

**THE HABITAT, NESTING AND FORAGING
REQUIREMENTS OF SOUTHERN GROUND-
HORN BILLS IN THE KRUGER NATIONAL PARK,
SOUTH AFRICA**

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ABSTRACT

Southern ground-hornbills *Bucorvus leadbeateri* are large, terrestrial, carnivorous birds that inhabit the savanna and bushveld habitats of much of Africa, south of the equator. They were once prevalent in north-eastern South Africa, but as a result of extensive habitat loss and persecution, their population has suffered a significant decline. They are currently listed nationally as *Endangered* and globally as *Vulnerable*. In an effort to curtail this decline in South Africa, a National Species Recovery Plan was developed, with reintroductions of the birds into suitable habitat outside of protected areas listed as a viable conservation intervention for the species. This plan also highlighted a number of knowledge gaps which need to be addressed and which are essential to the long-term conservation of the species. The exact habitat requirements (including specifics of nest cavities) and the foraging ecology of southern ground-hornbills were both listed as areas where data are lacking. Consequently the main aim of this study was to determine the habitat, nesting and foraging requirements of the southern ground-hornbills with the intention of developing management guidelines for areas planned as reintroduction sites for the species. Our study focused on the population of southern ground-hornbills located within the Kruger National Park.

We found that the particular characteristics of the southern ground-hornbill nest (cavity dimensions, tree species, height of cavity etc.) did not affect nesting success of the birds. The proximity of roads was important, with more successful nests being situated closer to roads. Habitat structure and diversity of vegetation around the nest also influenced the success of the particular group, with nests with more open habitats and a wider variety of vegetation types being more successful. Nest cavity temperatures were significantly different to ambient for selected nests studied across the 2013-2014 and 2014-2015 breeding seasons. We also found that nest temperature did not affect their nesting success. Interestingly, the artificial nest within our study area showed extremes in temperature (significantly higher and lower than ambient

maximum and minimum temperatures, respectively) despite this being one of the most successful nests studied.

As southern ground-hornbills are carnivorous, they are known to take a variety of prey items and have been considered generalists. One of the important current questions in foraging ecology is whether generalist populations consist of individuals (or in our case, groups) that are all generalists, or if the generalist population comprises a number of dietary specialists. We tested this theory for southern ground-hornbills using stable isotope analyses of feather and bill samples. Our results show that they are obligate generalists at the group level, suggesting that they access and consume prey species in accordance with their availability in the landscape. At the individual level, based on the two bill samples obtained, there could be some form of specialization occurring. With our relatively small sample size we were unable to determine whether this was in fact specialization or whether these results were reflecting local environmental changes, affecting the isotopic signatures of the vegetation and thereby, prey species of southern ground-hornbills.

We used satellite tracking technology to investigate home range sizes and habitat use of southern ground-hornbills within the Kruger National Park and surrounding conservation areas. We then used first-passage time analysis to determine whether certain movement behaviours were influenced by habitat type. We found that there were marked seasonal differences in home range size and that all groups showed a range restriction during the wetter months (coinciding with the breeding season), where activities are concentrated around the nest site. Grassland, open woodland and dense thicket habitats were found to be important habitats for foraging and grassland and open woodland areas were used in accordance with their availability within the groups' respective territories year-round. The results from this study have been consolidated into recommendations for areas being considered as potential release sites for captive-reared southern ground-hornbills.

This research investigated what the habitat, nesting and foraging requirements of southern ground-hornbills are with the aim of adding to the current data on the species as well as addressing these knowledge gaps as highlighted in the National Species Recovery Plan. Each aspect of this PhD study provided results that can be used in current and future conservation interventions, and in particular, reintroductions in areas outside of protected areas. These results are applicable to populations within South Africa, but can also be applied to the species across its range.

PREFACE

The data described in this thesis were collected in the Kruger National Park, Republic of South Africa from January 2008 until December 2014. Field work was carried out as part of the Endangered Wildlife Trust's Lowveld Large Bird Project (registered with SANParks Scientific Services) and while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs.

This thesis, submitted for the degree of Doctorate of Philosophy in Science in the College of College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.



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Leigh Combrink

November 2016

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.



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Professor Colleen T. Downs

Supervisor

December 2016

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DECLARATION 1 - PLAGIARISM

I, Leigh Combrink, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1

Combrink, L., Combrink, H.J., Botha, A.J. & Downs, C.T. Habitat structure and diversity influence the reproductive output of an endangered large cavity-nesting bird, the southern ground-hornbill (*Submitted*)

Author Contributions:

LC & CTD conceptualised the manuscript. LC, HJC and AJB conducted the field work. LC & HJC analysed the data. LC wrote the manuscript. All authors provided editorial input into manuscript.

Publication 2

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Author Contributions:

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Publication 3

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Author Contributions:

LC, CTD, GESR and SW conceptualised the paper. LC, HJC, GESR & AJB conducted the field work. SW & GH funded and ran the isotope and radiocarbon sample analyses. LC, HJC & SW analysed the data and wrote the manuscript; other authors provided editorial advice.

Publication 4

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(Submitted)

Author Contributions:

All authors conceptualised the manuscript. LC, HJC and AJB conducted the field work. LC & HJC analysed the data. LC wrote the manuscript. All authors provided editorial input into manuscript.



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Leigh Combrink

November 2016

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Chapter 1: Introduction

In this chapter, I detail factors affecting the persistence of terrestrial birds and then introduce the study species, the southern ground-hornbill *Bucorvus leadbeateri*. I review aspects of its ecology, including threats to the species and the current population conservation status in South Africa. A summary of past research is included and the findings and research recommendations listed in the National Species Recovery Plan for southern ground-hornbills in South Africa are discussed. The significance of this study in terms of complementing recent work and increasing our current knowledge of the species, as well as its relevance in terms of the knowledge gaps addressed, is then discussed. The specific research questions, aims and objectives of the research are outlined, with a complete thesis outline included at the end.

1.1 Threats to terrestrial avian species

An understanding of extinction risk, and the ecological mechanisms that cause extinction, are essential for species conservation (Owens & Bennet 2000). There are currently a number of threats facing the persistence of terrestrial biodiversity, and in particular, birds. These include climate change (Jetz et al. 2007), habitat loss (Sisk et al. 1994), competitive or predatory introduced species (Loope et al. 2001), hunting (Thiollay 2006a), use in wildlife trade and traditional medicine markets (Bruyns et al. 2013) and disease (Wikelski et al. 2004). Human activities have significantly influenced two of these major threats, being accelerated climate change and habitat loss and destruction (Jetz et al. 2007). With our ever-expanding human population, the effects of climate change and the associated loss of relatively pristine habitats, will result in countless species extinctions (Sisk et al. 1994).

Habitat loss, as a result of human-induced land use change, is predicted to predominantly affect bird populations in the lower latitudes, based primarily on the high levels of economic and population growth forecast for these areas (Owens & Bennett 2000). In the east African tropics, habitat loss from overgrazing by livestock and land cultivation are the major threats facing raptors (Virani & Watson 1998). Similarly, in central West Africa, the change in land use practices owing to the increase in human pressure, such as deforestation, overgrazing, an increase in the use of pesticides and in some cases, direct persecution of raptors, has resulted in substantial habitat changes and population declines in many bird species (Thiollay 2006a).

The decline of large terrestrial birds in West Africa has left these populations heavily reliant on protected areas for persistence and survival (Thiollay 2006b). Protected areas play a crucial role in protecting biodiversity from these human-induced threats (Cantú-Salazar & Gaston 2010). However, the majority of protected areas are small and as a result of threats such as habitat loss and climate change, can become increasingly isolated patches, often rendering them ineffective (Cantú-Salazar & Gaston 2010). Thus, the effectiveness of protected areas in future (and possibly currently) may lie disproportionately with very large contiguous protected areas (Cantú-Salazar & Gaston 2010).

Accelerated climate change and the associated changes in environmental conditions, in particular temperature, have been shown to affect birds in terms of the timing of egg laying (Both et al., 2004), timing of migration (Crick 2004), nestling condition (Perez et al. 2008), and nest survival (Guerena et al. 2016). With increasing global temperatures, tree cavities, with their buffering effect on ambient temperature extremes (Cooper 1999; Martin and Ghalambor 1999), are expected to become increasingly important to birds (Şekercioğlu et al. 2012). Birds that do not construct their own nests, such as secondary cavity nesters, are often limited by the availability of suitable nesting sites (Newton 1994; Cockle et al. 2010). When

suitable nests are limiting, stronger or fitter individuals will often occupy the best nests enhancing their reproductive output (Robertson and Rendell, 1990). Suitable cavities may become increasingly scarce owing to a loss of large trees, through logging and harvesting (Şekercioğlu et al. 2012) or through a lack of recruitment (Buitenwerf et al. 2012). This could mean that competition for the use of these hollows will become fierce, especially for temperature-sensitive species (Şekercioğlu et al. 2012).

Climate change can also contribute to habitat loss through bush encroachment, where increased CO₂ concentrations provide woody species with a competitive edge over grasslands (Wigley et al. 2010; Buitenwerf et al. 2012; Parr et al. 2014). This will become increasingly important for African savannas, where the increase in ambient temperature as a result of these increased CO₂ concentrations, could incur significant vegetation changes (Buitenwerf et al. 2012) and has the potential to severely affect bird reproductive output. Thiollay (2006b) showed that within savanna woodlands of Burkina Faso, the only significant and consistent bird species declines, when comparing the protected areas ranging from little disturbed to heavily exploited areas, were of the large terrestrial game birds, namely guineafowl, bustard, northern ground-hornbill, eagles and vultures. These birds were virtually extinct within the least protected areas (Thiollay 2006b).

The risk of extinction is not the same for all species of birds (Owens & Bennet 2000). Owens and Bennett (2000) showed that sources of extinction risk that relate to fecundity and longevity, such as persecution by humans and the impacts of introduced predators, affect mainly large bodied species with slow population growth rates. Conversely, extinction risk relating to habitat loss mainly affected smaller-bodied species with fairly specific habitat needs (Owens & Bennett 2000). Currently, 25 of the 57 known hornbill species, around 44%, are considered globally threatened or near threatened with extinction, with the major threat being habitat loss (Poonswad et al. 2013). The majority of these threatened hornbills occur in Asia

in forests, with only one species, the southern ground-hornbill *Bucorvus leadbeateri*, occurring in savannas (Poonswad et al. 2013).

1.2 The southern ground-hornbill

Southern ground-hornbills *Bucorvus leadbeateri* are large, terrestrial, carnivorous birds that inhabit savanna and bushveld habitats throughout much of Africa, south of the equator (Kemp 1995). The largest contiguous population of natural-nesting southern ground-hornbills in South Africa is found in the Kruger National Park.

Southern ground-hornbills have black plumage with white primaries (Kemp 1995), with males having pure red (bare) throat skin and females having a deep violet-blue patch under the lower mandible (Kemp & Kemp 1980). They are co-operative breeders, forming groups with an alpha breeding pair and up to nine helper birds, with the average group size being 3-5 birds (Kemp 1995). The birds are territorial and have home ranges from approximately 3 000 – 12 000 ha depending on the habitat (Combrink unpubl. data). In South Africa, they breed during the austral summer (December – March) which in the Lowveld region, coincides with the wet season (Kemp 1995). Rainfall has been shown to be an influential factor in the breeding of southern ground-hornbills, with egg laying only commencing after the first rains have fallen (Kemp 1976; Kemp & Kemp 1980; Kemp & Kemp 1991).

Incubation is only conducted by the alpha female, who remains in the nest for the 39-day period (Kemp 1995). During the breeding season, activity is concentrated in the vicinity of the nest site (Zoghby et al. 2015), with the group making numerous trips to provision for the incubating female and growing nestling. Southern ground-hornbills typically lay two eggs, usually 4-7 days apart. Incubation starts with the laying of the first egg and the chicks hatch asynchronously (Kemp 1995). The female only provisions for the first-hatched chick, with the

second usually succumbing to starvation and dehydration within seven days (Kemp 1995). The first-hatched chick remains in the nest for around 86 days (Kemp 1995).

Nests consist of large cavities either in trees, rock faces or earth banks (Kemp 1995), with the majority of known nests within the Kruger National Park being located in trees (Combrink pers. obs.). Southern ground-hornbill are secondary cavity nesters and need to find a suitable nest site within their respective territories in order to breed (Kemp 1995). Within the Kruger National Park, suitable nest-sites are thought to be limiting (Kemp et al. 1989; Kemp & Begg 1996) and have been considered the most important factor influencing southern ground-hornbill breeding success, with the availability of food resources being of secondary importance (Kemp 1988). Southern ground-hornbills feed on a range of prey items from hares, snakes, birds, tortoises and chameleons to frogs, scorpions, spiders, termites, beetles and grasshoppers (Kemp 1995). Southern ground-hornbill spend around 70% of their day walking, and forage as a cohesive unit, consuming whatever they can overpower (Kemp 1995).

They are threatened as a result of habitat loss and persecution and are considered *Vulnerable* globally (IUCN, 2016) and *Endangered* within South Africa (Taylor *et al.*, 2015). A National Species Recovery Plan was developed in South Africa for southern ground-hornbills in 2011 (Jordan, 2011).

1.2.1 Summary of past research in South Africa

Research on the ecology of southern ground-hornbills in South Africa was spear-headed by Alan and Meg Kemp, with particular emphasis on the population located within the Kruger National Park (Table 1.1). In 2005, a Population Habitat Viability Assessment (PHVA) for the species was completed (Morrison et al. 2005). Following this, research in South Africa focussed on the status of southern ground-hornbills in the Limpopo Province and analysing

some of the long-term data sets from the population monitoring in the Kruger National Park. Kemp and Webster (2008) analysed the population status of southern ground-hornbills in South Africa and noted that the species had suffered a decline of around 65%.

In 2011, a National Species Recovery Plan was developed, which highlighted research needs and knowledge gaps as well as possible conservation interventions for southern ground-hornbills in South Africa (Jordan 2011). This spurred a number of research papers to address these gaps and increase our understanding of aspects of the ecology of southern ground-hornbills.

Table 1.1. A summary of key South African research publications on aspects of southern ground-hornbill ecology

Authors	Year	Title
Kemp	1976	Factors affecting the onset of breeding in African hornbills
Kemp & Kemp	1980	The biology of the southern ground-hornbill <i>Bucorvus leadbeateri</i> (Vigors) (Aves: Bucerotidae)
Vernon	1986	The ground hornbill at the southern extremity of its range
Kemp	1988	The behavioural ecology of the southern ground hornbill: are competitive offspring at a premium?
Kemp et al.	1989	Distribution of southern ground hornbills in the Kruger National Park in relation to some environmental variables
Knight	1990	Status, distribution and foraging ecology of the Southern Ground Hornbill (<i>Bucorvus cafer</i>) in Natal.
Kemp & Kemp	1991	Timing of egg laying by southern ground-hornbills <i>Bucorvus leadbeateri</i> in the central-Kruger National Park, South Africa.
Kemp	1995	The hornbills: Bucerotiformes
Kemp & Begg	1996	Nest sites of the southern ground-hornbill <i>Bucorvus leadbeateri</i> in the Kruger National Park, South Africa, and conservation implications.
Kemp et al.	1998	Geographical analysis of vegetation structure and sightings for four large bird species in the Kruger National Park, South Africa
Kemp	2000	Southern ground-hornbill
Martin & Coetzee	2004	Visual fields in hornbills: precision-grasping and sunshades.
Kemp	2005	Ground hornbills.
Morrison et al.	2005	Southern Ground Hornbill (<i>Bucorvus leadbeateri</i>) PHVA.
Engelbrecht et al.	2007	The status and conservation of Southern Ground Hornbills <i>Bucorvus leadbeateri</i> in the Limpopo Province, South Africa.

Kemp & Kemp	2007	How often might southern ground-hornbills be expected to fledge two chicks? Data from the Kruger National Park, 1967-1999.
Kemp et al.	2007	What has become of eggs and chicks of southern ground-hornbill harvested from the Kruger National Park?
Kemp & Webster	2008	Latest analysis of southern ground-hornbill (SGH) distribution and population in South Africa: December 2008
Dickens	2010	How much is enough? Calibrating satellite telemetry for southern ground-hornbill
Wyness	2010	Home range use by southern ground-hornbills (<i>Bucorvus leadbeateri</i>) – quantifying seasonal habitat selection and vegetation characteristics.
Jordan	2011	Southern ground-hornbill (<i>Bucorvus leadbeateri</i>) Species Recovery Plan for South Africa.
Theron	2011	Genetic connectivity, population dynamics and habitat selection of the southern ground Hornbill (<i>Bucorvus leadbeateri</i>) in the Limpopo Province
Cilliers et al.	2013	Developing a site selection tool to assist reintroduction efforts for the southern ground-hornbill <i>Bucorvus leadbeateri</i> .
Theron et al.	2013	The home range of a recently established group of southern ground-hornbill (<i>Bucorvus leadbeateri</i>) in the Limpopo Valley, South Africa.
Wilson & Hockey	2013	Causes of variable reproductive performance by southern ground-hornbill <i>Bucorvus leadbeateri</i> and implications for management.
Broms et al.	2014	Spatial occupancy models applied to atlas data show southern ground-hornbills strongly depend on protected areas.
Zoghby et al.	2015	Patterns of roost site selection and use by southern ground-hornbills in north-eastern South Africa
Zoghby et al.	2015	Seasonal changes in movement and habitat use by southern ground-hornbills in the South African Lowveld.

1.3 Problem statement and significance of study

The southern ground-hornbill National Species Recovery Plan for South Africa highlights “the habitat requirements and what constitutes ideal Southern Ground Hornbill habitat” as a knowledge gap for the species (Jordan 2011). Specific aspects of their ecology that are mentioned as factors to be considered include availability of suitable nesting sites, food availability, effects of temperature and southern ground-hornbill population densities. Although some of these topics have been studied in South African southern ground-hornbill populations, these studies have either been based on a single group (Theron et al. 2013) or on groups that use artificial nest sites (Wilson & Hockey 2013; Zoghby et al. 2015) and where the densities were not determined before artificial nest sites were provisioned.

In this study, I investigated factors that affect the nesting success of southern ground-hornbills, including the potential effect of harvesting the second-hatched chick for captive rearing. I examined aspects of the nest cavity, location and proximity to a number of environmental, habitat and landscape features and the possible effects of temperature on nesting success. I used stable isotope analyses of feather and bill samples to answer questions relating to southern ground-hornbill foraging ecology, specifically whether they are dietary generalists or specialists. I then used tracking data to investigate their seasonal home range sizes and possible habitat preferences within the Kruger National Park. Using first-passage time analysis, I looked at the scales at which southern ground-hornbills concentrate their foraging efforts and whether certain movement behaviours, in particular, foraging, could be associated with habitat types.

My research complements previous works and builds on their findings based on the largest natural nesting population of southern ground-hornbills in South Africa. Owing to the geographic extent of the study area and the variety of habitat types available to the birds, my

findings are applicable to areas outside of protected areas and to sites beyond the borders of South Africa.

1.4 Aims and objectives

The main aim of this study was to determine the habitat, nesting and foraging requirements of the southern ground-hornbill with the intention of developing management guidelines for areas planned as reintroduction sites for the species. We aimed to base our study on the population of southern ground-hornbills located within the Kruger National Park. This population was chosen, as it is the largest contiguous natural nesting population of southern ground-hornbills in South Africa, with the Kruger National Park being home to more than half of the estimated national population (Kemp 2000). The Kruger National Park is around 2 million ha in extent with a variety of vegetation types, largely based on the two major soil types, being basalt and granite (Venter 1986). There is also a distinct rainfall gradient with areas in the south being progressively wetter than areas in the north (Smit 2011). This area provides us with a unique opportunity to study southern ground-hornbills across a variety of habitats in a natural setting.

My research objectives were:

- 1) To determine what factors (if any) affect the nesting success of southern ground-hornbills, with the factors being:
 - a. Nest site characteristics (measurements, tree species etc.);
 - b. Habitat or vegetation type;
 - c. Vicinity of water sources;
 - d. Vicinity of roads;
 - e. Nest treatment – harvesting of second-hatched chicks;

- 2) To investigate the temperature fluctuations within southern ground-hornbill nests, and specifically to determine
 - a. Differences between natural and artificial nests;
 - b. Differences between all nests;
 - c. Effects of temperature on nesting success;
- 3) To investigate the foraging ecology of southern ground-hornbills, using stable isotope analyses of naturally-shed feathers to determine
 - a. Whether southern ground-hornbills are all generalists or a generalist population comprising a number of specialists;
 - b. Whether there are age discrepancies in their diets;
 - c. What effect nesting habitat has on their diet;
- 4) To study southern ground-hornbill home range and habitat use, with the aim of determining
 - a. Whether there are seasonal differences in their territory sizes;
 - b. Whether they show any habitat selectivity throughout the different seasons;
 - c. At what spatial scale they concentrate their foraging efforts across the different seasons;
 - d. Whether movement behaviour is influenced by habitat type.

1.5 Study outline

This thesis is comprised of six chapters formatted as manuscripts for publication in relevant national and international peer-reviewed journals. As a result, there is some repetition within chapters. The various hypotheses and predictions are included in the individual chapters. The chapters included are as follows:

Chapter 2: Habitat structure and diversity influence the reproductive output of an endangered large cavity-nesting bird, the southern ground-hornbill.

Chapter 3: Nest temperature fluctuations in a cavity nester, the southern ground-hornbill.

Chapter 4: Isotopic proxy for the dietary niche of the endangered southern ground-hornbill.

Chapter 5: Aspects of the spatial ecology of southern ground-hornbills in the Kruger National Park, South Africa.

Chapter 6: This is a concluding chapter which summarises the research findings and resulting conservation recommendations for the species.

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Chapter 2: Habitat Structure and Diversity Influence the Reproductive Output of an Endangered Large Cavity-Nesting Bird, the Southern Ground-hornbill

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Running header: Habitat structure and ground-hornbills

2.1 Significance of work

Habitat structure and diversity surrounding southern ground-hornbill nests has a significant impact on their reproductive output. This highlights the importance of monitoring vegetation change in savanna habitats where they occur. Management of savanna areas should take factors that influence bush encroachment, such as fire and elephants, into account to ensure the long-term persistence of these birds.

2.2 Abstract

Changes in habitat structure can adversely affect the breeding success of birds, especially those dependent on specific habitat features for nesting. Bush encroachment, through an increase of woody species into grasslands, can switch areas from open savannas to closed canopy woodlands. Savannas are often managed with predators and large herbivores as priority species, with little thought to the many bird species that management decisions could affect. Using a data set spanning seven breeding seasons, we examined how nesting success of southern ground-hornbills *Bucorvus leadbeateri* varied according to various environmental and habitat factors within a radius of 3 km surrounding the nest site. Identifying which factors affect nesting success will allow for targeted management efforts to ensure the long-term survival of southern ground-hornbills both within and outside protected areas. Habitat structure and diversity of the vegetation surrounding the nest were the most influential factors on southern ground-hornbill nesting success. Southern ground-hornbills require open grassy areas for foraging and areas with large trees for nesting. Savanna habitat drivers, such as elephant and fire should be managed, and the effects of climate change monitored, to ensure that sufficient large trees are able to establish in the landscape and to control for bush encroachment. This is especially important in areas earmarked for reintroductions. Nest sites of southern ground-hornbills should be monitored to mitigate any structural changes in the habitat

surrounding the nests. Nests should be modified or artificial nest sites provided, where nests have been damaged or lost, to ensure the continued presence of these birds in African savannas.

Keywords: conservation, co-operative breeder, nesting success, savanna, southern ground-hornbill

2.3 Introduction

Identifying habitat characteristics that influence species and populations is important for management decisions for the conservation of these species (Martin 2014). Vegetation or habitat structure is one such characteristic that strongly influences the composition of bird communities in grasslands and savannas (Skowno & Bond 2003). A change in habitat structure, such as the loss of nesting trees, can be detrimental to the reproductive output or nesting success of a species (Martin 2014). Habitat structure can also influence foraging proficiency through decreasing the detectability of prey or the mobility of the bird searching for prey (Butler & Gillings 2004).

Over the past century, there has been an increase in woody plants in grasslands and savannas (Wigley et al. 2010; Buitenwerf et al. 2012; O'Connor et al. 2014). This woody or bush encroachment can significantly alter the biodiversity in the area (Buitenwerf et al. 2012) and have large consequences for conservation and protected areas (Wigley et al. 2010). Bush encroachment is often considered the result of changes in disturbance regimes, such as fire and herbivory (Wigley et al. 2010; Buitenwerf et al. 2012; Parr et al. 2014). In the Kruger National Park, elephants are considered a major cause of disturbance (du Toit et al. 2003) and are often labelled as ecosystem engineers (O'Connor et al. 2014). Climate change and an increase in atmospheric CO₂ concentrations could also play a role (Wigley et al. 2010) through the increased growth benefits that this provides to trees relative to grasses (Buitenwerf et al. 2012; Parr et al. 2014). This increase in woody cover can change the habitat structure and in extreme

cases lead to a biome switch from savannas to dense woodland (Hibbard et al. 2001; Parr et al. 2014) where the grass layer and its associated biota are lost completely (Wigley et al. 2010).

Often a shift in habitat structure has detrimental effects on the local biodiversity and in turn impacts the reproductive output of the associated bird species through loss of potential nesting habitat (Martin 2014), changes in prey base (Burke and Nol 1998), changes in foraging ability (Butler & Gillings 2004) and increased predation risk (Haensly et al. 1987; Badyaev 1995; Yurizharikov & Cooke 2007). For territorial species, which are already restricted to finding nest sites and sufficient prey within their territory, these impacts can be exacerbated, as changes in prey availability or accessibility or the availability of suitable nesting sites within their territory will lead to a reduction in productivity. This is particularly important when working with endangered birds, as conservation strategies aimed at saving these species will need to ensure that any factors affecting long-term reproductive output are mitigated where possible.

The southern ground-hornbill *Bucorvus leadbeateri* inhabits savannas throughout much of Africa and is currently listed as *Vulnerable*, mainly as a result of habitat loss, land-use change and persecution (Birdlife International 2016). In South Africa, the species is considered *Endangered* and suffered significant declines throughout its range (A.C. Kemp & R. Webster unpubl. data; Taylor, Peacock & Wanless 2015), with around 50% of the national population residing within the Kruger National Park (Kemp 1995). Southern ground-hornbills are terrestrial, carnivorous, co-operative breeders. They generally occur in groups of between 2-11 birds (Kemp et al. 1989), consisting of an alpha breeding pair and related subordinate helpers (Kemp 1995). They are secondary cavity nesters and occupy territories within the Kruger National Park ranging from 3000 – 12000 ha (L. Combrink unpubl. data). Nests are located in natural cavities in large trees, but are occasionally on cliffs or earth banks (Kemp 1988). The majority of known nests within the Kruger National Park are in trees, with only

one of the 38 nests referred to in this study being a nest in a cliff face. Females lay two eggs, 3-7 days apart. Only the first-hatched chick is provided for, with the second-hatched chick mostly perishing as a result of starvation (Kemp 1995).

The southern ground-hornbill National Species Recovery Plan for South Africa (Jordan 2011) highlights the use of captive-reared birds and reintroductions as conservation interventions for this species. However, the exact habitat requirements for southern ground-hornbills is considered a knowledge gap (Jordan 2011). Before reintroductions can occur, it is essential to first understand the factors that affect southern ground-hornbill nest site selection and that influence their reproductive output. Kemp and Kemp (1991) suggest that suitably sized nest cavities for southern ground-hornbill are limited within savannas. However, in their study from 1967-1995, Kemp & Begg (1996) did not find any of the nest site characteristics tested to have an influence on southern ground-hornbill nesting success. Recent changes in management strategies in the Kruger National Park, in particular those relating to fire and elephants (van Wilgen et al. 2008; Young et al. 2009), could have significantly affected the survival and recruitment of large trees. This in turn, could affect the availability of suitably-sized cavities in the landscape.

Wilson and Hockey (2013) found that southern ground-hornbill groups nesting in natural cavities were more successful when there was 3 km of open woodland surrounding the nest. They also found that southern ground-hornbill groups using artificial nests were more successful than those occupying natural nests. Their study was conducted in a private nature reserve adjacent to the central Kruger National Park which is 180 000 ha in extent (around 9% the size of the Kruger National Park).

Using data from seven complete breeding seasons of nest monitoring (2008 – 2015), we investigated what nest characteristics, habitat and environmental factors affected the overall reproductive output of southern ground-hornbill groups in the Kruger National Park.

Specifically, we wanted to determine whether aspects of the nest itself or food availability were more important predictors of nesting success for southern ground-hornbills. We also tested whether the habitat structure within 3 km surrounding the nest and aspects of the nest site itself affected southern ground-hornbill nesting success for all vegetation types with known southern ground-hornbill nests throughout the Kruger National Park. Using our results, we suggest possible management implications and interventions needed to ensure the long term sustainability of the southern ground-hornbill throughout its range.

2.4 Methods

2.4.1 Study area

This study was conducted within the Kruger National Park, South Africa (22-26°S, 30-32°E), which comprises around 2 million ha with an average annual rainfall of 350 – 750 mm (Gertenbach 1980). The park is largely divided longitudinally with more granitic soils in the west and basaltic soils in the east (Venter 1990). The habitat consists mainly of savanna, with pockets of dense woody vegetation within broader grasslands (Gertenbach 1983).

2.4.2 Nest surveys

We monitored all known and accessible southern ground-hornbill nesting sites within the Kruger National Park (n = 38) from the 2008/2009 breeding season until 2014/2015 (Fig. 2.1). The breeding season for southern ground-hornbills coincides with the wet season, from October through to April each year. Initial nest checks were usually conducted in November, with active nests being revisited throughout the breeding season to determine chick survival to fledging age. In some instances, the second-hatched chick was removed or harvested from the nest for the purposes of being included in the captive rearing and reintroduction programme

(Jordan 2011). Characteristics and measurements of each nest site were also collected. The nest site characteristics that we measured were: diameter of the base of the cavity (length and breadth), depth of the cavity (nest lip to base), volume of the nest (length x breadth x depth), height of the nest entrance from the ground and the diameter at breast height of the nest tree. We were only able to collect chick survival and nesting success data from one cliff nest, which is completely inaccessible for measurements to be taken. Only measurements from nest tree cavities were included in this analysis (n = 37).

2.4.3 Nest habitat

GIS layers obtained from the South African National Parks (SANParks) were used to extract environmental variables related to each southern ground-hornbill nest. As they are thought to be central-place foragers, concentrating their breeding season activity around the nest site, we included a buffer with a radius of 3 km around each nest for the purpose of extracting the related environmental variables and to test Wilson and Hockey's (2013) proposal about the area of open woodland surrounding each nest across the extent of the Kruger National Park.

Habitat was classified according to the 2013-2014 South African National Land Cover Dataset (GeoterraImage 2014). For each 3 km buffer zone, the proportions of the various land types were calculated. These data were then used to determine the vegetation diversity using the R package *vegan* (Oksanen et al. 2016) to calculate the Shannon-Weiner Diversity Index (Shannon & Weaver 1949; Spellerberg & Fedor 2003).

Insect species richness has been shown to be positively correlated with the Normalised Difference Vegetation Index (NDVI – measure of vegetation greenness) (Pettorelli et al. 2011). In the Kruger National Park, the NDVI calculated for the growing/wet season is highly correlated with above-ground biomass and rainfall (Wessels et al. 2006). In our chick survival models, we have used the NDVI and yield (biomass increase) within the buffer zone as a proxy

for food availability during the current breeding season. For the nesting success models, the NDVI and yield values were averaged for the seasons where the outcome or fate of the nest attempt was known. NDVI and yield measurements were obtained via the MODISTools package (Tuck & Philips 2015).

Soil type was classified as the proportion of granite, basalt, gabbro, eccla shale and rhyolite within the buffer zone and expressed as a percentage. The length (total number of kilometres) of all streams and rivers and the distance from the nest to the nearest stream were calculated using Quantum GIS (QGIS, version 2.4.0, Quantum GIS Development Team, 2016). Similarly, length (total number of kilometres) of all tourist and management roads, and distance from the nest to the nearest road (tourist or management) were included.

Rainfall for the current breeding season (mm), the previous breeding season (mm) and the previous non-breeding season (mm) was calculated using SANParks' rainfall data, collected at weather stations throughout the Kruger National Park. The rainfall data from the weather station closest to each nest site was used as a proxy for rainfall within the buffer zone for the particular time period. The mean annual rainfall (percentage of the buffer zone within the various rainfall categories – see Table 2.1) was calculated using the continuous vector layer of interpolated rainfall data provided by SANParks.

2.4.4 Reproductive output

The nestling period in southern ground-hornbills is around 86 days in length. Nestlings were fitted with alphanumeric metal rings and colour rings at 60-70 days for future individual identification. We considered the nestling to have fledged and the nest successful if the nestling reached ringing age. Reports of sightings of the fledged ringed chicks have confirmed that this is a reasonable assumption (L. Combrink unpubl. data). Chick survival was recorded as 0 if

the nest failed and 1 if the nest was successful. Nests were also considered to have failed if the eggs were infertile or the eggs or chicks were predated.

As a result of the large distances and travel times between southern ground-hornbills nests in the Kruger National Park, it was not possible to calculate daily nest survival rate. We calculated nesting success per group over the entire study period using the following formula: Nesting success is equal to the number of years where the chick survived divided by the number of years where the outcome was known. Years where the outcome was not known were excluded from the analyses. This yielded a proportion between 0 and 1. Models were weighted using the number of years of known outcome.

2.4.5 Data analyses

We conducted all statistical analyses using R (Version 3.2.2; R Core Team 2015). A generalised linear mixed model with a binomial distribution and logit link function was applied using the lme4 package (Bates et al. 2015) for both chick survival and nesting success. In the chick survival models, chick survival was the response variable and Group (defined using the nest name) and Year were included as random effects. For the nesting success models, nesting success was the response variable with Group included as a random effect.

Some of the predictor variables were found to be highly correlated ($r \geq 0.7$) and these were examined separately against the response variables to determine which produced the model with the lowest Akaike Information Criteria (AIC) ranking. Only those variables were kept in the model. Where two correlated variables had the same effect on the model, the variable that was present for the larger number of samples was retained. Similar variables were grouped together and models were compared and selected using AIC rankings.

For southern ground-hornbill chick survival we had four models, a TREATMENT model, looking at the effect that removing the second-hatched chick from the nest had on the

first hatched chick, a NEST model, investigating the influence of characteristics of the nest itself, a LAND model and a WATER model. For nesting success we had three models, a NEST model, a LAND model and a WATER model. Some variables in the LAND and WATER models, were excluded, owing to rank deficiency, as their contribution to the buffer zone area was negligible or only present for a small number of nests. For the NEST models, nest cavity width, breadth, depth and height of cavity entrance were all highly correlated with nest volume ($r \geq 0.7$). Only nest volume and diameter at breast height were included in the NEST models as fixed effects.

All models with significant variables were checked for over dispersion and Drop1 (Bates et al. 2015) was then used to determine the model with the best fit and lowest AIC value. The p values for the final models in each case were then adjusted using False Discovery Rate (FDR) to account for multiple comparisons on a small data set (Pike 2011) using the base package in R (R Core Team 2015). Table 2.1 details the fixed effects that were included in the respective LAND and WATER models for nesting success. Variables included in the LAND and WATER models for chick survival are included in Supplementary Material 1 Table S1.

2.5 Results

2.5.1 Chick survival

We monitored 100 southern ground-hornbill nesting attempts in the Kruger National Park during the study, for which the outcome of the nesting attempt was known. Of these 100 nesting attempts, 76 were successful and 24 failed. Second-hatched chicks were harvested from 32 of these nesting attempts (L. Combrink unpubl. data).

We tested the effect of the removal of the second-hatched chick on the survival to fledging age of the first hatched chick, but found no significant impact of the nest treatment

(Supplementary Material 1). We also modelled chick survival as a factor of the NEST, LAND and WATER variables. We found no significant effects of any of the WATER characteristics (Supplementary Material 1 Table S2). The results for the chick survival LAND model selection are presented in Online Resource 1 Table S3. Chick survival and nesting success were highly correlated and the significant LAND factors influencing chick survival were a subset of those found for overall nesting success (Supplementary Material 1 Table S4). NDVI and Yield (our proxies for food availability), although not significant, were retained in the model as removing them increased the AIC.

2.5.2 Nest site characteristics

Of the 37 southern ground-hornbill tree nests in our study, cavities had a mean length of 48.7 ± 2.0 cm (range 30 - 71 cm), a mean breadth of 43.1 ± 2.6 cm (25 - 102 cm) and a mean depth of 49.3 ± 4.2 cm (11 - 160 cm). All nests were situated in trees with a mean diameter at breast height of 129.6 ± 17.0 cm (64 - 544 cm) and cavities were located at a mean height of 5.6 ± 0.4 m from the ground (3 - 12 m). We modelled both chick survival and group nesting success as a factor of the various nest site parameters, but did not find that any played a significant role [Chick survival: nest volume ($P = 0.993$), DBH ($P = 0.341$); Nest success: nest volume ($P = 0.948$), DBH ($P = 0.179$)].

2.5.3 Nesting success

Nesting success was calculated for 38 southern ground-hornbill nests across the Kruger National Park. None of the variables included in the WATER model showed any significant effect on overall nesting success (Supplementary Material 2 Table S1). The best of the LAND models for nesting success (Tables 2.2 and 2.3) included all four of the major habitat classes (dense thicket, grassland, low shrubland and bare ground), latitude, longitude, percentage of

gabbro soils, distance from the nest to the nearest road and habitat diversity. Although longitude and the low shrubland habitat type did not have significant effects on nesting success, removing them from the model increased the AIC.

Latitude had a significant effect on southern ground-hornbills' nesting success, with nests in the north being less successful than those in the south. An increase in amount of thicket and dense bush, grassland or bare ground surrounding the nest caused nesting success to decrease. Similarly, the greater the percentage of gabbro soils within the buffer zone around each nest, the lower the overall group nesting success. Nests with a higher diversity of habitats within the buffer zone had a higher nesting success than those with more homogenous surrounding habitat. The proximity of nests to roads improved overall nesting success, with more successful nests being situated closer to road networks (Table 2.3).

2.6 Discussion

In this study, we analysed data spanning seven breeding seasons to determine whether nest sites or food availability were the primary resource contributing to southern ground-hornbill reproductive output in the Kruger National Park. Kemp (1988) suggested that nest sites were the most important resource for southern ground-hornbills, with food availability of secondary importance owing to the (a) southern ground-hornbill territory size being greater than the core foraging areas, (2) lone birds were allowed to trespass on territories and (3) that territory size was not influenced by group size. We found that none of the nest site characteristics nor our proxies for food availability (NDVI and Yield) had any effect on southern ground-hornbill reproductive output. Many of the variables that were significant were more related to food availability than to the actual nest site. Our results suggest that these two resources (food and nesting sites) are not mutually exclusive and may be of equal importance to southern ground-hornbill reproductive output. Specifically, our data showed that habitat

structure and diversity are of primary importance to overall nesting success of southern ground-hornbills. Consequently, habitat transformation from more open woodland areas to a dense thicket habitat, such as that associated with bush encroachment, will have a negative impact on southern ground-hornbill reproductive output.

Although none of the nest site characteristics tested were found to influence nesting success, the loss of a southern ground-hornbill nest site within a territory could be detrimental to the group's productivity. Following nest loss or collapse, some groups in Kruger National Park have failed to breed for the remainder of our study period – in one case, for a total of four seasons. As mentioned earlier, without recruitment, the loss of woody species and canopy trees can significantly alter the habitat composition with a potential change in habitat structure through bush encroachment (Smallie & O'Connor 2000; Baxter & Getz 2005). Fire and herbivory (with elephants *Loxodonta africana* in particular) are known to engineer savanna vegetation (Sankaran et al. 2008; O'Connor et al. 2014). With the increasing elephant densities in the Kruger National Park (Young et al. 2009) and the occurrence of frequent fires, many trees will have difficulty establishing (Helm et al. 2001). In order to establish successfully, savanna trees first need to escape the fire trap, where fire removes trees 1 - 3 m in height (Bond & Keeley 2005). Provided they survive this, they then need to escape the elephant trap, as described by Asner and Levick (2012), where elephants remove trees within the 5 - 9 m height class range. The combination of these two influences could result in the homogenisation of African savanna vegetation, which could negatively affect local biodiversity (du Toit *et al.* 2003; Asner & Levick 2012). Add to this the increase in woody biomass related to climate change and the impacts on southern ground-hornbills could be catastrophic.

Nest sites for southern ground-hornbills are thought to be limited in the Kruger National Park (Kemp et al. 1989) owing to a scarcity of suitably-sized cavities. Kemp and Begg (1996) found on average that nest cavities had a median diameter of 40 cm and were found in trees

with a diameter at breast height of at least 40 cm. We found that cavities had a median length of 45 cm and breadth of 40 cm. The median diameter at breast height was 103 cm (average of 129.6 cm), which is more than double that suggested by Kemp and Begg (1996). Our results suggest that southern ground-hornbill are now finding suitably-sized cavities within much older, more established trees. Although only speculative, this could mean that the current fire and elephant management policies (coupled with the effects of bush encroachment related to climate change) are suppressing the recruitment of large trees (diameter at breast height of around 40cm) in the landscape.

Elephant impacts on trees in the Kruger National Park were found to be more pronounced in drier areas (Asner & Levick 2012), which following Kruger National Park's rainfall gradient, would be as one moves northwards (Smit 2011). The combination of these two factors could explain the influence that latitude had on southern ground-hornbill nesting success. We found that the further south the nest site, the more successful the group. Although none of the rainfall variables were significant, an increase in rainfall would lead to an increase in vegetation biomass and thus, could influence prey availability, especially that of insects.

Habitat characteristics influence the foraging traits of birds and these in turn will affect habitat selection and community structure (Robinson & Holmes 1982). In particular food availability is influenced by habitat structure for many avian feeding guilds (Preston 1990; Whittingham & Evans 2004). Southern ground-hornbills require a delicate balance between more open grassy areas for foraging and woodland areas for nesting. Changes in habitat structure surrounding southern ground-hornbill nesting sites negatively impacted nesting success. Specifically, increases in thicket and dense bush, grassland and bare ground had the most influence on nest success rates.

Wilson and Hockey (2013) found southern ground-hornbill nesting success for natural nests to be significantly correlated with the amount of open woodland within 3 km of the nest

site. In our models, open woodland and grassland habitat types were negatively correlated. The grassland habitat type was retained in the model, as removing it increased the AIC. As we found that an increase in grassland has a negative effect on nesting success, we can deduce that an increase in open woodland around the nest will be beneficial. This means that open woodland surrounding the nest site is an important factor to consider for the placement of nest boxes or creation of nest sites for southern ground-hornbills, regardless of the vegetation type in which the nest is located.

Southern ground-hornbills spend around 70% of the day walking (Kemp 1995), and have been known to cover distances of around 7 km in a day (Wilson & Hockey 2013). Knight (1990) showed that southern ground-hornbills favour areas where the grass is less than 50 cm in height. Dense grass was associated with both vegetation types found on Gabbro soils (Venter 1986), which we found would negatively influence nesting success. An increase in grassland, and thicket or dense bush would likely impact southern ground-hornbill foraging efficiency. Not only would prey detection and acquisition be more difficult, but the denser habitat structure could increase the risk of ambush by predators (Butler & Gillings 2004; Wilson & Hockey 2013).

Proximity of the southern ground-hornbill nest to the road could also influence food availability within a territory. Kemp and Begg (1996) found that nests situated within 400 m of a tourist road were more attractive to southern ground-hornbills, they thought possibly as being closer to a road could lower the risk of depredation of the nest. Our data showed that being closer to the road offered a significant benefit to the group's overall nesting success. Road verges are often more vegetated as a result of increased precipitation runoff (Smit & Asner 2012), which could make these good foraging areas. Some southern ground-hornbill groups in the Kruger National Park beg from vehicles, mostly during the winter months (Combrink pers. obs.). In winter, when the abundance of available prey is at its lowest,

southern ground-hornbills are known to concentrate their foraging in areas around sources where prey abundance is higher (Kemp et al. 1989). Thus, a steady food source associated with roads in the winter months, could increase the health and fitness of the alpha pair and thereby, increase their nesting success.

Habitat diversity surrounding the nest site had a positive effect on nesting success, possibly owing to the greater number of niches available to a wider variety of prey items. Southern ground-hornbills consume a range of prey items, such as snakes, lizards, frogs, small mammals and invertebrates (Kemp 1995; L. Combrink unpubl. data). Our proxies for food availability (NDVI and Yield) had no significant effect on southern ground-hornbill nesting success, but they did influence chick survival (although again the results were not significant). We also did not find any aspects of the nest site itself having a significant effect on southern ground-hornbill reproductive output.

All the variables that we found to have a significant influence on nesting success were more related to food availability and the surrounding habitat than characteristics of the particular nest site. Hence, we suggest that food availability is equally important to southern ground-hornbills as the availability of a suitable nest site. Having either sufficient food resources with no suitable nest site, or having a suitable nest cavity with limited food resources would negatively affect southern ground-hornbill reproductive output.

Authorities responsible for vegetation management should take into account the possible influence that management decisions and actions can have on habitat composition and structure and the influence this has on overall biodiversity (Skowno & Bond 2003). The influence of climate change on bush encroachment into grasslands (and the subsequent changes to the structure of savanna vegetation) cannot be actively controlled. However, management authorities can control and even mitigate the influence of frequent fires and elephants. In Kruger National Park, where the elephant population is seemingly on the increase (Young

2009), the potential impact of high densities of elephants on the vegetation structure and subsequent impacts on overall species diversity should not be ignored. Elephant impacts on large trees in African savannas should therefore be monitored and managed where necessary to allow for the establishment of sufficient large trees. Similarly, in areas where southern ground-hornbill nests are located, and in particular, those known to be successful, fires should be managed so as not to damage the large nest trees and alter the habitat structure towards a more homogenous surrounding habitat.

2.7 Conclusions

Annual monitoring of southern ground-hornbill nest sites will allow for the early detection and possible mitigation of bush encroachment or changes in habitat structure surrounding nest sites. In addition, monitoring would detect when nest sites collapse or are no longer suitable. Maintenance of these nest sites and erection of artificial nest boxes, in cases where nests collapse, should be considered as a conservation intervention. Southern ground-hornbills readily take to nest boxes and groups nesting in artificial nests have been shown to have a significantly higher breeding success when compared with groups using natural nest sites (Wilson & Hockey 2013).

Our data also supported the harvesting of second-hatched chicks as a viable conservation initiative, as set out in the southern ground-hornbill National Species Recovery Plan for South Africa (Jordan 2011). Removal of second-hatched chicks from southern ground-hornbill nests was found to have no significant effect on the survival to fledging of the first-hatched chick. We therefore recommend that harvesting of second-hatched chicks from wild southern ground-hornbill nests continues to support the captive rearing and reintroduction programme (Jordan 2011).

Our results showed that habitat structure and diversity are critical when deciding on a suitable reintroduction site for southern ground-hornbills. As nest sites, in the form of artificial nests will most likely be provided, food availability and accessibility should be the primary resource of concern when assessing potential release sites.

Southern ground-hornbills, as with many other large bird species, are considered to be safe within protected areas, with most of the threats to the birds affecting those populations occurring in unprotected areas. We have shown that even within protected areas, without sufficient management interventions to control the drivers of bush encroachment and nest site losses, southern ground-hornbill reproductive output and population status will decline.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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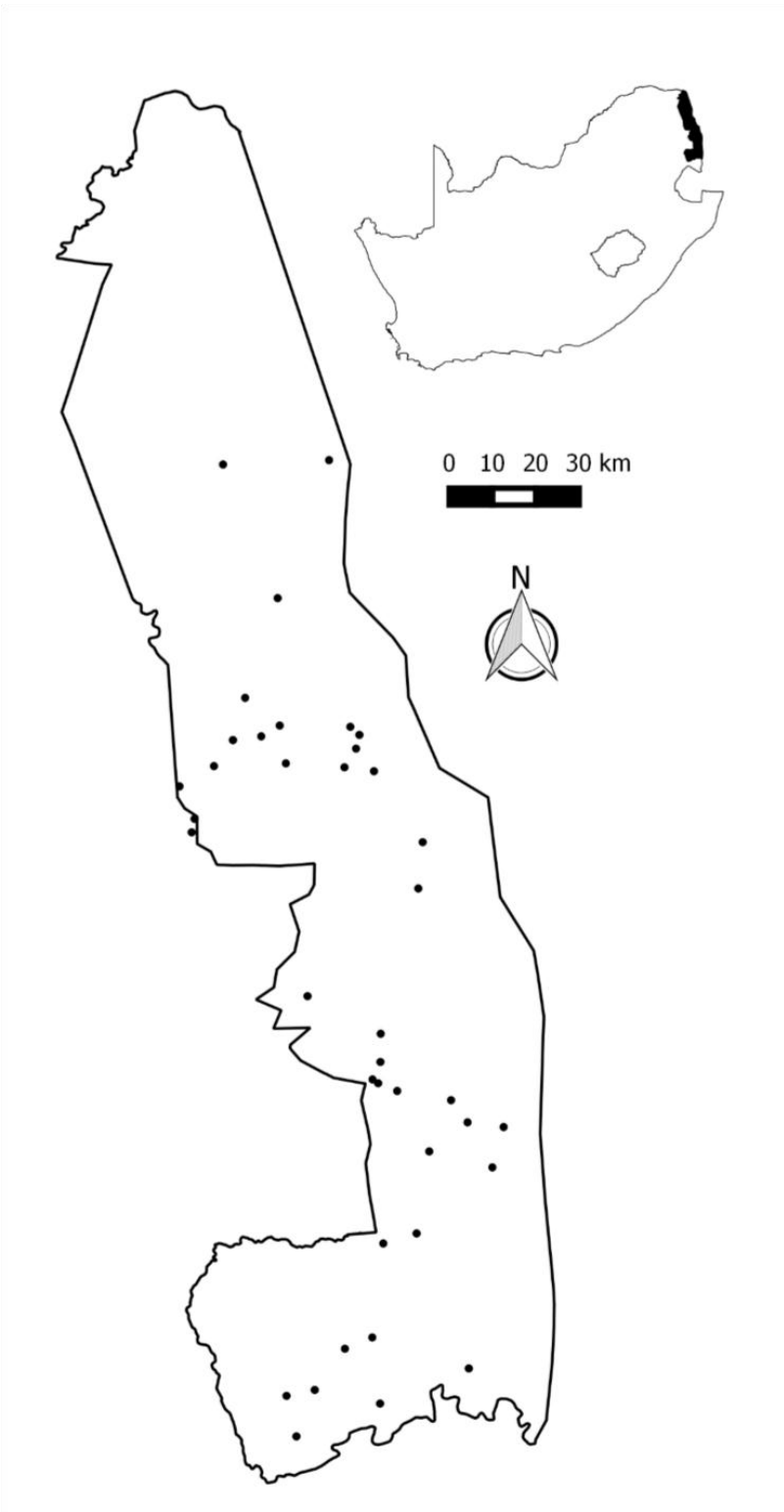


Fig. 2.1 The locations of southern ground-hornbill nesting sites investigated in this study within the Kruger National Park, South Africa.

Table 2.1 Fixed effects included in the southern ground-hornbill nesting success LAND and WATER generalised linear mixed models. An asterisk (*) denotes values obtained only for years where the fate of the nesting attempt was known.

LAND MODEL		Type
	Latitude	continuous
	Longitude	continuous
LAND COVER	Dense thicket (t)	percentage
	Grassland (g)	percentage
	Low shrubland (s)	percentage
	Bare ground (b)	percentage
SOILS	Granite (g)	percentage
	Ecca Shale (e)	percentage
	Gabbro (b)	percentage
ROADS	Length of Tourist Roads (t)	continuous
	Length of Management Roads (m)	continuous
	Distance from nest to nearest road (d)	continuous
	Mean NDVI *	continuous
	Mean Yield (biomass) *	continuous
	Diversity index	continuous
WATER MODEL		
MEAN ANNUAL RAINFALL	450-500 mm	percentage
	500-550 mm	percentage
	550-600 mm	percentage
	600-650 mm	percentage
	650-700 mm	percentage
	700-750 mm	percentage
STREAMS	Length of streams and rivers	continuous
	Distance from nest to nearest stream or river	continuous

Table 2.2 Output of GLMM model selection comparing nest success of southern ground-hornbills. All models included Group as a random effect. The last model with 15 estimable variables is the complete model.

Land Models	K	AIC	ΔAIC	Deviance
Lat + Long + LANDCOVER + SOILb+ Diversity + ROADd	9	144.6	0.0	122.6
Lat + Long + LANDCOVER + Diversity + ROADd	8	146.1	1.5	126.1
Lat + LANDCOVER + SOILb+ Diversity + ROADd	8	146.5	1.9	126.5
Lat + Long + LANDCOVER + SOILb+ Diversity	8	147.9	3.3	127.9
Lat + Long + LANDCOVERtgs + SOILb+ Diversity + ROADd	8	148.7	4.1	128.7
Lat + Long + LANDCOVER + SOIL + ROAD + Diversity + NDVI + Yield	15	154.6	10.0	120.6

Table 2.3 Parameter estimates, standard errors, z values, p values and adjusted p values (using False Discovery Rate) for variables in the best LAND model for southern ground-hornbill nesting success (with the lowest AIC). (Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1)

Variables	Estimate	Std. Error	z value	<i>P</i>	Adjusted <i>P</i> (FDR)	Signf.
Intercept	1.883	0.459	4.100	0.000	0.000	***
Latitude	-2.091	0.722	-2.897	0.004	0.007	**
Longitude	-0.977	0.528	-1.852	0.064	0.064	.
Dense thicket	-2.624	0.653	-4.021	0.000	0.000	***
Grassland	-1.562	0.549	-2.846	0.004	0.007	**
Low shrubland	-2.097	1.071	-1.957	0.050	0.056	.
Bare ground	-1.319	0.462	-2.852	0.004	0.007	**
Gabbro soils	-0.913	0.436	-2.092	0.036	0.046	*
Diversity index	2.663	0.744	3.581	0.000	0.001	**
Distance from nest to nearest road	-0.785	0.352	-2.232	0.026	0.037	*

2.10 Supplementary material 1. Results from analyses of southern ground-hornbill chick survival data

Using data from seven complete breeding seasons of southern ground-hornbill nest monitoring (2008 – 2015), we investigated what habitat and environmental factors affected the survival of the first chick to fledging age. We also examined the effects that harvesting of second-hatched chicks had on the survival to fledging age of the first-hatched chicks.

The southern ground-hornbill National Species Recovery Plan for South Africa (Jordan 2011) highlighted the use of captive-reared birds and reintroductions as conservation interventions for this species. Harvesting of these redundant second-hatched chicks from wild nests can provide a population for future reintroductions. Studies have shown that disturbances at the nest can impact bird nesting success (Poole 1981; Gibson *et al.* 2015). We tested whether removal of the second-hatched southern ground-hornbill chick had any significant impact on the survival to fledging of the first-hatched chick.

Methods

We conducted all statistical analyses in the program R (Version 3.2.2; R Core Team 2015). A generalised linear mixed model with a binomial distribution and logit link function was applied using the R package lme4 (Bates *et al.* 2015). For chick survival, we had four models, a TREATMENT model, a NEST model, a LAND model and a WATER model. The NEST model data are included in the main paper and not presented here. All models included Group and Year as random effects. The TREATMENT model compared the effect that harvesting of the second-hatched chick had on the survival of the first hatched chick to fledging age. Parameters included in the LAND and WATER models are presented in Table S1.

Results

The TREATMENT model comparing southern ground-hornbill chick survival between nests where harvesting was conducted with control nests, showed no significance (Estimate 0.8538, std. error 0.7704, z 1.108, P 0.2677). Although not significant, the log odds of the first hatched chick surviving to fledging age when harvesting is conducted were 83% and when the nests were only monitored, the log odds of the first hatched chick surviving to fledging age were 92%. This indicated that removing the second-hatched chick had no significant effect on the survival to fledging age of the first-hatched chick, although there does seem to be some benefit to the first hatched chick when the second hatched chick is removed. These data support the continuation of the harvesting scheme, where second-hatched chicks are removed from wild nests for captive rearing and reintroduction. We recommend continued southern ground-hornbill nest monitoring, and where necessary, modification of nests or the erection of nest boxes to support groups previously known to be successful.

For the WATER model, none of the variables showed any significance at the 0.05 level (Table S2.). The best LAND model (Table S3 and S4) showed that latitude, the amount of dense thicket and the habitat diversity had a significant effect on southern ground-hornbill chick survival. According to our results, as one moves further north, southern ground-hornbill chick survival decreased. Increases in the amount of dense thicket habitat had a negative influence on southern ground-hornbill chick survival to fledging age, whereas an increase in habitat diversity was positively correlated with southern ground-hornbill chick survival.

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Table S1.1 Fixed effects included in the southern ground-hornbill chick survival LAND and

WATER models

LAND MODEL		Type
	Latitude	continuous
	Longitude	continuous
LAND COVER	Dense thicket	percentage
	Grassland	percentage
	Low shrubland	percentage
	Bare ground	percentage
SOILS	Granite	percentage
	Ecca Shale	percentage
	Gabbro	percentage
ROADS	Length of Tourist Roads	continuous
	Length of Management Roads	continuous
	Distance from nest to nearest road	continuous
	Mean NDVI for current season	continuous
	Mean Yield (biomass) for current season	continuous
	Diversity index	continuous
WATER MODEL		
RAIN	Rainfall Previous breeding season	continuous
	Rainfall Previous non-breeding season	continuous
	Rainfall Current breeding season	continuous
MEAN ANNUAL RAINFALL	450-500 mm	percentage
	500-550 mm	percentage
	550-600 mm	percentage
	600-650 mm	percentage
	650-700 mm	percentage
	700-750 mm	percentage
STREAMS	Length of streams and rivers	continuous
	Distance from nest to nearest stream or river	continuous

Table S1.2 Parameter estimates, standard errors and p values for variables in the best WATER model (with the lowest AIC) for southern ground-hornbill chick survival.

WATER MODEL (n=100)	Estimate	Std. Error	z value	<i>P</i>
Intercept	4.904	8.243	0.595	0.552
Previous breeding season rainfall	0.544	0.476	1.143	0.253
Previous non-breeding season rainfall	0.560	0.445	1.259	0.208
Current breeding season rainfall	-0.492	0.476	-1.034	0.301
Ann. Rainfall 450-500mm	1.407	1.216	1.158	0.247
Ann. Rainfall 500-550mm	1.490	1.169	1.274	0.202
Ann. Rainfall 550-600mm	1.066	1.066	0.999	0.318
Ann. Rainfall 600-650mm	1.312	0.997	1.315	0.188
Ann. Rainfall 650-700mm	15.078	36.797	0.41	0.682
Distance from nest to the nearest stream	0.082	0.465	0.176	0.861
Length of all rivers and streams in buffer zone	0.507	0.505	1.006	0.315

Table S1.3 Output of LAND GLMM model selection comparing chick survival of southern ground-hornbills. Group and Year were included as random effects. The top five models are included with the last model (with 15 variables) being the complete model. Where not all variables are included in a group, these are specified e.g. LANDCOVERtgs is for dense thicket, grassland and low shrubland. LANDCOVER with no specifications will include all four variables.

LAND Model	K	AIC	ΔAIC	Deviance
Lat + Long + LANDCOVER + Diversity + NDVI + Yield	9	97.9	0.0	73.9
Lat + Long + LANDCOVER + Diversity + Yield	8	98.3	0.4	76.3
Lat + Long + LANDCOVER + Diversity + NDVI	8	99.4	1.5	77.4
Lat + Long + LANDCOVERtgs + Diversity + NDVI + Yield	8	100.1	2.2	78.1
Lat + LANDCOVER + Diversity + NDVI + Yield	8	100.1	2.2	78.1
Lat + Long + LANDCOVER + SOIL + ROAD + Diversity + NDVI + Yield	15	106.0	8.1	70.0

Table S1.4 Parameter estimates, standard errors and p values for variables in the best LAND model (with the lowest AIC) for southern ground-hornbill chick survival. (Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1)

LAND (n = 100)	Estimate	Std. Error	z value	<i>P</i>	Adjusted <i>P</i> (FDR)	Signf.
Intercept	1.889	0.446	4.237	0.000	0.000	***
Latitude	-2.069	0.779	-2.656	0.008	0.020	**
Longitude	-1.060	0.556	-1.908	0.056	0.070	.
Dense thicket	-1.693	0.520	-3.254	0.001	0.006	**
Grassland	-0.977	0.453	-2.155	0.031	0.057	.
Low shrubland	-1.193	0.644	-1.854	0.064	0.071	.
Bare ground	-0.660	0.320	-2.06	0.039	0.057	.
Diversity index	1.702	0.564	3.018	0.003	0.009	**
Mean NDVI	-0.931	0.539	-1.726	0.084	0.084	.
Mean Yield	0.946	0.460	2.055	0.040	0.057	.

2.11 Supplementary material 2. Results of the water variables on southern ground-hornbill nesting success

Table S2.1 Parameter estimates, standard errors, z values, p values and adjusted p values (using False Discovery Rate) for variables in the best WATER model for southern ground-hornbill nesting success (with the lowest AIC).

Variables	Estimate	Std. Error	z value	<i>P</i>
Intercept	9.608	19.514	0.492	0.622
Ann. Rainfall 450-500mm	2.166	1.590	1.362	0.173
Ann. Rainfall 500-550mm	1.868	1.508	1.239	0.215
Ann. Rainfall 550-600mm	2.046	1.524	1.342	0.18
Ann. Rainfall 600-650mm	1.875	1.424	1.316	0.188
Ann. Rainfall 650-700mm	26.402	66.924	0.394	0.693
Length of all rivers and streams in buffer zone	0.798	0.825	0.967	0.334
Distance from nest to the nearest stream	-0.103	0.802	-0.128	0.898

Chapter 3: Nest Temperature Fluctuations in a Cavity-Nester, the Southern Ground-hornbill

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3.1 Abstract

Southern ground-hornbills *Bucorvus leadbeateri* inhabit savanna and bushveld regions of South Africa. They nest in the austral summer which coincides with the wet season and hottest daytime temperatures in the region. They are secondary cavity nesters and typically nest in large cavities in trees, cliffs and earth banks, but readily use artificial nest boxes. Southern ground-hornbills are listed as *Endangered* in South Africa, with reintroductions into suitable areas highlighted as a viable conservation intervention for the species. Nest microclimate, and the possible implications this may have for the breeding biology of southern ground-hornbills, have never been investigated. We used temperature dataloggers to record nest cavity temperature and ambient temperature for one artificial and 11 natural southern ground-hornbill tree cavity nests combined, spanning two breeding seasons. Mean hourly nest temperature, as well as mean minimum and mean maximum nest temperature, differed significantly between southern ground-hornbill nests in both breeding seasons. Mean nest temperature also differed significantly from mean ambient temperature for both seasons. Natural nest cavities provided a buffer against the ambient temperature fluctuations. The artificial nest provided little insulation against temperature extremes, being warmer and cooler than the maximum and minimum local ambient temperatures, respectively. Nest cavity temperature was not found to have an influence on the breeding success of the southern ground-hornbill groups investigated in this study. These results have potentially important implications for southern ground-hornbill conservation and artificial nest design, as they suggest that the birds can tolerate greater nest cavity temperature extremes than previously thought.

Keywords: cavity nester, temperature fluctuation, nest temperature, hornbill, conservation

3.2 Introduction

The choice of a nest site can have a profound influence on energy expenditure during incubation, which in turn, can affect overall breeding success (D'Alba et al., 2009; Heenan, 2013; Hilton et al., 2004; Reid et al., 2000). Birds that do not construct their own nests, such as secondary cavity nesters, are often limited by the availability of suitable nesting sites (Cockle et al., 2010; Newton, 1994). When suitable nests are limiting, stronger or fitter individuals will often occupy the best nests enhancing their reproductive output (Robertson and Rendell, 1990).

During incubation, birds need to partition their energy resources to conserve body condition for future reproduction, as well as ensure that sufficient energy is allocated to the current breeding attempt (Heenan, 2013; Reid et al., 2000). Egg temperatures should be kept fairly constant to ensure optimal growth during incubation (DuRant et al., 2013; Hart et al., 2016; Kim and Monaghan, 2006). Tropical birds tend to expend less energy keeping their eggs at suitable temperatures owing to the prevailing climatic conditions (Hart et al., 2016). Even so, the amount of exposure to the elements that a nest receives could also influence breeding success (Hart et al., 2016).

An ideal nest site is one that offers shelter from direct sunlight and wind, and that provides some measure of insulation (DuRant et al., 2013). Cavity-nesters are somewhat buffered from the elements in this respect (Cooper, 1999; Martin and Ghalambor, 1999) and much work has been done studying the microclimates of, in particular, tree cavities used for nesting (Maziarz et al., 2017; Wiebe, 2001; Hooge et al., 1999), roosting (Cooper, 1999) and hibernating (Coombs et al., 2010).

In birds, nest microclimate or thermal environment has been shown to affect clutch size (Wiebe, 2001) and breeding success (Deeming et al., 2012; Kim and Monaghan, 2006; Reid et al., 2000). Nest construction and location can have a profound effect on nest microclimates (DuRant et al., 2013; Wiebe, 2001), with nest insulation thought to be a critical feature of nest

construction in many bird species (Deeming et al., 2012). Differences in insulation between natural cavity nests and artificial nest boxes are poorly documented, despite the role that this may play in nest site selection by birds (Maziarz et al., 2017). Most studies have shown that nest boxes are less insulated than natural tree cavities and, owing to their uniform design, would thereby provide limited variation in the quality of nest sites available for secondary cavity nesters (Maziarz et al., 2017). Ellis (2016) showed that nest boxes had similar microclimates irrespective of the size and shape of the design and suggested that placement and construction material of the nest box were far more important factors in determining nest microclimate. The quality of a particular nest site (Wiebe, 2001) and factors like climate change (Matthysen et al., 2011) would directly affect the nest microclimate and could influence incubation temperatures. This could then increase the selective pressures exerted on incubating adults to maintain optimal nest thermal conditions (DuRant et al., 2013).

Finding a suitable nest site to optimise incubation conditions can be especially challenging for large secondary cavity nesting birds that are territorial, such as the southern ground-hornbill *Bucorvus leadbeateri*. Southern ground-hornbills breed during the austral summer, from October to March each year, which coincides with the first annual rains in the South African Lowveld (Kemp, 1995). They typically nest in tree cavities, rock crevices and earth banks, but take readily to artificial nesting sites. The species has suffered a significant decline in South Africa owing mainly to habitat loss and persecution (A.C. Kemp and R. Webster, unpubl. data) and is listed nationally as *Endangered* (Taylor et al., 2015) and globally as *Vulnerable* (IUCN, 2016). A National Species Recovery Plan was developed in an effort to curtail this decline, with reintroductions of the birds into suitable habitat being listed as one of the primary conservation goals for South Africa (Jordan, 2011). The erection of artificial nests at these sites will increase the availability of suitably-sized nest sites. It is paramount that these

artificial nests offer the best conditions for nesting to ensure the persistence and long-term survival of the birds, as well as to optimise their breeding success at reintroduction sites.

We investigated the thermal fluctuations of southern ground-hornbill nest cavities during the breeding season to determine the current range of temperatures experienced by these birds. We predicted that their cavity nests would have more stable temperatures than the associated diel ambient temperatures. We also related their nesting success to cavity nest and ambient temperature maximums and minimums to see if these had any effect on overall reproductive output. We predicted that their nests in anthropogenic structures would have higher temperatures and experience greater extremes of temperatures than natural cavity nests in hollows of trees.

3.3 Methods

3.3.1 Study area

We conducted the study in Kruger National Park and associated conservation areas, South Africa (22-26°S, 30-32°E) in an area known as the South African Lowveld. The area is diverse, but has an average annual rainfall of 350-750 mm (Gertenbach, 1980), and consists mainly of savanna, with pockets of dense woody vegetation within broader grasslands (Gertenbach, 1983).

3.3.2 Nest temperatures

We recorded southern ground-hornbill nest temperatures and associated ambient temperatures during two breeding seasons (2013-2014, 2014-2015) with calibrated data logger i-Buttons® (Model DS 1922L \pm 0.06°C, Dallas Semiconductor, Sunnyvale, CA) in natural nests in Kruger National Park and one artificial nest in an associated conservation area (Fig.

3.1). All i-Buttons® were calibrated with mercury thermometers (0.05°C) in a water bath at temperatures from 5 to 45°C. i-Buttons® were programmed to take a temperature reading every 15 min.

For nest cavity temperatures, i-Buttons® were secured on the inside wall of the nest cavities, just underneath the layer of nesting material, with epoxy glue. Suitable locations outside the nest cavity, but out of direct sunlight, were sought to secure i-Buttons® (again with epoxy glue) to record ambient temperature. Initially, nine natural southern ground-hornbill nests were selected, but owing to the loss of i-Buttons® during the 2013-2014 breeding season, nest and ambient temperature data were only collected from six natural nest sites. In the 2014-2015 breeding season, we were again unable to recover all of the i-Buttons® and nest temperature data were only collected for four natural southern ground-hornbill nests, with ambient temperature data only collected from three natural nests. There was only one artificial nest available within the study area. i-Buttons® were deployed at the artificial nest site to record both ambient and nest cavity temperature in both the 2013-2014 and 2014-2015 breeding season. Although a total of 20 i-Buttons® were deployed throughout this study, only 10 were recovered (many only as a result of using a metal detector) owing to the birds discovering them and actively pecking them off from the nests cavity walls. Nest activity and success for each breeding season were also recorded.

3.3.3 Statistical analyses

Initially, we calculated hourly mean temperatures for each day in each month. We then determined the daily minimum and maximum hourly mean nest temperature for each month. We performed Analysis of Variance (ANOVA) and Repeated Measures Analysis of Variance (RMANOVA) to determine whether there was a significant difference in southern ground-hornbill nest temperatures. Data from both active and inactive nests for the 2013-2014

breeding season were pooled for the RMANOVA analyses, as Post-hoc Scheffe tests showed that this was not a dividing factor. We used Tukey Post-hoc tests to determine among which sites significant differences in temperatures occurred. The above statistics were performed using the Statistica 7 package (Statsoft Inc., Tulsa, OK, USA). All graphs were plotted using the ggplot2 (Wickham, 2009) and cowplot (Wilke, 2016) packages in R (Version 3.2.2; R Core Team, 2015).

A generalised linear mixed model with a binomial distribution and logit link function was applied using the R lme4 package (Bates et al., 2015) to determine if either nest or ambient minimum and maximum temperatures had any effect on nesting success. Nest success was the response variable and Nest and Year were included as random effects. A nest was considered successful if the nestling reached ringing age (60 - 70 days).

3.4 Results

3.4.1 Nest characteristics and success

The measurements and characteristics of the various southern ground-hornbill cavity nest sites are included in Table 3.1, with data on the activity and success of each nesting attempt presented in Table 3.2. None of the nest characteristics were shown to have an effect on nesting success for southern ground-hornbills in the Kruger National Park (Combrink, unpubl. data). We tested the effect of maximum and minimum cavity nest and ambient temperatures on nest success and found no significant impact [Nest success: nest maximum temperature ($P = 0.311$), nest minimum temperature ($P = 0.168$), ambient maximum temperature ($P = 0.267$), ambient minimum temperature ($P = 0.250$)].

3.4.2 Nest temperatures

The mean hourly temperature showed that most southern ground-hornbill cavity nest temperatures fluctuated daily (Fig. 3.2) with the artificial nest (PMC) showing the greatest fluctuation. The temperature ranges recorded for both ambient and nest cavity temperatures are presented in Table 3.3. The mean hourly nest temperature differed significantly between the southern ground-hornbill nests across both seasons (2013 – 2014: $F_{(6, 468)} = 53.879$; 2014 – 2015: $F_{(4, 324)} = 35.25$, $P < 0.05$). In addition, mean hourly nest temperature differed significantly from mean hourly ambient temperature for both seasons (Figs. 3.3a, 3.4a), with ambient temperature being below nest temperature for all nests excepting Mpfuleni in the 2013-2014 breeding season.

Similarly, mean minimum and maximum cavity nest temperatures of southern ground-hornbills differed significantly between the nests for both seasons (Figs. 3.3b, 4b). The artificial nest maximum was significantly warmer than nest minimum temperature in both breeding seasons (Post-hoc Scheffe, $p < 0.05$). Maximum cavity nest temperatures of southern ground-hornbill nests differed significantly to maximum ambient temperatures for both breeding seasons (Figs. 3.3c, 3.4c). Ambient maximum temperature was higher than the nest maximum temperature for all nests excluding Mudzadzene nest (2014-2015 season), where the temperatures were almost equal, and the artificial nest (both seasons). The artificial nest maximum temperature was significantly higher than the maximum ambient temperature in both breeding seasons (Post-hoc Scheffe, $p < 0.05$). Similarly, minimum nest temperatures of southern ground-hornbill nests differed significantly to minimum ambient temperatures for both breeding seasons (Figs. 3.3d, 3.4d). Generally, the nest minimum temperatures were warmer than the minimum ambient temperatures for all nests in both breeding seasons, with the exception of the artificial nest.

3.5 Discussion

Changes in local environmental conditions, in particular temperature, have been shown to affect birds in terms of the timing of egg laying (Both et al., 2004), timing of migration (Crick, 2004), nestling condition (Perez et al., 2008), and nest survival (Guerena et al., 2016). In savannas, the increase in ambient temperature as a result of increased CO₂ concentrations, could incur significant vegetation changes (Buitenwerf et al., 2012) which could severely affect bird reproductive output. Southern ground-hornbills time their breeding to coincide with the first seasonal rainfall (Kemp and Kemp, 1991), which in the South African Lowveld occurs in late spring and early summer. Rainfall, is considered an influential factor in the breeding biology of southern ground-hornbills, as nesting only starts once the first rains of the wet season have fallen (Kemp and Kemp, 1991). This is most likely in response to the increased abundance of their typical prey (Kemp and Kemp, 1991). However, this also coincides with increased temperature during the daytime.

Climate change is expected to cause an overall increase in temperature and greater extremes in wet and dry seasons, as well as fluctuations in extreme temperatures (Thuiller et al., 2008). Our results showed a high plasticity and range in southern ground-hornbill cavity nest temperatures with some nests having stable nest temperatures both day and night, others decreased nest temperature at night, whereas others showed increased nest temperatures at night. This was interesting as we expected nest cavity temperatures to be more stable than ambient temperatures. We did, however, find that tree cavities provided a buffer against the maximum and minimum ambient temperatures for southern ground-hornbills in the South African Lowveld, although the mean hourly cavity nest temperatures were generally warmer than the mean hourly ambient temperatures.

When comparing the ambient maximum and ambient minimum temperatures to the nest maximum and minimum temperatures, the buffering effect of the natural tree cavities against

the heat and cold for southern ground-hornbills during incubation is evident. For the Mudzadzene nest in the 2014-2015 breeding season, the ambient and nest maximum and minimum temperatures were similar. This is the only natural nest in our study that is located in a dead snag, without a canopy. Not having adequate shade during the hottest part of the day or a canopy for cover at night could have affected the nest temperatures. The artificial nest was the only nest where the nest maximum was significantly higher than the ambient maximum across both breeding seasons. Similarly, there was a marked difference between the nest minimum and ambient minimum temperatures for the artificial nest across both seasons, with the artificial nest minimum being lower than ambient minimum. For the natural tree cavities, the nest minimum temperatures were higher than ambient minimum temperatures in both seasons.

Our results showed that the artificial nest, constructed from a 52 gallon plastic drum, provided little insulation against the extreme temperature fluctuations, day and night, experienced in the South African Lowveld. This nest was erected on privately-owned land by the land managers, as part of an experiment to see whether southern ground-hornbills would nest there. Surprisingly, this was one of the most consistently successful nests (based on number of seasons where nestlings reached ringing age) out of the 30-40 southern ground-hornbill nests that have been monitored in this region over the past seven years. Nest cavity temperature maximums in the artificial nest (PMC) were 14.5 °C and 8°C higher than ambient temperature maximums for the 2013-2014 and 2014-2015 breeding seasons, respectively. These temperatures, however, were not the highest recorded nest cavity temperatures in the 2013-2014 breeding season, with two natural nests (Hlahlene (failed) and Nwaswitsontso (inactive)) reaching maximums above 56 °C. These results are encouraging, as they suggest that southern ground-hornbills can breed successfully at extreme temperatures.

Many areas that would previously have supported southern ground-hornbills have been found unsuitable (Cilliers et al., 2013), limiting the potential range expansion of the species outside of protected areas. In an effort to enhance breeding, the use of artificial nest boxes for southern ground-hornbills has been implemented within areas of the Lowveld with great success (Wilson and Hockey, 2013). Much time and effort has been spent on determining the best design for a southern ground-hornbill artificial nest box to promote successful breeding. A workshop held in 2013 listed 10 points to consider when designing artificial nest boxes for southern ground-hornbills (Kemp et al., 2013, unpublished workshop report). The dimensions of the cavity, entrance perches, roof structure and the attachment point were included, although the actual material used to construct the nest was not listed as a priority consideration (Kemp et al., 2013, unpublished workshop report).

Although we only had one artificial nest site within our study area, our results suggest that groups will choose to use a sub-optimal nest in terms of ideal microclimate, if there is no suitable alternative nest within their territory. As a result of the fact that the group was able to nest successfully in these sub-optimal conditions, the dimensions of the nest cavity seem to be a more important factor than the construction material used for the nest for southern ground-hornbills. We would, however, still recommend constructing artificial nests out of natural materials, where possible, purely for the comfort of the birds and to better mimic the conditions (in particular the buffering effect) shown in natural tree cavities. Further research should investigate the effect of different nest box construction materials on nest microclimate towards providing southern ground-hornbills with high quality artificial nest sites at reintroduction sites.

3.6 Acknowledgements

We thank the Ford Wildlife Foundation and the First Rand Foundation for providing financial support for our research. This work was part of a registered research project with SANParks (POTT988) that was approved by the relevant animal ethics committee. We thank SANParks for allowing access to the Kruger National Park and providing various GIS layers.

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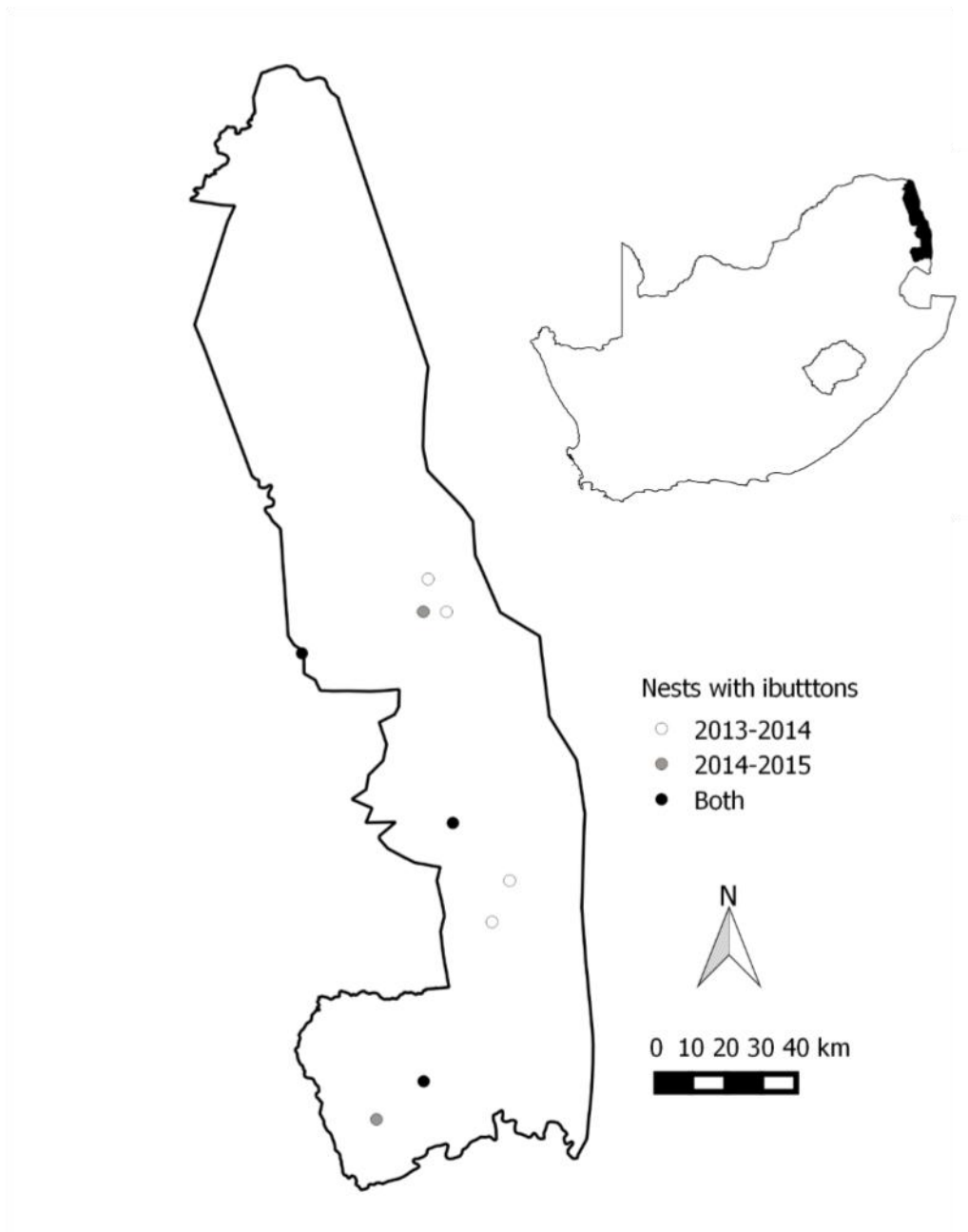
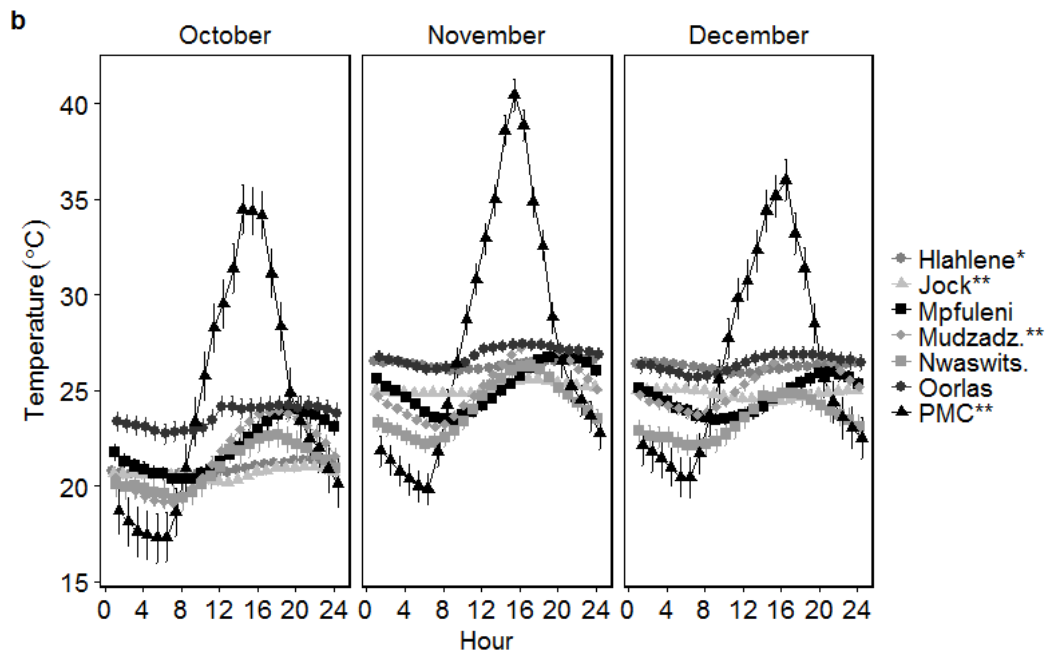
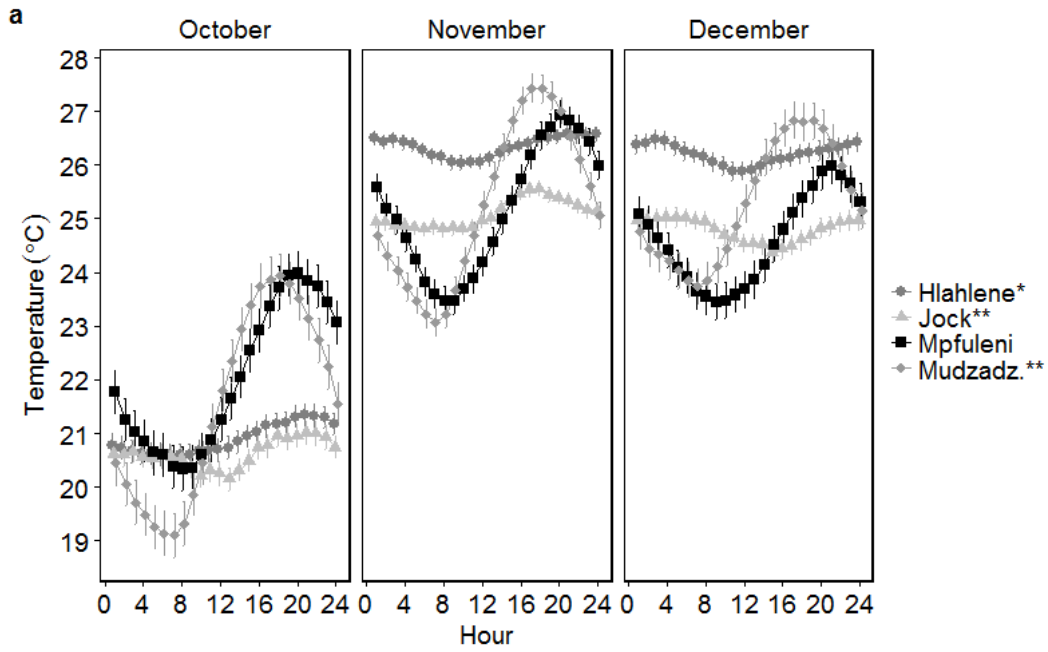


Fig. 3.1 The locations of southern ground-hornbill nest sites sampled within the Kruger National Park and associated conservation areas, South Africa.



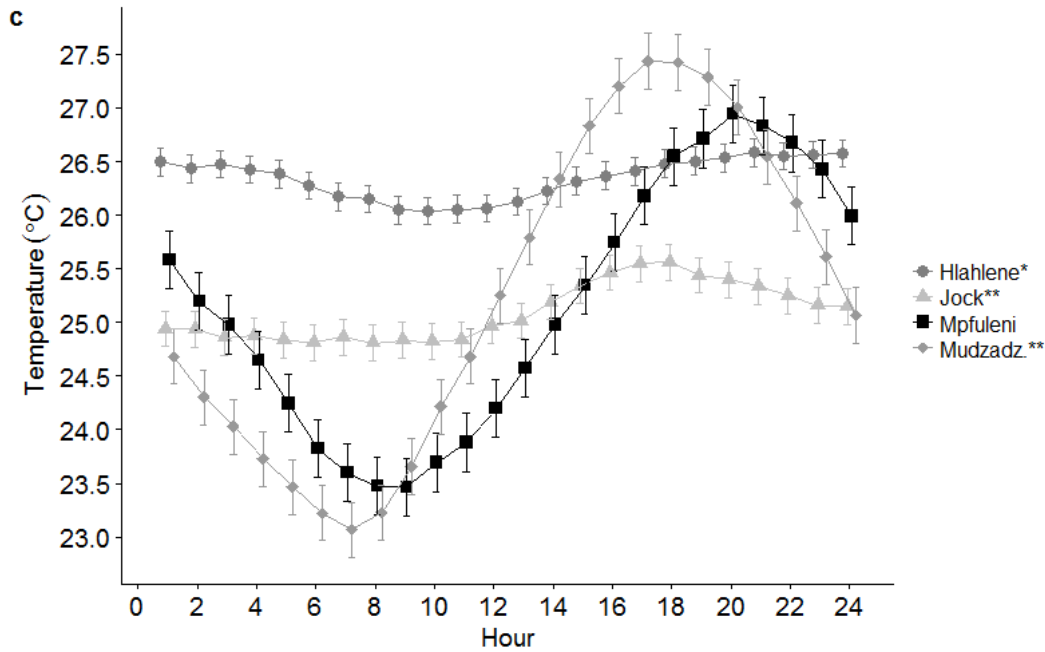
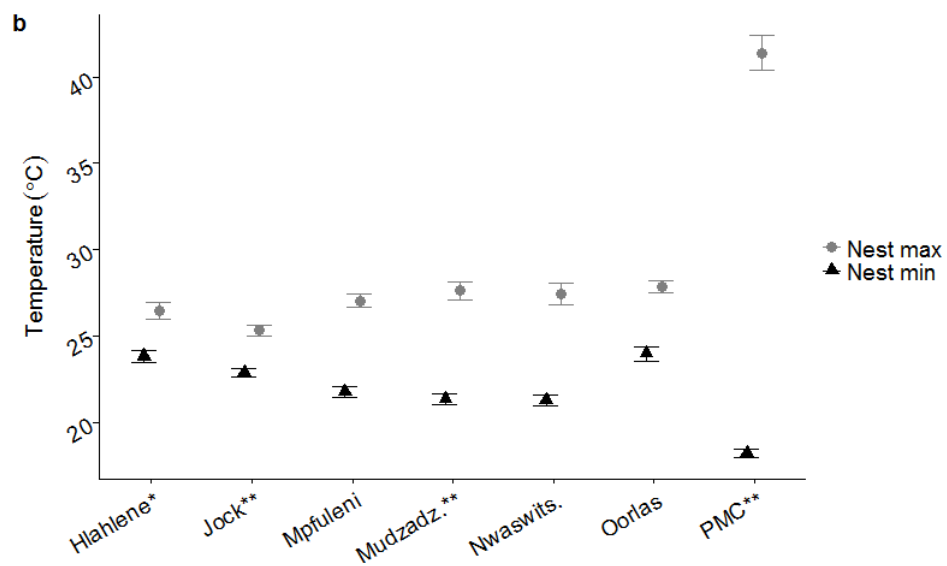
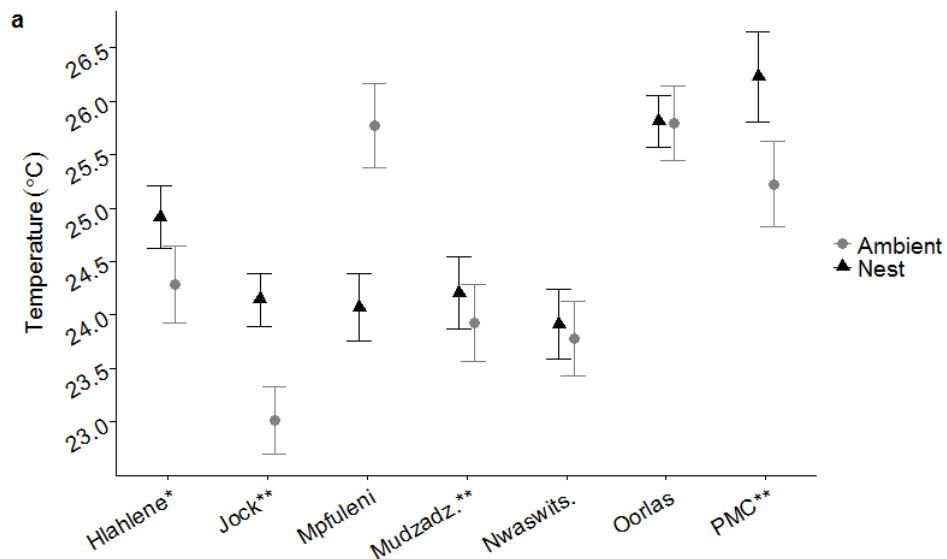


Fig. 3.2 Mean (\pm SE) hourly nest temperature of a range of southern ground-hornbills nest cavities in the Kruger National Park and associated conservation areas, South Africa, in the 2013-2014 breeding season where a. shows the fluctuations in some natural cavities, b. shows all the nests including the artificial one (PMC) for the duration of study period in the breeding season ($F_{(6,468)} = 53.879$, $p < 0.05$), and c. the mean hourly fluctuations for some of the nests during December 2013 in the breeding season. (Note: * indicates an active but unsuccessful nest, ** is an active and successful nest, no markings indicate inactive nests).



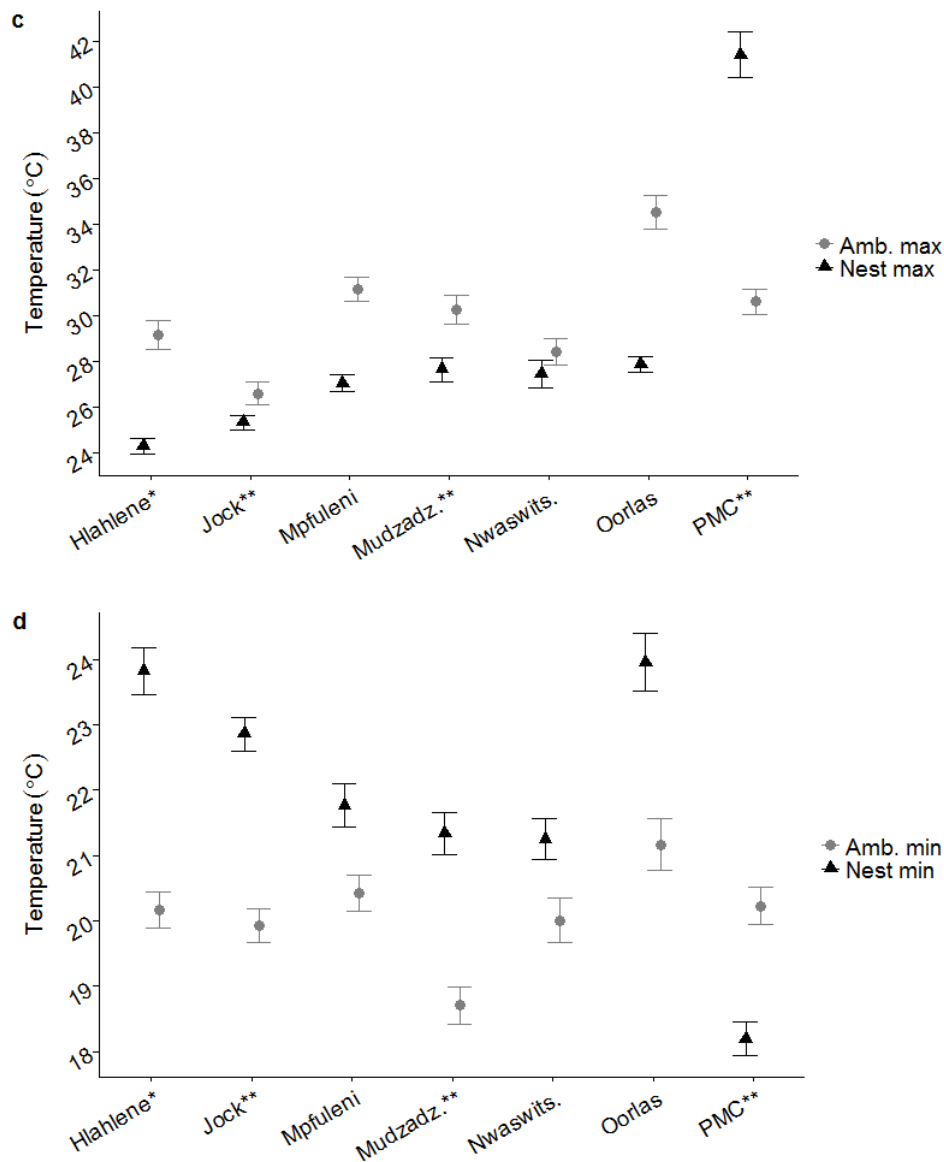
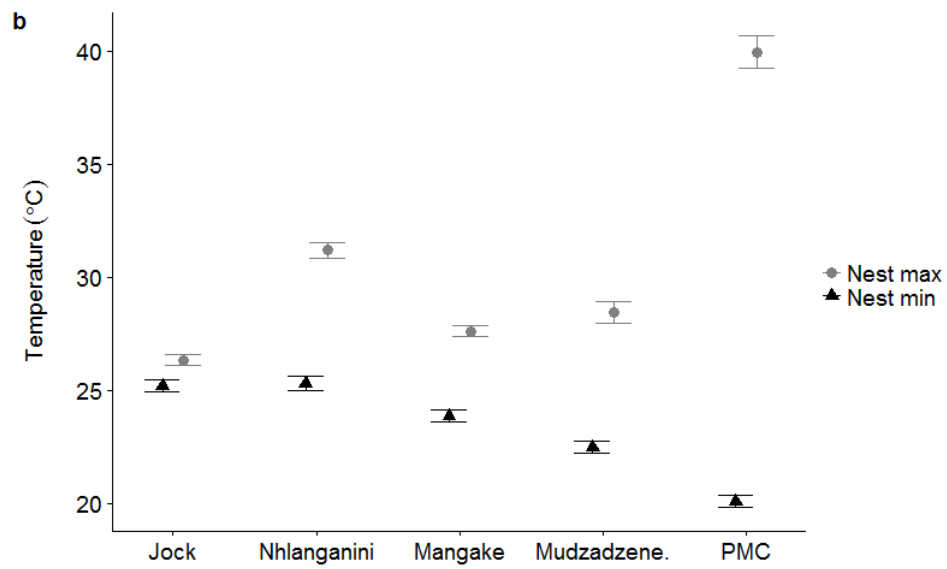
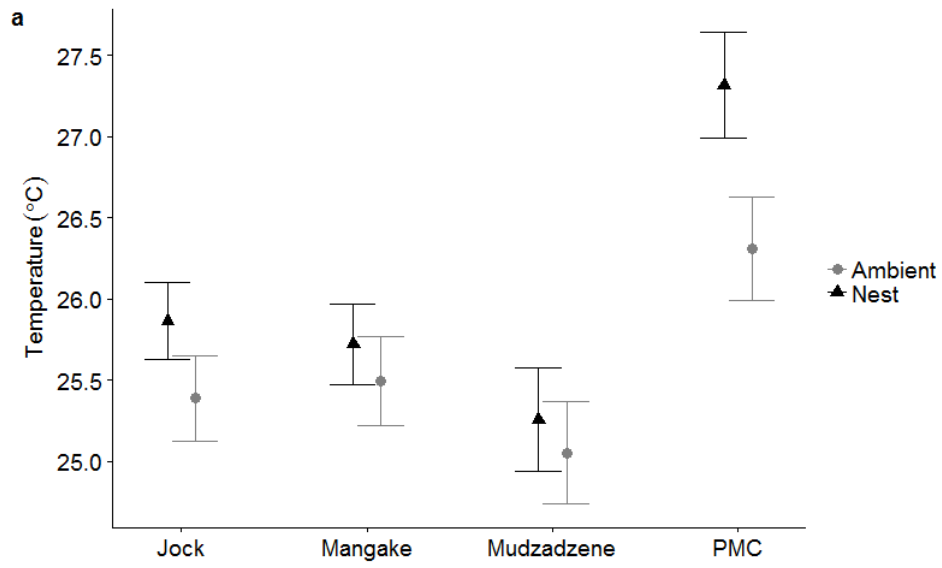


Fig. 3.3 Comparison of southern ground-hornbill nest temperatures in the 2013-2014 breeding season where a. is mean hourly temperature of each nest versus mean hourly ambient temperature for each nest ($F_{(6,468)} = 53.879$, $p < 0.05$), b. is mean minimum temperature versus mean maximum temperature of each nest ($F_{(6,468)} = 223.11$, $p < 0.05$), c. is nest maximum temperature versus ambient maximum temperature for each nest ($F_{(6,468)} = 199.02$, $p < 0.05$), and d. is nest minimum temperature versus ambient minimum temperature for each nest ($F_{(6,468)} = 173.93$, $p < 0.05$). (Note: All values are mean \pm SE. * indicates an active but unsuccessful nest, ** is an active and successful nest, no markings indicate inactive nests).



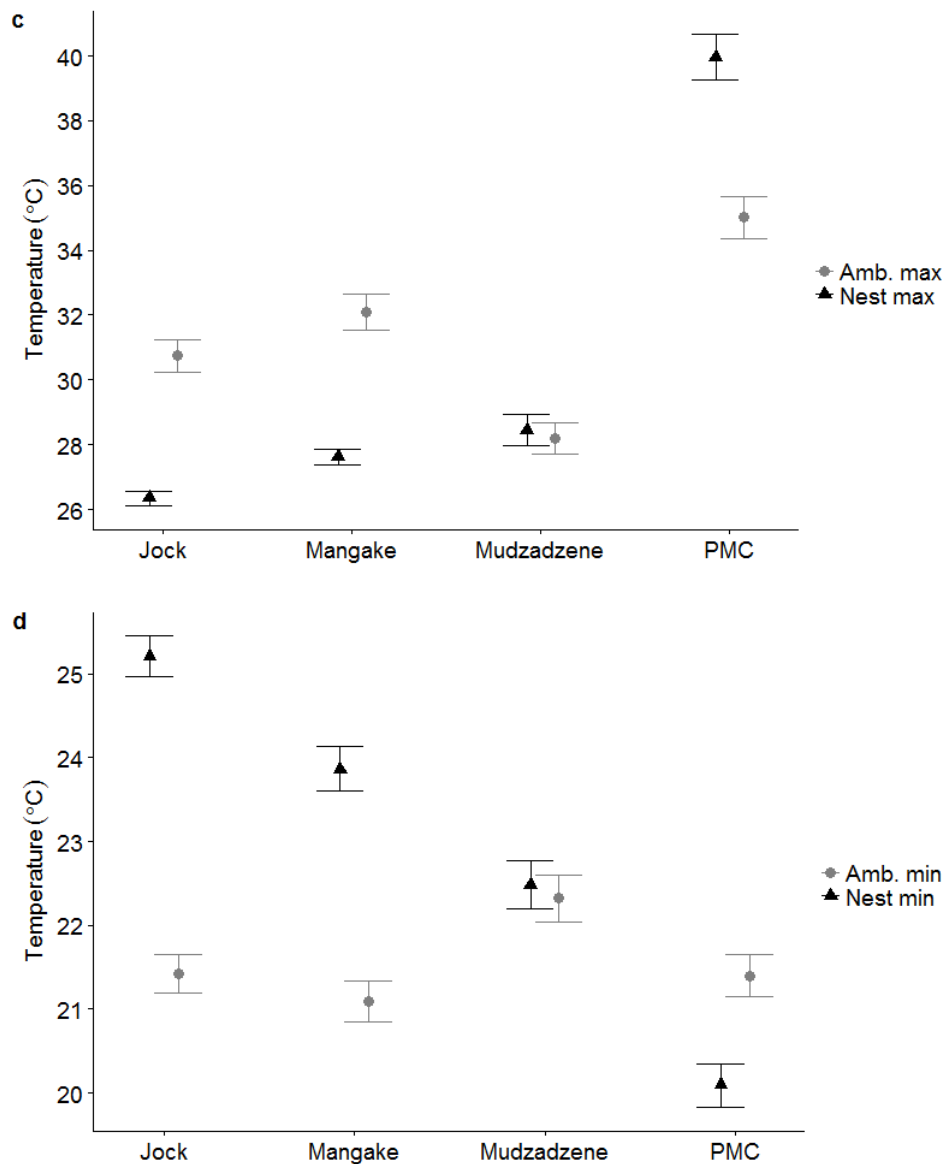


Fig. 3.4 Comparison of southern ground-hornbill nest temperatures in the 2014-2015 breeding season where a. is mean hourly temperature of each nest versus mean hourly ambient temperature for each nest ($F_{(3,255)} = 8.352$, $p < 0.05$), b. is mean minimum temperature versus mean maximum temperature of each nest ($F_{(3,255)} = 365.62$, $p < 0.05$), c. is nest maximum temperature versus ambient maximum temperature for each nest ($F_{(3,255)} = 186.22$, $p < 0.05$), and d. is nest minimum temperature versus ambient minimum temperature for each nest ($F_{(3,255)} = 448.40$, $p < 0.05$). (Note: All values are mean \pm SE. All nests measured in the 2014-2015 breeding season were active and successful).

Table 3.1 Characteristics of the southern ground-hornbill nests used in this study

Nest	Tree measurements		Nest cavity measurements		
	Tree species	Diameter at Breast Height (cm)	Diameter base (l) (cm)	Diameter base (b) (cm)	Depth (lip to base) (cm)
Hlahlene	<i>Diospyros mespiliformis</i>	127	42	53	65
Jock	<i>Diospyros mespiliformis</i>	151	60	35	36
Mangake	<i>Diospyros mespiliformis</i>	65	55	40	40
Mpfuleni	<i>Ficus sycomorus</i>	127	35	45	50
Mudzadzene	<i>Combretum imberbe</i>	83	55	49	79
Nhlanganini	<i>Philenoptera violacea</i>	95	37	45	38
Nwaswitsontso	<i>Diospyros mespiliformis</i>	141	66	28	29
Oorlas	<i>Philenoptera violacea</i>	99	45	45	50
PMC	Artificial	NA	57.2	57.2	52.5

Table 3.2 Activity and nesting success of southern ground-hornbill nests used in this study

Nest	2013-2014 season		2014-2015 season	
	active	successful	active	successful
Hlahlene	yes	no	-	-
Jock	yes	yes	yes	yes
Mangake	-	-	yes	yes
Mpfuleni	no	no	-	-
Mudzadzene	yes	yes	yes	yes
Nhlanganini	-	-	yes	yes
Nwaswitsontso	no	no	-	-
Oorlas	no	no	-	-
PMC	yes	yes	yes	yes

Table 3.3 Nest and Ambient temperature ranges (°C) for southern ground-hornbill nests during the 2013-2014 and 2014-2015 breeding seasons

Nest	2013-2014 season		2014-2015 season	
	Cavity temperatures	Ambient temperatures	Cavity temperatures	Ambient temperatures
Hlahlene	11.7 – 57.0	12.2 – 58.6	-	-
Jock	17.7 – 36.1	14.6 – 38.6	19.7 – 29.7	15.7 – 42.2
Mangake	-	-	17.1 – 32.6	14.6 – 46.1
Mpfuleni	11.1 – 33.1	12.1 – 40.6	-	-
Mudzadzene	11.7 – 53.1	11.6 – 53.5	16.2 – 40.2	17.1 – 40.1
Nhlanganini	-	-	17.2 – 10.2	-
Nwaswitsontso	11.6 – 62.5	11.1 – 52.6	-	-
Oorlas	5.6 – 45.1	5.7 – 46.6	-	-
PMC	11.7 – 56.6	11.6 – 42.1	13.7 – 54.6	14.7 – 46.6

Chapter 4: Isotopic Proxy for the Dietary Niche of the Endangered Southern Ground-hornbill

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LC, CTD, GESR and SW conceptualised the paper. LC, HJC, GESR & AJB conducted the field work. SW & GH funded and ran the isotope sample and radiocarbon dating analyses. LC, HJC & SW analysed the data and wrote the manuscript; other authors provided editorial advice.

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4.1 Abstract

Of interest in foraging ecology is whether all individuals in a dietary generalist population are generalists or whether they are a generalist population as a result of the combination of the varied diets of many specialists. The foraging ecology of the southern ground-hornbill *Bucorvus leadbeateri* has been highlighted as a knowledge gap for the species. Being an endangered bird that moves extensively during the day, studying their diet through stomach content analysis is not feasible, and through observation alone, is challenging. Consequently, we used naturally-shed feathers, bill samples from carcasses and feather samples collected from nestlings during ringing to investigate the isotopic niche of southern ground-hornbill in the Kruger National Park, South Africa. We showed that southern ground-hornbills are obligate generalists that consume a wide range of prey, yet they can focus on a particular prey resource if it is in abundance within their respective territories. Age also affected niche width, with nestlings having significantly smaller isotopic niches than adults. We found that the mean annual rainfall and the geological substrate for the area surrounding the nest significantly affected niche width. These results indicated that southern ground-hornbills can survive and reproduce successfully across a range of habitats and with a variety of food sources, which has implications for future planned reintroductions of these birds.

Keywords: diet, SIBER, feather, bill, carnivorous bird

4.2 Introduction

An animal's dietary niche comprises the entire range of food resources included in its diet, which is influenced by the quality, quantity and availability of these resources (Lehmann et al. 2015). Individuals within a population may develop a preference for one or another food type. Therefore, it may be more accurate to define a species' trophic niche as that obtained from summing the collection of individual dietary niches (Lehmann et al. 2015). When a

species shows a large trophic niche width, it is important to determine whether that is the result of all individuals being generalists or certain individuals or family groups / populations specialising in different food types (Bearhop et al. 2004). Consequently, of interest in foraging ecology, is whether all individuals are generalists or whether they are a generalist population consisting of many specialists.

Stable isotope ratios, particularly those involving carbon and nitrogen, have become a useful tool for ecologists for determining animal diets (McKechnie 2003, Bearhop et al. 2004, Thomson et al. 2005), primarily as the ratios in the proteins of consumers reflect those of the proteins of their prey in a predictable way (Bearhop et al. 2004). Although not the same as the ecological niche, the isotopic niche of a consumer contains ecological information (Jackson et al. 2011), and the variance exhibited between individuals in isotope or δ -space can be linked to among-individual variation in diet (e.g. specialist versus generalist) (Bearhop et al. 2004, Jackson et al. 2011).

The range in $\delta^{15}\text{N}$ values generally denotes the trophic length of a population, whereas the $\delta^{13}\text{C}$ range shows the variety of carbon pools or sources utilised (Bearhop et al. 2004, Layman et al. 2007). Thus stable isotope values of a tissue reflect the diet during the time in which that tissue was formed (Bearhop et al. 2004). Inert tissues such as keratin, found in feathers, and bills, will preserve this signature indefinitely (Bearhop et al. 2004, Fraser et al. 2008). For the purposes of our study, feathers are presumed to represent the diet over a relatively short period of time (weeks), whereas bills, which grow incrementally and therefore show temporal variation in the diet of the individual, are thought to represent the diet throughout the lifetime of the bird.

Southern ground-hornbills *Bucorvus leadbeateri* are large, terrestrial, carnivorous birds that inhabit the savanna and bushveld habitats of much of Africa south of the equator (Kemp 1995). They were once prevalent in north-eastern South Africa, but as a result of extensive

habitat loss and persecution, their population has suffered a significant decline (A.C. Kemp & R. Webster, unpubl. data). They are currently listed nationally as *Endangered* (Taylor et al. 2015) and globally as *Vulnerable* (IUCN 2016). In an effort to curtail this decline in South Africa, a National Species Recovery Plan was developed (Jordan 2011), with reintroductions of the birds into suitable habitat outside of protected areas listed as a viable conservation intervention for the species. This plan also highlighted a number of knowledge gaps which need to be addressed and which are essential to the long-term conservation of the species. The foraging ecology of southern ground-hornbills was one area where data were lacking.

Southern ground-hornbills are co-operative breeders that occur in groups of 2-11 birds (Kemp et al. 1989). The largest contiguous population of natural-nesting southern ground-hornbills in South Africa is found in the Kruger National Park. The birds are territorial and have home ranges from approximately 3 000 – 12 000 ha depending on the habitat (Combrink unpubl. data). During the breeding season, activity is concentrated in the vicinity of the nest site (Zoghby et al. 2015).

Southern ground-hornbills forage as a cohesive unit and will consume whatever they can overpower (Kemp 1995). They feed on a range of prey items from hares, snakes, birds, tortoises and chameleons to frogs, scorpions, spiders, termites, beetles and grasshoppers (Kemp 1995). However, there are no detailed studies of their diet. Their range of prey items consumed would suggest that as a species, southern ground-hornbills are generalists. Pagani-Núñez et al. (2016) suggest that generalists can be either facultative or obligate. Facultative generalists are species which can evolve dietary specialisations to exploit additional resources (Pagani-Núñez et al. 2016). Obligate generalists are species which exploit a wide variety of resources, but can concentrate on one particular resource if in abundance (Pagani-Núñez et al. 2016). Pagani-Núñez et al. (2016) also suggest that obligate generalists will be more limited in developing foraging innovations. Based on these definitions, we predicted that southern ground-hornbills

would be obligate generalists. Consequently, in this study, we investigated the isotopic niches of southern ground-hornbills in the Kruger National Park through feather and bill samples. This work is novel, as to the best of our knowledge, no such analyses have been performed for this species, nor similar large terrestrial bird species. We aimed to determine the isotopic dietary niche widths of individuals and family groups of southern ground-hornbills. We characterised these using the surface area within the boundaries of the 95% confidence intervals (CI) of Bayesian ellipses in the two-dimensional ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) isotopic space. Specifically, we asked (1) are all southern ground-hornbills generalist feeders or do certain individuals or groups specialise on certain food sources; (2) are there age discrepancies in southern ground-hornbill diets; and (3) what influence does nesting habitat have on dietary niche width?

4.3 Materials and methods

4.3.1 Study site

This study was conducted in the Kruger National Park which is situated in the Lowveld region of the Limpopo and Mpumalanga Provinces of South Africa, ranging between 22-26°S, 30-32°E. Samples were collected at southern ground-hornbill nesting sites (Fig. 4. 1) located throughout the park. The Kruger National Park is approximately 20 000km² in extent. The vegetation in the park varies, but is generally regarded as savannas (Gertenbach 1983), characterised by the granitic soils in the west and basaltic clays in the east (Venter 1990). The mean annual rainfall ranges from 350 - 700 mm, north to south and falls during the austral summer months from November through March (Gertenbach 1980).

4.3.2 Sample collection

Naturally-shed feathers from southern ground-hornbills ($n = 157$) were collected at nest sites during routine nest monitoring from January 2011 to July 2015. Feathers were collected during the breeding season, which for southern ground-hornbills in the Kruger National Park is during the rainy season from October/November until March. All naturally-shed feathers were from adults, presumed to be from males, as females will most likely suspend their moult during the breeding season (Kemp 1995). Southern ground-hornbills forage in groups (Kemp 1995) and would have access to the same prey items over the same period. All feathers collected at a nest site were therefore presumed to represent the group's diet, although these feathers could all be from one individual. Nestling feathers ($n = 41$) were collected from the birds during ringing, just prior to fledging. Bill samples were collected from two natural mortality carcasses of southern ground-hornbill females found at nest sites during routine monitoring. We have not included data on potential southern ground-hornbill prey items, owing to the lack of adequate data on the range of possible prey consumed by this species. Our aim was rather to conduct a preliminary investigation of variation in the isotopic niche of the southern ground-hornbill population in the Kruger National Park, providing a basis for future, more detailed isotopic research.

4.3.3 Chronological control

All feather samples are presumed to have formed in the year in which they were recovered. The bill samples represent the contemporary keratin formed through the life of the respective birds. The year of death is presumed to be the year in which the carcasses were recovered. The year of hatching was determined by radiocarbon dating the tip of the bills. This approach is affected by the wear of the bill, and accordingly the radiocarbon ages provide a

minimum estimation of the bill age. The radiocarbon analyses were calibrated using the Southern Hemisphere SHZ1_2 bomb calibration dataset of Hua et al. (2013) using the Calibomb program (<http://calib.org/CALIBomb/>).

4.3.4 Stable isotope analyses

Isotopic analyses were conducted at the University of Pretoria, Pretoria and iThemba LABS, Johannesburg. Feathers were washed in a 2:1 / ethanol:chloroform solution to remove surface oils before being dried in a drying oven at 50°C. Representative samples (0.5 ± 0.05mg) were weighed in tin capsules (pre-cleaned using toluene). Samples were combusted in a Flash EA 1112 Series Elemental Analyser coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (Thermo™; Thermo Fisher Scientific, Bremen, Germany). A laboratory running standard and blank sample were run after every 12 unknown samples. Stable isotope $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$ ratios are reported in per mille units (‰) using standard delta (δ) notation with all analyses normalised against laboratory running standards that are in turn referenced to Vienna Pee Dee Belemnite and air for carbon and nitrogen, respectively.

4.3.5 Isotopic niches

Isotopic dietary niche metrics were calculated using stable isotope Bayesian ellipses using the package SIBER (Jackson et al. 2011) in R (version 3.3.0; R Core Team 2016). This programme randomly samples the dataset for each group repeatedly and then draws the ellipse which best represents the dietary niche width of the group. The area encompassed by each ellipse is used as a measure of dietary niche width. Standard ellipse areas (SEA) were corrected for small sample sizes (SEAc) (Jackson et al. 2012) and the 95 % confidence intervals (CIs) were defined as the actual boundaries of the dietary niches throughout our study period

(Jackson et al. 2012). Parametric bootstrapping was used to create Bayesian estimations of SEAc (SEA.B) and produce density plots of the isotopic niche widths based on group, age and various environmental variables. The SEA.B also allowed for comparisons of the 95% CIs to determine any isotopic dietary niche overlap. For the individual female bills, we plotted the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in time order to see how these fluctuated over time.

To determine what influence the isotopic niche of the southern ground-hornbill group had on their nesting success, we applied a generalised linear mixed model with a binomial distribution and logit link function using the lme4 package (Bates et al. 2015). We included nesting success (calculated as the number of years a group fledged a chick divided by the number of years where the fate of the nesting attempt was known) as the response variable, isotopic niche width as the explanatory variable and southern ground-hornbill group as the random effect.

4.4 Results

The feather isotopic compositions for all 198 southern ground-hornbill feather samples collected (representing 44 different groups) had a mean of -16.8 ± 1.7 ‰ for $\delta^{13}\text{C}$ (range -20.3 to -12.1 ‰); and a mean of 8.3 ± 1.5 ‰ for $\delta^{15}\text{N}$ (range 4.7 to 17.2 ‰) respectively. Ellipses could only be calculated for 22 southern ground-hornbill groups, as a minimum number of three samples was required per group for the analyses (Supplementary material 1). The bivariate plot of C and N for all 22 southern ground-hornbill groups is shown in Fig. 4.2a, although only ellipses for a subset of the groups are shown (The plot with ellipses for all southern ground-hornbill groups, is shown in Supplementary material 1). The density plots (Fig. 4.2b) showed that although there were some groups with different isotopic niche widths, the majority of the groups had similar niche widths. When comparing the probability that a particular group's isotopic niche width was smaller than another group's (Supplementary

material 2), six groups were significantly different from more than 50% of the groups in total, three being significantly smaller and three significantly larger (Table 4.1). Southern ground-hornbill groups showed a mean of 5.7 +/- 8.1 % overlap in their isotopic niches. The amount of overlap between two groups was represented as a percentage of the area of the 95% CIs for both ellipses (Supplementary material 3). Six groups showed no overlap with more than 50% of the groups, suggesting that these groups specialised on certain prey items (Table 4.1). Group 18, which was located in the Pafuri region of the Kruger National Park, only shared a 0.5% overlap with one other group (Group 2), which was located near to Hamiltons Private Concession, approximately 247 km south of the Pafuri group.

The radiocarbon age of the bill tip from female 1 was measured on the residual of isotope samples 40-44. The result obtained was 109.1±1.5 pMC (iTC-156) which calibrated to 1997-2005 CE. Female 1 was found dead on 26 September 2011 in the presence of a dead juvenile black mamba *Dendroaspis polylepis*, believed to be the cause of her death. Comparing the approximate date of her death to the estimated minimum age of the oldest bill samples suggests that the age of female 1 was between 6 and 14 years. Although the amalgamation of several samples and wear of the tip of the bill implies that this is an underestimate of the age, it is unlikely that the bird was significantly older than this. The radiocarbon age of the bill tip from female 2 was 106.1±1.5 pMC (iTC-153) on isotope residual samples 108-110. This calibrated to 2005-2011 CE. Female 2 died while sitting on her egg between 12 December 2013 and 5 January 2014. Her inferred age is between 3 and 9 years, with the same minimum age estimate.

Isotopic analyses from the bill from female 1 (n = 44) had a mean of -15.6 ± 0.7 ‰ for $\delta^{13}\text{C}$ (range -16.9 to -13.8 ‰) and a mean of 8.8 ± 2.1 ‰ for $\delta^{15}\text{N}$ (range 5.1 to 13.0 ‰) respectively, whereas those from the bill from female 2 (n = 108) had a mean of -13.1 ± 1.4 ‰ for $\delta^{13}\text{C}$ (range -17.3 to -11.1 ‰) and a mean of 7.5 ± 0.6 ‰ for $\delta^{15}\text{N}$ (range 6.2 to 8.9 ‰)

respectively (Fig. 4.3a). Female 1 showed greater variation in $\delta^{15}\text{N}$ values than female 2, while the converse was true for $\delta^{13}\text{C}$ values, suggesting a wider range of carbon sources within the diet of female 2. Although the bivariate plots of these two individual females were quite different, the density plots showed that their niche widths were almost identical (SEA.B female 1 = 2.70 ‰^2 ; SEA.B female 2 = 2.74 ‰^2 ; $p = 0.47$; Fig. 4.3b). There was no overlap between the 95% CIs for their two diets based on the Bayesian ellipses calculated (SEA.B). When comparing the distributions of the $\delta^{13}\text{C}$ values over time (Fig. 4.4a), female 1 showed a transition from foraging in a more C_4 dominated habitat to a more C_3 dominated habitat. The $\delta^{15}\text{N}$ values for female 1 (Fig. 4.4b) indicated a possible cyclic distribution. The results from the bill of female 2 over time showed a clear cyclic pattern for both the $\delta^{13}\text{C}$ (Fig. 4.5a) and $\delta^{15}\text{N}$ values (Fig. 4.5b).

Adult feathers ($n = 156$) had a mean of $-16.5 \pm 1.8 \text{ ‰}$ for $\delta^{13}\text{C}$ (range -20.3 to 12.1 ‰) and a mean of $8.2 \pm 1.6 \text{ ‰}$ for $\delta^{15}\text{N}$ (range 4.7 to 17.2 ‰) respectively, and showed a wider isotopic niche when compared with feathers from nestlings ($n = 41$) (Fig. 4.6a), which had a mean of $-17.6 \pm 1.2 \text{ ‰}$ for $\delta^{13}\text{C}$ (range -19.2 to -13.9 ‰) and a mean of $8.5 \pm 1.1 \text{ ‰}$ for $\delta^{15}\text{N}$ (range 6.0 to 11.2 ‰) respectively. The difference in niche width between adults and nestlings was significant (SEA.B adults = 8.96 ‰^2 ; SEA.B nestlings = 3.96 ‰^2 ; $p < 0.05$; Fig. 4.6b), with the overlap between adult and nestling diet being 24.9% (calculated as a percentage of the 95% credible intervals of the area of both ellipses).

When comparing isotopic niche widths with aspects of the particular nesting habitat of southern ground-hornbill, only rainfall and soil type showed any significant differences. For rainfall, samples were grouped into <500 mm mean annual rainfall ($n = 51$) or ≥ 500 mm mean annual rainfall ($n = 146$). The niche widths for birds on territories where the mean annual rainfall was <500 mm were significantly larger than those in areas with ≥ 500 mm mean annual rainfall (SEA.B <500 mm = 8.56 ‰^2 ; SEA.B ≥ 500 mm = 6.51 ‰^2 ; $p < 0.05$; Fig. 4.7a).

Samples were also grouped according to the two major soil types within the Kruger National Park, being granite (n = 158) and basalt (n = 39). Southern ground-hornbills on territories with granitic soils had significantly smaller isotopic niches than those with territories on basaltic soils (SEA.B granite = 6.08 ‰²; SEA.B basalt = 13.42 ‰²; $p < 0.05$; Fig. 4.7b) SEA.B values for each group were used for the isotopic niche width in our generalised linear mixed model. Nesting success could only be calculated for 18 of the 22 groups. The isotopic niche width of a group was not found to have any significant effect on nesting success ($p = 0.31$).

4.5 Discussion

We assessed the isotopic niches of southern ground-hornbill groups within the Kruger National Park using naturally-shed feathers and bills from adults and chest feathers from nestlings. We aimed to determine whether southern ground-hornbills were a generalist population consisting of dietary generalists or whether they were a generalist population as a result of the combination of many dietary specialists, whether there were any age discrepancies in their diets and what influence nesting habitat has on southern ground-hornbill niche width.

4.5.1 Generalists or specialists

The difference in $\delta^{15}\text{N}$ between consumers and their resources is often used to denote trophic level (Post 2002, Newsome et al. 2007). This difference is exhibited by a stepwise enrichment (2.5-5‰ for $\delta^{15}\text{N}$ and by approximately 1‰ in $\delta^{13}\text{C}$). Southern ground-hornbills showed a broad spectrum of $\delta^{15}\text{N}$ values, spanning at least four trophic levels (assuming one trophic level is equivalent to a change of $\sim 3\text{‰}$). However, if $\delta^{15}\text{N}$ values change with foraging location, then differences in these values could be more representative of changes in habitat than of trophic level feeding differences, as the isotopic signature of prey species will change in different locations (vander Zanden et al. 2010). The $\delta^{13}\text{C}$ values for southern ground-

hornbills spanned a broad range and covered almost the entire C₃ to C₄ spectrum, from regions resembling strictly savanna habitat to areas which are almost pure grassland, respectively. This variety in isotopic signature suggests that southern ground-hornbills in the Kruger National Park can be considered habitat generalists (Bearhop et al. 2004).

Our results showed a small percentage of overlap amongst most southern ground-hornbill groups' diets, although certain groups did exhibit isotopic niches with no overlap with more than 50% of the groups studied. These differences in isotopic niches could best be explained by the geographic extent of the study population and by southern ground-hornbills being obligate generalists, exploiting a wide variety of resources or concentrating on a few that are in abundance (Pagani-Núñez et al. 2016). This opportunistic foraging behaviour can account for why certain groups showed either significantly smaller or larger niche widths although their C and N sources were similar to those of other groups.

The variance displayed between individuals (or in our case, groups) within δ -space can be used as a proxy for dietary niche width (Bearhop et al. 2004, Newsome et al. 2007). Matthews and Mazumder (2004) state that within populations the isotopic variance of consumers is dependent on the isotopic composition of their prey sources. In addition, variation within the population diet is also dependent on the feeding behaviour (generalist or specialist) of the consumer (Matthews & Mazumder 2004). In order to accurately determine the level of dietary specialisation within the southern ground-hornbill population in the Kruger National Park and within particular groups, prey sources from territories throughout the Kruger National Park would need to be analysed. However, given their broad diet and habitat range this is difficult.

The bill samples taken from the two individual female southern ground-hornbill showed that although their niche widths were almost identical in size, the distribution of their isotopic signatures in δ -space was significantly different. From a purely isotopic point of view,

the time series data from the two female bills sampled could suggest individual specialisation. If the individual females are indeed generalists, and randomly sampling the full dietary spectrum that the feathers portray, then we would expect the time series data to randomly walk through the population's isotopic dietary niche and through their respective realised niches (see Fig. 4.3). The time series data did not show this. Instead, the data suggest that, at any point in time, the females may be specialising. This may be as a result of environmental constraints, such as the differences between soil types and related habitat types, but without additional bills for which the ages of the females at death are known or another way to determine individual specialisation, this is only speculative.

Alternatively, comparing the $\delta^{13}\text{C}$ values of the two female bills over time suggests that female 1 is shifting her foraging from a grassier (C_4 dominated) to a more wooded (C_3 dominated) habitat. This could indicate dispersal from the natal territory or could simply be an indication of bush encroachment within the natal territory. Similarly, the $\delta^{15}\text{N}$ values for female 1 showed a possible cyclic distribution. This could, again, be attributed to a change in habitat (vander Zanden et al. 2010). Taken in isolation, the $\delta^{13}\text{C}$ distribution for female 1 could indicate monotonic drift, again suggesting specialisation on certain prey items at different times. However, examination of female 2's bill time series, the cyclical nature of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values is obvious. Similar cyclical distributions in $\delta^{13}\text{C}$ values have been shown in other savanna animals, such as elephants *Loxodonta africana*. Koch et al. (1995) found that these cyclic variations were most likely attributed to seasonal changes in the elephant's diet, with shifting amounts of grass and browse being incorporated in their diets.

The cyclical changes in southern ground-hornbill diet could result from seasonal vegetation changes (and subsequent changes in prey availability) based on changes in rainfall. Southern ground-hornbills may be accessing whatever prey is most abundant in the surrounding habitat, at that particular point in time, as the $\delta^{15}\text{N}$ values changed even when the

habitat ($\delta^{13}\text{C}$) values were the same (Fig. 4.5 a, b). Although only speculative, this suggests that southern ground-hornbills could be taking prey items in proportion to their abundance, making them obligate generalists.

We cannot be certain whether individual southern ground-hornbills are specialising based on these two bills. Not only is the sample size insufficient to make such claims, but even with the radiocarbon dating, we are uncertain as to the period of time that the samples represent.

4.5.2 Age discrepancies in southern ground-hornbill diet

Individual specialisation is thought to account for a proportion of the residual variance in the diet of a population, provided age, sex and morph have been taken into account (Bolnick et al. 2003). In southern ground-hornbills, adult niche widths were significantly larger than nestlings, with the entire nestling diet being contained within the adult's diet in δ -space. The nestling period for southern ground-hornbills is approximately 86 days in length (Kemp 1995). Nestlings start to show feather-quills from around 7 days of age (Kemp 1995; Combrink pers. obs.) with feathers covering most of the body by 30 days of age (Kemp 1995). This suggests that nestling feathers only provide information on prey sources for the earlier stages of the nestling period.

During the first seven days, southern ground-hornbills provide small reptiles and insects almost exclusively to their nestlings (Combrink unpublished data). Prey items are then increased in size as the nestling grows (Combrink unpublished data). In the early nestling period, the female stays with the nestling and the group will provide her with prey items during her relative confinement. We have observed that the female selectively feeds the smaller items to the nestling and consumes any larger prey items herself (Combrink unpublished data), although smaller items similar to what she feeds the nestlings are also consumed. Consequently

in the case of southern ground-hornbills, nestling diet does not accurately represent the breeding season prey selection of southern ground-hornbill adults.

In some studies, nestling diet is taken as a proxy for adult foraging behaviour during the breeding season (Romanek et al. 2000). As southern ground-hornbills are territorial (Kemp 1995) their dietary needs must be met within this restricted area. Bearhop et al. (2004) suggested that “foraging location” could affect the isotopic variance of a consumer population when individuals forage across an isotopically heterogeneous landscape. Under such conditions, wide-ranging individuals would exhibit more variation in their isotopic signatures than those that were more sedentary (Bearhop et al. 2004). Southern ground-hornbill foraging movements are further restricted during the breeding season with activities concentrated around the nest, as the group has to continuously provision for both the incubating female and growing nestling (Zoghby et al. 2015). This could also explain the discrepancy in adult and nestling dietary niche width in that not all areas of their territories can be accessed during the breeding season, leaving certain potential prey sources unattainable. This restriction on southern ground-hornbill foraging movement is lifted as soon as the nestlings fledge, allowing the birds full use of all habitats available to them within their respective territories.

4.5.3 Influence of habitat on niche width

Habitat and vegetation across the Kruger National Park varies quite dramatically along both the edaphic (east-west), and rainfall (north-south) gradients (Venter et al. 2003). Both soil type and rainfall had an effect on the isotopic niche width of southern ground-hornbills. Rainfall, is considered an influential factor in the breeding biology of southern ground-hornbills, as nesting only starts once the first rains of the wet season have fallen (Kemp & Kemp 1991). Wilson and Hockey (2013) found that groups whose territories experienced \geq 500 mm of rainfall during the breeding season were less successful reproductively than those

with 300 – 500 mm of rainfall. Although we could find no correlation between niche size and nesting success in our study, our results showed that groups with territories with < 500 mm mean annual rainfall had significantly larger isotopic niche widths. Rainfall is also thought to influence southern ground-hornbill prey availability (Kemp & Kemp 1991). Too much rainfall can inhibit foraging ability, especially for terrestrial birds that spend most of their time (70% of the day) walking (Kemp 1995) and affects prey activity, especially those that are ectotherms.

Soil type influences the vegetation composition and structure in the Kruger National Park, with granites generally having higher tree densities and basalts, a higher grass component (Colgan et al. 2012). Basaltic soils are also more nutrient rich, making the vegetation of higher forage quality and therefore, more attractive to herbivores, particularly in the dry season (Asner et al. 2015, Smit & Prins 2015). Smit (2011) showed concentrations of herbivores (ruminants) to be significantly higher on basalts as opposed to granites within the Kruger National Park. We can expect these differences between the vegetation and large herbivore numbers to reflect differences in southern ground-hornbill faunal prey diversity (insects, birds, reptiles and small mammals) between the two soil types. Unfortunately, comparisons of biodiversity across these two soil types have not been studied in any great depth.

If biodiversity is greater on basaltic soils, small niche width on granitic soils could be indicative of specialisation in diet, owing purely to the lack of variety of prey available to the birds in those territories. This would still support our prediction that southern ground-hornbills are opportunistic feeders and obligate generalists in that should additional prey species become available within territories on granites, we would expect the group's isotopic signatures to reflect these new food sources. Similarly, the wider niche width on basaltic soils could indicate a more obligate generalist foraging behaviour in that all available prey species are consumed in these territories.

4.6 Conclusion

Stable isotope analyses are a good proxy for an animal's diet, as isotopic variation reflects both prey-related and habitat-related influences (Newsome et al. 2007). This can make interpretation of the results difficult and it is important to combine stable isotope results with traditional observational data regarding the behaviour and diet of the species when evaluating individual foraging patterns (Thomson et al. 2012). In addition, some variation in the isotopic signatures of individuals could be due to individual variation in physiology or isotopic discrimination rather than differences in foraging patterns (Barnes et al. 2008). In this study, we showed that southern ground-hornbills exhibit a wide isotopic niche on both the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ axes. Their nitrogen sources suggest that they consume prey from a range spanning around four trophic levels, although these values could be more indicative of changes in habitat. Similarly, for carbon sources, they access prey from almost the entire C_3 to C_4 spectrum. Individual female diets were also shown to vary considerably within isotopic space, even though their niche widths were relatively similar. Age did affect diet in that adult southern ground-hornbill niche widths differed significantly from those of nestlings, with nestling diet being completely incorporated within adult diets in isotopic space. Habitat and location (with regards to rainfall and soil type) also played a role in the extent of the niche widths, with territories in areas with granitic soils and > 500 mm of mean annual rainfall having significantly smaller niche widths.

Our results suggest that southern ground-hornbills are obligate generalists owing to the wide range of carbon sources that they exploited. The limited overlap between certain groups supports this and suggests that some groups are exploiting an abundant resource within their territories. The bill data showed the possibility of specialisation at the individual level or changes in diet in response to climatic variables. Without sufficient sample sizes and a more detailed chronology of the formation of the bills, these interpretations are only speculative.

Our findings are relevant because they not only add to the relatively scarce existing knowledge of southern ground-hornbill diet, but they will aid the choice of suitable sites for reintroductions of the birds. Our results showed that southern ground-hornbills can survive and reproduce successfully across a range of habitats and with a variety of food sources. Thus, provided the chosen site is large enough and the variety of potential niches for prey species high enough, they should be successful if reintroduced there.

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Ethical Approval

All applicable institutional and/or national guidelines for the care and use of animals were followed. Ethical approval was provided by the University of KwaZulu-Natal and the relevant SANParks animal ethics committee. This project was registered with SANParks' Scientific Services and samples were collected under the SANParks Resource Use permits No.SK038 & SK026

4.8 References

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Table 4.1 Mean stable isotope values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with standard deviations (s.d) for groups that had isotopic niche widths significantly larger and significantly smaller than 50% of the southern ground-hornbill groups, and groups that showed no overlap in isotopic niche width with at least 50% of the southern ground-hornbill groups studied.

Group	Name	Mean $\delta^{13}\text{C}$ (s.d)	Mean $\delta^{15}\text{N}$ (s.d)	Isotopic niche width
3	Hlahlene	-16.1 (2.8)	9.1 (1.4)	Larger
4	Jock	-16.6 (2.0)	7.6 (1.1)	
19	Lindanda	-15.7 (2.2)	7.8 (2.3)	
5	Jumbo	-18.5 (0.5)	8.4 (0.7)	Smaller
10	Ngwenyene	-17.8 (0.2)	8.6 (1.0)	
14	Orpen Dam	-17.2 (1.6)	7.8 (0.1)	
5	Jumbo	-18.5 (0.5)	8.4 (0.7)	No overlap with 50% of groups studied
7	Mangake	-15.9 (1.4)	6.6 (0.8)	
12	Nkombe	-17.0 (0.5)	7.3 (0.5)	
18	Pafuri	-16.0 (1.2)	11.3 (0.3)	
21	Nwaswitsontso	-15.8 (0.9)	9.5 (1.0)	
22	Trichard Road	-13.4 (1.6)	9.5 (1.4)	

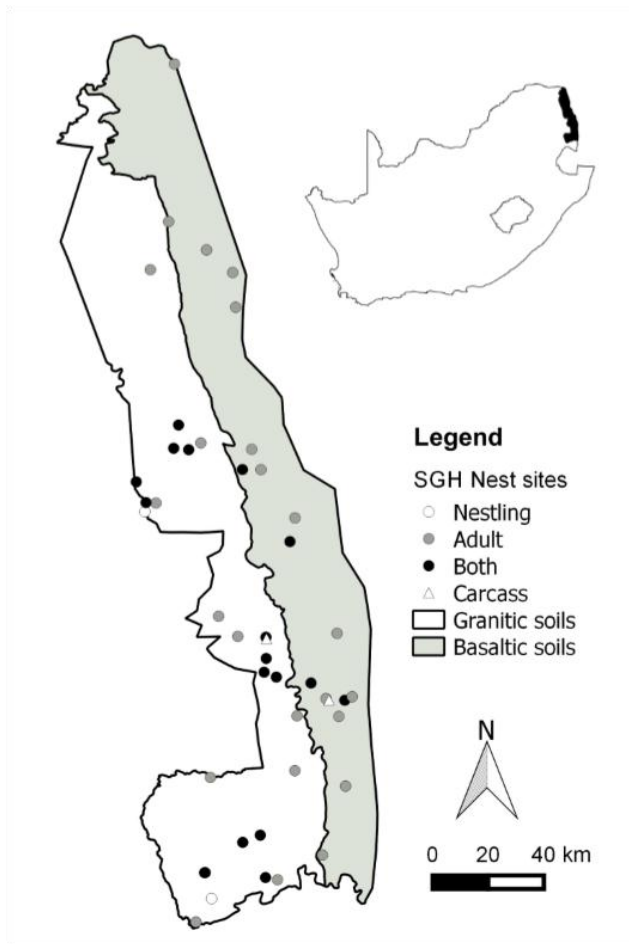


Fig. 4.1 Map of southern ground-hornbill nesting sites in the Kruger National Park showing where the various samples were collected and the relevant soil type in the area. Sites where only nestling feathers were collected are represented by open circles, where only adult feathers collected, by filled grey circles and where both adult and nestling feathers were collected, by filled black circles. Sites where carcasses were recovered are represented by open triangles. The grey shaded area represents basaltic soils, with the white shaded area representing granitic soils.

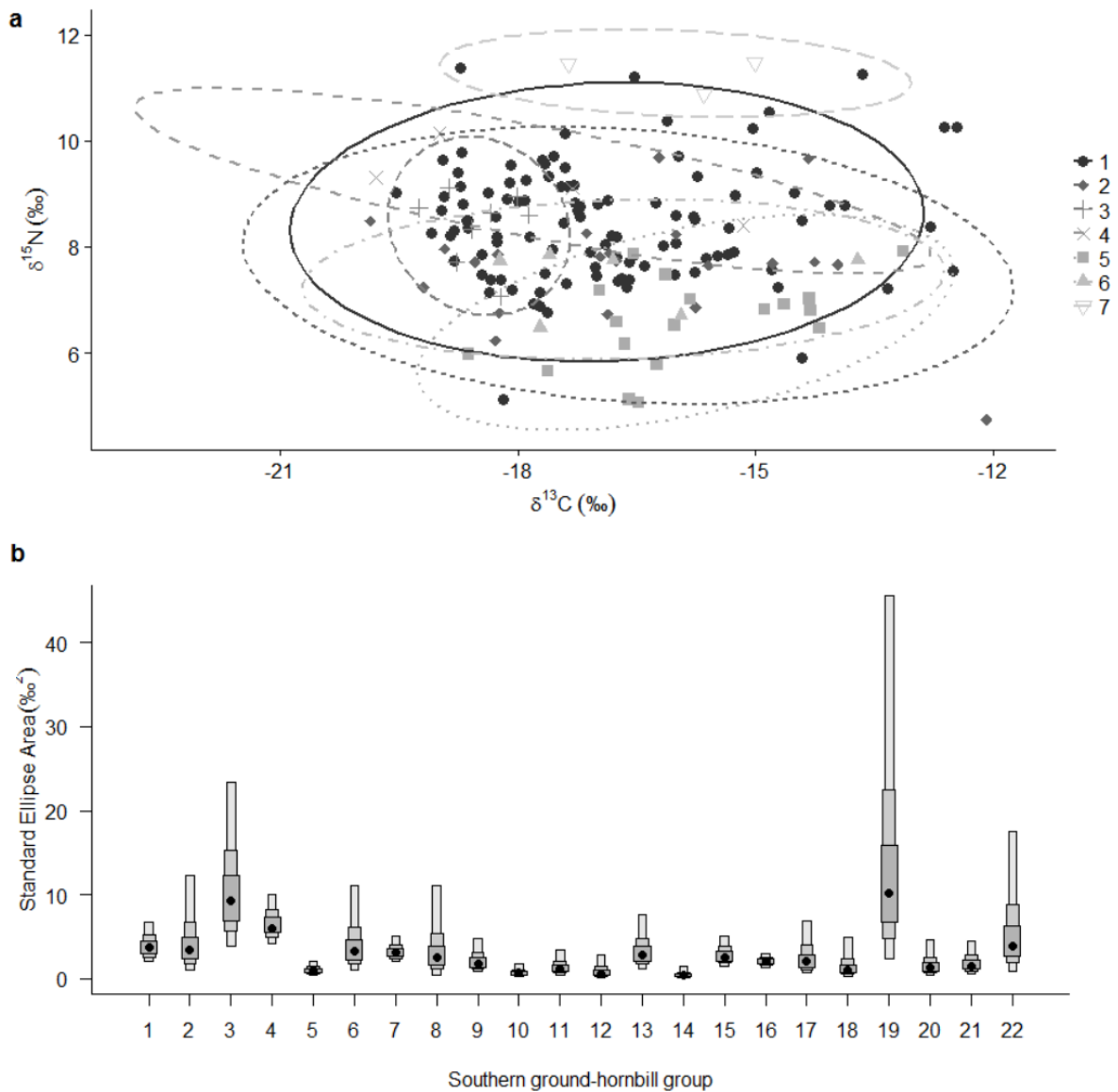


Fig. 4.2 Data from the analysis of feather samples showing (a) the bivariate plot of stable C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) isotope ratios, and (b) the isotopic niche sizes for the 22 southern ground-hornbill groups studied in the Kruger National Park. In (a) only ellipses of the six groups where the isotopic niches were significantly different to the majority of other groups are shown. Here, 2 (filled diamonds) represents the Hlahlene group, 3 (+ signs) is the Jock group, 4 (x's) if the Jumbo group, 5 (filled squares) is the Lindanda group, 6 (filled triangles) represents the Ngwenyene group and, 7 (inverted open triangles) represents the Orpen Dam group. The data points for the remaining 16 groups were pooled and plotted as one ellipse (group 1 - filled

circles). Each Bayesian standard ellipse for the group was calculated using all data for each southern ground-hornbill group. In (b), isotopic niche sizes were estimated by the area of ellipses (‰^2) in two-dimensional isotopic space. The mean is represented by a black dot, with shaded boxes indicating the 50% (dark grey), 75% (medium grey) and 95% (light grey) credible intervals.

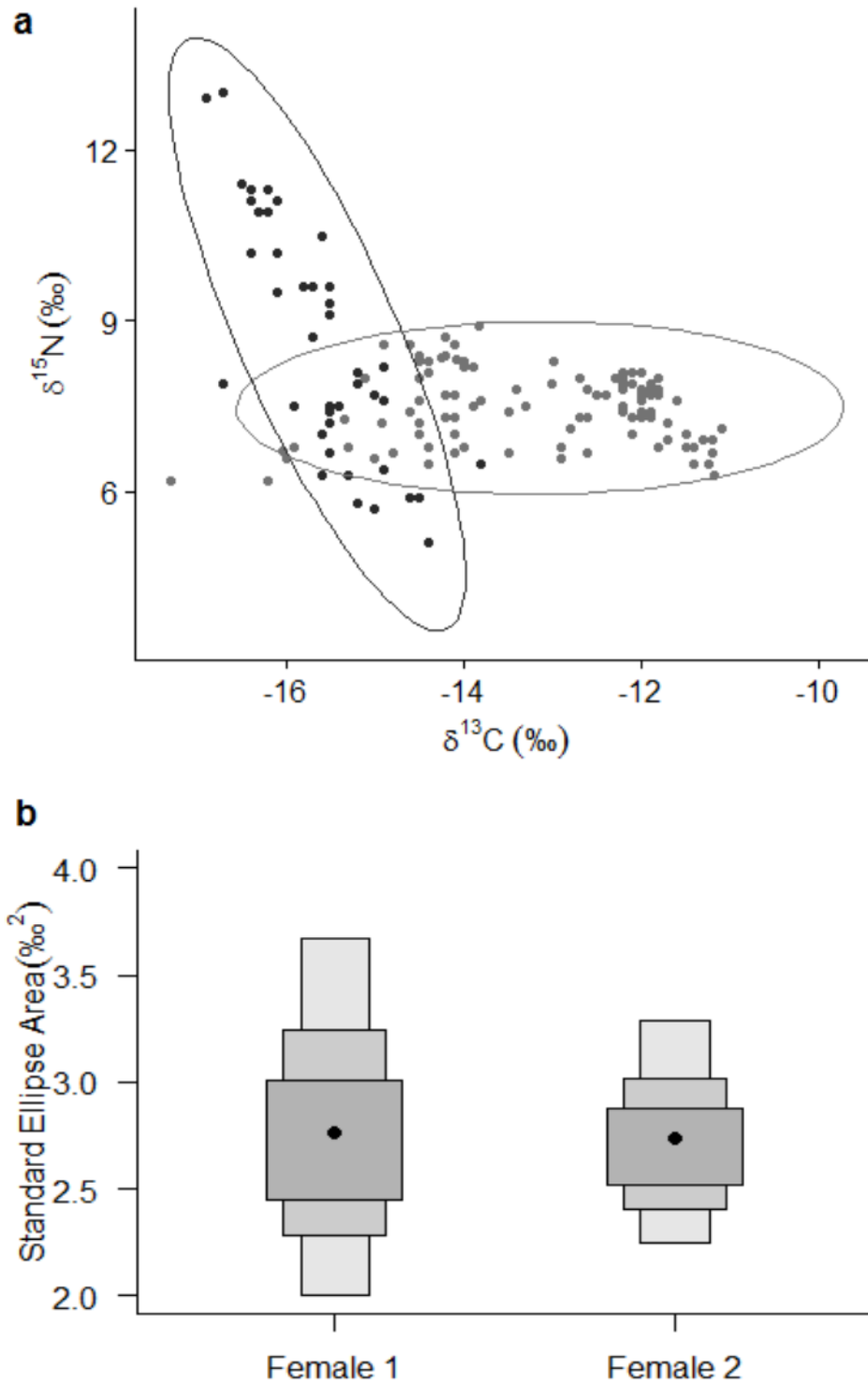


Fig. 4.3 Data from the analysis of bill samples showing (a) the bivariate plot of stable C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) isotope ratios and (b) the isotopic niche sizes for the two female southern ground-hornbills. Each Bayesian standard ellipse was calculated using all data from each individual

female bill, with data points from female 1 represented by black filled circles and data points from female two, grey filled circles. Isotopic niche sizes were estimated by the area of ellipses (‰^2) in two-dimensional isotopic space. The mean is represented by a black dot, with shaded boxes indicating the 50% (dark grey), 75% (medium grey) and 95% (light grey) credible intervals.

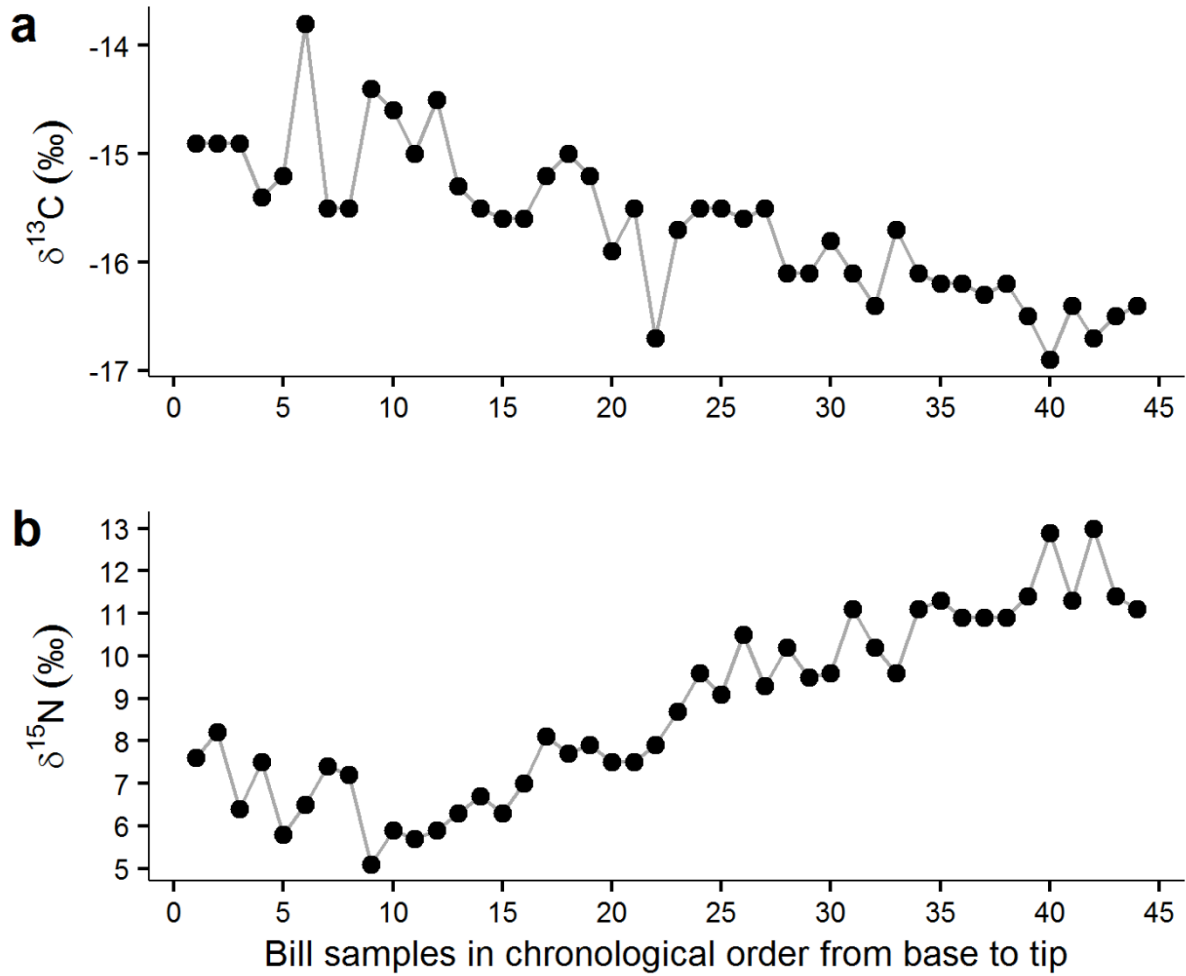


Fig. 4.4 Bill samples (n=44) from southern ground-hornbill female 1 plotted in time order from left to right, with (a) showing the changes in stable C ($\delta^{13}\text{C}$) isotopes and (b) the changes in stable N ($\delta^{15}\text{N}$) isotopes.

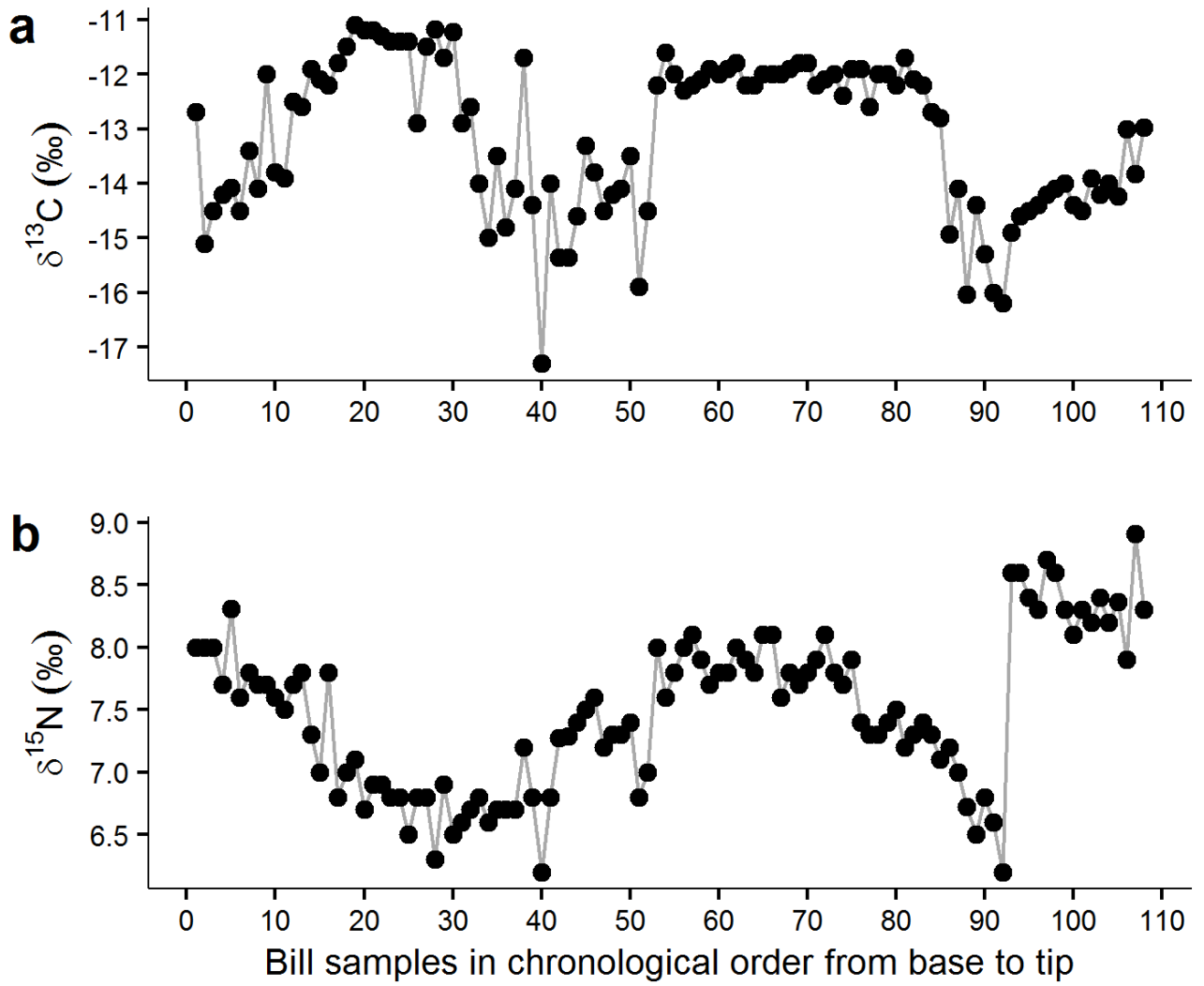


Fig. 4.5 Bill samples (n=108) from southern ground-hornbill female 2 plotted in chronological order from left (base) to right (tip), with (a) showing the changes in stable C ($\delta^{13}\text{C}$) isotopes and (b) the changes in stable N ($\delta^{15}\text{N}$) isotopes.

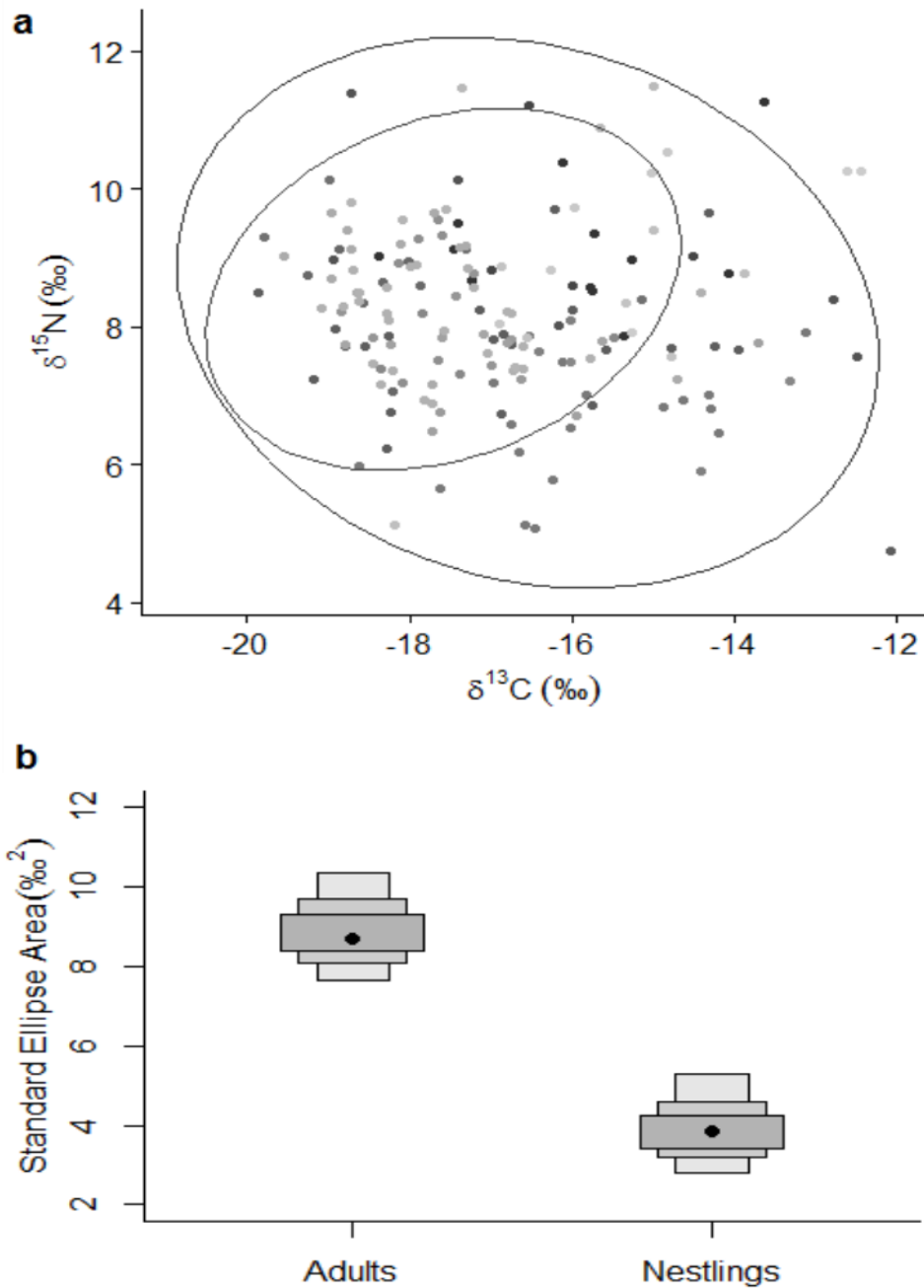


Fig. 4.6 Data from the analysis of feather samples showing (a) the bivariate plot of stable C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) isotope ratios and (b) the isotopic niche sizes for adult and nestling southern ground-hornbills. Each Bayesian standard ellipse was calculated using all data for each age class, with adult data points represented by black filled circles and nestling data points, grey filled circles. Isotopic niche sizes were estimated by the area of ellipses (‰^2) in two-dimensional isotopic space. The mean is represented by a black dot, with shaded boxes indicating the 50% (dark grey), 75% (medium grey) and 95% (light grey) credible intervals.

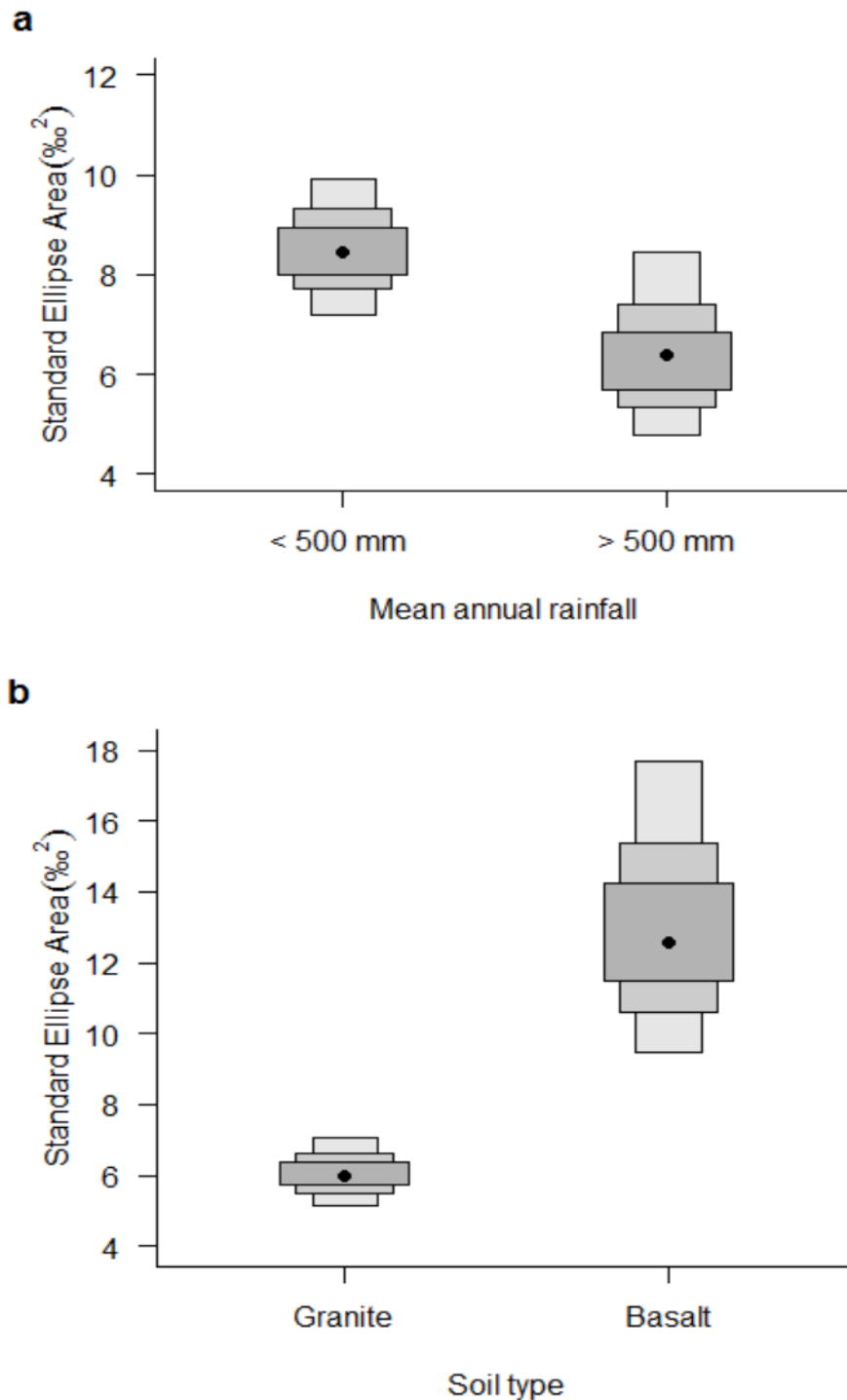


Fig. 4.7 Isotopic niches of southern ground-hornbill groups calculated in terms of environmental factors measured around the nest sites, being (a) mean annual rainfall and (b) soil type. Isotopic niche sizes were estimated by the area of ellipses (‰²) in two-dimensional isotopic space. The mean is represented by a black dot, with shaded boxes indicating the 50% (dark grey), 75% (medium grey) and 95% (light grey) credible intervals.

4.9 Supplementary material 1. Bivariate plot and ellipses for all 22 southern ground-hornbill groups

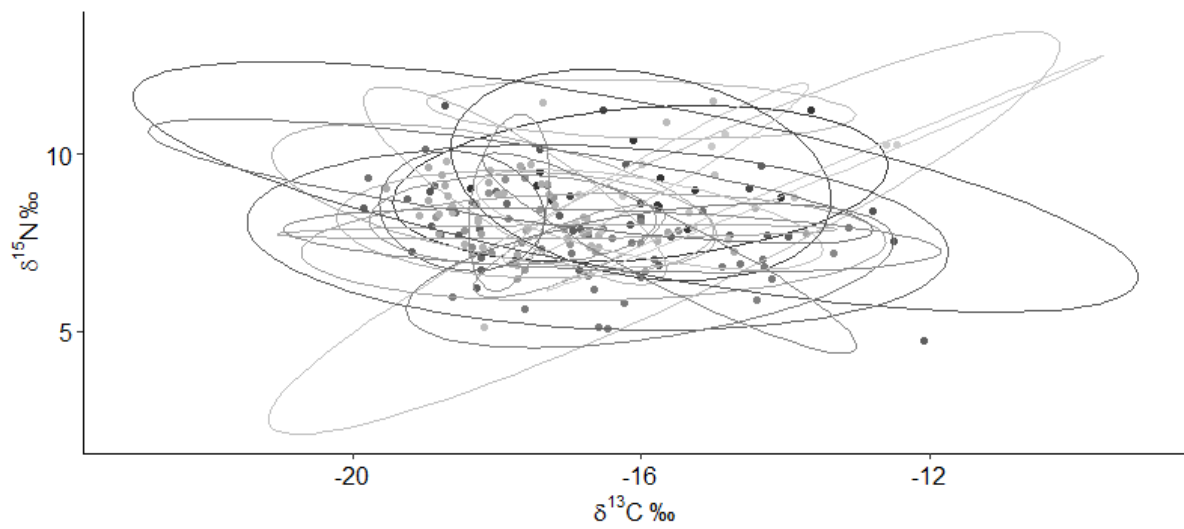


Fig. S1. Data from the analysis of feather samples showing the bivariate plot of stable C ($\delta^{13}\text{C}$) and N ($\delta^{15}\text{N}$) isotope ratios for the 22 southern ground-hornbill groups studied in the Kruger National Park.

4.10 Supplementary material 2. Probabilities of dietary niche width differences between southern ground-hornbill groups

Table S1 Probabilities that the southern ground-hornbill groups listed on the vertical axis have a larger niche width than those on the horizontal axis. Significant differences between niche widths are highlighted.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1		0.43	0.02	0.08	1	0.48	0.69	0.59	0.87	1	0.96	0.98	0.63	1	0.77	0.97	0.77	0.92	0.01	0.9	0.9	0.3
2	0.57		0.1	0.24	0.99	0.55	0.71	0.63	0.85	1	0.94	0.97	0.67	1	0.77	0.93	0.77	0.92	0.06	0.9	0.89	0.38
3	0.98	0.9		0.86	1	0.92	1	0.93	1	1	1	1	0.98	1	1	1	0.98	0.99	0.36	0.99	1	0.81
4	0.92	0.76	0.14		1	0.79	0.98	0.83	0.98	1	1	1	0.92	1	0.99	1	0.94	0.98	0.09	0.98	0.98	0.61
5	0	0.01	0	0		0.01	0.01	0.04	0.1	0.73	0.3	0.62	0.01	0.87	0.02	0.06	0.07	0.33	0	0.21	0.15	0.01
6	0.52	0.45	0.08	0.21	0.99		0.65	0.59	0.83	1	0.94	0.97	0.61	0.99	0.71	0.9	0.73	0.9	0.05	0.88	0.86	0.35
7	0.31	0.29	0	0.02	0.99	0.35		0.47	0.79	0.99	0.93	0.96	0.47	0.99	0.63	0.93	0.67	0.88	0	0.86	0.85	0.19
8	0.41	0.37	0.07	0.17	0.96	0.41	0.53		0.75	0.98	0.87	0.94	0.51	0.99	0.6	0.79	0.65	0.85	0.05	0.82	0.79	0.28
9	0.13	0.15	0.01	0.02	0.91	0.17	0.21	0.26		0.96	0.75	0.89	0.23	0.97	0.29	0.54	0.41	0.72	0	0.64	0.59	0.08
10	0	0	0	0	0.27	0	0.01	0.02	0.04		0.15	0.43	0.01	0.75	0.01	0.03	0.03	0.19	0	0.11	0.07	0
11	0.04	0.06	0	0	0.7	0.06	0.07	0.13	0.25	0.85		0.75	0.09	0.92	0.11	0.23	0.19	0.5	0	0.39	0.33	0.03
12	0.02	0.03	0	0	0.38	0.03	0.04	0.06	0.11	0.57	0.25		0.04	0.77	0.06	0.1	0.09	0.28	0	0.19	0.15	0.02
13	0.37	0.33	0.02	0.08	0.99	0.39	0.53	0.49	0.77	0.99	0.91	0.96		0.99	0.62	0.86	0.67	0.87	0.02	0.85	0.83	0.24
14	0	0.01	0	0	0.13	0.01	0.01	0.01	0.03	0.25	0.08	0.23	0.01		0.01	0.03	0.02	0.09	0	0.05	0.05	0
15	0.23	0.23	0	0.01	0.98	0.29	0.37	0.4	0.71	0.99	0.89	0.94	0.38	0.99		0.83	0.58	0.84	0	0.81	0.78	0.15
16	0.03	0.07	0	0	0.94	0.1	0.07	0.21	0.46	0.97	0.77	0.9	0.14	0.97	0.17		0.36	0.73	0	0.64	0.58	0.04
17	0.23	0.23	0.02	0.06	0.93	0.27	0.33	0.35	0.59	0.97	0.81	0.91	0.33	0.98	0.42	0.64		0.77	0.02	0.71	0.66	0.16
18	0.08	0.08	0.01	0.02	0.67	0.1	0.12	0.15	0.28	0.81	0.5	0.72	0.13	0.91	0.16	0.27	0.23		0.01	0.4	0.35	0.06
19	0.99	0.94	0.64	0.91	1	0.95	1	0.95	1	1	1	1	0.98	1	1	1	0.98	0.99		1	1	0.86
20	0.1	0.1	0.01	0.02	0.79	0.12	0.14	0.18	0.36	0.9	0.61	0.81	0.15	0.95	0.19	0.36	0.29	0.6	0		0.44	0.06
21	0.1	0.11	0	0.02	0.85	0.14	0.15	0.21	0.41	0.93	0.67	0.85	0.17	0.95	0.22	0.42	0.34	0.65	0	0.56		0.07
22	0.7	0.62	0.19	0.39	0.99	0.65	0.81	0.72	0.92	1	0.97	0.98	0.76	1	0.85	0.96	0.84	0.94	0.14	0.94	0.93	

4.11 Supplementary material 3. Percentage of overlap between southern ground-hornbill dietary niches

Table S2 Percentages of overlap between the dietary niches of the 22 southern ground-hornbill groups for which ellipses could be calculated in the Kruger National Park

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1		36.4	26.0	6.1	0	19.7	0	5.0	0	0	1.2	0	0	0	5.5	1.2	5.2	0	7.5	12.5	14.7	0
2	36.4		28.0	6.9	0	13.7	0	4.0	0	0	0	0	0.5	0	0.7	0	0.1	0.5	9.5	13.8	11.9	0
3	26.0	28.0		8.5	0	19.7	0	3.8	1.1	3.0	0.8	0	1.3	0.8	8.4	0.8	13.2	0	14.6	12.3	5.7	1.8
4	6.1	6.9	8.5		4.9	4.0	13.3	19.5	26.1	5.5	17.5	12.7	35.4	8.8	9.7	22.1	8.1	0	19.9	20.8	1.4	0.8
5	0	0	0	4.9		2.0	0	0	1.5	3.2	19.1	0	0	5.2	15.5	15.1	0	0	0	0	0	0
6	19.7	13.7	19.7	4.0	2.0		0	2.7	0	7.7	0.9	0	0	0	21.9	0	20.3	0	2.1	9.1	5.4	0
7	0	0	0	13.3	0	0		17.1	5.1	0	0	0	11.5	0	0	0	0	0	13.1	0	0	0
8	5.0	4.0	3.8	19.5	0	2.7	17.1		15.5	0	0.5	3.9	17.4	5.3	2.9	3.0	2.3	0	9.2	17.8	2.0	0.2
9	0	0	1.1	26.1	1.5	0	5.1	15.5		0.0	0.1	0.2	34.0	17.6	0.1	19.0	2.4	0	10.6	10.8	0	0.6
10	0	0	3.0	5.5	3.2	7.7	0	0	0.0		0.2	0	1.8	4.2	16.2	14.7	15.2	0	0	0	0	0
11	1.2	0	0.8	17.5	19.1	0.9	0	0.5	0.1	0.2		0	6.8	12.2	20.6	41.5	14.5	0	0	0.7	0	0
12	0	0	0	12.7	0	0	0	3.9	0.2	0	0		20.1	7.1	0	6.1	0.8	0	7.4	1.7	0	0
13	0	0.5	1.3	35.4	0	0	11.5	17.4	34.0	1.8	6.8	20.1		0.1	0.3	13.5	2.4	0	16.6	10.4	0	0.5
14	0	0	0.8	8.8	5.2	0	0	5.3	17.6	4.2	12.2	7.1	0.1		0	14.3	2.5	0	2.4	7.5	0	1.0
15	5.5	0.7	8.4	9.7	15.5	21.9	0	2.9	0.1	16.2	20.6	0	0.3	0		17.4	27.6	0	0	3.1	0.3	0
16	1.2	0	0.8	22.1	15.1	0	0	3.0	19.0	14.7	41.5	6.1	13.5	14.3	17.4		14.2	0	1.1	2.7	0	0
17	5.2	0.1	13.2	8.1	0	20.3	0	2.3	2.4	15.2	14.5	0.8	2.4	2.5	27.6	14.2		0	0.2	2.3	0	0
18	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0
19	7.5	9.5	14.6	19.9	0	2.1	13.1	9.2	10.6	0	0	7.4	16.6	2.4	0	1.1	0.2	0		10.8	0	3.1
20	12.5	13.8	12.3	20.8	0	9.1	0	17.8	10.8	0	0.7	1.7	10.4	7.5	3.1	2.7	2.3	0	10.8		5.4	2.3
21	14.7	11.9	5.7	1.4	0	5.4	0	2.0	0	0	0	0	0	0	0.3	0	0	0	0	5.4		0
22	0	0	1.8	0.8	0	0	0	0.2	0.6	0	0	0	0.5	1.0	0	0	0	0	3.1	2.3	0	

Chapter 5: Aspects of the Spatial Ecology of Southern Ground-hornbills in the Kruger National Park, South Africa

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Running header: Spatial Ecology of Ground-hornbills

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5.1 Abstract

Understanding how a species utilizes its habitat and the processes that give rise to its movement and pattern of space use is critical for its conservation. Southern ground-hornbills *Bucorvus leadbeateri* are listed as Endangered in South Africa, as a result of habitat loss and persecution. The National Species Recovery Plan highlighted “understanding the exact habitat requirements of southern ground-hornbills” as a knowledge gap. In this study, we used tracking data from six southern ground-hornbill groups (a total of 37060 GPS locations) in the Kruger National Park to investigate their seasonal home range differences and habitat preferences. We used first-passage time analysis to determine the scale at which southern ground-hornbills concentrate their foraging efforts and whether specific movement behaviours were linked to habitat types. We found that there were marked differences in seasonal home ranges, with all groups showing a range contraction during the breeding season. Grassland and open woodland habitat types were used throughout the year in accordance with their availability within the territory. Grassland, open woodland and dense thicket were favoured habitats for foraging. When selecting a potential release site for reintroductions, based on our habitat preference results, we determined that the ideal ratio of grassland:open woodland:low shrubland in the release area should be 1.00:6.10:0.09 ha for southern ground-hornbills.

Key words: home range, movement, habitat use, conservation, first-passage time, hornbill

5.2 Introduction

Habitat selection compares the use of a particular habitat with the availability of that habitat to the species within a prescribed area (Jones, 2001). How a species utilises its habitat and understanding the processes that give rise to its movement and pattern of space use, is paramount to its conservation (Beyer *et al.*, 2010; Kie *et al.*, 2010; Byrne & Chamberlain, 2012). The purpose of movement is to optimise individual fitness through the exploitation of resources within these habitats, the availability of which changes in space and time (van Moorter *et al.*, 2013). With the advent of advances in satellite tracking technology and the accompanying improvements in analytical tools, the field of movement ecology has developed rapidly over the last decade (Allen & Singh, 2016).

Movement patterns and space use determine species distributions and home ranges (Frair *et al.*, 2005). Most species have spatially heterogeneous home ranges, where resources are not evenly distributed in space or time (Byrne & Chamberlain, 2012). A large number of species will alter their speed of movement or the tortuosity of their movement paths in response to the abundance of local resources (Frair *et al.*, 2005). Optimal foraging will result in animals conducting intensive searches in patches of high resource density and minimising time spent in lower resource density areas (Byrne & Chamberlain, 2012). This particular movement pattern, termed an area-concentrated search, results in slow, tortuous paths within a particular resource patch and fast, direct paths between patches (Fauchald & Tveraa, 2003; Frair *et al.*, 2005). Another measure of search effort is first-passage time, which is the time taken for a species to cross a circle with a given radius (Fauchald & Tveraa, 2003). This also provides information on the spatial scales at which species concentrate their search effort (Johnson *et al.*, 1992; Fauchald & Tveraa, 2003).

The use of tracking technology has allowed researchers to link movement patterns and relocation data with global information systems (GIS) mapping, habitat and environmental

variables, providing a useful way of determining the influence of habitat and environmental features on animal movement (Kie *et al.*, 2010; Morales *et al.* 2010). Understanding these patterns of movement and habitat use and relating these to environmental variables and habitat heterogeneity will assist in modelling and predicting species home ranges in different regions and determining their minimum habitat requirements (Byrne & Chamberlain, 2012). This is particularly important in the conservation of endangered species.

Southern ground-hornbills *Bucorvus leadbeateri* are large, terrestrial, carnivorous birds that inhabit savanna and bushveld habitats throughout much of Africa, south of the equator (Kemp, 1995). They are co-operative breeders, forming groups with an alpha breeding pair and up to nine helper birds, and they forage as a cohesive unit (Kemp 1995). They are threatened as a result of habitat loss and persecution and are considered Vulnerable globally (IUCN, 2016) and Endangered within South Africa (Taylor *et al.*, 2015). A National Species Recovery Plan was developed in South Africa for southern ground-hornbills in 2011 (Jordan, 2011). This plan highlighted a number of knowledge gaps for the species, one being an understanding of the habitat requirements of these birds, as well as important conservation initiatives that could be implemented, such as active relocations of groups to suitable areas within their historical distribution (Jordan, 2011).

Consequently, we tracked the movements and habitat use of six southern ground-hornbill groups within the Kruger National Park, where more than 50% of the South African population of southern ground-hornbills are located (Kemp 2005). Past research on southern ground-hornbills suggests that both group and seasonal effects influence home range sizes and habitat use (Wyness, 2011; Zoghby *et al.*, 2015). We investigated their seasonal space use and habitat selectivity in the Kruger National Park with groups of differing size. Specifically, we aimed to determine (1) if they have any seasonal home range differences across the extent of the Kruger National Park, and (2) if they show any seasonal habitat preferences in the Kruger

National Park. We then used first-passage time analysis to determine (3) at what scale they concentrated their foraging movement, and how this varied with season and between groups. Lastly, we determined (4) if southern ground-hornbill's movement behaviours were linked to habitat types. It is hoped that the results of our research will inform management decisions both within and beyond the borders of protected areas towards the conservation of this endangered bird.

5.3 Methods

5.3.1 Study area

This study was conducted within the Kruger National Park, South Africa (22 – 26°S, 30 – 32°E), which comprises around 2 million ha with an average annual rainfall of 350 – 750 mm (Gertenbach 1980). The park is largely divided longitudinally with more granitic soils in the west and basaltic soils in the east (Venter 1990). The habitat consists mainly of savanna, with pockets of dense woody vegetation within broader grasslands (Gertenbach 1983).

5.3.2 Home range and habitat use

We used 70g solar Argos/GPS PTT satellite transmitters (Microwave Telemetry Inc., Columbia, MD) to track the movements of five groups of southern ground-hornbills within Kruger National Park and associated conservation areas, namely Cleveland, Mangake, Mudzadzene, Shingwedzi and Ngotso Camp (Fig. 5.1). An additional group (Jock) was monitored using a 105g GSM tracking device (VECTRONIC Aerospace GmbH, Berlin, Germany). Groups were named after prominent natural features or infrastructure within their territories. Birds were lured into a domed-shaped walk-in trap (6m (l) x 3m (b) x 2m (h)) using decoy southern ground-hornbills made of fibreglass and simultaneously playing their territorial

call. The trap was closed with a curtain which was pulled across the entrance once the birds had entered the trap. One bird per group was fitted with a GPS satellite tracking device using a tubular 16" Teflon[®] backpack harness design, with the Teflon[®] criss-crossed across the chest and secured around the bird's wings. All devices were not programmed according to the same schedule for GPS fixes, as most were donated to the Kruger Southern Ground-hornbill Project following the termination of other respective tracking projects. Tracking data were prepared for trajectory analysis as per the instructions in the *adehabitatLT* package (Calenge, 2006), accounting for missing fixes and irregular time intervals.

GPS fixes from the Microwave Telemetry Inc. (MTI) devices were decoded using their MTI Argos-GPS Parser software, whereas the data from the Vectronic-Aerospace (V-A) device used the V-A GPS-Plus software package for GPS data extraction. All statistical analyses were conducted in R version 3.3.1 (R Core Team, 2016). GIS analyses were conducted using Quantum GIS (version 2.4.0, Quantum GIS Development Team, 2016) and the R package *adehabitatHR* (Calenge, 2006) and *adehabitatHS* (Calenge, 2006). Kernel use density estimates (KDEs) (95%) were calculated using the h_{ref} smoothing factor for the overall home, breeding season and seasonal home ranges using the *adehabitatHR* package (Calenge, 2006). Habitat use was determined using a combination of the Points in Polygon plugin for QGIS and the areas of used and available habitat types within these KDEs.

Habitat preference was determined using a habitat selectivity index (E_i), calculated per tracked southern ground-hornbill. We used Jacobs's (1974) modification of Ivlev's Electivity Index, comparing availability of food types and their utilization in the diet, modified to reflect habitat preference (Velasquez *et al.*, 1991), according to the following formula

$$E_i = (p_i - q_i) / (p_i + q_i - 2p_iq_i)$$

Where $p_i = \text{number of satellite fixes per habitat type } (N_i) / \text{Total number of satellite fixes } (N_t)$;
and $q_i = \text{area (ha) of habitat type in home range } (A_i) / \text{Total area (ha) of home range } (A_t)$

The results of this index (E_i) range from -1 to +1, with values $>+0.25$ taken to indicate habitat preference and < -0.25 taken as habitat avoidance. Values of >-0.25 to $<+0.25$ indicate neutral habitat attraction. Habitat was classified according to the 2013-2014 South African National Land Cover Dataset (GeoterraImage, 2014). For each KDE, the proportions of the various land types within the KDE were calculated by clipping the land cover layer with the KDE polygons for each southern ground-hornbill group generated from the `adehabitatHR` package. Southern ground-hornbills coincide their breeding season with the onset of the rainy season, which in South Africa falls within the austral summer. For the purposes of our study, home ranges were estimated for four seasons: late wet (January to March), early dry (April to June), late dry (July to September) and early wet (October to December).

For each GPS location, the corresponding habitat type was digitally extracted from the land cover layer. The GPS locations contained within the various home and seasonal ranges for each southern ground-hornbill group were clipped with the respective polygons and the number of points per habitat type, summed. We also calculated the percentage of woody cover associated with each GPS location. Only a section of the territory of the Cleveland southern ground-hornbill group fell within Kruger National Park. As the woody cover layer does not extend beyond the Kruger National Park boundary, the percentage of woody cover within the Cleveland home ranges could not be calculated, necessitating excluding this group from any analyses involving woody cover.

To determine whether compositional foraging habitat proportions, woody cover, season and group had any effect on the breeding seasonal home ranges of southern ground-hornbills, we applied linear regressions to the data using the `lme4` package in R (Bates *et al.*, 2015). All

variables included in the models were log transformed and their distributions then approached normality. Separate models for woody cover and habitat composition were run owing to there being no woody cover data for the Cleveland group as mentioned.

5.3.3 First-passage time analysis

We followed the methods of Fauchald and Tveraa (2003) and used first-passage time (FPT) analyses to determine whether southern ground-hornbills exhibit area-restricted search (ARS) behaviour. This analysis places circles of a specified range of radii on the GPS location and calculates the time the particular animal takes to traverse to the centre of the circle and back. Using the `adehabitatLT` package (Calenge, 2006) for R, we plotted the variance of the log-transformed FPT of ten daily seasonal trajectories per southern ground-hornbill group, as a function of the radius. The scale at which the birds concentrated their search (ARS behaviour) corresponded to the value of the radius associated with the peak of the variance of each log-transformed FPT graph (Fauchald & Tveraa, 2003), hereafter referred to as rv_{\max} . We used the mean rv_{\max} for each group per season to determine movement behaviour patterns between successive GPS fixes. We classed movement behaviour as “resting” if the distance between fixes was <100 m, “foraging” if the distance was ≥ 100 m but $<$ seasonal rv_{\max} for the group, or as “relocating” if the distance moved was \geq the seasonal rv_{\max} value. We then used multinomial logistic regression (R package `nnet`, Venables & Ripley, 2002), with “foraging” included as the reference category, to determine the effects of habitat type on southern ground-hornbill movement behaviour.

5.4 Results

5.4.1 Home range and habitat use

A total of 37 060 GPS locations were obtained for the six southern ground-hornbill groups, accounting for 3 143 group-days. All birds were tracked for a minimum of 11 months, although these months were not always concurrent. An additional 8 746 fixes (19%) were not recorded as a result of satellite signal acquisition failure or battery malfunction. Home ranges of southern ground-hornbills determined using KDE ranged from 2866 ha to 12145 ha (mean \pm SD = 5974 \pm 3058 ha; Table 5.1). All groups showed restricted ranges during the intensive breeding season months (December to March), with the percentage of the overall home range used varying from 21% to 97% (mean \pm SD = 63 \pm 27.0%). In the early and late dry seasons, groups expanded their ranges with many groups covering areas larger than the extent of their KDE home ranges (101% to 131%, n = 4).

Southern ground-hornbill territories comprised only eight of the 72 land cover habitat types with most groups not having equal access to all types. The eight habitat types defined according to the land cover layer were (1) “permanent water”, (2) “seasonal water”, (5) “dense bush, thicket and tall dense shrubs” (hereafter referred to as dense bush), (6) “woodland and open bushland” (hereafter referred to as open woodland), (7) “grassland”, (9) “low shrubland: other” (hereafter referred to as low shrubland), (36) “Mine (2) semi-bare” (hereafter referred to as gravel mine, and (41) “bare (non-vegetated)” (hereafter referred to as bare ground). The Ivlev scores for the preference of these habitat types for the various seasons per southern ground-hornbill group are given in Table 5.2. The Shingwedzi and Cleveland groups were the only groups with access to permanent water, although the Ivlev scores show that these areas were strongly avoided year round. With seasonal water, the Ivlev’s scores are more mixed with some groups actively avoiding these areas and other selecting these habitats. Although

available to all groups year round, bare ground (which includes roads) was strongly avoided. Only the Jock southern ground-hornbill group had access to the mine area, which they selected for in the late dry and early wet seasons, and strongly avoided for the remainder of the year. Dense bush and low shrubland were mostly used in proportion to their availability, although some seasonal preferences were evident. Open woodland and grassland were generally used by all groups in proportion to their availability.

The best linear regression model for seasonal southern ground-hornbill home range size (AICc = 157.2; Table 5.3) showed that seasonal home range sizes differed significantly amongst the six southern ground-hornbill groups studied. The amount of low shrubland ($p < 0.005$), and grassland ($p = 0.014$) also influenced seasonal home range size, with home ranges decreasing in size with increase in the proportion of low shrubland available and increasing in size when home ranges contained a higher proportion of grassland habitat. Although not significantly influencing the seasonal home range size, the percentage of dense thicket and open woodland areas were left in the model, as removing these increased the AICc values.

Woody cover was divided into the percentage area of the seasonal home range per southern ground-hornbill group that fell into the following categories, <25%, 25 - 50% and 51 - 75%. The best model explaining the influence of woody cover on seasonal southern ground-hornbill home range size included only the 25 - 50% woody cover category ($p = 0.004$, AICc = 159.8) with the percentage area within the 25 - 50% woody cover category decreasing as seasonal territory size increased.

5.4.2 First-passage time analysis

There were no clear patterns in the seasonal mean rv_{\max} values for the various southern ground-hornbill groups (Table 5.4). Some groups' rv_{\max} values were fairly constant year round

(e.g. Cleveland) whereas others (e.g. Jock and Mangake) fluctuated seasonally. The mean distances moved in the “resting” movement category were consistent across seasons, with mean “foraging” distances being similar in the late wet and early dry seasons and in the late dry and early wet seasons. The mean distances for the “relocation” movement category (\geq seasonal $r_{v_{max}}$) were lowest in the early dry season and highest in the early wet season.

The results from the multinomial regression showed that time spent within the low shrubland, gravel mine and bare ground habitats had a higher likelihood of being classed within the “relocation” category as opposed to the foraging category of southern ground-hornbills (Table 5.5). Conversely, time spent within the grassland, open woodland and dense bush habitat types more likely belonged to the “foraging” category as opposed to the “relocation” category. When comparing the “resting” behaviour to active “foraging”, all available habitats were preferentially selected for “foraging” as opposed to “resting”.

5.5 Discussion

The decision by an individual to move from one area to another is influenced by a number of factors, such as resource quality and availability, predation risk and local environmental conditions, all of which will influence its survival and reproductive output (van Moorter et al., 2013; Allen & Singh, 2016). The challenge for conservationists is understanding how these individual decisions influence population dynamics, home ranges and ultimately species survival (Allen & Singh, 2016).

The southern ground-hornbill breeding season coincides with the warm, wet summer months, when prey availability, and especially that of invertebrates, would be generally higher (Theron et al., 2013, Zoghby et al., 2015). We found that seasonal home ranges during the early and late dry seasons were larger than in the wet season, with groups using between 76 and 115% of their home ranges during the late dry season. This could be as a result of southern

ground-hornbills having to increase their search for food, as well as no longer being restricted to the area surrounding the nest, during this time.

Previous research on southern ground-hornbill home ranges has recorded group densities of one group every 4 000 ha (communal areas in Zimbabwe, Witteveen et al., 2013), to one group every 10 000 ha (Kruger National Park, Kemp & Kemp, 1980), with one group in the Limpopo Valley having a home range close to 20 000 ha (Theron et al., 2013). These results were obtained by direct observations of active nest sites or using radio transmitters. In our study using GPS data, we showed that home range sizes of southern ground-hornbills within Kruger National Park vary. However, all groups demonstrated a restricted and contracted home range during the breeding season, when they concentrate their movements around the nest site as found in other studies (Theron et al., 2013; Zoghby et al., 2015). Wyness (2011) reported that of four southern ground-hornbill groups studied in the Association of Private Nature Reserves (APNR) adjacent to the Kruger National Park, the three that bred successfully in the year of their study, showed a reduction in breeding range size ranging from 24 - 36% of their home range. The unsuccessful group used 70% of their home range during this time (Wyness, 2011), suggesting that breeding success could influence wet season home range size, possibly as the birds would no longer be bound to the nest site for prey provisioning. The groups within the Kruger National Park did not show such a definitive pattern in home range size reduction, based purely on breeding success. Of the six southern ground-hornbill groups monitored in our study, four groups bred successfully, one group's attempt failed (Ngotso Camp) and the breeding status for the third group (Shingwedzi) was unknown. The groups that bred successfully used 21 - 97% of their respective home ranges, with the unsuccessful group using 85% of their home range (See Table 5.1). These results suggest that factors other than breeding success influence the home range size during the wet period.

Southern ground-hornbills are known to favour more open habitats for foraging (Knight, 1990; Zoghby et al., 2015). Our results supported this, with groups selecting the open woodland and grassland habitat types year round, in accordance with their availability within the home range. Although southern ground-hornbill seasonal territory size differed significantly amongst the groups, they all showed a decrease in the amount of low shrubland and an increase in the amount of grassland habitat used with increased territory size. Similarly, as seasonal territory sizes increased, the amount of low-medium woody cover (25-50%) decreased. Thus, when selecting or evaluating an area as a reintroduction site for southern ground-hornbill groups, the ratio of low-medium woody cover (low shrubland) to grassland should be taken into account, as this will likely influence the home range size and number of groups that could be supported in an area.

Although an understanding of the changes and restrictions in territory size is important for the management of a species, the types of movements adopted within a population will influence the management actions needed for their conservation, such as ensuring connectivity or access to certain resources (Allen & Singh, 2016). Management actions have been shown to be less effective when interventions do not take the spatial and temporal changes in habitat use and scale of species movements into account (Allen & Singh, 2016). The results from the first-passage time analysis of southern ground-hornbill movements showed that the different groups did not consistently demonstrate seasonal patterns in the scale at which they concentrated their foraging efforts. The mean distance travelled for all trajectory paths classified as active “foraging” behaviour were similar and lower in the late wet and early dry seasons compared with the late dry and early wet seasons. The mean distances travelled allocated to the “relocation” category, or movement between foraging resource patches, were highest in the wet season months, with the maximum mean distances travelled during the early wet season and the start of the breeding period. Prey abundance is generally higher in the

wetter months, and so relocation distances are expected to decrease. We found that wet season movements were most likely influenced by the need to travel to and from the nest site to provision prey to the incubating female and growing nestling. Once resources closer to the nest were depleted, the distances travelled to access additional habitats and prey would also likely increase.

Habitat structure and the diversity of habitat types within a 3 km radius around the nest site have been shown to positively influence southern ground-hornbill nesting success (Combrink et al. in prep.). Southern ground-hornbills also showed a preference for the amount of open woodland habitat surrounding the nest site (Combrink et al. in prep.; Wilson & Hockey, 2013). An increase in the density of woody habitat surrounding the nest site negatively influenced breeding success (Combrink et al. in prep.), which could be as a result of decreased foraging opportunities, an increased risk of predation or an increase in foraging effort beyond a value which is beneficial. The results from the multinomial regression (Table 5.5) demonstrated that the likelihood of a movement behaviour being classified as “foraging” within the open woodland, grassland and dense thicket habitat types was higher than the behaviour being attributed to “relocating”. The selection of open woodland and grassland habitats for “foraging” over “relocating” was expected as these are the ideal open foraging habitats for southern ground-hornbills (Knight, 1990; Zoghby et al., 2015) and used year round in proportion to their availability. Southern ground-hornbills spend around 70% of their day walking (Kemp, 1995), and have been shown to travel distances of up to 10.6 km in a day (Zoghby et al., 2015). Having to navigate through dense thicket vegetation in an area may increase the amount of time spent there. This could account for why this habitat type is predicted to be used more for “foraging”-type behaviour as opposed to “relocating” behaviour. Travel through areas of low shrubland habitat would more likely be allocated to the “relocating”-behaviour category. This suggests that in this habitat type it is more profitable to

move further, and the corresponding chance of finding food greater, than conducting area-restricted searches and spending relatively greater time in one patch. When comparing movements between habitats allocated to “resting” as opposed to “foraging”, the time spent in all habitats was most likely as a result of “foraging”. The reason for this could be that the GPS locations were only recorded during the day and nightly roost sites, which may indicate habitat preferences for these were not recorded. During the day, southern ground-hornbills may not be selecting for specific habitat types as roost or resting sites during the heat of the day and may simply be roosting or resting at a chosen site within the habitat type in which they were “foraging” or “relocating”.

5.5.1 Management implications

Our results demonstrated that the ratio of low-medium woody cover (low shrubland) to grassland in an area selected for a potential reintroduction site of southern ground-hornbill groups is critical, as this influences the home range size, and number of groups that can be supported in an area. The amount of open woodland and grassland area are also of importance, as these areas are selected for as primary foraging habitat and are used in proportion to their availability in the landscape. From the compositional percentages of land cover types in the seasonal home ranges for southern ground-hornbills in the Kruger National Park, we calculated that for every 1 ha of grassland habitat, potential release site areas should contain a mean of 6.1 ± 3.07 ha of open woodland and a mean of 0.09 ± 0.13 ha of low shrubland. The fact that southern ground-hornbill home ranges differed greatly between seasons, largely owing to habitat type and not breeding success, also indicated that the habitat diversity within a potential home range for southern ground-hornbills should be considered.

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5.7 References

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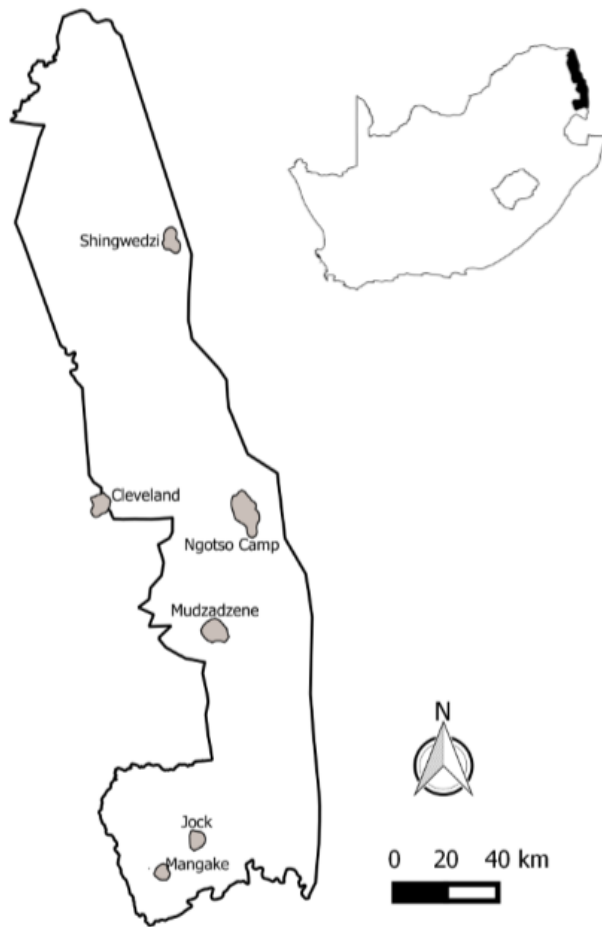


Fig. 5.1 Home ranges of the groups of southern ground-hornbills in the Kruger National Park tracked during the study period.

Table 5.1 Home, breeding and seasonal ranges of southern ground-hornbills in Kruger National Park, measured using Kernel Density Estimates in hectares with the percentage of the home range used in parentheses.

	Cleveland	Jock	Mangake	Mudzadzene	Ngotso Camp	Shingwedzi
Home range (ha)	5080	3757	2866	7154	12145	4843
Breeding range (Dec-Mar) (ha)	4931 (97%)	2040 (54%)	615 (21%)	5632 (78%)	10427 (85%)	1974 (40%)
Early wet	3938 (77%)	3417 (91%)	2176 (76%)	4787 (67%)	12279 (101%)	5749 (118%)
Late wet	4983 (98%)	1976 (52%)	244 (8%)	6509 (91%)	11673 (96%)	1113 (23%)
Early dry	5862 (115%)	3626 (96%)	3767 (131%)	7230 (101%)	9748 (80%)	3644 (75%)
Late dry	4927 (96%)	3963 (105%)	3298 (115%)	5437 (76%)	13212 (108%)	4972 (103%)

Table 5.2 Ivlev scores of habitat selectivity of southern ground-hornbills in Kruger National Park during the various seasons, with no symbols indicating areas used in proportion to their availability; “-“ indicating areas not available to the particular group; “‡” = areas used preferentially in relation to their availability and “*” = areas avoided compared with their availability.

Season	Group	Permanent Water	Seasonal Water	Dense Bush	Open Woodland	Grassland	Low Shrubland	Gravel Mine	Bare Ground
Early wet	Cleveland	-1.00*	-0.56*	0.11	-0.08	0.11	-1.00*	-	-0.79*
	Jock	-	-	0.11	-0.01	-0.04	-0.15	0.66‡	-1.00*
	Mangake	-	-1.00*	0.01	-0.03	0.06	-1.00*	-	-1.00*
	Mudzadzene	-	-1.00*	0.08	-0.06	0.03	0.28‡	-	-1.00*
	Ngotso Camp	-	0.14	0.58‡	-0.29*	0.02	0.14	-	-0.47*
	Shingwedzi	-1.00*	-0.02	0.31‡	-0.23	-0.22	0.34‡	-	0.16
Late wet	Cleveland	-1.00*	-0.90*	-0.09	-0.05	0.19	-1.00*	-	-0.58*
	Jock	-	-	0.00	-0.11	0.14	-0.20	-1.00*	-1.00*
	Mangake	-	-	0.15	-0.11	-0.11	-0.13	-	-
	Mudzadzene	-	-1.00*	-0.02	-0.20	0.23	0.70‡	-	0.61‡
	Ngotso Camp	-	0.28‡	0.40‡	-0.15	-0.16	0.26‡	-	-0.81*
	Shingwedzi	-1.00*	0.23	0.16	-0.14	-0.23	0.58‡	-	-0.27*
Early dry	Cleveland	-1.00*	-0.80*	-0.23	0.05	0.14	-1.00*	-	-0.84*
	Jock	-	-	-0.38*	-0.09	0.23	-1.00*	-1.00*	-1.00*
	Mangake	-	-1.00*	0.08	-0.04	-0.08	0.19	-	-1.00*
	Mudzadzene	-	-1.00*	-0.22	0.12	-0.07	0.20	-	-1.00*
	Ngotso Camp	-	0.28‡	0.31‡	0.10	-0.35*	0.12	-	-0.33*
	Shingwedzi	-1.00*	0.53‡	0.13	-0.16	-0.17	0.55‡	-	0.59‡
Late dry	Cleveland	-1.00*	-1.00*	-0.33*	0.11	0.07	-1.00*	-	-1.00*
	Jock	-	-	-0.28*	-0.19	0.27‡	-0.35*	0.35‡	-1.00*
	Mangake	-	-	0.09	0.01	-0.27*	0.15	-	-
	Mudzadzene	-	-1.00*	-0.01	0.06	-0.08	-0.29*	-	-1.00*

Ngotso Camp	-	-0.16	0.30	0.01	-0.09	0.00	-	-0.80
Shingwedzi	-1.00*	-0.22	0.08	-0.01	-0.18	-0.02	-	0.05

Table 5.3 Parameter estimates, standard errors and p values for variables in the best model (with the lowest AICc) relating the percentage of available foraging habitat with seasonal home range size of southern ground-hornbills. (Significance codes: ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1).

	Estimate	Std. Error	t value	<i>p</i>	Significance
Intercept	-104.44	84.229	-1.24	0.23537	
Dense thicket	-21.767	16.356	-1.331	0.20453	
Open woodland	18.214	14.603	1.247	0.23276	
Grassland	19.204	6.873	2.794	0.01434	*
Low shrubland	-36.141	6.08	-5.944	3.58E-05	***
Jock group	55.093	11.598	4.75	0.00031	***
Mangake group	47.347	8.591	5.511	7.67E-05	***
Mudzadzene group	58.338	12.936	4.51	0.00049	***
Ngotso Camp group	106.849	19.132	5.585	6.73E-05	***
Shingwedzi group	76.676	9.112	8.415	7.57E-07	***

Table 5.4 Mean rv_{\max} values obtained from the 10 trajectories randomly selected per group, and mean distance moved per movement behaviour by southern ground-hornbill group in the Kruger National Park, South Africa. These were identified using first-passage time and hourly location intervals, per season.

	Late wet	Early dry	Late dry	Early wet
Group	Mean rv_{\max} (m) per group per season - mean (SD)			
Cleveland	507.7 (343.1)	568.6 (299.8)	549.0 (132.4)	533.3 (281.8)
Jock	538.5 (291.9)	337.3 (163.8)	611.8 (318.7)	494.1 (203.2)
Mangake	415.4 (228.1)	517.7 (249.8)	431.4 (244.9)	729.4 (287.7)
Mudzadzene	511.5 (393.8)	549.0 (248.0)	780.4 (306.0)	725.5 (358.7)
Ngotso Camp	523.1 (399.0)	392.2 (149.8)	588.2 (202.3)	670.6 (401.2)
Shingwedzi	580.8 (443.7)	560.8 (323.9)	658.8 (305.2)	545.1 (116.9)
Movement mode	Distance moved (m) per season - mean (SD)			
Resting	46.4 (30.5)	41.1 (32.3)	37.2 (33.2)	38.8 (28.7)
Foraging	294.8 (120.0)	292.6 (119.3)	369.2 (144.8)	371.9 (157.2)
Relocating	908.9 (441.5)	715.9 (325.5)	821.6 (350.9)	1024.4 (538.2)

Table 5.5 Results from the multinomial model for the probability of hourly movement within various habitat types being associated with resting or relocating vs. foraging behaviour for southern ground-hornbill groups in Kruger National Park. The estimated coefficients (β) are given with standard errors (SE) and significance levels (p).

Variable	Relocating vs. foraging			Resting vs. foraging		
	β	SE	p	β	SE	p
(Intercept)	-0.0461	0.3051	0.8799	0.780	0.257	0.002
Dense thicket	-0.2827	0.3079	0.3586	-1.614	0.262	0.000
Open woodland	-0.2232	0.3055	0.4650	-2.418	0.259	0.000
Grassland	-0.1453	0.3065	0.6354	-2.283	0.262	0.000
Low shrubland	0.0775	0.3108	0.8030	-2.360	0.277	0.000
Gravel mine	9.6565	67.0236	0.8854	-3.185	6.003	0.596
Bare ground	0.0464	0.4289	0.9139	-3.871	1.054	0.000

Chapter 6: Discussion & Conclusions

6.1 Introduction

Habitat loss and climate change are two of the major threats currently facing bird species (Sisk et al. 1994; Owens & Bennett 2000; Jetz et al. 2007). Species located within protected areas are often considered safe, even though the majority of protected areas are small and growing evermore isolated, rendering them relatively ineffective (Cantú-Salazar & Gaston 2010). Much of Africa, in particular savanna areas, has shown a decline in large terrestrial birds, with the long-term survival of these populations heavily reliant on protected areas (Thiollay 2006a, 2006b). Consequently, conservation efforts to protect large terrestrial birds in future, may need to focus on very large contiguous protected areas in order to be effective (Cantú-Salazar & Gaston 2010).

Currently, around 44% of all hornbill species are considered globally threatened or near threatened with extinction, with the major threat being habitat loss (Poonswad et al. 2013). The majority of these threatened hornbills occur in Asian forests, with only one species, the southern ground-hornbill *Bucorvus leadbeateri*, occurring in savannas (Poonswad et al. 2013).

My PhD study aimed to determine the habitat, nesting and foraging requirements of southern ground-hornbills, based on the population located within the Kruger National Park. This population was studied, as it is considered the stronghold for the South African southern ground-hornbill population, with around 50% of the national population being located there (Kemp & Begg 1996). This research explored factors that could have affected southern ground-hornbill breeding success (determined based on the number of nestlings to reach ringing age during the study period), including aspects relating to the nest site location, type, cavity dimensions, nest treatment (potential effects of the removal of the second-hatched chick for

captive rearing) and the possible effects of temperature. Using stable isotope analyses of naturally-shed feathers and bill samples, I investigated the dietary niches of southern ground-hornbills, in particular, whether they are dietary generalists or specialists and what factors affected their dietary niche width. I used satellite tracking data to look at the seasonal home ranges and habitat use and preferences of southern ground-hornbills. Lastly, using first-passage time analysis, I determined the scale at which southern ground-hornbills concentrated their foraging efforts and whether habitat type had any influence on movement behaviour, and in particular, foraging.

This chapter provides a summary of the research objectives and findings, as well as overall management and conservation recommendations. Possible directions for future research are all discussed.

6.2 Research findings

Our research investigated aspects of southern ground-hornbill ecology, namely their habitat, foraging and nesting requirements, to address knowledge gaps highlighted within the National Species Recovery Plan for southern ground-hornbills (Jordan 2011). The overall aim of the research was to develop management guidelines and recommendations to assist the reintroduction of captive-reared southern ground-hornbills outside of protected areas within South Africa. This study had four main objectives.

Our first objective aimed to determine factors contributing to or influencing the nesting success of southern ground-hornbills in the Kruger National Park (Chapter 2). We considered a nest successful if the nestling reached ringing age (60-70 days). None of the features relating to rainfall or the availability of water sources (streams, dams etc.) contributed to nesting success (Chapter 2). This was surprising, as rainfall is known to influence southern ground-

hornbill breeding, with the onset of laying occurring only after the first rains of the season have fallen (Kemp & Kemp 1980; Kemp & Kemp 1991). In addition, Wilson and Hockey (2013) found that nests on territories which received more than 500mm of rain in a season were less successful.

We found that the amount of grassland habitat within 3 km surrounding the southern ground-hornbill nest site negatively affected their nesting success (Chapter 2). Our data showed that grassland was negatively correlated to the amount of open woodland habitat. Our results concur with Wilson and Hockey's (2013) findings that the amount of open woodland surrounding a southern ground-hornbill nest site positively influenced nesting success. We also found that habitat structure played a role, i.e. the denser the vegetation surrounding the nest, the less successful the group using that particular nest site (Chapter 2). Conversely, the greater the habitat diversity surrounding the nest, the more successful the group. Kemp & Begg (1996) found that nests near to roads were more attractive to southern ground-hornbills, although this did not influence the nesting success of the group. Our results suggest that proximity to roads has a positive influence on how successful a group is, possibly owing to the productivity of the road verge areas (Smit & Asner 2012) and the fact the groups are known to beg from tourists, especially during the dry season (Chapter 2).

Our data also supported the harvesting of southern ground-hornbill second-hatched chicks as a viable conservation initiative, as set out in the southern ground-hornbill National Species Recovery Plan (Jordan 2011). Removal of second-hatched chicks from southern ground-hornbill nests was found to have no significant effect on the survival to fledging of the first-hatched chick (Chapter 2).

Our results showed that habitat structure and diversity are critical when deciding on a suitable reintroduction site for southern ground-hornbills (Chapter 2). Nest site dimensions had no effect on southern ground-hornbill nesting success (Chapter 2). As nest sites, in the

form of artificial nests will most likely be provided, food availability and accessibility should be the primary resource of concern when assessing potential release sites.

Our second objective was to investigate the thermal fluctuations of southern ground-hornbill nest cavities during the breeding season to determine the current range of temperatures experienced by these birds in the Kruger National Park (Chapter 3). We found significant differences in nest cavity temperatures between groups and across both breeding seasons studied (Chapter 3). The artificial nest showed extremes in temperature, with the nest minimum and nest maximum being significantly lower and higher than ambient minimum and maximum temperatures, respectively. We showed that natural nests provide an important buffer against extremes in ambient temperatures, although nest cavity temperature had no effect on overall nesting success. (Chapter 3). Our results are encouraging as they suggest that an increase in ambient temperature, as predicted by climate change models (Thuiller et al., 2008), may not have a severe effect on southern ground-hornbill reproductive output.

Our third research objective was to explore the foraging ecology of southern ground-hornbills in the Kruger National Park (Chapter 4). We used stable isotope analyses of naturally-shed feather and bill samples to see what factors influenced southern ground-hornbill dietary niche width and to determine whether the birds are all dietary generalists or a generalist population consisting of a number of dietary specialists (Chapter 4). We showed that southern ground-hornbills exhibit a wide isotopic niche on both the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ axes (Chapter 4). Their nitrogen sources suggest that they consume prey from a range spanning around four trophic levels and for carbon sources, they access prey from almost the entire C_3 to C_4 spectrum. Age affected dietary niche width, with adults having wider niches than those of nestlings, and with nestling diet being completely incorporated within the adults' diet in isotopic space. Habitat and location (with regards to rainfall and soil type) also affected niche widths, with territories in areas with granitic soils and > 500 mm of mean annual rainfall having significantly

smaller niche widths. The results from the samples from the two female bills, suggest the possibility of specialisation at the individual level or could represent changes in diet in response to climatic variables and possible reactions to changes in abundance of specific prey species. Overall, our results suggest that southern ground-hornbills are obligate generalists owing to the wide range of carbon sources that they exploit and that they could be accessing prey species in accordance with their abundance (Chapter 4).

Our fourth objective was to determine southern ground-hornbill home range sizes and habitat use in the Kruger National Park (Chapter 5). We found that southern ground-hornbill home ranges differed seasonally, with all groups showing a range restriction during the breeding season (Chapter 5). Overall home range sizes ranged from 2866 – 12145 ha, with breeding season ranges being 615 – 10427 ha. Habitat preferences differed across the groups studied, but in all cases, grassland, open woodland and dense thicket areas were used in proportion to their availability year round. Our movement analyses showed again that grassland and open woodland were primary foraging habitats, highlighting the importance of these vegetation types in potential reintroduction sites (Chapter 5). We determined that the ideal ratio of grassland:open woodland:low shrubland in the release area should be 1.00:6.10:0.09 ha (Chapter 5). This again supports needing to control bush encroachment drivers, such as elephants *Loxodonta africana* and fire, to ensure that this balance and structural diversity is maintained.

6.3 Discussion and recommendations

Southern ground-hornbills, as with many other large bird species, are considered to be safe within protected areas, with most of the threats to the birds affecting those populations occurring in unprotected areas. We have shown that even within protected areas, without

sufficient management interventions southern ground-hornbill reproductive output and population status will decline.

We recommend annual monitoring of southern ground-hornbill nest sites to allow for the early detection and possible mitigation of bush encroachment or changes in habitat structure surrounding nest sites. This would also allow for the detection of nest site collapse or deterioration. In savannas, elephants (du Toit et al. 2003; O'Connor et al. 2014) and fire (Wigley et al. 2010; Buitenwerf et al. 2012; Parr et al. 2014) are important drivers of vegetation change and thereby, bush encroachment. If bush encroachment is identified as a problem in an area, especially where successful southern ground-hornbill groups are known to reside, efforts to control the influence of elephants or adjust the fire regime should be implemented.

As suitable nest sites are thought to be limiting (Kemp & Begg 1996), maintenance of these nest sites and erection of artificial nest boxes, in cases where nests collapse, should be considered as a conservation intervention. Southern ground-hornbills readily take to nest boxes and groups nesting in artificial nests have been shown to have a significantly higher breeding success than groups using natural nest sites (Wilson & Hockey 2013). Our results have shown that nest temperature does not affect nesting success and, although we only had data from one artificial nest, these results suggest that predicted increases in ambient temperatures as a result of climate change (Thuiller et al., 2008) may not adversely affect southern ground-hornbill breeding success. This further supports the provisioning of artificial nest boxes at potential reintroduction sites.

We recommend that the harvesting of second-hatched chicks from wild nests is continued, to increase the captive-rearing and captive-breeding stock. It is also important to keep recording sightings of southern ground-hornbill groups, especially during the breeding season, as these could lead to the discovery of new nests, which could potentially provide new genetic stock for these programmes.

In terms of assessing potential sites for reintroductions of southern ground-hornbills, our foraging and tracking data provided some useful insights into southern ground-hornbill diet, movements and behaviour. Southern ground-hornbills are known to take a variety of prey species and will consume anything that they can overpower (Kemp 1995). Our stable isotope results suggest that southern ground-hornbills are obligate generalists, being a species that exploits a wide variety of resources, but can concentrate on one particular resource if it is in abundance (Pagani-Núñez et al. 2016). Although rainfall and soil type influenced niche width, with groups with territories in areas receiving > 500mm of rain in a year and territories on granitic soils having significantly smaller niche widths, our results showed that southern ground-hornbills can survive and reproduce successfully across a range of habitats and on a variety of available food sources. Thus, provided the chosen site is large enough and the variety of potential niches for prey species high enough, they should be successful if reintroduced there.

Home range sizes of southern ground-hornbills differed between groups and seasonally, with the overall home range being 2866 – 12145 ha and the breeding season range being 615 – 10427 ha. In terms of habitat requirements, our results showed that the ratio of low-medium woody cover (low shrubland) to grassland in an area is critical, as this influences the home range size, and thereby, the number of southern ground-hornbill groups that can be supported in an area. Although nest sites are often found along drainage lines or in riparian areas (Kemp & Begg 1996), mainly due to the fact that these areas contain many large trees, we found that areas with permanent and seasonal water were mostly avoided. Open woodland and grassland habitats were selected for as primary foraging habitat and were used in proportion to their availability in the landscape year round. We determined that for every 1 ha of grassland habitat, potential release site areas should contain a mean of 6.1 ± 3.07 ha of open woodland and a mean of 0.09 ± 0.13 ha of low shrubland. The fact that southern ground-hornbill home ranges

differed greatly between seasons, largely owing to habitat type and not breeding success, also indicated that the habitat diversity at a potential release site should be considered.

6.4 Future work

Although this research on southern ground-hornbills in the Kruger National Park, a protected area, has addressed a number of noted knowledge gaps for this species, it has also raised certain additional questions. We have shown based on our nest temperature data (Chapter 3) that southern ground-hornbills can handle extremes of temperature within the nest cavity, which does not seem to have any effect on nesting success. We only had access to one artificial nest site for this study and would suggest that further research on temperature fluctuations for additional or other artificial nests be conducted to determine the best design (in terms of size, material used and insulation) for the provisioning of southern ground-hornbill nests at reintroduction sites.

Our foraging research also yielded a number of additional questions. Firstly, every effort should be made to collect any carcasses of southern ground-hornbills to further investigate the interesting relationships in isotopic signature that were demonstrated with the two female bill samples included in this study (Chapter 4). We were unable to ascertain whether these individual birds were showing patterns of specialist feeding behaviour or whether the changes in isotopic signatures were simply related to environmental factors. In addition, it would be very beneficial for the South African National Parks (SANParks) to commission a study focusing on the biodiversity differences between the two major soil types within the Kruger National Park, being granite and basalt. As soil types determine the vegetation (Colgan et al. 2012), which in turn affects the animal species distributions and abundance, understanding the biodiversity implications of the different soil types would support a number of studies conducted within the Kruger National Park.

6.5 Concluding remarks

This dissertation furthers our knowledge about the ecology of southern ground-hornbills. Through investigating their habitat requirements in the Kruger National Park, we have identified key habitat preferences and highlighted management interventions, such as controlling drivers of bush encroachment, that will ensure areas remain or can be made suitable for these birds. Our results also show that southern ground-hornbills are able to adapt to changes in their environment, like extremes in nest cavity temperature, and that provided they have a suitable nest site within a sufficiently large territory, ample food supply and a good mix of grassland and open woodland habitats within their territory, they will be able to survive in an area for the foreseeable future.

6.6 References

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