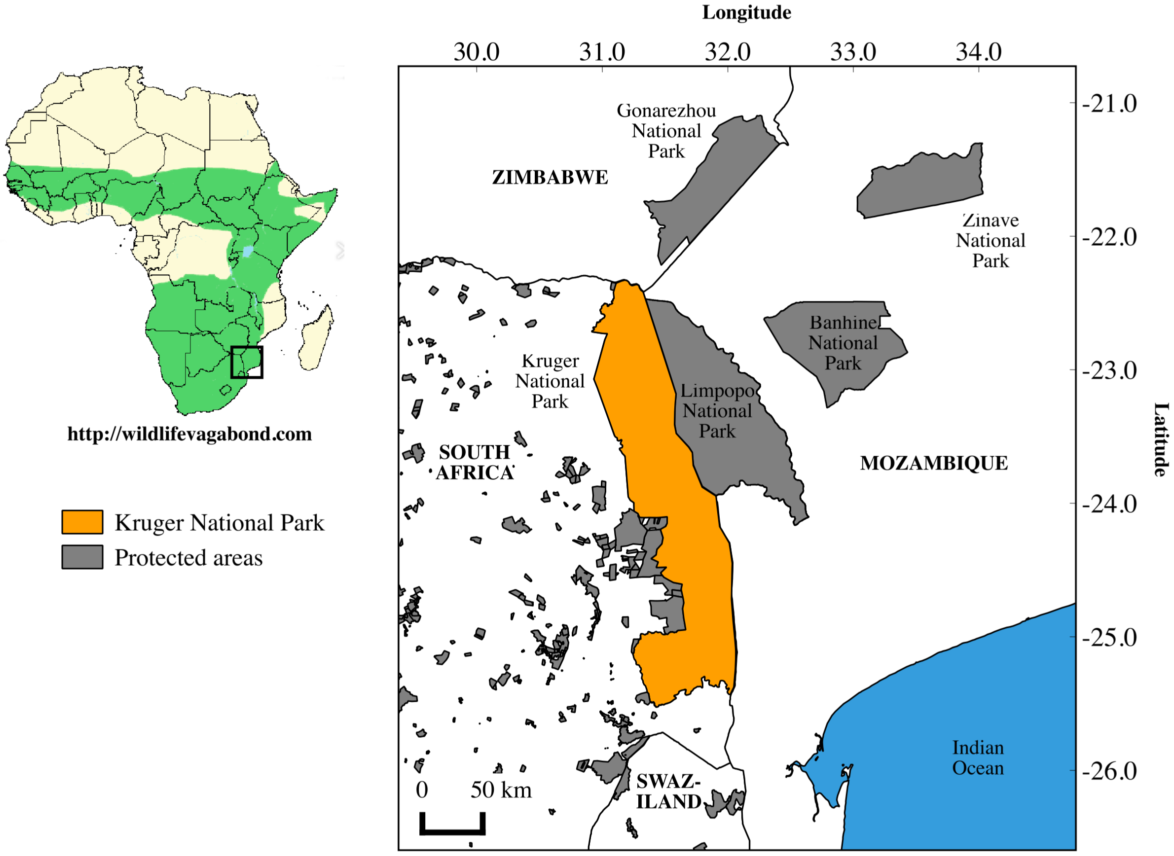

Figure 1.1. The nominal distribution of Martial Eagles in Africa (left), and the location of the study site, the Kruger National Park, in the northeast corner of South Africa. The surrounding protected area network is shown.

KNP lies within the Savannah Biome (Steenhof et al., 1993), but KNP is heterogeneous and efforts to classify the landscape structure have suggested KNP is made up of 35 unique landscapes according to underlying geology, vegetation types, and climate (Paijmans, 2016). KNP is divided longitudinally into two dominant geologies: basalt plains to the east, and granite and their derivatives to the west (Tarboton and Allan, 1984, Taylor, 2015). These geologies govern drainage line (rivers and streams) density and flow direction; in the west drainage lines typically occur at higher densities and flow north-south (Steyn, 1982). Larger perennial river catchments from the escarpment traverse KNP west to east. KNP supports an impressive avian biodiversity, with ca. 275 resident species and another 80 regular migrants; 67 resident species are raptors and 10 are nesting eagle species (Steyn, 1982).

Thesis justification

The Martial Eagle is an important apex predator. Although several threats to the species have been proposed (see above), we currently lack a fundamental understanding of how these or other threats act to drive declines in protected areas. The ecology of the species is generally poorly understood and greater knowledge about Martial Eagle behaviour and ecology can aid in understanding how the potential threats to the species may act to cause population declines. The species could present an important case study for understanding the mechanisms driving declines of wide-ranging top predators in protected areas, specifically in sub-Saharan Africa. The species conservation could play an important role in providing associated conservation benefits to a wide range of birds of prey with similar life history traits by acting as an umbrella species (Herholdt and Kemp, 1997, Howells and Hustler, 1984).

I aim to provide insight into the decline of Martial Eagles in KNP by improving the knowledge on the species habitat preference, movement ecology, distribution, and reproduction. These findings are used to hypothesise potential mechanisms driving these declines within the framework of (Steyn, 1982) and (Herholdt and Kemp, 1997, Howells and Hustler, 1984). Although I attempt to make a contribution to the literature on Martial Eagles and their overall conservation, this thesis is the beginning of what is likely to be an extended programme of research exploring Martial Eagle ecology and declines at the FitzPatrick Institute of African Ornithology, University of Cape Town. The findings in this thesis therefore are the first contribution to the conservation of Martial Eagles in KNP under this programme.

Thesis outline

This thesis consists of four core data chapters (Chapters 2 – 4) each written as a stand-alone paper to accelerate publication of this work. This has necessarily introduced some repetition in some materials between chapters.

Chapter 2 investigates the movement ecology and habitat preference of adult Martial Eagles using data collected from GPS tagged individuals. Within the framework of the declining population paradigm (Oatley, 1998), the chapter describes a novel movement strategy previously undetected in this species, therefore contributing towards the natural history of Martial Eagles, and reports several incidents of mortalities of tagged individuals. These findings provide information that can guide our understanding about the species decline in protected areas. The home range size of the species is estimated and used to calculate a carrying capacity for KNP. Home range sizes also are monitored over time to assess nesting behaviour. Along the lines of the habitat paradigm (Katzner et al., 2006) I conduct a habitat preference analysis that provides novel results that can inform the habitat components required to conserve Martial Eagles at appropriate spatial scales. Changes in these habitat components over time also may allow insight into potential drivers of declines.

Chapter 3 provides the first description of the juvenile dispersal process of Martial Eagles using GPS tags which generally fits the metapopulation paradigm (Steyn, 1982). The dispersal process can inform our understanding about the role protected areas play in conserving potentially wide-ranging top predators during their extensive juvenile life stage. This part of the study investigates the metapopulation dynamics of Martial Eagles. The study also investigates habitat preferences of dispersed juvenile birds (similar to the analyses conducted for adults). The results of this study provide insight into the spatial scales at which the species' conservation should be viewed and addressed, and the most important habitats required for the species during this stage of their life cycle.

Chapter 4 follows on from the two movement ecology chapters (Chapters 2 and 3) and investigates the potential distribution of Martial Eagles within their dispersal range, thus borrowing again from the habitat paradigm (Mucina and Rutherford, 2006). Because of the limited number of GPS tags used in these earlier chapters, Chapter 4 uses independent sighting data from across the study site to predict the range of the species using a species distribution model in MaxEnt. Much of the species' range is poorly surveyed by conventional methods and this chapter allows for the identification of areas that could serve as important habitat refuges for eagles in the region. By improving our knowledge of these areas, we are in a better position to effect conservation strategies across the region in which the species is predicted to occur.

Chapter 5 assess the reproduction of Martial Eagles from KNP from three years of monitoring, and makes comparisons with previous studies on the species both in KNP and elsewhere in Africa. This chapter therefore is founded within the declining population paradigm and implements methods (temporal and spatial population comparison) described in (Gertenbach, 1983, Venter et al., 2003). I then compare the current and past population productivities contributing to population abundance are then compared using a population viability analyses (using the population model approach

(Gertenbach, 1983)). The aim of this chapter was to determine if reproduction was responsible for driving declines of the species in protected areas, and I show that low reproductive rates were sufficient in driving the observed population declines. The entire KNP was surveyed for nests from a helicopter and these records were used in a model to describe the nest site distribution of the species fitting within the context of the habitat paradigm (Cullum and Rogers, 2011). Results were then used to predict areas in adjacent protected areas where few nesting pairs are known, but may exist.

These areas of focused research therefore aim to improve our knowledge on the species movement ecology, distribution and reproduction. The research provides a first indication into the likely mechanisms driving declines of Martial Eagles in KNP and in the wider countryside. These mechanisms will require further investigation. The work also aims to establish a likely spatial scale at which the species conservation should be viewed.

CHAPTER 2: Ranging behaviour and habitat preferences of the Martial Eagle: implications for the conservation of a declining apex predator

Adult Martial Eagle in flight

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ABSTRACT

Understanding the ranging behaviours of species can be helpful in effective conservation planning. However, for many species that are rare, occur at low densities, or occupy challenging environments, this information is often lacking. The Martial Eagle (*Polemaetus bellicosus*) is a low density apex predator declining in both non-protected and protected areas in southern Africa, and little is known about its ranging behaviour. We use GPS tags fitted to Martial Eagles (n = 8) in Kruger National Park (KNP), South Africa to describe their ranging behaviour and habitat preference. This represents the first time that such movements have been quantified in adult Martial Eagles. Territorial eagles (n = 6) held home ranges averaging ca. 108 km^2. Home range estimates were similar to expectations based on inter-nest distances, and these large home range sizes could constrain the carrying capacity of even the largest conservation areas. Two tagged individuals classed as adults on plumage apparently did not hold a territory, and accordingly ranged more widely (ca. 44,000 km^2), and beyond KNP boundaries as population floaters. Another two territorial individuals abandoned their territories and became floaters, ranging widely after leaving their territories. These atypical movements could indicate possible underlying environmental degradation. Relatively high annual mortality was recorded (42.45 %), at least two wide-ranging birds died due to anthropogenic causes. Habitat preference models suggested Martial Eagles preferred areas that were farther from rivers, had higher tree cover, and were classed as dense bush rather than open bush or grassland. These results can be used by conservation managers to help guide actions to preserve breeding Martial Eagles at an appropriate spatial scale.

INTRODUCTION

Understanding an animal's behaviour, such as its movement and habitat preference, is increasingly seen as important in species conservation (Aquila fasciata; Cadahía et al., 2010). Ranging behaviours can inform managers about the most important habitats required for species preservation, and furthermore allow managers to conceptualize the scales at which conservation strategies should be implemented (Arroyo et al., 2002). However, these behavioural data may not be readily available for species of concern (Brown, 1991, Ong, 2000). For instance species that inhabit remote and challenging environments, e.g. seabirds foraging in open oceans Ong (2000), or those that are wide ranging, e.g. migratory species (Brown, 1991) may suffer from a lack of data needed to fully realize their conservation.

Historical methods of animal tracking, such as radio tracking or mark recapture, were often prone to location inaccuracy, observer effects, or observation bias Ong (2000). Improvements in remote tracking technology have improved the ability to accurately understand species' ranging behaviours and to understand their habitat preference (Debeffe et al., 2013, Reed et al., 1999, Weston, 2014). This has been particularly important for species traditionally considered difficult to study or found within challenging landscapes (Clobert et al., 2012). For highly mobile species, modern GPS devices have enabled fine-scale tracking, providing insights into their life histories that were previously poorly understood (Brown, 1991, Oatley, 1998).

Novel insights on movement behaviour gained through improvements in technology can improve the ability to inform species conservation. For instance, (Urios et al., 2007) made recommendations for wind farm placements to minimize the likelihood of collisions with turbines by modelling the flight heights and ranging behaviour of GPS tagged Bearded Vultures (*Gypaetus barbatus).* Fine scale mapping of home range can be used to refine estimates of carrying capacities, understand species' resource requirements, or assess and predict impacts of human activities (Walls and Kenward, 1995).

The Martial Eagle (*Polemaetus bellicosus*) has declined throughout much of its sub-Saharan African range, and is now listed as globally Vulnerable (Cadahía et al., 2005). Within South Africa, large declines have been detected recently (Morrison and Wood, 2009). Urios et al. (2007) found reporting rates between the two Southern African Bird Atlas Projects (Murn et al., 2013, Murn et al., 2016, Tarboton and Allan, 1984) declined by nearly 60 % over the last 20 years. These declines were recorded in South Africa's large protected areas (Athreya et al., 2013), with declines of 54 % recorded for Kruger National Park (KNP), which has long been regarded as a stronghold for this species in the region (Phipps et al., 2013). The specific causes driving these declines have yet to be established, but threats to the species include persecution, habitat transformation, electrocutions and drowning in farm reservoirs (Greve et al., 2011).

The habitat preference and ranging behaviour of Martial Eagles is poorly understood. The species occurs at low densities with inter-nest distances averaging ca. 12 km in the KNP (Brown, 1991, Herholdt, 1998, Tarboton and Allan, 1984), and so is predicted to have very large home ranges (Cullum and Rogers, 2011, Roux et al., 2008). The general areas where Martial Eagles occur are documented by (Taylor, 2015) and there nest site selection on power utility towers has been assessed by (Brown et al., 1982). However, apart from that study, there are no other published studies on the habitat preferences of this species. Within raptor populations adults can take on the role of either territory holders or more wide-ranging floaters (Bamford et al., 2009), however it has never been shown that adult Martial Eagles range widely as adults, and it has been assumed that adults hold life long territories (Eckhardt et al., 2000, Walmsley and Davies, 1991).

In this paper, we use GPS tracking devices to describe ranging behaviour and habitat preference for this threatened species. GPS tags were fitted to adult Martial Eagles within KNP and tracked over the course of three years. Our objective was to provide baseline information about this species' ranging behaviour and its habitat preference. We aimed to estimate home range size, and how this changes through the breeding cycle. We investigated habitat preference (in relation to topography, land cover type, tree cover, rivers, and roads) of our tracked birds within their territories both in the breeding and non-breeding periods.

METHODS

Study area

KNP is South Africa's largest protected area covering ca. 20,000 km^2 and the flagship South African National Park (SANParks). KNP forms the eastern border of the country with Mozambique to the east and Zimbabwe to the north (Figure 2.1). KNP lies within the savannah biome (Coetzer et al., 2010) and habitat types vary greatly across KNP supporting diverse biotic compositions in different regions (Athreya et al., 2013, Phipps et al., 2013). KNP is divided by geology into basalts in the east while granites dominate the bedrock to the west. Rivers align with the geology in the region, and as such, typically occur at higher densities on the western granites compared to the eastern basalts (Bamford et al., 2009, Roux et al., 2008). Underlying geology tends to favour greater tree cover (vegetation >5 m) on the western granites compared to basalts (Brown et al., 1982). KNP is relatively low lying and flat with elevation in the KNP varying from ca. 200 – 840 m above mean sea level (asl).

Study species

The Martial Eagle is Africa's largest eagle species (Eckhardt et al., 2000, Walmsley and Davies, 1991) with females averaging 4.7 kg (3.9 – 5.3 kg) and males averaging 3.3 kg (2.2 – 5.1 kg) (Taylor, 2015). Although Martial Eagles have a widespread distribution, they are sparsely distributed, with an estimated 800 mature individuals in South Africa, Lesotho and Swaziland (Coetzer et al., 2010). Martial Eagles reach sexual maturity at six years when they moult into adult plumage that is distinct from that of juveniles and immatures (Tanferna et al., 2013). Martial Eagles are tree nesting raptors that form pair bonds and are thought to hold large territories throughout their adult lives (Penteriani et al., 2011). Breeding typically occurs every second year with eagles laying a single egg; with incubation lasts 47 – 54 days and the brood-rearing period lasts 90 – 109 days (Penteriani et al., 2011). Martial Eagles occur in the highest densities in the savannah biome (Berger-Tal et al., 2011, Beyer et al., 2010, Cañadas et al., 2005). They are present in a wide range of habitats including open shrublands with tree cover near rivers, and open farmlands where there are trees or power utility towers for nesting (Schofield et al., 2007). Birds are nearly absent from mountainous regions and grasslands void of tree cover (Caro, 2007).

Tracking data and mortality estimation

Six adult Martial Eagles were trapped between late July and early August 2013, and a further two individuals were trapped in March 2016 using a bal-chatri (Burger and Shaffer, 2008) containing small chickens (*Gallus gallus domesticus*). All were fitted with 70 g GPS satellite tags (PTT 100, Microwave Telemetry, Columbia, Maryland, U.S.A.). The trapping method used is an internationally recognised and ethical procedure (Bridge et al., 2011) carried out under relevant permits and licenses from local authorities: The research was approved by South African National Parks Animal Use and Care Committee (Reference No. 13-5); University of Cape Town Science Faculty Animal Ethics Committee (Approval number: 2013/V7/AA); Department of Environmental Affairs and Tourism: Threatened or Protected Species (ToPS) (Permit number WM 1297/2013). GPS units were fitted using a backpack-mounted harness made from 0.55" Teflon® Ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A). We selected adult eagles (> 6 years old) for capture when they were found perched along tourist roads in KNP during daily fieldwork. Adults are easily classified as such from plumage as they are distinct from immatures or juveniles. Birds were sexed based on mass, which in cases involving breeding birds was verified from behaviour at the nest. In addition to a GPS tag, birds were fitted with alphanumerically unique 26 mm stainless steel rings (SAFRING authority card 12956). GPS tags recorded hourly positions, accurate to ±18 m (http://microwavetelemetry.com). These fixes were obtained between 5:00 and 17:00 during winter months (starting 21 April) and between 5:00 and 18:00 during summer months (starting 03 September). Tracking data were inspected on a regular basis and we tried to recover tags that indicated that they were no longer moving. When an eagle carcass was recovered we attempted to deduce the cause of mortality.

We calculated annual mortality rates following methods in Chapter 2. Therefore we divided the number of mortalities (d) during the study by the sum of each birds total months (m) tracked during the study. This was multiplied by 12 to get an annual mortality rate, and then again by 100 to convert a proportion into a percentage (mortality rate = d/m * 12 * 100). This is similar to the method used to calculate survival rates in Bearded Vultures (Coelho et al., 2007, Cooke et al., 2004, Tomkiewicz et al., 2010).

Ranging behaviour and home range estimation

Although Martial Eagles are typically thought to hold territories from adulthood (Cagnacci et al., 2010), it is unknown if a section of the adult population range more widely as floaters. Therefore we first defined the movement strategy for each individual using net squared displacement (NSD) and a latent state model using the 'lsmnsd' package (Cagnacci et al., 2010, Schofield et al., 2007) in R (Bridge et al., 2011, Krüger et al., 2014, Murgatroyd et al., 2016a, Wilson et al., 2008).

The latent state component defines movements based on discrete characteristics such as turn angle and step length between successive locations (Coelho et al., 2007, Cooke et al., 2004, Tomkiewicz et al., 2010).

NSD measures the squared distance between each location and the first location, and when plotted over time provides insight into specific movement strategies. The shape of a modelled curve fit to the data can reveal patterns Reid et al. (2015) e.g. migration (cyclic departure and return to and from the same geographic space, represented by a double-sigmoid), dispersal (departure from one geographic space to another, represented by a sigmoid), nomadism (represented by a linear curve; in raptor biology nomadic movements can be characteristic of population floaters (Cagnacci et al., 2010, Morales et al., 2010)), and resident (represented by an asymptotic curve). We visually inspected the NSD plots and compared them to those in (Birdlife International, 2013) to ensure correct classification by the latent state model.

To investigate ranging behaviour and calculate home range sizes we used the adehabitatHR package in R to estimate Minimum Convex Polygons (MCP) and Kernel Density Estimates (KDE) of the species Utilization Distribution (UD) (Underhill, 2012). UDs are the most common method used to visualize and calculate home ranges Cloete (2013), and more generally express the traditional concept of a home range (Boshoff, 1997). UDs were calculated using the h_{ref} method (grid = 100 m, or if the grid size was too small to allow estimation the grid size was increased by 50 m increments until the estimation was made). We calculated 95, 75 and 50 % utilization distributions to map the areas used for all individuals in QGIS (Quantum GIS Development Team, 2015). Furthermore we estimated a 100 % MCP which encloses all GPS fixes in the smallest possible convex polygon and as such includes fixes that may be atypical to an individual's predominant home range. MCPs have been used historically for radio tracking studies on Martial Eagles (Amar et al., 2015, Cloete, 2013) and we therefore calculated these to enable comparisons with these historical findings.

To explore whether home range sizes changed in relation to the different stages of breeding (non-breeding vs. breeding period, as determined by nest checks) we calculated monthly home range sizes. For individuals tracked for more than one year we calculated annual home range sizes using 95 % utilization distributions. For individuals that had more than one movement behaviour (e.g. territorial and floater – see Results), home range sizes were calculated separately for each behaviour.

Lastly we assessed individuals' movement step lengths (distance moved between hourly locations). We compared their movements among months to assess seasonal effects, the breeding period and non-breeding period, and different movement strategies (territorial and floater). This comparison was made using a generalised linear mixed model in R package lme4 (Tarboton and Allan, 1984).

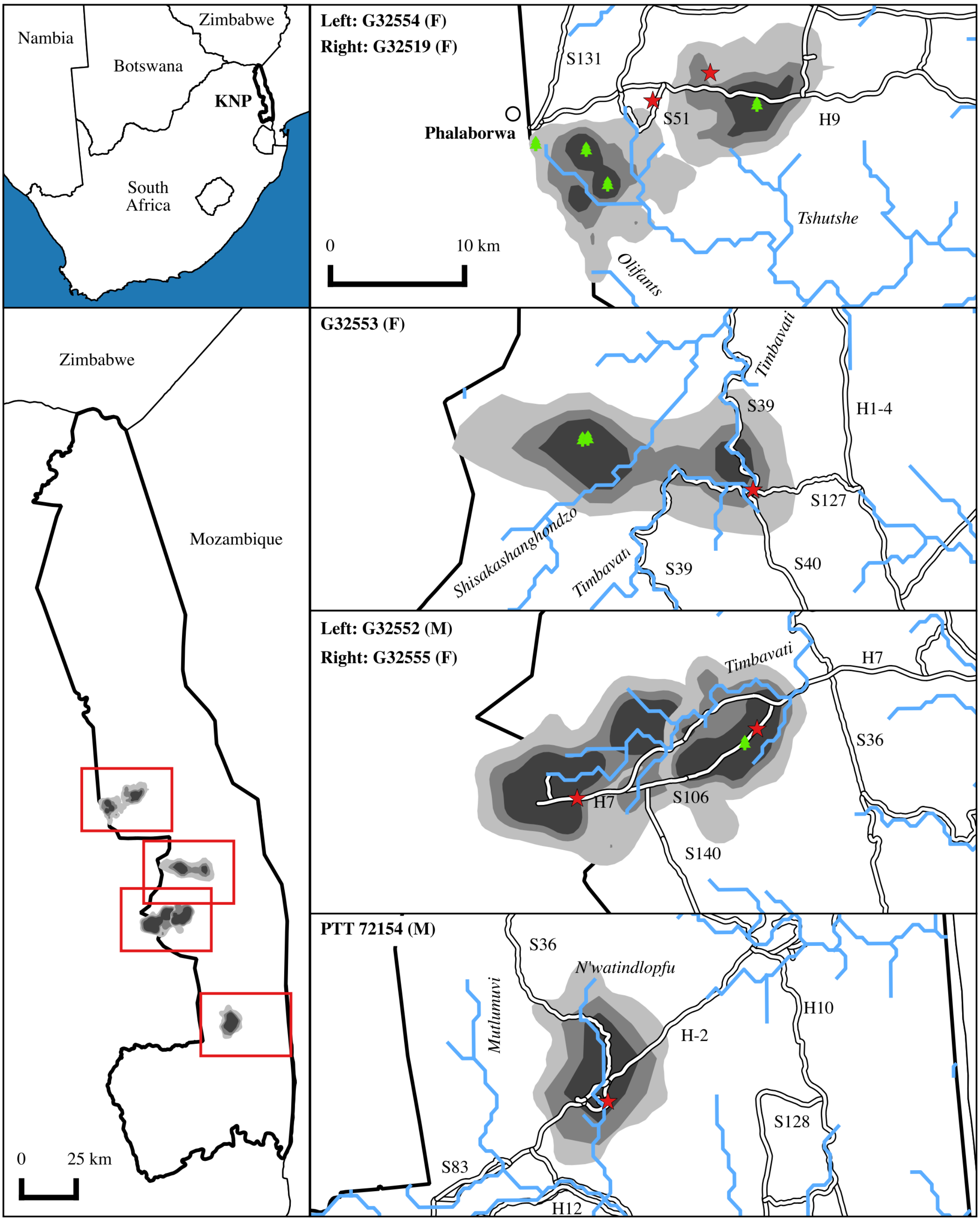

Figure 2.1. Home range estimators (50, 75, 95% Kernel Density Estimates) for six of eight adult Martial Eagles classed as territorial. Eagles were GPS tracked in KNP, South Africa (top left). Home ranges are shown in relation to KNP borders. Expanded plots of home ranges are shown (right) in relation to the KNP boundary (thick black line), main rivers (blue lines e.g. Timbavati), roads (thin parallel black lines e.g. S39, nest sites (green trees), and capture locations (red stars). Panels on the right showing home ranges are set to the same scale as given in the upper right panel.

Distance between points (step lengths) was the dependent variable, and individual ID was fitted as a random effect. To calculate step lengths we measured the straight-line distance between successive hourly GPS locations between 6:00 and 18:00. Where more than one hour elapsed between two GPS locations, the distance travelled between these hours was excluded so that only hourly movements were conserved for analysis (n = 35371/44594). We assessed models using AICc scores calculated during model comparison in the R package MuMIn (Anderson et al., 1999, Brown, 1991, Herholdt, 1998, Herholdt and Kemp, 1997, Van Rooyen and Ledger, 1999). If two or more candidate models were within 4 AICc, we then performed model averaging on these candidate models (Tarboton and Allan, 1984).

Habitat preference: environmental variables

We assessed habitat preference using a number of environmental variables (Figure S2.1). To describe topographic influences (elevation and slope) we used a 90-m digital elevation model (Newton, 1979). Tree cover preferences were investigated using a 30-m resolution continuous fields of tree cover map that describes the proportion of vegetation >5 m in height Taylor (2015). The importance of rivers was inferred using a 1:50 000 resolution HydroSHEDS river network layer Machange et al. (2005) that has global coverage. As roads are known to influence hydrology, tree height and species assemblages (Penteriani et al., 2011) we incorporated a roads layer into our environmental dataset. Lastly, we included a recent (2013/2014) 72-class South African National land cover dataset (Steyn, 1982) that categorizes South Africa into land classes at a 30 m resolution (S1 Table). Categories include vegetation type e.g. grassland, open bush, dense bush, and anthropogenic categories such as urban development.

Habitat preference: statistical analyses

Habitat preference of Martial Eagles was investigated by calculating the likelihood of occurrences of GPS tracking fixes and a set of randomly distributed points which fell within each individuals 95 % KDE to describe the use of the environmental variables described above (Mucina and Rutherford, 2006). Thus the presence/pseudo-absence of Martial Eagles was modelled as a function of the elevation, slope, % tree cover, and land cover class at each presence/pseudo-absence location, and the distance from each presence/pseudo-absence location to the nearest road, and river. In addition we included the distance to the edge of the 95 % KDE territory to account for territorial behaviour. The probability of occurrence in relation to these habitat variables was modelled using binomial generalised linear mixed-effects models. This is the same approach as used by (Gertenbach, 1983) to model habitat preference by Bearded Vultures fitted with identical tags programmed with the same duty cycle of hourly fixes. Data from the breeding period were excluded from this specific model and treated separately (see below) because breeding birds experience different constraints that can affect the interpretation of habitat preference models (Cullum and Rogers, 2011). Similarly, for birds that vacated their territories (n = 2), the data associated with their floater movements were excluded from the analyses, but the data associated with their territorial behaviours were retained.

We ran a separate model to describe the breeding period. Because only three individuals bred during the study, the breeding period habitat preference was modelled using a general linear model, and individual ID was fitted as a fixed effect. In this second model we fitted distance to the nest as an additional explanatory variable. The separation between breeding and non-breeding periods was made by examining nest centric behaviour; the onset and cessation of daily visits of the tagged bird to within 500 m of the nest described the start and end of each individuals' breeding season. A 100 m buffer was placed around nests to exclude data biased towards the nest e.g. during incubation.

Numerical variables were centred and standardised: $V_2 = \frac{(V_1 - \bar{x})}{s(V_1)}$, where V_1 is the unstandardised variable, $\bar{x}$ is the mean of V_1, and s is the standard deviation of V_1. For factor data (e.g. NLC), categories that contained less than 2 % of all data (e.g. "permanent water" which classifies water bodies such as lakes) were grouped and assigned into a category "other" (Table S2.1). The random points (pseudo-absences) were generated using QGIS (Quantum GIS Development Team, 2015). We generated three times the number of random points to real bird fixes for each bird (Bucini et al., 2010).

Model selection was based on the model with the lowest AICc using the MuMIn package in R to compare all possible model combinations. If models were within 4 AICc, we then model averaged the top model candidates within 4 AICc to get averaged fixed effects estimates and calculated the fixed effects confidence intervals (lower: 2.5%, upper: 97.5%) using MuMIn.

We assessed model fit using receiver operator curves (ROC) in R package ROCR (Brown et al., 1982). ROC assesses the predicted classification of absences and presences into their correct categories, and the area under curve (AUC) was thus used to determine model performance; values over 0.9 are typically associated with an accurate model and AUCs of 0.7–0.9 categorize models with moderate predictive power, and models with an AUC <0.7 are generally considered to have relatively poor predictive power (2005). We tested correlation between independent variables and used a correlation coefficient of 0.3 as a cut off for assessing relationships between variables.

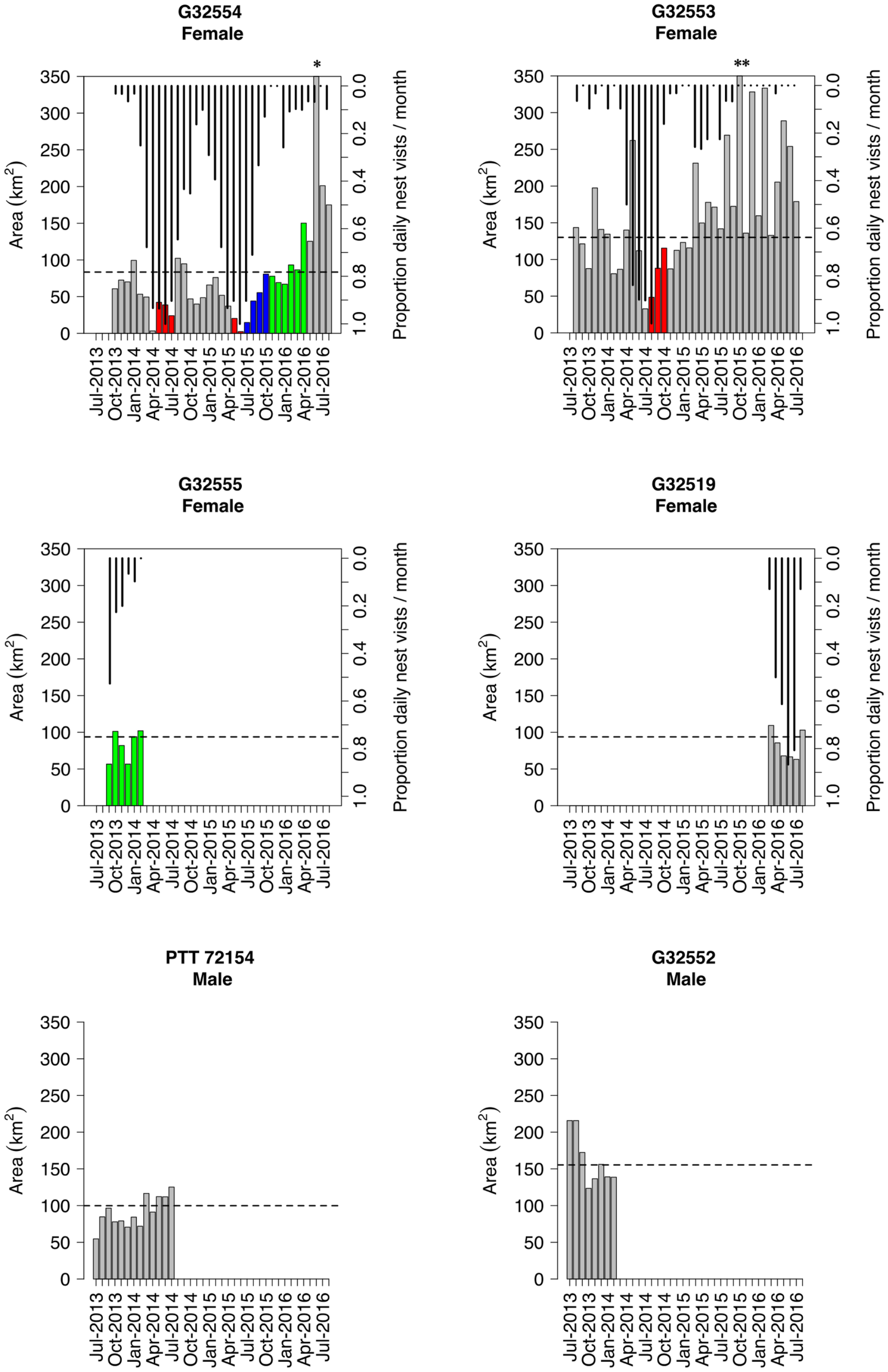

Figure 2.2. The 95 % kernel density estimate (KDE) home range size for each territorial individual by month. Missing bars indicate no data due to cessation of tag transmission. Coloured bars indicate months in which the individual bird was recorded to incubate (red), raise a fledgling (blue) or provision a fledged young in post fledging dependency (green). Horizontal dashed lines indicate the 95% KDE for the entire dataset of each individual. Vertical lines indicate the proportion of days per month that a nest site was visited by the individual. * 1493 km2; ** 2319 km2

RESULTS

Tracking data and mortality estimation

Individual Martial Eagles were tracked for a mean duration of 479 ± 374 days (range = 160 - 973 days; Table 3.1). We tracked six females and two males. Three female individuals (G32554, G32519, and G32553) were tracked through at least one breeding cycle (Figure 2.2). Another female (G32555) was tagged whilst she was still provisioning a fledged chick. The remaining two females (G32551 and G32516) and the two tracked males (PTT 72154 and G32552) did not have known nests, nor did their tracking data indicate an obvious nest location.

During the course of the study we confirmed mortalities four mortalities resulting in an annual mortality of 42.48 % (Table 3.1). Another individual (PTT72154) went offline near a power distribution line in Swaziland but because no carcass was recovered the definitive reason that the tag stopped transmitting is unknown. Of the four confirmed mortalities, one eagle (G32156) was found dead in a hunting snare in Mozambique, one eagle (G32551) was not recovered but its tag was found cut off in a local village in Mozambique. The bird was moving in a regular fashion before its last location in a field adjacent to the local village. The GPS locations of two individuals (G32555 and G32552) tagged in adjacent territories show that they made contact an hour before G32552 stopped moving. G32555 stopped moving 12 days later. Neither bird was recovered early enough to confirm wounds were inflicted during conspecific conflict but this is the most likely cause. Therefore, 50 % of confirmed mortalities were unnatural and occurred beyond KNP boundaries.

Table 3.1. Tracking data summary for adult Martial Eagles GPS tracked in KNP. The attributed causes of transmission cessation are shown where applicable; devices still transmitting at the time of publication are represented by NA.

Individual	Sex	Dates tracked	# Days	# GPS locations	Transmission cessation (cause)
G32554	F	09/10/2013 – 21/09/2016	1078	11758	NA
G32553	F	26/08/2013 – 22/09/2016	1123	14874	NA
G32551	F	01/08/2013 – 06/07/2014	339	4064	Yes (Hunted/persecuted)
G32555	F	12/09/2013 – 19/02/2014	160	2358	Yes (Conspecific conflict)
G32519	F	16/03/2016 – 22/09/2016	187	2673	NA
G32516	F	22/03/2016 – 20/05/2016	59	869	Yes (Hunted)
G32552	M	23/08/2013 – 07/02/2014	168	2532	Yes (Conspecific conflict)
PTT72154	M	30/07/2013 – 20/08/2014	386	5466	Yes (Unknown, possible electrocution)

Home ranges

Six individuals were classed as territory holders and remained in spatially confined regions or home ranges for most of their time (Figure 2.1 and S2.2). The 95 % kernel density estimated home range size for these individuals averaged 108.42 ± 29.51 km^2 (Table 2.2). Home range sizes for two individuals tracked over multiple years differed among years with an increasing home range size trend from 2013 to 2016 (G32554: 2013 = 69.12 km^2, 2014 = 71.69 km^2, 2015 = 74.7 km^2, 2016 = 107.33 km^2; G32553: 2013 = 137.87 km^2, 2014 = 110.86 km^2, 2015 = 281.84 km^2, 2016 = 204.96 km^2).

Another two females (G32551 and G32516) did not remain on a territory and were classed as floaters; these individuals ranged widely, covering a 95 % KDE area of 44,194.93 ± 1615.73 km^2 before they were both killed in Mozambique (Figure 2.2; Table 2.2). Although our sample size (n = 2) was too small for any formal comparison, visual inspection of monthly home range sizes indicated that female home ranges became smaller prior to and during incubation. Monthly home ranges increased again during the nestling period (Figure 2.2). It was not possible to formerly compare home range sizes between the sexes but average home ranges of males were slightly larger than females (95 % KDE; males: 128.86 ± 41.06 km^2, females: 98.21 ± 21.71 km^2). 100 % MCPs were many times larger than 95 % KDEs (Table 2.2). MCPs enclosed temporary movements beyond their normal range that were excluded by 95% KDEs (Figure S2.3).

Table 2.2. Home range estimations (Minimum Convex Polygon: MCP and Kernel Density Estimators: KDE) for each adult Martial Eagle tracked in the KNP showing the extent of areas used (km^2) under different GPS location densities (50 – 95%).

Individual	Sex	MCP 100 %	KDE 95 %	KDE 75 %	KDE 50 %
Territorial					
G32554	F	489.55	83.49	31.47	11.56
G32553	F	4 279.37	185.12	80.48	37.56
G32555	F	316.91	93.78	49.21	26.00
G32519	F	415.31	85.47	37.13	14.01
G32552	M	174.40	157.90	86.39	45.48
PTT72154	M	155.40	99.83	50.89	24.35
Floater					
G32551	F	46 860.2	43 052.44	19 812.69	8 781.842
G32516	F	23 368.65	45 337.43	19 012.47	7 103.56
G32553	F	22 943.05	10 830.8	2 503.894	1 048.142
PTT72154	M	713.3828	-	-	-

Eagle G32553 left its territory after 1087 days of tracking and moved north into Zimbabwe; the eagle did not return before the end of this study. In the previous 2 years she had been unsuccessful in rearing any young and failed on incubation during the first year (Figure 2.3). Eagle PTT 72154 left its territory and made a long ranged movement into Swaziland where its tag stopped transmitting under a power distribution line shortly afterwards but the tag was not recovered despite efforts.

Hourly step lengths in Martial Eagles were generally small; ca. 57 % of hourly movements were less than 200 m apart (Figure 2.4). Step lengths were smaller in the breeding-period compared to the non-breeding period and tended to increase in winter months compared to the summer months (Table S2.2; Figure 2.4). There were no clear differences between the step lengths of territorial birds or floaters.

Habitat preference

Habitat preference by territorial adults during the non-breeding period was associated with all seven environmental variables, with the top model incorporating all terms (Table S2.4). However the next best model (which excluded distance to roads) was within 4 AICc and therefore we model averaged the top two models. The average model indicated that habitat preference was associated with higher percentage tree cover, areas farther from main rivers, higher elevations, steeper slopes, and areas farther from the territory edge (Table 2.3, Figure 2.5). Because the confidence intervals for the distance to roads variable overlapped zero, we cannot attribute this variable to having any influence over the species habitat preference. Additionally, dense bush areas tended to be selected over areas comprising of open bush, grassland, or other habitat types (Table 2.3, Figure 2.5).

During the breeding period, habitat preferences were similar to the non-breeding period, and again the top two models were averaged because they were within 4 AICc from the top model. However, during the breeding period, bird's showed preference for lower elevations within their breeding home ranges. Furthermore, as expected, birds tended to be found closer to their nests.

The non-breeding period model with the lowest AIC had an AUC = 0.73, and the breeding period model had an AUC = 0.89, suggesting these models had relatively good predictive power i.e. the models' ability to discern between presence and pseudo-absence locations was relatively strong.

DISCUSSION

Mortality estimation

Annual mortality rates recorded during this study were far higher than the expected mortality rates for large, low-density eagles with delayed breeding and low fecundity. Mortality rates in species such as Golden Eagles typically range between 10 – 3 % per annum (Taylor, 2015), even when high unnatural mortalities are factored in (Steyn, 1982).

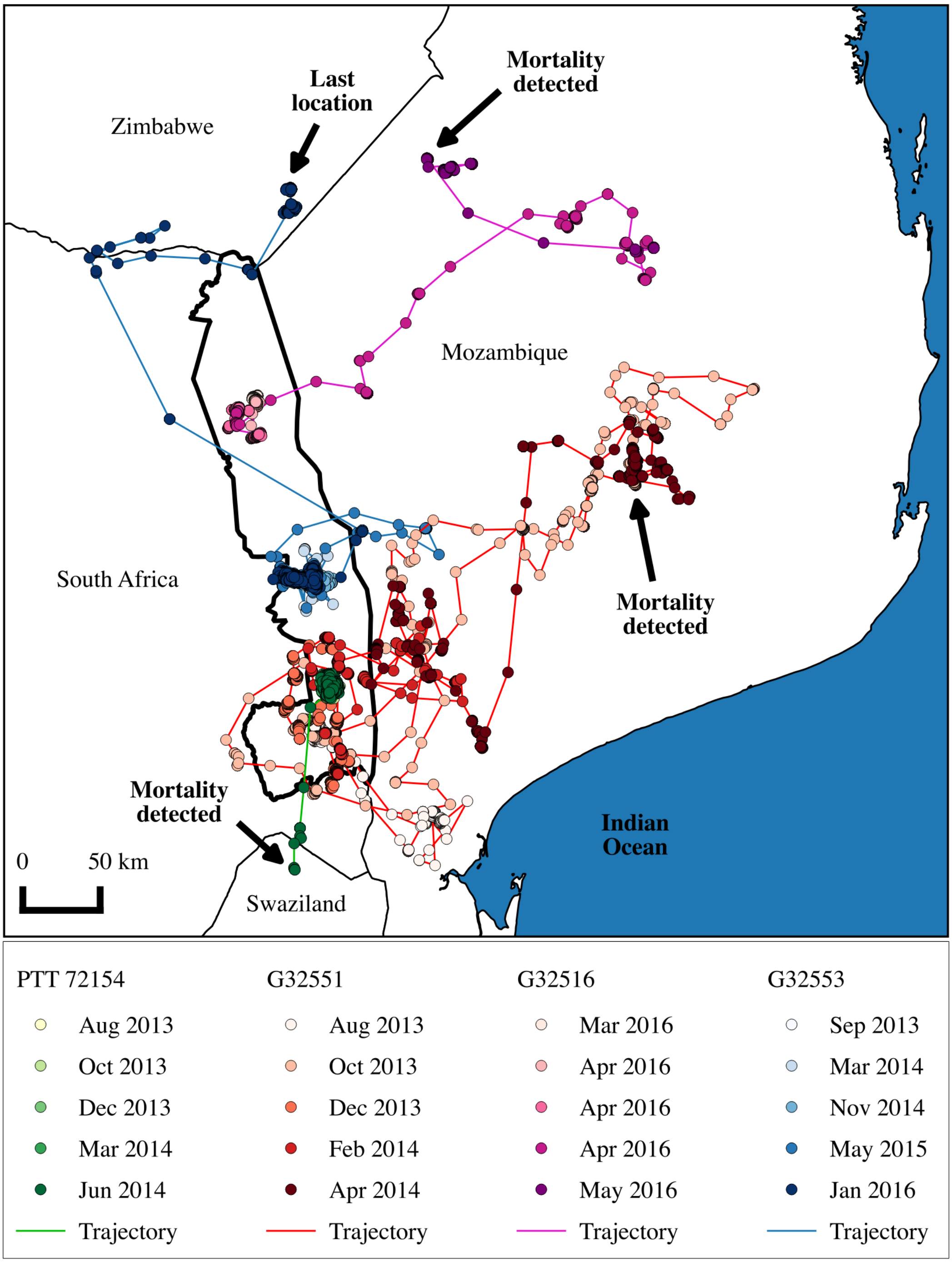

Figure 2.3. Movements of floater adult Martial Eagles (G32551 and G32516), and those that were territorial but vacated their territories (PTT 72154 and G32553) from KNP, showing the area covered during tracking. GPS locations are coloured by month to visualize movements through time (see bottom legend). The location of each bird's death, or last known location, is indicated.

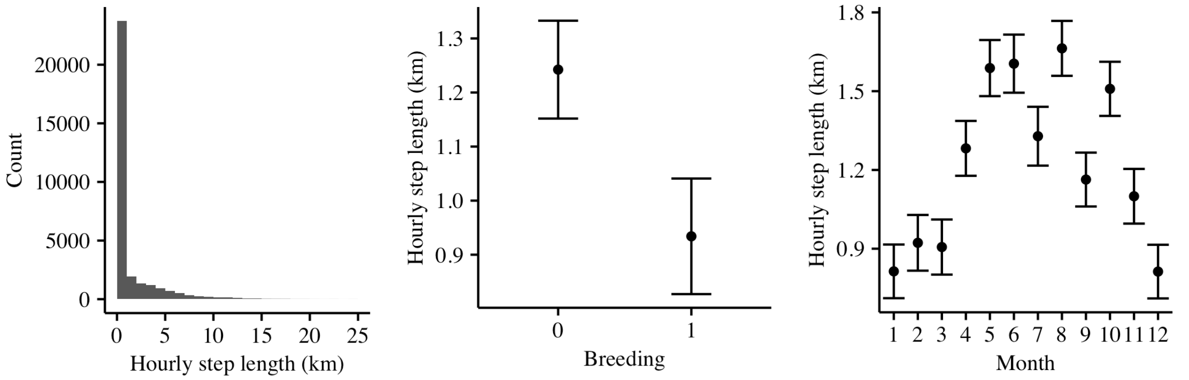

Figure 2.4. Frequency of step lengths in 200m intervals (left), and fixed effects plots from a generalised linear mixed model investigating step lengths between the breeding and non-breeding period (centre) and between months to assess seasonality (right).

Table 2.3. GLMM results showing the model averaged fixed effects (scaled) estimates used to predict the occurrence of Martial Eagles during the non-breeding period and the results from the general linear model investigating breeding period habitat preference. The models included, tree cover, elevation, topographic slope, distance to the nearest river, distance to the nearest road, distance to the territory edge, and four National Land Cover classes shown relative to class ‘other’ which described all categorizes that had less than 2 % of the total data. Estimates are ranked from high to low. The breeding period model included distance to the nest.

Model: Non-breeding period

Variable	Estimate	Std. Error	CI (2.5 %)	CI (97.5 %)	z value	Pr(>|z|)
Intercept	-1.37	0.12	-1.61	-1.12	11.02	< 0.001
Distance to territory edge	0.87	0.01	0.85	0.88	104.47	< 0.001
Land cover: Dense bush	0.57	0.07	0.43	0.71	7.97	< 0.001
Land cover: Grassland	-0.55	0.07	-0.69	-0.40	7.40	< 0.001
Elevation	0.18	0.02	0.14	0.21	9.49	< 0.001
Distance to river	0.06	0.01	0.03	0.08	4.52	< 0.001
Slope	0.05	0.01	0.04	0.07	7.43	< 0.001
Land cover: Open bush	0.05	0.07	-0.09	0.19	0.74	0.46
Tree cover	0.03	0.01	0.02	0.05	4.33	< 0.001
Distance to road	0.01	0.01	0.00	0.03	0.82	0.41

Model: Breeding period

Variable	Estimate	Std. Error	CI (2.5 %)	CI (97.5 %)	z value	Pr(>|z|)
(Intercept)	-3.01	0.44	-3.88	-2.14	6.78	< 0.001
Land cover: Dense bush	2.79	0.50	1.81	3.76	5.58	< 0.001
Land cover: Open bush	2.63	0.50	1.65	3.61	5.28	< 0.001
Land cover: Grassland	2.20	0.50	1.22	3.19	4.40	< 0.001
Distance to territory edge	2.10	0.04	2.02	2.19	47.71	< 0.001
ID: G32554	-1.98	0.10	-2.19	-1.78	18.92	< 0.001
Elevation	-1.05	0.14	-1.33	-0.77	7.37	< 0.001
ID: G32553	-0.85	0.10	-1.04	-0.65	8.47	< 0.001
Distance to nest	-0.43	0.04	-0.50	-0.35	10.89	< 0.001
Distance to river	0.40	0.04	0.32	0.48	9.47	< 0.001
Distance to road	0.29	0.03	0.23	0.34	10.14	< 0.001
Tree cover	0.08	0.03	0.02	0.13	2.77	< 0.001
Slope	0.01	0.02	-0.03	0.08	0.46	0.64

Individual G32516 was found caught in a hunting snare and only G32551's tag was recovered from a hunting outpost and the harness was clearly cut off. In this study two individuals for whom we recorded possible conspecific conflict both died from their encounter (Table 2.1). Anecdotal reports of Martial Eagles in conflict with conspecifics and other raptor species suggest that these behaviours are not rare and it should be tested how common these behaviours are (Ong, 2000, Steyn, 1982, Tarboton and Allan, 1984).

Home ranges

Using GPS tracking data we were able to describe the home range size of adult Martial Eagles. Our tracking data suggested adults held home ranges of ca. 108 km^2. The home ranges we observed were similar in size to those of other large eagles such as Golden Eagles (Steyn, 1982) but much larger than African species such as Crowned Eagles (*Stephanoaetus coronatus*) or Verreaux's Eagle (*Aquila verreauxii*) (Taylor, 2015). Based on a simple circular area, our home range sizes would represent territories of ca. 6 km radius. Although our study represents the first home range estimation of this species from GPS tracking data, the results compare well with previous home range estimates based on inter-nest distances for this species (Boshoff, 1997, Brown et al., 1982, Machange et al., 2005, 2005, Taylor, 2015) as well as estimates from VHF radio-tagged birds (Taylor, 2015). For example, (Berger and Mueller, 1959) found inter-nest distances in the local region (KNP and Transvaal Province) of ca. 12 km (radius = 6 km). The species inter-nest distance varies considerably in different landscapes with larger inter-nest distances (ca. 19 km) in the drier regions of the Nama-Karoo and Namibia (Bloom et al., 2007). Previous home range estimates for the species using radio tags on four individuals estimated that Martial Eagles in Kenya (Gypaetus barbatus; Krüger, 2014) had home ranges described by MCPs averaging 120 km^2 (sd: 59 km^2, range: 74 – 205 km^2), with male home ranges larger than females within pairs. These home range sizes compare well with our KDE home range sizes, but poorly with our MCP home ranges.

Our MCP estimates were often many times larger than our KDE estimates due to occasional movements far beyond the typical home range identified from our GPS fixes (Figure S2.3). These types of large infrequent movements would unlikely be detected by conventional VHF radio tracking used in other studies highlights the discrepancy in accuracies between these two methods (Penteriani et al., 2011).

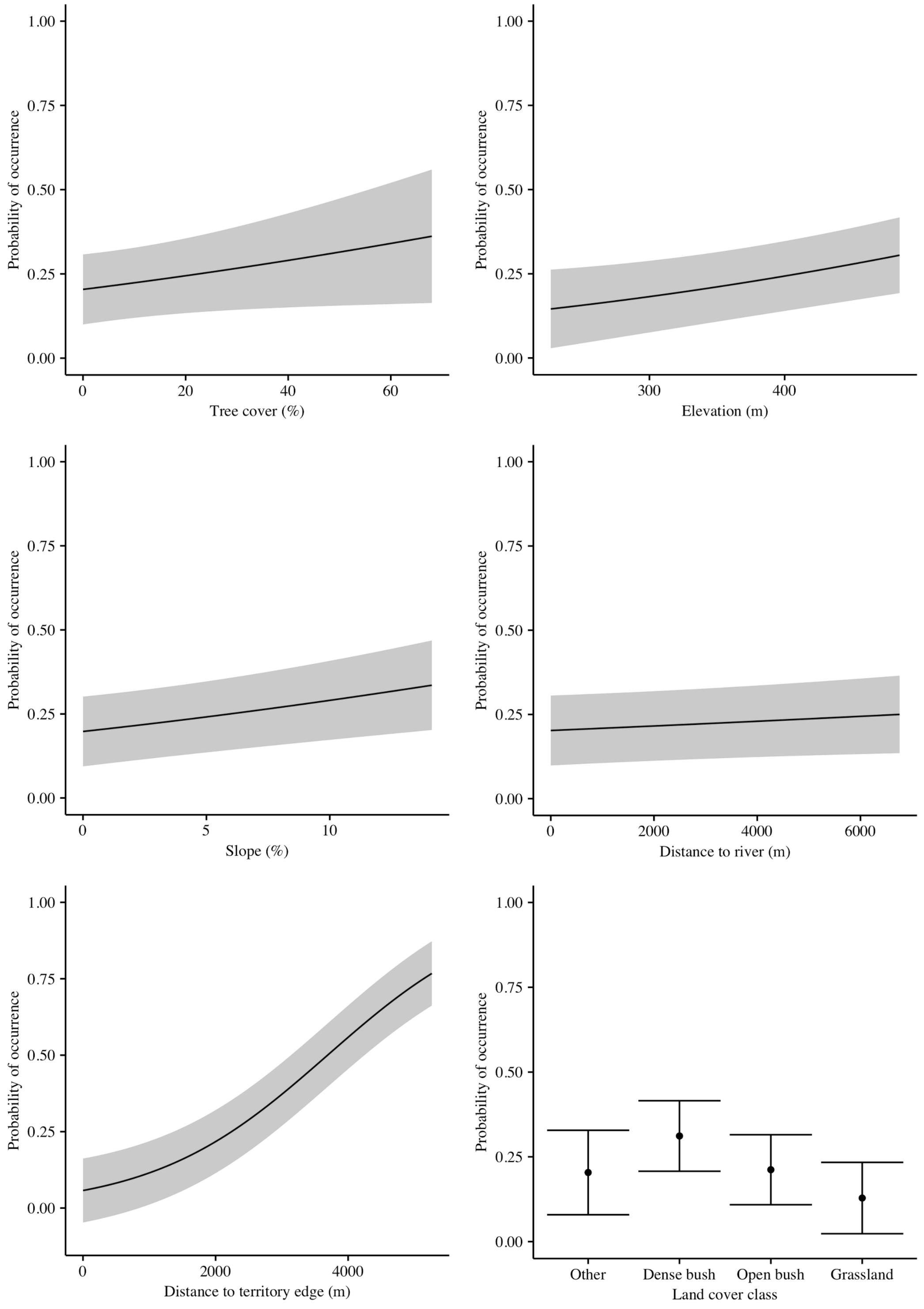

Figure 2.5. Generalized linear mixed model (GLMM) predictive fixed-effects plots showing the modelled habitat preference of territorial Martial Eagles tracked after their capture in KNP according to several habitat features: tree cover, elevation, topographic slope, distance to nearest river, distance to nearest road, and land cover. Solid lines show the predicted relationships, with 95 % CL captured within grey shaded areas. The bottom right panel shows the predicted probability for the categorical factor, land cover, with 95 % CL represented by vertical lines.

Extra territory movements are known to occur in other raptor species and may be linked to extra pair copulations (Steyn, 1982) or explorations of neighbouring territories or food patches (Bastille-Rousseau et al., 2016). In one of these long-range movements a male individual travelling into Swaziland stopped transmitting shortly afterwards (Figure 2.3).

Although any conclusions were severely limited by our sample size of only four breeding female birds, home range estimates were lowest during and before incubation and the early brood-rearing phase. Birds tended to make shorter trips during the breeding period. Such a finding is hardly surprising given that females of most eagle species undertake the most of the incubation and stay at the nest to care for young nestlings (R Core Team, 2015), and will therefore spend more of their time in close proximity to their nests during the early stages of the breeding cycle (Bastille-Rousseau et al., 2016). After the nestling was older than 4 weeks, the females' home range sizes increase presumably as they spent less time brooding and more time away from the nest, this also coincided with a decrease in nest visits per month. Nest visits by our tagged birds dropped sharply after 12 weeks, supporting observations by (Bastille-Rousseau et al., 2016, Bunnefeld et al., 2011). Similar patterns in reduction of home range size during the breeding season have been observed in Golden Eagles (Bastille-Rousseau et al., 2016). These results therefore emphasize the importance of studying ranging behaviour through a full breeding cycle to gain a more complete understanding of behaviour (Wheat et al., 2017). Furthermore, step lengths tended to increase during the dry winter months. It should be tested what factors are driving these behaviours, for instance when prey is scarce birds may need to traverse more of their territory to hunt (Bastille-Rousseau et al., 2016).

Two individuals were floaters, both ranging into Mozambique where they died due to anthropogenic causes. These wide ranging behaviours were not expected for adult Marital Eagles given that a floater population has not been identified previously in the region. It was assumed that adults likely held territories for most of their breeding lives Bunnefeld et al. (2011). Although our sample size is small, these behaviours appear to increase the risk of mortality, given that both the floater individuals died in areas adjacent to KNP. Increasing our sample size of tracked adults would be useful to determine how common these kinds of behaviours are amongst adults of this species. Understanding the survival and movements of this sector of the population will likely improve our ability to understand the current population declines (Calenge, 2006). The movements into neighbouring countries and the detected mortalities in these regions highlights the importance of trans-boundary conservation efforts (Laver and Kelly, 2008, Worton, 1989).

The presence of adult floaters in a declining population is surprising because population equilibrium theory dictates these individuals should mostly be present in a saturated breeding population where new territories are unavailable; otherwise these individuals should be expected to take up vacant territories (Burt, 1943). We did not detect any ousting of individuals, as regular nest checks did not detect breeding in these territories after individuals emigrated from their territories. Thus, in this declining population, the abandonment of territories and a possible increase in the floater population may signal underlying environmental limitations to breeding such as shortages of prey, mate loss, low reproductive success, or limited appropriate breeding habitat in the KNP (Ong, 2000). These possible explanations will require robust testing, for instance by comparing home range sizes and nomadism between high and low rainfall years.

Floaters may reject settling in unsuitable vacant territories as the costs of holding a territory may outweigh the expected lifetime reproductive rate; joining the floater population could improve overall individual fitness (Bates et al., 2014, R Core Team, 2015). However, an addition of floaters to the population may further affect the breeding population through disruption via competition for more suitable territories being held by breeders thus adding an additional stress to those individuals that choose to remain in a territory and attempt to breed (Bartoń, 2015), or through competition for mates (Bartoń, 2015). In a declining population, it could be expected that these behaviours may increase as a function of reduced mate availability.

Habitat preference

The habitat preferences of Martial Eagles found in this study indicates that the species typically preferred areas with greater tree cover, dense bush over open bushveld or grassland, away from the territory edge, areas with increased elevation, steeper slopes, and away from rivers and roads.

The reliance on tree cover and dense bushveld areas is concerning as tree cover in KNP has undergone substantial change over the last half century, with some areas reducing in woody cover by up to ca. 64 % (USGS, 2008). These declines have been attributed largely to interactions between increasing elephant densities and frequent fires driven by historical management decisions (Sexton et al., 2013). Elephants (*Loxodonta africana*) tend to impact maturing trees in the 5 - 9 m height range and tree fall rates in areas accessible to elephants may be up to six times higher (Lehner et al., 2006). Increases in elephant numbers may have decreased the quality of habitat or reduced nest tree availability for Martial Eagles in KNP. This finding is supported by a previous analysis (Smit and Asner, 2012), which found that declines of Martial Eagles within KNP were highest in areas with highest elephant densities. This issue therefore clearly merits further research.

Martial Eagles avoided their territory edge and this is likely to avoid conspecific conflict. Some raptors are highly territorial and display little territory overlap with their neighbours (GeoTerra Image (GTI) Pty Ltd). Martial Eagles preferred areas with higher elevation and steep slopes, and these areas may provide vantage points for intruder detection and greater visibility of prey. However it is more likely that these features may aid in flight for instance by providing orographic lift (Aarts et al., 2008). Distance to the territory edge greatly improved the ability of the model to discern between pseudo-absence and presence locations (without this variable the AUC decreases by 13 % points – not reported). Unfortunately this variable is not readily available to others, thus reducing the generality of the model for others to predict Martial Eagle occurrence.

Avoidance of rivers was interesting as models of juvenile habitat preference indicate that Martial Eagles are more likely to be found closer to rivers. It is likely that the large rivers used in the analyses were less accessible to adults as they are constrained by their territory. Finer river layers e.g. Reid et al. (2015) could show that adults also prefer areas closer to riverine habitat, however these finer scale layers are constrained to the extent of KNP.

Conclusions

The conservation of Martial Eagles will likely be challenging given their large ranging behaviour both when holding territories, but also when present as floaters in the population. Efforts to mitigate habitat loss e.g. tall tree loss and dense shrubland, and improving trans boundary conservation efforts e.g. mitigating wildlife conflict will be important factors in the species conservation plans. Future research should investigate seasonal affects on ranging behaviour and determine how common nomadic behaviour is in this population. Studies should focus on how nomadism can affect the population dynamics and whether nomads are at increased risk of mortality beyond protected area boundaries.

ACKNOWLEDGMENTS

We thank the South African National Parks (SANParks) Management, Rangers, Veterinary Wildlife Services, and Scientific Services for supporting this research; in particular Sharon Thompson (Scientific Services). We are grateful for the many field assistants who assisted with captures and attempts, notably Shane McPherson and Megan Murgatroyd who provided valuable mentorship and advise in capture techniques and harnessing. Gareth Tate and John Davies for assistance with captures and tag recoveries. Timothy Reid and Petra Sumasgutner provided statistical advice.

SUPPLEMENTARY MATERIAL – CHAPTER 2

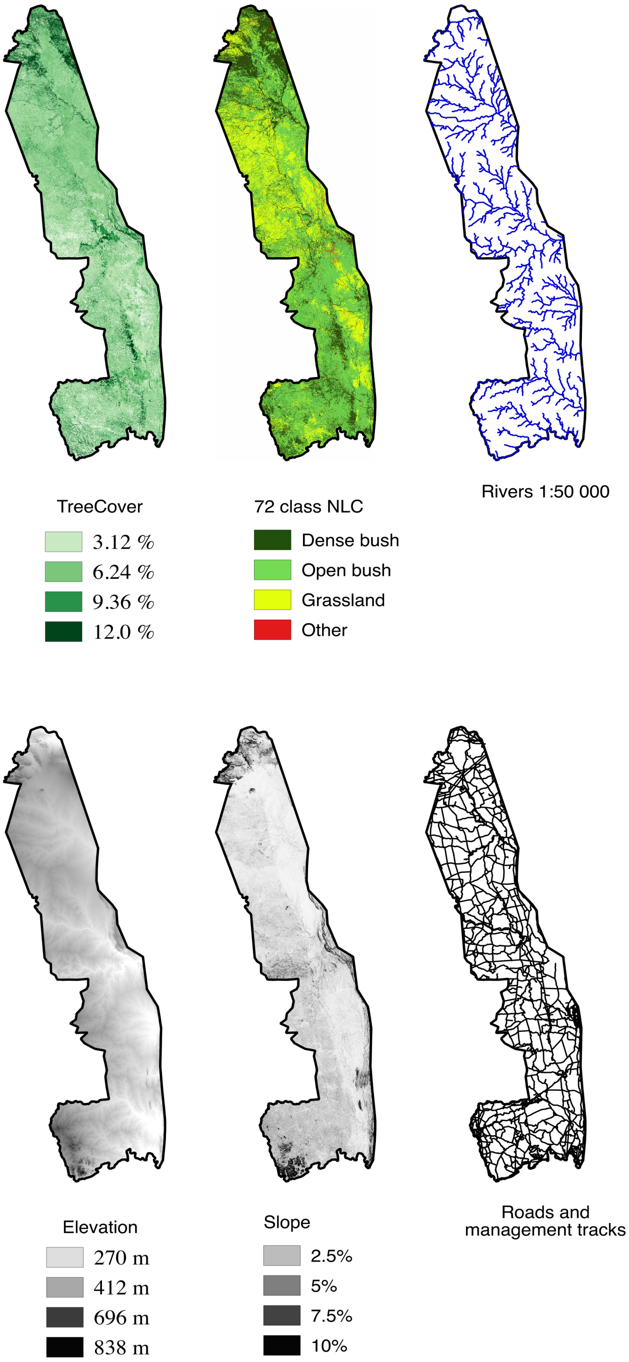

Figure S2.1. Mapping of data used in modeling Martial Eagle habitat preference showing the hetrogeneity of the landscape in KNP. Tree cover was sourced from (Beyer et al., 2010), a 72-class National Land Cover (72-class NLC, from http://bgis.sanbi.org) was used to understand the preferred landscape types. A 1:50 000 river map was used to inform river importance (Wakefield et al., 2011). A 90 m Digital Elevation Model (Sing, 2005) and the derived slope were uses to understand topographic influences. Roads and management tracks were provided by SANParks GIS Services and used to understand road effects.

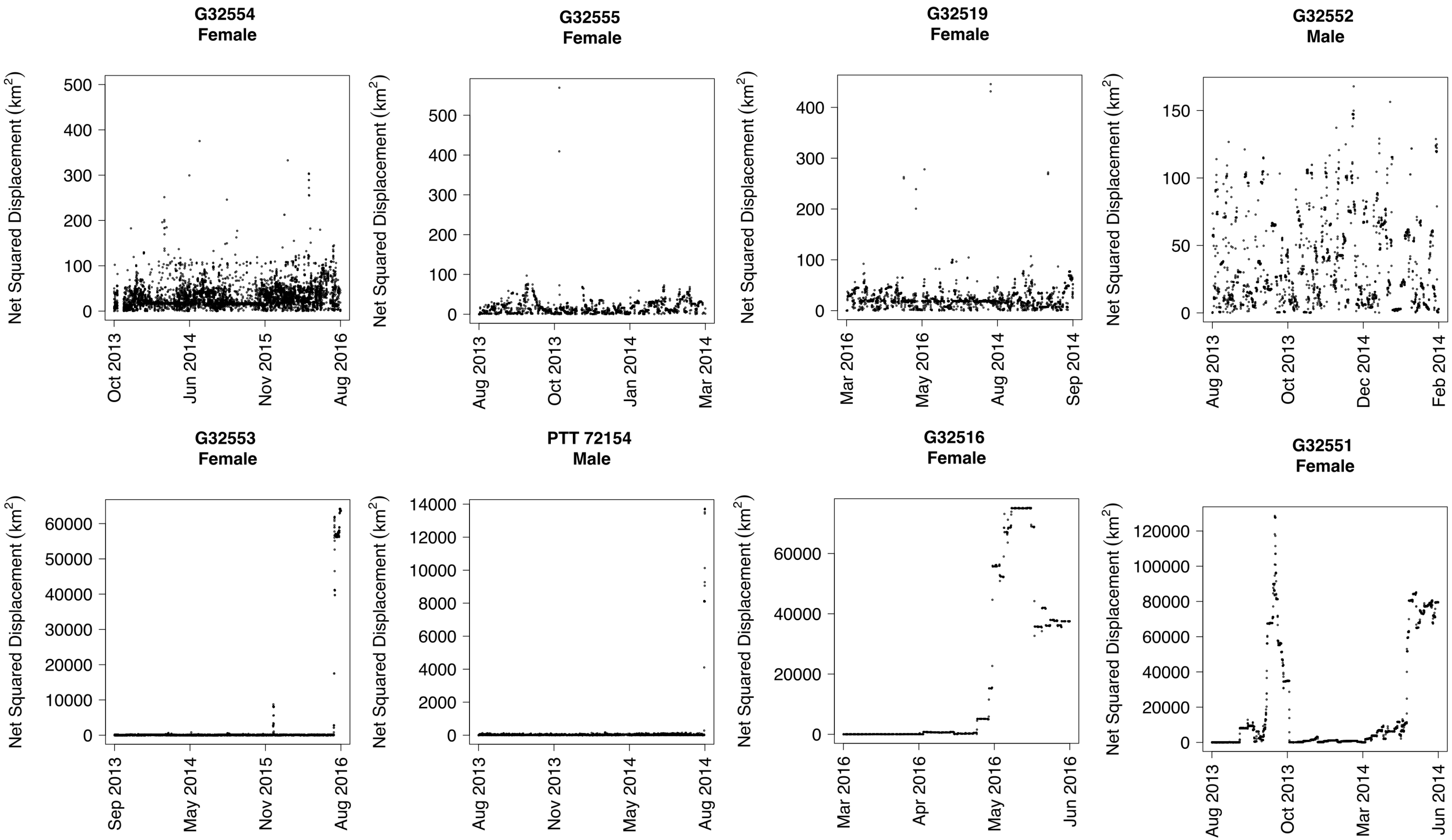

Figure S2.2. Net Squared Displacement (square distance between each point and the first location, plotted over time) of Martial Eagles tracked from KNP showing five individuals that remained in spatially confined areas and one individual (72150) that roamed widely. Plots are not to the same scale due to the large variation among individuals' movements through time.

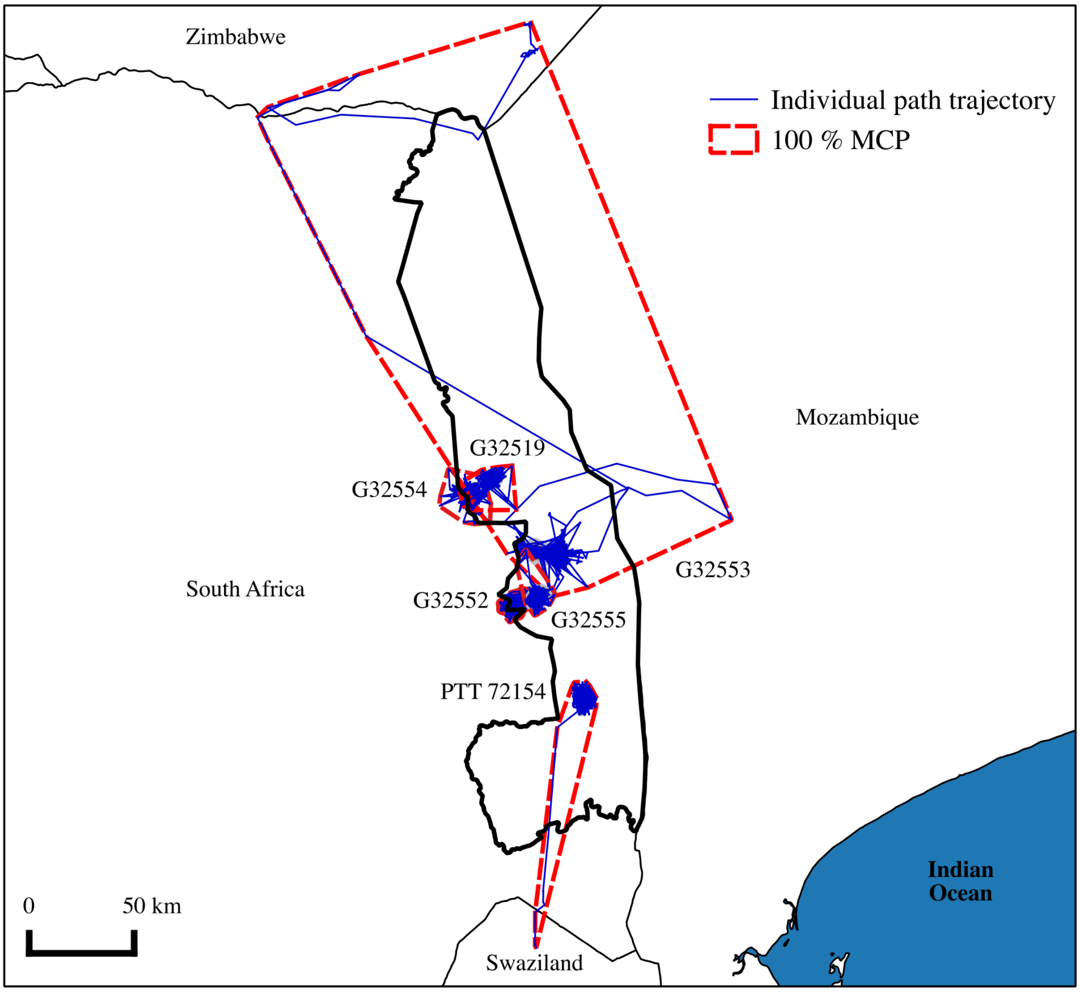

Figure S2.3. Minimum Convex Polygon (dashed red lines) enclosing all (100 %) tracking locations of Martial Eagles that held stable home ranges and the movement path (blue lines) along those locations showing movements over the course of each individuals tracking period.

Table S2.1. A 72-class National Land Cover map (SANBI) was used to inform habitat preferences of Martial Eagles. Categories that contained < 2% of absence and presence points were collapsed into a class "other".

Class	Description	Presence points	Absence points
36	Mines – semi-bare	1	12
53	Urban smallholding (dense trees / bush)	1	
58	Urban sports and golf (open trees / bush)	1	47
69	Urban built-up (dense trees / bush)	2	17
72	Urban built-up (bare)	2	2
57	Urban sports and golf (dense trees / bush)	3	120
48	Urban residential (dense trees / bush)	4	
70	Urban built-up (open trees / bush)	5	9
40	Erosion	11	40
35	Mines – bare	13	237
41	Bare / non vegetated	15	87
2	Water permanent	18	69
9	Low shrubland	154	290
7	Grassland	1826	9017
5	Thicket /dense bush	6319	11775
6	Woodland /open bush	15329	49376
1	Water seasonal		3
3	Wetlands		
4	Indigenous forest		
8	Shrubland fynbos		
10	Cultivated commercial fields (high)		
11	Cultivated commercial fields (med)		
12	Cultivated commercial fields (low)		
13	Cultivated commercial pivots (high)		
14	Cultivated commercial pivots (med)		
15	Cultivated commercial pivots (low)		
16	Cultivated orchards (high)		
17	Cultivated orchards (med)		
18	Cultivated orchards (low)		
19	Cultivated vines (high)		
20	Cultivated vines (med)		
21	Cultivated vines (low)		
22	Cultivated permanent pineapple		
23	Cultivated subsistence (high)		
24	Cultivated subsistence (med)		
25	Cultivated subsistence (low)		
26	Cultivated cane pivot - crop		
27	Cultivated cane pivot - fallow		
28	Cultivated cane commercial - crop		
29	Cultivated cane commercial - fallow		
30	Cultivated cane emerging - crop		
31	Cultivated cane emerging - fallow		
32	Plantations / woodlots mature		
33	Plantations / woodlots young		
34	Plantations / woodlots clear-felled		
37	Mines - water seasonal		2
38	Mines – water permanent		2
39	Mine buildings		
42	Urban commercial		
43	Urban industrial		
44	Urban informal (dense trees / bush)		
45	Urban informal (open trees / bush)		
46	Urban informal (low veg / grass)		
47	Urban informal (bare)		

Class	Description	Presence points	Absence points
49	Urban residential (open trees / bush)		
50	Urban residential (low veg / grass)		
51	Urban residential (bare)		
52	Urban school and sports		
54	Urban smallholding (open trees / bush)		
55	Urban smallholding (low veg / grass)		
56	Urban smallholding (bare)		
59	Urban sports and golf (low veg / grass)		5
60	Urban sports and golf (bare)		1
61	Urban township (dense trees / bush)		
62	Urban township (open trees / bush)		
63	Urban township (low veg / grass)		
64	Urban township (bare)		
65	Urban village (dense trees / bush)		
66	Urban village (open trees / bush)		
67	Urban village (low veg / grass)		
68	Urban village (bare)		
71	Urban built-up (low veg / grass)		

Table S2.2. Generalised linear mixed model showing how Martial Eagle hourly step lengths are affected by breeding status (breeding vs. non-breeding period), month of the year, and territorial behaviour.

Variable	Estimate	Std. Error	CI 2.5 %	CI 97.5 %	z value	Pr(>|z|)
(Intercept)	0.89	0.13	0.64	1.14	7	< 0.001
Breeding: Yes	-0.31	0.07	-0.44	-0.18	4.78	< 0.001
Month: 2	0.11	0.08	-0.04	0.26	1.44	0.15
Month: 3	0.09	0.07	-0.05	0.24	1.26	0.21
Month: 4	0.47	0.08	0.32	0.62	6.19	< 0.001
Month: 5	0.78	0.08	0.62	0.94	9.65	< 0.001
Month: 6	0.79	0.09	0.62	0.96	9.27	< 0.001
Month: 7	0.52	0.09	0.34	0.69	5.92	< 0.001
Month: 8	0.85	0.07	0.7	1	11.35	< 0.001
Month: 9	0.35	0.07	0.21	0.49	4.87	< 0.001
Month: 10	0.7	0.07	0.55	0.84	9.64	< 0.001
Month: 11	0.29	0.07	0.14	0.43	3.88	< 0.001
Month: 12	0	0.07	-0.14	0.14	0.01	0.99
Territorial: Yes	-0.03	0.11	-0.55	0.25	0.27	0.79

Table S2.3. Table showing the number of GPS locations (presence points) used in the habitat preference models for each bird. Data that are used in the breeding period model are shown in bold.

	Year: 2013											
ID	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
G32554										220	112	478
G32553								72	401	414	366	407
G32552								120	453	456	451	471
G32555									156	479	407	476
PTT 72154							19	425	463	480	443	480

	Year: 2014											
ID	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
G32554	441	405	406	192	**98**	**55**	115	315	358	437	427	423
G32553	458	419	451	**404**	**358**	**335**	**319**	399	406	457	446	484
G32552	459	94										
G32555	467	250										
PTT 72154	490	434	458	232	427	414	421	280				

	Year: 2015											
ID	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
G32554	456	372	416	**389**	**323**	**345**	**272**	216	317	336	335	412
G32553	415	332	405	355	390	330	336	378	344	415	332	405

	Year: 2016											
ID												
G32554	378	373	347	394	256	286	145	211	158			
G32553	444	418	445	398	303	313	228	259				
G32519			191	456	**428**	**411**	**423**	428	310			

Table S2.4. Akaike Information Criteria (AIC) and associated statistics for the top five GLMMs for the habitat preference of Martial Eagles in relation to tree cover (TC), National Land Cover class (LC), distance to nearest river (DRi), elevation (El), slope (Sl), and distance to nearest road (DRo).

Model	Df	AICc	ΔAICc	Weight
El + LC +Sl + DRo + DRi + TC	8	132745.92	0.00	0.98
LC +Sl + DRo + DRi + TC	7	132754.35	8.42	0.01
El + LC + DRo + DRi + TC	7	132758.27	12.35	< 0.001
El + LC +Sl + DRi + TC	7	132762.24	16.32	< 0.001
LC + DRo + DRi + TC	6	132765.42	19.50	< 0.001

CHAPTER 3: Dispersal and habitat preferences of pre-adult Martial Eagles in Kruger National Park, South Africa

Juvenile Martial Eagle fitted with a 45g Microwave Telemetry solar GPS/PTT.

© Ziggi Hugo, 2015

ABSTRACT

Martial Eagles are low-density predators declining across their African range as well as in some of the largest protected areas. Little is known about their dispersal, juvenile ranging behaviour, or habitat preferences. Such knowledge may inform the potential causes for the decline, for instance birds ranging into non-protected areas may be at increased risk of unnatural mortality. We used GPS tags (n = 8) to explore movements during the post fledging dependency period (PFDP) and subsequent dispersal in Kruger National Park. Four juveniles were tagged during the PFDP and these eagles undertook exploration trips away from the nest, often into non-protected areas, that lasted up to 93 hours and ranged ca. 150 km away from the nest. We recorded the dispersal of two of the four juveniles tagged in the PFDP. These eagles moved as far as ca. 390 km from their natal territory, but the average of their relocations during the study was ca. 100 km to their natal nest during the dispersal period. Dispersal home ranges for the two individuals from known nest locations were ca. 5,900 km^2. Another three juveniles tagged during their dispersal period maintained home ranges similar to their counterparts with known origin. During the three-year study individual ranges did not reduce to that of known nesting home range sizes and neither was settlement detected. Home ranges overlapped ca. 55 % with the current protected area network. No mortalities were detected in non-protected areas. Habitat preference analysis showed that tagged individuals preferred areas close to rivers, with moderate tree cover and avoided areas influenced by human activity.

INTRODUCTION

Protected areas are considered an important conservation tool in the preservation of habitats and their wildlife (Tarboton and Ryan, 2016). Under the current pressures of global change, habitat fragmentation and degradation, protected areas are increasing in importance (Crooks and Soule, 1999). However, not all species may benefit from protected areas. For instance species that are wide ranging may traverse areas in the surrounding landscape where they may be at increased risk of mortality due to the increased anthropogenic pressures in these areas (Sergio et al., 2008). Fenced protected areas (often termed “fortress conservation”) in which wildlife is constrained to a specific area, and where human impacts are maintained to a low level, may assist in the protection of some species (Sergio et al., 2008), but inhibit the natural movements of others Caughley (1994). For example species that undertake long distance migrations or movements require a different conservation approach, and there has been substantial focus on creating corridors to allow these directional movements Peery et al. (2004). Large protected areas may be sufficient at maintaining breeding populations of wide ranging species (Caughley, 1994), but certain life history strategies such as juvenile dispersal may predispose a species to risks beyond protected area boundaries. Unlike predictable migrations, dispersal may occur in multiple directions and at large spatial scales, which presents an even greater conservation challenge and needs to be accounted for if managers are to be effective in their conservation efforts for such species (Armstrong, 2005).

Dispersal is a process that is characterized by departure from a natal territory, which leads to a vagrant period and a final settlement period when an individual settles to breed (Armstrong, 2005). Dispersal of pre-breeding individuals from natal sites to spatially separate breeding areas (Armstrong, 2005) plays an important role in maintaining the viability of small isolated populations Peery et al. (2004) and has therefore been recognized as a crucial element in conservation biology. However, the increased risk of mortality to individuals dispersing across degraded habitats can contribute to declines of populations in protected areas when they fail to recruit back into protected breeding populations (Peery et al., 2004). This notion is exemplified by birds of prey, as juveniles of this group typically disperse over wide areas (Armstrong, 2005). The dispersal period for larger species can span long temporal periods before individuals are recruited into the breeding population because of their deferred maturity (Gaston et al., 2008, Watson et al., 2014a). Protected areas established to conserve breeding populations therefore may not be adequate for juveniles dispersing across non-protected areas (Rodrigues et al., 2004). Birds of prey in Africa, in particular, rely heavily on protected areas as they are sensitive to the high human pressures in the surrounding matrix (Woodroffe and Ginsberg, 1998). Thus, for declining birds of prey, it is important that we fully understand dispersal as a life stage, the resources required during this period, and the threats faced by dispersing individuals. Such knowledge allows conservation measures to be targeted most appropriately (Packer et al., 2013).

The recent use of GPS tracking devices has greatly improved our ability to understand the dispersal of large raptors over large spatial and temporal scales (Douglas-Hamilton et al., 2005, Hayward and Kerley, 2009, Wilcove and Wikelski, 2008). Such technology can provide insight into natal movements, help determine settlement behaviour in relation to specific landscape features and determine habitat preferences, as well as provide empirical data for survival rates and causes of mortality (Berger, 2004, Bildstein, 2006, Runge et al., 2015).

Martial Eagles (*Polemaetus bellicosus*) are widely distributed across sub-Saharan Africa, where they are the largest eagle species (Newmark, 1995). The species' conservation status has recently been elevated to vulnerable due to declines in their populations (Benz et al., 2016, Cadahía et al., 2010, Parrish et al., 2003). Within South Africa, the species is believed to have declined by up to 60 % over the last 20 years (Cloete, 2013). These declines have been apparent within protected areas such as the Kruger National Park (KNP; 54 % decline), where declines might be expected to be less severe (Cloete, 2013, Amar et al. 2015). Protected areas have the potential to act as refuges for breeding adults of this species, but it is not clear whether they perform the same function for juvenile birds. Based on ring recoveries and re-sightings of ringed birds, dispersing juveniles may travel substantial distances outside of protected areas where they may be at increased risk of un-natural mortalities, such as persecution or electrocutions Ronce (2007). Currently no empirical data exists on the movements of juvenile Martial Eagles away from the nest or during the dispersal period, so this is an important avenue for future research (Ronce, 2007). A better understanding of dispersal behaviour may therefore provide important conservation insight and may illuminate potential mechanisms driving declines within protected areas (Greenwood, 1980).

In this study we use GPS tags attached to juvenile (birds in their first moult cycle) and immature (plumage proceeding first moult cycle and preceding definitive adult plumage, following (Armstrong, 2005)) Martial Eagles in KNP, South Africa, to understand whether protected areas alone can be sufficient to protect this non-breeding section of the population. We explore early movement behaviours during the post fledging dependency period (PFDP). The PFPD, the period from fledging to independence, is an important period in a raptors life cycle. During this period juvenile birds typically spend their time improving hunting skills and developing their flight ability while being provisioned for by adults (Penteriani et al., 2005b, Pulliam, 1988, Ronce, 2007, Woodroffe, 2003). We then investigate the movements of GPS tagged juveniles during the dispersal period away from the natal territory. We use these data to estimate home range size of independent juveniles, the proportion of fixes within and outside protected areas, and the species habitat preferences.

METHODS

Study site and species description

KNP is the largest (ca. 20,000 km^2) national park in South Africa. It is in the north east of the country and is bordered by Zimbabwe to the north and Mozambique to the east. The habitat is defined by the Savannah biome (Balbontín and Ferrer, 2009, Cadahía et al., 2010, Ferrer, 1993, Real and Mañosa, 2001, Soutullo et al., 2006a). KNP is suggested to be a stronghold for Martial Eagles with a likely carrying capacity of 110 - 137 nesting pairs (Cadahía et al., 2009, Urios et al., 2007). KNP forms part of a larger network of contiguous protected areas. The Associated Private Nature Reserves (ca. 1,800 km^2) to the west of KNP forms the Greater Kruger National Park. The Limpopo National Park (ca. 10,000 km^2) in Mozambique to the east of KNP forms part of the Limpopo Transfrontier Park.

Martial Eagles are long-lived (Penteriani et al., 2005b) and reach sexual maturity at ca. 6 years (Herremans and Herremans-Tonnoeyr, 2000, Thiollay, 2006). Adults build large stick nests in the forks of tall trees. Martial Eagles lay a single egg from April to July with a peak in May (Morrison and Wood, 2009, Penteriani and Delgado, 2009). The incubation period lasts 47 – 54 days, followed by a nestling period of 90 - 109 days, and a lengthy post fledging dependency period (PFDP) that may last up to 9 months (Matthysen, 2012). If a pair raises a young to fledging, then they typically forgo breeding in the next season.

Trapping and tagging

We fitted GPS tags to 9 young Martial Eagles between 2012 and 2015 that were either still in the nest (n = 2), had recently fledged (n = 2) and could be caught in the vicinity (ca. 200m) of their nest, or were recently fledged juvenile (n = 4) or immature (n = 1) eagles dispersing through the study area with no known nest origin (n = 5) (Table 3.1). The latter birds were caught opportunistically as we came across them during daily fieldwork because we were unable to locate enough nests that had accessible young for this study (Figure 3.1; Table 3.2).

Table 3.1. Years and development stages that young Martial Eagles were tagged in to understand dispersal, ranging behaviour, and habitat preference.

Year	Tagged on nest	Tagged during PFDP	Tagged during dispersal
2013	1	0	0
2014	1	1	4
2015	0	1	1
Total	2	2	5

Eagles were fitted with GPS units using a backpack-mounted harness made from 0.55” Teflon® Ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A). Juveniles tagged on the nest (n = 2) were fitted with units when 70-80 days old based on known hatching dates calculated from regular nest checks (Chapter 5). Eagles were classed as juveniles (first moult cycle) or immatures (completed the first moult cycle) following guidelines in (Cagnacci et al., 2010, Matthysen, 2012). Individuals that had already fledged from their nests were trapped using a bal-chatri (Cadahía et al., 2008, Cagnacci et al., 2010, Wabakken et al., 2007) baited with two young chickens (*Gallus gallus domesticus*) under the relevant permits (SANParks Animal Use and Care Committee Reference No. 13-5; University of Cape Town Science faculty Animal Ethics Committee approval number: 2013/V7/AA; Threatened or Protected Species (ToPS) permit number WM 1297/2013).

We used two types of tracking units: Solar powered GPS-GSM (n = 7; CTT-1080, 80 g Cellular Tracking Technologies, U.S.A; accuracy: <2 m horizontal, <3 m vertical) and GPS/PTT (n = 2; PTT 100, 45 g Microwave Telemetry, U.S.A; accuracy: ± 18 m) tracking devices. GPS-GSM units recorded a GPS location every 15 min between 05:00 and 18:00 UTC+2. GPS/PTT tracking devices recorded a GPS location every hour between 07:00 and 20:00 UTC+2 in winter (>21 April), and 06:00 and 21:00 UTC+2 in summer (> 03 September). In order to standardize data between the two tracking devices, we used the datum from the GSM tags that were closest to each hour between 06:00 and 18:00 UTC+2.

Mortality estimates

The GPS data transmitted from tagged eagles was assessed every three days to determine the mortality status of each eagle. When an eagle was seen to remain in the same location for more than two days or a tag suddenly stopped transmitting data, we searched the last known location for the individual. If an eagle was found dead, the cause of death was determined and where possible a necropsy was conducted by KNP Veterinary Wildlife Services. For individual eagles whose tags transmitted infrequently or had low battery capacity, we attributed cessation of transmissions to tag failure. Where a tag failed to transmit data but the tag was functioning correctly prior to the cessation of transmissions we could not attribute a cause of cessation.

Dispersal period

Because our paper only covers the early juvenile period (see Results) of Martial Eagle life history we separated our data into the period of time leading up to 'departure' from the natal site (where available), known as the PFDP, and a 'vagrant' period, from hereon referred to as the (juvenile) dispersal period.

The beginning of the PFDP was estimated from regular nest checks and young were presumed to have fledged 109 days after hatching. Where birds were tagged on the nest we calculated a more accurate fledging date based on the first movement away from the exact nest location (change in speed > 0 m.s^{-2} and a movement > 18 m equal to the GPS error of PTTs). We calculated annual mortality rates by dividing the number of mortalities (d) during the study by the total number of months (m) tracked during the study, multiplied by 12 to get an annual mortality rate, and then again by 100 to convert a proportion into a percentage (mortality rate = d/m * 12 * 100). This is similar to the method used to calculate survival rates in Bearded Vultures (Brown et al., 1982).

Explorations beyond the natal area are often regarded as part of the dispersal process (Birdlife International, 2013) prior to departure, and these were investigated for birds with known nest locations. An exploration was defined as a bird leaving the natal territory and then returning. As such we calculated the date a bird first left the natal territory as the date of the individuals first exploration and any movements beyond the natal territory that returned as subsequent explorations.

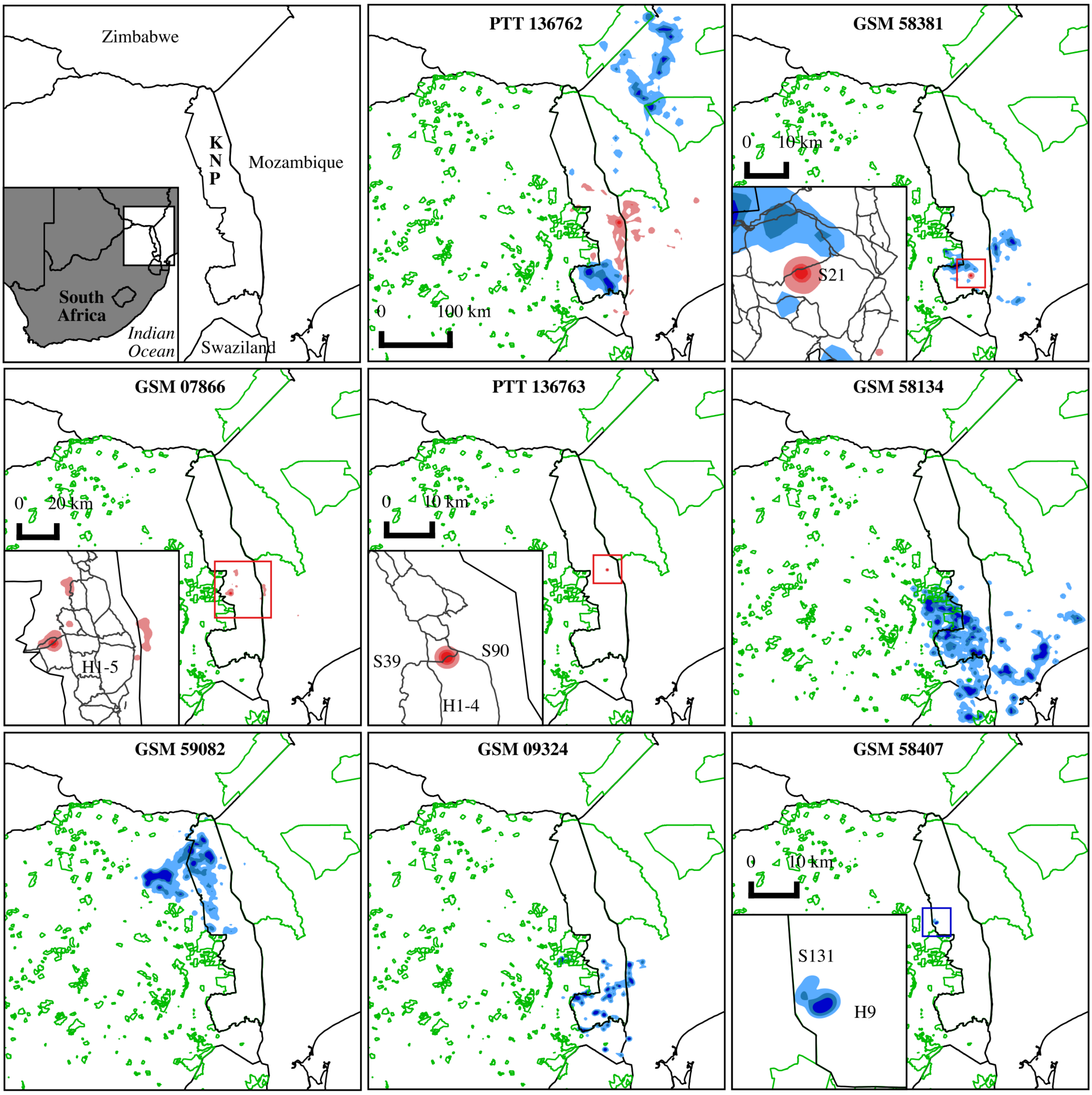

Figure 3.1. Home ranges of juvenile and immature Martial Eagles GPS tagged in Kruger National Park, South Africa. Each panel represents one individual's 95, 75 and 50% kernel density estimated home range during the PFDP (red polygons) and dispersal period (blue polygons). These home ranges are shown in relation to protected area coverage (green polygons). Main panels are set to the same scale and extent for comparison among individuals. Insets (not to same scale) show detail for small home ranges and roads e.g. S131 are provided for spatial context.

Table 3.2. Summary of the juvenile Martial Eagles tracked to understand dispersal behaviour, and post dispersal habitat preference. Prefixes (GSM/PTT) of individual identity numbers represent the type of tracking device used (see Methods). Where mortalities or tag failures were detected the cause is indicated in parentheses. Age classes indicate at what stage of the birds' life GPS tags were fitted.

Individual	**Deployment date**	**Sex**	**Age**	**Development period**	**Days tracked**	**GPS fixes**	**Transmission cessation (cause)**
GSM 58381	09/12/2013	M	Nestling	Nest	1026	6406	No
PTT 136763	18/08/2014	F	Nestling	Nest	178	1966	Yes (Unknown)
PTT 136762	24/02/2015	F	Juvenile	PFDP	586	6687	No
GSM 07866	09/01/2014	F	Juvenile	PFDP	101	1213	Yes (Unknown)
GSM 58134	07/02/2014	M	Juvenile	Dispersal	967	5196	No
GSM 59074	13/03/2014	M	Juvenile	Dispersal	0	0	Yes (Tag lifespan)
GSM 59082	16/03/2014	M	Juvenile	Dispersal	929	10273	No
GSM 09324	15/03/2015	M	Juvenile	Dispersal	369	1359	Yes (Tag lifespan)
GSM 58407	02/02/2014	F	Immature	Dispersal	228	2655	Yes (Starvation)
Total					**4384**	**32897**	

The frequency, distance and length of time away from the natal territory (using the nest location for distance measurements) of these explorations, prior to dispersal proper, were calculated. The natal territory was calculated using known nesting Martial Eagle home range sizes (see Chapter 2). These average ca. 108 km^2, thus representing territories with a radius of ca. 6 km, assuming that a nest is centred within a home range and that territories are circular. The end of the PFDP and beginning of the dispersal period was based on the maximum amount of time spent away from the natal territory that a bird can survive without adult provisioning (Barnes, 2000, Oatley, 1998, Steyn, 1982). Golden Eagles (*Aquila chrysaetos*) are similar in size to Martial Eagles and in many of their life history traits (Hustler and Howells, 1987), therefore in this study we use 10 days as the maximum period that a juvenile eagle can go without provisioning, following (Penteriani et al., 2005b).

Lastly, to understand the dispersal behaviour employed by Martial Eagles, we constructed movement paths, also known as trajectories, from the hourly GPS fixes in the adehabitatLT package in R Clark and Pyle (2015). GPS locations were used to create net squared displacement (NSD) plots, which show displacement from the first location over time. Patterns in these plots can indicate movement strategies such as migration, dispersal, nomadism, and home range (Ferrer, 1992). Dispersal is characterised by a sigmoidal NSD curve. Our plots were visually compared to the NSD plots in (Rutherford et al., 2006) which describe the various movement behaviours.

Home range analyses

We calculated home range sizes separately for the PFDP and dispersal period using 100% Minimum Convex Polygons (MCP) as well as for the 50, 75 and 95% contours of the species utilization distribution (UD) using the adehabitatHR package in R (Murn et al., 2012, Tarboton and Allan, 1984). The UDs were calculated using biased random bridges (ca. 30 years; Paijmans, 2016). We calculated MCP, although considered obsolete with modern GPS and home range estimators such as BRB, so that we could compare our findings with the home range sizes of Martial Eagles that have previously been tracked with radio telemetry during their PFDP (Steyn, 1982). BRB are based on brownian bridges that expand the location based kernel density estimates by including the path between points used in calculating the probability density function. BRB are built using a diffusive model similar to brownian bridges, but drift towards the next location in a trajectory is included in the model rather than drift towards the end point of a trajectory. We calculated trajectories using the adehabitatLT package in R (Tarboton and Allan, 1984). Because BRB allows for temporal constraints on the time between locations in the construction of bridges we set the maximum time allowed to elapse between points in the creation of bridges, Tmax, = 3 hrs. The minimum distance allowed between points to be defined as a movement was set to 18 m (Lmin = 18 m) as this is equal to the error of our GPS tags. D, the diffusion parameter was calculated using the BRB.D function in the adehabitatHR package.

We calculated monthly home range estimates for each individual and plotted these from the estimated date of fledging (0 months) to assess home range size changes through the PFDP and dispersal period. For birds that we determined using plumage characteristics to be in their first moult cycle we plotted their home range sizes from 12 months. Lastly, we plotted the monthly home range of one individual tagged in the third moult cycle from 36 months. These monthly home range sizes were compared to the known average home range sizes of breeding age adults in KNP (Chapter 2).

Lastly to determine if bids intensely used one patch or more different patches within their dispersal range over time, we calculated the central GPS location in each month by taking the average longitude and latitude of all GPS locations in a month and measured the distance (displacement) between these average points. If a home range remains in the same spatial area from one month to the next we would expect the distance between the centres of each monthly home range to converge towards zero. The displacement between monthly home ranges was plotted over age in months, similarly to the plots exploring home range size with age (see above).

Protected area coverage

Within the 95 and 50 % UD contours calculated for birds in the dispersal period, we calculated the proportion of area covered by protected areas using the World Dataset on Protected Areas (WDPA). We filtered the WDPA to use only areas designated as ‘National Park’ or ‘Nature Reserve’ to exclude areas that are not under formal management (Hustler and Howells, 1987, Steyn, 1982). This was similar to the method of protected area selection used by Clark and Pyle (2015) to calculate the population size of White-headed Vultures (*Trigonoceps occipitallis*), as many parks in Africa are technically paper parks with no formal management plan. Additionally, the proportion of individual GPS locations was calculated within these protected areas. Furthermore, to assess whether juveniles birds in the PFDP were leaving protected areas during their explorations, we calculated the proportion of these movements that extended into non-protected areas.

Habitat preference: environmental variables

We used global satellite derived environmental layers to determine habitat preferences (the likelihood of selecting one habitat feature over another (Berger and Mueller, 1959)) of juvenile Martial Eagles during their dispersal period. Topographical information (elevation and slope) was derived from a 90 m digital elevation model (Gypaetus barbatus; Krüger, 2014). Tree cover was estimated from a 30-m resolution continuous fields of tree cover layer Ronce (2007). Information on rivers was derived from a 1:50 000 HydroSHEDS river network layer (Steyn, 1982).

Additionally, to allow habitat preference to be explored in more detail, we undertook an analysis using only locations within South Africa where additional GIS products were available. Thus we assessed habitat preference, in addition to our other variables above, using a 72-class South African land cover map (Matthysen, 2012). This dataset categorizes South Africa into 72 land types at a 30-m resolution, including categories such as natural vegetation categories (e.g. 'dense bush', 'open bush', 'grassland'), agriculture categories (e.g. 'cultivated'), and urban development categories (e.g. 'urban village', 'urban built up'). Therefore the 72-class land cover map was collapsed into 6 broader categories, namely 1) natural vegetation, 2) water bodies, 3) cultivated land, 4) forestry plantations, 5) mines, and 6) urban (Table S3.1).

Habitat preference models

Habitat preferences of juvenile Martial Eagles was investigated using a binomial generalized linear mixed model (GLMM) (Weston et al., 2013). As a response variable, GPS fixes and a set of randomly distributed points generated within the 100 % MCP of individuals in the dispersal period were modelled in relation to underlying environmental variables, and individual ID was modelled as a random effect (Brown et al., 1982). Random points were generated in QGIS and for each real fix, three random points were generated Weston et al. (2013). GLMMs were run in R using the lme4 package (Calenge, 2006). Model assumptions were checked, thus we ensured that there was no co-correlation (co-efficient > 0.3) between continuous variables. Continuous variables were scaled and centred to improve estimate comparisons.

The environmental variables used in the first model spanning political borders were elevation, slope, % tree cover, and distance to rivers. Martial Eagles are typically absent from true forests or very mountainous environments (Bunnefeld et al., 2011), thus % tree cover and elevation were included as quadratic terms. The second model using only points from within South African borders used habitat classes from the land cover map to investigate response to human transformed landscapes in addition to variables used in the cross border model.

Model selection was based on the model with the lowest AICc using the MuMIn package in R to compare all possible model combinations Bunnefeld et al. (2011). Model fit was assessed using receiver operator curves (ROC) in R (R Core Team, 2015) package ROCR (Calenge, 2006, R Core Team, 2015). The area under curve (AUC) was used to determine model performance; values over 0.9 are typically associated with an accurate model and AUCs of 0.7 – 0.9 categorizing models with moderate predictive power, while models with an AUC < 0.7 are generally considered to have poor predictive power (BRB; Benhamou, 2011, Benhamou and Cornélis, 2010)

RESULTS

Mortality estimates

Eight out of the nine eagles transmitted data and were tracked for a minimum of 101 days and up to 1026 days. We confirmed the mortality of one eagle (GSM 58407): an immature eagle that veterinary reports indicate died due to starvation. Another two individuals (GSM 07866 and PTT 136763) suddenly stopped transmitting data during the PFDP and it was not clear what caused these tags to stop transmitting as they were functioning correctly prior to this point. The individuals were not seen subsequently. Additionally, two other tags (one without transmitting any data) failed due to confirmed technical problems. We estimated an annual mortality of 8.13 % using only confirmed mortalities (1/8 tracked individuals over 147.64 bird months).

Fledging movements

Of the four individuals tagged at known natal territories, we recorded the dispersal away from the natal home range for two individuals (GSM 58381 and PTT 36763) as the other two individuals (PTT 36763 and GSM 07866) tags suddenly stopped transmitting during the PFDP (Figure 3.1 and Figure S3.1). Individual GSM 58381 tagged as a nestling made 10 explorations before dispersing. Individual PTT tagged during the PFDP made 20 explorations but may have made additional explorations before it was tagged. These two individuals spent ca. 22 and 270 days from fledging in the natal territory before departing (Table 3.3). Exploratory trips beyond the natal territory varied in length from 1 – 70 hrs and reached distances up to 147.5 km away from the nest before returning to the natal territory (individual means in Table 3.4). Individuals that stopped transmitting data before departure (PTT 36763 and GSM 07866) made at least 5 exploratory trips before transmission cessation. Exploratory trips for these individuals lasted 1 – 93 hrs and reached up to ca. 47 km from the nest before returning to the natal territory.

Dispersal period

The two individuals that successfully dispersed from their natal territory travelled to a maximum distance of 102 (GSM 58381) and 393 km (PTT 36762) from the nest within the first and fourth month after dispersing, respectively (Figure S3.1). NSD plots for individuals GSM 58381 and PTT 36762 showed a pattern of long distance movements in relation to the starting position after departure; however they returned to areas close to their starting location. The average distance that these individuals ranged from the nest after dispersal onset was 100.32 ± 80.83 km (N = 2 individuals, n = 38 months; Figure S3.1). NSD plots for the other two individuals whose tags stopped transmitting prior to departure (PTT 36763 and GSM 07866; Figure 3.2 and Figure S3.1) show that they moved little away from their nests during their PFDP.

Table 3.3. The estimated number of days Martial Eagles took to perform their first exploration and the number of days spent in the PFDP before dispersal proper occurred. Asterisks (*) represent individuals for which accurate fledge dates could not be estimated as birds were trapped during the PFDP. Double asterisks (**) represent individuals for which the timing to first exploration or dispersal onset could not be recorded because of tag transmission cessation during the PFDP.

Individual	**Sex**	**Fledge date**	**Days to 1st exploration**	**Days to dispersal**
GSM 58381	M	17/01/2014	209	270
PTT 136763	F	15/09/2014	122	**
PTT 136762 *	F	8/11/2014	**	220
GSM 07866 *	F	19/09/2013	176	**

Table 3.4. The number of explorations (Expl.) recorded during the PFDP of juvenile Martial Eagles. For each individual the minimum, maximum and mean time away from the natal territory (hours), and distances travelled (km) away from the nest during explorations are shown.

ID	Sex	Expl.	Time (hrs)			Distance (km)		
			Min	Max	Mean	Min	Max	Mean
GSM 58381	M	10	1	25	8.5 ± 9.8	6.3	60.3	27.1 ± 15.7
PTT 136763	F	5	1	4	1.8 ± 1.3	6.2	19.0	9.8 ± 5.3
PTT 136762	F	20	1	73	24.7 ± 26.2	6.7	147.5	49.5 ± 41.8
GSM 07866	F	5	1	93	20.4 ± 40.6	6.5	46.9	17.3 ± 17.3

Movements for the remaining individuals, that were captured during their dispersal period (GSM 58134, GSM 59082, GSM 58407, GSM 09324) suggest they all remained within areas in close proximity to their respective points of capture which is also indicated in NSD plots as a cloud of locations that did not show movement away from the first (capture) location (Figure S3.1).

Home ranges

As would be expected, home range sizes during the PFDP were smaller compared to the dispersal period (Figure 3.1 and Table 3.5). During the PFDP home range sizes increased in size after fledging from less than 100 m^2 in the first month up to 1 km^2 by month 4 (Figure 3.2). In month 5, individuals used up to 10 km^2 around their nest, and up to 10 000 km^2 before the onset of dispersal (Figure 3.2).

The dispersal period home range sizes of two individuals tagged as juveniles (GSM 58381 and PTT 136762) averaged 5895 ± 4211 km^2. The four individuals, which were trapped during the dispersal period (GSM 58134, 59082, 58407, 09324), had home ranges averaging 7331 ± 2482 km^2 (Figure 3.1, Table 3.5). One bird trapped in the dispersal period in immature plumage (GSM 58407) maintained a relatively small home range of less than 70 km^2 before it died of starvation (95% UD contour; Figure 3.1 and Table 3.5). Because individual GSM58407 was of unknown age it was excluded from monthly home range and movement analysis.

Table 3.5. Minimum convex polygon (MCP) and biased random bridge utilization distribution (BRB) home range estimators for juvenile Martial Eagles during the post fledging dependency phase (PFDP) and during the dispersal period demonstrating the area usage (km^2) for each individual (ID).

ID	PFDP MCP 100%	BRB 95 %	BRB 75 %	BRB 50 %
GSM 58381	1210.90	95.04	20.68	8.63
PTT 136762	24093.65	2993.67	125.24	24.54
GSM 07866	4425.94	295.27	22.58	7.05
PTT 136763	161.75	24.08	10.43	5.09
	Dispersal period MCP 100%	BRB 95 %	BRB 75 %	BRB 50 %
GSM 58381	15912.05	2917.66	731.72	217.89
PTT 136762	60483.21	8873.226	2367.521	661.8342
GSM 58134	54845.46	8106.428	1913.376	568.7491
GSM 59082	27208.94	8366.29	2869.911	947.4447
GSM 09324	15080.27	8392.937	3570.634	1524.914
GSM 58407	45.00	66.99	28.12	11.52

Despite covering large areas over the tracking period, individuals intensively used smaller areas on a month-by-month basis during the dispersal period (Figure 3.2). These smaller areas of intensive use averaged 1282.60 ± 1402.96 km^2 per month (Figure 3.2; range: 66.47 – 7546.79 km^2). The distance between the centres of monthly home ranges averaged 43.58 ± 54.8 km^2 (Figure 3.2; range: 0.78 – 328.17 km^2) from one month to the next. Individuals ($n = 5$) in their first year of dispersal (13 – 24 months) apparently had significantly different variation in monthly home range sizes ($F = 7.01$, $df = 4$, $p < 0.001$) but there was no significant difference in the variation in distances travelled between these monthly ranges (F = 0.037, df = 1, p = 0.85). The difference in monthly home range sizes was attributed to individual GSM59082 because this individual used much larger home ranges on monthly bases than GSM58381, GSM58134, and GSM09324 (Table S3.2) Therefore the individuals tagged without prior knowledge of their nest mostly reflected the behaviour of individuals tagged at natal areas following their dispersal onset.

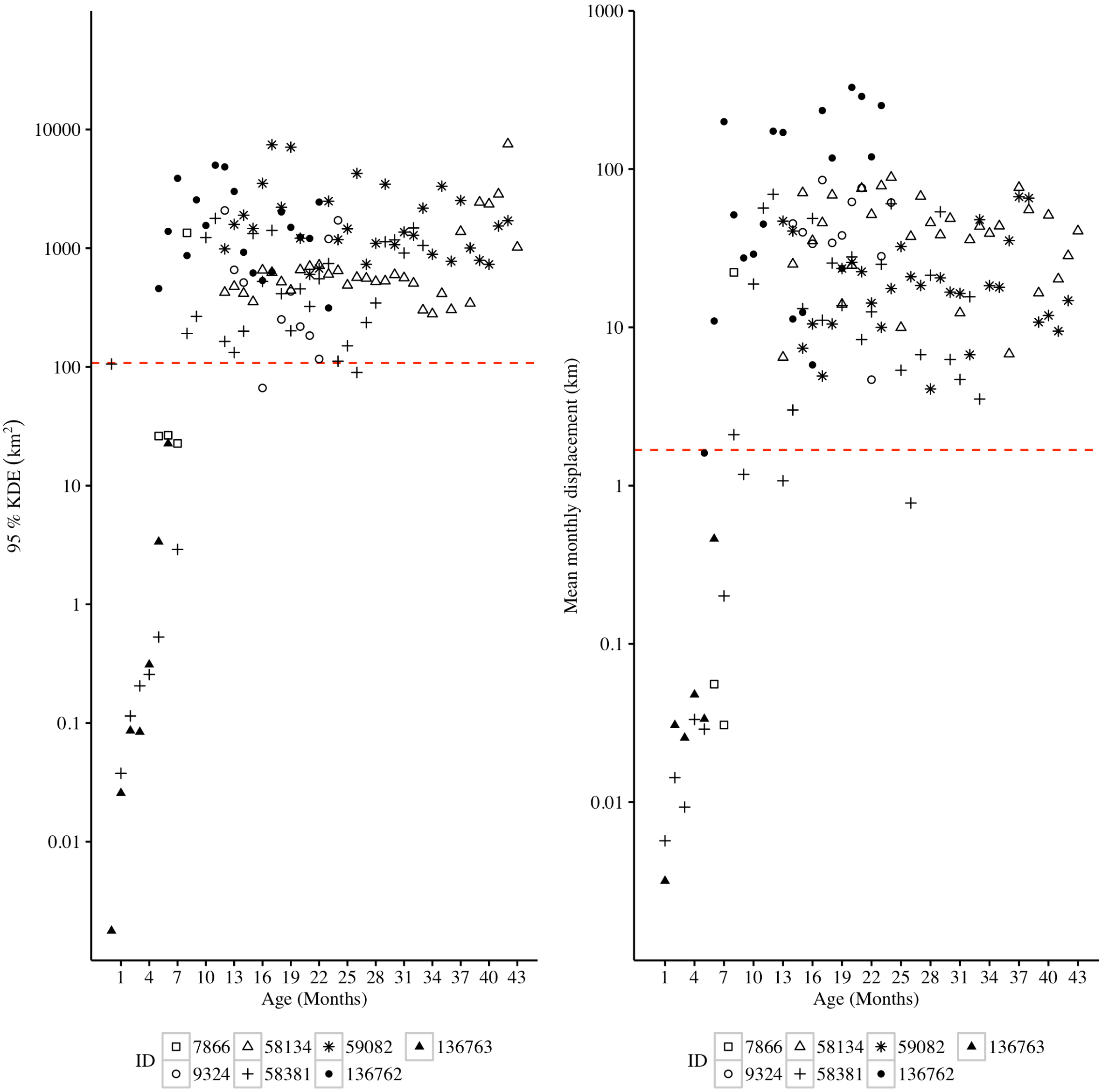

Figure 3.2. Monthly home range sizes of juvenile Martial Eagles (95 % kernel density estimates), left, and the distance moved between months, right, plotted against eagle age. Y-axis is on a $\log_{10}$ scale. The average breeding adult home range (108 km^2), and average adult monthly displacement is illustrated using a red horizontal dashed line for comparison.

Protected area coverage

The general area used (95 % UD contour) during the dispersal period overlapped protected areas by 55 ± 23 % (range: 36 – 100 %) and the core area used (50 % UD contour) overlapped by 64 ± 29 % (range: 31 – 100 %). Similar results were seen when examining simply the proportion of points inside or outside of protected areas, with 60 ± 22 % of all dispersal period locations (range: 33 – 100 %) being inside protected areas. Four individuals used the network (Associated Private Nature Reserves) of protected areas to the west of KNP (Figure 3.1). The western side of individual GSM 59082's home range was not covered by any protected area. The range of PTT 136762 was conserved in two of Mozambique's large protected areas, Banhine and Limpopo National Parks, but the core of its home range west of Zinave National Park was not under any apparent formal protection. Eleven of 40 explorations from the natal territories left KNP and extended into a non-protected area.

Habitat preference

Analysing all tracking locations in the dispersal period (n = 17600), juvenile habitat preference was associated with 4 key features. They preferred areas that were 1) intermediate in elevation (indicated by a quadratic relationship with elevation, where a peak usage occurs when elevation was ca. 560 m), 2) closer to rivers, 3) had intermediate tree cover (indicated by a quadratic relationship with tree cover, where a peak usage occurs when tree cover was ca. 40 %), and 4) had lower inclined slopes (Table 3.6). The top model containing these terms had an AUC = 0.66 and there were no competing models (< 2 ΔAIC) (Table S3.3).

Table 3.6. Generalized linear mixed-effect model results showing the occurrence likelihood of juvenile Martial Eagles in relation to elevation, distance to rivers, slope, elevation^2, tree cover and tree cover^2 listed in their relative order of importance.

Fixed effect	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	-0.92	0.11	-8.35	< 0.001
Elevation	0.59	0.01	43.88	< 0.001
Distance to river	-0.37	0.01	-37.47	< 0.001
Slope	-0.33	0.02	-18.11	< 0.001
Elevation^2	-0.24	0.01	-26.65	< 0.001
Tree cover	0.07	0.02	4.44	< 0.001
Tree cover^2	-0.02	0.00	-4.98	< 0.001

A second model set examining habitat preference in more detail using a land classification map of South Africa (thus excluding presence and absence points beyond the South African border, n = 12508), indicated that relative to natural habitats (e.g. bushveld) juvenile Martial Eagles were less likely to occur in areas of plantations, urban, or cultivation and were more likely to occur near water bodies (Table 3.7). This model showed similar relationships with the variables reported in the first model (Table 3.6) and this model had an AUC = 0.69. There were no competing models (< 2 ΔAIC) in this second model (Table S3.4).

DISCUSSION

Mortality estimates

We hypothesised that a potential driver of Martial Eagle declines in KNP is that juvenile and immature eagles are at increased risk of unnatural mortality during dispersal beyond protected area boundaries, therefore resulting in recruitment failure. Our study results do not support this hypothesis, as only one individual was confirmed dead and therefore annual mortality rates were similar to the natural mortality rates of other large species, e.g. Golden Eagles (Brown, 1991, Ong, 2000), after their first year of life. The study, however, was limited by low recovery rates of eagles that stopped transmitting data (n = 2) with no definitive explanation, and furthermore by tag failures (n = 2). Because of these shortcomings, the mortality of juveniles should continue to be assessed through ring re-sighting data or GPS tracking.

Table 3.7. Generalized linear mixed-effect model results for the occurrence likelihood of juvenile Martial Eagles within the borders of South Africa in relation to elevation, distance to river, tree cover, slope, elevation^2, tree cover^2 (listed in their order of importance), and in relation to a category collapsed National Land Cover class map.

Fixed effect	Estimate	Std. error	z value	Pr (>|z|)
Intercept	-0.86	0.18	-4.92	< 0.001
Elevation	0.76	0.03	23.69	< 0.001
Distance to river	-0.48	0.01	-37.57	< 0.001
Tree cover	0.38	0.02	17.37	< 0.001
Slope	-0.32	0.02	-15.44	< 0.001
Elevation^2	-0.26	0.02	-14.80	< 0.001
Tree cover^2	-0.05	0.00	-10.52	< 0.001
Land cover: plantations	-3.59	0.73	-4.95	< 0.001
Land cover: urbanised	-1.73	0.12	-14.33	< 0.001
Land cover: cultivated	-1.12	0.08	-14.47	< 0.001
Land cover: mines	-0.45	0.26	-1.71	0.09
Land cover: water bodies	0.41	0.18	2.29	0.02

Previous studies have indicated that the juvenile life stage is a vulnerable period for Martial Eagles, with annual mortalities as high as 40 % (Calenge, 2006). Brown (1991) noted that farmers shot most birds during the onset of dispersal, whilst an individual tracked by (Brown, 1991, Ong, 2000) was killed by a pair of Verreaux's Eagle Owls (*Bubo lacteus*). In another study (Chapter 2) we found that annual adult mortality rates were high (ca. 42 %) and that at least two of the four confirmed mortalities in that study were due to unnatural causes; specifically these individuals were killed by persistence hunting activities. Therefore we likely under estimated the true immature mortality rate in this population.

Fledging movements

Previously, little was known about the fledgling dependence of juvenile Martial Eagles. Although our sample size was only two, we found that juveniles had long PFDP (ca. 7 – 9 months) similar to nest observations by (IUCN and UNEP-WCMC, 2016) who recorded PFDP lasting up to 8 months. Golden Eagles, which are similarly sized, have a similarly long PFDP that may range from 5 – 8 months Murn et al. (2016). But some individuals in migratory populations of Golden Eagles initiate dispersal as early as 39 days after fledging, suggesting other factors can drive earlier dispersal rather than size of a species (Beyer et al., 2010). Variations in the length of the PFDP may reflect variation of environmental conditions in the natal area (USGS, 2008). For instance, prey availability is often regarded as a predictor for PFDP length in other species such as Montagu's Harriers (vegetation >5 m tall; Sexton et al., 2013) or Eurasian Kestrels (Lehner et al., 2006); these species which have longer PFPD when prey availability is higher. Future studies on Martial Eagles could test whether the length of the PFDP is governed by prey availability. The PFDP is correlated with hatching date in both Montagu's Harriers, migratory Golden Eagles and Spanish Imperial Eagles (*Aquila adalberti*), with individuals that hatch later having shorter dependency periods (GeoTerra Image (GTI) Pty Ltd). Unfortunately our sample size was too small to determine the effects of time of hatching on the length of the PFDP and this too should be considered in future studies.

Home range sizes during the PFDP were initially small but increased gradually until dispersal. Gradual movements away from the nest also occur in Golden (Bates et al., 2014) and Bonelli's Eagles (Aarts et al., 2008, Reid et al., 2015). Gradual increases in area use generally coincides with increased independence, exploration, and a decline in provisioning from adults (Wakefield et al., 2011). However in this study adults were not tagged simultaneously and it was not possible to test this. It will be important to verify how parents and juveniles interact during the PFDP in future studies. For instance, another study (Chapter 2) has shown that adult Martial Eagles rapidly reduce the number of visits to the nest while the nestling is still on the nest, and visits to the nest after the young has fledged are infrequent (Chapter 2; Steyn, 1982); thus reduced visitation may drive the onset of dispersal in Martial Eagles if juveniles are not being provisioned for away from the nest.

The movements of juvenile Martial Eagles during the PFDP have previously been assessed using radio tracking (Bates et al., 2014). (Taylor, 2015) tracked one juvenile individual that covered 11 km^2 (MCP) in its first 2 months after fledging, and up to 29 km^2 in its 6th month after fledging. Our individuals did not use areas of this size until their 4th month. However, one individual trapped during the PFPD was using an area of > 3000 km^2 (MCP) from the time of capture at 5 months old and thus may have made similarly large movements earlier on than the individuals tagged in the nest.

Dispersal period

Ring re-sightings of juveniles have suggested that individuals may travel 47 – 351 km from the nest; however these re-sightings only represent the species dispersal potential and do not highlight the areas traversed over time or the timing of dispersal (Bartoń, 2015). Our study supports data from ring recovery programmes as two individuals tracked to dispersal reached up to 393 km from the nest. However, both used areas over the course of the study that was closer to their nest. Similarly, a study of a single Golden Eagle documenting dispersal from fledging to its first breeding attempt showed similar long range movements in the first year, followed by a reduced range in the later years before settling closer to the natal territory (Sing, 2005). This behaviour also is observed in Common Buzzards (*Buteo Buteo*), and this behaviour may hinder the re-colonisation of other areas (Swets, 1988). In contrast, juvenile Bonelli's Eagles increase the distance from the natal territory over time leading to settlement areas distant from the natal territory (Hunt et al., 1998, Newton et al., 2016). Because of sample size and temporal constraints on this study, the settlement of Martial Eagles in relation to the natal site was not recorded and which dispersal strategy used by Martial Eagles is still poorly understood. As time goes on we hope that our tracked birds will be recruited into the population and will enhance our understanding of the natal dispersal process in this population.

Protected area coverage

Protected areas in the Lowveld region of South Africa are important for the conservation of birds of prey to the extent that some species are absent beyond protected area boundaries (Brown, 1991). Martial Eagles during their dispersal period used the protected areas (Figure 3.1) west of KNP, formally known as the Associated Private Nature Reserves, and in Mozambique. However, individuals in the north of KNP are less conserved by protected areas in the region west of KNP around the town of Giyani. This region should therefore be a focus for new protected areas.

Although our study had a relatively low mortality rate of dispersing birds currently using these areas (although accepting that sample size is small) wide ranging eagles will unlikely benefit from protected areas alone (Chapter 2), and greater emphasis should be placed on conservation strategies in the surrounding landscape, such as improving tolerance to top predators Ong (2000), and mitigating threats associated with electrical infrastructure (Ferrer, 1992).

Habitat preference

Our habitat preference analysis was able to reveal some of the environmental parameters associated with Martial Eagles during the dispersal period. This understanding should be used to inform the conservation of the species and predict their spatial requirements. Juvenile Martial Eagles in both the model using all their locations, and the model using only locations confined to South Africa indicate that areas with an elevation similar to KNP (280 – 840m asl), in areas with gentle slopes, close to rivers and with intermediate tree cover. These results were dissimilar to adult Martial Eagles who preferred areas further from rivers, with increasing tree cover, elevation and slopes (Chapter 2). The reasons for this dissimilarity may stem from the range of data used in the juvenile and adult models. For instance the availability of habitats that juveniles can spend their time in is not constrained by defending a territory.

KNP is situated in an area that not only satisfies juvenile Martial Eagle altitudinal preferences, but also satisfies their tree cover preferences and availability of large rivers with many tributaries Hustler and Howells (1987). To the west of KNP elevation and slope increase towards the escarpment, and the area also is dominated by indigenous and plantation forests (Chapter 4). These factors may limit the dispersal of Martial Eagles to the west of the escarpment, where surveys have indicated that the species occurs at lower densities (Bahat, 1992, Soutullo et al., 2006b, Weston, 2014).

Although the species was previously known to avoid forested areas (McIntyre and Collopy, 2006), Martial Eagles, like other raptors (Soutullo et al., 2006b), depend on some tree cover for perching, hunting and roosting close to rivers. These results are important in the context of tree cover change and threats to rivers in KNP. Tree cover alone in KNP has declined by ca. 64% over the last half century, and South Africa's river systems currently face a number of threats including high levels of pollution and water shortages from upstream activities such as mine run off and agriculture (Circus pygargus; Arroyo et al., 2002).

Martial Eagles preferred areas classed as natural vegetation over areas dominated by human transformed landscapes such as cultivation, mining, and urbanisation. These results again demonstrate the importance of natural habitats in the Lowveld region for dispersing juvenile Martial Eagles. Rapid development is currently occurring around the KNP (Falco tinnunculus; Vergara et al., 2010) and habitat loss associated with development is likely to increase the threats faced by dispersing eagles.

In conclusion, the wide-ranging behaviour of juvenile eagles poses a considerable conservation challenge (Arroyo et al., 2002, Ferrer, 1992, McIntyre and Collopy, 2006). Although our hypothesis that juvenile eagles would incur high rates of unnatural mortality was not supported, protection of potential settlement areas where birds explored and may later breed should be a priority in order to realise the best conservation outcomes when addressing declining species(Soutullo et al., 2006b). However, these areas still need to be fully identified for Martial Eagles. This can be achieved in part by increasing sample size of tracked individuals and by monitoring currently tagged individuals until they enter the breeding population. The study was severely limited by sample size and was constrained by the number of tags that went offline with no explanation. However, this paper provides the first insight into the dispersal process of Martial Eagles. Results suggest that protected area networks alone are unlikely to fully conserve eagles during their dispersal, with a large proportion of their time (ca. 55 %) currently spent outside of protected areas. Conservationists should also look to improving social attitudes towards top predators in the landscape surrounding protected areas.

ACKNOWLEDGMENTS

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SUPPLEMENTARY MATERIAL – CHAPTER 3

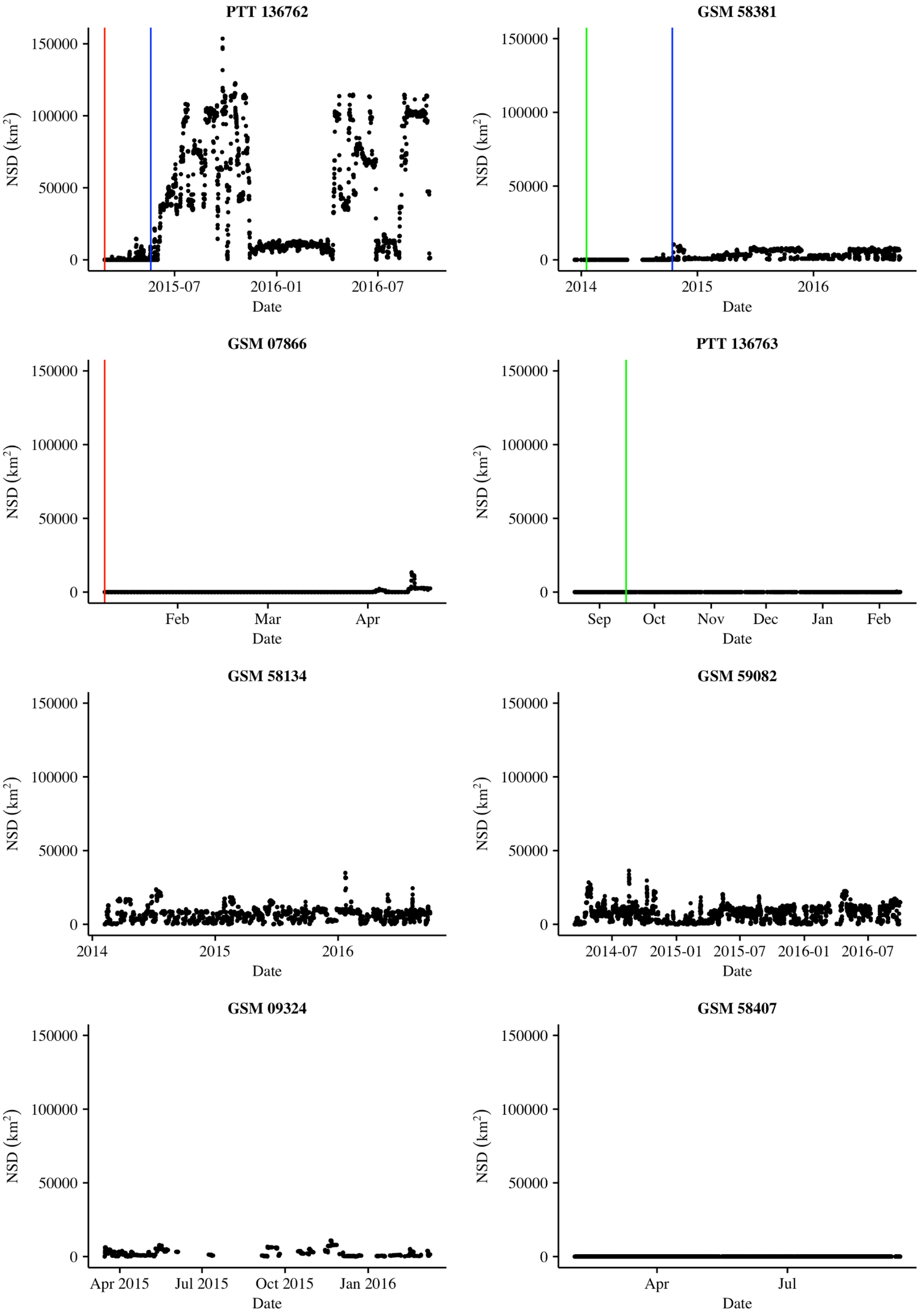


Figure S3.1. Net squared displacement (NSD) plots detail the dispersal process and ranging behaviour of juvenile and immature` Martial Eagles. Red vertical lines represent the start tracking for individuals caught at nests during the post fledging dependency period (PTT 136762 and GSM 07866); green vertical lines indicate the estimated fledging date for individuals tagged on the nest as nestlings (GSM 58381 and PTT 36763), blue vertical lines indicate the dispersal date and onset of the dispersal period.

Table S3.1. A 72-class National Land Cover map (SANBI) was used to inform habitat preferences of dispersing juvenile Martial Eagles within the confines of South Africa. Land class categories 1 - 72 were grouped based into 6 broader categories based on their similarity.

Class	Description	Presence points	Absence points
4 - 9	Natural vegeteation	27279	12099
1 - 3	Water bodies	99	93
10 – 31	Cultivated land	1348	210
32 -34	Plantations	277	2
35 - 41	Mines	88	26
42 - 72	Urban	1027	78
1	Water seasonal	5	1
2	Water permanent	58	41
3	Wetlands	36	51
4	Indigenous forest	41	2
5	Thicket /dense bush	7245	5415
6	Woodland /open bush	14345	5474
7	Grassland	5532	1169
8	Shrubland fynbos		
9	Low shrubland	116	39
10	Cultivated comm fields (high)	5	
11	Cultivated comm fields (med)	43	5
12	Cultivated comm fields (low)	17	4
13	Cultivated comm pivots (high)	3	
14	Cultivated comm pivots (med)	1	
15	Cultivated comm pivots (low)	1	1
16	Cultivated orchards (high)	169	10
17	Cultivated orchards (med)	54	6
18	Cultivated orchards (low)	6	0
19	Cultivated vines (high)		
20	Cultivated vines (med)		
21	Cultivated vines (low)		
22	Cultivated permanent pineapple		
23	Cultivated subsistence (high)	32	7
24	Cultivated subsistence (med)	251	82
25	Cultivated subsistence (low)	265	76
26	Cultivated cane pivot - crop	100	9
27	Cultivated cane pivot - fallow	15	1
28	Cultivated cane commercial - crop	292	6
29	Cultivated cane commercial - fallow	59	1
30	Cultivated cane emerging - crop	23	2
31	Cultivated cane emerging - fallow	12	
32	Plantations / woodlots mature	240	2
33	Plantations / woodlots young	34	
34	Plantations / woodlots clearfelled	3	
35	Mines – bare	23	1
36	Mines – semi-bare	6	
37	Mines - water seasonal	1	
38	Mines – water permanent	5	
39	Mine buildings	2	
40	Erosion	27	5
41	Bare / non vegetated	24	20
42	Urban commercial	6	
43	Urban industrial	5	
44	Urban informal (dense trees / bush)	3	
45	Urban informal (open trees / bush)	1	
46	Urban informal (low veg / grass)	1	
47	Urban informal (bare)		
48	Urban residential (dense trees / bush)	30	4

Class	Description	Presence points	Absence points
49	Urban residential (open trees / bush)	7	2
50	Urban residential (low veg / grass)	1	
51	Urban residential (bare)	2	
52	Urban school and sports	3	
53	Urban smallholding (dense trees / bush)	1	
54	Urban smallholding (open trees / bush)	1	
55	Urban smallholding (low veg / grass)	2	3
56	Urban smallholding (bare)	1	
57	Urban sports and golf (dense trees / bush)		
58	Urban sports and golf (open trees / bush)		
59	Urban sports and golf (low veg / grass)		
60	Urban sports and golf (bare)		
61	Urban township (dense trees / bush)	21	
62	Urban township (open trees / bush)	8	
63	Urban township (low veg / grass)	9	
64	Urban township (bare)	1	
65	Urban village (dense trees / bush)	191	16
66	Urban village (open trees / bush)	331	24
67	Urban village (low veg / grass)	362	13
68	Urban village (bare)	1	
69	Urban built-up (dense trees / bush)	17	8
70	Urban built-up (open trees / bush)	10	4
71	Urban built-up (low veg / grass)	11	4
72	Urban built-up (bare)	1	

Table S3.2. Tukey HSD Post-Hoc analyses showing differences in individual monthly home ranges amongst juvenile Martial Eagles during there first year away from the natal territory (13 – 24 months).

Comparison	Difference	Lower	Upper	p – value
GSM58134 – GSM 09324	31.95	-1384.61	1448.51	0.999
GSM 58381 – GSM 09324	-2.35	-1418.90	1414.21	0.999
GSM 59082 – GSM 09324	2079.37	662.81	3495.93	0.001
PTT 136762 – GSM 09324	777.22	-668.31	2222.75	0.555
GSM 58381 – GSM58134	-34.30	-1384.93	1316.34	0.999
GSM 59082 – GSM58134	2047.42	696.79	3398.05	< 0.001
PTT 136762 – GSM58134	745.27	-635.72	2126.26	0.551
GSM 59082 - GSM 58381	2081.72	731.08	3432.35	< 0.001
PTT 136762 - GSM 58381	779.56	-601.42	2160.55	0.507
PTT 136762 - GSM 59082	-1302.15	-2683.14	78.84	0.073

Table S3.3. Top five candidate models ranked by AIC investigating the habitat preference of juvenile Martial Eagles in relation to the percentage tree cover (TC), elevation (El), slope (Sl) and distance to a river (Ri).

Model	Df	AICc	ΔAICc	Weight
$TC + TC^2 + El + El^2 + Sl + Ri$	8.00	74751.53	0.00	1
$TC^2 + El + El^2 + Sl + Ri$	7.00	74769.28	17.75	< 0.001
$El + El^2 + Sl + Ri$	6.00	74776.13	24.60	< 0.001
$TC + El + El^2 + Sl + Ri$	7.00	74777.27	25.74	< 0.001
$TC + TC^2 + El + El^2 + Ri$	7.00	75153.09	401.55	< 0.001

Table S3.4. Top five candidate models ranked by AIC investigating the habitat preference of juvenile Martial Eagles in South Africa, where in addition to tree cover (TC), elevation (El), slope (Sl), distance to a river (Ri), an additional land cover (LC) map was available to assess the use of natural and transformed habitats

Model	Df	AICc	ΔAICc	Weight
$TC + TC^2 + El + El^2 + Sl + Ri + LC$	13	47404.77	0.00	1.00
$TC + El + El^2 + Sl + Ri + LC$	12	47534.11	129.34	< 0.001
$TC + TC^2 + El + El^2 + Ri + LC$	12	47680.82	276.05	< 0.001
$TC^2 + El + El^2 + Sl + Ri + LC$	12	47710.02	305.25	< 0.001
$El + El^2 + Sl + Ri + LC$	11	47713.67	308.90	< 0.001

CHAPTER 4: Predicted distribution of Martial Eagles in south-east Africa: modelling occurrence under a shortage of surveys

Martial Eagle ringed for unique identification, mobbed by a Lilac-breasted Roller (*Coracias caudatus*)

© Rene van der Schyf, 2015

ABSTRACT

Understanding the area that a species can inhabit is helpful in implementing effective conservation strategies, especially when, biology or socio-economics limits surveys. The Martial Eagle is a wide-ranging predator, declining in Africa. Few dedicated surveys of its distribution exist, however, beyond some protected areas. To address this deficiency, we used maximum entropy models incorporating locations from road surveys and citizen science platforms together with underlying habitat variables to understand the distribution across the known dispersal range (ca. 390 km) from Kruger National Park, an important breeding area. Because adults and immatures may have different habitat requirements, we ran a model for each age class, and a final model using all data. Predicted adult and immature distributions generally overlapped. The overall model predicted the species is distributed across 25 % of the total model region. Models confirmed the importance of KNP; the predicted area within KNP made up 10 % of the total predicted range, and 39 % of the predicted range in all protected areas. Independent tests using known nests in KNP indicated most nests occurred within (77 %) or very close to the predicted species range. The species was predicted to occur across much of western Mozambique and many non-surveyed large reserves in the country. Eagles were predicted to occur in areas at lower elevations, closer to rivers, with intermediate tree cover, and a climate that was hotter, with greater diurnal temperature variation, lower annual rainfall and greater annual rainfall variation (high seasonality). Our analyses indicate the value of using predictive distribution models when survey data are rare: we predict that Martial Eagles may have a wider distribution in south-east Africa than has been appreciated previously.

INTRODUCTION

To conserve wide ranging threatened species effectively, conservation initiatives are often required to be implemented at large (e.g. continental) spatial scales (Swets, 1988). Achieving this depends on an adequate understanding of a species' distribution (Newton et al., 2016). Understanding a species distribution at broader scales is particularly relevant for conservation of migrants (Hunt et al., 2002), species that exhibit extensive dispersal (Latest Sightings, 2016), or wide ranging species that are prone to the threats beyond protected area boundaries (Aquila chrysaetos; Watson et al., 2014b).

Quantifying the potential distribution of species can be tackled by implementing broad scale species distribution models (SDMs) (McPherson, 2016, Murgatroyd et al., 2016a). These models have proved useful for predicting the distribution of species across large areas based on known (surveyed) distribution and an understanding of habitat and climatic variables associated with this distribution (Boshoff, 1993, Tarboton and Allan, 1984). This information is then used to predict outwards into novel space that was either not surveyed or where the species was not detected. Modern methods used to understand habitat preference such as habitat preference modelling of telemetry data can prove valuable in determining a species preferred niche, but often too few individuals are tracked to understand the range of environmental niches a species may occupy. This can make extrapolating these results across populations, landscapes or geo-political boundaries challenging (Ong, 2000).

SDMs can therefore provide an indication of a species' possible range where there might be substantial uncertainty. For example, low density, rare or threatened species are often poorly studied or difficult to locate throughout the species possible range. Similarly, in areas where survey effort is constrained by economic or social factors SDMs can improve our ability to identify areas that the species is likely to occupy, thus highlighting possible priority conservation areas Tarboton and Allan (1984). SDMs can be used to predict future ranges in the face of habitat loss and climate change (Boshoff, 1993). Therefore, these models can improve our knowledge about a species niche, which may aid in improving reserve selection, design, and management (Ong, 2000). Protected area networks across Africa play an important role in the conservation of many raptors often providing some of the last remaining habitat suitable for breeding, so identifying similar areas could play an important role in their conservation (Ong, 2000).

The Martial Eagle (*Polemaetus bellicosus*), Africa's largest eagle, is regarded as a top predator occurring at low densities in its savannah habitat, and has experienced considerable declines during the last two decades (Meyburg et al., 2007, Pérez-García et al., 2013, Rosenfield et al., 2015). Comparing reporting rates from citizen science survey data collected during the first (1987 - 1992) and second (2007 – present day) South African Bird Atlas Project have indicated that the species may have declined by 60% between the two surveys (Fernández et al., 2009, Meyburg et al., 2007). Declines in the species reporting rates in the wider countryside have been attributed to habitat loss, direct persecution, electrocution, and drowning in farm reservoirs (Newton, 1979), and potentially poor reproductive output (Chapter 5). To a lesser extent declines up to 54 % have been detected within some of South Africa's largest protected areas, such as the Kruger National Park (KNP).

KNP has been considered a stronghold for Martial Eagles in Southern Africa, hosting up to ca. 140 breeding pairs and the region has been identified as a priority for conservation efforts (Katzenberger et al., 2015), Adults of the species in KNP have large (ca. 108 km^2) home ranges, and both adults and immatures can range widely from KNP (ca. 390 km) when acting as adult non-breeding floaters or during juvenile dispersal respectively (Chapter 2 and 3). We have a better understanding of how the species is distributed within KNP through nest surveys (see Chapter 5) and beyond the borders of KNP through a limited number of GPS tracked individuals (Chapter 2 and 3), but it is still poorly understood how the species is distributed elsewhere in the region. In Swaziland, all Martial Eagle nests recorded during aerial surveys were found in protected areas Steyn (1982). Little information exists for the large protected areas in Mozambique, as the last comprehensive survey of the region preceded establishment of protected areas such as Zinave, Banhine and Limpopo National Park (Marzluff et al., 1997).

By identifying areas likely to be suitable for Martial Eagles, conservation practitioners will be better positioned to implement conservation initiatives in the region. These may include managing habitats or mitigating threats such as new wind farms (Braham et al., 2015, Haworth et al., 2006, Sumasgutner et al., 2016). Conservationists can assess the risks of habitat fragmentation (Penteriani et al., 2013) or implementing education programmes to reduce direct or indirect persecution (Steyn, 1982) in areas where the models indicate Martial Eagles are likely to be present.

Thus, the aim of this study was to predict which areas in the regions surrounding KNP are likely to be suitable for the species. To achieve this aim, we develop SDMs from sightings of the species in the region, and built our models using climatic, environmental and topographic information available both for KNP and for surrounding areas in Mozambique, Swaziland and southern Zimbabwe. These models were then validated using independent information from GPS tracked individuals and known nests within KNP. We further evaluate predicted distribution in the context of current protected area networks and highlight gaps for the species' conservation.

METHODS

Study area

We modelled species distribution over an extent similar to the known range of dispersing juvenile and adult non-breeding floater Martial Eagles from KNP (Chapter 2 and 3). Areas were then selected based on political boundaries (from here on referred to as 'regions') as this provided the most coherent framework for describing results and for managers to implement our findings at a local level. We therefore chose to model the species distribution across Limpopo and Mpumalanga Provinces in South Africa, the Gaza and Maputo Provinces in Mozambique, across Swaziland, and Masvingo and Matabeleland South Provinces in Zimbabwe, providing 7 distinct regions (Figure 4.1).

Occurrence data

Martial Eagle sightings were recorded at random during daily fieldwork and in KNP and in the Limpopo and Mpumalanga Provinces where the majority of Martial Eagle research was conducted. Locations were logged using a GPS (Garmin Oregon® 600). To improve our database we drew on `citizen scientist bird survey efforts as an additional source of occurrence data. We sourced data from the Birdlasser app developed for the recording of South African Bird Atlas Project (SABAP) data (http://birdlasser.com), and the African Raptor Databank app (http://habitatinfo.com), which both provided GPS location data. Occurrences also were collated from wildlife sightings app Latest Sightings Inc. A poster and media campaign was launched to encourage tourists to KNP to record and submit their Martial Eagle sightings. Observers provided either a GPS co-ordinate or recorded the distance along a road to the nearest road intersection. The latter reports as well as those submitted via Latest Sightings were then geo-referenced. Only one record of each sighting was included in the dataset. Age classes of birds were recorded where possible and grouped into adult or immature age classes based on plumage characteristics (Penteriani et al., 2011, Penteriani et al., 2005a).

Model approach

We calculated the predicted species distribution using presence only MaxEnt (Maximum Entropy) models (Lambertucci et al., 2014) in the R (Hunt, 1998, Penteriani et al., 2011) package 'dismo' (Carrete et al., 2002, Forero et al., 1999, Jiménez-Franco et al., 2011, Rutz and Bijlsma, 2006). The dismo package provides an R environment that communicates to the Java based MaxEnt programme. The settings and protocols were guided by recommendations in (Braham et al., 2015), (Hunt, 2015) and (Ferrer et al., 2015). MaxEnt uses species presences in a grid placed out across a landscape with each grid cell having a prescribed set of environmental values. These are used to predict the environmental niche of a species. We used a grid with cells 450m x 450m as this best fit the resolution of available environmental data (see below). To avoid pseudo-replication we removed duplicate Martial Eagle occurrences in each grid cell. We selected the model features that were biologically meaningful and suitable for the number of presence points in our dataset, thus we allowed the model to incorporate hinge, quadratic and product features, but not linear or threshold features, as these are redundant with hinge features. Regularization values were held at their default settings (0.05 for product and quadratic; 0.5 for hinge). We performed 500 model iterations. We generated three sets of models for (1) all our occurrence data regardless of age class, (2) for only immature eagles and (3) for only adult eagles.

The areas suitable for Martial Eagle occupancy was selected by calculating a cut-off predicted likelihood of occurrence value that maximized the training sensitivity and specificity during model evaluation (Lowney et al., 2017). Values above and below this likelihood of occurrence probability were recalculated into a present/absent binary.

Sampling bias

SDMs can be sensitive to the locations of occurrence data, and it is generally advised to collect data from as much of the study area as possible (Ferrer et al., 2015). Here not all areas were surveyed and this does not indicate that the species is absent in some habitat types (Figure S4.1).

This raises concerns for the interpretation of the model and much focus has been placed on developing methods for correcting this bias (Robertson et al., 1998). Methods to deal with biased occurrences include: subsampling the occurrence data to even out samples across space, selecting background samples with the same spatial bias as the occurrence data, or accounting for survey effort by selecting background data from areas where taxonomically similar species were observed (Target Group Sampling: TGS) (van Niekerk, 2011).

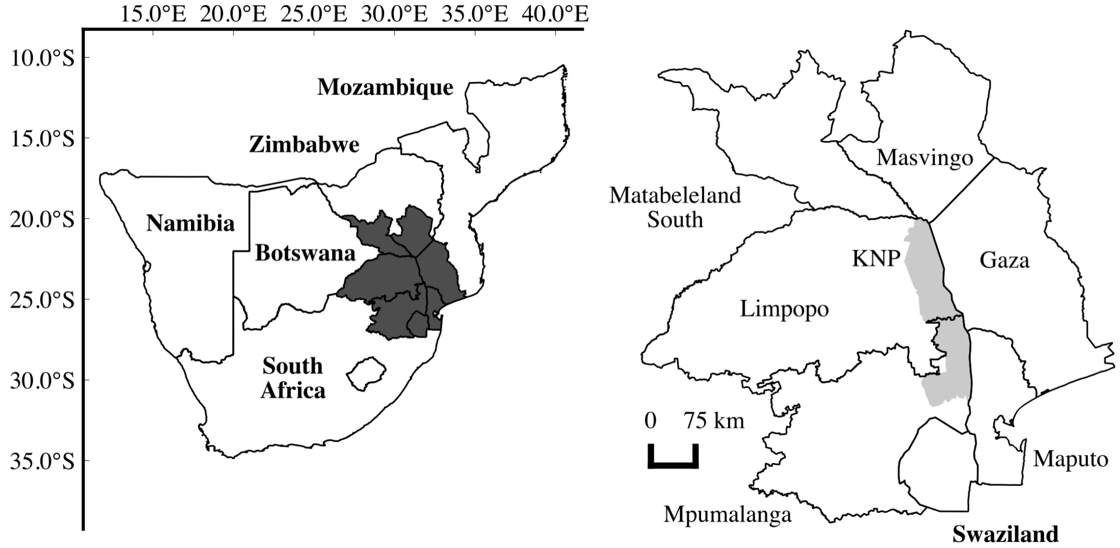


Figure 4.1. Map of southern Africa (left) and the regions (right; dark grey) where distribution of Martial Eagles was modelled. In the map to the right, the position of Kruger National Park (light grey) is shown in relation to the other study regions.

We chose to select our 10,000 background points using the TGS method (Machange et al., 2005). Background sampling was based on 23,877 locations of raptors in all taxonomic groups recorded for the Limpopo and Mpumalanga Provinces in the African Raptor Data Bank (Figure S4.1), thus providing a measure of survey effort that improves our ability to recognize if Martial Eagle occurrence bias is a result of biased sampling effort or natural distribution. To do this we created a heat map around all locations of similar species, which we used to weight our background point selection. Therefore our background samples represent areas where similar species were recorded and Martial Eagles could have also been recorded if they were present.

Environmental data

Our previous research on Martial Eagle habitat preference and ranging behaviour using GPS tracked eagles showed that the species preferred to use areas with intermediate elevation, gradual slopes, closer to rivers, and with intermediate tree cover (Chapter 2 and 3). Therefore distribution models were fitted using a 90-m resolution Shuttle Radar Topographic Mission derived Digital Elevation Model (Hustler and Howells, 1990) to infer elevation preferences (Figure S4.2) and the slope across this elevation model was calculated using the 'terrain' function in the R package 'raster' (Brown et al., 1982). To infer tree cover importance, we used a 30-m resolution tree cover map that details the proportion of tree cover over 5 m in height (Cresswell, 1996) To infer the importance of rivers, we used a 1:50 000 resolution rivers layer (Herholdt and Kemp, 1997). The rivers layer was transformed into a raster by generating a grid with a resolution of 450 m and for each grid cell we calculated the distance from the cell centre to the nearest river feature. We used four Bioclim (Bisson et al., 2002, Chandler et al., 1995, Suárez et al., 2000) layers to infer climatic preferences; these were BIO1 (annual mean temperature), BIO2 (mean diurnal range (mean of monthly (max temp – min temp))), BIO12 (annual precipitation) and BIO15 (precipitation seasonality (coefficient of variation)), which were available at a resolution of ca. 1 km. To infer land cover preferences we used the 300 m resolution Globcover (Eckhardt et al., 2000) map for 2009 which classifies land cover into 22 classes covering vegetation type, agriculture and urban areas. All environmental rasters were then aggregated to 450 m using the mean raster cell value for continuous variables, and the modal i.e. dominant categorical variable. Finally, we set all rasters to the same spatial extent.

Predicting to novel regions

When environmental background data in a novel space is under represented in the area used to train the model, it can be difficult to interpret how well the model is performing in the novel space (Eckhardt et al., 2000, Vanak et al., 2012). We produced Multivariate Environmental Similarity Surface (MESS) maps (Figure S4.3) that indicate regions of similarity to help understand how similar the environments in the novel space (e.g. Swaziland) are to the model space (e.g. Mpumalanga Province) (Asner and Levick, 2012).

Variable and model validation

Variables used in the SDM were assessed for their importance using jackknife tests. Jackknife tests allow us to understand the variables that carry the most information about the species distribution by assessing the training gain with and without this variable (Ogada et al., 2008). We assessed the correlation between variables as, even though correlation does not impede the models to predict distribution, the interpretation of response curves can be challenging when two or more variables are correlated (Cloete, 2013).

We assessed the model's predictive power using the area under receiver operator characteristic curve (often abbreviated to AUC), an approach often used in species distribution modelling (Smit and Asner, 2012). The AUC provides a measure of model performance by assessing the correct classification of presences and absences. Such that, the proportion of presence instances classified correctly (also known as sensitivity or true positive rate) are plotted against the proportion of absence instances that are classified correctly (also known as specificity or false positive rate). In presence only modelling such as MaxEnt, the AUC is calculated by distinguishing presence instances from random background rather than absences (Broomhall et al., 2004). Random predictions of presence correspond to an AUC of 0.5 and models with more predictive power have AUC scores converging towards 1. Models with good predictive power are characterized by AUC greater than 0.7 (Bautista et al., 2004). Our models were assessed by withholding 15 % of the data as test data and calculating the AUC values for both test and training datasets.

Models were further validated using an independent set of GPS tracking locations of immature eagles (n = 5) and another set using GPS tagged territory-holding adults (n = 5) from the KNP (Chapter 2 and 3). Using a binomial generalized linear mixed model (GLMM) we assessed the pseudo absence/ presence (independent variable) of tracked eagles in relation to the underlying predicted likelihood of occurrences (response variable) generated from the SDM. For each immature eagles' presence point we generated three random points (pseudo absences) within the 95 % Brownian Random Bridge Utilization Distributions (BRB UD) surrounding that individuals tracking locations. Similarly for each adult eagle we generated three random points for each tracking location within that individuals 95 % Kernel Density Estimated Utilization Distribution (KDE UD). BRB UDs and KDE UDs were calculated using the adehabitatHR package (Lian et al., 2011, Van Niekerk and Van Ginkel, 2003) in R . Individual ID was used as a random effect. The explanatory variable was the species distribution likelihood from either the immature model or adult model for the respective tracking datasets, followed by a further model for each tracking dataset where the explanatory variable was the species distribution likelihood from the overall (that used both adult and immature locations) model. The model with the explanatory variable that best predicted eagle occurrences was determined using AIC model comparison.

Lastly we used a large set (n = 65) of known nest locations across the entire KNP (Chapter 5) to model the probability of nest occurrence relative to the overall SDM predicted likelihood of occurrence. This was done using a general linear model (GLM) with absence/presence of nests as a response and SDM likelihood of occurrence as a dependent variable. Lastly, we calculated the proportion of nests within a cell above the threshold predicted likelihood of occurrence. If a nest occurred outside the threshold predicted area we calculated the distance to the nearest cell that indicated the species was likely to be present.

RESULTS

Occurrence data

Data collection across the Limpopo and Mpumalanga Provinces returned 1167 independent Martial Eagle occurrence records (i.e. no duplicates of the same individual on any one day, as far as we could reasonably determine). 1099 (93.5 %) of sightings were recorded in KNP. Author efforts accounted for 21.6 % of all sightings, and the remainder of sightings were extracted from citizen scientist databases, including 10.8 % of the sightings made by A. Botha whose records were extracted from the ARDB (Table 4.1). After removing multiple records for the same cell and accounting for age classes where this was recorded, 885 records remained for the overall model, 289 records for the adult only model, and 112 records for the immature model.

Table 4.1. The number of observations collated from varying sources used in the overall SDM.

Sightings source	Total	Adult	Immature
Latest Sightings (WhatsApp Group)	379	33	44
Birdlasser (Mobile App)	280	7	4
Authors	378	208	80
African Raptor Data Bank (Mobile App)	18	11	1
Email	94	67	15
Social Media (Facebook groups and pages)	15	13	2
Other	3	1	0
Total	**1 167**		

Environment similarity and correlation

The regions (Limpopo and Mpumalanga, South Africa) from which background data were sampled were well represented in the rest of the regions, as shown by Multivariate Environmental Similarity Surfaces (Figure S4.3). Some variables, however, showed strong patterns of dissimilarity. For instance, elevation and BIO1 in the eastern areas of Gaza Province were most dissimilar to the sampled area. Elevation and BIO1 were the only two variables that were highly correlated (R = -0.95). However we chose to keep BIO1 in the model because it provided additional information that improved prediction of the species distribution by increasing the models training gain (see below). Furthermore, distance to the nearest river is greater in the north of KNP compared to the south.

Species distribution models

Model support

The overall model (Figure 4.2) was well supported during model validation with an AUC = 0.853. Furthermore, the test data AUC closely matched that of the training data (AUC = 0.83). Similarly

AUC scores supported the adult (training AUC = 0.833; test AUC = 0.866) and immature (training AUC = 0.922; test AUC = 0.871) models equally well.

The distribution models also were supported by independent tracking data for both juvenile dispersing eagles, and territory holding adults (Table S4.1). The modelling exercise using known presences of adult and juvenile tracked birds in relation to the underlying predicted distribution showed that the overall predicted species distribution was a better predictor compared to the age class specific distributions as indicated AIC scores (Table S4.2). Martial Eagles were more likely to build their nests in areas that had a higher SDM predicted likelihood of occurrence (estimate: 1.63, Std. Err: 0.92, z value: 1.768, $p < 0.001$; Figure 4.5). Of 66 nests in the model, 71% nested within the threshold predicted area of occurrence, and it was evident that many of those in the area excluded by the threshold were close (971.58 ± 755.15 m) to overall threshold-selected cells/areas (Figure 4.4).

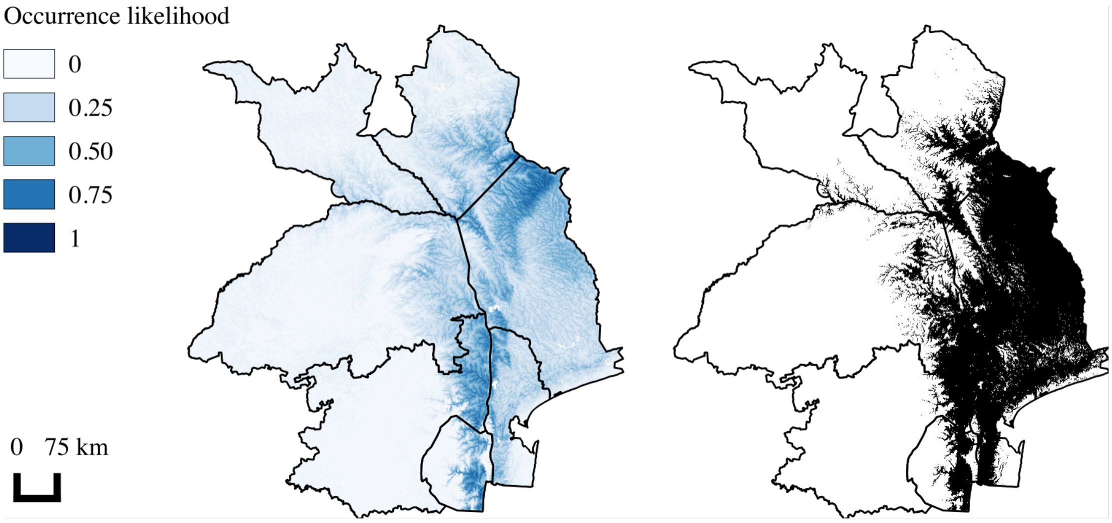


Figure 4.2. Likelihood of occurrences across the predicted regions (left) and the threshold (Maximum Sensitivity plus Specificity) selected area of occurrence for the overall model (right).

Variable importance and response

In all models, elevation contributed the most to the model (Table S4.3), and jackknife tests (Figure S4.4.1 – S4.4.3) revealed elevation was the variable that contributed to the highest gain when used in isolation and thus provides the most information about the species occurrence. The rivers layer was the second most important variable in the overall and adult models, and the third most important in the immature model. When omitted, the rivers layer contributed to the greatest decrease in gain in all models, thus the rivers layer contains the most information not present in other variables. Temperature (BIO1) was the third most important variable in the overall and adult model, and the fourth most important in the immature model. The other variables made relatively little contribution to the model and their importance varied between models.

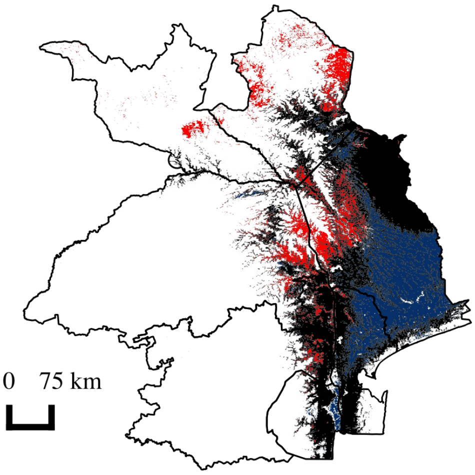


Figure 4.3. The threshold (Maximum Sensitivity plus Specificity) selected area of occurrence for the overall model. Differences in predicted areas for adults and immatures are shown. Areas in red indicate where only adults were predicted to occur in the adult only model. Similarly areas in blue indicate where only immatures were predicted to occur and not adults.

Response curves (Figure S4.5.1 – S4.5.3) suggest eagles were more likely to occur in areas with lower elevations, less steep slopes and closer to rivers. From the overall model (Figure S4.5.1), Martial Eagles preferred warmer (> 25 °C) areas (BIO1), with greater (> 10 °C) mean diurnal range (BIO2), with intermediate tree cover (0 – 10 %), with low (< 500 mm) annual rainfall (BIO12), and areas with greater variation in rainfall (BIO15). Variable responses showed that eagles were least likely to occur in closed forest areas (Globcover category 50) and most likely to occur in mosaic shrubland/grassland (Globcover category 110).

From the adult model, adult eagles (Figure S5.2) preferred cooler (< 25 °C) areas (BIO1), with less (< 15 °C) mean diurnal range (BIO2), with intermediate tree cover (0 – 10 %), in areas with low annual rainfall (BIO12), and preferred areas with greater variation (> 90 mm) in rainfall (BIO15). Again, as with the overall model, adult eagles were least likely to occur in closed forest areas (Globcover category 50) and most likely to occur in mosaic shrubland/grassland (Globcover category 110).

Immature eagles (Figure S5.3) preferred warmer (> 20 °C) areas (BIO1), with less (< 15 °C) mean diurnal temperature range (BIO2), with intermediate tree cover (0 – 10 %), with intermediate (550 mm) annual rainfall (BIO12), and areas with less variation (< 90 mm) in rainfall (BIO15). As, with the two previous models, immature eagles were least likely to occur in open forest areas (Globcover category 60) and most likely to occur in mosaic grassland/shrubland (Globcover category 120).

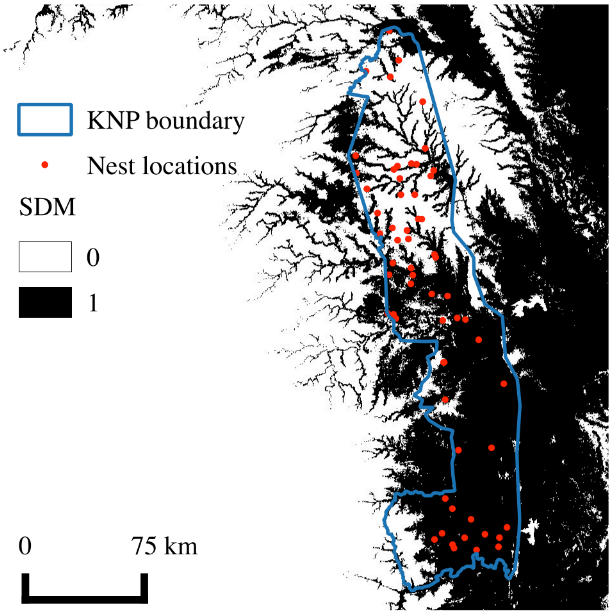


Figure 4.4. Distribution of known nests in KNP in relation to the threshold predicted species distribution within and immediately beyond KNP.

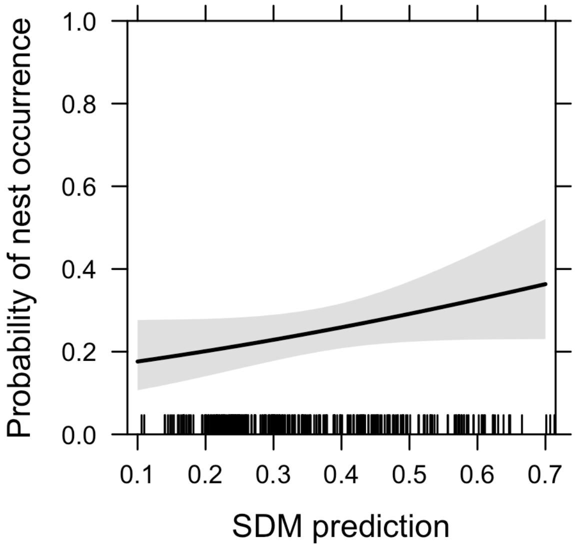


Figure 4.5. General linear model indicating the increased likelihood of nests occurring in areas predicted to have a high species occurrence probability

Predicted area of occurrence

We modelled species distribution across ca. 428,185 km^2 of which Martial Eagles were predicted to occupy ca. 122,788 km^2 (ca. 29 %). Adults were predicted to occupy ca. 89,183 km^2 and immature eagles ca. 99,071 km^2. Overall, the likelihood of occurrences was highest in the Gaza Province of Mozambique (Table 4.2, Figure 4.2). Limpopo and Mpumalanga Provinces of South Africa had high occurrence likelihoods in the eastern areas of the Lowveld where the KNP is situated (Figure 4.1). Similarly models predicted occurrences for the Lowveld region of Swaziland, and Maputo Province of Mozambique. There were differences apparent amongst areas predicted as suitable for immature and adult eagles; large areas of south-eastern Gaza Province, Mozambique, were predicted to be suitable for immature eagles, but not for adults (Figure 4.3). This area was characterized by large diurnal temperature ranges (BIO2) and low precipitation seasonality (BIO15). Furthermore, adults were predicted to occur across northern KNP, but this area was predicted as less suitable for immature eagles.

Table 4.2. The regions and the size of the regions (estimated from the number of 450 x 450 m grid cells) where the distribution of the species was modelled and area of those regions that eagles were predicted to occur by the overall model incorporating both adults and immatures.

Region	**Area (km^2)**	**Predicted area (km^2)**	**Percent of region**	**Percent of model extent**
Limpopo, South Africa	123 135	10851	8.81	2.53
Mpumalanga, South Africa	79 256	11086	13.99	2.59
Swaziland	17 341	5487	31.64	1.28
Matabeleland South, Zimbabwe	54 825	1199	2.19	0.28
Masvingo, Zimbabwe	56 080	12591	22.45	2.94
Gaza, Mozambique	74 966	65130	86.88	15.21
Maputo, Mozambique	22 596	16455	72.82	3.84
Total	**428 199**	**122 798**		

Using the overall model as the most representative model for the species distribution, protected areas covered 30,951 km^2 (ca. 25 %) of the areas where Martial Eagles were predicted to occur. These protected areas were mostly made up of KNP – South Africa (ca. 39 %), Limpopo National Park - Mozambique (ca. 21 %), and Banhine National Park - Mozambique (19 %) (Table 4.3). The area predicted for KNP accounted for ca. 10 % of the total predicted area of occurrence, and ca. 21 % of the predicted area that fell within protected areas. 65 % of KNP was predicted to be suitable habitat for Martial Eagles.

Table 4.3. Main protected areas in each region used to predict Martial Eagle distribution summarizing the area (estimated from the number of 450 x 450 m grid cells) of each protected area, and the predicted area of occurrence within protected areas.

Protected area	**Area (km^2)**	**Predicted area (km^2)**	**Percent of PA**	**Percent of all PAs**
Kruger National Park, South Africa	18 981	12 244	64.51	21.57
APNR, South Africa	2 066	1 591	77.01	2.8
Limpopo National Park, Mozambique	10 448	6 504	62.25	11.46
Banhine National Park, Mozambique	6 049	6 024	99.59	10.61
Mkhaya Game Reserve, Swaziland	100	99	98.99	0.18
Gonarezhou, Zimbabwe	4 920	3 330	67.69	5.87
Other	14 202	1 159	8.16	2.04
Total	56 766	30 951		

DISCUSSION

The distribution of Martial Eagles beyond the borders of KNP has been poorly understood until recently (Pérez-García et al., 2013). Using SDMs for the first time we were able to predict the occurrence likelihood for much of the region surrounding KNP where survey efforts have been poor (e.g. SABAP: http://sabap2.adu.org.za/coverage.php, accessed August 2016; ARDB: http://gis.habitatinfo.com/java/ardb_viewing, accessed August 2016). The predicted species distribution indicates that the Lowveld region of Swaziland and much of the Gaza and Maputo Provinces of Mozambique are potentially important regions for the species. Within South Africa and Swaziland, the results are consistent with atlas reporting rates for the species (Katzner et al., 2012). Much of western Limpopo and Mpumalanga Provinces, and western Swaziland were predicted to have no Martial Eagles, and this is well supported by historical records of nesting Martial Eagles Cullum and Rogers (2011). However, in the former Sul do Save Province of Mozambique (now Gaza, Maputo, and Inhambane Provinces) the species was suggested to be scarce, whereas our model predicts large areas of these regions have a high probability of Martial Eagle occurrence (Sexton et al., 2013). (Lehner et al., 2006) proposed that the region (including Inhambane Province to the east of Gaza) may hold as few as 200 birds, similar to that of KNP (USGS, 2008). The recorded absence of the species in areas where we predicted it should occur may be due to poor survey effort. The species could also be genuinely rare due to high mortality rates as a consequence of persecution, or because their prey base has been depleted by local hunters (Bretagnolle and Inchausti, 2005, Radford et al., 2005).

Large national parks such as KNP are important areas for the species' conservation (Franklin, 2010, Guisan et al., 2013). Within our study region, of all parks, the KNP conserved the most area where the species was predicted to occur. Similarly KNP has been identified as an important area for a number of other threatened species of raptors, e.g. White-headed Vultures (Bildstein, 2006, Faaborg et al., 2010) and should therefore receive appropriate conservation attention. Martial Eagles were not predicted to occur in large areas of northern KNP and this may be because the species was strongly predicted to occur near rivers. In the north of KNP river density is less than the south and here Martial Eagles may use smaller tributaries not mapped by the 1:50 000 rivers layer. Known nests in the northern area of KNP were often located within or very close to areas along rivers that were predicted by the threshold occurrence maps as suitable for the species.

It is worrying that the species is declining in the KNP given its highlighted importance (Elorriaga et al., 2009). These declines have been hypothesized to be due to source sink dynamics in the surrounding region as the home range and dispersal of the species extends beyond KNP borders (Riggio et al., 2013, Woodroffe and Ginsberg, 1998). The habitat in the Gaza and Maputo Provinces of Mozambique was indicated as an attractive area for KNP eagles. Mortalities detected from GPS tagged adult birds have indicated that the species is prone to unnatural mortality in Mozambique (Chapter 2), therefore supporting this hypothesis for the species decline.

In southern Zimbabwe, Martial Eagles were predicted to occur in Masvingo Province where the Gonarezhou National Park is located, but not southern Matabeleland Province. Martial Eagles are known to breed in high densities elsewhere in Zimbabwe, e.g. Hwange National Park which borders the north of southern Matabeleland Province (Bustamante and Seoane, 2004, Phillips et al., 2006, Vetaas, 2002). Gonarezhou has few records for the species in both the SABAP and ARDB, but no information in the literature could be found for the breeding status of Martial Eagles in the region.

Some of the variables that had the greatest influence over distribution were consistent with results from fine scale habitat preference modelling for both adult (Chapter 2) and immature (Chapter 3) eagles. However, the SDM predicted that eagles would avoid higher elevations that were preferred by territory holding adults. This difference likely stems from the availability of high elevations within individual territories. This is a common problem with habitat preference models using GPS tracked individuals as the results are often location specific and cannot easily be transferred to other regions or populations (Hijmans et al., 2015). Models of dispersing immature eagle habitat preference also show avoidance of high elevations. The escarpment to the west of KNP likely forms a barrier to movement for eagles in the low veld.

Martial Eagles are known live in a wide range of thermal and rainfall regimes from mesic savannah to xeric semi-desert areas where the species nests along prominent rivers (Beyer et al., 2010). Where age class was known, adults were predicted to occur in cooler regions with less diurnal variability. The differences in environmental preference between adult and immature eagles affected their predicted distribution. Although this is the first time that it is indicated that immature and adult birds may inhabit different environments, spatial separation between adult and immature age classes is not uncommon in raptors. For example, immature Spanish Imperial Eagles (*Aquila adalberti*) tend to seek temporary settlement areas that are void of adult eagles (Bustamante and Seoane, 2004, Rodríguez‐Soto et al., 2011). The ability of immature eagles to travel substantial distances during dispersal, and their reduced need for the specific habitats compared to adults seeking breeding territories, could enable immature eagles to exploit a greater range of habitats (Araújo et al., 2004, Guisan and Thuiller, 2005, VanDerWal et al., 2013). The differences in predicted area may be attributed to bias in the locations of the immature and adult records relative to environmental predictors, and may not fully represent the distribution of these age classes fairly. Future models can benefit from a wider survey effort across southern Africa.

In conclusion, these results highlight the importance of KNP within the South African context. KNP may be the most viable landscape for the persistence of Martial Eagles, providing important breeding grounds and habitat for dispersing individuals. Conservation strategies should focus on this area to mitigate further declines. This can be achieved by preserving large tracts of protected areas in the mapped areas of South Africa suggested to be suitable to the species. These maps can inform the placement of new power distribution lines, wind farms, and where to limit urban sprawl. Within the broader study region, future research should focus on trans boundary conservation efforts such as education and stricter environmental law enforcement, and identify potential Martial Eagle nest locations in predicted areas beyond KNP.

ACKNOWLEDGMENTS

Thank you to Dr. Rob Davies and Dr. Vernon Visser who helped with species distribution modelling. Rob provided data through the African Raptor Databank. Distribution models were made possible through data provided by Henk Nel (Birdlasser) and Nadav Oddendryver (Latest Sightings).

SUPPLEMENTARY MATERIAL – CHAPTER 4

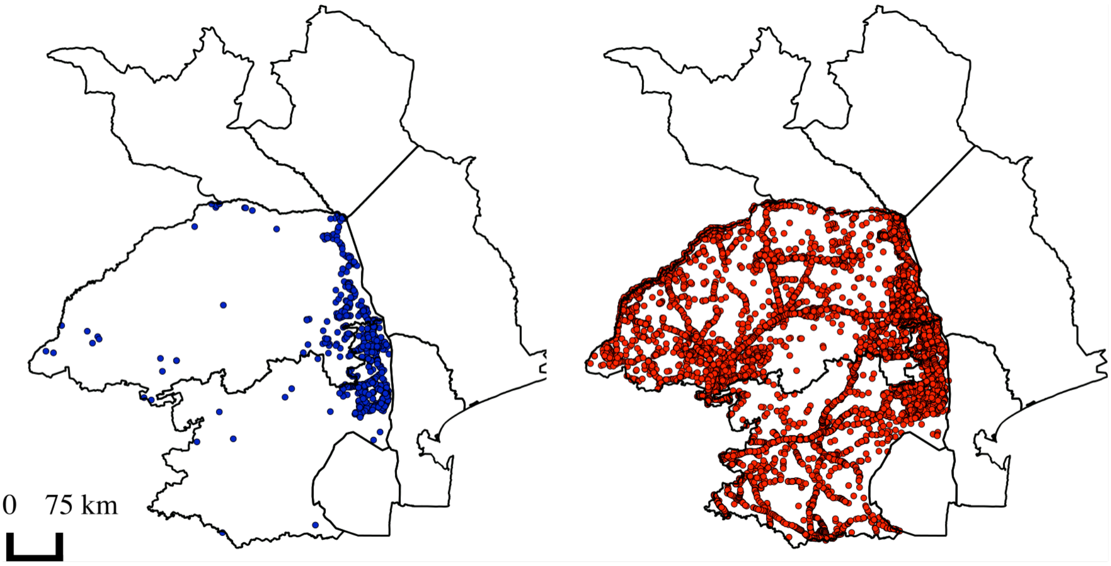


Fig S4.1. The distribution of the 1176 presence locations (left) used in the overall species distribution model, and the distribution of the 23,878 Taxonomically Similar Group locations (right) used in the creation of a bias background data set.

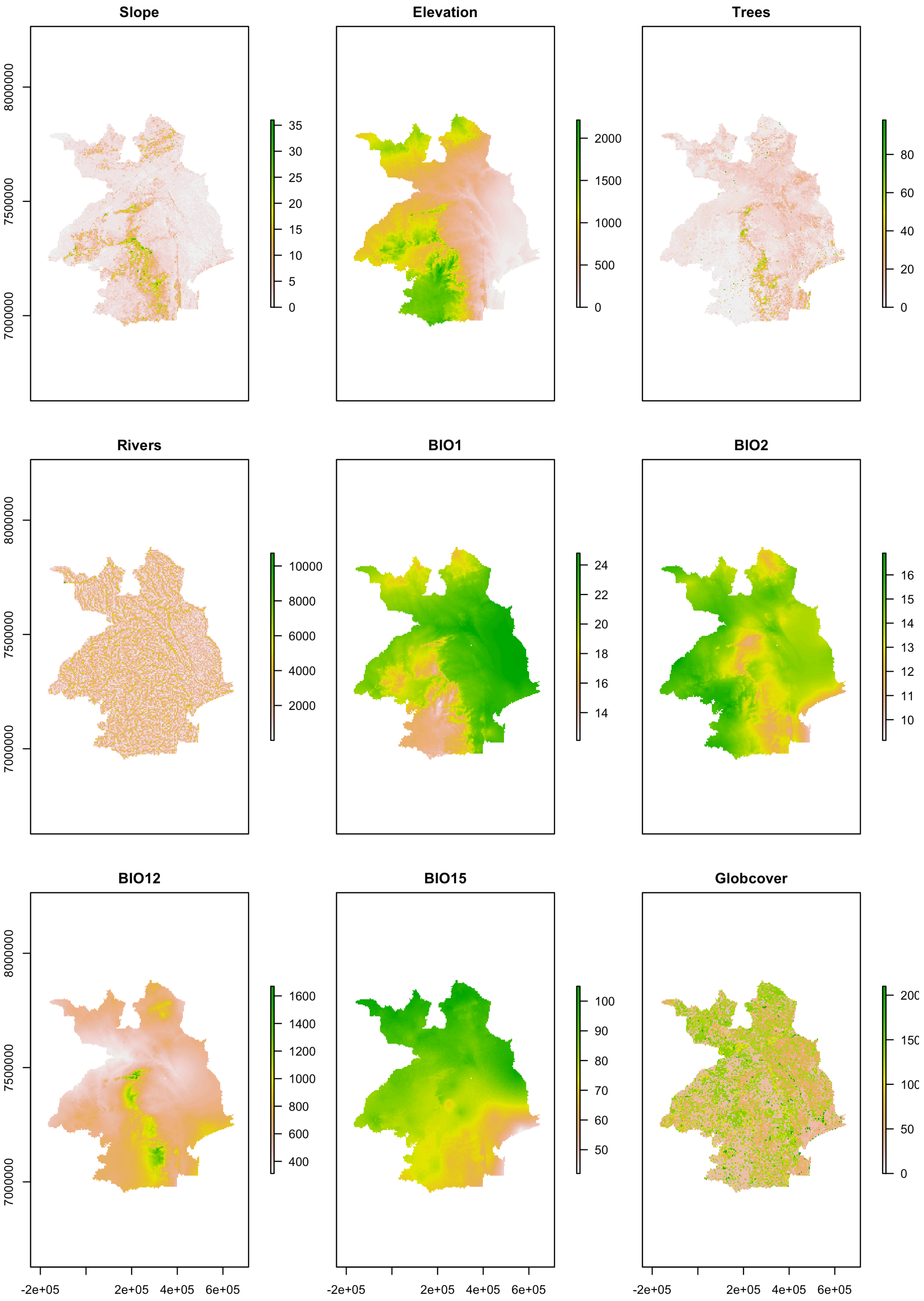


Figure S4.2. Environmental layers used in the Martial Eagle species distribution model.

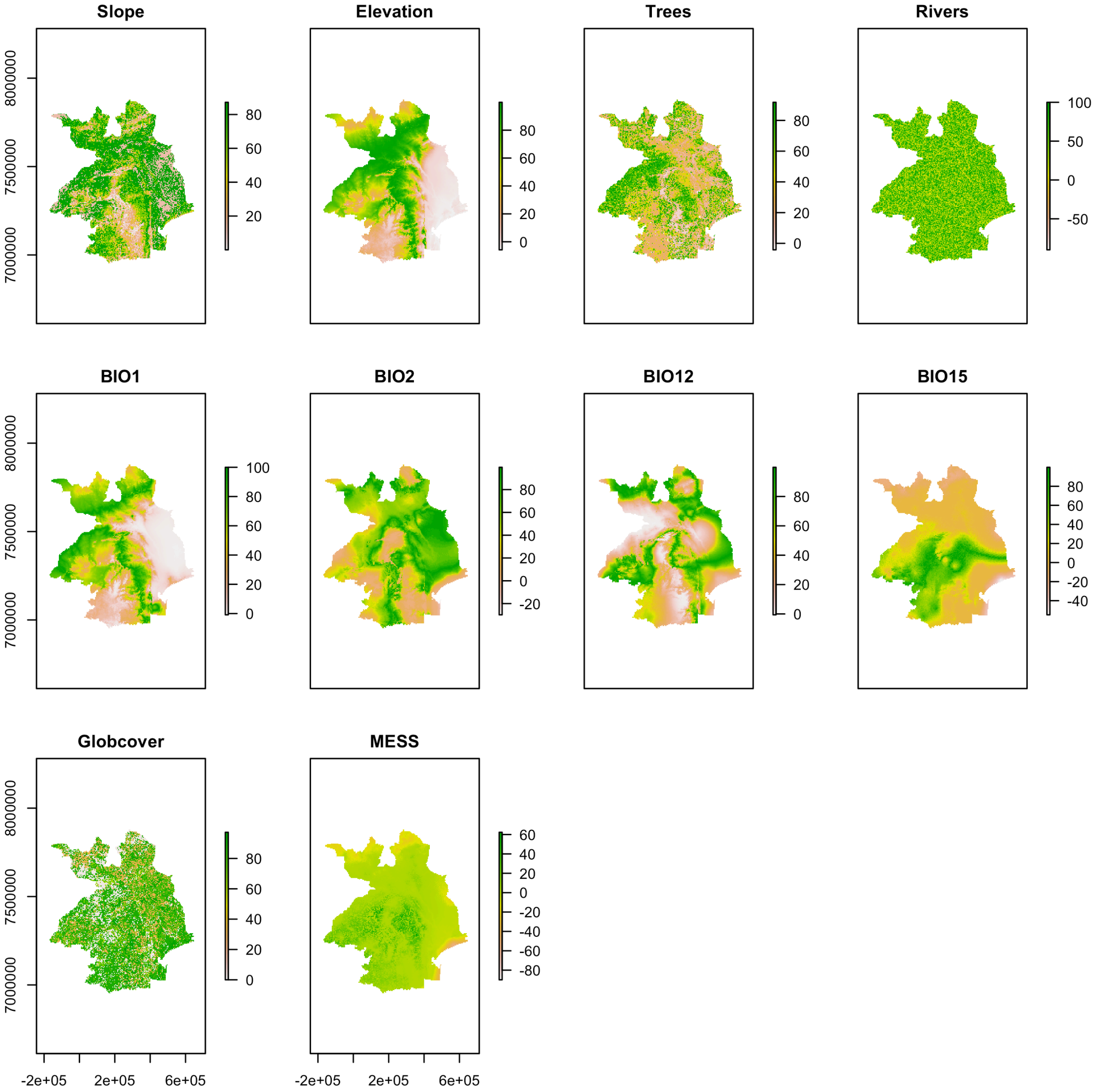


Figure S4.3. Environmental similarity between areas where background data was sampled and where models extrapolated to depicted using a Multivariate Environmental Similarity Surface (MESS; last panel). The similarity between the sample area and the predicted area are shown for each variable that made up the MESS.

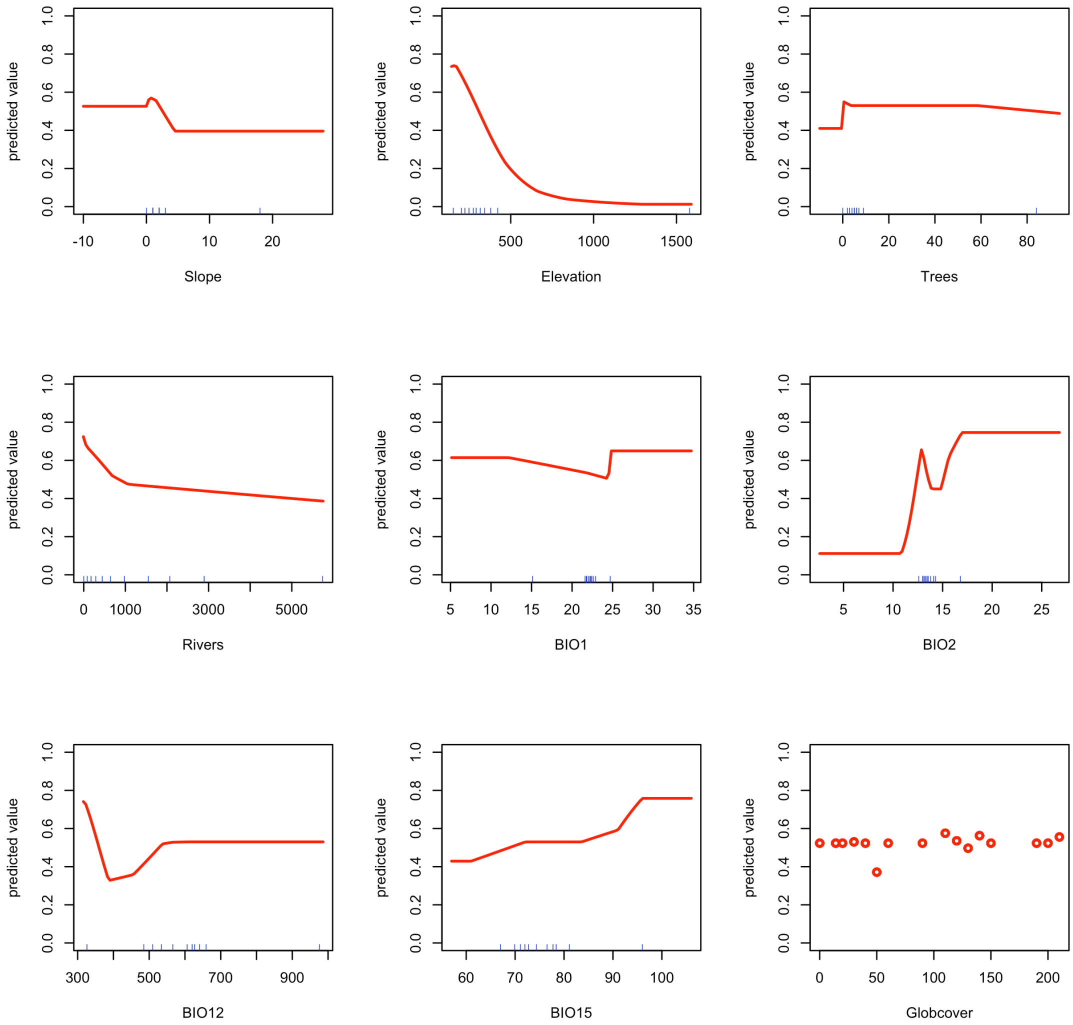


Figure S4.3.1. Response curves showing the relationship between the presence locations and each environmental variable used in the overall SDM

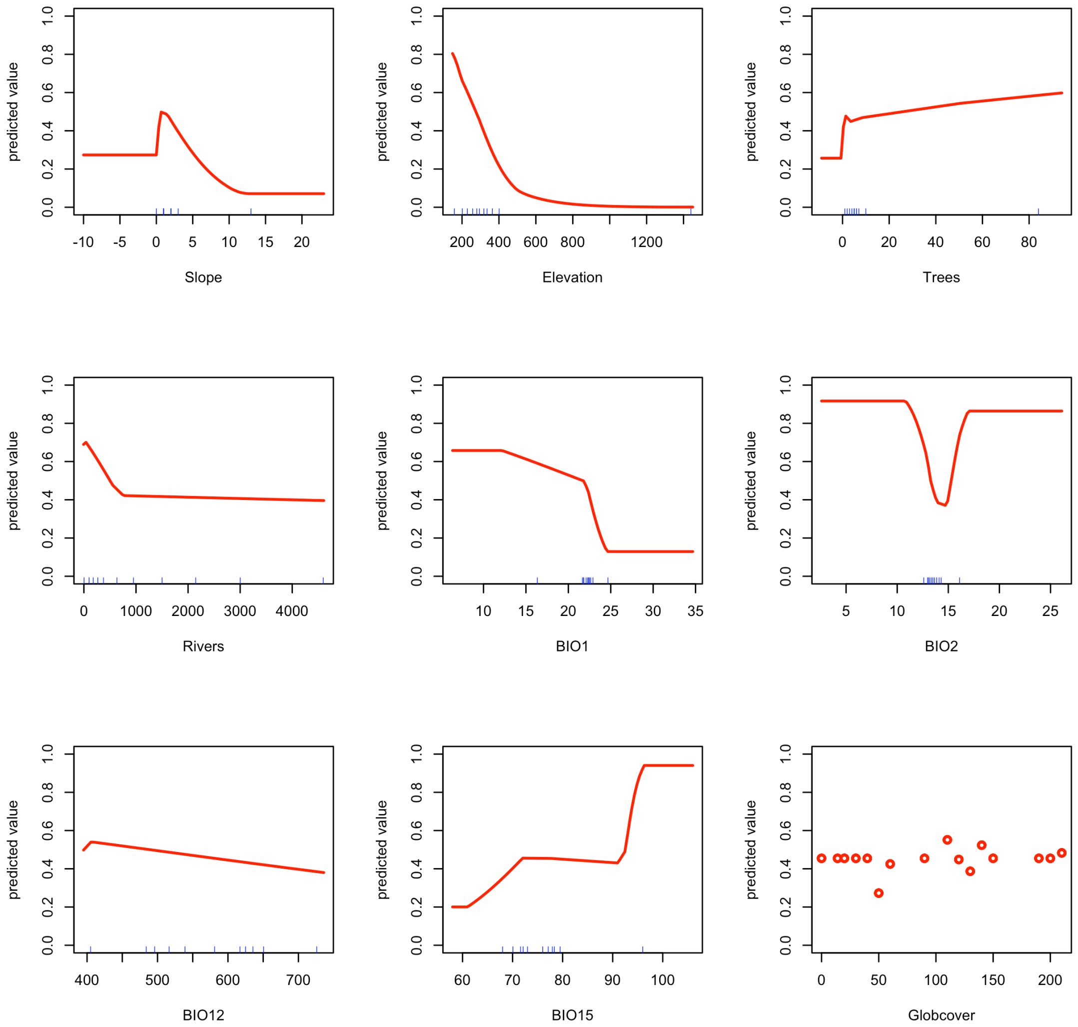


Figure S4.3.2. Response curves showing the relationship between the presence locations and each environmental variable used in the adult SDM.

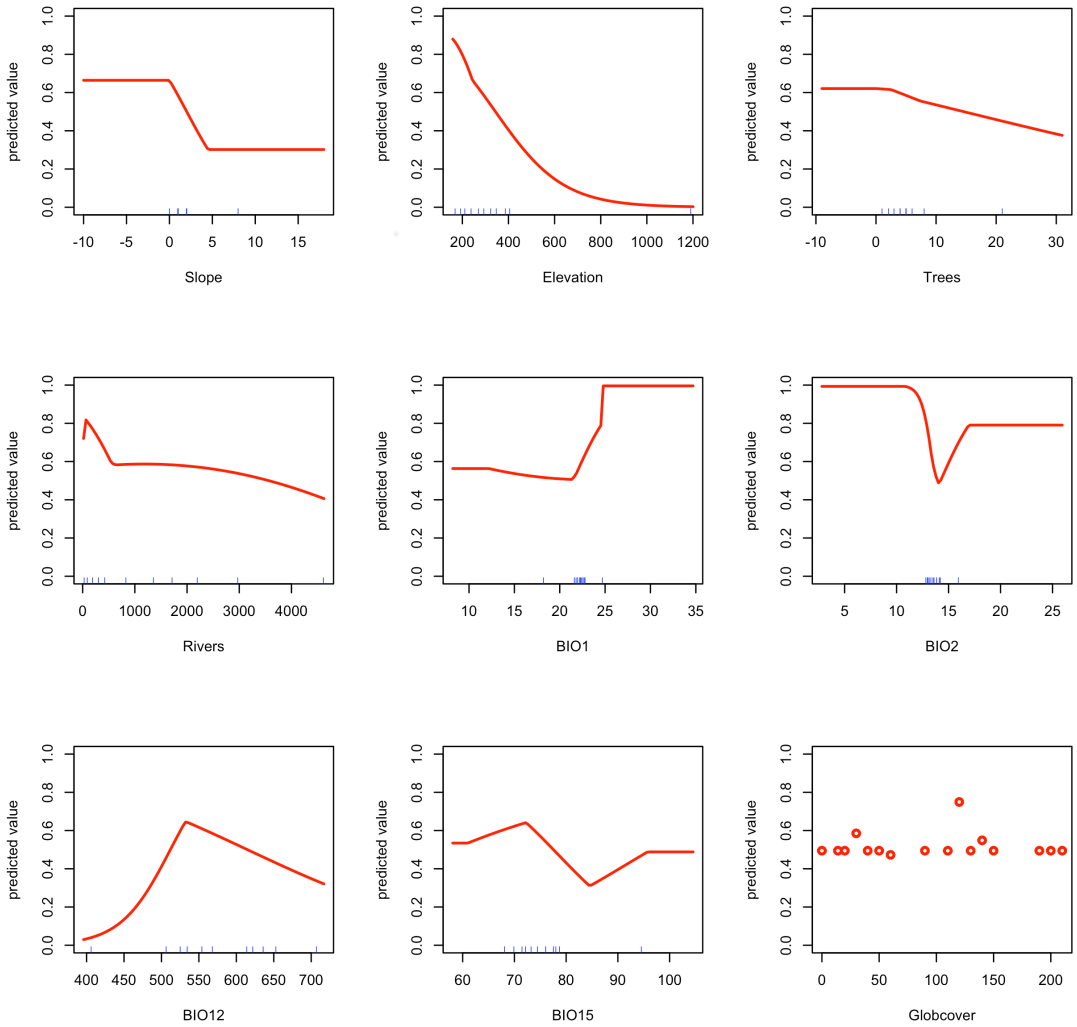
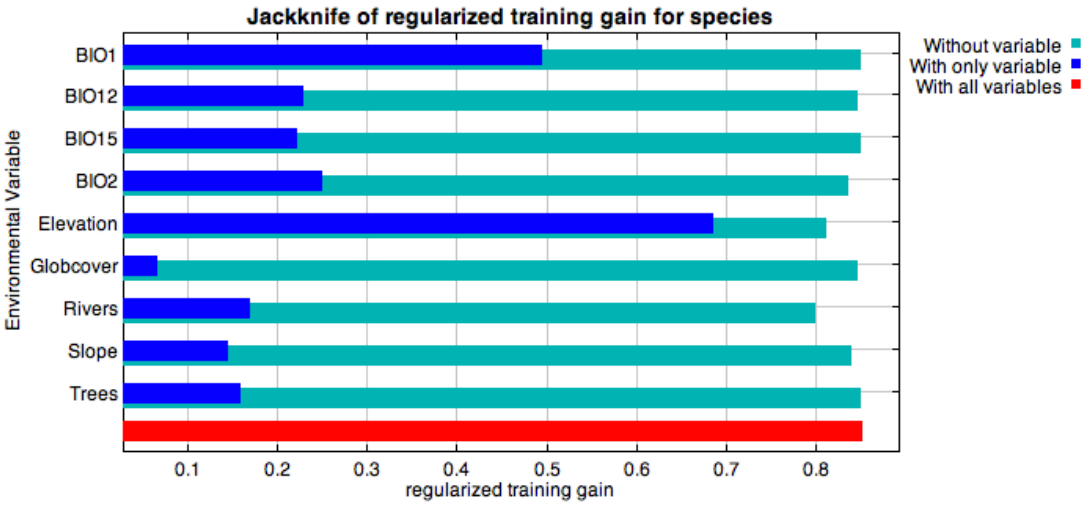
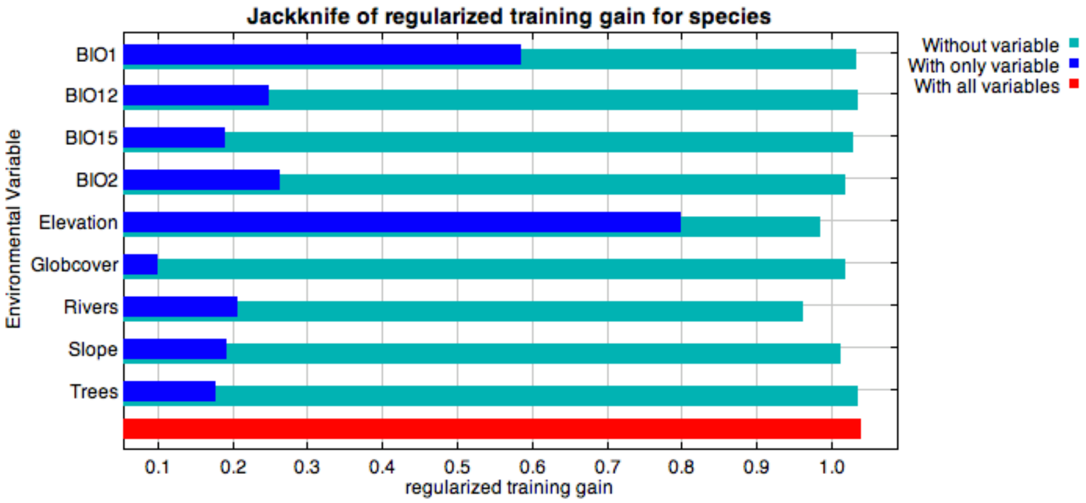


Figure S4.3.3. Response curves showing the relationship between the presence locations and each environmental variable used in the immature SDM





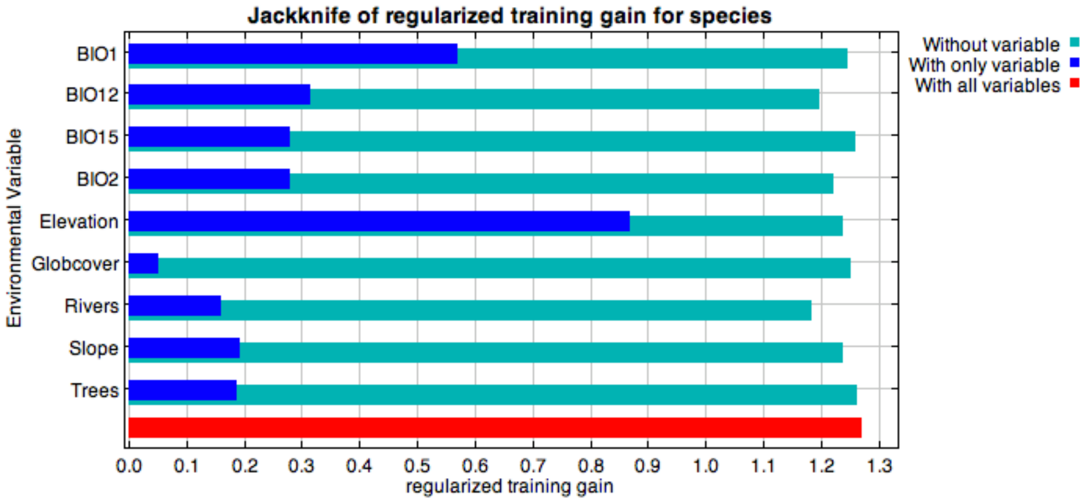


Figure S4.4.1 – 4.4.3 Variable jackknife graph for the overall model depicting relative variable importance in isolation and when excluded.

Table S4.1. Generalized linear mixed model (GLMM) predicting the likelihood of tracked eagles occurring in relation to the species distribution predicted likelihood.

Fixed effect	Estimate	Std. error	z value	Pr (>|z|)
Model: Adult presence ~ overall SDM prediction				
Intercept	1.80709	0.07481	-24.16	< 0.001
SDM prediction	1.64092	0.07197	22.80	< 0.001
Model: Adult presence ~ adult SDM prediction				
Intercept	-1.55765	0.06835	-22.79	< 0.001
SDM prediction	1.11129	0.05706	19.48	< 0.001
Model: Immature presence ~ overall SDM prediction				
Intercept	-1.74551	0.07264	-24.03	< 0.001
SDM prediction	1.50947	0.05577	27.07	< 0.001
Model: Immature presence ~ immature SDM prediction				
Intercept	-1.17547	0.02162	-54.36	< 0.001
SDM prediction	0.21833	0.04815	4.53	< 0.001

Table S4.2. AIC model comparisons explaining which distribution model best explains the locations of GPS tracked adult (model comparison 1) and immature (model comparison 2) Martial Eagles.

Model comparison 1	Df	AIC	BIC	logLik	Deviance	Chisq	Pr(>Chisq)
Adult presence ~ Adult SDM	3	108120	108148	-54057	108114		
Adult presence ~ Overall SDM	3	107979	108008	-53987	107973	140.66	> 0.001
Model comparison 2							
Immature presence ~ Immature SDM	3	78872	78899	-39433	78866		
Immature presence ~ Overall SDM	3	78162	78189	-39078	78156	709.95	> 0.001

Table S4.3. Relative variable importance in each Martial Eagle species distribution model set

Variable	Percent contribution	Permutation importance
Model: All presence		
Elevation	68	83.7
Rivers	11.2	5
BIO1	5.8	0
BIO15	5.3	0.5
BIO12	4.8	2.6
BIO2	2.2	4.8
Slope	1.7	1.9
Globcover	0.8	0.9
Trees	0.1	0.7
Model: Adult presence		
Elevation	71.7	75.2
Rivers	13.5	3.5
BIO1	4.6	3.3
Slope	2.9	5.9
Globcover	2.6	2.2
BIO15	2.4	1.2
BIO2	1.9	5.5
Trees	0.3	1.2
BIO12	0.1	
Model: Immature presence		
Elevation	59.4	59.7
BIO12	9	12.9
Rivers	8.4	3.8
BIO1	6.6	2.1
BIO15	6.3	7.4
Slope	3.8	4.4
BIO2	3	7.9
Globcover	2.1	1.1
Trees	1.3	0.7

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CHAPTER 5: Martial Eagle reproduction and nest site selection in Kruger National Park, South Africa

A young Martial Eagle engages in wing flapping over a fresh Monitor Lizard (*Varanus albigularis*) prey delivery, Longueville Bird and Wildlife Sanctuary, Zimbabwe.

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ABSTRACT

Productivity is important in population regulation, and low fecundity is known to contribute towards population declines. Understanding the reproduction of threatened species is thus an important step in identifying the potential demographic drivers of population declines. Martial Eagles are currently declining across their range, including within large protected areas such as the Kruger National Park (KNP). It is unknown what role poor productivity may play in these declines. We monitored nesting territories in the KNP over three consecutive seasons (2013 – 2015) and compared reproductive parameters to those reported for other populations and those recorded in a historical study in KNP. Although the proportion of occupied nests were similar those of other populations, productivity (0.19 young per pair per year) was lower than any study has previously reported. This productivity alone was predicted to drive population declines similar to those reported by comparing species reporting rates amongst surveys. Productivity was limited by a high failure to lay after lining a nest (38 %), and low hatching success (64 %). However, two of the three years over which data were collected were severe drought years, and it remains uncertain how representative this productivity is. Lastly we model the nest distribution of Martial Eagles using a MaxEnt model to predict the areas suitable for the species in KNP and connected reserves. At least 35 % of KNP, 58 % of the Limpopo National Park, and 38 % of the Associated Private Nature Reserves were predicted to be suitable nesting habitat and greater efforts should be made to find and assess nests in the Greater KNP region.

INTRODUCTION

Population declines can be understood in part by assessing factors that regulate population growth, such as survival and reproductive output, and assessing which of these factors contribute to negative growth rates (Ferrier, 2002, Guisan et al., 2013). For large long-lived species, adult survival is typically the most important driver of population trends; however productivity also can be a potentially important demographic variable in determining population growth (Herremans and Herremans-Tonnoeyr, 2000, Murn et al., 2016, Thiollay, 2006). Data on this component of a species life cycle are often collected in studies on low density or wide ranging species where other parameters can be challenging to collect (Amar et al., 2015, Cloete, 2013). Furthermore, long term datasets of productivity have been used to understand a wide range of ecological questions that shape population patterns and trends (Cloete, 2013, Underhill, 2012). Productivity can often be related to environmental conditions and therefore changes in productivity may act as an early indicator for environmental change (Anderson et al., 1999, Boshoff, 1993, Kemp and Kemp, 1977, Tarboton and Allan, 1984, Van Rooyen and Ledger, 1999).

For instance, reduced productivity can indicate shortages in prey availability (Cloete, 2013, Underhill, 2012), and in the late 1960s the negative effects of pesticides were identified due to the temporal links between their intense use and the large decline in hatching success in raptors (Barnes, 2000, Tarboton and Allan, 1984, Taylor, 2015). Reproduction studies may provide an opportunity to further understand the negative effects of climate change as these changes may affect productivity in some species (Monadjem and Rasmussen, 2008). Furthermore, productivity can help identify important habitats for threatened birds as it is well known that productivity may differ under different habitat conditions (Parker, 1999).

Martial Eagles *Polemaetus bellicosus* have experienced dramatic (ca. 60 %) population declines over the last 20 years, both beyond and within the boundaries of protected areas (as has been done for Bearded Vultures Gypaetus barbatus; Reid et al., 2015). Kruger National Park (KNP), often considered to be a stronghold for the species (Coetzer et al., 2010), has experienced declines in species reporting rates recorded during citizen science based atlas projects of up to 54 % (Lagendijk and Gusset, 2008). The main causes of mortality for this species have been identified as electrocution (Chapter 2, Steyn, 1982), drowning in farm reservoirs (Phillips et al., 2006) and persecution (R Core Team, 2015), which can affect birds from protected areas due to their large home ranges and the movements of dispersing young (Chapter 2 and Chapter 3). However, quantifying the mortality rates of the species are currently challenging and an on-going avenue of research (Chapter 6). Although these mortalities may increase the likelihood of population declines as the species is a k selected species (Hijmans et al., 2015), it is also unknown whether these declines are possibly driven by low productivity. Unlike mortality rates, reproduction has been better studied for other Martial Eagle populations in southern Africa Merow et al. (2013). This provides an important benchmark that can be used to determine if productivity is possibly contributing towards the observed population decline.

Martial Eagles are a low density species (one territory averages ca. 108 km^2; Chapter 2) and the number of nesting birds in KNP (ca. 137 pairs) has been estimated by extrapolating inter-nest distances across KNP Phillips and Dudík (2008). It is still poorly understood whether this upper limit is a true reflection of the carrying capacity of KNP, as the full extent of KNP may not be suitable for nesting birds (Chapter 4). Assessing the availability of habitat for nesting birds will improve our understanding of the population size and aid in targeting species conservation Phillips (2005). For instance, large trees used by nesting eagles (Liu et al., 2013, Roxburgh and Buchanan, 2010) are currently declining across KNP (Phillips et al., 2006) as a function of increasing elephant (*Loxodonta africana*) numbers and fire interactions (Chapter 2, Steyn, 1982). It has been suggested that elephant impacts could have negative implications for biodiversity required to support Martial Eagles in KNP (Phillips et al., 2006). Understanding their nesting distribution will improve our knowledge on the spatial scale at which these impacts could take place.

In this study, we first assess the productivity of Martial Eagles in the KNP. This productivity is assessed in relation to previous studies in the KNP region and elsewhere. We then use this productivity together with other estimated population variables to build a population model to assess whether productivity is sufficient alone to have driven the population declines. Second, we model the species predicted nesting distribution. By understanding the spatial distribution of nests, it is possible to estimate the likely nesting population size. Furthermore, by assessing which areas of KNP are suitable for nesting eagles, conservation mangers will better understand the regions in which to implement management strategies to reverse the species decline. These models are extended to surrounding conservation areas where little to no information on nests exists.

METHODS

Study species

Martial Eagles are long-lived (Beck et al., 2014, Kramer-Schadt et al., 2013, Merow et al., 2013, Phillips et al., 2009, Yackulic et al., 2013), reach sexual maturity at 6 years old and are considered to be sporadic breeders with some pairs passing through a number of seasons without a nesting attempt (Beck et al., 2014, Kramer-Schadt et al., 2013, Merow et al., 2013, Phillips et al., 2009). The species lays a single egg predominantly during the dry winter (April – July) months (Merow et al., 2013, Phillips and Dudík, 2008). After a successful nesting attempt Martial Eagles may forgo breeding in the next season, therefore a single fledgling is produced every second year suggesting a maximum productivity of 0.5 young per pair year over the long term (USGS, 2008). Martial Eagles build large nests (> 2 m wide and deep) in the fork of tall (> 7 m) trees (Hijmans, 2015). Nests are easily identifiable in the region because no other eagles build large stick nests in KNP other than African Hawk Eagles (*Aquila spilogaster*), however their nests are constructed from smaller sticks. Incubation periods have been estimated to last 47 – 51 days (Sexton et al., 2013). Martial Eagles have variable productivities in different regions (Lehner et al., 2006) and this may be due to differences in habitat quality, prey availability or rainfall (http://www.worldclim.org; Hijmans et al., 2005).

Study area

KNP is a 20,000 km^2 (ca. 400 km north to south and ca. 50 km east to west) national park (IUCN category II, http://www.iucn.org) and South Africa's flagship protected area. It is located on the eastern boundary of South Africa and forms the border with neighbouring countries Mozambique to the east and Zimbabwe to the north (Figure 5.1). KNP forms part of the Greater Kruger National park, an unfenced 35,500 km^2 conservation area that incorporates a network of private reserves to the west collectively known as the Associated Private Nature Reserves (APNR), and forms part of the

Limpopo Transfrontier Park, incorporating the Limpopo National Park (Limpopo NP) to the east of KNP. KNP is characterized by relatively low elevations (ca. 200 - 840 m ASL). The region receives austral summer rainfall with a distinct rainfall gradient from 450 mm in the north to 700 mm in the south of KNP (Bontemps et al., 2011). Annual rainfall in the region typically shifts between above and below average rainfall on a 10 year wet (above average rainfall) and dry (below average rainfall) cycle (Phillips et al., 2009, Zurell et al., 2012). For practical management, KNP is divided into 22 sections, each with a section ranger responsible for the integrity of the management unit.

Nest locations

Martial Eagle nests were located during three aerial surveys to determine densities of tree nesting vulture and eagle species in KNP (Elith et al., 2010). Each survey covered ca. 1/3 of KNP to reach complete coverage across three years (2011, 2014, 2015). Surveys were conducted during September when most raptors, including Martial Eagles, are brooding young or have large nestlings. Surveys were conducted as a series of east-west transects flown from a helicopter with transect paths spaced 2 km apart, flying ca. 300 m above ground level and at a speed of ca. 140 km.h^{-1} following methods in (Phillips, 2005).

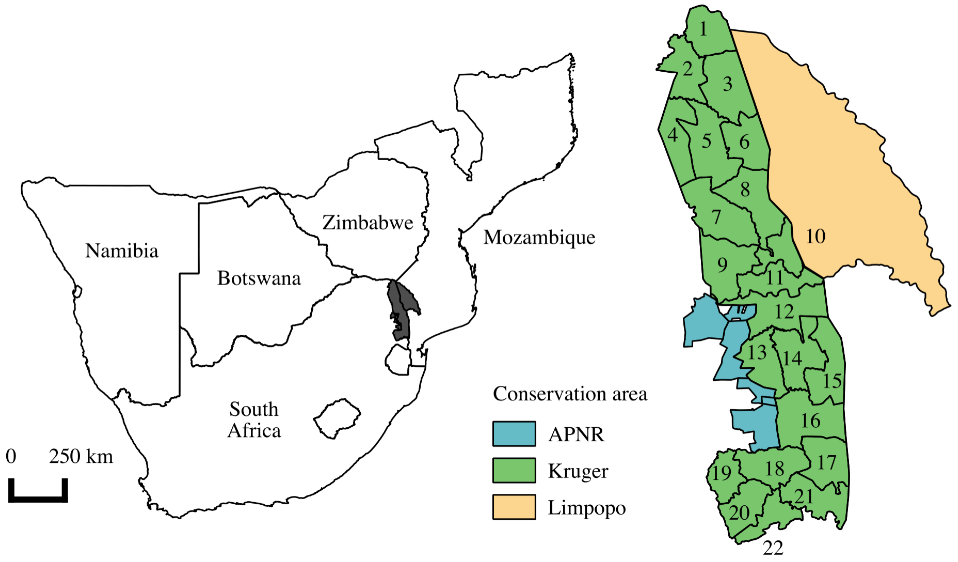


Figure 5.1. The location of Kruger National Park (KNP), Limpopo National Park and the Associated Protected Nature Reserves relative to neigbouring countries (left) and the division of KNP into 23 management sections (right), namely: 1. Pafuri, 2. Punda Maria, 3. Vlakteplaas, 4. Shangoni, 5. Woodlands, 6. Shingwedzi, 7. Mahlangeni, 8. Mooiplaas, 9. Phalaborwa, 10. Letaba, 11. Olifants, 12. Houdtbosrand, 13. Kingfisherspruit, 14. Satara, 15. N'wanetsi, 16. Thsokwane, 17. Lower Sabie, 18. Skukuza, 19. Pretoriuskop, 20. Stolsnek, 21. Crocodile Bridge, 22. Malelane.

When a nest was located we recorded the location, circling the nest as closely as possible to get an accurate location. Additional nests were located by chance and reported by rangers when performing aerial anti-poaching patrols or other aerial surveys (e.g. annual Rhinoceros (*Ceratotherium simum*) surveys). Nests also were located from road transects conducted on tourist roads and management tracks, and by searching areas on foot where eagles had been seen carrying prey during the breeding season. Furthermore, several nests were located by monitoring the movements of GPS tracked female eagles (Chapter 2). Where possible, tree species was recorded and nest locations were ground truthed using a GPS. The height of nest trees was recorded where possible using a 15 m telescopic pole as reference.

Terminology

We define reproductive terms (Table 5.1) based on recommendations by Steenhof et al. (2017), Steenhof and Newton (2007) and (Postupalsky, 1974). In some cases descriptions are expanded to accommodate methods used in this study. In other cases new terms (e.g. hatching success, nestling survival, reproductive parameter) are introduced that were not satisfied by established descriptions.

Defining a territory and calculating nest densities

Martial Eagles may have multiple nests within the same territory that are used alternatively (Chapter 2). To calculate productivity per occupied nesting territory we were required to account for the possibility that two or more nests may belong to the same nesting territory (pair). Therefore using GPS tracking data for four adult female eagles, we measured the distance from each of their nests to the edge of their 95 % kernel density estimated territory boundary (Chapter 2). This defined the minimum distance between a nest and the next nesting territory, and twice this distance was therefore used to group nests that may belong to the same pair, thus defining a group of nests in the same nesting territory. Inter-nest distances were then calculated between each nest and the nearest neighbour in a different territory to calculate inter territory nest distance, a measure that has often been used to calculate territory sizes of Martial Eagles.

Nest observations and territory occupancy

Nest checks took place from 2013 – 2015. Initially we aimed to visit as many nests as possible from the beginning of the breeding season (April), visiting each nest once per month until late November when most young fledge. When a nest was determined to be unoccupied for the season, these nests were visited less regularly due to logistical challenges in monitoring a large number of nests in an area as large as KNP. Nest contents were checked using a 15 m telescopic pole fitted with a GoPro HD video camera (Hero 4, GoPro Inc., California, USA). Nest contents were recorded into stages as:

Table 5.1. Reproductive terms used to describe breeding behaviour of Martial Eagles. Descriptions in italics are quoted from Steenhof et al. (2017). Terms and descriptions in bold are either our expansions one the quoted descriptions or terms that are relevant to this work.

Term	**Description**
Alternative nest	*"One of potentially several nests within a nesting territory that is not being used for laying eggs in current or given year"* (Millsap et al. 2015)
Apparent Nesting Success	*"The ratio of the number of successful pairs to the total number of pairs in a population with known outcomes. (Can be based on all territorial pairs or only laying pairs; Steenhof and Newton 2007)."* **We base our nesting success on only laying pairs.**
Breeding season	*"A synonym for nesting season: the time from courtship through dispersal of young".*
Hatching success	**The proportion of eggs laid that hatch; calculated as the proportion of eggs per nesting attempt or the proportion of eggs in a population. Here we define hatching success as the proportion of eggs hatched in the population.**
Minimum Acceptable Age for Assessing Success	*"A standard nestling age* (**56 d of age for Martial Eagles (Hustler and Howells, 1987)**) *at which a nesting attempt can be considered successful. An age when young are well grown but not old enough to fly: often defined as 80% of the age that young of a species normally leave the nest of their own volition, but may be lower (65–75%) for species in which age at fledging varies considerably or for species that are more likely to leave the nest prematurely when disturbed* (Steenhof and Newton 2007)".
Nesting attempt	*"Any activity involving egg-laying as determined by observation of an egg, young, a bird in incubation posture, or other evidence indicating recent use of a nest for incubation of eggs or rearing of young".*
Nesting success	"*The proportion of territorial pairs or laying pairs that raise at least one young to the minimum acceptable age for assessing success* (Steenhof and Newton 2007)", **which we define as 56 d of age for Martial Eagles. We define nesting success based on the proportion of laying pairs (Apparent nesting success).**
Nestling	*"A young eagle that has not fledged from the nest. The terms 'eaglet' or 'young' can be used as substitutes for nestling. The term 'young' is a broader term that can be used to describe either nestlings or fledglings".*
Nestling survival	**The proportion of hatched nestlings that survive to fledging. Suggested as 56 d for Martial Eagles (Hustler and Howells, 1987)**
Non-laying pair	*"A territorial pair of eagles that does not lay at least one egg in a given year".*
Occupied nest	*"A nest that contains eggs, young, or an incubating bird, or has a pair of birds on or near it, or has been recently repaired or decorated"* (Postupalsky 1974, Millsap et al. 2015)". **We include white wash and recent prey remains as evidence for an occupied nest.**
Occupied nesting territory	*"A nesting territory inhabited by a pair of birds, as evidenced by an occupied nest (see above), or a pair of birds copulating, displaying, or defending a nest."* **A nesting territory was assumed to be occupied throughout the study period if occupation was noted in at least one year.**
Pair years	**Cumulative number of years in a population that a territory was occupied.**

Term	Description
Productivity	*"The number of young that reach the minimum acceptable age for assessing success (56 days for Martial Eagles); usually reported as the number of young produced per territorial pair (occupied nesting territory) in a particular year"* (Steenhof and Newton, 2007). **We report productivity as the number of young produced per occupied territory over the course of the study (pair years).**
Reproductive parameter	**We define a parameter as any factor that makes up the reproductive cycle e.g. the proportion of individuals that lay eggs, those eggs that hatch, those young that survive to fledging, or the factors by which success is measured including nesting success and productivity.**
Successful nest	*One in which at least one young reaches the minimum acceptable age for assessing success"* (Steenhof and Newton, 2007). **Suggested as 56 d for Martial Eagles.**

empty, lined (when visible green sprigs were present), an egg, or nestling. The nestling age was determined using a photographic reference in (Phillips, 2005). Occupied nests were visited once per month up until incubation, and then once in each reproductive stage after incubation onset to minimize disturbance.

To calculate productivity it was important to define territory occupancy because the presence of a nest may not signal the presence of a nesting pair. Newly discovered nesting territories that showed no signs of occupation were therefore excluded from analysis until they showed signs of occupancy. If a territory was occupied at least once in the study we based our calculations (e.g. productivity) on the full territory history, assuming occupation throughout the study period.

Reproductive parameters and periodicity

To determine at what stages of the reproductive cycle nests failed to be successful we calculated the percentage of pairs at occupied nests that failed to hatch an incubated egg (hatching success), or fledge a brooded young (nestling survival). Furthermore we calculated the proportion of occupied nests that resulted in a nesting attempt. Productivity (young per pair year; ypy) was calculated as the number of chicks fledged from the number of occupied territories following (Barnes, 2000, Boshoff, 1997, 2005, Taylor, 2015). If a nest was monitored up to a point where the success of a nest could not be recorded due to logistics (e.g. a pair was still incubating or a nestling was less than 56 days old at the time of the last nest check), then these nests were excluded from the productivity and success calculations in the given year. To determine breeding periodicity we assessed the interval between nesting attempts.

Population modelling

We tested whether the productivity in KNP was sufficient to sustain the population, and whether past declines could be explained by productivity alone using a stochastic population model in programme VORTEX 10 (Monadjem and Rasmussen, 2008, Tarboton and Allan, 1984). We assessed the population extinction risk using our productivity measure and those measured in various other studies (Figure 5.2) by holding the other population parameters constant and assessing the changes in the probability of extinction. To standardise productivity measures, we recalculated productivity from other studies where detailed data tables were available, for instance other studies have included derelict or collapsed nests in their productivity calculations (Parker, 1999) and we exclude these. If predicted population declines were observed using the productivity measured in our study, we increased the productivity by one percent point increments to calculate a minimum productivity required to maintain a stable population growth rate ($\lambda = 1$).

We used an estimated nesting population (110 pairs) of Martial Eagles in KNP Parker (1999) to establish baseline demographic parameters for our population model. We used the best-known demographic measures for Martial Eagle adult mortality (137 pairs; Tarboton and Allan, 1984) and because immature mortality rates are poorly known for the species because of small sample sizes (Chapter 2) we used those from other, well-studied, large eagle species with similar life history traits to Martial Eagles. Therefore we used the best case mortality rates from the biologically similar Golden Eagle (*Aquila chrysaetos*) which can be as high as 10 % for immature, and 16.6 % in the first year of life (Parker, 1999). Additional parameter settings can be found in supplementary Table S5.2.

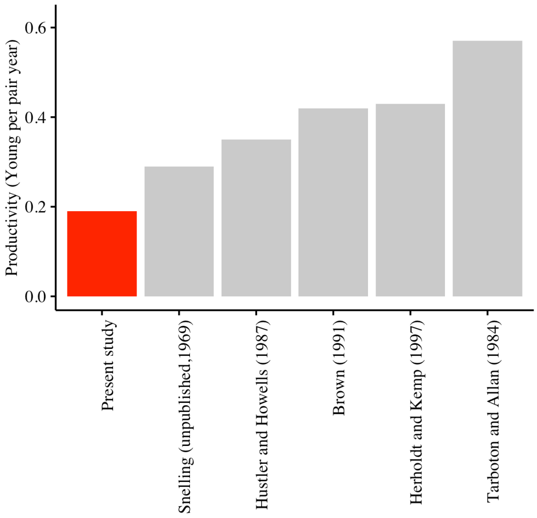


Figure 5.2. Martial Eagle productivity in the Kruger National Park (KNP) during this study (red) compared to the productivity recorded during past studies.

Nest distribution model

To model nest site selection we assessed nest site characteristics in relation to habitat availability within KNP with a MaxEnt (Taylor, 2015) distribution modelling algorithm in programme R (Trignoceps occipitalis; Murn et al., 2016), using the dismo package (Cloete, 2013). The model then predicted into the novel space of the APNR and Limpopo NP in Mozambique. Martial Eagles are thought to typically nest in tall trees close to drainage lines on flat or undulating ground, but this requires empirical investigation (Chapter 2, Chapter 3, Penteriani et al., 2005b). To test these assumptions we used GIS layers with regional coverage in our nest distribution model as was done for modelling the predicted distribution of the species from sightings (Chapter 4). These variables (Table S5.3) included elevation, the derived slope, % tree cover (Monadjem and Rasmussen, 2008), distance to major rivers (Parker, 1999), climatic variables (Hustler and Howells, 1990), and a map of land cover (Herremans and Herremans-Tonnoeyr, 2000, Murn et al., 2016, Thiollay, 2006). Environmental data was aggregated to a 450-m grid, thus even the few nest locations taken from aerial surveys that were not ground truthed were likely represented within the correct grid cells describing the environment around the nest (Figure S5.1).

The area considered suitable for nesting was established using the threshold of predictions that maximized the model training sensitivity plus specificity (max SSS), and a second less strict threshold, the equal training sensitivity and specificity (equal SS) threshold (Beyer et al., 2010). The percent of area suitable for Martial Eagles to nest in was then calculated for KNP. The percent of each of the 22 management sections of the KNP was calculated in order to help inform management decisions at a local level. We calculated the percent of areas suitable in the Limpopo NP and the APNR as almost no information exists about the possible nest distribution in these potentially important conservation areas. Lastly the number of possible territories in each conservation area (KNP, APNR, Limpopo NP) was calculated using the average territory size (ca. 108 km^2) for nesting Martial Eagles (Chapter 2).

Model fit was evaluated using Area Under the Receiver Operator Curve (AUC). Models with strong predictive power typically have AUC values greater than 0.9, moderate predictive power between 0.7 - 0.9, and poor predictive power when the AUC value is < 0.7 (Herholdt and Kemp, 1997).

RESULTS

Reproductive parameters and periodicity

We conducted nest checks at 57 nests in 48 territories (Table S5.3). Thirty-five of 48 territories were occupied (73 % occupancy) at least once during the study period. In total we recorded 81 pair years of data. Pairs lined a nest in 48 instances (59 %), and laid an egg in 30 instances (37 %) (Table 5.1).

From the 30 laid eggs, 18 hatched; another 2 nests were not checked subsequently and it was unclear if hatching took place so we excluded them from our calculations (hatching success: 18/28 = 64 %). From the 18 eggs that we confirmed to have hatched, 15 young fledged. Another two were younger than 56 days old during the last nest check and it was unclear if they survived to fledging, so we excluded them from our nestling survival calculation (nestling survival: 15/16 = 94 %).

Table 5.1. Number of pair years and the proportion of individuals that laid an egg, an egg hatched successfully, and proportion of nestlings that survived to minimum acceptable age for assessing success in Kruger National Park (KNP) compared to historical studies in KNP and elsewhere. The present study is shown in bold and records are ranked to emphasise comparisons with previous studies.

Pair years		
Location		Reference
Zimbabwe, Hwange	144	(Ferrer and Harte, 1997)
South Africa, Kalahari Gemsbok National Park	88	(Nijman and Van Balen, 2003)
Present study	**81**	
South Africa, Transvaal	63	(Beissinger and Westphal, 1998, Hunt, 1998, Peery et al., 2004)
South Africa, Kruger National Park	24	Snelling (unpublished, 1969)
Namibia, Central Namibia	12	(Katzner et al., 2006, Ortega et al., 2009)

Nesting attempts		
Location		Reference
Zimbabwe, Hwange	58	(Katzner et al., 2006, Murgatroyd et al., 2016b, Pulliam, 1988)
South Africa, Transvaal	54	(Katzner et al., 2007)
South Africa, Kalahari Gemsbok National Park	53	(Westemeier et al., 1998)
Present study	**30**	
Namibia, Central Namibia	6	(Crawford et al., 2006, Rodríguez and Bustamante, 2003)
South Africa, Kruger National Park	12	Snelling (unpublished, 1969)

Hatching success (%)		
Location		Reference
Namibia, Central Namibia	100	(Amar et al., 2005, Crawford et al., 2006, Steenhof et al., 1997)
South Africa, Transvaal	92	(Ratcliffe, 1970)
South Africa, Kalahari Gemsbok National Park	89	(Stevenson and Bryant, 2000)
South Africa, Kruger National Park	82	Snelling (unpublished, 1969)
Present study	**64**	
Zimbabwe, Hwange	50	(Amar et al., 2008, Murgatroyd et al., 2016b, Pulliam, 1988)

Nestling survival (%)		
Location		Reference
Zimbabwe, Hwange	95	(Amar et al., 2015, Cloete, 2013, Underhill, 2012)
Present study	**94**	
Namibia, Central Namibia	89	(Taylor, 2015)
South Africa, Kalahari Gemsbok National Park	81	(Cloete, 2013, Underhill, 2012)
South Africa, Transvaal	83	(Oatley, 1998, van Rooyen and Grantham, 1998, Van Rooyen and Ledger, 1999)
South Africa, Kruger National Park	67	Snelling (unpublished, 1969)

The proportion of successful nests over the course of the study was therefore 58 %, lower than any previous study (15 fledglings from 26 eggs with known outcome; Table 5.2). Overall, we recorded a productivity of 0.19 ypy (15 fledglings from 81 pair years), lower than any other previous study (Figure 5.2). If both nestlings younger than 56 days fledged, productivity may have been higher (17/81 = 0.21 ypy). In no cases did a pair attempt incubation in a year following a successful nesting attempt.

Table 5.2. Nesting success of Martial Eagles in Kruger National Park (KNP: 2013 - 2015) compared to historical records in KNP and elsewhere in Africa. Records are ranked from high to low to emphasize where the present study (in bold) ranks in comparison with historical studies. Table is updated from (Anderson et al., 1999).

Nesting success		
Location	Success (%)	Reference
South Africa, Kalahari Gemsbok National Park	72	(Barnes, 2000, Brown, 1991, Herholdt, 1998, Oatley, 1998, Tarboton and Allan, 1984)
South Africa, Kruger National Park	67	Snelling (unpublished, 1969)
South Africa, Transvaal	78	(Pulliam, 1988)
Zimbabwe	78	(Herholdt and Kemp, 1997, Hustler and Howells, 1987, Tarboton and Allan, 1984)
Present study, Kruger National Park	**58**	

Population model

Our population model indicated that under the current level of productivity (0.19 ypy) the population would decline, but would not result in extinction within 50 years (Figure 5.3; Table 5.3). Similarly, one previous study in the KNP had a productivity sufficient to drive declines (Figure 5.3; Table 5.3). After 20 years the KNP population was predicted to decline by 39.7 % (N = 87). A productivity of at least 0.37 ypy was required to maintain a stable population growth rate (λ = 1, probability extinction = 0, N-extant = 220 ± 36), similar to studies elsewhere in Africa (Figure 5.3; Table 5.3).

Table 5.3. VORTEX model results showing the probability of extinction (PE), deterministic growth rate (λ), and predicted number of extant individuals after 50 years under the current productivity in KNP compared to the productivity reported in previous studies.

Productivity	Reference	λ	PE	N-extant ± SD
0.57	(Tarboton and Allan, 1984)	1.03	0	345 ± 7
0.43	(López-López et al., 2007)	1.01	0	273 ± 59
0.42	(Tarboton and Allan, 1984)	1.01	0	256 ± 60
0.35	(Eckhardt et al., 2000, Levick and Asner, 2013)	0.99	0	132 ± 42
0.29	Snelling (unpublished, 1969)	0.98	0	66 ± 24
0.19	**Present study**	0.95	0.008	**22** ± 10

Nest distribution

65 nests were recorded in KNP (during the three aerial surveys: 43, and during other survey methods: 22). Based on our definition of nests belonging to a territory, we recorded one territory containing three nests (ca. 1.7 %) and seven territories containing two nests (ca. 12.5 %), with the remainder (48) only containing one nest as far as we could reasonably ascertain. The distance between nests we assumed to belong to the same pair averaged 2.88 ± 1.78 km, while the minimum inter-nest distance between different pairs averaged 5.71 ± 0.97 (min: 4.61, max: 6.8 km). During the study period 8 nests were lost (ca. 17 %): 4 nests collapsed, 3 nesting trees were lost with unknown cause, and 1 nesting tree was lost to fire.

Tree species was recorded for 47 of the 65 known nests (Table S5.6). Martial Eagles used seven species of trees; *Acacia nigrescens* (38.3 %) and *Combretum imberbe* (34.0 %) were the predominant species used (Table S5.6). Nest trees were 15 ± 2 m tall (n = 33).

Our MaxEnt model predicting the distribution of nests was well supported, with an AUC = 0.731. The variables that best predicted the nests distribution of Martial Eagles, in order of their contribution, were areas with relatively shallow slopes, a low mean diurnal temperature range, lower annual rainfall, low elevation, close to rivers, with intermediate tree cover (ca. 10%), with greater rainfall seasonality, and areas with higher annual temperature (Figure S5.2). However there was almost no discernable preference for any specific annual mean temperature. Martial Eagles tended to avoid nesting in grasslands. Slope contributed the most gain when retained in the model as the only predictor (i.e. excluding all other variables; Figure S5.3), thus slope provided the most information about the species nesting distribution. The variable that contributed to the greatest decrease in gain

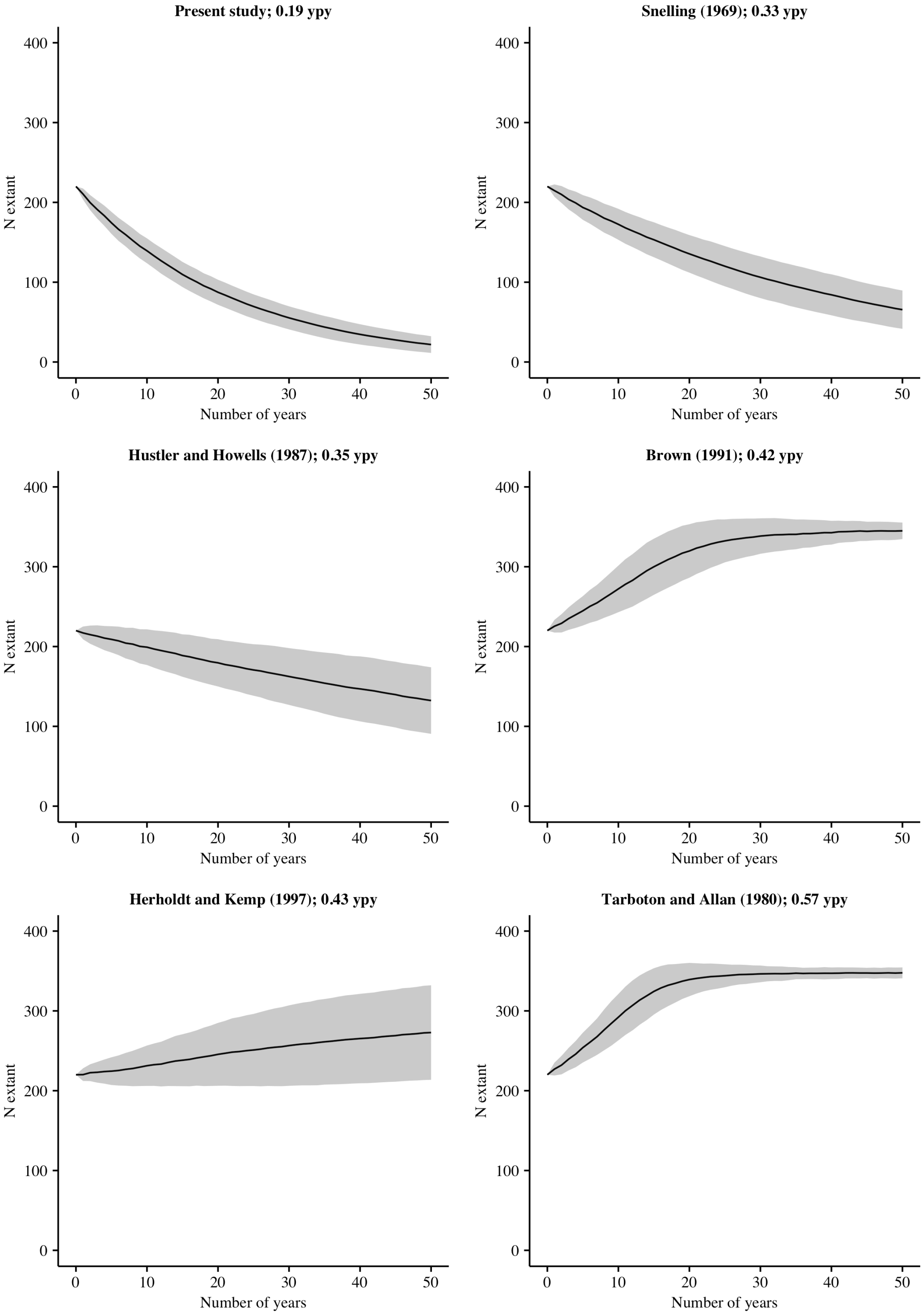


Figure 5.3. Population size (number of extant eagles) over time predicted from a stochastic population model using various productivity measures recorded for Martial Eagles.

when omitted from the full model and thus provides the most information not present in other variables was the climatic variable BIO12 which describes annual precipitation.

By applying the max SSS threshold (0.608), only 43 % of nests occurred in areas predicted to be suitable for nests (Figure 5.4). Applying the more relaxed equal SS threshold (equal SS; 0.484), 75 % of nests were within an area the model predicted to be suitable. Therefore we continued to use the equal SS method in all other calculations as we felt that it would be less likely to exclude areas that may be suitable for nesting. Thus, the model predicted that at least 6629.2 km^2 of KNP (34.9 %), 6084 km^2 of Limpopo NP (58.2 %), and 777.6 km^2 of the APNR (37.6 %) were suitable for nest placement. KNP could thus support ca. 60 nesting pairs (or 67 when calculated for each management section as the number of 450 m cells; Table 4), Limpopo NP ca. 55 pairs and the APNR ca. 7 pairs. The proportion of each section predicted to be suitable for nests (Table 5.4), suggested that Mahlangeni section was the section with the highest suitability for nests; Pretoriuskop section was the least suitable section for eagles to nest in.

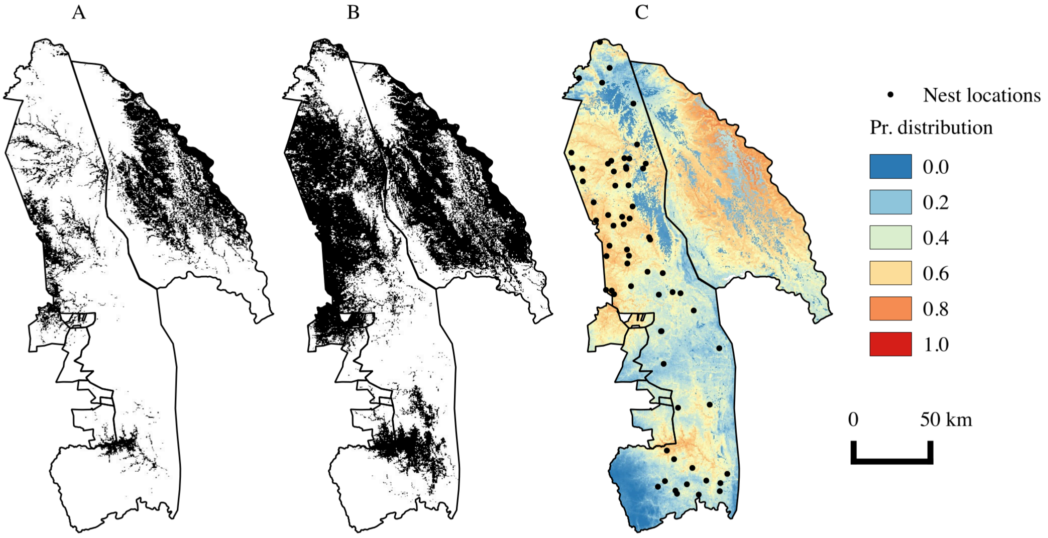


Figure 5.4. Predicted distribution of nesting habitat based on (A) the maximum sensitivity plus specificity (max SSS), and (B) the equal sensitivity and specificity threshold selection methods. The probability of occurrence is depicted relative to known nest locations used in the model (C).

Table 5.4. Predicted area of martial eagle nesting habitat and the likely number of nests in each section

Section	Area[1] (km^2)	Predicted area[1] (km^2)	% Coverage	Predicted pairs	Known nesting pairs
Pretoriuskop	2585	4	0.15	1	0
Stolsnek	3344	5	0.15	1	2
N'wanetsi	4514	24	0.53	1	1
Malelane	2621	16	0.61	1	0
Kingfisher Spruit	3796	68	1.79	1	1
Satara	4631	96	2.07	1	0
Crocodile Bridge	4031	222	5.51	1	7
Houtboschrand	5709	580	10.16	1	2
Olifants	3444	470	13.65	1	2
Letaba	2755	503	18.23	1	1
Vlakteplaas	5420	1108	20.44	2	1
Pafuri	3665	828	22.59	2	3
Thsokwane	5785	1712	29.59	3	2
Lower Sabie	3960	1550	39.14	3	1
Skukuza	4169	1667	39.99	3	2
Punda Maria	3900	1568	40.21	3	1
Mooiplaas	5097	2277	44.67	4	2
Shingwedzi	3818	2754	72.13	5	4
Phalaborwa	5090	3693	72.55	7	6
Woodlands	5631	4833	85.83	9	5
Shangoni	4060	3487	85.89	6	4
Mahlangeni	5731	5269	91.94	10	9
Total				67	56

1. Area based on the number of 450 m cells covering each section and may vary from true section polygon area

DISCUSSION

Once species declines are detected, understanding the mechanism causing the decline requires multiple avenues of research that identify the agents using temporal e.g. before or after declines are detected, or spatial comparisons e.g. declining vs. stable populations (Asner and Levick, 2012). The reproductive ecology of Martial Eagles has been studied historically (see references in Table 5.1), providing some comparison with current productivity and reproductive parameters. Therefore we aimed to assess if this component of their life cycle was potentially responsible for driving declines and compared reproductive parameters to previous studies. One study by (Cloete, 2013) assessed productivity in KNP and the surrounding Province (former Transvaal Province). Within KNP, three unpublished studies have recorded the reproduction of the species (J Snelling, A Kemp and T Cade: 1966 – 1969; J van Jaarsveld and A Kemp: 1982 – 1991; A Kemp and K Begg: 1991 - 1993). Data were retrieved from one of these studies, Snelling et al. (1966 - 1969).

KNP Martial Eagles in this study had a nesting success and productivity lower than any of the previous studies that have been carried out across Africa, as well as in the KNP. However the proportion of pairs that lined their nests (59 %) was most similar to (ca. 32 years; Paijmans, 2016)

(46 %) and Snelling (unpublished data) (50 %). The study by (Steyn, 1982) which took place 1975 – 1981 in the KNP and surrounding Province, showed that the region previously had the highest recorded productivity of any Martial Eagle population. However their productivity was unlikely a realistic measure and most likely over represented individuals in a nesting year, as 87 % of birds tended to their nests in that study. Low productivity may have been driven by a large proportion of individuals that failed to lay an egg (63 %) after lining a nest. In other raptor species, the propensity to breed has been shown to be related to local habitat condition (Tarboton and Allan, 1984), prey availability, and male provisioning rates (Herholdt and Kemp, 1997, Hustler and Howells, 1987); in some cases when these factors are constraining, population declines can occur (Steyn, 1982). The current study was carried out during a period of drought, particularly in two of the three years which had the lowest rainfall recorded in over 15 years (Tarboton and Allan, 1984). The low rainfall conditions during this study may explain the very low productivity estimate in KNP, as primary production is low during droughts and could have potentially reduced prey availability.

Failure during nesting may have resulted in low productivity. Nesting pair success was lower than that recorded in any historical study, and a low hatching success rate (64 %) ultimately limited the productivity of the population. Hatching success has been estimated to be over 80 % in some populations (Steyn, 1982). Low hatching success rates in other avian species may be linked to unfavourable climatic conditions and shortages in prey (Herholdt and Kemp, 1997), low reproductive success as a result of an aging population (Howells and Hustler, 1984, Hustler and Howells, 1987, Hustler and Howells, 1990), or a low genetic diversity within small and declining populations (Hustler and Howells, 1987). Therefore the low hatching success could be linked to unfavourable nesting conditions in KNP. Further research is required to determine which habitat variables could potentially constrain reproduction. For instance a prey provisioning experiment at nests during the breeding season may improve productivity. This was successful in increasing the productivity of Spanish Imperial Eagles (Gertenbach, 1980), and may demonstrate that prey availability is a limiting factor for Martial Eagles in KNP.

In contrast to poor hatching success, nestling survival was high in KNP. Only one failure to fledge occurred at this stage when a large nestling likely fell from the nest. Despite an abundance of predators that may impact nesting Martial Eagles (Gertenbach, 1980), no evidence for nestling predation was recorded.

Martial Eagles are typically sporadic breeders and it has been stressed that long term datasets are needed in order to make substantial conclusions when assessing productivity in relation to local prey, climatic conditions etc. (Murn and Botha, 2016, Murn et al., 2013). Our results stem from a short study period and it remains unclear if these results are a true reflection on long-term productivity. The low productivity recorded could be a result of two caveats. First, it is possible given the large territory sizes of Martial Eagles that pairs may have bred at alternative nests not identified during aerial surveys or other nest searches. Few pairs (ca. 12.5 %) had known alternative nests compared to other studies in the region; alternative nests were present in at least 18 % (van Jaarsveld, unpublished notes) to 44 % Murn et al. (2013) of the population historically. From four adults GPS tagged during this study and that had known nests, two (50 %) had alternative nests (Chapter 2). It is likely that more pairs may have had alternative nests and thus we underestimated productivity when birds bred at alternative nests. However, the productivity of these individuals was similar to the overall monitored population (Chapter 2). Second, the addition of new nesting territories into our study as they were discovered could have over-represented pairs in a non-breeding year, effectively reducing our productivity estimate.

Although we observed a population decline using this productivity measure, the modelled population trend may have been influenced by the chosen demographic variables. Although we modelled a best-case scenario using mortality rates from robust studies of similar species, such a sporadic breeding species is likely to have very high survival rates across its life cycle. In the KNP, first year mortality of GPS tagged birds, (reported in Chapter 2), was relatively low and we may have over estimated this component of the model. Future studies can benefit from more robust population parameters and a complete modelling approach that incorporates elastic tests of parameter sensitivity to determine the most important variables driving population trends Steenhof et al. (2017), Steenhof and Newton (2007). If however our estimates are a true reflection of long-term productivity, this may very well contribute to the observed declines in the KNP population by reducing the number of new individuals present in the population, and thus limiting recruitment of new breeders (Postupalsky, 1974). The productivity in KNP is therefore cause for concern and the underlying drivers need to be more thoroughly investigated.

Nest site selection and distribution

Martial Eagles predominantly nested in *A. nigrescens and C. imberbe*. Similarly, in previous studies Martial Eagles predominantly nested in these tree species Steyn (1982). The loss of tall trees in KNP with limited recruitment is concerning provided the importance of tall trees for a multitude of nesting birds of prey (Steenhof and Newton, 2007). Tall trees in KNP are often pushed over by elephants Hustler and Howells (1987), and as a result, Martial Eagle declines may be driven by a shortage of appropriate nesting sites Tarboton and Allan (1984). Over the course of the study, 17 % of nests were lost, with tree fall contributing to almost half of these losses. Fire was the main driver of tree loss, however the interaction between fire and elephant damage on trees has been well established (Steenhof and Newton, 2007). Fire impacts may limit the nesting pair success of eagles (Hustler and Howells, 1987) and this should be investigated for Martial Eagles as fire plays an important role in savannah systems and an adaptive management plan for fire for KNP is under continuous development Herholdt and Kemp (1997).

A high proportion of one-nest territories compared to previous studies, as an alternative to the explanation provided above, could signal a shortage of suitable nest sites on a territory scale. Modern imaging (e.g. airborne LiDAR) products are able to map tree species such as *A. nigrescens* with high precision at the landscape scale (Lacy and Pollak, 2014) providing an opportunity to assess the availability of nesting sites for Martial Eagles. However, albeit on a small scale (10 km^2) (Hustler and Howells, 1987) reported that there were ca. 125 *A. nigrescens* trees in the 12 m and taller height class in a 1000 individual sample. Nevertheless, tree height alone may not be the sole predictor for nest tree selection, as eagles need a prominent tree fork or limb to build their nest on (Murn et al., 2012). Alternative nests in eagles are important for reducing parasite loads in nests and for reducing nest site competition (6.7 %; Herholdt and Mendelsohn, 1995), and are important in the conservation of species where nest sites are limited (Hunt et al., 1998, Newton et al., 2016). Therefore, future research should consider the differences in nesting success of pairs with more than one nest, and assess the nest site availability for the species.

KNP sections with the highest likely nest presence were found on the western boundary, north of the Olifants River. Sections associated with the Sabie River were predicted to be favourable sections. Sections around and including Satara, as well as areas around Malelane, had the lowest relative predicted areas for nesting. Conversely, surveys of tree nesting vultures suggest that densities are typically higher in the south of KNP than in the north (Maximum Entropy; Phillips et al., 2006). However, the habitat preferences of these species may be largely driven not only by tree availability, but also by greater scavenging opportunities (R Core Team, 2015); mammal and predator densities are typically higher in the south of KNP compared to the north (Hijmans et al., 2015). Within the management of KNP, these sections can be managed accordingly to preserve the features that influence nest site distribution.

Raptor nest site selection is typically constrained by nest site and prey availability (Herholdt and Kemp, 1997, Steyn, 1982, Tarboton and Allan, 1984). Thus, the variables predicted to be important for eagles theoretically should positively influence nest site availability and prey. The structural composition of the vegetation across KNP, and the factors influencing this composition has been well established (USGS, 2008). Tree (height > 5.5 m) cover for species used by Martial Eagles, such as *A. nigrescens,* are often associated with riverine habitat and the extreme south of KNP where rainfall is higher (Sexton et al., 2013). Martial Eagles nested closer to rivers, thus matching the distribution of their main nest tree species. Alarmingly, elephant (*Loxodonta africana*) impacts on trees tends to increase closer to rivers thus possibly impacting nesting raptors (Lehner et al., 2006).

(http://www.worldclim.org; Hijmans et al., 2005) noted that the reporting rates of Martial Eagles experienced greater declines in areas with higher elephant impact. This again indicates that nest site availability or ecological degradation in areas suitable for nesting may be, in part, driving the declines of the species through reduced productivity. As a management strategy, nest platforms could be installed in areas where nests have collapsed to encourage breeding (Bontemps et al., 2011). The influence of prey availability on nest site selection requires further assessment and the abundance of prey may either limit Martial Eagles in their choice of nesting sites (Liu et al., 2013) or have little effect as shown for Bonelli's Eagles (Swets, 1988).

Martial Eagle nest selection was associated with low annual rainfall with high seasonality and *A. nigrescens* trees are more likely to be present in areas with late dry season rainfall, supporting the influence of rainfall seasonality on nest site selection. This seasonality may benefit nesting eagles which tend to incubate during the dry winter, and fledge young in the wet summer Hustler and Howells (1987). Tall trees in general are typically located in areas with lower woody cover < 10 % Herholdt and Kemp (1997), similar to the tree cover nest site selection of Martial Eagles.

Mean temperature did not strongly predict the distribution of nests, however Martial Eagles preferred to nest in areas with a low diurnal temperature range. Although the variability in temperature has not been used to describe tree distributions in KNP, temperature seasonality can influence the distribution of some tree species Tarboton and Allan (1984). Climate is an important factor that may influence the nesting pair success in eagles Brown (1991). A low diurnal temperature range could benefit eagles during incubation by reducing thermal stress and the associated metabolic effect when adjusting between very cool or very warm conditions Hustler and Howells (1987). Over the last ca. 30 years in the KNP region of South Africa, temperatures are generally cooling, however rainfall is declining Tarboton and Allan (1984). The ability for Martial Eagles to thus locate and allocate sufficient resources to reproduction may be compromised as was suggested by Herholdt and Kemp (1997) for Tawny Eagles (*Aquila rapax*) nesting in arid habitats.

Conclusion

In conclusion, the productivity and nesting success of Martial Eagles requires continued monitoring to determine if the low reproductive parameters observed in this study are consistent through time and not due to a small sample size or short term ecological conditions such as drought. If the current performance levels do hold, the populations' low productivity may be contributing towards population declines and will limit the species recovery. This should be taken into account in a species recovery plan. Other factors driving declines such as adult survival should be assessed as these parameters typically drive declines in large raptors. Martial Eagles are possibly constrained by nest site selection at the territory scale, and this is concerning in the context of large tree loss in KNP.

Greater attention should be paid to the preservation of nests and an assessment of nest site availability. A supplementary feeding experiment, although challenging to implement, could determine whether the population is limited by prey availability and could provide important direction for this species conservation.

ACKNOWLEDGMENTS

We thank Dr. Campbell Murn for nest location data and discussion. We thank SANParks and pilot Charles Thompson as well as the Bateleurs and pilot Eugene Couzyn for assistance with aerial surveys. Scott Ronaldson and Leigh Combrink provided aerial survey support.

SUPPLEMENTARY MATERIAL – CHAPTER 5

Table S5.1. VORTEX stochastic population model parameters

Simulation input	Setting
Scenario settings	
Number of iterations	100
Number of years	50
Duration of each year	365
Run as population based model	No
Extinction definition	One sex remains
Number of populations	1
Species description	
Inbreeding depression	No
EV correlation	0.5
Reproductive system	
Relationship	Monogamous
Age of first offspring females	6
Age of first offspring males	6
Maximum lifespan	32
Maximum number of broods per year	1
Maximum number of progeny per brood	1
Sex ratio at birth (%)	50
Density dependent reproduction	No
Reproductive Rates	
% Adult females breeding	57; 43; 42; 35; 29; 19
Distribution of broods per year	0; 1
Mortality rates (%)	
Mortality 0 – 1 years	16.6 ± 2
Mortality 1 – 5 years	10 ± 2
Mortality ≥ 6 years	6.7 ± 2
Catastrophes	
Number of catastrophes	0
Mate monopolization	
% Males in breeding pool	100
Initial population size	
Distribution	Stable age distribution
Population size	220
Carrying capacity	350

Table S5.2. Habitat variables used in the MaxEnt nest site distribution model

Variable	Description	Resolution	Reference
Elevation	Digital elevation model	90 m^2	Brown (1991)
Slope	Derived slope from a digital elevation model	90 m^2	Brown (1991)
Tree cover	% Vegetation cover > 5 m in height	30 m^2	Tarboton and Allan (1984)
Distance to rivers	Rasterized distances (m) to the nearest 1: 50 000 rivers layer	450 m^2	Herholdt and Kemp (1997)
WorldClim: BIO1	Interpolated weather station data describing mean annual temperature (°C)	300 m^2	Hustler and Howells (1987)
WorldClim: BIO2	Interpolated weather station data describing mean diurnal temperature range (°C)	1 km^2	
WorldClim: BIO10	Interpolated weather station data describing mean annual precipitation (mm)	1 km^2	
WorldClim: BIO12	Interpolated weather station data describing the seasonality of precipitation (mm; coefficient of variation)	1 km^2	
GlobCover: Land cover class	Land cover map representing 22 land cover classes mapped by the MERIS sensor	300 m^2	Hustler and Howells (1987)

Table S5.3. Martial Eagle nesting history showing territories where a nest indicated the territory was occupied by a nesting pair (pair present, droppings, feathers, prey remains), or lined with greenery for nesting. The final outcome of each nesting attempt (egg, young, fledgling) is shown and where the final outcome could not be determined an asterisk indicates this. Territories where all known nests were lost or had collapsed are indicated by an X.

Territory	Nests	2013	2014	2015
1	1	Un-occupied		Occupied
2	1	Lined	Lined	Lined
3	1	Not active	Lined	Lined
4	1	Fledgling	Un-occupied	Egg
5	1	Un-occupied	Egg	Lined
6	1	Un-occupied	Egg	Lined
7	1	Occupied	X	X
8	2	Un-occupied	Egg	Young*
9	1	Un-occupied	Un-occupied	Un-occupied
10	1	Fledgling	Un-occupied	Fledge
11	1	X	X	X
12	1	X	X	X
13	1	Occupied	Fledgling	Occupied
14	3		Lay	Fledgling
15	1	Un-occupied	X	X
16	1	Lined	Lined	Lined
17	2	Lined	Un-occupied	Un-occupied
18	1	Un-occupied	Un-occupied	Occupied
19	1	Lined	Egg	Fledgling
20	1	X	X	X
21	1	Occupied	Fledgling	Occupied
22	1			Fledgling
23	1	Un-occupied	Fledgling	Un-occupied
24	1	Un-occupied	Young	Occupied
25	1	Fledgling	Occupied	X
26	1	Egg	Egg	Occupied
27	1	Lined	Un-occupied	Un-occupied
28	1	Fledgling	Un-occupied	Occupied
29	1	Occupied	Egg	Lined
30	2		Egg	Lined
31	1		Egg	Occupied
32	1			Occupied
33	1		Fledgling	Occupied
34	1		Fledgling	Un-occupied
35	2		Lined	Lined
36	1			Fledgling
37	1			Un-occupied
38	1			Young*
39	1			Un-occupied

Territory	Nests	2013	2014	2015
40	1			Un-occupied
41	1			Un-occupied
42	2			Un-occupied
43	1			Fledgling*
44	2			Fledgling*
45	1			X
46	2			Un-occupied
47	1			Fledgling
48	1			Un-occupied

Table S5.4. Tree species used for nesting by Martial Eagles

Species	Number of nests	Tree height (m)
Acacia nigrescens	18	14 ± 2
Balanites maughamii	2	14 ± 1
Colophospermum mopane	2	13 ± 1
Combretum imberbe	16	16 ± 2
Diospyros mespiliformis	1	10 ± 1
Kirkia wilmsii	1	No data
Philonoptera violacea	7	16 ± 2
Not recorded	18	

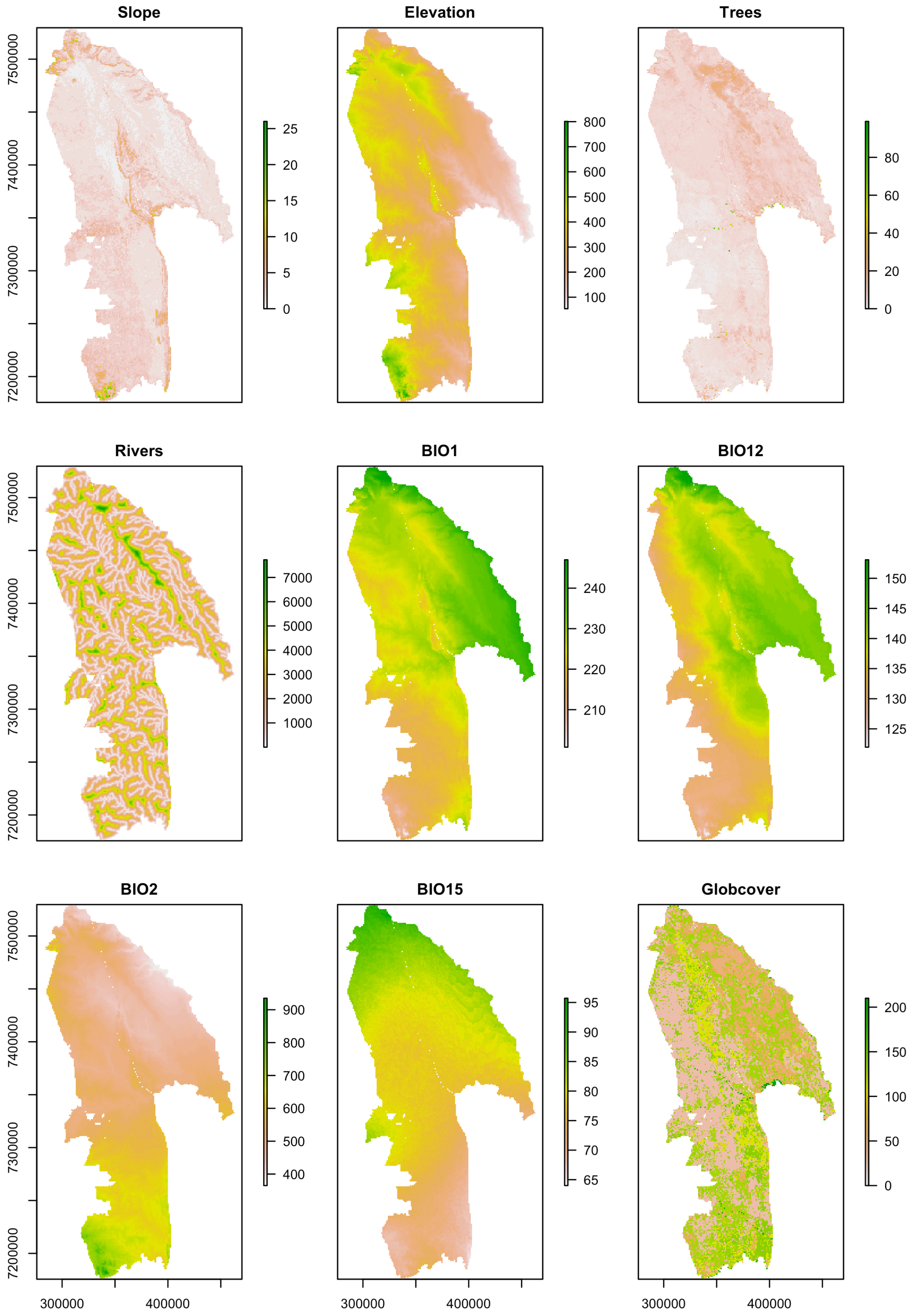


Figure S5.1. Habitat variables used to predict the nesting distribution of Martial Eagles in the KNP, namely slope (°), elevation (m), tree cover (%), distance to rivers (m), BIO1 (annual mean temperature, °C multiplied by 10), BIO2 (mean diurnal temperature range, °C multiplied by 10), BIO12 (annual precipitation, mm), BIO15 (precipitation seasonality, coefficient of variation), GlobCover (23 class global land cover).

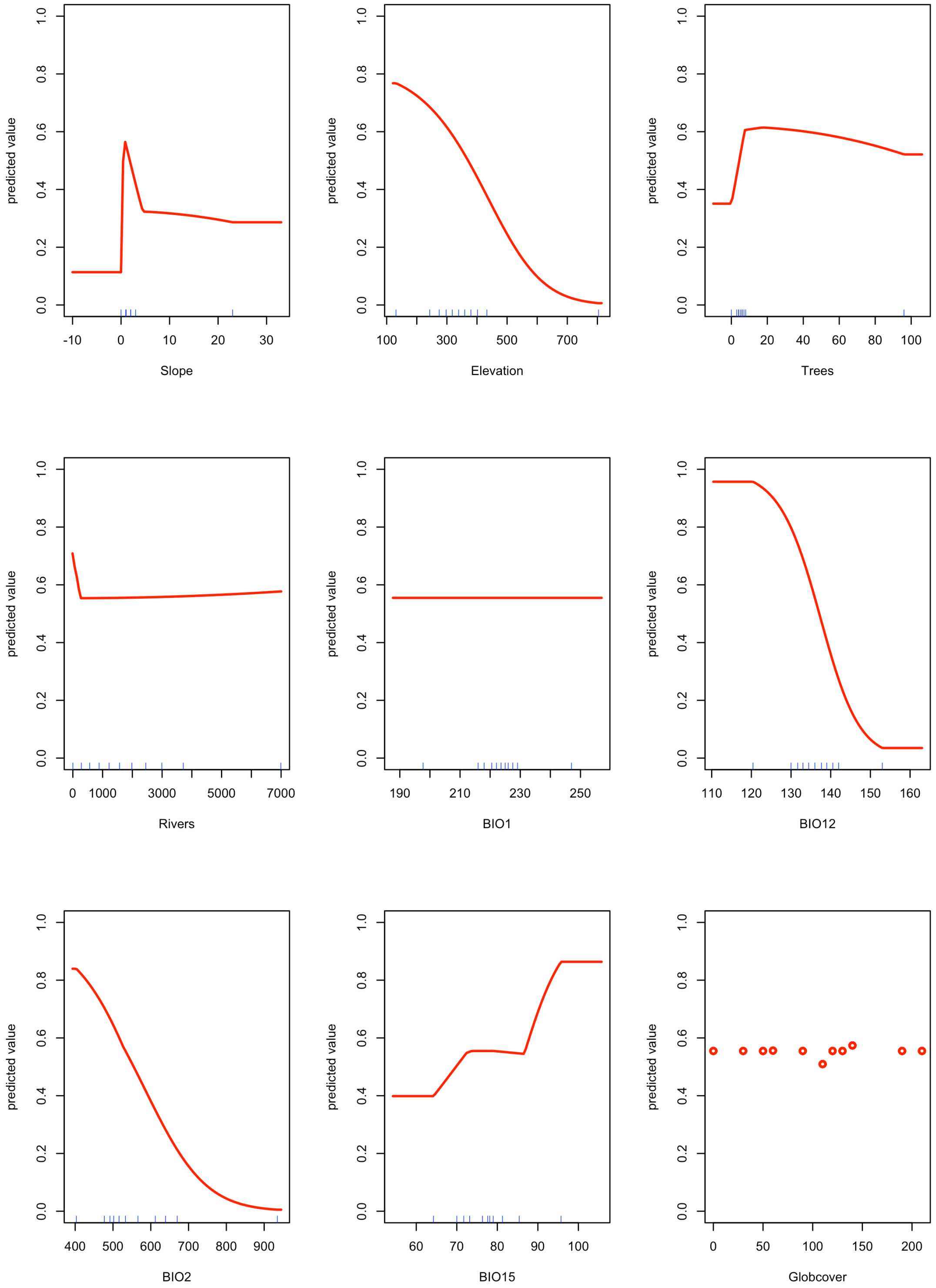


Figure S5.2. Response curves for MaxEnt nest site distribution model showing the relationship between predicted occurrence and habitat variables used in the model.

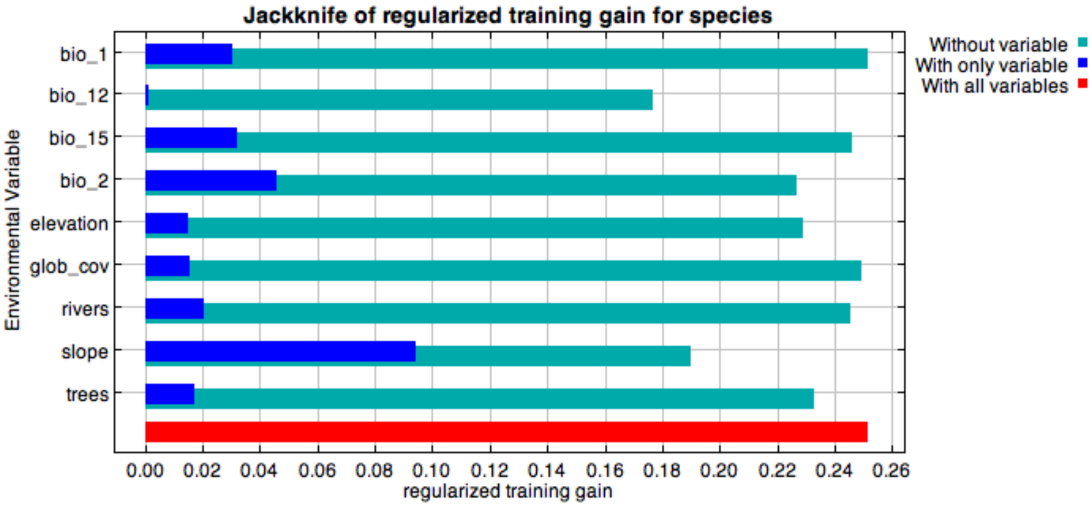


Figure S5.3. Jackknife test depicting variable importance assessing the models regularized training gain with only one variable of interest, and the full model without that variable.

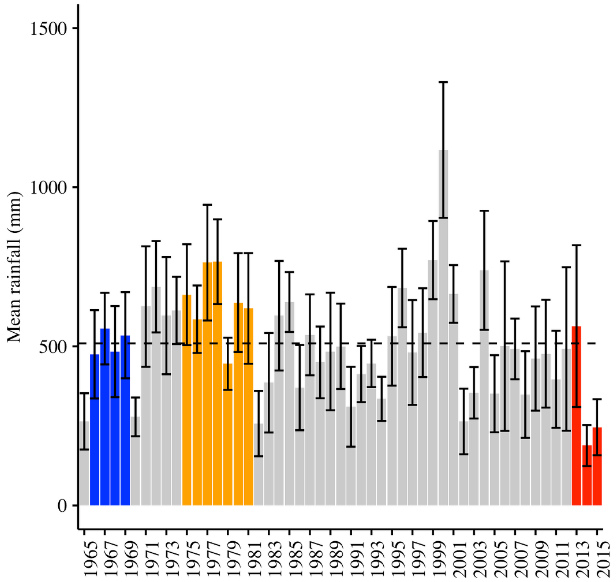
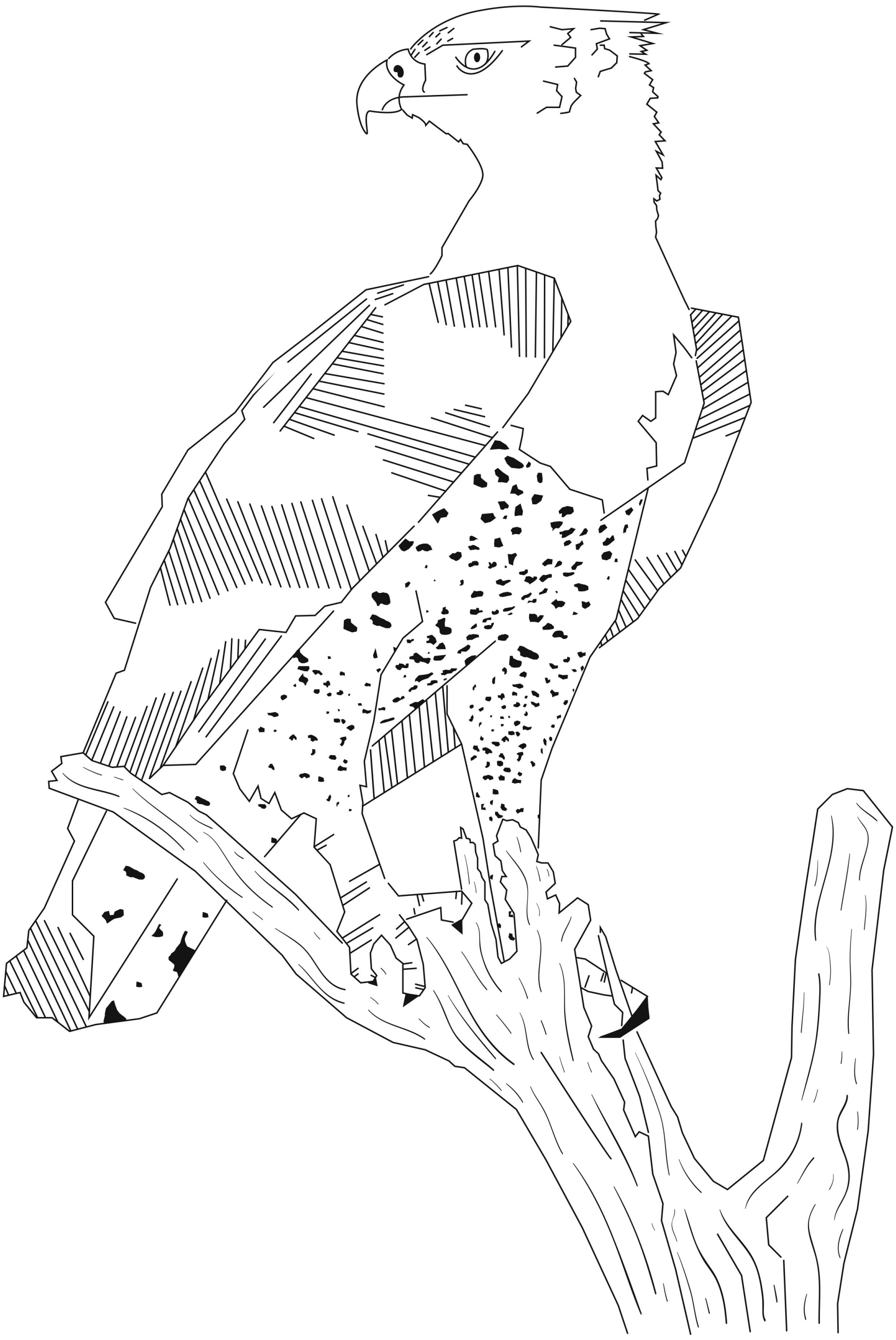


Figure S5.4. Mean annual rainfall across Kruger National Park from 1965 - 2015 (grey bars). The 26-year mean is shown by black dashed line. Blue bars indicate years in which data was collected by Snelling (unpublished), orange bars years in which data was collected by Tarboton and Alan (1984), and red bars in which data was collected in the present study.

CHAPTER 6: Synthesis



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SYNTHESIS

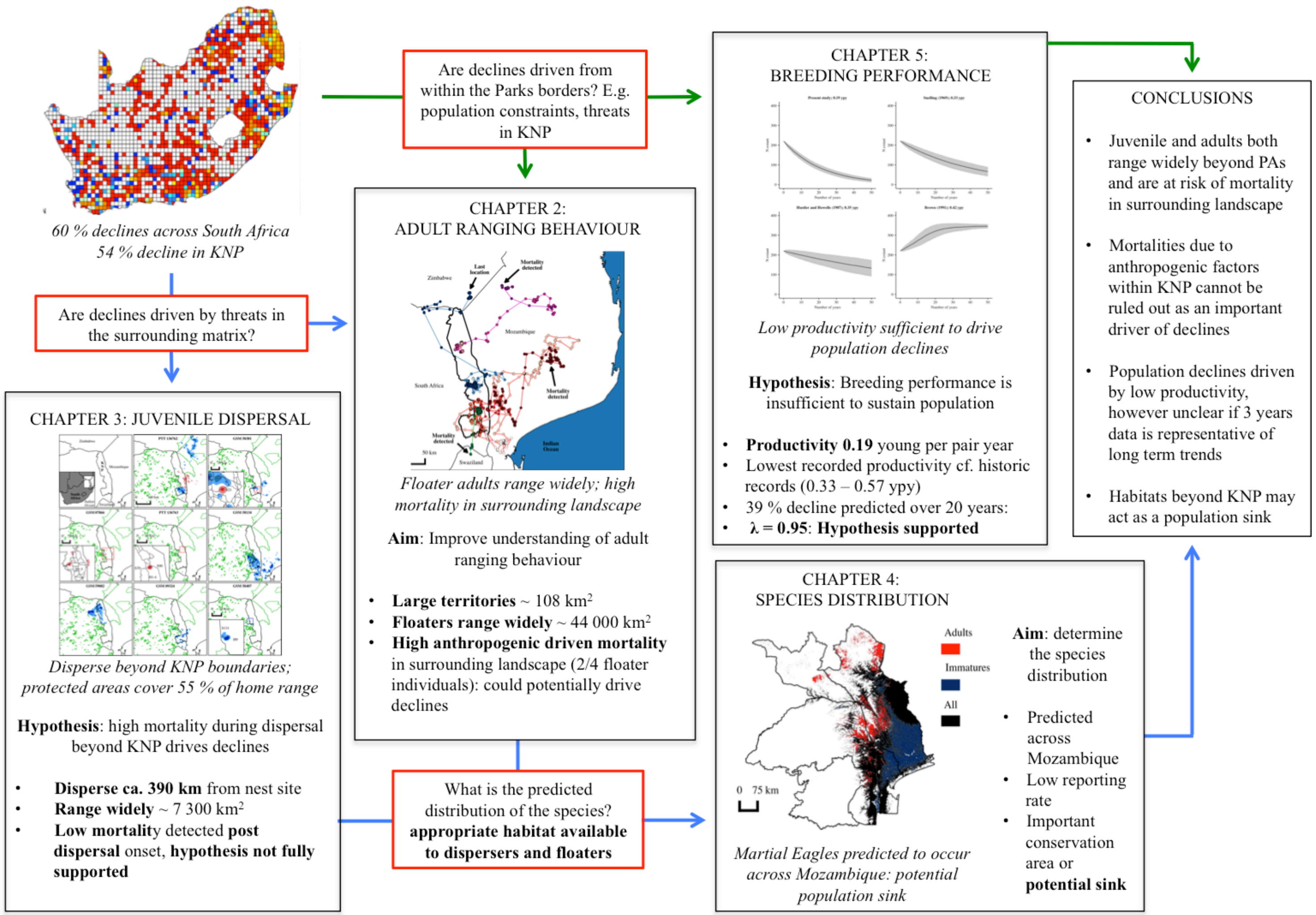
The project behind this thesis was established after the discovery of a 60 % decline in Martial Eagle reporting rates over a 20-year period between the first and second Southern African Bird Atlas Project, together with a concomitant 54 % decline across the species' stronghold, the Kruger National Park Brown (1991). Thus, the central aim of my thesis was to investigate the causes driving these declines. Protected areas are regarded as important refuges for Martial Eagles: a species that is particularly sensitive to the effects of habitat degradation in areas surrounding protected areas Herholdt and Kemp (1997). However, from the analysis of the SABAP data (Cloete 2013), and those of Tarboton and Allan (1984), protected areas only act to buffer declines observed in the surrounding landscape. My research addressed the different components of the species life cycle (reproductive output, juvenile dispersal and adult ecology) to investigate at which stage the potential drivers of the decline within KNP are likely to be operating. In non-protected areas Martial Eagles are prone to a number of threats e.g. electrocution, persecution, habitat loss, and drowning in farm reservoirs Herholdt and Kemp (1997). In a very large protected area such as the KNP (ca. 20,000 km^2) it is less clear which, or if any, of these potential drivers of declines could impact on KNP's population within its borders. Thus, my research explores:

- Firstly, whether declines are driven by factors beyond the protected area boundaries operating on individuals that leave KNP. To explore this issue, it is therefore crucial to understand the movement ecology of species (Figure 6.1).
- Secondly, I explore whether declines are driven by factors operating from within KNP. Here I focused on answering the question whether the population may be declining because productivity is too low (Figure 6.1).

Given the wide ranging nature of dispersing juveniles of large eagle species Herholdt and Kemp (1997), I first hypothesised that the most likely reason for the decline in KNP is that juvenile eagles disperse beyond KNP's borders, where they have unnaturally high mortality caused by anthropogenic threats in the surrounding landscape. This high mortality thus leads to recruitment failure back into KNP and ultimately the population decline seen inside the KNP (Chapter 3). This hypothesis has been previously established for another raptors species, the Spanish Imperial Eagle Tarboton and Allan (1984) and tested using a population model. I also investigated whether adult ranging behaviour may affect the species beyond the boundaries of KNP. For instance, wide ranging individuals may be at increased risk from impacts at park edges or the immediate surrounds (Chapter 2 and 3). I also investigated adult and immature habitat preference to determine how this may be involved in the declines (Chapter 2 and 3). By understanding a species' habitat requirements it becomes possible to establish whether any of their preferred habitats may have changed in abundance over the period of the decline, or could be currently limiting the population (Amar & Redpath 2005, Amar et al. 2008). These ideas were then extended by assessing the availability of habitat for the species within KNP, contiguous reserves, and across the species' likely dispersal range (Chapter 4). Last, because reproductive output is one of the important parameters for sustaining the growth rate of populations Tarboton and Allan (1984), I investigated (Chapter 5) whether the current reproductive output in KNP is adequate to sustain the population, and how it compares to other populations and to past productivity within KNP.

Prior to this research the dispersal behaviour of juvenile Martial Eagles was poorly understood. Recoveries of individuals ringed as juveniles, however, suggested that the species had the potential to move large distances (ca. 350 km) away from their natal nests. These distances would likely lead to Martial Eagles dispersing beyond most protected area boundaries. How protected areas act to conserve very wide ranging species is a topic of continued research in conservation biology in both terrestrial and marine systems Herholdt and Kemp (1997). From my research, I observed that during the post fledging dependency phase, and at around 4 months, juveniles began to move distances up to ca. 150 km beyond the natal range and the boundaries of KNP before returning to the natal area, therefore my expectation that individuals ranged beyond protected areas was met. Movements away from the natal territory appeared to be a vulnerable period in the development of juvenile Martial Eagles as during these movements two of the four juveniles tracked from the nest disappeared under suspicious circumstances. Juvenile raptors are typically vulnerable to mortality earlier on in their post fledging dependency phase with increasing survival probabilities as they age Brown (1991), Brown et al. (1977), Brown et al. (1982).

The two juvenile individuals that suddenly stopped transmitting may have died in KNP. Tags that stop transmitting with no explanation could be as a result of a blunt impact or electrocution. However neither individual was recovered and these remain suggestions. Threats such as electrocution and within KNP may play a role in the population declines, and should be minimised where possible as a first practical step in improving the conservation of the species. Issues within the borders of many protected areas can often affect the species they are designed to conserve Hustler and Howells (1987). For instance substantial tourism infrastructure within parks, such as roads and power lines, can have a considerable impact on wildlife, as is sometimes the case in KNP (Caughley, 1994). One approach to overcome these issues is to implement wilderness areas, which essentially limit any human induced threats to species Tarboton and Allan (1984). However, given the economic importance of KNP for South Africa, this approach is unlikely to be feasible. Other mitigation measures, such as ensuring all energy infrastructures are bird friendly, would seem to be a practical and sensible approach.



60 % declines across South Africa
54 % decline in KNP

Are declines driven by threats in the surrounding matrix?

Are declines driven from within the Parks borders? E.g. population constraints, threats in KNP

CHAPTER 3: JUVENILE DISPERSAL

Disperse beyond KNP boundaries; protected areas cover 55 % of home range

Hypothesis: high mortality during dispersal beyond KNP drives declines

- **Disperse ca. 390 km** from nest site
- **Range widely** ~ 7 300 km^2
- **Low mortality** detected **post dispersal** onset, **hypothesis not fully supported**

CHAPTER 2:
ADULT RANGING BEHAVIOUR

Floater adults range widely; high mortality in surrounding landscape

Aim: Improve understanding of adult ranging behaviour

- **Large territories** ~ 108 km^2
- **Floaters range widely** ~ 44 000 km^2
- **High anthropogenic driven mortality** in surrounding landscape (2/4 floater individuals): could potentially drive declines

What is the predicted distribution of the species? **appropriate habitat available to dispersers and floaters**

CHAPTER 5:
BREEDING PERFORMANCE

Low productivity sufficient to drive population declines

Hypothesis: Breeding performance is insufficient to sustain population

- **Productivity 0.19** young per pair year
- Lowest recorded productivity cf. historic records (0.33 – 0.57 ypy)
- 39 % decline predicted over 20 years:
- **λ = 0.95**: **Hypothesis supported**

CHAPTER 4:
SPECIES DISTRIBUTION

Martial Eagles predicted to occur across Mozambique: potential population sink

Aim: determine the species distribution

- Predicted across Mozambique
- Low reporting rate
- Important conservation area or **potential sink**

CONCLUSIONS

- Juvenile and adults both range widely beyond PAs and are at risk of mortality in surrounding landscape
- Mortalities due to anthropogenic factors within KNP cannot be ruled out as an important driver of declines
- Population declines driven by low productivity, however unclear if 3 years data is representative of long term trends
- Habitats beyond KNP may act as a population sink

Figure 6.1. The flow of chapters and the main questions posed (red boxes) to explain the decline of the Martial Eagle in Kruger National Park. I assessed whether declines were driven by threats in the surrounding landscape (blue arrows) during movements beyond protected area boundaries, or by factors within KNP's borders (green arrows), such as poor reproductive output or high mortality of adults.

Following the onset of dispersal, juvenile eagles ranged even farther (ca. 390 km) away from the natal nest, similar to the maximum distances from nests that ringed birds have been recovered Hustler and Howells (1987). These results indicate that even the largest protected areas are unlikely to provide complete protection for Martial Eagles during dispersal. The inability to protect wide-ranging species is perhaps one of the biggest fundamental drawbacks or limitations of protected areas. For animals that migrate or disperse over long distances, one solution has been to create networks of reserves that can act as stepping-stones and temporary settlement areas Tarboton and Allan (1984). Trans boundary policies also will need to be implemented (Amar et al., 2008, Crandall et al., 2015, Whitfield et al., 2001) as Martial Eagles from KNP range over multiple countries, which can make achieving conservation goals challenging.

Besides the potential risks faced during initial ranging behaviour of dispersing juveniles, one interesting outcome of this study was that the dispersing juveniles were not connected to any other known substantial nesting Martial Eagle population, as they all returned or remained closely linked to the KNP-centric population. From Chapter 4, species distribution models predicted that the habitat west of the escarpment dividing the Low Veld and the High Veld was largely unsuitable for the species. Other research has demonstrated a sizable population (ca. 130 – 159 pairs) on the electrical infrastructure in the Northern and Western Cape, South Africa (Amar et al., 2003). Further research should determine what connectivity exists between the KNP population and other populations via juvenile dispersal as low dispersal may have consequences for the overall genetic structure of the population (Thorup et al., 2010), especially given the observed declines. According to the metapopulation paradigm, isolated populations are more likely to face extinction (Figure S4; SANParks Corporate Communications, 2015), therefore it will be important to investigate where immature eagles settle in relation to the natal area or the study population in the future. Unfortunately, the duration of this PhD was not sufficient to follow tracked birds to their eventual nesting areas. Spanish Imperial Eagles in Parque Nacional de Doñana provide a good example of a population with low genetic diversity as a consequence of a small effective population size and low immigration rates (e.g. Herholdt and Kemp, 1997). It has been suggested that emigration is facilitated to avoid inbreeding depression in this population of Spanish Imperial Eagles, and a similar strategy could be implemented for Martial Eagles. Other top predators in the KNP e.g. African lion (*Panthera leo*), all likely face similar dispersal constraints. This has spurred some research groups, e.g. the Lion Management Forum, to consider relocations of top predators between reserves (Martin, 1987, Newton, 1979, Steenhof et al., 1997). However, small populations of other large eagles e.g. White-tailed Eagle (*Haliaeetus albicilla*) have maintained genetic diversity despite going through large population declines (Newton and Rothery, 1997); if the period of constricted population size is small in relation to the species generation time, then less diversity is likely to be lost. Therefore, it will be important to ensure rapid recovery of the KNP population so that diversity is maintained, or conservationist should ensure that genetic diversity is maintained in different populations before consequences of the population declines are experienced.

In summary, immature home ranges averaged ca. 6,500 km^2 and these home ranges were only partially (ca. 55 %) covered by protected areas. These findings support my expectations that juvenile eagles range beyond the boundaries of KNP. However immature eagles that ranged far appeared to have low mortality rates calculated using known mortalities (8.48 %) as reported in Chapter 3. Therefore my hypothesis that juveniles would incur high rates of un-natural mortality was not supported. Despite the birds ranging beyond protected area boundaries, I did not detect any unnatural mortality subsequent to dispersal from the natal area. Immature mortality rates in other large eagles such as Golden Eagles (*Aquila chrysaetos*) is estimated to be ca. 21 % per annum in Western Scotland (Briskie and Mackintosh, 2004), and in California can range from ca. 16 % in juveniles to 10 % in immatures (Aquila adalberti; González et al., 2006, Negro et al., 2007). Even when the two individuals that disappeared without an explanation are factored in, mortality rates were still low for this age group (ca. 24 %). Therefore, despite our low sample size, the annual mortality rates in this study are similar to biologically similar species and may in fact be a true reflection of the population (Herholdt and Kemp, 1997). The mortality of immature birds may not be the main driving force behind the species decline within KNP if this is the case, but additional survival studies are needed to establish this.

This lower than expected mortality of immature eagles, was unfortunately not the case for adult Martial Eagles which experienced higher rates of mortality during this study (42.48 % per annum) as was reported in Chapter 2. Mortality rates in other large and threatened eagles are substantially lower. For example annual mortality rates in Golden Eagles and Spanish Imperial Eagles range between 9 and 2.5 % (Herholdt and Kemp, 1997, Steyn, 1982). The possibility of a high mortality rate in adult Martial Eagles is particularly worrying since we know that populations of K-selected species, like eagles, which are usually long lived and slow to reproduce, can be most susceptible to increases in adult mortality rates (Tarboton and Allan, 1984). For example increasing annual mortality rate by 3 – 5 % in Golden Eagles ascribable to persecutions is sufficient to drive population declines, even when reproduction is very good (Katzner et al., 2006).

During this study, I unexpectedly found that some of the adult population do not continually hold territories, as was previously thought (Amar et al., 2005, Newton, 2004). This behaviour has been observed for other eagle species that can abandon territories due to disturbance, or when ousted by another individual competing for a territory (van Jaarsveld unpublished report; Tarboton and Allan, 1984). I found that a high proportion of individuals (4/8 tagged adults) became floaters that were not permanently resident in territories. The movements of these individuals were best described by a nomadic movement strategy that ranged beyond protected area boundaries. Compared to the relatively lower mortality rates observed in immature eagles in Chapter 3, adults incurred higher rates of mortality attributed to anthropogenic sources within the borders of neighbouring countries (2/4 confirmed deaths recorded). This again indicates the importance of implementing trans boundary conservation policies, as discussed above for dispersing immature eagles.

Protected area coverage in the region that this study took place is vast; the contiguous Greater Kruger and Limpopo National Park system effectively makes up a conservation area of ca. 32,000 km^2. Areas accessible to Martial Eagles during dispersal or nomadism are sparsely populated (only 0.25 % of the area is classified as “urban” (Levick and Asner, 2013, Murn et al., 2013)). Despite this high availability of protected areas and low human population density, adult eagles still tended to be at threat from human related activities. This is what was expected for less experienced immature eagles, suggesting an alternative hypothesis that adult individuals acting as population floaters are prone to unnatural mortality in the surrounding landscape, therefore driving population declines directly through adult mortality.

Large movements by adults were not expected because the population was not, and still is not, expected to be saturated due to the observed declines. Floaters play an important role in replacing aging birds in a saturated population (Moncrieff et al., 2008, Shannon et al., 2008), and I expected that many of the previously occupied nesting territories would be available to floaters because of the observed population decline. Chapter 5 indicated that 27% of territories showed no signs of re-occupation over the course of the study, suggesting that there was a plentiful supply of unoccupied territories with suitable nests. Territory abandonment may have been driven by poor habitat conditions as the study took place during a drought. Although this hasn’t been investigated for Martial Eagles, territorial abandonment in other species can occur when conditions are poor (Krüger et al., 2015, Mateo-Tomás and Olea, 2010). The increased step lengths observed during the dry winter indicates that changes in seasonality can influence Martial Eagle movement ecology. This aspect of their ecology should be a focus for further research, given the increasing variability of the region’s climate as a consequence of global change (Newton, 1979).

Non-breeding floaters may be more common than previously thought, mainly because of their mobile nature which can make them less detectable and harder to study (Shannon et al., 2011). The presence of floaters in a population that is unlikely to be saturated indicates that the KNP population may be under ecological constraints; a shortage of mates or poor prey availability for instance may have driven birds to abandon their territories (Kochert et al., 1999) in search of alternative food or nesting opportunities. However, in doing so, these birds are falling victim to external threats operating outside the boundaries of KNP. My limited sample size (n = 8), however, means that I cannot be sure how representative my sample is in describing mortality rates in the wider KNP Martial Eagle population.

Adult mortality due to anthropogenic causes is concerning and may be one of the drivers of declines, suggesting that drivers in the landscape surrounding KNP may still be responsible for declines as originally hypothesised – just acting on a different section of the population than originally foreseen. Models of population declines in long-lived eagles typically indicate that adult survival is a far stronger driver of population declines than immature survival and productivity (van Wilgen et al., 2014).

In terms of the species' conservation, in light of these results, it is evident that both floating adults and immature range over similar distances away from KNP (max ca. 390 km). This could be used to define spatial limits when implementing conservation strategies to reverse the KNP population decline. The practical applications of behavioural data in conservation is under appreciated and this result improves our knowledge for conservation of the species (Cho et al., 2012). Similarly, and along the lines of the habitat paradigm Levick et al. (2015), it is important to recognise the habitats required to sustain a Martial Eagle population in the KNP and beyond its borders. This was the main focus of both the habitat preference analyses in Chapters 2 and 3, and the species distribution model largely based on citizen science datasets in Chapter 4, and the nest site distribution model in Chapter 5. These chapters link to provide a better understanding of the species spatial and habitat requirements (Figure 6.1).

Chapter 2 and 3 showed that both adult and immature Martial Eagles used habitats that had moderate tree cover, were in low-lying areas with gentle slopes, and that they preferred dense bush veld compared to open bush veld and grasslands. Within KNP availability of this habitat likely limits the population and any changes in this habitat may have consequences for the ability of KNP to support Martial Eagles. For example tall tree loss could eventually limit nesting sites, or reduce perch availability therefore reducing the quality of the landscape for hunting birds (Herholdt and Kemp, 1997). The Lowveld area of South Africa in which KNP is situated has experienced a decline in rainfall over the last two decades (Ontiveros et al., 2008). Reduced rainfall as a consequence of climate change also may limit water availability in riverine habitats, therefore potentially reducing prey abundance (e.g. small mammals and game birds) in this system.

Habitats preferred by Martial Eagles are often poorly conserved beyond protected area boundaries (Millsap et al., 2015). In Gaza Province, Mozambique, for instance, charcoal production is decreasing woodland habitat in areas predicted to support Martial Eagles (Murn et al., 2013). Therefore, protected areas, although not fulfilling a complete role in the species conservation as outlined above, will likely remain an important component in the preservation of Martial Eagles as for other top predators in Africa that are sensitive to the impacts of man (Newton, 1979, Parra and Tellería, 2004). The importance of protected areas will likely become ever more evident in Africa as protected areas become increasingly isolated (Chirima et al., 2012).

The widespread predicted distribution of Martial Eagles across Mozambique in Chapter 4 was an important finding as it indicates that these landscapes could support Martial Eagles. However, previous surveys have suggested that the species is apparently scarce across our predicted model region (Newton, 1979, Redpath et al., 1998). The region may have supported Martial Eagles historically. A number of the tracked individuals (n = 8/16) did indeed travel over the predicted region of occurrence. I recorded two un-natural mortalities from these individuals. Therefore the area may in fact act as a population sink, rather than the potential source it should be.

Immature Martial Eagles tended to avoid landscapes within their dispersal home ranges that fitted the urban category (Chapter 3). It was evident in Chapter 3 that where anthropogenic areas existed eagles avoided these areas. Avoidance of these highly transformed areas may have alleviated some of the human-wildlife conflict commonly driving eagle declines in populated areas, where a few intolerant land owners can have substantial impacts on local eagle populations (Kiker et al., 2014). Martial Eagles typically nest away from urban centres, unlike the similarly sized Crowned Eagle (*Stephanoaetus coronatus*) which nests in urban environments (Kiker et al., 2014, Scholtz et al., 2014). Therefore it will be critical to limit human disturbance around known nests.

The availability of habitat for Martial Eagles calculated in Chapter 4, together with the estimated home range sizes from Chapter 2, allow better population estimates to be made (Shannon et al., 2008). Adults held large (ca. 108 km^2), apparently non-overlapping home ranges, which likely limits the carrying capacity of even some of the largest protected areas. If all areas were suitable within KNP, KNP could support ca. 180 pairs, but this could be an over estimate because not all habitats will be suitable. Cloete (2013) estimated 137 pairs across KNP. However, my distribution models in Chapter 4 suggest as little as 29 % of KNP is suitable for nesting Martial Eagles, thus supporting ca. 52 pairs. Nest distribution models in Chapter 5 predict approximately 60 suitable nesting territories in the KNP. During aerial surveys and other modes of nest searches I detected 56 occupied territories. Therefore the likely number of pairs in the KNP (ca. 52 – ca. 60 pairs) is far less than what has been predicted previously by simple extrapolations of home range sizes across KNP's surface area. The number of nesting pairs of Martial Eagles is therefore far fewer than the predicted number of lions (ca. 1700) (Cade and Temple, 1995, McClure et al., 2016, Olendorff et al., 1989) or leopards (*Panthera pardus pardus*) (ca. 700) in KNP (Zub et al., 2010). Martial Eagles are therefore highly prone to entering an extinction vortex and their conservation may need to be viewed within the framework of Caughley's

(1994) small population paradigm rather than the declining population paradigm as originally considered at the start of this thesis.

Few protected areas in South Africa are large enough to sustain a substantial nesting population of Martial Eagles, supporting the fact that KNP. Because of its size and habitat availability for Martial Eagles, the KNP should serve as a stronghold for the species and an area of focused conservation efforts. Other substantial populations in South Africa include the ca. 9,500 km^2 Kalahari Gemsbok National Park which is predicted to support ca. 30 pairs (Aquila fasciata; Ontiveros and Pleguezuelos, 2000) and the 960 km^2 Hluhluwe-iMfolozi Game Reserve which could carry at most 9 pairs. All of these conservation areas have experienced declines (Tarboton and Allan, 1984). Martial Eagles are evidently such a low density species, with fragmentation of suitable habitats and particular habitat preferences so the species may be prone to the effects of genetic drift and may be more prone to stochastic events within the framework of the small population paradigm (Kiker et al., 2014). The small isolated population of Spanish Imperial Eagles and Iberian Lynx (*Lynx pardinus*) in Doñona National Park, Spain, face similar population constraints and special management, e.g. mitigating human induced mortalities and ensuring ample habitat, is needed to prevent the declines of these species. Game farming and private protected areas in South Africa has provided a means for maintaining habitat (Scholtz et al., 2014), but some drawbacks may exist for Martial Eagles. Martial Eagles could use farms rearing rare colour varieties of antelope e.g. Springbok (*Antidorcas marsupialis*) for the hunting market and could pose a threat to the lambs on these farms, therefore increasing the risk of persecution by property owners.

In Mozambique, the establishment and maintenance of private game lodges could provide both a source of income to locals and preserve wildlife areas. Martial Eagles could potentially perform the role of a flagship species in Africa, similar to the role the Spanish Imperial Eagle has performed in Europe. Essentially if ecosystems should be preserved in Africa, the management of habitats for Martial Eagles could assist in the conservation for a wide range of raptors, vultures e.g. White-backed Vultures (*Gyps africanus*), and other top predators that operate at broad spatial scales, but for which we have limited knowledge (Ontiveros and Pleguezuelos, 2003).

Despite the spatial issues involved in conserving Martial Eagles, one of the most surprising results stemmed from the investigating reproductive rates in Chapter 5. This chapter was founded within the declining population paradigm (Caughley, 1994) using both a temporal and spatial comparison (Briga and Verhulst, 2015) of recent data with previous studies carried out both within KNP and elsewhere in Africa. The comparison revealed that recent productivity in the KNP was lower than reported by any other study on the species, including within KNP historically. Based on this finding, I then explored whether low productivity alone was sufficient to drive declines, applying a population model approach as advocated by Peery et al. (2004) to explore causes of declines. Under the current average productivity of 0.22 young per pair per year, and holding all other population variables at expected levels, I found that the species decline that has occurred over the last 20 years could almost entirely be explained by low productivity, without the need to invoke other factors affecting other sections of the population. Low productivity is typically a result of environmental constraints such as low prey availability (Cunningham et al., 2016), poor weather conditions Wichmann et al. (2003) or human persecution USGS (2008). My data on productivity were collected during three of the lowest rainfall years in recent history, and it is likely that this may have facilitated the low productivity. The idea that poor habitat conditions may have driven poor reproductive output is supported by territorial abandonment Hijmans (2015), USGS (2008) that was witnessed, with two of the eight tracked individuals abandoning their territories during the study (Chapter 2).

After fledging, juveniles enter a long post fledging dependency phase that may last up to 9 months. During this period a small area (1 km^2) around the nest was used for the first four months (Chapter 3). Martial Eagles to only breed every second year following a successful nesting attempt, thus equating to roughly 0.5 young per pair per year as reported by Sexton et al. (2013). In Chapter 5 a population model demonstrated that declines are driven when productivity is lower than 0.37 young per pair per year, even when all other population parameters reflect a population with the lowest natural mortality rates for large eagles. Therefore, improving reproductive rates is likely to be an important part of any potential species management plan.

Mortalities and mitigation

The thesis Chapters 2 - 5 largely assessed behavioural aspects of Martial Eagle ecology that could facilitate declines, however the fundamental causative agents contributing to mortalities need a unifying clarification. Of the 8 immature individuals that were GPS tagged and for which data were collected, three mortalities were recorded in total. One immature individual (ca. 3 years old) likely suffered from starvation or was suffering from an underlying condition as recorded in KNP Veterinarian report.

Of the eight GPS tagged adults four confirmed mortalities were detected. Two of these mortalities occurred in rural Mozambique: one individual was found in a hunting snare, and the second individual’s tag was found cut off the bird at a hunting outpost. Another individual that travelled to Swaziland sent a last transmission next to a power line transformer box but the carcass was not recovered. Another two individuals died due to conspecific conflict. During my research in KNP (2013 – 2015), I was made aware of another three adult Martial Eagle mortalities related to power line collisions or electrocutions within the confines of KNP. One of these individuals was found dead in 2015 close to the site where it was originally ringed in 1991 as a full adult Lehner et al. (2006).

In summary of the 8 confirmed mortalities (4 tracked adults, 1 tracked immature, and 3 unmarked adults) that I was aware of during my study, reported above, three were most likely attributed to electrocution, two to hunting or persecution, one starvation, and two were natural. In terms of GPS tagged bird mortalities due to anthropogenic sources, 50 % occurred beyond protected area boundaries. Mortalities within KNP associated with electrocutions (3 electrocutions in KNP) are perhaps most worrying and even greater effort should be made to mitigate these incidents. Currently ESKOM the national power utility company has changed electrical distribution line structures to assist in mitigating electrocution. However further mitigation can be achieved by taking rest camps off the grid, or by making electrical infrastructure even safer for eagles by insulating the section of line near to poles where eagles perch Hijmans et al. (2005). Preventing hunting and persecution is an important avenue to ensure the survival of dispersing and floating individuals. This can be done through education, livestock compensation, reducing the availability of snare wires, and law enforcement Bontemps et al. (2011).

Study limitations

This study was limited primarily by sample size. More tracked birds would have allowed more inferences about the source-sink dynamics of immature eagles dispersing beyond protected area boundaries. This small sample size prevented me from establishing robust mortality rates for adult and immature birds. The expense of GPS tagging is often a constraining factor in telemetry studies (KNP; Amar et al., 2015, Cloete, 2013). In this study I encountered a high proportion of tag failures (n = 3). Furthermore, the length of the tracking study (ca. 36 months) was too short to identify the settlement areas of immature birds. The movement ecology study was made challenging given the very low productivity of the population, limiting the number of young available for tagging. Nests with young were not always safely accessible to a climber, and were not always positioned appropriately for bal-chatri trapping (e.g. close to a road). I underestimated the challenges in finding Martial Eagles to trap and GPS tag throughout KNP, owing to their scarcity. In addition to GPS tagging, I ringed 24 adult eagles to better understand survival rates. However, despite efforts to promote the reporting of ringed birds by the public, few individuals were re-sighted often enough to calculate survival rates. A number of birds also managed to remove their colour ID rings, compromising the value of these data. Therefore survival rates from this dataset were not included in this thesis. The study was limited by the number of breeding seasons over which nest checks were conducted. This prevented a modelling approach to assess productivity in relation to habitat variability, or long-term trends in reproductive output. KNP is a very large area to cover, and the resources required to work across KNP made data collection challenging. This was made even more challenging as the study took place during high levels of rhino poaching. As a result, access to nests was not always possible when anti-poaching patrols were in place.

Recommendations for future research

- Because the study focused on the KNP, I only recorded nests in the confines of KNP. However, models predicted that neighbouring conservation areas likely support nesting pairs. Therefore, a survey for nests in contiguous protected areas should be conducted in order to provide an improved regional estimate of the overall nesting population in and around KNP.

- Models suggested that large areas of Mozambique were likely to support Martial Eagles. A survey across the predicted area of Martial Eagle occurrence should be undertaken to confirm these models and to establish the likely numbers of pairs in the region. This will help understand if the area is an important refuge for dispersing and floater individuals, or is a potential sink.

- I was constrained by both the number of juvenile eagles that were fitted with GPS tags and the length of the study in my efforts to understand dispersal and settlement areas. Genetic analyses should be undertaken to examine links with other populations and to determine the genetic diversity of the population. The small size of the KNP population makes it vulnerable to genetic constraints e.g. bottle necks. Genetic analyses of the population should be done to determine parentage and sex ratios. Collecting feathers at nests could improve genetic material collection compared to physical captures across the species range (Herremans and Herremans-Tonnoeyr, 2000, Murn et al., 2016, Thiollay, 2006, Thiollay, 2007).

- Low productivity in KNP is a concern. A study explicitly testing the causes for low reproductive rates should be conducted. This study should use an experimental approach to determine if food or nesting sites are a limiting factor in Martial Eagle reproduction. A modelling approach can be used to determine if climatic variability or habitat composition influences productivity.

- Reliable demographic parameters are required to inform the population structure and survival rates so these data should be collected through unique ID ringing of nestlings. A more robust PVA analyses should be conducted using all the data collected to determine the population trend. A parameter sensitivity test sensu Katzner et al. (2006) can be conducted to establish the most important variables driving population trends.

- Additional adult eagles should be tracked to determine how common nomadism is in the population and to explore possible environmental drivers for territory abandonment. The dynamics between floaters and territory holders should be investigated.

Conclusion

In summary, this research highlights the most likely mechanisms driving Martial Eagle declines in KNP, improves the context of protected areas as a useful tool for conservation of wide-ranging top predators in Africa, and provides further information about the ecology of Martial Eagles. Further research should investigate whether Martial Eagles are declining due to high adult mortality and determine what proportion occurs due to unnatural mortality beyond protected area boundaries. Additional studies are also required to determine if declines are driven by low productivity and if this is confirmed to be a factor driving declines the likely causes of low productivity should be tested. The ranging behaviour of Martial Eagles likely constrains the carrying capacity of even the largest protected areas, as the species has enormous territories. Birds range so widely, both as floaters and during juvenile dispersal, that protected areas may only act to conserve nesting pairs. Environmental degradation may limit the productivity of nesting birds within parks. Therefore conservationists should aim to mitigate threats to Martial Eagles in Parks, as well as in the wider countryside by identifying and mitigating threats, and they should ensure that appropriate habitat is provided for the species.

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