Investigating the effects of environmental variables on martial eagle breeding performance in the Kruger National Park

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Abstract

Within South Africa martial eagles reporting rates have decreased by almost 60% over the last two decades. Similar declines have also been reported within Kruger National Park (KNP), which is regarded as a stronghold for this species. Declines within KNP have been attributed to the low productivity rates. As apex predators, marital eagles are considered to be good indicators of ecosystem health, being sensitive to the cumulative effects of disturbance down the food chain. Changes in the breeding performance of martial eagles may therefore indicate broader environmental change within the ecosystem. In this study, we aim to explore which environmental variables (e.g. climate, land cover, tree cover, fire and elephant abundance) within each territory correlated with martial eagle breeding performance in the hope that we may better understand which variables affect martial eagles breeding performance and whether these may have changed over time to cause the low levels of fecundity presently seen within KNP. We found that breeding productivity (young per territorial pair) was positively influenced by higher precipitation and Normalized Difference Vegetation Index (NDVI) and negatively impacted by high temperatures during the previous year. Breeding rate (breeding attempt per territorial pair) appeared to be negatively influenced by higher tree cover within 6 km of the nest site. Nesting success (outcome of a breeding attempt) was correlated with higher NDVI and lower relative levels of precipitation during the previous year. Using longer term climatic data and the relationship between climate in the previous year and productivity, (the variable which directly relates to annual fecundity), we hindcast the predicted productivity over the last three decades (2018-1986) to explore whether change in climate conditions (precipitation, temperature and NDVI) might reveal declines in productivity. No such declines were predicted, thus, our results do not explain why productivity has declined within KNP.

Contents

Introduction

Global biodiversity is currently under threat as species from diverse taxa are undergoing dramatic population declines (Mora & Sale 2011; Waldron et al. 2017). These declines are largely driven by anthropogenic activities associated with landscape modifications, over-exploitation, direct persecution, climate change and the introduction of alien species (Eglington & Pearce-Higgins 2012; Hooper et al. 2012; Newbold et al. 2015). Unfortunately the acceleration of extinctions is projected to continue into the coming century, threatening to dismantle vital ecosystem processes and services (Sekercioglu et al. 2004; Hooper et al. 2012; Ceballos et al. 2015).

Birds are one of the most well studied group of major organisms, with the conservation status of most bird species being assessed at least twice (Gentry 1992; Sekercioglu et al. 2004). Anthropogenic activities are known cause broad-scale changes in the community composition of birds and have been documented around the globe (Eglington & Pearce-Higgins 2012; Donázar et al. 2016). Recent estimates suggest 12 % of bird species are threatened with extinction, a further 12 % have restricted ranges threatened by landscape modification and lastly, major reductions of 20 – 35 % in the global abundances of birds have been noted (Sekercioglu et al. 2004; Pimm et al. 2006).

Raptors appear to be particularly susceptible to declines due to their high trophic level and generally slow life history traits (Paviour 2013; Krüger & Amar 2017; McClure et al. 2018). As indicators of biodiversity and ecosystem health loss of raptors may lead to reductions of some ecosystem functions and services (Buechley et al. 2019). Currently

18% of the worlds raptors are threatened with extinction, while a further 52% have declining populations (McClure et al. 2018). Large raptor declines have been reported in west Africa (Thiollay 2006, 2007), east Africa (Ogada & Keesing 2010) and southern Africa (Amar & Cloete 2018; Garbett et al. 2018). In West Africa and for the martial eagle in South Africa declines were markedly higher outside of protected Areas (Thiollay 2007; Amar & Cloete 2018).

Protected areas have been at the core of conservation strategies for more than a century (Rayner et al. 2014) and are an important tool for tackling global biodiversity loss at a local level (Beresford et al. 2011). The primary objective of protected areas is to ensure the long term persistence of nature and its associated ecosystem services (Rayner et al. 2014). However, as natural expanses beyond protected area boundaries continue to contract and fragment (Watson et al. 2014a) biodiversity loss continues at a considerable rate (Butchart et al. 2010). As a result the ability for protected areas (alone) to maintain biodiversity has been questioned (Rayner et al. 2014; Watson et al. 2014). Nonetheless, the role protected areas play in the conservation of raptors is becoming increasingly apparent, because in many areas they hold the bulk of most raptor species populations (Thiollay 2006; Ogada & Keesing 2010; Amar et al. 2016).

Quantifying the reproductive rates of raptors can provide valuable information on the status of a population and can help understanding the variables that may be responsible for any population decline (Steenhof & Newton 2007). For raptors, persistent reductions in breeding productivity can lead to regional population declines and impact long-term population persistence. For example, population declines of multiple raptor species have been linked to reduced productivity (Liven-schulman et al. 2004; Amar et al. 2011). Moreover, changes in their reproductive parameters over time may indicate broader environmental change (Moloney et al. 2004).

The Martial eagle (*Polemeatus bellicosus*) is an African endemic and one of the largest raptor species on the continent (Amar & Cloete 2018). Martial eagles were up-listed from “Near-Threatened” to “Vulnerable” by the IUCN (International Union for the Conservation of Nature) in 2013 due to rapid population declines that have occurred throughout its range over the last three generations (56 years) (IUCN 2018; Taylor et al. 1997).

Within South Africa martial eagle reporting rate declines of more than 60% have occurred between two repeat surveys, SABAP 1 (South African Bird Atlas Project 1) (1987-1992) and SABAP 2 (2007-2012) (Amar & Cloete 2018). Following these findings the martial eagle was upgraded from “Vulnerable” to “Endangered” within the Southern Africa region (Taylor et al. 2015; Amar & Cloete 2018). During this 25 year period, declines in reporting rates (albeit lower) were also observed within protected areas (42%). Within the KNP, which was considered a stronghold for the species, declines of 54 % were observed (Amar & Cloete 2018). The current South African population is thought to be less than 600 pairs, mostly restricted to conservation areas in the Lowveld and Kalahari regions where it is thought that the species can escape human persecution (Machange et al. 2005), though a large population is also thought to occur nesting on powerlines in the Karoo region (Machange et al. 2005; Berndt 2015).

Van Eeden *et al*. (2016) collected data on the ranging behavior, habitat preference and productivity of martial eagles within the KNP from 2013 – 2015. During this time he estimated an unsustainably low productivity of martial eagles within the KNP of 0.19 - 0.23 y.p.y (young per pair year), the lowest productivity recorded for martial eagles of any previous studies, including for previous studies within KNP. Using this estimate to build a population model, suggested that the observed population decline within the KNP may be due to low productivity without the need to invoke changes to any other demographic parameters.

Although Van Eeden (2016) identifed low productivity of martial eagles as the potential driver of the KNP population decline, the study did not attempt to explore what factors that might be driving such low productivity. Furthermore, Van Eeden (2016) only captured data over three breeding seasons and thus, the low estimates obtained could have been due to particularly poor years. Thus, further years of monitoring data are required in order to establish how robust these low estimates are. Understanding of which environmental variables influence productivity in this population could be useful to identify what changes may have occurred to reduce the productivity of this population (Skowno & Bond 2003; Burgess et al. 2011; Vanak et al. 2012; Väli 2013; Skagen & Yackel Adams 2017; Smith et al. 2017). Such and understanding could therefore potentially help devise conservation strategies to improve productivity and thus halt the declines of this population (Peery et al. 2004; Coulson et al. 2005).

In semi-arid locations, such as the KNP, climatic influences on primary production, food abundance and predation may lead to changes in reproductive outputs of birds (Keane et al. 2006; Eglington & Pearce-Higgins 2012; Skagen & Yackel Adams 2017). The influence of temperature may present trade-offs with regard to its effect on productivity of birds (Skagen & Yackel Adams 2017). High temperatures have been associated with increased prey activity or changes in incubation activity, allowing adults to forage for longer periods without their eggs or nestlings being subjected to the negative effects of cold (Skagen & Yackel Adams 2017). Yet, high extremes, may also cause embryos of nestlings to overheat, forcing adults to attend the nest for longer periods (Väli 2013).

Precipitation is considered the most important environmental variable within arid environments, because of its influence on vegetation growth and structure, widely acknowledges as primary determinants of bird communities, as well as the timing of breeding (Skowno & Bond 2003; Wichmann et al. 2009; Burgess et al. 2011; Smith et al. 2017). This trend, although often showing a lagged effect, is also reflected in secondary and tertiary production (Bolger et al. 2005; Skagen & Yackel Adams 2017). Higher precipitation leads to increases in the amount of plant biomass, for which NDVI is sometime used as a proxy, and with it the abundance of insects, passerines and gamebirds (prey availability), which may increase foraging success of martial eagles (Arroyo & Garcia 2001; Young et al. 2009; Väli 2013; Smith et al. 2017).

Habitat quality is often linked to reproductive success and survival through the direct influence of habitat on food availability (Burgess et al. 2011). GPS tracked martial eagles showed a preference of habitats with higher tree cover; this is concerning as tree cover has decreased by as much as 60% within the last 50 years on basalt soils, which cover a large portion of eastern KNP. Correspondingly a 12% increase in tree cover has occurred on granitic soils on the western portion of the KNP (Eckhardt et al. 2000; Van Eeden et al. 2017). The changes to tree cover may have altered community composition and prey abundance on which martial eagles rely (Van Eeden et al. 2017). Tree cover declines have been attributed to interactions between Elephants (*Loxodonta africana*) and fire regimes imposed by past management decisions (Eckhardt et al. 2000; Vanak et al. 2012). Large herbivores have the potential to drive changes in vegetation structure, composition and ecosystem function (Young et al. 2009; Pellegrini et al. 2017). Elephants are unique as they have the ability to topple large trees, which they will preferentially target (Pellegrini et al. 2017). Previous research has indicated that martial eagle declines have been greatest in areas where elephant densities are highest (Cloete 2015).

In this study, we first of all explore the annual rates of productivity (young produced per territorial pair), breeding rate (breeding attempts per territorial pair) and nesting success (successfully fledging per breeding attempt) within KNP each year over a six year period between 2013-2018; to establish whether the previously low breeding performance recorded for this population over a shorter time period was representative of the longer term breeding performance of this population. Secondly, we explore which environmental variables (temperature, precipitation, NDVI, tree cover, land cover type, elephant abundances, river length and fire – all within 6 km of the nest sites), and over which period (previous year, pre-lay or breeding) for temporally dynamic variables (temperature, precipitation, NDVI) were most closely associated with our three breeding performance measures.

Methods

Study species

Martial Eagles' are one of largest eagle in Africa (females: C. 4.7 kg, males: 3.3 kg (Brown et al. 1977; Van Eeden et al. 2017). They are long lived, with some individuals reaching ages of more than 30 years in the wild (Taylor et al. 2015). They have a wide distribution across Sub-Saharan Africa, however, they generally occur at low densities (Hustler & Howells 1987; Brown et al. 2015). In the KNP inter-nest distances of approximately 12 km have previously been recorded (Tarboton & Allan 1984). In the drier savannah of the Kgalagadi Transfrontier Park and Namibia inter-nest distances of C.24km have been noted (Herholdt & Kemp 1997). Home ranges of territorial adults within the KNP estimated through GPS tracking were 117 ± 29.51 km^2 (95% KDE) (Van Eeden et al. 2017).

Martial eagle pairs usually build large, sturdy nest platforms from large sticks in tall trees (6m - 20m) (Brown 1970; Van Eeden 2016). The nests can be approximately two meters in diameter and two meters in depth, usually in the main fork of the tree or on a lateral branch (Tarboton & Allan 1984; Berndt 2015). Prior to breeding, nests can be decorated with sprigs of green leaves for two months within the 60 cm depth nest bowl without an attempt (Steyn 1982). A territorial pair will sometimes have more than one nest within their home range which they alternate between in successive breeding attempts (Steyn 1982; Tarboton & Allan 1984).

Female martial eagles lay a single egg, if the breeding attempt is successful the adults will forgo breeding in the following year (Hustler & Howells 1987). Laying generally occurs between April and July, with peak laying occurring in May (Hustler & Howells 1987). Incubation lasts for 47 – 51 days, with nestlings remaining on the nest for C. 90 – 109 days (Steyn 1982; Van Eeden et al. 2017). The post fledging period lasts around seven to nine months where fledglings will remain being fed at the nest, without any adult aggression, sometimes extending into the following years breeding period (Hustler & Howells 1987; van Eeden 2016).

Study area

The KNP covers C. 20 000 km^2 in north eastern South Africa (Kemp & Begg 2001), bordering Mozambique to the east and Zimbabwe to the north (fig 1.). The National Park, managed by South African National Parks (SANParks), is an IUCN category II protected area extending C. 400 km from north to south and 50 km east to west. The general landscape of the park comprises of undulating plains of granite and basaltic soils vegetated by various forms of savanna (South African National Biodiversity Institute 2011).

Nest site locations

Martial eagle nest locations were identified from ongoing field monitoring between 2013 – 2018 as well as from three aerial surveys, completed in 2011, 2014 and 2015 (Murn et al. 2013). Each of the aerial surveys covered a third of the park. Surveys took place during September when most raptors, including martial eagles, were brooding or had large nestlings. Surveys were conducted using a helicopter flying east-west transects spaced two km apart, flying at an altitude of C. 300 m above ground level at an approximate speed of 140 km.h^{-1} (Murn et al. 2013). Further nests were also identified by SANParks rangers and members of the project team through chance observations during the study period (fig 1.).

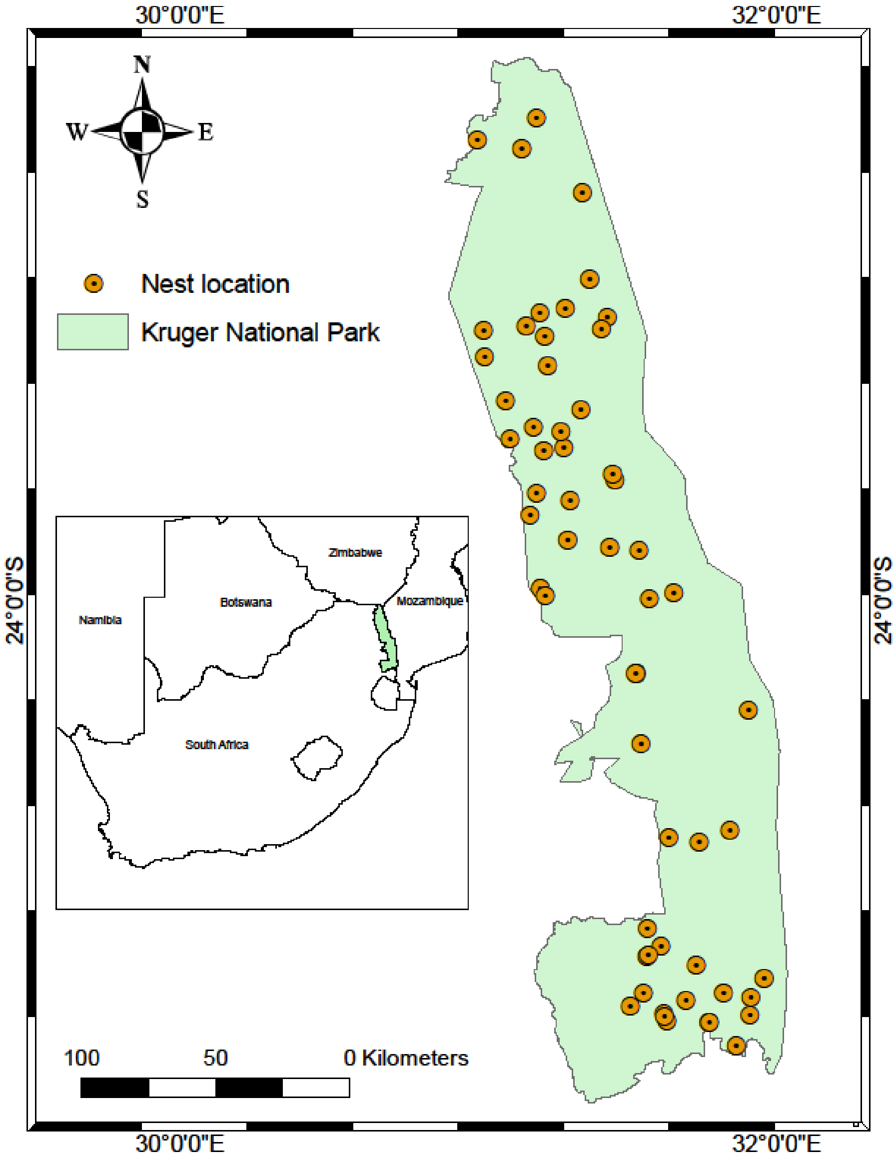

Figure 1. Map indicating the location of the KNP within Southern Africa. All martial eagle nest locations (n=58) from 48 territories in KNP. Nests locations indicated were monitored at least once between 2013 – 2018.

Breeding performance observations

Breeding performance parameters were monitored over six breeding seasons (2013 – 2018) through nest observations in 48 territories. During this period martial eagle nests where visited between one and six times in the breeding season (April – November), depending on activity at the nest. Due to the large study area, not all territories were visited each year, and not all territories had repeat visits each year. Less attention was paid to nests, which were successful in the previous year, since martial eagles do not breed the following year after being successful (Hustler & Howells 1987). Nests which were not successful in the previous year were checked in April – June each year to determine if they were 'active'. The number of nest visits conducted thereafter depended on logistical constraints as well as whether sites were considered 'active' on the first survey visit. Whether a nest was active was determined based on the presence of i) fresh nest lining (determined from the ground or through a video camera mounted on an extendable pole), ii) fresh white wash on the nest tree or ground below, iii) fresh prey remains under the nest tree, iv) the presence of martial eagle feathers and lastly, v) the presence of at least one martial eagle at the time of the nest visit. Subsequent nest visits confirmed whether 1) birds were incubating, or an egg had been produced and 2) whether a chick had hatched, and 3) whether a chick had successfully fledged, defined as reaching 56 days old (Minimum Acceptable Age for Assessing Success) (Hustler & Howells 1987).

A territory was considered to be occupied – and thus used to estimate productivity and breeding rate, if it was occupied at least once during the study, and it was deemed to be active (see above) within a five year period. If a period of more than five years passed without the territory being ‘active’ we considered the territory to be abandoned and that territory was excluded from our calculations.

This information allowed us to determine for each territory in each year i) whether an attempt had been made – breeding rate and ii) whether an attempt was successful – nesting success, iii) overall productivity (Table 1).

Breeding parameters

We used three breeding parameters in our analysis, all were scored as either 0 or 1 (NA if unknown – due to lack of repeat visits) for each territory that was sufficiently monitored in each year: 1) Breeding rate – the proportion of occupied territories which made a breeding attempt i.e. incubation confirmed: egg or incubating adult martial eagle present, 2) Productivity – the proportion of territories which fledged a chick and 3) Nesting success – the proportion of breeding attempts which fledged a chick. In some years where occupation, attempt or success could not be confirmed with certainty due to logistical constraints, the territories in those years were excluded from some of the parameters analyzed – hence we had highly variable sample sizes between years and parameters.

Table 1. Reproductive terms used to describe the breeding behavior of martial eagles.

Term	Description
Minimum Acceptable Age for Assessing Success	Nestlings older than 56 days were considered to have fledged successfully (Hustler & Howells 1987).
Success	Breeding attempt in which the fledgling reaches Minimum Acceptable Age for assessing Success (MAAS, 56 days old).
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)
Breeding season	April – November annually: from egg laying to successful fledging
Pair years	Cumulative number of years in a population that a territory was occupied.
Breeding rate	Breeding rate is the proportion of the monitored nest years in which a breeding attempt is made (Murgatroyd et al. 2016).
Occupied	Territories where at least one adult had been seen on the nest tree or in the proximate area, or if martial eagle feathers, fresh white wash or fresh plant material was observed on the nest indicating use. Where no activity was seen for five years a territory was considered abandoned (Krüger & Amar 2017).
Attempt	Incubation confirmed: egg or incubating martial eagle present.
Productivity	Productivity is the proportion of the adequately monitored territories in each year that successfully fledge a chick.
Nesting success	Nesting success is proportion of breeding attempts that raise a hatchling to the MAAS (Steenhof & Newton 2007).

Environmental variables: All environmental variables were extracted from a circular buffer centered on the nest location with a radius of 6.1 km (6 km hereafter). The radius of the buffer corresponds to the 95% (117 km^2) KDE home range size estimate for adult territorial martial eagle GPS tracked within the KNP (Van Eeden et al. 2017).

Land cover types surrounding each nest site was estimated using the South African National land cover dataset (GeoTerra Image (GTI) Pty Ltd 2015) which classifies land cover into 72 core classes at a 30m resolution from data derived in 2013/2014. Because of the mostly natural landscape that exists within the KNP, land cover types were reduced to four classes, namely: thicket (dense bush), woodland (open bush), grassland and other. Thicket and grassland vegetation types are a core land cover types. Woodland is another core cover type and was combined with indigenous forest, which only included in two nests (<1%). Land cover type “other” was an amalgam of the remaining land cover types (and only made up on average 1.5% (range 0% – 40.6%). The percentage of each land cover class within each buffer was calculated (Table S25).

The mean percentage tree cover (tree cover) in each buffer was derived from Landsat Tree Cover Continuous Fields (VCF) 30 m resolution tree cover map (Table S25). VCF estimates the percentage of each 30 m pixel that is covered by woody vegetation greater than 5 m in height (Sexton et al. 2013).

To determine the length of rivers (river length) surrounding each nest site we used the 1:50 000 HydroSHEDS river network map, which illustrates streams and rivers globally (Lehner et al. 2008).

Lastly, we calculated the average abundance of elephants counted, from point count data, within the nest buffer during-aerial surveys conducted in 2010, 2012, 2015 and 2017. This provided a single average abundance from the four mega faunal aerial surveys (SANParks unpublished data) for each nest buffer.

Information on habitat characteristics, tree cover and extent of rivers, were considered 'landscape variables', which for the purpose of this study were considered to be constant between years, and thus had only a single measure for each nest site during the six years of monitoring.

Additionally, we extracted information on the amount of fire around the nest sites for three relevant time periods: 1) pre-lay period (Nov – Apr), 2) breeding period (May - Oct) and 3) average conditions throughout the previous year (Jan – Dec). The percentage of the area burned within the buffers for each time period was extracted from Moderate Resolution Imaging Spectrometer (MODIS) Burned Area product which has a 250 m resolution (2012 – 2018) (Giglio et al. 2009).

Climatic variables: We also obtained information on climatic variables in the buffers for the three time periods: 1) pre-lay period (Nov – Apr), 2) breeding period (May - Oct) and 3) average conditions throughout the previous year (Jan – Dec). For each nest year (2012 – 2018) we extracted average temperature (GLDAS Noah Land Surface Model L4 monthly 0.25 x 0.25 degree V020 (GLDAS_NOAH025_M) at GES DISC **"avetemp"** (equivalent to 25.5 km x 25.5 km)) (Rodell et al. 2004).

To extend the time period to allow hindcasting, we also obtained the average-maximum daily temperature (1986 – 2018) from CPC Global Daily Temperature at a 0.5 degree resolution **"maxtemp"** (equivalent to 67.4 km x 67.4 km) (NOAA/OAR/ESRL PSD, Boulder, Colorado 2019). Average precipitation estimates (1986 – 2018) were extracted from the Climate Hazards Group InfraRed Precipitation with Station dataset (CHIRPS) provided at a resolution of 0.05 degrees(equivalent to 5.8 km x 5.8 km) (Funk et al. 2015).

We obtained mean NDVI for each time period in the buffers using the MOD13A1 Version 6: 16-day product, at a resolution of 500 m **"aNDVI"** (covering the years 2012 – 2018) (Didan, 2015).

To extend the time period to allow hindcasting, we also obtained daily NOAA Climate Data Record (CDR) of Normalized Difference Vegetation Index, Version 4 which is produced at 0.05 degree (approx. 5.1 km x 5.1 km) resolution **"bNDVI"** (1986 – 2018) (Vermote et al. 2014).

Variable layers avetemp and aNDVI provided the finer scale resolution than their extended counterparts and were used during the analysis determining which time periods are important for martial eagles breeding performance. Climatic variables maxtemp and bNDVI covered longer time scales necessary for hindcasting. Data for bNDVI years 2001, 2002, 2003, 2008, 2009 and 2010 were missing and thus excluded from subsequent analysis.

Statistical analysis:

All analyses were performed in R version 1.2.1335 (R core team 2019). Many of our land cover and climate variables were correlated with each other. Thus we used two ordination approaches to deal with these correlations and to reduce the overall number of variables in the final models. Firstly, for the four land cover variables we performed a Canonical Correspondence Analysis (CCA) using the "vegan" package (Oksanen et al.

2014). Using this approach we reduced the original four land cover classes to two meaningful dimensions (CCA1 and CCA2) which we utilized in the analysis of breeding performance parameters to explore for any association between breeding performance and different land covers.

For, the climate variables (temperature, precipitation and NDVI) within each time period we used a Principal Component Analysis (PCA) with package SensoMineR (Le & Husson 2008). We again used the scores from the first two PCA dimensions (PCA1 and PCA2) in our subsequent analysis. These PCA's were done on both the short-term data covering our monitoring period (2013 – 2018; PCA1 and PCA2) and the longer-term data (1986 – 2018; $PCA1^{hist}$ and $PCA2^{hist}$) to allow hindcasting.

Our analyses aim to identify which variables, and for those that were temporally variable (e.g. climate, NDVI and fire), over which time periods were most closely associated with breeding performance (Table 2). For these analyses we used generalized linear mixed effect models (GLMMs) for productivity and breeding rate and univariate Generalized Linear Models (GLMs) for nesting success because of the lower sample size (n = 35). We explored whether the productivity, breeding rate and nesting success were related to any of our environmental variables in the three time periods by constructing models separately for variables in i) the pre-lay period (Nov - Apr), ii) the breeding period (May - Oct), and iii) the previous year (Jan - Dec).

The top models for productivity and breeding rate were compared between time periods via their Akaike's Information Criterion scores, corrected for small sample size (AIC_c), and explored in depth later, after determining which time period was most influential on those breeding parameters. The GLMMs were constructed with a binary response variable (e.g. 1 = attempt/success, 0 = no attempt/failure), specifying a binomial family and a logit-link function using the package “lme4” (Bates et al. 2015). Territory was included as a random effect to account for the repeated measurement from the same territories between the years. When necessary model convergence was reached using the “optimx” package (John et al. 2018). To examine which variables best explained breeding performance, we used an Information Theoretic approach whereby all potential variable combinations were tested and the models were ranked by their Akaike’s Information Criterion scores corrected for small sample size (AIC_c) using the dredge function with the “MuMIn” package (Barton 2014). Where necessary, for our final models, model averaging was performed across the top candidate models ($\Delta AIC_c < 2$) and conditional averages of the models and their 95% confidence intervals were reported. All variables, except territory, were standardized by centering (subtracting sample mean) and scaling (dividing by sample standard deviation) (Schielzeth 2010). For nesting success, univariate GLMs AIC_c scores were compared to find the best model for each time period. The GLMs were constructed with a binomial response variable (e.g. 1 = attempt/success, 0 = no attempt/failure) and the best overall model was explored in depth thereafter. As no random terms could be included in the GLMs the issue of repeated measures from the same territories was ignored. This was less problematic as it only occurred for five territories with nine observations in total.

To generate the estimated averages for our three breeding performance measures, whilst correcting for the unbalanced sampling between territories, we also ran null GLMMs with territory as a random term. Further models, with territory as a random term and year as a fixed effect were generated for each breeding measure to determine whether there were any significant between years differences in the breeding performance measures (Table 2). The productivity estimate was compared with other estimates generated for martial eagles throughout southern Africa.

To determine whether productivity differed by region we split the KNP along 24 degree south line of latitude, into north and south, to determine if breeding performance was spatially influenced (Table 2). We performed a GLM with binomial response variable (e.g. 1 = success, 0 = failure) specifying a binomial family and a logit-link function.

Hindcasting significant environmental variables

For variables that were temporally dynamic (i.e. climate, NDVI or fire) and that were associated with variation in the breeding productivity, we also repeated our final models substituting the data sourced over the longer time period (i.e. 1986 – 2018) with that of the finer resolution short term data (i.e. 2012 – 2018). This time period, 1986 – 2018, aims to cover the period from SABAP 1 to SABAP 2 and thus the period of the large documented decline of martial eagles in KNP. If the temporally dynamic variable maintains an association with breeding productivity we then used that model together with the predict function, from “stats” package (Chambers & Hastie 1992), to hindcast breeding performance that would be predicted each year between 2018 and 1986. This will be done to determine if breeding productivity measures may have changed throughout the time period due to changes in climate. Furthermore, we used these predicted annual estimates as response variables with year as a continuous predictor variable to determine whether productivity is likely to have changed over the time period from 1986 – 2018 using a GLM (Table 2).

Table 2: Table outlining all the key analysis completed. Explanatory variables tree cover, fire, river length and average elephant abundances were not manipulated. PCA and CCA were the scores extracted from the CCA and PCA analyses. CCA1, CCA2, PCA1 and PCA2 represent the first and second dimension from each analysis respectively. *All explanatory variables included for each model in each time period. **Univariate analyses performed for each explanatory variable in each time period.

Breeding parameter/ Time period	Model	Response	Explanatory variable	Random	Distribution	Sample size	Dataset
Productivity*							
Pre-lay Breeding period Previous year	GLMM	Success	PCA1, PCA2, CCA1, CCA2, River length (m), Fire (%), Elephant abundance, Tree cover (> 5m)	1)Territory	Binomial	135	All territories where any sign of martial eagle occupation has been observed in the last five years. That were adequately monitored to know if a young was fledged
Null	GLMM	Success	NA	1)Territory 2) Territory and year	Binomial	156	
Breeding rate*							
Pre-lay Previous year	GLMM	Attempt	PCA1, PCA2, CCA1, CCA2, River length (m), Fire (%), Elephant abundance, Tree cover (> 5m)	Territory	Binomial	118	Territories where incubation was initiated (adult martial eagles either flushed off the nest or incubating).
Null	GLMM	Attempt	NA	1) Territory	Binomial	118	

Nesting success**							
Pre-lay Breeding period Previous year	GLM	Success	PCA1, PCA2, CCA1, CCA2, River length (m), Fire (%), Elephant abundance, Tree cover (> 5m).	NA	Binomial	35	Territories with breeding attempts, where success or failure could be established.
Null	GLMM	Success	NA	1) Territory 2)Territory and year	Binomial	35	
Additional analysis**							
Hindcasting Productivity Previous year	GLMM	Success	**PCA1	Territory	Binomial	135	All territories where any sign of martial eagle occupation has been observed in the last five years.
Region (North / South)	GLM	Success	Region	NA	Factor	156	All territories where any sign of martial eagle occupation has been observed in the last five years.
Productivity over time (1987 - 2018)	GLM	Predicted annual productivity	Year	NA	Continuous	27	Model predictions using all territories where any sign of martial eagle occupation has been observed in

the last five years.

Results

Habitats - Canonical correspondence analysis

Our CCA explored the variation between the four land cover variables (thicket, woodland, grassland and other) (Table 3). Dimensions 1 and 2 explained 86 % of the variation in the data and were used for the breeding parameter analysis. CCA1 (dimension 1) separated sites with more thicket and woodland *Vs* those with more grassland; whereas CCA2 separate sites with more thicket from those with more woodland (Table 4, fig 2.).

Table 3: Results of the CCA analysis on the four land cover types: woodland, thicket, grassland and other, measured as a percentage of each nest buffer. Eigenvalue indicates the proportion of the variance explained by the CCA.

	Inertia	Proportion	Rank
Total	0.45	1	
Constrained	0.45	1	3
Unconstrained	0	0	0

Eigenvalues and their contribution to the scaled Chi-square

Importance of components:	CCA 1	CCA 2	CCA 3
Eigenvalue	0.27	0.12	0.062
Proportion explained	0.60	0.26	0.14
Cumulative proportion explained	0.60	0.86	1

Table 4: CCA scores for land cover classes and biplot scores for constraining variables retrieved from the CCA analysis of land cover types. Land cover percentages in the buffer were extracted around each nest.

Land cover scores for each land cover class			
	CCA1	CCA2	CCA3
Thicket	0.46	-0.14	-0.44
Woodland	0.23	0.15	0.17
Grassland	-0.87	-0.05	-0.06
Other	0.46	-2.57	0.67
Biplot scores for the constraining variables			
Thicket	0.71	-0.22	-0.67
Woodland	0.71	0.47	0.52
Grassland	-0.10	-0.06	-0.07

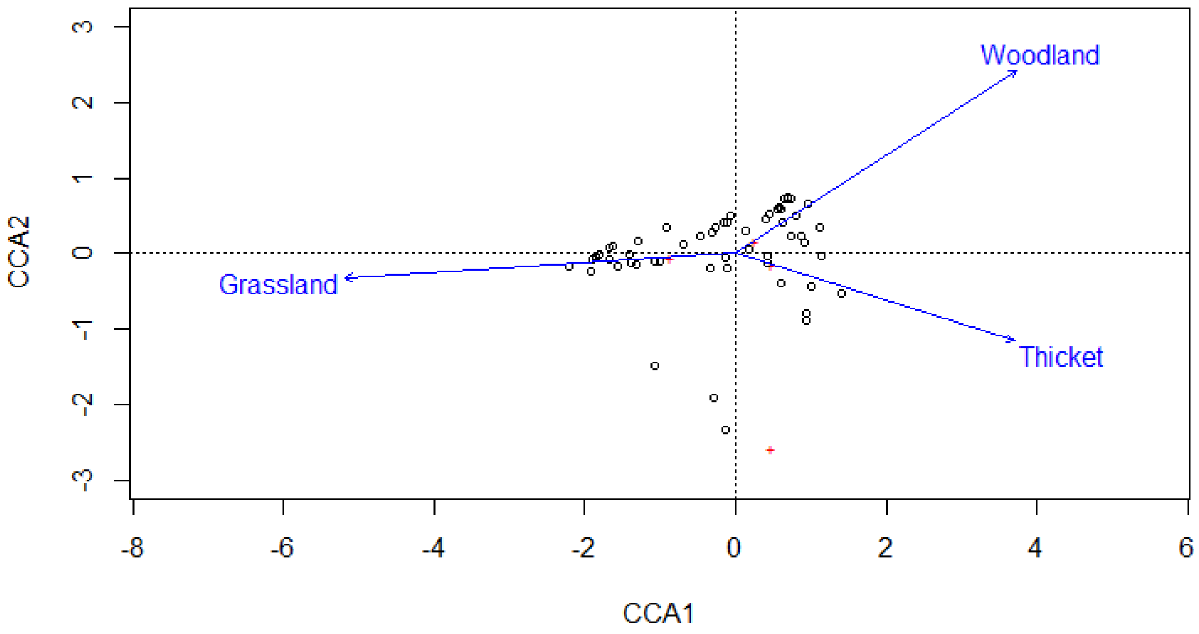

Figure 2: Plot of CCA land cover analysis. Arrows indicate the directions of the constraining variables in space**.** Only constraining variables are labeled. Red crosses indicate the scores of each land cover.

Climate – Principal Component Analyses

The first two dimensions of our PCA on climate accounted for 91.9 % of the variation in the data (Table 5). These two dimensions were therefore used in our subsequent analyses. PCA1 largely separated sites/years with higher level of precipitation and NDVI and lower temperatures, from those with higher temperatures and lower precipitation and lower NDVI. PCA2 largely separated sites/years with high precipitation and low NDVI from those with higher NDVI and lower precipitation (fig 3.).

We ran the same PCA but for during the six month pre-lay period and the six month breeding period of that year. These PCA dimensions produced were very similar to those for the previous year (Table 5 and S2-3, fig 3. and S1-2.).

Table 5: Results of the PCA analysis on three temporally dynamic variables captured during the previous year period: mean annual precipitation, mean annual average temperature and mean annual NDVI, showing the percentage variance explained by each dimension (% variance) and the cumulative percentage of variance explained by each dimension (Cum. % of variance). The relative contribution of each variable to each dimension is also presented (Ctr).

Eigenvalues	Dimension 1		Dimension 2		Dimension 3	
Eigenvalue	2.15		0.6		0.24	
% of variance	71.81		20.05		8.14	
Cumulative % of variance	71.81		91.86		100	
Variables	**Dim 1**	**Ctr**	**Dim 2**	**Ctr**	**Dim 3**	**Ctr**
Precipitation	0.858	34.16	-0.417	28.915	0.3	36.925
NDVI	0.761	26.883	0.639	67.823	0.114	5.293
Temperature	-0.916	38.957	0.14	3.262	0.376	57.781

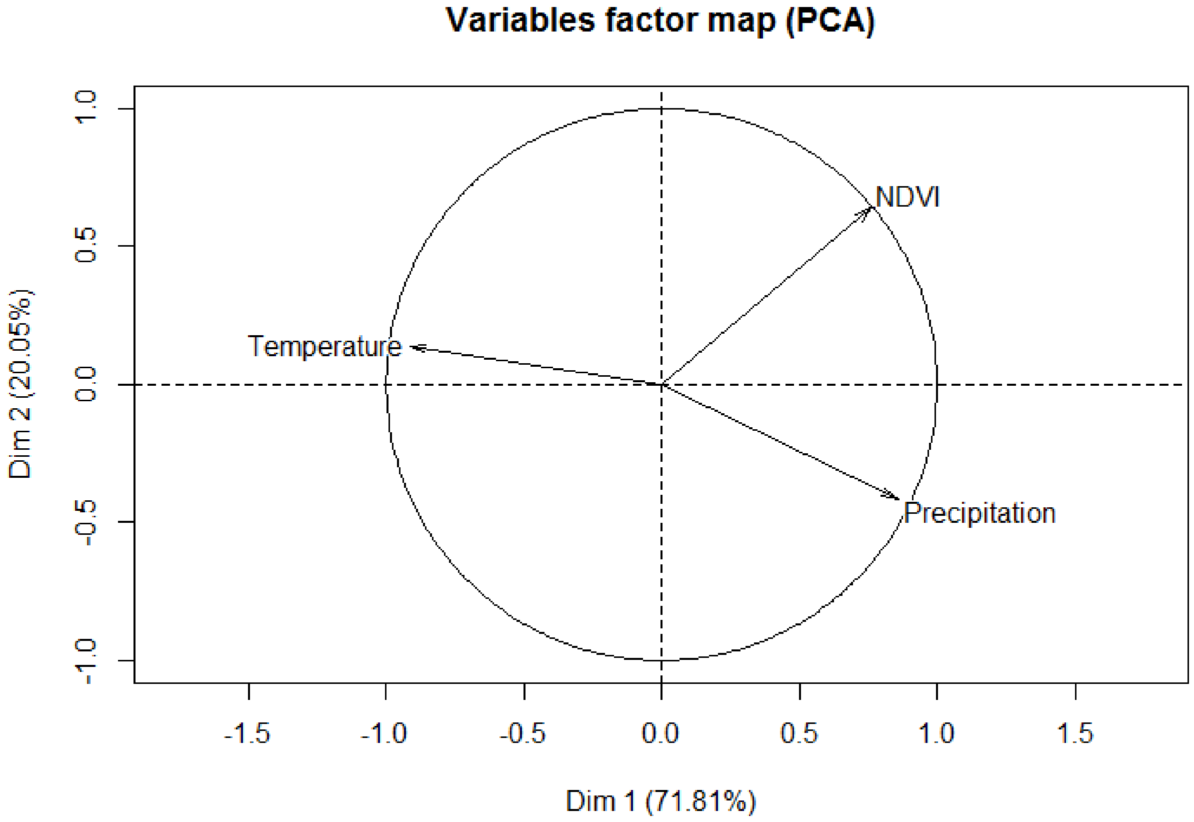

Figure 3: Diagram illustrating the separation of climatic variable results from the PCA.

Breeding parameters

Nest visits were conducted at 48 territories, over the six years. A total of 175 pair years were monitored (Table S1). From these 175 observations, there were 22 instances were breeding attempts could not be confirmed due to insufficient visits and 35 instances when the success of breeding attempts the previous season could not be concluded (for the first year of monitoring all nests were assumed not to have produced a chick the previous year – due to no knowledge on this). Thus there were 37 attempts from 118 complete monitoring observations giving an overall breeding rate across all the years and all observations of 31.4 %.

Of the 43 confirmed breeding attempts, success could not be determined definitively in eight of the nests due to insufficient monitoring, which were thus excluded. A total of 16 chicks successfully fledged from the remaining 35 territories, resulting in a nesting success across all years of 45.7 % per breeding attempt.

Lastly, from the 175 pair years monitored, the outcome of 19 nests could not be conclusively confirmed due to insufficient monitoring. Of the remaining 156 pair years, a total of 27 chicks successfully fledged (reaching at least 56 days old); giving an overall productivity of 0.17 young per pair year.

The overall measures outlined above were similar to the estimates for these same parameters from the models which corrected for repeated measures by territory and year as random terms. Estimates from null GLMM models which describe these parameters correcting for repeated measures of territories were: breeding rate (β **±** SE = 0.28 **±** 0.03, z = -2.49, p = 4.28e-08, vs. 0.31 %), nesting success (0.49 ± 0.15, z = -2.49, p = 0.937, vs 45.7 %) and productivity (0.16 **±** 0.03, z = -7.02, p = 4.28e-08, vs 0.17 %) (Table 6 and S4, S5, S8, S9, S10 and S11). The productivity estimate is the lowest recorded between any studies done to date for martial eagles (fig 6.).

Using these same models, but including year as a fixed effect, we also tested for any significant differences between years. Only nesting success showed a significant differences between years (p = 0.03) (Table S12-13), annual nesting success in 2018 was higher than 2014 (p = 0.04). No significant differences were observed between years for productivity (p = 0.26) or breeding rate (p = 0.21) (Table S6, S7, S12 and S13).

Table 6: Summary of martial eagle pairs monitored in KNP from 2013-2018, and estimates of average breeding performance per year (± SE). These estimates are from null GLMMs fitting the random term 'territory' and thus controlling for unbalanced sampling from different territories. Except for Breeding rate – which are the average from the raw values.

	2013	2014	2015	2016	2017	2018	Total ± SE
Pair years	20	28	40	31	28	28	175
Attempt	0/16	11	7	4	9	12	43
Fledged young	3/19	5	5	1	5	8	27
Productivity	0.15 ± 0.08	0.16 ± 0.07	0.14 ± 0.06	0.04 ± 0.04	0.17 ± 0.07	0.26 ± 0.09	0.16 ± 0.03
Breeding rate	0	39.3	17.5	12.9	32.1	42.9	31.4
Nesting success	0	0.12 ± 0.10	0.83 ± 0.20	1 ± 0.0002	0.18 ± 0.15	0.81 ± 0.13	0.49 ± 0.15

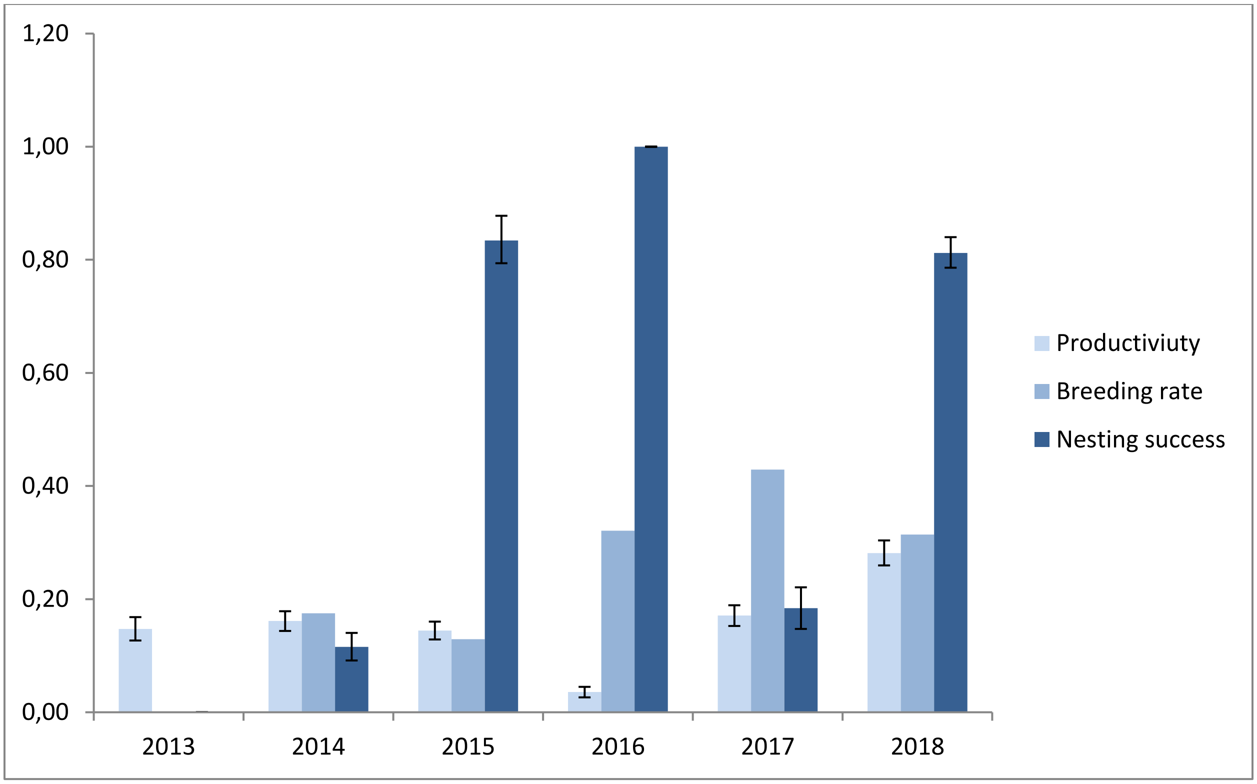

Figure 4: Breeding performance of martial eagles in the KNP from 2013 -2018 from the GLMM, raw data and GLM analysis with year as a fixed effect for. a) Productivity (n =156), b) breeding rate (n=118) and c) nesting success (n=35) respectively. Where possible the standard error around the estimates has been included. Only nesting success varied significantly between the years monitored. Only raw values are illustrated for breeding rate as model convergence with year as a fixed effect could not be reached. Only productivity estimates were generated for 2013 as sampling was not sufficient to determine breeding rate and nesting success.

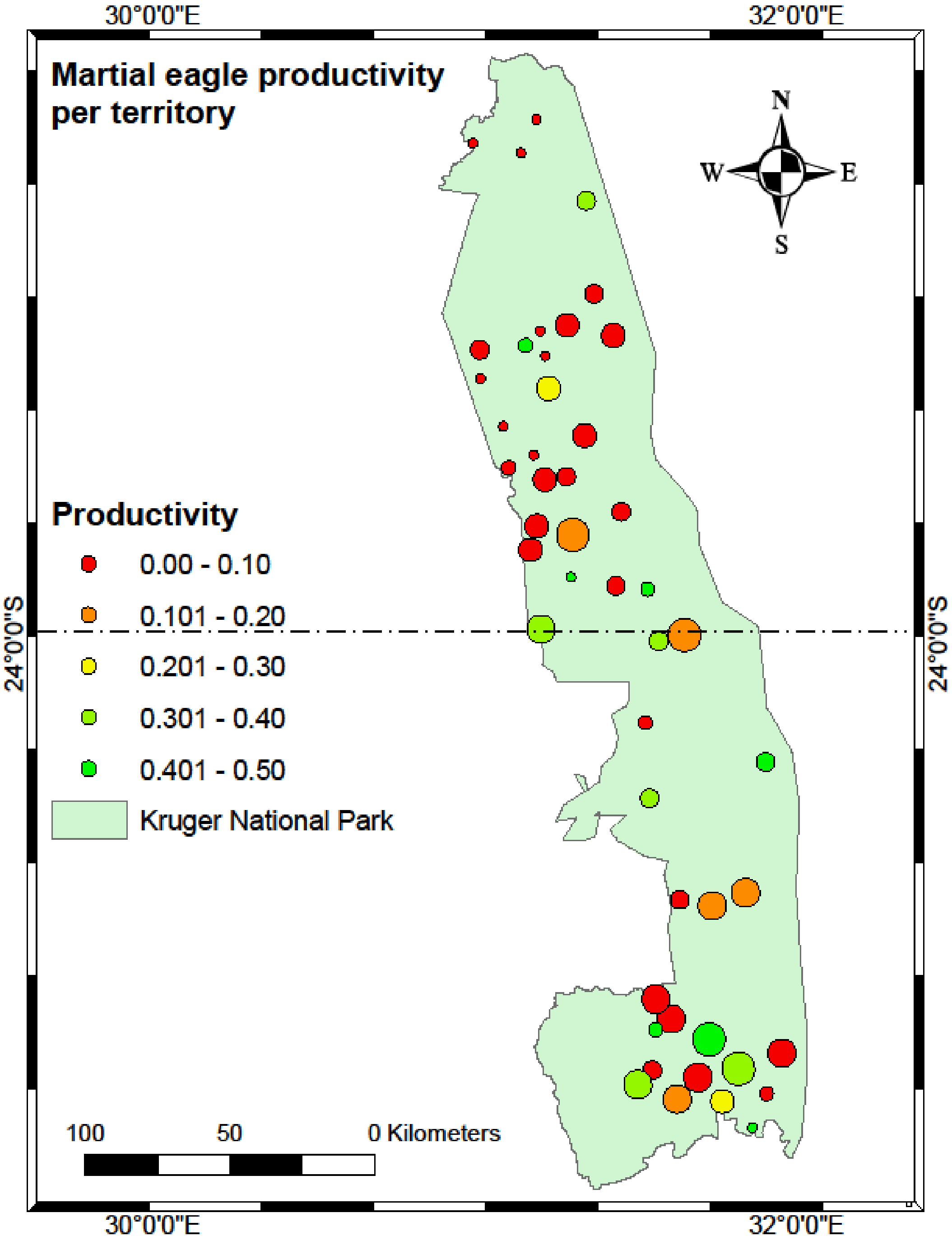

Figure 5: Map indicating the relative productivity of each martial eagle territory (n = 48) within the KNP where success or failure in at least one pair year was known. Productivity is the proportion of monitored territories that successfully fledged a chick. Circles indicate the location of a territory. Circle colours indicated the relative productivity (number of chicks fledged divided by the number of years monitored). Larger circles indicate territories monitored more often, proportionally.

Visually examining the relative productivity of each monitored territory (fig 5.), no obvious clustering of successful or unsuccessful territories were apparent, nor can any spatial variation in the relative productivity be observed. No difference in productivity could be detected between the northern and southern portions of the KNP (p=0.09), though a slight trend for higher productivity in the south of the KNP was observed (Table S14).

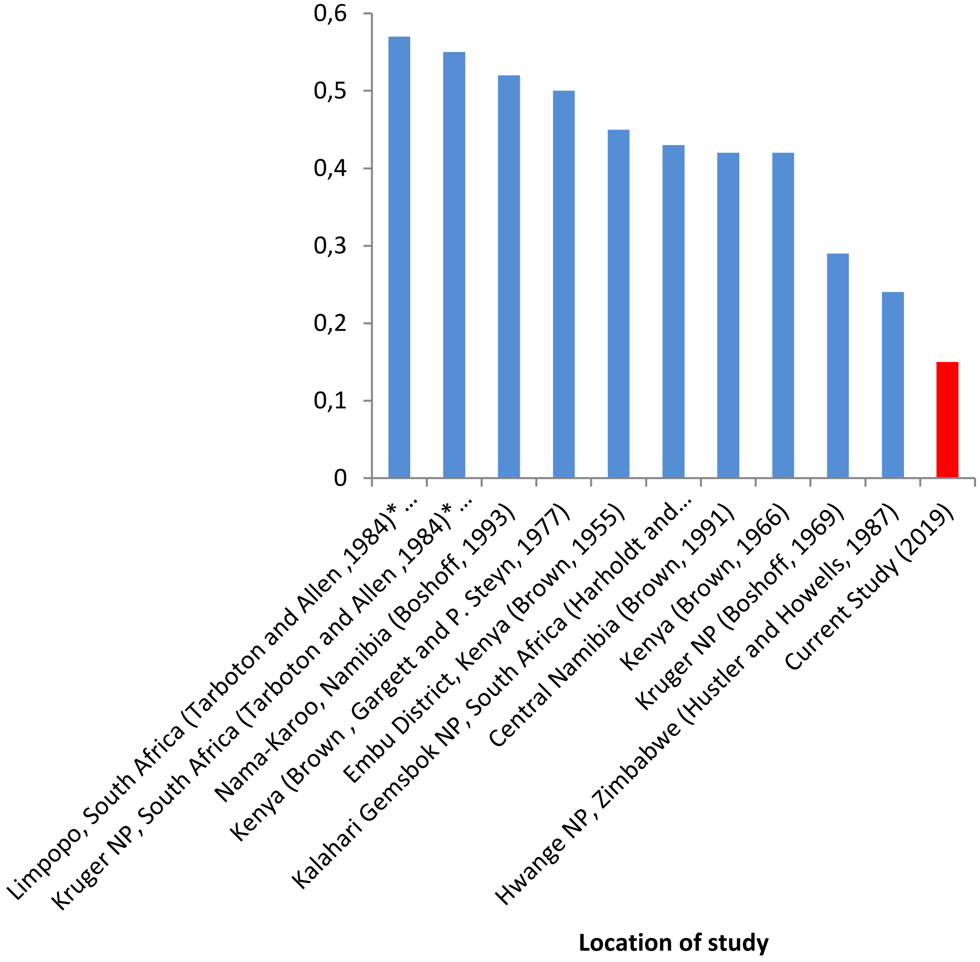

Figure 6: Martial eagles breeding productivity in the KNP (red) compared to previous estimates recorded throughout southern and east Africa.

Temporal analyses on breeding parameters

For breeding productivity and success we tested the effect of environmental variables during three time periods (i.e. pre-lay, during the current breeding period, during the previous year) to explore whether conditions during a certain time period had the greatest influence on breeding performance. We ran these same analyses for breeding rate, although we excluded conditions during the current breeding period since these conditions relate to a period after incubation and thus could not conceivably influence this parameter. The AICc of the top models for productivity and breeding rate, and the best univariate model for nesting success were compared between the three time periods (Table 7).

For productivity the top candidate model, containing PCA1 with a relative importance of one, suggested that environmental conditions during the previous year had the greatest influence on whether a territory fledged a chick (Table 7 and S15-S18) (ΔAIC_c: prelay: 4.03; breeding period: 4.03).

The top candidate model for breeding rate featured mean tree cover, CCA1, CCA2 and PCA2. The time period which featured the lowest AICc was during the pre-lay period, but only performed slightly better than the model featuring dynamic variables from the previous year (Table 7 and S19-S20) (ΔAIC_c: previous year: 0.94).

Nesting success, undertaken with univariate analysis of our variables indicated that conditions during the previous year provided the best model with the lowest AICc (PCA2) (ΔAIC_c: prelay: 2.81; breeding period: 3.03). This time period performing considerably better than during the pre-lay and breeding periods in influencing whether a pair fledged a chick after making an attempt (Table 7 and S21-S22).

Table 7. Findings of the breeding performance analysis performed using GIS layers PCA (aNDVI, avetemp, precipitation), CCA (woodland, thicket, grassland and other), average elephant abundances, percent tree cover (>5m), % of buffer area burnt and river length (m). PCA1 and PCA2 are the dimensions extracted from the principal component analysis using NDVI, temperature and precipitation values. CCA1 and CCA2 are the dimensions extracted from the Canonical correspondence analysis of land cover variables (Woodland, Thicket, grassland and other). Explanatory variables were extracted per each time period.

	Top model								
	Previous year			Pre-lay			Breeding period		
GLMM	variables	RI	AICc	variables	RI	AICc	variables	RI	AICc
Productivity	PCA1	1	**130.38**	CCA1 CCA2	0.56 0.46	134.41	CCA1 CCA2	0.64 0.43	134.41
Breeding rate	Tree cover CCA1	1 1	144.05	Tree cover CCA1 CCA2 PCA2	0.68 0.63 0.82 0.93	**143.11**	NA	NA	NA
GLM	Variable	AICc		Variable	AICc		Variable	AICc	
Nesting success	PCA2	**45.58**		PCA1	48.39		PCA2	48.61	

Productivity (Previous year's conditions)

The productivity analyses, included climate conditions experienced during the previous year. This analyses included 14 top candidate models with a $\Delta AIC_c < 2$ (Table 8) (ΔAIC_c: prelay: 4.03; breeding period: 4.03). Following model averaging, the most important variable, included in all of the top models, was PCA1, and was the only variable whose estimates did not overlap zero. The relationship was positive, indicating increased productivity in years following conditions that had higher precipitation and NDVI levels with lower mean temperatures (Table 9; fig 7).

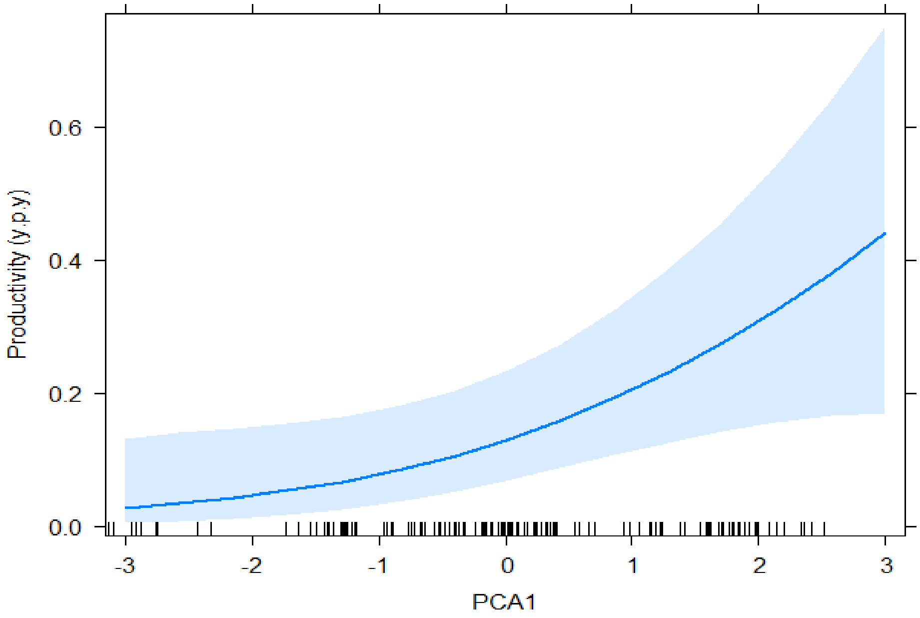

Figure 7: Effects plot of the GLMM showing the modeled effect of PCA1 on martial eagle breeding productivity. The solid line shows the predicted relationship with 95% confidence intervals shaded in blue.

Table 8. Results from the top 14 GLMMs models, where $\Delta AIC_c < 2$, comparing model fit of productivity in martial eagles (n = 135 observation from 2013 – 2018). Model parameters recorded from the previous year: PCA1, PCA2, CCA2, river length (m - Riv), fire (% buffer burnt - Fire), average elephant abundance per buffer (Eleph) and mean percentage tree cover (>5m height - TreeC). W_i = Component weight.

Model	df	logLik	AICc	Δ AICc	Weight
PCA1	3	-62.1	130.38	0	0.12
CCA2 + PCA1	4	-61.12	130.55	0.17	0.11
PCA1 + Riv	4	-61.27	130.84	0.46	0.1
Eleph + PCA1 + Riv	5	-60.22	130.9	0.52	0.1
TreeC + PCA1	4	-61.54	131.38	1	0.08
CCA2 + PCA1 + Riv	5	-60.59	131.64	1.25	0.07
Eleph + PCA	4	-61.67	131.64	1.26	0.07
Fire + PCA1	4	-61.8	131.9	1.52	0.06
TreeC + CCA2 + PCA1	5	-60.73	131.93	1.55	0.06
Fire + CCA2 + PCA1	5	-60.85	132.17	1.79	0.05
PCA1 + PCA2	4	-61.93	132.17	1.79	0.05
Eleph + CCA2 + PCA1	5	-60.88	132.23	1.84	0.05
CCA1 + PCA	4	-61.98	132.27	1.89	0.05
TreeC + PCA1 + Riv	5	-60.91	132.28	1.9	0.05

Table 9. Parameter estimates from model averaging of the ranked models in Table 10 explaining the variation in martial eagle productivity. Parameters: PCA1, PCA2, CCA1, CCA2, river length (m), percentage buffer burnt, mean tree cover (%) and average elephant abundance per buffer (ab/117km^2) reported from the conditional averages. RI = Relative importance. Variables in bold show those who 95% CI do not overlap zero

Variable	Estimate	Std.Error	CI(2.5%)	CI(97.5%)	Z value	RI
(Intercept)	-1.93	0.35	-2.62	-1.22	5.42	-
PCA1	**0.81**	**0.34**	**0.09**	**1.50**	**2.36**	**1.00**
CCA2	-0.37	0.32	-1.00	0.31	1.13	0.34
River length (m)	0.48	0.37	-0.27	1.21	1.28	0.31
Elephant (ab/117km^2)	-0.41	0.39	-1.19	0.36	1.03	0.21
Tree cover (%)	-0.30	0.32	-0.99	0.35	0.95	0.18
Fire (%)	-0.20	0.27	-0.74	0.38	0.73	0.11
PCA2	0.17	0.29	-0.39	0.78	0.58	0.05
CCA1	0.18	0.38	-0.51	1.13	0.47	0.05

Breeding rate (Pre-lay period conditions)

This analysis of breeding rate, included climatic variables taken during the pre-lay period. Model averaging generated seven top candidate models with a $\Delta AIC_c < 2$ (Table 10) (ΔAIC_c: previous year: 0.94). Subsequent to model averaging the variables included in the top candidate model were mean tree cover, CCA1, CCA2 and PCA2. Mean tree cover and CCA1 occurred in all the top models and each had a relative importance of 1 (Table 11). Breeding rate had a negative estimate with tree cover indicating more breeding attempts in locations with less tree cover (Table 13), this was the only variable who 95% CI's didn't overlap zero (Table 11; fig 8.). Histograms of the average tree cover per territory, where an attempt was made and in territories where no attempt to breed was made, indicates that territories where no attempt to breed was made in a particular year had a slightly more left skewed tree cover distribution (fig 9a-b).

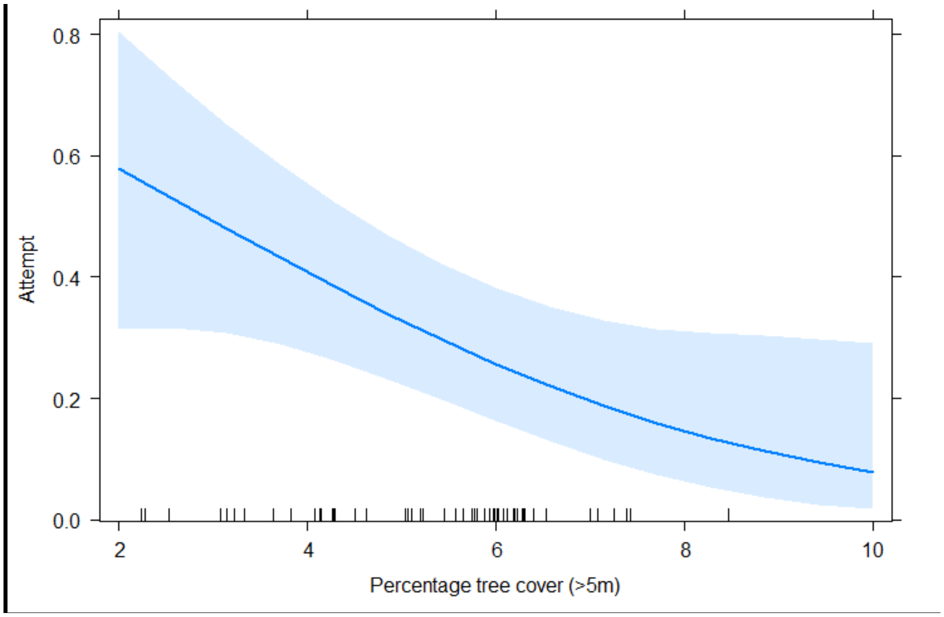

Figure 8: Effects plot of the GLMM showing the modeled effect of tree cover on martial eagle breeding rate. The solid line shows the predicted relationship with 95% confidence intervals shaded in blue.

Table 10. Results from the top seven GLMMs models, where ΔAIC$_c$ < 2, comparing model fit of breeding rate in martial eagles (n = 118 observation from 2013 – 2018). Model parameters recorded from the previous year: PCA2, CCA1, CCA2, fire (% buffer burnt - Fire) and mean percentage tree cover (>5m height - TreeC). W$_i$ = Component weight.

Model	df	LogLik	AIC$_c$	ΔAIC$_c$	Weight
TreeC + CCA1 + CCA2 + PCA2	6	-65.18	143.11	0	0.22
TreeC + Fire + CCA1 + CCA2 + PCA2	7	-64.29	143.6	0.49	0.17
TreeC + CCA1 + PCA2	5	-66.54	143.62	0.51	0.17
TreeC + CCA1	4	-67.85	144.05	0.94	0.14
TreeC + Fire +CCA1 +PCA2	6	-65.83	144.42	1.31	0.11
TreeC+ CCA1 + CCA2	5	-66.97	144.47	1.36	0.11
TreeC + Fire + CCA1	5	-67.21	144.96	1.85	0.09

Table 11. Parameter estimates from model averaging of the ranked models in Table 12 explaining the variation in martial eagle breeding rate. Parameters: Tree cover (%), CCA 1, CCA 2, PCA 2 and fire (% buffer burnt). RI = Relative importance.

Variable	Estimate	Std.Error	CI(2.5%)	CI(97.5%)	Z value	RI
(Intercept)	-0.88	0.23	-1.32	-0.42	3.86	-
Tree cover (%)	**-0.60**	**0.24**	**-1.05**	**-0.07**	**2.45**	**1.00**
CCA1	0.53	0.25	-0.03	1.01	2.09	1.00
CCA2	-0.39	0.30	-1.00	0.18	1.27	0.67
PCA2	0.40	0.22	-0.03	0.85	1.80	0.50
Fire (%)	0.37	0.49	-0.64	1.47	0.74	0.37

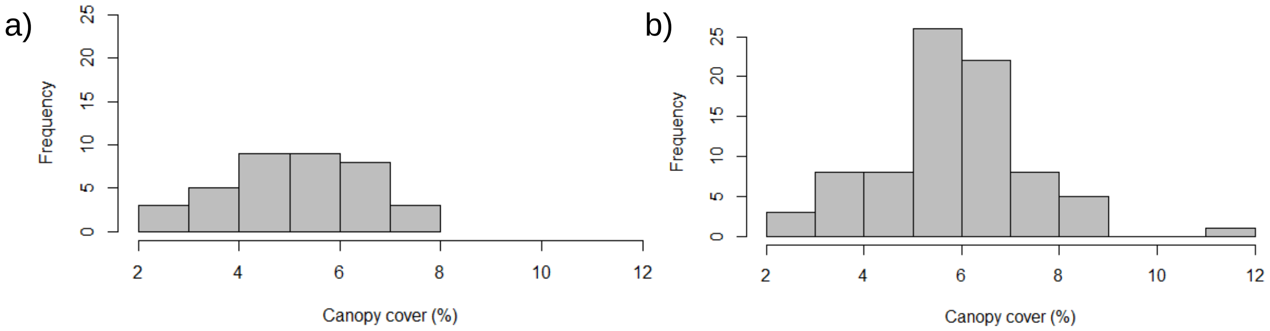

Figure 9a-b: Histogram of average canopy cover where: a) an attempt to breed was made (n = 37) and b) no attempt to breed was not made (n = 81).

Nesting success (Univariate analysis of the previous year's conditions)

Examining the AIC_c scores for the best model for nesting success, PCA2 from the previous year's conditions produced the lowest AIC_c for any of the variables of the three time periods. This model performed much better than the best models from the pre-lay and breeding period (Table 12) (ΔAIC_c: prelay: 2.81; breeding period: 3.03). The effect was positive (fig 10.) suggesting that breeding attempts were more successful at fledging young when the previous year's conditions had relatively higher levels of NDVI and relatively lower levels of precipitation (Table 12).

Table 12. Results of the top five GLM models examining variable effects on martial eagle breeding rate using logit link function and binomial error (n = 33).

	Estimate	Std. Error	z value	CI(2.5%)	CI(97.5%)	Null AIC	Residual deviance	AICc
(Intercept)	-0.19	0.37	-0.50	-0.94	0.55			
PCA2 Previous year	**1.03**	**0.46**	**2.25**	**0.23**	**2.06**	**48.26**	**41.58**	**45.58**
(Intercept)	-0.18	0.36	-0.506	-0.90	0.52			
PCA1 Pre-Lay	**-0.74**	**0.41**	**-1.81**	**-1.64**	**-0.003**	**48.26**	**44.39**	**48.39**
(Intercept)	-0.18	0.36	-0.51	-0.90	0.52			
PCA2 Breeding period	-0.71	0.40	-1.78	-1.57	0.02	48.26	44.61	48.61
(Intercept)	-0.29	0.40	-0.72	-1.29	0.44			
Fire % buffer breeding period	-0.95	0.88	-1.09	-3.77	0.13	48.26	45.54	49.54
(Intercept)	-0.14	0.35	0.69	-0.85	0.57			
CCA2	-0.62	0.52	0.24	-1.93	0.18	48.26	46.15	50.15

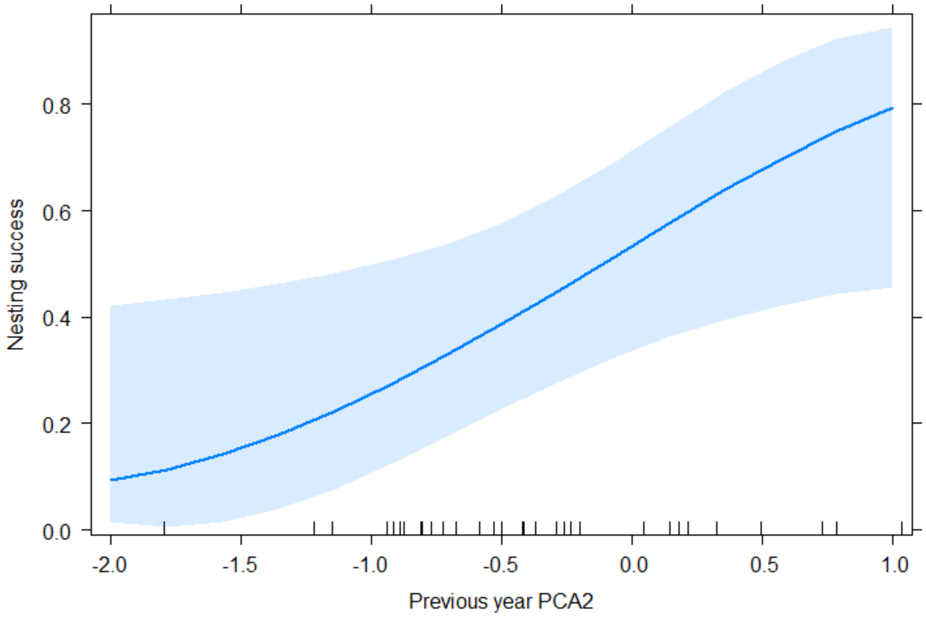

Figure 10. Predicted effects of climatic conditions experienced in the previous year on nesting success of martial eagles. The solid lines indicate the predicted relationship with both upper and lower confidence intervals (95%) shaded in blue.

Hindcasting prediction

Results from the productivity analysis indicated that PCA1 of conditions captured the previous year had the strongest effect on martial eagle productivity (Table 7 and 9). In order to hindcast productivity predictions based on past climate conditions, we therefore built a univariate GLMM for productivity as the response variable and only PCA^{hist} as a fixed explanatory variable. This analysis indicated that PCA1 remained a good predictor of productivity (Table 13). Results again estimated a positive trend whereby higher productivity occurred with higher NDVI and precipitation together with lower temperatures in the previous year (fig 11. and S3.).

Table 13. Results from the GLMM models comparing model fit of productivity in martial eagles. Model parameters recorded from the previous year: PCA1.

Variable	Estimate	Std.Error	CI(2.5%)	CI(97.5%)	Z value	Pr(>|z|)
(Intercept)	-1.86	0.34	-3.04	-1.18	-5.53	3.29e-08
$PCA1^{hist}$	0.80	0.29	0.23	1.52	2.73	0.006

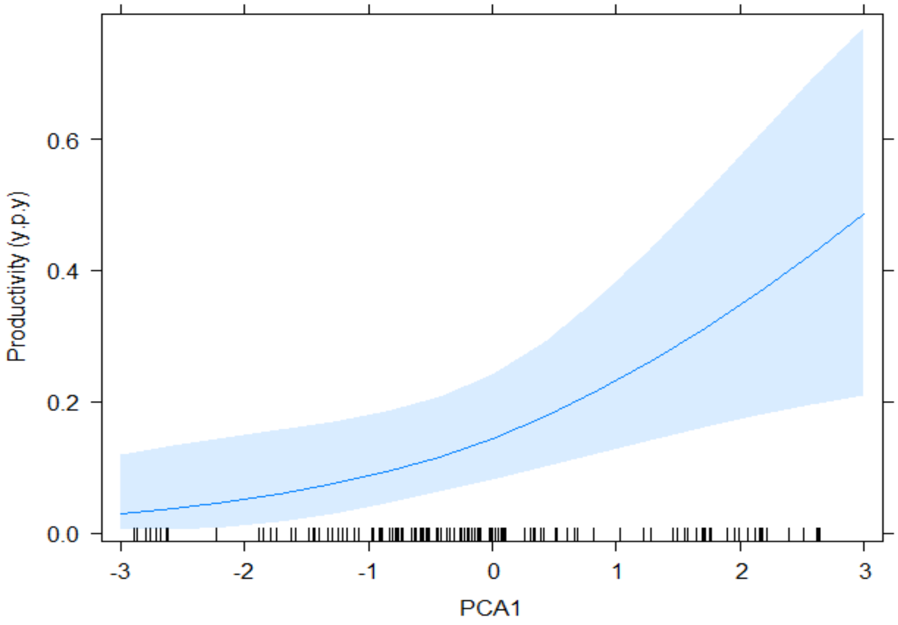

Figure 11. Predictive effects plot of the GLMM showing the modeled effect of PCA1^{hist} on martial eagle breeding productivity. The solid line shows the predicted relationship with 95% confidence intervals shaded in blue.

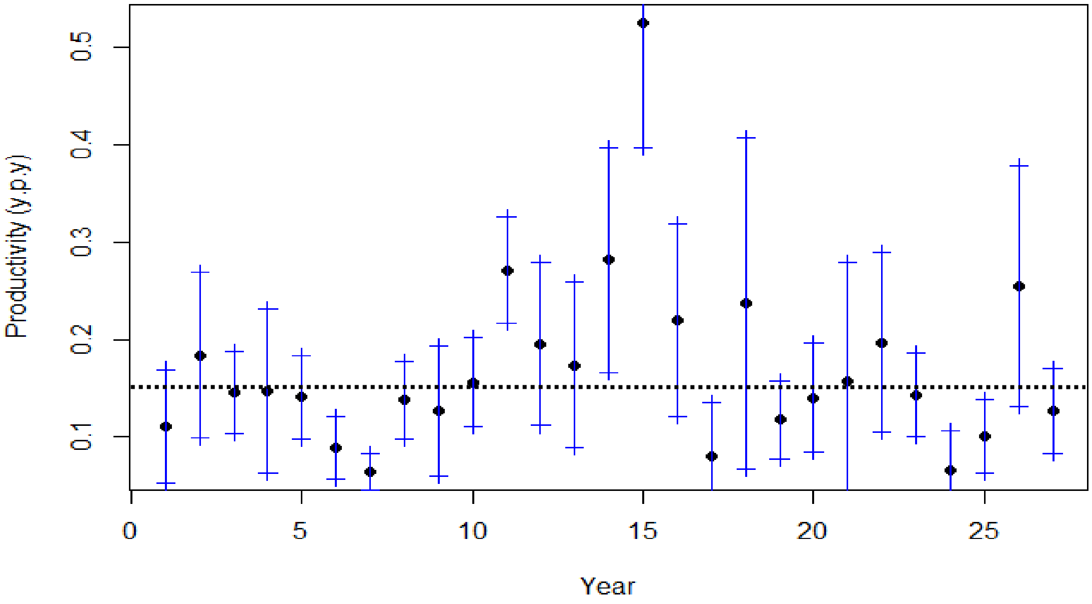

Figure 12. Predicted productivity of martial eagles in the KNP from 1986 - 2018. Red circles show the standard deviation around estimated productivity for each year. Productivity predictions were generated using GLMM model estimates hindcast with the predict function. No discernible increase or decrease can be detected through visual observation of the figure.

Productivity estimates generated for the KNP from 1986 to 2018 using the predict function indicate no changes are likely to have occurred within this time period (t = 0.72) (Table 14; fig 12.).

Table 14. Results of the GLM examining whether changes in productivity are likely to have occurred since 1987. Year was a continuous explanatory variable with predicted annual productivity as the response variable.

	Estimate	Std. Error	t value	CI (2.5%)	CI (97.5%)	Pr(>|t|)	Null deviance	Residual deviance	AICc
(Intercept)	0.16	0.04	4.25	0.08	0.23	0.0002			
Year	0.0008	0.002	0.37	-0.003	0.005	0.72	0.22	0.22	-47.2

Discussion

Overall, our analyses suggested that martial eagle productivity was most closely associated with climatic conditions in the previous year. Whereby higher precipitation and higher levels of NDVI in one year lead to higher productivity in the next year.

This delayed effect of climate conditions is not wholly surprising, and most likely occurs since precipitation in the previous year may drive prey abundance experience in this following year, through the delayed breeding responses of the larger prey consumed by martial eagles (Kruger et al. 2002). To a degree, this key finding supports the previous finding by Kruger et al. (2002), which found that for most large raptors in an arid zone environment, abundance was most strongly associated with precipitation in the previous year. Although for marital eagle they actually found abundance was most strongly linked to precipitation in the current year. However, it is important to recognize that these two results are not in contrast to one another, since they were measuring abundance, not breeding performance as was the case with our study.

Another explanation, for the delayed impact of climate, may link to female condition, since the vital conditions experienced in the lead up to egg formation may extend beyond the few months prior to breeding. The energy requirements needed to reach minimum body condition by the female to produce an egg is high. These requirements exceed those during the rest of the breeding cycle (Ross et al. 2017; Tapia & Zuberogoitia 2017). Thus, poor conditions in one year may result in poorer body conditions of the female in the subsequent year, meaning they have less energy available for egg production (Hustler & Howells 1987; Taylor et al. 1997; Tapia & Zuberogoitia 2017).

Precipitation is often considered the most important environmental variable for a species performance because of its influence on vegetation structure as well as the timing of breeding (Skowno & Bond 2003; Moloney et al. 2004; Wichmann et al. 2009; Burgess et al. 2011). In arid and semi-arid locations, such as KNP, this is likely to be the case, since primary production, on which the food web is built, generally fluctuates synchronously with precipitation (Moloney et al. 2004). Higher levels of NDVI, which have been used as a surrogate to represent primary production and prey availability, may indicate why higher martial eagle productivity rates were attained in areas where precipitation and NDVI were higher the previous year (Young et al. 2009; Kosicki 2010; Kopsová-Storchová et al. 2017).

Hustler and Howells (1990) investigated the effect of precipitation on breeding productivity of three raptor species (tawny eagles (*Aquila rapax*), african hawk eagles (*Hieraetus spilogaster*) and the martial eagle) and concluded that the number of chicks produced per breeding attempt was significantly greater in years of higher precipitation. Though not consistent with our results, as they did not measure effects according to the previous year’s conditions, their conclusion for tawny and African hawk eagles’ was that in years of low precipitation, primary productivity and prey availability was lower. However, as Kruger (2002) suggested for martial eagles larger prey likely experience a lagged effect with regard to abundance of prey for years following higher rainfall and

NDVI. Though not compatible the findings of both papers allow us to elucidate possible mechanisms for higher martial eagle productivity following high rainfall and NDVI during the previous year (Table 12: fig 10).

In our analysis, we used a PCA ordination, due to correlations between the climate variables, thus we cannot ultimately be sure whether the influence is most strongly linked with either NDVI, precipitation or indeed temperature, although it might well be a cumulative effect of all three. High temperatures together with low precipitation and low NDVI could cumulatively reduce prey abundance for martial eagles in the subsequent year. Similar results were observed for nesting success.

Nesting success

Our analysis of breeding success necessitated a more simplistic analytical approach due to the lower sample size. This univariate analysis revealed that the probability of a nesting attempt being successful was also most strongly influenced by climate conditions in the previous year. However, this analysis selected a different dimension (PCA2), suggesting that higher NDVI in the previous year, was the most influential climate variable affecting this breeding performance measure for similar reasons as discussed for above for productivity.

Breeding rate

From our analysis on breeding rate – which was the probability of a territorial pair producing a clutch, suggested that territories with higher tree cover had fewer breeding attempts.

Martial eagles are generally sedentary (Brown et al. 2015; Van Eeden et al. 2017) and can be found perched around their nests, normally in tall trees, throughout the year (Brown et al. 2015). Although large trees are necessary for martial eagles nesting sites, increased canopy cover may reduce prey visibility. Andersson *et al*. (2009) illustrated that prey detectability increased with increasing perch height in open habitats, however, they indicated that at further distances vegetation and topography can eclipse the prey's stature concealing it from view. Reduced tree cover may be favourable to martial eagles as it may increase food availability, which is not only determined by prey density, but also by accessibility of prey (Ontiveros et al. 2005). High tree cover may allow prey to forage under cover making it difficult for raptors to access (Ontiveros et al. 2005; Jaksic et al. 2010). American kestrel (*Falco sparverius*), a perch hunter, showed greater hunting success in locations with shorter vegetation as increases in vegetation height reduced prey detectability and increased the difficulty of capturing it (Toland 1987). Predation rates have occasionally been shown to be higher in more open areas regardless of prey availability (Tapia & Zuberogoitia 2017). As one of the functions of territoriality is to principally provide sufficient resources, usually food and nest-site locations, martial eagles may be preferentially targeting habitats of less tree cover for breeding as they provide better forage opportunities optimizing prey delivery to the nest (Ontiveros et al. 2005; Zub et al. 2010).

Within KNP between 1984 and 1996 decreases in larger trees (>5m), on which martial eagles rely as perches and for nesting sites, have been observed (Eckhardt et al. 2000; Tapia and Zuberogoitia 2017). Alternatively, the increases in woody cover of smaller trees (0 – 5m) observed over the same period may reduce the ability of martial eagle to detect prey and their ability to successfully capture prey (Eckhardt et al. 2000; Ontiveros et al. 2005). More recently indications of decreased woody vegetation on southern granites and southern basalts of KNP have been observed with increases in woody vegetation on granites and basalts in the north (Munyati & Sinthumule 2016). Raptors have specific nest site requirements, which are limited by suitable breeding habitat (Tapia and Zuberogoitia 2017). Each species shows preferences for height, position, orientation, accessibility, visibility and shelter for the nest site (Tapia and Zuberogoitia 2017). Within populations, variations in individual breeding success have been attributed to nesting-habitat features (Kostrzewa 1996). Moreover, habitat quality is often linked to reproductive success and survival through the direct influence of habitat on food availability (Burgess et al. 2011). Large increases in woody vegetation density, largely driven by the interactions of elephants and fire return periods (Scholtz et al. 2014), may reduce the number of martial eagle breeding attempts and may lead to territory abandonment where habitats no longer favour breeding.

These results suggesting a negative effect of tree cover on breeding rates do appear to run counter to the findings by van Eeden et al. (2017). In that study, van Eeden et al. (2017) looked at habitat use by adult territorial martial eagles and found that they preferentially used tree cover during both the breeding and non-breeding periods. Although tree cover was a significant variable in their model, its effect size was relatively small.

Conservation implications

Our analysis on martial eagle productivity observed the lowest annual productivity rate measured to date (0.16 y.p.y) which is lower than any other study done to date in Southern and Eastern Africa (fig 6) and is low enough to drive the observed population declines (van Eeden 2016; Amar & Cloete 2018). Our estimate of productivity was conservative in comparison most studies on martial eagles where productivity was measured only when activity was recorded that year, while we considered that territories were occupied until activity had not been seen around the nest for five consecutive years. However, our estimate of productivity does fit better with the erratic and slow breeding behavior of martial eagles', where birds do not always attempt to breed every other year (Taylor et al. 1997; Brown 1965) as is commonly suggested (Hustler & Howells 1987). As climatic variables appear to be most influential in martial eagle demography conservation measures can only focus on direct persecution on martial eagles and reducing land use change beyond protected area boundaries.

Hindcasting – does climate change explain the lower levels of productivity in KNP?

Our hindcasting analysis did not predict that productivity has declined over time due to changing climate conditions over the last 30 years. In fact temperature, precipitation and NDVI do not appear to have changed considerably during this period, further studies have also observed that little change has occurred within KNP over this time though more frequent extreme are likely (MacFayden et al. 2018; van Wilgen et al. 2016) (fig. S4-S6.). This suggests that whilst climate factors may influence between year variability in productivity, factors beyond climatic variables are likely responsible for the decline in martial eagles at this site (Tarboton & Allan 1984; Van Eeden et al. 2017; Amar & Cloete 2018).

Beyond low productivity, martial eagle declines may stem from a number of sources, however, illegal killing is considered to be the main cause of population declines beyond protected areas (Machange et al. 2005; Van Eeden et al. 2017). Another possibility for the continued decline of martial eagles is the high mortality rate of individuals who range beyond the KNP boundaries. Of the eight GPS tracked adult martial eagles five died. Three of the deaths were attributed to unnatural causes; two adults were hunted while ranging in Mozambique while the third individual was thought to be electrocuted, although this could not be confirmed (van Eeden et al. 2017). These results indicated an annual mortality rate of 42.48% for the confirmed deaths. Although a small sample size the high mortality rate beyond the KNP boundary illustrates the limits of protected areas to wide ranging species (Van Eeden et al. 2017).

Illegal killing may occur for multiple reasons; because of their reputation as predators of small domestic stock animals, martial eagles are often shot or poisoned by private land owners (Machange et al. 2005). They have also been recorded caught in snares intended to capture bush meat (Van Eeden et al. 2017), and martial eagle parts have been recorded at black market in West Africa where parts are likely sold for use in traditional medicine (Atuo et al. 2015; Buij et al. 2016). Further threats include electrocutions and collisions with electricity pylons and drowning in sheer sided farm reservoirs (Van Eeden et al. 2017; Amar & Cloete 2018).

Conclusion

Our results align with previous hypothesis regarding the effect of previous year precipitation on raptor productivity for species feeding on large prey-items in semi-arid environments (Krüger et al. 2002; Zabala & Zuberogoitia 2014). They hypothesized that a) “larger prey-items show a longer lag between abundance and precipitation, thus species feeding on larger prey-items are more prone to be affected by delayed precipitation and species feeding on small prey-items are more likely to be affected by direct precipitation; (b) larger prey-items are more mobile and hence have a greater ability to move with precipitation, thus species feeding on larger prey items are more prone to be affected by precipitation than species feeding on small prey-items”. Evidence for their hypothesis was found for 14 out of the 15 species studied, except the martial eagle. Research on small mammal responses to precipitation have indicated that outbreaks or abundances are influenced by precipitation during the preceding year or wet season (Krüger et al. 2002; Luque-Larena et al. 2013; Byrom et al. 2014) Unfortunately, little work have been done on small mammals population dynamics in arid ecosystems, even though they are a source food (Byrom et al. 2014). None the less the climatic conditions experienced in the year prior to breeding are important for martial eagle’s productivity and nesting success as they likely influence prey availability. Tree cover appears to be more in influential in determining whether a martial eagle will attempt to breed. Conceptually, the former two are more important measures than breeding rate as they account for additions to a population.

Closing statement

Understanding the variables which affect productivity is important for integrated population models. Parameters inputs for such models can be important in determining the population dynamics of a species. For endangered species understanding gained into aspects of demography may be crucial for developing conservation strategies which aim to halt such declines. Moreover, it allows us to determine where to input limited resources for conservation more effectively and efficiently or where influential variables on breeding performance are beyond our control.

Study limitation and future research avenues

1) Better measures for elephant density should be generated in future to better understand the potential effects of elephants on martial eagle productivity.

2) The GIS analysis on rivers should be broken up into stream order to determine whether the size and flow of river may have any influence on martial eagle breeding parameters.

3) Climatic conditions in terms of climatic extremes should be considered as a future avenue of research. Extreme high or low temperatures and high rainfall events should be considered as these likely will affect young chicks or martial eagles which have not yet fledged.

4) This study was limited by the GIS layers which were available before January 2019. Because the dataset ended in 2018 finding fine scale data that was cleaned was not possible. Recent more fine scale layers should be considered for future research.

5) The influence of woody vegetation increases and decreases within KNP will likely impact on martial eagle productivity and should be investigated further.

6) Lastly, it would be useful to relate prey abundance of the main prey types to weather variables – for example guineafowl, monitor lizards or small antelope.

References

Amar A, Cloete D. 2018. Quantifying the decline of the Martial Eagle *Polemaetus bellicosus* in South Africa. Bird Conservation International **28**:363–374.

Amar A, Cloete D, Whittington M. 2016. Using independent nest survey data to validate changes in reporting rates of Martial Eagles between the Southern African Bird Atlas Project 1 and 2. Ostrich **87**:1–5.

Amar A, Davies J, Meek E, Williams J, Knight A, Redpath S. 2011. Long-term impact of changes in sheep *Ovis aries* densites on the breeding output of the hen harrier *Circus cyaneus*. Journal of Applied Ecology **48**: 220–227.

Andersson M, Wallander J, Isaksson Daniel. 2009. Predator pershes: a visual perspective. Functional Ecology **23**:373–379.

Arroyo BE, Garcia JT. 2001. Comparative analysis in sympatric harriers effect of abiotic factors on reproduction in the centre and periphery of breeding ranges : a comparative analysis in sympatric harriers. Ecography **24**:393–402.

Atuo FA, Timothy J. O, Peter U. A. 2015. An assessment of socio-economic drivers of avian body parts trade in West African rainforests. Biological Conservation **191**:614–622.

Barton K. 2014. MuMIn: Multi-model inference R package 1.9.13.

Bates D, Machler M, Walker S, Bolker B. 2015. Fitting linear mixed-effects models using (lme4). Journal of Statistical Software **67**:1–48.

Beresford AE, Buchanan GM, Donald PF, Butchart SHM, Fishpool LDC, Rondinini C. 2011. Poor overlap between the distribution of Protected Areas and globally threatened birds in Africa. Animal Conservation **14**:99–107.

Berndt J. 2015. Martial Eagles and the national power grid in South Africa: the implications of pylon-nesting for conservation management. Available from https://open.uct.ac.za/bitstream/item/16656/thesis_sci_2015_berndt_jessie.pdf?sequence=1.

Bolger DT, Patten MA, Bostock DC. 2005. Avian reproductive failure in response to an extreme climatic event. Oecologia **142**:398–406.

Brown CJ, Kemper J, Simmons RE. 2015. Martial eagle | *Polemaetus bellicosus*. Pages 135–137 Birds to Watch in Namibia: Red, Rare and Endemic Species. Ministry of Environment & Tourism, Namibia Nature Foundation, Windhoek, Namibia.

Brown LH. 1955. Supplementary notes on the biology of the large birds of prey of Embu Distirct, Kenya Colony. Ibis **97**:185–221.

Brown LH. 1966. Observations on some Kenya eagles. Ibis **108**:531–572.

Brown LH. 1970. African Birds of Prey. Collins, London.

Brown LH, Gargett V, Steyn P. 1977. Breeding success in some African eagles related to theories about sibling aggression and its effects. Ostrich **48**:65–71.

Buechley ER, Santangeli A, Girardello M, Neate-Clegg MHC, Oleyar D, McClure CJW, Sekercloglu CH. 2019. Global raptor research and conservation priorities: Tropical raptors fall prey to knowledge gaps. Diversity and Distributions **25**:856–869.

Buij R, Nikolaus G, Whytock R, Ingram DJ, Ogada D. 2016. Trade of threatened vultures and other raptors for fetish and bushmeat in West and Central Africa. Oryx **50**:606–616.

Burgess MD, Nicoll MAC, Jones CG, Norris K. 2011. Multiple environmental gradients affect spatial variation in the productivity of a tropical bird population. Journal of Animal Ecology **80**:688–695.

Butchart SHM et al. 2010. Global Biodiversity: Indicators of Recent Declines. Science **328**:1164–1168.

Byrom AE, Craft ME, Durant SM, Nkwabi AJK, Metzger K, Hampson K, Mduma SAR, Forrester GJ, Ruscoe WA, Reed DN, Bukombe J, Mchetto J, Sinclair ARE. 2014. Episodic outbreaks of small mammals influence predator community dynamics in an east African savanna ecosystem. Oikos **123**:1014–1024.

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science Advances **1**:1–5.

Chambers JM, Hastie TJ, editors. 1992. Statistical Models in S. Wadsworth & Brooks/Cole Advanced Books & Software.

Cloete D. 2015. Investigating the decline of the martial eagle (*Polemaetus bellicosus*) in South Africa. University of Cape Town. Available from http://nivenlib.pfp.uct.ac.za/pdf/Cloete_Danial_2016_MSc_thesis.pdf.

Coulson T, Gaillard JM, Festa-Bianchet M. 2005. Decomposing the variation in population growth into contributions from multiple demographic rates. Journal of Animal Ecology **74**:789–801.

Didan K. 2015. MOD13A1 MODIS/Terra Vegetation Indices 16-Day L3 Global 250m SINgrid V006. NASA EOSDIS Land Process DAAC.

Donázar JA, Cortes-Avizanda A, Fargallo JA, Margalida A, Moleon M, Morales-Reyes Z, Moreno-Opo R, Perez-Garcia JM, Sanchez-Zapata, Zuberogoitia I, Serrano D.

2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. Ardeola **63**:181–234.

Eckhardt HC, Van Wilgen BW, Biggs HC. 2000. Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. African Journal of Ecology **38**:108–115.

Eglington SM, Pearce-Higgins JW. 2012. Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. PLoS ONE **7**:1–8.

Funk C, Peterson P, Landsfeld M, Pedreros D, Verdin J, Shukla S, Husak G, Harrison L, Hoell A, Michaelsen J. 2015. The climate hazards infrared precipitation with stations - A new environmental record for monitoring extremes. Scientific Data **2**:1–21.

Garbett R, Herremans M, Maude G, Reading RP, Amar A. 2018. Raptor population trends in northern Botswana: A re-survey of road transects after 20 years. Biological Conservation **224**:87–99.

Gentry AH. 1992. Tropical forest biodiversity: distributional patterns and their conservational significance. Wiley on behalf of Nordic Society Oikos **63**:19–28.

GeoTerra Image (GTI) Pty Ltd. 2015. 2013-14 South African National Land-Cover Dataset.

Giglio L, Loboda T, Roy DP, Quayle B, Justice CO. 2009. An active-fire based burned area mapping algorithm for the MODIS sensor. Remote Sensing of Environment **113**:408–420.

Herholdt J, Kemp AC. 1997. Breeding status and ecology of the Martial Eagle in the Kalahari Gemsbok National Park , South Africa. Ostrich **68**:80–85.

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, Connor MI. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature **486**:105–108.

Hustler K, Howells WW. 1987. Breeding Periodicity, Productivity and Conservation of the Martial Eagle. Ostrich **58**:135–138.

Hustler K, Howells WW. 1990. The influence of primary production on a raptor community in Hwange National Park, Zimbabwe. Journal of Tropical Ecology **6**:343–354.

IUCN. 2018. Interantional Union for Conservation of Nature. Available from http://www.iucnredlist.org/details/22696116/0 (accessed September 6, 2018).

Jaksic FM, Gutiérrez JR, Meserve PL, Kelt DA, Engilis JR A, Previtali MA, Milstead WB.

2010. Long-term research in Bosque Fray Jorge National Park: Twenty years studying the role of biotic and abiotic factors in a Chilean semiarid scrubland. Revista chilena de historia natural **83**:69–98.

John A, Nash C, Varadhan R. 2018. Package ‘ optimx .’

Keane JJ, Morrison ML, Fry DM. 2006. Prey and weather factors associated with temporal variation in Northern Goshawk reproduction in the Sierra Nevada, California. Studies in Avian Biology **31**:85–99.

Kemp AC, Begg KS. 2001. Comparison of time-activity budgets and population structure for 18 large-bird species in the kruger national park, south africa. Ostrich **72**:179–184.

Kopsová-Storchová L, Storch D, Brotons L, Hořák D. 2017. Geographical variation in reproductive investment across avian assemblages in Europe: effects of environmental drivers differ between altricial and precocial species. Journal of Avian Biology **48**:976–987.

Kosicki JZ. 2010. Reproductive success of the White Stork Ciconia ciconia population in intensively cultivated farmlands in western Poland. Ardeola **57**:243–255.

Krüger O, Liversidge R, Lindström J. 2002. Statistical modelling of the population of dynamics a raptor community in a semi-desert environment. Journal of Animal Ecology **71**:603–613.

Krüger SC, Amar A. 2017. Productivity of the declining bearded vulture *Gypaetus barbatus* population in southern Africa. Ostrich **88**:139–145.

Le S, Husson F. 2008. Sensominer: A package for sensory data analysis. Journal of Sensory Studies **23**:14–25.

Lehner B, Verdin K, Jarvis A. 2008. New Global Hydrography Derived From Spaceborne Elevation Data. Eos, Transactions American Geophysical Union **89**:93–94.

Liven-schulman I, Leshem Y, Alon DAN, Yom-tov Y. 2004. Causes of population declines of the Lesser Kestrel. Ibis:145–152.

Luque-Larena JJ, Mougeot F, Viñuela J, Jareño D, Arroyo L, Lambin X, Arroyo B. 2013. Recent large-scale range expansion and outbreaks of the common vole (*Microtus arvalis*) in NW Spain. Basic and Applied Ecology **14**:432–441.

MacFayden S, Zambatis N, Van Teeffelen AJA, Hui C. 2018. Long-term rainfall regression surfaces for the Kruger National Park, South Africa: a spatio-temporal review of patterns from 1981 to 2015. International Journal of Climatology **38:**2506–2519.

Machange RW, Jenkins AR, Navarro RA. 2005. Eagles as indicators of ecosystem health: Is the distribution of Martial Eagle nests in the Karoo, South Africa, influenced by variations in land-use and rangeland quality? Journal of Arid Environments **63**:223–243.

McClure CJW, Westrip JRS, Johnson JA, Schulwitz SA, Virani RD, Davies R, Symes A, Wheatley H, Thorstrom R, Amar A, Buij R, Jones VR, Williams NP, Buechley ER butchart SHM. 2018. State of the world's raptors: Distributions, threats, and conservation recommendations. Biological Conservation **227**:390–402.

Millsap BA, Grubb TG, Murphy RK, Swem T, Watson JW. 2015. Conservation significance of alternative nests of golden eagles. Global Ecology and Conservation **3**:234–241.

Moloney KA, Wichmann MC, Dean WRJ, Wissel C, Jeltsch F. 2004. Implication of climate change for the persistence of raptors in arid savanna. Oikos **102**:186–202.

Mora C, Sale PF. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: A review of the technical and practical shortcomings of protected areas on land and sea. Marine Ecology Progress Series **434**:251–266.

Munyati C, Sinthumule NI. 2016. Changes in woody cover at representative sites in the Kruger Natinal Park, South Africa, based on historical imagery. SpringerPlus **5:**1417.

Murgatroyd M, Avery G, Underhill LG, Amar A. 2016. Adaptability of a specialist predator: the effects of land use on diet diversification and breeding performance of Verreaux's eagles. Journal of Avian Biology **47**: 1–12.

Murn C, Combrink L, Ronaldson GS, Thompson C, Botha A. 2013. Population estimates of three vulture species in Kruger National Park, South Africa. Ostrich **84**:1–9.

Newbold T et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature **520**:45–50.

NOAA/OAR/ESRL PSD, Boulder, Colorado U. 2019. CPC Global Temperature data. Available from https://www.esrl.noaa.gov/psd/ (accessed October 1, 2019).

Ogada DL, Keesing F. 2010. Decline of Raptors over a Three-Year Period in Laikipia, Central Kenya. Journal of Raptor Research **44**:129–135.

Oksanen AJ, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H. 2014. Vegan: Community Ecology Package. R Package Version 2.2-0.

Ontiveros D, Pleguezuelos JM, Caro J. 2005. Prey density, prey detectability and food habits: The case of Bonelli's eagle and the conservation measures. Biological

Conservation **123**:19–25.

Paviour J. 2013. Key factors that influence breeding performance in raptors. The Plymouth Student Scientist **6**:386–399.

Peery MZ, Beissinger SR, Newman SH, Burkett EB, Williams TD. 2004. Applying the Declining Population Paradigm: Diagnosing Causes of Poor Reproduction in the Marbled Murrelet. Conservation Biology **18**:1088–1098.

Pellegrini AFA, Pringle RM, Govender N, Hedin LO. 2017. Woody plant biomass and carbon exchange depend on elephant-fire interactions across a productivity gradient in African savanna. Journal of Ecology **105**:111–121.

Pimm S, Raven P, Peterson A, Sekercioglu CH, Ehrlich PR. 2006. Human impacts on the rates of recent, present, and future bird extinctions. Proceedings of the National Academy of Sciences **103**:10941–10946.

R core team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org.

Rayner L, Lindenmayer DB, Wood JT, Gibbons P, Manning AD. 2014. Are protected areas maintaining bird diversity. Ecography **37**:43–53.

Rodell BYM, Houser PR, Jambor U, Gottschalck J, Mitchell K, Meng C-J, Arsenault K, Cosgrove B, Radakovich J, Bosilovich M, Entin JK, Walker JP, Lohmann D, Toll D. 2004. The global land data assimilation system. American Meteorological Society **85**:381–394.

Ross MV, Alisauskas RT, Douglas DC, Kellett DK. 2017. Decadal declines in avian herbivore reproduction: density-dependent nutrition and phenological mismatch in the Arctic. Ecology **98**:1869–1883.

Schielzeth H. 2010. Simple means to improve the interpretability of regression coefficients. Methods in Ecology and Evolution **1**:103–113.

Scholtz RG, Kiker GA, Smit IPJ, Venter FJ. 2014 Identifying drivers that influence the spatial distribution of woody vegetation in Kruger National Park, South Africa. Ecosphere **6**:1–12.

Sekercioglu CH, Daily GC, Ehrlich PR. 2004. Ecosystem consequences of bird declines. Proceeding of the National Acadamy of Sciences of the United States of America **101**:18042–18047.

Sexton JO, Song X-P, Feng M, Noojipady P, Anand A, Huang C, Kim D-H, Collins KM, Channan S, DiMiceli C, Townsend JR. 2013. Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. International Journal of Digital Earth **6**:427–448.

Skagen SK, Yackel Adams AA. 2017. Weather effects on avian breeding performance and implications of climate change. Ecological Applications **22**:1131–1145.

Skowno AL, Bond WJ. 2003. Bird community composition in an actively managed savanna reserve, importance of vegetation structure and vegetation composition. Biodiversity and Conservation **12**:2279–2294.

Smith SH, Steenhof K, McClure CJW, Heath JA. 2017. Earlier nesting by generalist predatory bird is associated with human responses to climate change. Journal of Animal Ecology **86**:98–107.

South African National Biodiversity Institute. 2011. The Vegetation of South Africa, Lesotho and Swaziland. Page (Mucina L, Rutherford MC, editors). Strelitzia 19, Pretoria. Available from http://bgis.sanbi.org/MapViewer.

Steenhof K, Newton I. 2007. Assessing Nesting Success and Productivity. Pages 181–192 in D. Bird and K. Bildstein, editors. Raptor Research and Management Techniques. Hancock House.

Steyn P. 1982. Birds of Prey of Southern Africa - Their identification and life histories. David Philip, Cape Town and Johannesburg.

Tapia L, Zuberogoitia I. 2017. Breeding and Nesting Biology in Raptors. Pages 63–94 in J. H. Sarasola, J. M. Grande, and J. J. Negro, editors. Birds of Prey: Biology and conservation in the XXI century, 2018th edition. Springer International Publishing AG, part of Springer Nature 2018.

Tarboton WR, Allan DG. 1984. The status and conservation of birds of prey in the Transvaal. Species accounts - secretary bird, vultures, kites, hawks, eagles, bateleur. Transvaal Museum Monographs **3**: 6–61.

Taylor MR, Peacock F, Wanless RM, editors. 2015. The 2015 Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. Birdlife South Africa, Johannesburg.

Taylor P, Herholdt JJ, Kemp AC. 1997. Breeding status and ecology of the Martial Eagle in the Kalahari Gemsbok National Park , South Africa. Journal of African Ornithology **68**:80–85.

Thiollay JM. 2006. The decline of raptors in West Africa : long-term assessment and role of protected area. Ibis **148**:240–254.

Thiollay JM. 2007. Raptor declines in West Africa: Comparisons between protected, buffer and cultivated areas. Oryx **41**:322–329.

Toland BR. 1987. The effect of vegetative cover on foraging strategies, hunting success and nesting distribution of American Kestrels in central Missouri. Journal of Raptor Research **21**:14–20.

Väli Ü. 2013. Factors Limiting Reproductive Performance and Nestling Sex Ratio in the Lesser Spotted Eagle Aquila pomarina at the Northern Limit of Its Range: the Impact of Weather and Prey Abundance . Acta Ornithologica **47**:157–168.

van Eeden R. 2016. Understanding the decline of Martial Eagles *Polemaetus bellicosus* in the Kruger National Park, South Africa. University of Cape Town. Available from http://nivenlib.pfp.uct.ac.za/pdf/Van_Eeden_Rowen_2016_PhD_thesis.pdf.

Van Eeden R, Whitfield DP, Botha A, Amar A. 2017. Ranging behaviour and habitat preferences of the Martial Eagle: Implications for the conservation of a declining apex predator. PLoS ONE **12**:1–22.

Van Wilgen NJ, Goodall V, Holness S, Chown SL, McGeoch MA. 2016. Rising temperatures and changing rainfall patterns in South Africa’s national parks. International journal of Climatology **36**: 706–721.

Vanak AT, Shannon G, Thaker M, Page B, Grant R, Slotow R. 2012. Biocomplexity in large tree mortality: Interactions between elephant, fire and landscape in an African savanna. Ecography **35**:315–321.

Vermote E, Justice C, Csiszar I, Eidenshink J, Myneni R, Baret F, Masuoka E, Wolfe R, Claverie M, Program NC. 2014. NOAA Climate Data Record (CDR) of Normalized Difference Vegetation Index (NDVI), Version 4.

Waldron A, Miller DC, Redding D, Mooers A, Kuhn TS, Nibbelink N, Roberts JT, Tobias JA, Gittleman JL. 2017. Reductions in global biodiversity loss predicted from conservation spending. Nature **551**:364–367.

Watson JEM, Dudley N, Segan DB, Hockings M. 2014. The performance and potential of protected areas. Nature **515**:67–73.

Wichmann MC, Dean WRJ, Jeltsch F, Predicting FJ. 2009. Predicting the breeding success of large raptors in arid southern Africa : a first assessment a first assessment. Ostrich **6525**:22–27.

Young KD, Ferreira SM, Van Aarde RJ. 2009. The influence of increasing population size and vegetation productivity on elephant distribution in the Kruger National Park. Austral Ecology **34**:329–342.

Zabala J, Zuberogoitia I. 2014. Individual quality explains variation in reproductive success better than territory quality in a long-lived territorial raptor. PLoS ONE **9**:1–10.

Zub K, Pugacewicz E, Jędrzejewska B, Jędrzejewski W. 2010. Factors affecting habitat selection by breeding lesser spotted eagles *Aquila pomarina* in northeastern Poland. Acta Ornithologica **45**:105–114.

Supplementary material:

Nest information

Table S1: Martial eagle territory information used during this analysis. Refer to methods for term explanations.

Territory	Year	Nest	Visits	Attempt	Success	Years monitored
1	2016	MEnest2016_01	2	0	0	3
1	2017	MEnest2016_01	2	0	0	3
1	2018	MEnest2016_01	1	0	0	3
2	2014	MEnest2014_02	3	1	0	5
2	2015	MEnest2015_01	3	1	1	5
2	2016	MEnest2015_01	2	0	0	5
2	2017	MEnest2015_01	3	1	1	5
2	2018	MEnest2015_01	1	0	0	5
3	2013	MEnest2011_01	4	0	0	3
3	2014	MEnest2011_01	2	0	0	3
3	2015	MEnest2011_01	3	0	0	3
4	2015	MEnest2015_21	1	0	0	4
4	2016	MEnest2015_21	2	0	0	4
4	2017	MEnest2015_21	2	0	0	4
4	2018	MEnest2015_21	2	0	0	4
5	2013	MEnest2011_15	4	0	0	6
5	2014	MEnest2011_15	3	0	0	6
5	2015	MEnest2011_15	3	na	na	6
5	2016	MEnest2011_15	2	0	0	6
5	2017	MEnest2011_15	2	1	na	6

5	2018	MEnest2011_15	3	1	0	6
6	2013	MEnest2011_18	4	0	0	6
6	2014	MEnest2011_18	5	1	0	6
6	2015	MEnest2011_18	3	na	1	6
6	2016	MEnest2011_18	2	0	0	6
6	2017	MEnest2011_18	3	1	0	6
6	2018	MEnest2011_18	3	0	0	6
7	2013	MEnest2011_17	2	0	0	4
7	2014	MEnest2011_17	2	0	0	4
7	2015	MEnest2011_17	2	0	0	4
7	2016	MEnest2011_17	2	0	0	4
8	2016	MEnest2015_20	2	0	na	3
8	2017	MEnest2015_20	2	0	0	3
8	2018	MEnest2015_20	2	0	0	3
9	2014	MEnest2014_09	1	0	0	5
9	2015	MEnest2014_09	2	na	na	5
9	2016	MEnest2014_09	2	0	0	5
9	2017	MEnest2015_13	2	0	0	5
9	2018	MEnest2014_09	1	0	0	5
10	2015	MEnest2009_01	2	0	0	3
10	2016	MEnest2014_01	2	0	0	3
10	2017	MEnest2014_01	1	0	0	3
11	2016	MEnest2016_04	2	1	na	3
11	2017	MEnest2016_04	4	na	1	3
11	2018	MEnest2016_04	1	0	0	3
12	2015	MEnest2015_11	1	0	0	4

12	2016	MEnest2015_11	2	0	0	4
12	2017	MEnest2015_11	3	1	0	4
12	2018	MEnest2015_11	1	1	0	4
13	2013	MEnest2013_02	2	0	0	4
13	2014	MEnest2013_02	2	1	0	4
13	2015	MEnest2013_02	2	0	0	4
13	2016	MEnest2013_02	2	0	0	4
14	2013	MEnest2011_06	1	0	0	3
14	2014	MEnest2014_05	1	0	0	3
14	2015	MEnest2014_05	3	na	na	3
15	2015	MEnest2011_21	4	1	1	4
15	2016	MEnest2011_21	2	0	0	4
15	2017	MEnest2011_21	2	1	0	4
15	2018	MEnest2011_21	2	0	0	4
16	2013	MEnest2012_01	1	0	0	6
16	2014	MEnest2012_01	3	1	1	6
16	2015	MEnest2012_01	5	0	0	6
16	2016	MEnest2012_01	2	1	na	6
16	2017	MEnest2012_01	2	1	0	6
16	2018	MEnest2012_01	3	0	0	6
17	2013	MEnest2011_08	1	0	0	5
17	2014	MEnest2011_08	2	0	0	5
17	2015	MEnest2011_08	3	0	0	5
17	2016	MEnest2011_08	2	0	0	5
17	2017	MEnest2011_08	2	1	0	5
18	2013	MEnest2013_04	2	0	0	5

18	2014	MEnest2013_04	1	0	0	5
18	2015	MEnest2013_04	3	0	0	5
18	2016	MEnest2013_04	2	na	na	5
18	2018	MEnest2018_02	4	1	1	5
19	2013	MEnest2011_07	1	0	0	6
19	2014	MEnest2011_07	5	1	0	6
19	2015	MEnest2015_02	2	1	na	6
19	2016	MEnest2015_02	2	0	0	6
19	2017	MEnest2017_01	2	na	1	6
19	2018	MEnest2017_01	1	0	0	6
20	2013	MEnest2012_02	1	0	0	3
20	2014	MEnest2012_02	4	1	0	3
20	2015	MEnest2012_02	3	0	0	3
21	2013	MEnest2011_09	4	na	1	6
21	2014	MEnest2011_09	1	0	0	6
21	2015	MEnest2011_09	4	1	1	6
21	2016	MEnest2011_09	2	0	0	6
21	2017	MEnest2011_09	2	na	1	6
21	2018	MEnest2011_09	1	0	0	6
22	2014	MEnest2011_03	1	0	0	5
22	2015	MEnest2011_03	6	1	0	5
22	2016	MEnest2011_03	2	0	0	5
22	2017	MEnest2011_03	2	0	0	5
22	2018	MEnest2011_03	2	1	0	5
23	2013	MEnest2011_05	2	0	0	6
23	2014	MEnest2011_05	4	1	0	6

23	2015	MEnest2011_05	4	na	1	6
23	2016	MEnest2011_05	2	0	0	6
23	2017	MEnest2011_05	2	0	0	6
23	2018	MEnest2011_05	3	1	1	6
24	2014	MEnest2014_08	2	na	1	5
24	2015	MEnest2014_08	1	0	0	5
24	2016	MEnest2014_08	2	0	0	5
24	2017	MEnest2014_08	2	0	0	5
24	2018	MEnest2014_08	3	1	1	5
25	2015	MEnest2015_03	2	1	na	4
25	2016	MEnest2015_03	2	0	0	4
25	2017	MEnest2015_03	3	1	0	4
25	2018	MEnest2015_03	2	0	0	4
26	2014	MEnest2014_07	2	na	1	3
26	2016	MEnest2014_07	3	1	1	3
26	2018	MEnest2014_07	3	1	1	3
27	2013	MEnest2011_04	2	0	0	6
27	2014	MEnest2011_04	6	0	0	6
27	2015	MEnest2011_04	5	0	0	6
27	2016	MEnest2011_04	2	na	na	6
27	2017	MEnest2011_04	1	0	0	6
27	2018	MEnest2011_04	3	0	0	6
28	2013	MEnest2011_02	2	0	0	5
28	2014	MEnest2011_02	2	0	0	5
28	2015	MEnest2011_02	4	0	0	5
28	2016	MEnest2011_02	2	0	0	5

28	2017	MEnest2011_02	2	0	0	5
29	2016	MEnest2016_05	2	0	0	3
29	2017	MEnest2016_05	3	1	1	3
29	2018	MEnest2016_05	2	0	0	3
30	2014	MEnest2014_03B	2	1	0	5
30	2015	MEnest2014_03B	2	na	na	5
30	2016	MEnest2014_03A	1	1	na	5
30	2017	MEnest2014_03A	2	0	0	5
30	2018	MEnest2014_03B	2	1	na	5
31	2017	MEnest2017_02A	1	0	0	2
31	2018	MEnest2017_02B	4	1	1	2
33	2013	MEnest2011_12	1	0	0	6
33	2014	MEnest2011_12	3	1	1	6
33	2015	MEnest2011_12	2	0	0	6
33	2016	MEnest2011_12	1	0	0	6
33	2017	MEnest2011_12	2	0	0	6
33	2018	MEnest2011_12	3	0	0	6
35	2013	MEnest2011_16	2	0	0	3
35	2014	MEnest2011_16	1	0	0	3
35	2015	MEnest2015_04	1	0	0	3
36	2013	MEnest2011_20	2	na	na	3
36	2014	MEnest2011_20	2	na	1	3
36	2015	MEnest2011_20	3	0	0	3
37	2013	MEnest2013_01	2	na	1	4
37	2014	MEnest2013_01	2	na	0	4
37	2016	MEnest2013_01	1	na	na	4

37	2017	MEnest2013_01	1	0	0	4
38	2013	MEnest2013_05	1	na	1	3
38	2014	MEnest2013_05	1	0	0	3
38	2015	MEnest2013_05	1	0	0	3
39	2014	MEnest2013_06	4	1	0	5
39	2015	MEnest2013_06	2	na	na	5
39	2016	MEnest2013_06	1	0	0	5
39	2017	MEnest2013_06	2	0	0	5
39	2018	MEnest2013_06	2	na	na	5
40	2014	MEnest2014_04	4	1	0	5
40	2015	MEnest2014_04	2	0	0	5
40	2016	MEnest2014_04	1	0	0	5
40	2017	MEnest2014_04	1	0	0	5
40	2018	MEnest2014_04	6	1	1	5
41	2015	MEnest2015_05	1	0	0	1
42	2015	MEnest2015_06	1	0	0	1
43	2015	MEnest2015_07	1	1	na	1
44	2015	MEnest2015_08	1	0	0	1
45	2015	MEnest2015_09	1	0	0	1
46	2015	MEnest2015_10	1	0	0	1
48	2015	MEnest2015_15	1	0	0	1
49	2015	MEnest2015_18	1	0	0	1
47	2015	MEnest2015_19	1	0	0	1
50	2018	MEnest2018_01	3	1	1	1
51	2018	MEnest2018_03	2	1	1	1

Table S2: Results of the PCA analysis on the temporally dynamic variables (mean annual precipitation, mean annual average temperature and mean annual NDVI) captured during the pre-lay period. The percentage variance explained by each dimension (% variance) and the cumulative percentage of variance explained by each dimension (Cum. % of variance) are presented. Ctr designates the relative contribution of each variable to the dimensions 1, 2 and 3.

Eigenvalues	Dimension 1		Dimension 2		Dimension 3	
Eigenvalue	2.39		0.50		0.11	
% of variance	79.77		16.56		3.67	
Cumulative % of variance explained	79.77		96.33		100	
Variables	**Dim 1**	**Ctr**	**Dim 2**	**Ctr**	**Dim 3**	**Ctr**
Precipitation	0.802	26.855	0.596	71.566	-0.042	1.58
NDVI	0.951	37.781	-0.188	7.087	0.246	55.132
Temperature	-0.92	35.364	0.326	21.348	0.218	43.288

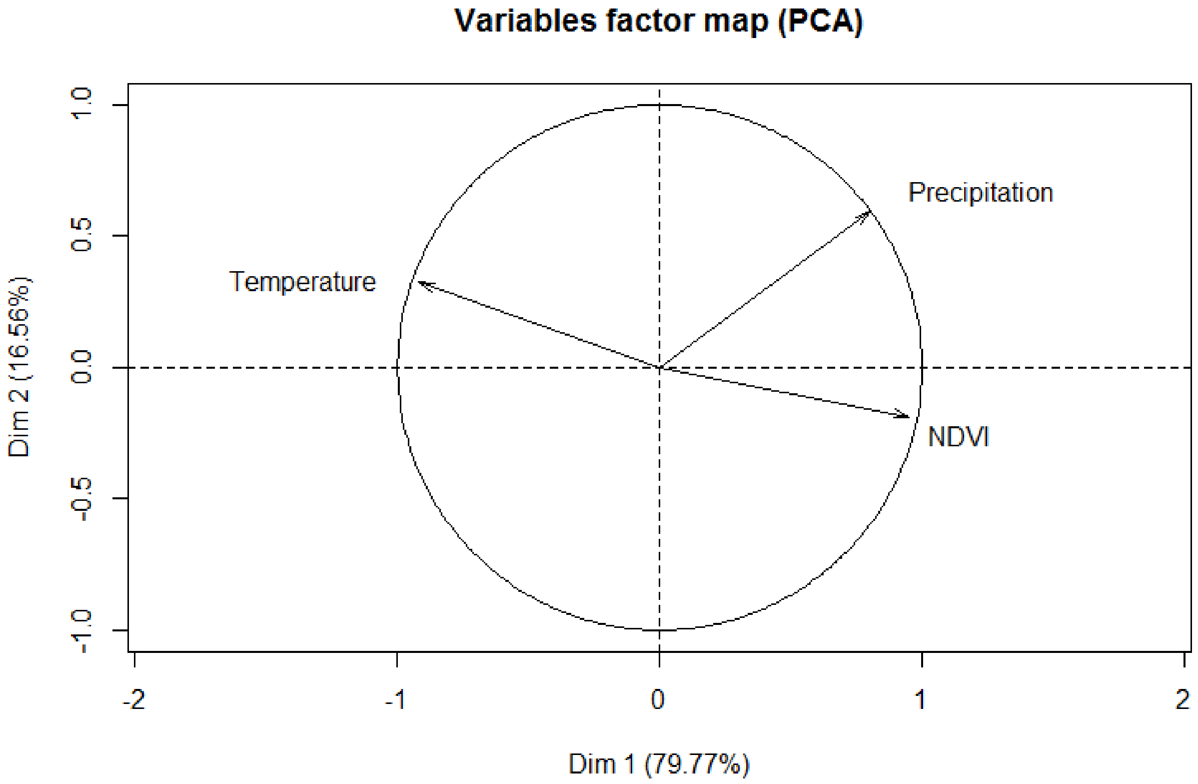

Figure S1: Diagram of the PCA analysis illustrating the separation of temporally dynamic variables (mean temperature, NDVI and precipitation).

Table S3: PCA analysis results on the three temporally dynamic variables captured during the breeding period: mean annual precipitation, mean annual average temperature and mean annual NDVI, presenting the percentage variance explained by each dimension (% variance) and the cumulative percentage of variance explained by each dimension (Cum. % of variance). The relative contribution of each variable to each dimension is also shown (Ctr).

Eigenvalues	Dimension 1		Dimension 2		Dimension 3	
Eigenvalue	1.68		0.68		0.06	
% of variance	55.88		22.5		21.61	
Cumulative % of variance explained	55.88		78.38		100	
Variables	**Dim 1**	**Ctr**	**Dim 2**	**Ctr**	**Dim 3**	**Ctr**
Precipitation	0.745	33.115	-0.531	41.764	0.404	25.121
NDVI	0.741	32.715	0.621	57.162	0.256	10.123
Temperature	-0.757	34.171	0.085	1.073	0.648	64.756

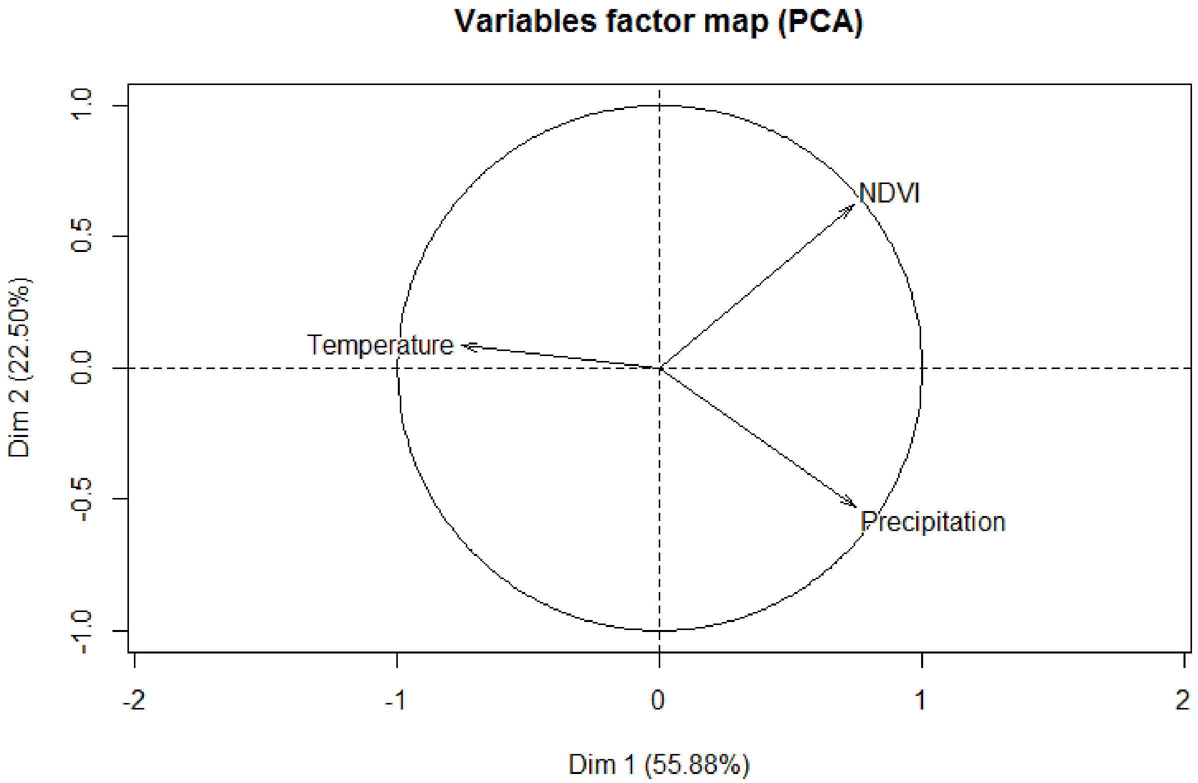

Figure S2: Diagram illustrating the separation of temporally dynamic variables results from the PCA.

Null models

Table S4: Productivity analysis from null GLMM model for the KNP population with territory and year as random terms.

Random effects	Estimate	Std. Error	Z value	AICc	BIC	LogLik	deviance	R df	Variance	Std dev
Territory									3.9e-01	6.25e-1
Year									1.30e-13	3.61e-07
Fixed effects										

Intercept	-1.69	0.24	-7.02	149.2	158.4	-71.6	143.2	153

Table S5: Estimate productivity of martial eagles in the Kruger National Park from 2018 - 2018. Standard error (SE) and the confidence limits have been presented (CL - confidence limit)

	Probability	SE	lower CL	upper CL
Overall	0.16	0.03	0.08	0.24

Table S6: Annual martial eagles productivity estimates from the null GLMM model from observations during from 2013 – 2018. Territory is included as a random term and year as a fixed term.

Random effects	Estimate	Std. Error	Z value	AICc	BIC	LogLik	deviance	R df	Variance	STD dev
Territory									2.02	1.42
Fixed effects										
Intercept	-1.75	0.66	-2.65	150.5	171.9	-68.3	136.5	149		
2014	0.10	0.83	0.13							
2015	-0.2	0.83	-0.2							
2016	-1.54	1.26	-1.22							
2017	-0.17	0.83	0.21							
2018	0.82	0.79	1.04							

Table S7: Estimated annual productivity of martial eagles in the Kruger National Park from 2018 -2018. Standard error (SE) and the confidence limits have been presented (CL -confidence limit)

Year	Probability	SE	lower CL	upper CL

2013	0.15	0.09	0.05	0.39
2014	0.16	0.07	0.06	0.35
2015	0.14	0.06	0.06	0.32
2016	0.04	0.04	0.004	0.24
2017	0.17	0.07	0.07	0.36
2018	0.28	0.09	0.14	0.48

Table S8: Breeding rate analysis from null GLMM model for the KNP population with territory and year as random terms.

Random effects	Estimate	Std. Error	Z value	AICc	BIC	LogLik	deviance	R df	Variance	STD dev
Territory									0.47	0.69
Year									0.54	0.74
Fixed effects										
Intercept	-0.97	0.39	-2.49	149	157.3	-71.5	143	115		

Table S9: Estimate breeding rate of martial eagles in the Kruger National Park from 2013 - 2018. Standard error (SE) and the confidence limits have been presented (CL - confidence limit)

	Probability	SE	lower CL	upper CL
Overall	0.28	0.08	0.15	0.45

Table S10: Nesting success analysis from null GLMM model for the KNP population with territory and year as random terms.

Random effects	Estimate	Std. Error	Z value	AICc	BIC	LogLik	deviance	R df	Variance	STD dev

Territory									7.84e-14	2.79e-07
Year									8.81e-01	9.39e-1
Fixed effects										
Intercept	-0.046	0.583	-0.079	51.7	56.4	-22.9	45.7	32		

Table S11: Nesting success of martial eagles in the Kruger National Park from 2018 - 2018. Standard error (SE) and the confidence limits have been presented (CL - confidence limit)

	Probability	SE	lower LCL	upper CL
Overall	0.49	0.15	0.23	0.75

Table S12: Annual nesting success estimates from GLMM models recorded during the study period with territory as a random term and year as a fixed term. No data were collected on this in 2013 – so 2014 is the reference year in this model

Random effects	Estimate	Std. Error	Z value	AICc	BIC	LogLik	deviance	R df	Variance	STD dev
Territory									1.53	1.24
Fixed effects										
Intercept	-2.03	0.96	-2.13	48.5	57.8	-18.2	36.5	29		
2015	3.65	1.71	2.13							
2016	19.00	5433.32	0.003							
2017	0.54	1.32	0.41							
2018	3.50	1.25	2.80							

Table S13: Annual nesting success of martial eagles in the Kruger National Park from 2018 -2018. Standard error (SE) and the confidence limits have been presented (CL - confidence limit)

Year	Nesting success	SE	lower LCL	upper CL
2014	0.12	0.10	0.02	0.46
2015	0.83	0.20	0.23	0.99
2016	1	0.0002	0.0003	1
2017	0.18	0.15	0.03	0.61
2018	0.81	0.13	0.46	0.96

Table S14: GLM determining the whether any difference in productivity existed between the northern and southern portion of the KNP.

	Estimate	Std. Error	z value	CI (2.5%)	CI (97.5%)	Pr(>|t|)	Null AIC	Residual deviance	AICc
(Intercept)	-1.96	0.34	-5.80	-2.68	-1.35	6.51e-09			
South	0.73	0.47	1.69	-0.11	1.62	0.09	48.26	41.58	45.58

Temporal analysis (Previous year, pre-lay and breeding period)

Pre-lay

Table S15. Parameter estimates from model averaging of the ranked models in Table S16 explaining the variation in martial eagle productivity. Parameters: PCA 2, CCA2, River length (m), Fire (% of buffer burnt) and mean tree cover. RI = Relative importance.

Variable	Estimate	Std.Error	A St Er	CI(2.5%)	CI(95%)	Z value	RI
(Intercept)	-1.77	0.32	0.32	-2.40	-1.14	5.49	-
CCA1	0.52	0.35	0.35	-0.19	1.23	1.49	0.56
CCA2	-0.40	0.30	0.30	-0.97	0.22	1.31	0.46
Tree cover	-0.39	0.31	0.32	-0.97	0.28	1.25	0.24
PCA1	0.34	0.30	0.30	-0.29	0.92	1.13	0.22
Elephant abundances	-0.39	0.36	0.36	-1.08	0.37	1.06	0.21
River length (m)	0.34	0.34	0.34	-0.33	1.04	1.00	0.18
Fire	0.21	0.21	0.22	-0.21	0.63	0.96	0.16
PCA2	0.12	0.25	0.26	-0.45	0.57	0.46	0.02

Table S16: Top candidate models from the pre-lay period for martial eagle productivity.

Model	df	LogLik	AIC_c	ΔAIC_c	Weight
CC1 + CC2	4	-63.05	134.41	0	0.05
CC2	3	-64.18	134.55	0.14	0.05
CC1	3	-64.2	134.59	0.18	0.05
TreeC + CC1	4	-63.15	134.6	0.19	0.05
(Null)	2	-65.31	134.71	0.3	0.05
TreeC + CC1 + CC2	5	-62.24	134.94	0.53	0.04
CC2 + PC1	4	-63.32	134.96	0.55	0.04

PC1	3	-64.61	135.4	0.99	0.03
Eleph + CC1	4	-63.57	135.45	1.04	0.03
Eleph + CC1 + Riv	5	-62.51	135.49	1.08	0.03
Fire + CC2	4	-63.65	135.61	1.2	0.03
Riv	3	-64.75	135.68	1.28	0.03
TreeC + Eleph + CC1	5	-62.65	135.76	1.36	0.03
CC1 + Riv	4	-63.73	135.76	1.36	0.03
Eleph + CC1 + CC2	5	-62.66	135.78	1.37	0.03
TreeC	3	-64.81	135.81	1.4	0.03
Fire + CC1 + CC2	5	-62.68	135.83	1.42	0.03
Fire	3	-64.88	135.94	1.53	0.03
CC1 + CC2 + PC1	5	-62.75	135.96	1.55	0.03
Fire + CC2 + PC1	5	-62.75	135.97	1.56	0.03
TreeC + Fire + CC1	5	-62.76	135.99	1.58	0.02
CC2 + Riv	4	-63.87	136.04	1.64	0.02
TreeC + CC2	4	-63.87	136.06	1.65	0.02
CC1 + CC2 + Riv	5	-62.81	136.09	1.68	0.02
Fire + CC1	4	-63.91	136.14	1.73	0.02
PC1 + Riv	4	-63.92	136.15	1.75	0.02
TreeC + CC1 + Riv	5	-62.87	136.2	1.79	2.00E-02
TreeC + Fire + CC1 + CC2	6	-61.79	136.23	1.82	0.02
Eleph	3	-65.03	136.25	1.84	0.02
CC1 + PC1	4	-63.99	136.29	1.88	0.02
CC2 + PC1 + Riv	5	-62.93	136.32	1.91	0.02

CC1 + CC2 + PC2	5	-62.95	136.36	1.95	0.02
Eleph + PC1 + Riv	5	-62.96	136.39	1.98	0.02

Breeding period

Table S17. Parameter estimates from model averaging of the ranked models in Table S18 explaining the variation in martial eagle productivity. Parameters: PCA 1, PCA2, CCA1, CCA2, River length (m) and Average tree cover. RI = Relative importance.

Variable	Estimate	Std.Error	CI(2.5%)	CI(95%)	Z value	RI
(Intercept)	-1.77	0.32	-2.40	-1.14	5.48	-
CCA1	0.55	0.35	-0.15	1.31	1.54	0.64
CCA2	-0.39	0.30	-0.97	0.22	1.30	0.43
Tree cover	-0.39	0.31	-0.98	0.29	1.23	0.28
Elephant abundances	-0.37	0.36	-1.07	0.38	1.02	0.21
River length (m)	0.32	0.34	-0.36	1.02	0.95	0.19
PCA2	-0.22	0.26	-0.71	0.36	0.83	0.13
PCA1	-0.20	0.34	-0.73	0.71	0.57	0.06

Table S18: Top candidate models from the breeding period for martial eagle productivity.

Model	df	LogLik	AIC_c	ΔAIC_c	Weight
CC1 + CC2	4	-63.05	134.41	0	0.07
CC2	3	-64.18	134.55	0.14	0.07
CC1	3	-64.2	134.59	0.18	0.07
TreeC + CC1	4	-63.15	134.6	0.19	0.07
(Null)	2	-65.31	134.71	0.3	0.06
TreeC + CC1 + CC2	5	-62.24	134.94	0.53	0.06

Eleph + CC1	4	-63.57	135.45	1.04	0.04
Eleph + CC1 + Riv	5	-62.51	135.49	1.08	0.04
Riv	3	-64.75	135.68	1.28	0.04
PC2 + CC2	4	-63.7	135.7	1.29	0.04
PC2 + CC1 + CC2	5	-62.63	135.73	1.33	0.04
TreeC + Eleph + CC1	5	-62.65	135.76	1.36	0.04
CC1 + Riv	4	-63.73	135.76	1.36	0.04
Eleph + CC1 + CC2	5	-62.66	135.78	1.37	0.04
TreeC	3	-64.81	135.81	1.4	0.04
CC2 + Riv	4	-63.87	136.04	1.64	0.03
TreeC + CC2	4	-63.87	136.06	1.65	0.03
CC1 + CC2 + Riv	5	-62.81	136.09	1.68	0.03
TreeC + CC1 + Riv	5	-62.87	136.2	1.79	0.03
Eleph	3	-65.03	136.25	1.84	0.03
PC2	3	-65.06	136.3	1.89	0.03
PC2 + CC1	4	-64	136.31	1.9	0.03
PC1 + CC1 + CC2	5	-62.93	136.32	1.91	0.03
TreeC + PC1 + CC1	5	-62.95	136.36	1.95	0.03

Breeding rate

Previous year

Table S19. Parameter estimates from model averaging of the ranked models in Table S20 explaining the variation in martial eagle productivity. Parameters: PCA 1, CCA2, River length (m), Area burnt (%) and Average tree cover. RI = Relative importance.

Variable	Estimate	Std.Error	A St Er	CI(2.5%)	CI(95%)	Z value	RI

(Intercept)	-0.8899	0.2318	0.2343	-1.35	-0.42	3.798	-
Tree cover	-0.6427	0.2564	0.2591	-1.12	-0.07	2.481	1
CCA1	0.5494	0.2596	0.2624	-0.04	1.06	2.094	1
CCA2	-0.3544	0.2967	0.2999	-0.97	0.20	1.182	0.43
PCA2	-0.2756	0.2234	0.2258	-0.78	0.14	1.221	0.31
Fire	0.2319	0.2278	0.2303	-0.28	0.66	1.007	0.26
PCA1	0.1703	0.2632	0.266	-0.25	0.87	0.64	0.08
Rivers	0.1042	0.2305	0.233	-0.38	0.61	0.447	0.07

Table S20: Top candidate models from previous year conditions

Model	df	LogLik	AIC_c	ΔAIC_c	Weight
TreeC + CC1	4	-67.85	144.05	0	0.2
TreeC + CC1 + CC2	5	-66.97	144.47	0.42	0.16
TreeC + CC1 + CC2 + PC2	6	-66.15	145.05	1	0.12
TreeC + CC1 + PC2	5	-67.33	145.2	1.15	0.11
TreeC + Fire + CC1	5	-67.39	145.31	1.26	0.11
TreeC + CC1 + PC1	5	-67.65	145.83	1.78	0.08
TreeC + Fire + CC1 + CC2	6	-66.59	145.93	1.88	0.08
TreeC + Fire + CC1 + CC2 + PC2	7	-65.47	145.97	1.92	0.08
TreeC + CC1 + Riv	5	-67.75	146.03	1.98	0.07

Nesting success

Prelay period

Table S21. Results of the GLM examining the effects of conditions experienced the previous year on the nesting success of martial eagles using logit link function and binomial error. (n = 33)

	Estimate	Std. Error	z value	CI (2.5%)	CI (95%)	Null AICc	Residual deviance	AICc
(Intercept)	-0.18	0.36	-0.51	-0.90	0.52			
PCA1	-0.74	0.41	-1.81	-1.64	0.00	48.26	44.39	48.39

Breeding period

Table S22. Results of the GLM examining the effects of conditions experienced the previous year on the nesting success of martial eagles using logit link function and binomial error. (n = 33)

	Estimate	Std. Error	z value	CI(2.5%)	CI(95%)	Null AICc	Residual deviance	AICc
(Intercept)	-0.18	0.36	-0.51	-0.90	0.52			
PCA2	-0.71	0.40	-1.78	-1.57	0.02	48.26	44.61	48.61

Climate – Principal Component Analyses (Previous year 1986 - 2018)

Table S23: Results of the PCA analysis on the three climatic variables: mean annual precipitation, mean annual maximum temperature and NDVI.

Eigenvalues	Dimension 1		Dimension 2		Dimension 3	
Eigenvalue	1.94		0.71		0.35	
% of variance	64.75		23.51		11.75	
Cumulative % of variance explained	64.75		88.25		100	
Variables	Dim 1	Ctr	Dim 2	Ctr	Dim 3	Ctr

NDVI	0.69	24.74	0.71	72.05	-0.11	3.21
Max Temperature	-0.83	35.52	0.41	23.46	0.38	41.02
Precipitation	0.88	39.73	-0.18	4.49	0.44	55.78

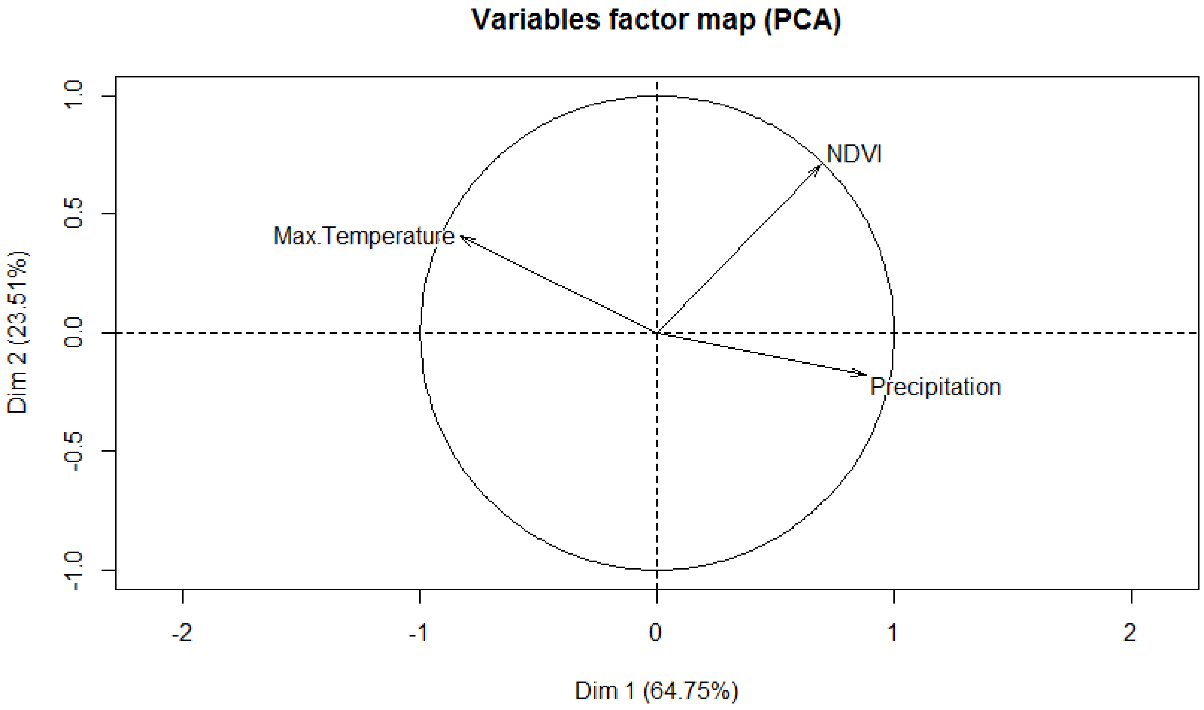

Figure S3: Diagram illustrating the separation of historic climatic variable results from the PCA.

Table S24. Model selecting table of parameter estimates from model averaging, between PCA1 and the model of no effect, explaining the variation in martial eagle productivity (n = 135 observation from 1987 – 2018).

Intercept	PCA1	Df	AICc	ΔAIC_c	logLik	Weight
-1.86	0.80	3	128.9	0.00	-61.38	0.95
-1.75	Null	2	134.7	5.77	-65.31	0.5

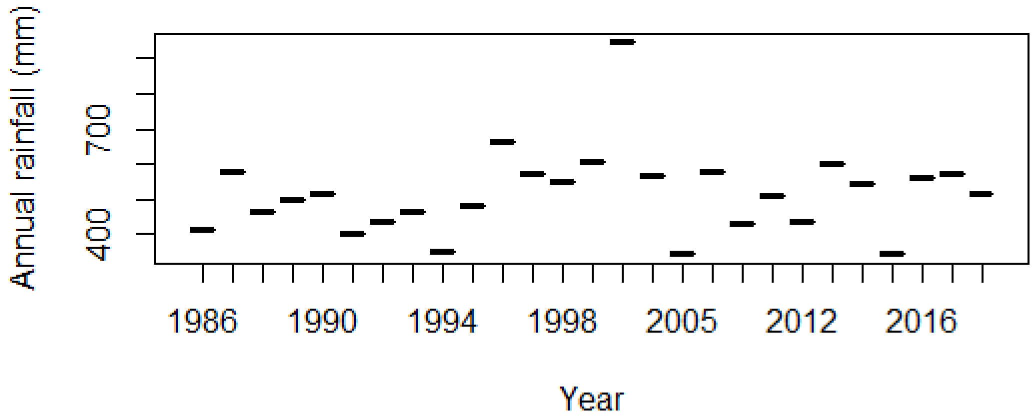

Figure S4: Mean annual rainfall recorded in the martial eagle nest buffers from 1986 – 2018.

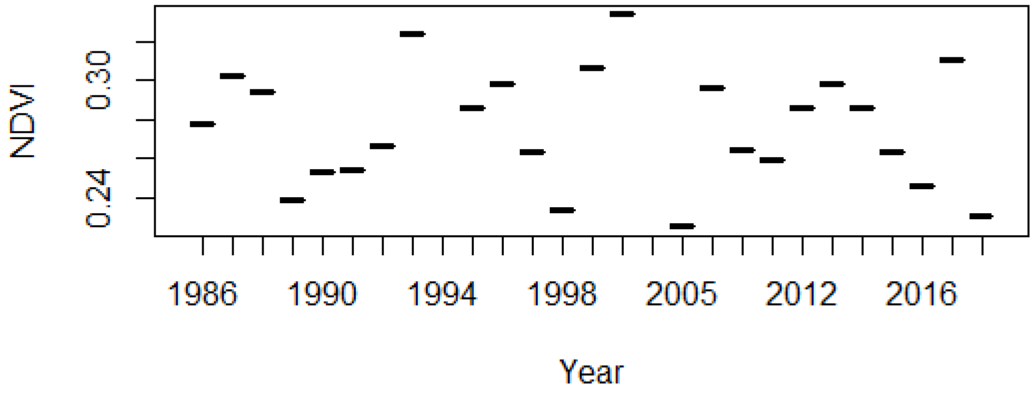

Figure S5: Mean annual NDVI recorded in the martial eagle nest buffers from 1986 – 2018.

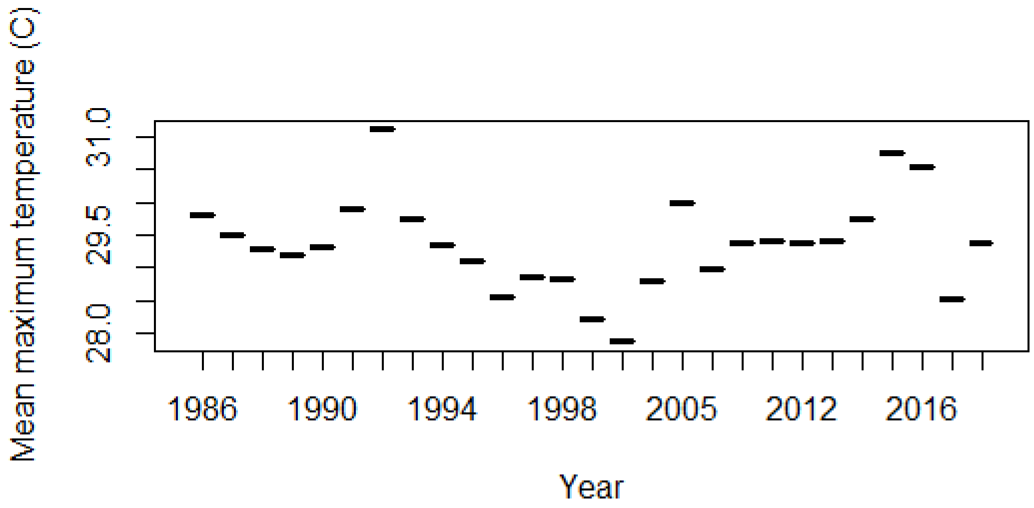

Figure S6: Mean annual maximum temperatures recorded in the martial eagle nest buffers from 1986 –2018.

Table S25. Percentage land cover for each nest buffers recorded from the monitored nests within the Kruger National Park 2013 – 2018. Mean percentage tree cover is also indicated.

Territory	Thicket dense bush	Woodland open bush	grassland	Other	Average percentage canopy cover
MEnest2016_01	11.47	26.42	61.70	0.41	6.29
MEnest2014_02	22.81	35.04	31.24	10.91	2.24
MEnest2015_01	18.41	38.16	34.03	9.40	2.27
MEnest2011_01	6.75	48.11	45.14	0.00	2.54
MEnest2015_21	4.22	31.63	63.41	0.74	3.15
MEnest2011_15	7.10	51.88	39.73	1.29	4.08
MEnest2011_18	12.17	38.02	48.72	1.08	4.28
MEnest2011_17	4.12	33.74	62.11	0.02	5.10
MEnest2015_20	5.36	37.07	56.72	0.84	3.83

MEnest2014_09	28.82	52.89	16.90	1.39	7.00
MEnest2015_13	10.32	64.30	24.96	0.42	6.30
MEnest2009_01	12.94	51.16	35.32	0.58	5.77
MEnest2014_01	13.75	53.72	32.02	0.50	6.01
MEnest2016_04	8.61	33.14	57.36	0.88	6.20
MEnest2015_11	30.02	33.51	35.99	0.48	6.18
MEnest2013_02	6.37	39.43	54.08	0.13	5.97
MEnest2011_06	28.73	64.39	5.36	1.51	5.22
MEnest2014_05	24.09	65.97	8.57	1.37	5.65
MEnest2011_21	5.21	18.65	76.14	0.00	5.77
MEnest2012_01	47.70	48.36	3.60	0.35	6.23
MEnest2011_08	14.07	77.09	8.53	0.31	5.04
MEnest2013_04	24.45	64.45	4.64	6.46	5.06
MEnest2018_02	24.41	64.88	4.58	6.13	5.06
MEnest2011_07	8.42	60.71	29.93	0.95	4.29
MEnest2015_02	8.99	63.96	26.17	0.87	4.50
MEnest2017_01	8.93	62.95	27.31	0.81	4.46
MEnest2012_02	15.32	68.95	14.88	0.86	4.14
MEnest2011_09	21.21	76.32	2.15	0.32	5.98
MEnest2011_03	15.55	78.03	5.00	1.43	6.23
MEnest2011_05	23.26	74.27	2.41	0.05	7.43
MEnest2014_08	17.74	67.71	14.20	0.34	3.33
MEnest2015_03	14.11	78.30	7.19	0.40	4.14
MEnest2014_07	17.55	60.04	21.57	0.84	4.27

MEnest2011_04	36.15	62.24	1.50	0.11	6.30
MEnest2011_02	37.10	54.83	4.93	3.14	8.47
MEnest2016_05	23.91	53.02	21.93	1.14	5.45
MEnest2014_03B	21.00	68.33	10.66	0.01	3.23
MEnest2014_03A	19.87	69.04	11.08	0.01	3.24
MEnest2017_02A	15.36	76.77	7.74	0.13	5.57
MEnest2017_02B	17.14	75.69	7.04	0.13	5.65
MEnest2011_12	23.40	45.79	29.75	1.06	7.08
MEnest2011_16	5.79	26.30	67.80	0.10	6.03
MEnest2015_04	6.21	24.83	68.87	0.09	5.94
MEnest2011_20	22.16	46.92	29.10	1.82	4.70
MEnest2013_01	12.34	76.25	10.48	0.94	2.67
MEnest2013_05	71.63	26.84	1.52	0.00	11.28
MEnest2013_06	33.30	59.35	6.82	0.53	6.54
MEnest2014_04	20.23	68.31	10.55	0.90	5.20
MEnest2015_05	4.65	32.42	62.93	0.00	5.80
MEnest2015_06	6.10	26.15	67.75	0.00	6.41
MEnest2015_07	43.66	12.47	3.26	40.61	5.89
MEnest2015_08	44.60	38.33	15.79	1.28	7.38
MEnest2015_09	40.31	40.34	19.07	0.29	7.25
MEnest2015_10	24.85	16.40	53.42	5.33	4.62
MEnest2015_15	11.79	36.89	50.39	0.93	6.13

MEnest2015_18	13.16	30.01	56.25	0.58	6.09
MEnest2015_19	10.08	19.40	70.25	0.28	5.75
MEnest2018_01	29.05	40.07	0.81	30.08	3.08
MEnest2018_03	5.61	27.88	66.49	0.02	3.64