Breeding and dispersal implications for the conservation of the Southern Ground Hornbill *Bucorvus leadbeateri*

Kate Carstens

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FitzPatrick Institute of African Ornithology
DST-NRF Centre of Excellence
Department of Biological Sciences, Faculty of Science
University of Cape Town

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Supervised by Professor Peter Ryan
Co-supervised by Dr Rob Little and Dr Robert Thomson

Declaration

This thesis reports original research that I conducted under the auspices of the Percy FitzPatrick Institute, University of Cape Town. All assistance received has been fully acknowledged. This work has not been submitted in any form for a degree at another university.

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Kate Carstens

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Abstract

Populations of secondary tree-cavity nesting bird species are often limited by a shortage of natural nesting sites. For the Southern Ground Hornbill *Bucorvus leadbeateri* that typically nests in natural tree cavities, the shortage of nesting sites is one factor potentially limiting population growth. The species is listed as endangered in South Africa, and vulnerable throughout the rest of its range. Nest boxes can improve the conservation status of threatened birds that are limited by nest-site availability. However, nest boxes or other types of artificial nests are not always beneficial to the target species, and their value as a conservation tool needs to be tested for each species. Wooden nest boxes were installed for ground hornbills in a study area in north eastern South Africa with a paucity of natural nest sites. In this thesis, I assess productivity, timing of breeding, and dispersal in the Southern Ground Hornbill in a study area supplemented with nest boxes and discuss the implications for the conservation of this endangered species.

Nest boxes are an effective conservation tool to improve productivity in areas lacking natural tree cavity nesting sites. Breeding success (calculated as the proportion of nesting attempts that fledged a chick) and predation levels were similar for groups using nest boxes and natural nests. Natural nests were more buffered against cooling night temperatures, but otherwise nest boxes provided nesting conditions that were no better than natural nests. Timing of breeding for nests in natural tree cavities and nest boxes were similar. However, groups with access to a nest box attempted breeding more often than groups with access to a natural nest only, resulting in an 15 % increase in the number of fledglings per group compared to an adjacent protected area with no artificial nests. The number of breeding groups in the study area increased by 460 % over 12 years.

However, there is a limit to the density of breeding groups. Breeding success was highest when breeding density was one breeding group per 90–120 km^2, so nests should be spaced ~10 km apart. Given that the threats to ground hornbills include persecution and poisoning, increasing the reproductive rate by providing nest boxes should assist in slowing the decline by the increased recruitment of offspring into the population.

Timing of breeding varied across years. The first eggs laid each year ranged from 9 September to 14 November, and median lay date was 03 November. Breeding attempts that were initiated early in the season were more likely to fledge a chick than those initiated later in the season. Timing of breeding was delayed during warmer springs, particularly under dry conditions. In savannas, hotter spring temperatures could limit food availability, for example, if higher temperatures cause the vegetation to dry out, resulting in a rapid decline in insect flush, especially in the phytophagous insect groups that form a large part of the ground hornbill diet.

Factors to consider when constructing and placing nest boxes include thickness of the cavity walls, entrance height above ground and density of nest boxes placed in the landscape. Breeding attempts in natural nests and nest boxes with thicker nest walls and those positioned with higher entrances above the ground increased breeding success. Therefore, nests should be constructed with cavity walls at least 6 cm thick and placed so that the entrances are situated > 6 m above the ground.

With 186 ringed chicks fledging from the study area after the installation of nest boxes, it was possible to observe their dispersal within the study area and farther away into the adjacent Kruger National Park. There was no evidence for sex-biased dispersal. Males and females dispersed at similar ages, and over similar distances, raising interesting questions about inbreeding avoidance mechanisms in this species. If females do not disperse beyond the range of related males, how do related individuals avoid pairing, and what forms of individual recognition exist?

Acknowledgements

I owe a great deal to the many people who were involved in the making of this PhD. First and foremost, my significant other, Cassie Carstens, for being by my side every step of the way. I am grateful that he shares my fascination with these modern-day pterodactyls, and for his love and support during this journey. To my supervisor, Peter Ryan, for his impeccable guidance. He allowed me to shape this PhD in my own way, but at the same time provided just enough steering to make sure my thoughts didn't drift too far of course. To Rob Little, who gave me the chance to do this PhD, and who assisted me to edit countless versions of chapters. His help and guidance from the very beginning made this journey fun. To Robert Thomson, who came on board as an unofficial co-supervisor a little later during my PhD journey, but who provided useful comments on the chapters when my logic was sometimes flawed. To the support staff of the Fitz: Hilary Buchanan, Anthea Links, Tania Jansen, Chris Tobler, Margaret Koopman, Susan Mvungi, Denise Scheepers and Gonzalo Aguilar; knowing they were there to help was always a huge relief. And to Phil Hockey for his support during my early days with the study.

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Chapter 1 An introduction to artificial nests as a conservation tool

Thirteen per cent of bird species are currently listed as globally threatened (1375 of 10424 species are vulnerable, endangered or critically endangered, IUCN 2016). Habitat loss is the primary cause of population declines, affecting 87 % of threatened species globally (Williams et al. 2013). However, strategic conservation interventions can be effective at reducing the decline of threatened avian species (Williams et al. 2013).

Habitat loss has necessitated the declaration of protected areas to conserve vital tracts of natural habitat for threatened species. This type of intervention is effective in protecting a suite of species that utilise habitats within these protected areas. In 2009, 14 % of terrestrial habitat was under formal protection globally (Watson et al. 2016). In South Africa, 7 % of the country's terrestrial habitat has been designated as formally protected areas (IUCN & UNEP-WCMC 2014), with an additional 17 % that is privately owned and protected, such as private nature reserves or wildlife ranches (Cousins et al. 2008). The extent of formally protected areas needs to continuously expand to maintain current levels of avian species richness (Evans et al. 2006). By 2020, target 11 of the CITES Strategic Vision is to have 17 % of terrestrial environments protected globally (CITES & CBD COP 2011). Although the establishment of protected areas is currently outpacing habitat transformation (Watson et al. 2016), the increasing human population size and demands for natural resources make it unlikely that the 2020 target to reduce biodiversity loss will be met (Tittensor et al. 2014). A fresh approach is needed to reduce biodiversity loss (Seddon et al. 2016), where slowing and reversing the decline of threatened species may require short-term, direct, species-specific interventions.

Direct interventions to reduce the decline of avian populations

Where habitat preservation and legal protection are insufficient, direct human interventions can be applied, with conservation measures targeted at specific threatened or near-threatened bird species (Cade & Temple 1995). Direct human interventions include translocations, harvesting of redundant offspring, and the removal of predators. Translocations aim to re-establish a population that was extinct in the wild or that has been reduced to numbers identified as being too small for future population persistence (Williams et al. 2013). Another example of a direct human intervention is the harvesting of redundant offspring to be incorporated in wild-release and captive breeding programs (L Kemp pers. comm.). These approaches have resulted in recoveries of several species that were on the brink of extinction. Some of the most famous examples come from the island of Mauritius, where captive breeding and wild releases restored populations of the Mauritius Kestrel *Falco punctatus,* Echo Parakeet *Psittacula eques* and Pink Pigeon *Nesoenas mayeri* (Jones & Merton 2012). In New Zealand, predation by introduced mammals such as rats and cats caused population declines of species such as the Kakapo *Strigops habroptila* (Lloyd & Powlesland 1994), Red-fronted Parakeet *Cyanoramphus novaezelandiae* (Oritz-Catedral & Brunton 2010) and Black Robin *Petroica traversi* (Butler & Merton 1993). By transferring rapidly declining bird populations to predator-free islands succeeded in saving these species. In the USA, translocations have assisted population recovery of the Red-cockaded Woodpecker *Picoides borealis,* by increasing the number of breeding pairs and the population size, as well as by minimising the potential negative genitive consequences of small population size (Franzreb 1997) World-wide, the costly and time-consuming eradication of introduced cats, rats and mice on ecologically sensitive islands is assisting the recovery of several threatened bird species (Nogales et al. 2004; Howald et al. 2007; Ratcliffe et al. 2010). For example, Galapagos Petrel *Pterodroma phaeopygia* breeding success increased and predation of adults decreased following the control of introduced mammalian predators (Cruz & Cruz 1996). These are just some examples of the hundreds of threatened species that are currently benefitting from targeted efforts to mitigate population extinction risks (Williams et al. 2013). In addition to translocations, harvesting of redundant offspring and predator control, another direct intervention to reduce the decline in avian populations is the installation of artificial nest sites to assist with the recovery of threatened populations that have suitable habitat, but are limited by a lack of suitable nesting sites. Suitable habitat is an important prerequisite, to avoid creating an ecological trap, which is drawing pairs or groups into areas to breed where they may not be adequate forage or roosting sites for example.

Nest boxes as a conservation tool

Nest boxes have been used as a conservation tool for a wide range of taxa, including mammals, insects and birds. In Australia, nest boxes have been used as a research and management tool for arboreal marsupial for over 30 years (Beyer & Goldingay 2006). IN addition, nest boxes are used as a research tool for insects such as bees (Lopez-Vaanmonde et al. 2004), with hives being used as a cost-effective management tool to deter elephants from raiding crop fields (King et al. 2009). But by far the most number of studies involving nest boxes have been those on birds.

Birds make use of a wide-range of man-made structures for nesting that were not intended for this purpose. Familiar sites include buildings, bridges, pylons and hollow fence posts (Mainwaring 2015). However, nest sites can be created specifically for occupation by birds. These artificial nests include, but are not limited to, burrowing chambers for seabirds and owls (Smith & Belthoff 2001; Belthoff & Smith 2003; De León & Mínguez 2003; Bolton et al. 2004; Sherley et al. 2012; Nadeau et al. 2015; Bourgeois et al. 2015), platforms for birds of prey (Schmutz et al. 1984) and man-made islands for flamingos (Anderson & Anderson 2010). But the most wide-spread and familiar type of artificial nest is the nest box that provides nesting sites for cavity nesting birds.

Populations of at least some tree-cavity nesting bird species are limited by the shortage of natural nesting sites (Newton 1994, but see Wiebe 2011 for mature, unmanaged forests). Cavity nesting species include some of the most exploited and threatened groups of birds including parrots and hornbills. The loss of old trees, and thus the loss of natural tree cavities, has occurred largely because of logging, the felling of trees for firewood, and forest clearing for agricultural practices (du Plessis 1995; Lindenmayer et al. 2012). The formation of protected areas assists with conserving tracts of existing and future large trees (Lindenmayer et al. 2014), but in some cases, such as the loss of large trees due to impacts by African Elephant, the threats persist regardless of the designation of the protected area (Mograbi et al. In press).

Direct approaches, such as the installation of nest boxes, have been used to provide immediate solutions to the shortage of nesting sites. Apart from the obvious benefit of allowing individuals to breed in areas where natural cavities occur at low densities or not at all, nest boxes have three additional benefits. For example, providing nest boxes can decrease intra-specific competition for cavities and allow additional individuals to breed (Newton 1994). This can be beneficial in areas where the breeding density is low, and nest boxes assist to increase breeding densities to levels that would be expected prior to the loss of natural nesting sites. In addition, nest boxes provide cavities that are typically more suitable for nesting than natural cavities thereby increasing reproductive output (Korpimäki 1985; Mitrus 2003; Sherley et al. 2012; Briskie et al. 2014). For field biologists, nest boxes also provide a tool with which to increase the amenability and efficiency with which a species can be studied (Griffith et al. 2008). This is especially true in long-term studies of passerines such as the Pied Flycatcher *Ficedula hypoleuca* (Lundberg & Alatalo 2010), Tree Swallow *Tachycineta bicolor* (Robertson & Rendell 1990; Ardia et al. 2006), House Sparrow *Passer domesticus* (Griffith et al. 1999; Nakagawa et al. 2007, 2008) and Great Tit *Parus major* (Perrins 1965; Visser et al. 1998).

Many empirical studies have used nest boxes to understand their contributions to nesting success (Brazill-Boast et al., 2013; Griffith et al., 2008; Miller, 2002; Stamp et al., 2002) or to compare the breeding performance between pairs using natural nests versus nest boxes (Robertson & Rendell 1990; Purcell et al. 1997; Mitrus 2003). Other studies have investigated the differences, if any, in predation rates (Storaas 1988; Rangen et al. 2000; Mezquida & Marone 2003; Nana et al. 2014) and parasite loads between the two nest types (Møller 1989; Thompson & Neill 1991; Wesołowski & Stańska 2001).

Importantly, nest boxes can be a useful conservation tool to assist the recovery of declining populations of threatened species (Williams et al. 2013). The provision of nest boxes has assisted population increases in birds of prey (Toland & Elder 1987; Fargallo et al. 2001; Catry et al. 2007), cavity-nesting waterfowl (Dennis & Dow 1984; Pöysä & Pöysä 2002), and woodpeckers (Walters et al. 1991; Franzreb 1997). Local increases in a critically threatened population of Red-cockaded Woodpeckers *Picoides borealis* occurred following the installation of nest boxes in South Carolina (Franzreb 1997). Nest boxes enhanced the reproduction in the endangered Gouldian Finch *Erythrura gouldiae* (Brazill-Boast et al. 2013), and the near-threatened Great Hornbill *Buceros bicornis* (Pasuwan 2000).

However, nest boxes or other types of artificial nests are not always beneficial to the targeted species. Of 120 studies describing the effect of artificial nests on breeding success and population size, 81 % reported positive effects on breeding success or population growth compared to natural cavities, 4 % reported similar levels of breeding success or no change in population size, while 15 % reported negative effects (Williams et al. 2013). Maladaptive outcomes of installing artificial nests have been attributed to increased competition for nests (Finch 1990), breeding densities that are too high and that result in decreased reproductive output (supra-optimal breeding densities, Mänd et al. 2005), poor habitat (Mänd et al. 2005; Smallwood & Collopy 2009; Demeyrier et al. 2016), increased harvesting of eggs or poaching by humans (Feekes 1991; Sanz et al. 2003; Briceño-Linares et al. 2011), higher temperature fluctuations inside the nest which, if extreme enough, can bring the temperature of egg or nestling to critical thermal maximums or minimums causing failure to hatch or death(Brightsmith & Figari 2003), high levels of predation (Finch 1990; Botelho & Arrowood 1998; Dailey 2003) which can result from the conspicuous placement of nests (Evans et al. 2002). Since nest boxes have had adverse effects on some species, the levels of success, such as how breeding success compares between pairs or groups using nest boxes and natural nests should be tested in each case.

In addition to investigating the success of providing nest boxes, the cost effectiveness of doing so should also be investigated (Lindenmayer et al. 2009), especially in cases where artificial nest boxes are to be maintained over extended periods. Costs to be considered include the cost of nest box construction, installation, maintenance and replacement (Lindenmayer et al. 2009). It is also worth considering the benefits of additional or alternative approaches to promote the development of natural nesting hollows, such as land management strategies aimed at conserving mature trees (Gibbons et al. 2008).

Nest boxes for ground hornbills

The Southern Ground Hornbill *Bucorvus leadbeateri* (hereafter ground hornbill) is the largest cooperatively breeding bird globally, and it is a flagship species of the African savanna biome (Figure 1.1**Error! Reference source not found.**). The species occurs in 13 countries in Africa, from Kenya in the north to South Africa in the south. The core of the South African population occurs in the north-eastern regions of the country (Figure 1.1), with the entire South African population estimated to be 1290–2380 individuals and declining (Taylor & Kemp 2015).

Habitat loss is one of the most important threats facing ground hornbills. The species has undergone a range reduction of ~66 % in 115 years, and the species is currently listed as endangered in South Africa (Taylor & Kemp 2015). The typical and preferred habitats of this species are the tropical and subtropical savannas. However, 79 % of these habitats have been converted and only 20 % is protected, including grasslands and shrublands (Watson et al.

2016). Ground hornbills require large territories of roughly 100 km^2 (Kemp & Kemp 1980; Knight 1990). They are secondary cavity nesters (although they can dig their own nests in mud banks), mainly relying on large natural cavities in trees or rock crevices, which are scarce in the landscape in Kruger National Park (Kemp & Begg 1996).

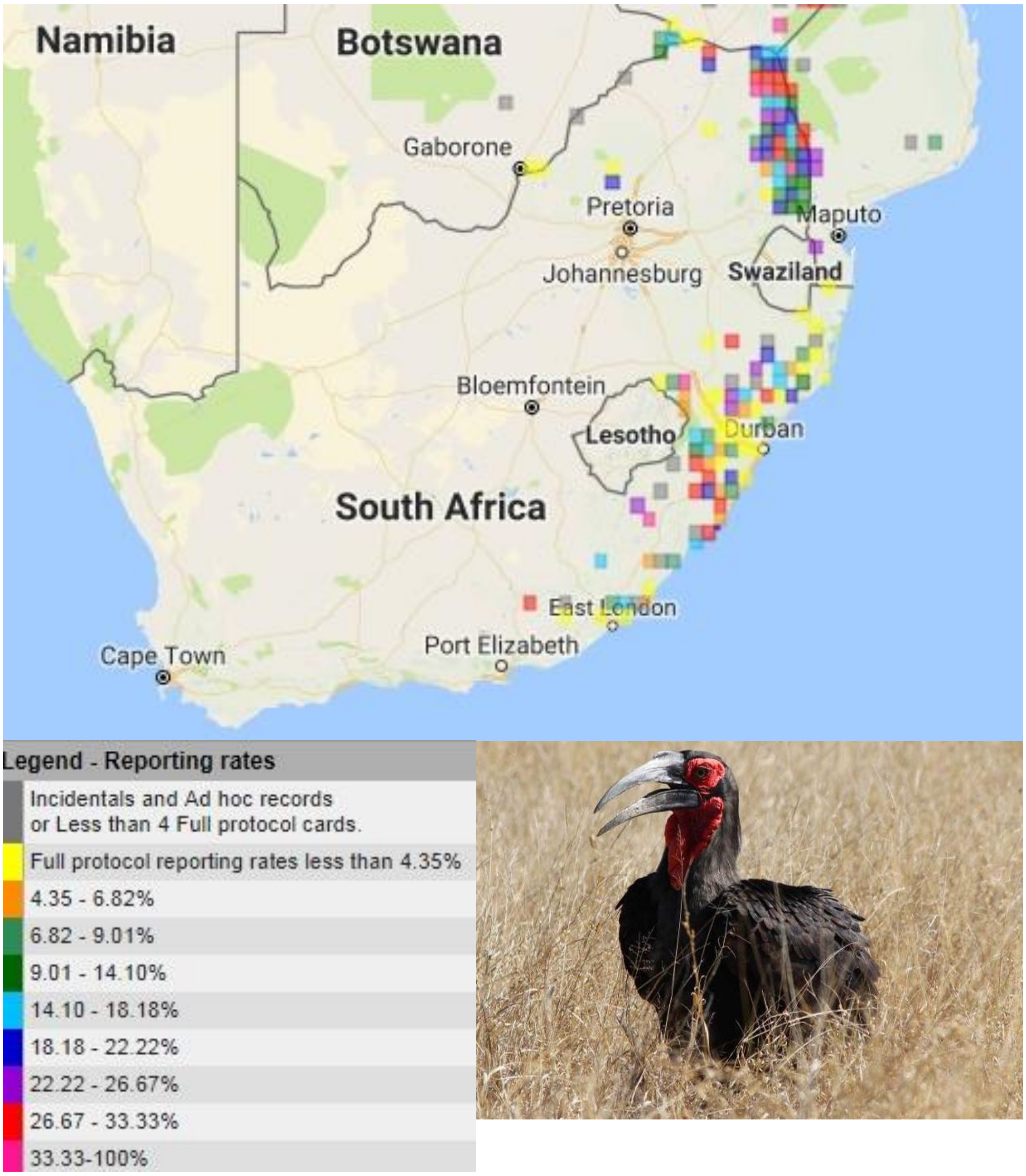

Figure 1.1. Distribution of the Southern Ground Hornbill *Bucorvus leadbeateri* in South Africa, showing the core of the population in the north-east of the country. (Map and legend: Southern African Bird Atlas Project, 2017. Photo: Southern Ground Hornbill, Johann Carstens 2016).

In the African savannas, large trees are removed from the landscape mostly by humans and African Elephants *Loxodonta africana*, and less so by wind or fire (Mograbi et al. in press). Several factors have contributed to the decline in the ground hornbill in South Africa. Direct threats contributing to ground hornbill declines nationally include persecution, secondary poisoning, electrocution (Taylor & Kemp 2015), lead toxicosis (Koeppel & Kemp 2015), and the killing of individuals for traditional medicine (Bruyns et al. 2013; Coetzee et al. 2014). However, the major factors contributing to their population decline are the loss of suitable habitat and a shortage of suitable nesting sites (Jordan 2011).

The aims of the Southern Ground Hornbill Species Recovery Plan (Jordan 2011) are to slow, halt and eventually reverse the population decline of the species in South Africa. The six objectives of the plan are to: (1) understand the genetic relationships across the populations, within family groups and the mechanisms behind female and immature dispersal, (2) collect information on population threats and mortalities to determine their importance, (3) increase awareness and the threats acting upon the species to increase tolerance towards the species and reduce persecution, and (4) provide an insurance against future declines in the wild population by managing a viable *ex situ* population, (5) generate an increase in the population by expanding it into parts of its historic range and, (6) investigate and implement *in-situ* and *ex-situ* management and conservation interventions to increase populations in South Africa and neighbouring countries. This study relates particularly to the last two points.

There are an estimated ~660 ground hornbill groups in South Africa, based on a maximum population estimate of 2380 individuals and a mean group size of 3.6 individuals per group (Vernon 1986, Kemp et al. 1989, Knight 1990). Given that the population is declining (Taylor & Kemp 2015), a critical step in slowing this decline is to ensure that all groups can breed. But since natural nesting sites are in short supply (Kemp & Begg 1996), the effective number of breeding groups is likely to be considerably smaller than 660. Thus, providing artificial nests could increase the number of breeding groups in the country. Secondly, the current reproductive rate is relatively slow, with estimates of groups raising one chick on average every nine years in the Kruger National Park (Kemp 1990). Finding a way to increase this reproductive rate would further slow the decline, as the loss of individuals through poisoning and persecution would be balanced at least in some way by the increased recruitment of offspring into the population.

An intervention currently underway to increase the number of breeding groups is the release of groups back into suitable habitats in parts of the species' historic range in South Africa, such as in the Waterberg areas (Limpopo Province) and Loskop Dam area (Mpumalanga

Province). The reintroduction areas targeted so far also lack natural nesting sites, highlighting the lack of nesting sites as a population limiting factor (Kemp & Begg 1996, Jordan 2011), and necessitating the use of artificial nests to facilitate the reintroduced groups to contribute by adding progeny to the population. Nest boxes also have been installed as a conservation intervention in the Limpopo River Valley (~ 20 boxes) and the Associated Private Nature Reserves (APNR, the area used for this study; 31 nest boxes) during the past two decades, where wild groups occur but where natural nesting sites were in short supply. In the Limpopo River Valley, nest boxes remain unoccupied. The few breeding groups that occur there nest in Baobab tree cavities and have low breeding productivity (Theron 2011). In the APNR in north-eastern South Africa, only 13 natural nests were discovered in 1800 km^2 (180 000 ha). A total of 28 nest boxes installed during 2003–2008 (25 installed during 2003 and 2004), and 64 % were subsequently occupied by groups by 2008 (Wilson & Hockey 2013). In the APNR study site, Wilson & Hockey (2013) identified environmental and social factors affecting breeding success, such as rainfall over the season, group size, and the amount of open habitat around nests. Now, an evaluation of nest boxes as a conservation tool is needed to guide future nest box provision programmes, that includes an investigation into additional nest-related factors that may influence reproductive productivity, as well as an assessment of the impact that providing nest boxes had on groups in the study area.

This study characterises breeding biology and dispersal in the only occurring ‘nest-box’ population of ground-hornbills. This study draws together analyses on reproductive productivity, laying dates, breeding group density and group size

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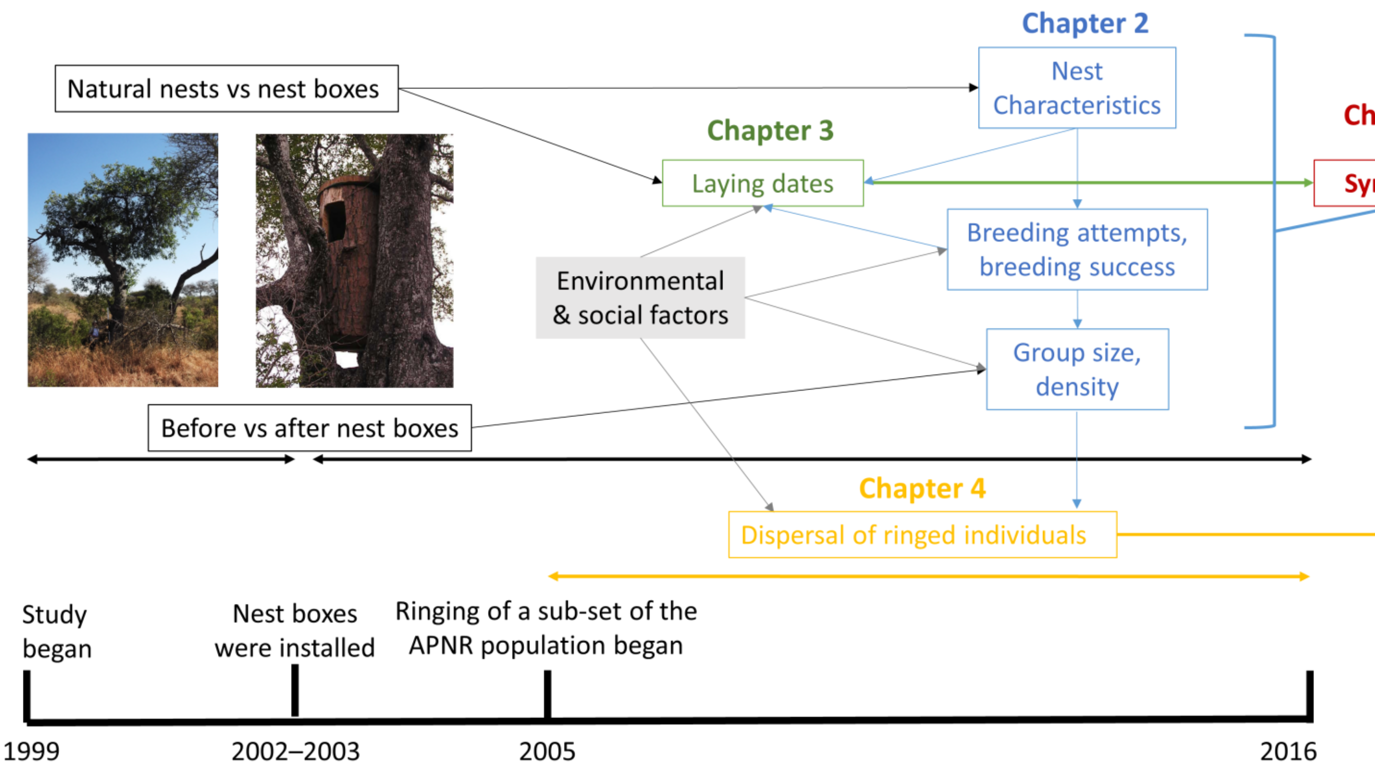

Figure 1.2**Error! Reference source not found.**). In addition, it will describe how this intervention allowed for the ringing of a relatively high number of chicks and older individuals which allowed, for the first time, a study on the movement of ringed individuals within the study area and into an adjacent protected area

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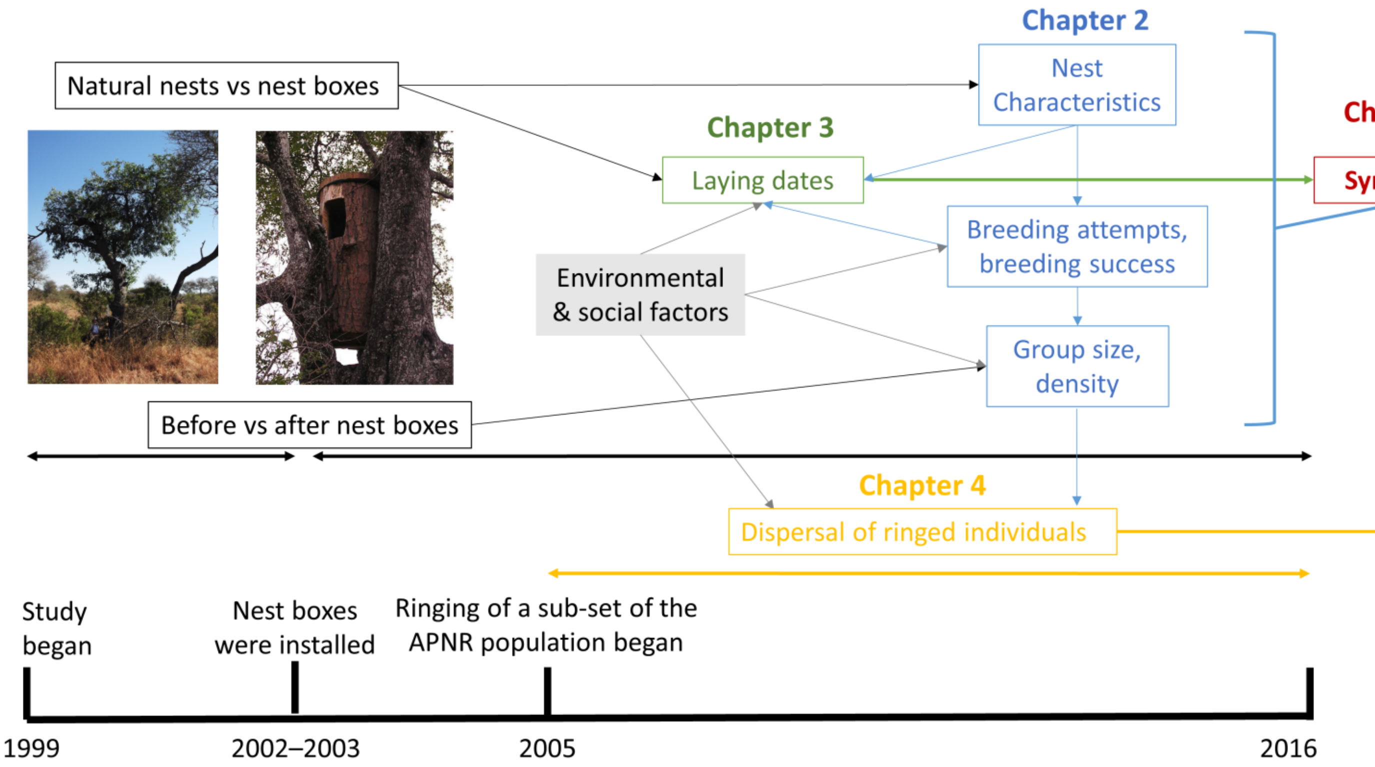

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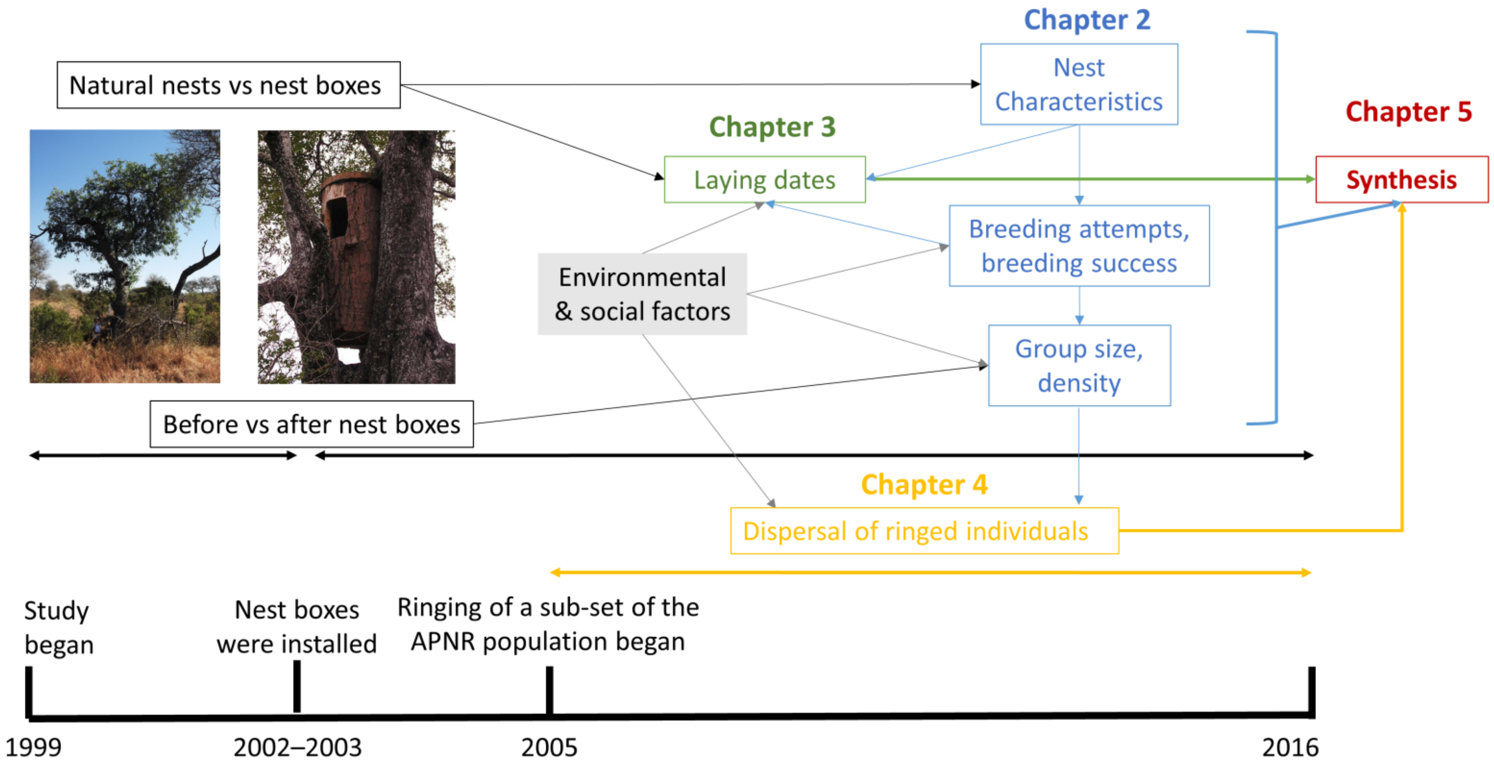


Figure 1.2. Mind map of the topics covered within each data chapter (chapters 2–4), ultimately being drawn together in the synthesis (chapter 5).

Ground hornbill general biology

The two ground hornbill species that comprise the family Bucorvidae are restricted to sub-Saharan Africa (Poonswad et al. 2013). The Abyssinian Ground Hornbill *Bucorvus abyssinicus* occurs from Senegal to Ethopia, and forms an allospecies with the Southern Ground Hornbill, which replaces it to the south, occurring from Kenya to South Africa (Figure 1.3**Error! Reference source not found.**). The global population sizes of neither species have been quantified (Hoyo et al. 2001; IUCN 2016).

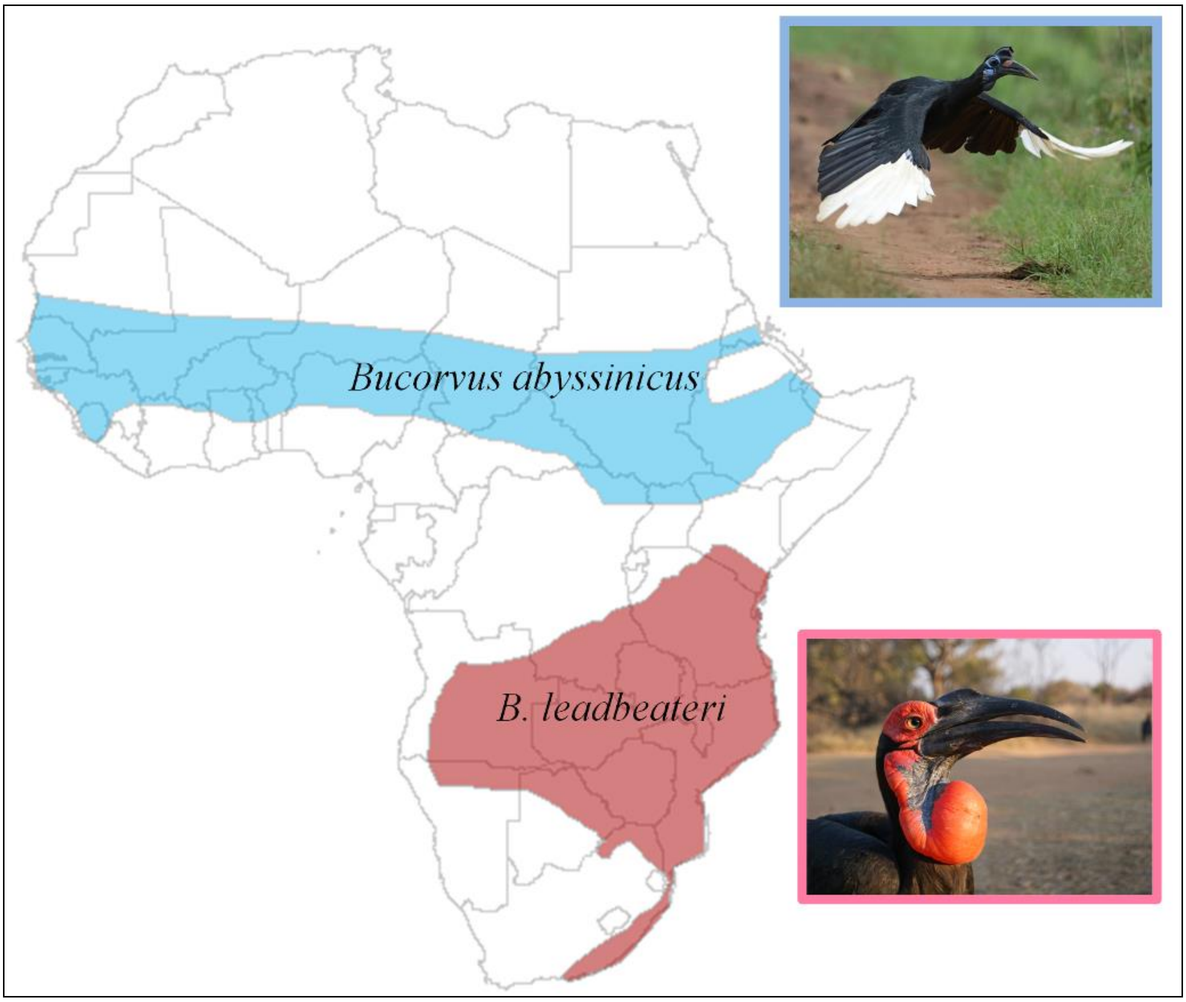


Figure 1.3 Distribution of the Southern Ground Hornbill *Bucorvus leadbeateri* (red), showing non-overlapping range with the Northern Ground Hornbill *B. abyssinicus* (blue). Photos: Krzysztof Błachowiak (Northern Ground Hornbill) and Kate Carstens (Southern Ground Hornbill).

Ground hornbills have a life-span of up to 50 years and reach maturity between 4–6 years (Kemp 1990). Adult males weigh up to 5.5 kg and adult females up to 3.5 kg (Morrison et al. 2005). They live in groups of 2–11 individuals which consist of a breeding pair, non-breeding sub-adults (mostly male helpers) and immature individuals (Kemp 1990). They are slow-breeding and fledge only one chick every 2–9 years (Kemp 1990). Breeding takes place in the austral spring and summer (September–March) with females typically laying two eggs, 2–5 days apart (**Error! Reference source not found.**Figure 1.4, Kemp 1990). Incubation begins when the first egg is laid, and lasts 38–42 days. Hatching is asynchronous and the female feeds mostly to the older, larger chick. Due to lack of food, the second-hatched chick succumbs to starvation a few days after hatching (Kemp & Kemp 1980). However, if the first chick perishes, the second chick is fed and raised. Consequently, only one chick is raised to fledging per breeding attempt, and fledging takes place at 80–90 days after hatching.

Ground hornbills consume any prey small enough to be overpowered, such as insects, snails, reptiles, amphibians, birds (including eggs and chicks), and small mammals (Kemp 2005). Groups usually remain within a 3-km radius of the nest when breeding (Wyness 2011), and travel up to 6–8 km per day to and from the nest (Zoghby et al. 2015). During winter, groups use the maximum extent of their ~100 km^2 home range (Wyness 2011), but significantly reduce their daily foraging movements (Zoghby et al. 2015).

Figure 1.4 A Jackalberry Tree *Diospyros mespiliformes* that contains a natural Southern Ground Hornbill nest. Top right: two eggs laid in a nest typically lined with Mopane *Colophspermum mopane* leaves. Bottom right: two ground hornbill chicks showing the difference in size between the large first-hatched chick and the much smaller, second-hatched chick. Photos by Cassie and Kate Carstens.

Timing of breeding and dispersal in the Southern Ground Hornbill

Ground hornbills are long-lived (60+ years, Kemp 1990), slow breeding (1 chick every 9 years, Kemp 1990), and occupy vast home ranges (100 km^2, Kemp & Kemp 1980). Acquiring enough data to investigate relatively basic biological questions on the species, such a factor affecting breeding success, timing of breeding and dispersal of individuals, therefore requires input from long-term studies operating in a relatively large area. Ground hornbills in the 1800 km^2 Associated Private Nature Reserves in north-eastern South Africa have been monitored since 2000, providing more than a decade of breeding data and resightings of ringed individuals. The APNR population is unique in that it is an area where > 75 % of groups breed in nest boxes. Consequently, it provides an opportunity not only to investigate the role of nest boxes as a conservation tool, but to also investigate little-known aspects of the species biology, such as the timing of breeding and dispersal, using the data collected from this monitored population occupying nest boxes over a relatively long period (since 2002).

Timing of breeding

For most bird species that live in seasonal environments, nests initiated in the first half of the season are more likely to fledge a chick and have offspring that survive to the next season than breeding attempts in the latter part of the breeding season (Perrins 1970; Daan et al. 1989; Verhulst & Nilsson 2008). Anthropogenic climate change is affecting the timing of breeding in many bird species with mostly negative consequences (Dunn & Winkler 2010). For example, inducing earlier egg-laying caused by warmer weather which then causes mis-timing between breeding and peaks in food supply, which can cause breeding attempts to fail (Møller et al. 2010) Since most studies emanate from the northern temperate regions, there is a need to better understand the effects of environmental conditions on avian phenology across a wider geographic scale (Dunn & Winkler 2010), and in bird species other than passerines, such as Hornbills.

Ground hornbills in South Africa occurs during the wet, austral spring and summer months (September–March) and typically only a single breeding attempt is made per season. Breeding females generally lay two eggs. At most, one chick, usually the first-hatched, is raised to fledging. With time and energy focussed on only a single breeding attempt per season, timing the breeding attempt to maximise the likelihood of fledging a chick is crucial to achieve maximum fitness benefits.

Kemp and Kemp (1991) investigated the timing of breeding of ground hornbills in the Kruger National Park, north-eastern South Africa, from breeding attempts that took place during 1966–1989. The authors investigated whether rainfall over the previous year (July–June) affecting the timing of breeding, or rainfall over the winter prior to egg-laying, and found that neither effected the timing of breeding (Kemp & Kemp 1991). Rather, timing of breeding generally coincided with the first rains of summer: laying was late when summer rains were late, and heavy rain appeared to synchronise laying (Kemp & Kemp 1991). Kemp & Kemp (1991) conclude that rainfall is not directly involved in effecting timing of breeding, but rather indirectly by effecting food supply for laying females. Not addressed in their study were other factors that may be associated with the timing of breeding, such as ambient temperature, nest type, group size and female identity. The association between timing of breeding and each of these additional factors are discussed in greater detail in Chapter 4, and investigated in a ground hornbill population supplemented with nest boxes.

Dispersal

Natal dispersal in animals is the permanent movement of individuals away from their natal site to the first site where they attempt to breed, and breeding dispersal is the movement of individuals among breeding sites (Greenwood & Harvey 1982). Individuals disperse for example to avoid pairing with close kin (Howard 1960; Woxvold et al. 2006; Ortego et al. 2008; Nelson-Flower et al. 2012), since inbreeding has high costs such as reduced hatch rate, brood size and survival (Keller & Waller 2002). Understanding a species ability to disperse and what conditions favour or limit dispersal, is important to understand the species' ability to track environmental shifts and thus the likelihood of a species persistence (Ferriere et al. 2000).

Birds in general mostly exhibit delayed dispersal by males (male philopatry) and most of the dispersing individuals are females (female-biased dispersal, Greenwood & Harvey 1982; Williams & Rabenold 2005; Temple et al. 2006). Male birds typically have greater ease of acquiring a territory closer to home than further away (Greenwood 1980), and therefore it pays to stay (Koenig et al. 1992). Females, to avoid pairing with male relatives, generally (but not always) disperse further than males. But not all species show this difference in dispersal distances between the sexes, with some studies revealing systems where males and females disperse equally far (Blackmore et al. 2011; Nelson-Flower et al. 2012; Engler et al. 2014). In some cases, the dispersal distances are similar because of a distance limitation, such as on relatively small islands (Engler et al. 2014). In another case, females may not have to disperse far to avoid pairing with close relatives, due to their ability to recognise and avoid familiar group members as mates (Nelson-Flower et al. 2012).

Kemp (1990) monitored 12 groups of unmarked individuals in central Kruger National Park. He found that ground hornbill groups typically comprise a breeding pair and a variable number of mostly male non-breeding helpers (Kemp 1990). Remembering the limitation of observing movements of unmarked individuals (some of which were identifiable by unique physical characteristics), he found that males and females appeared to have different dispersal strategies (Kemp 1990). Young females were thought to disperse once mature, which is reached at approximately 6 years of age (Kemp 1990). Males were thought to delay dispersal, remaining in their natal territories for at least six years, after which they presumably inherited the natal or a neighbouring territory (Kemp 1990). The long-term study in the APNR provided an opportunity to test the generality of Kemp’s (1990) inference of male philopatry and female-biased dispersal, and expand that study to explore causes of dispersal age and distance, as well as the selection of new groups by dispersing individuals. For the first time, this study describes dispersal events of ringed ground hornbill individuals, using resightings of ringed individuals since ringing in the study area began in 2005.

Thesis outline

Chapters are largely written in a style to ease subsequent publication; however large pieces of repetitive text have been removed to ease readability. The full description of the study area and study species appears once in the thesis. The description of nest boxes and their installation is described in full in Chapter 2 but not in the other chapters.

In the first data chapter, Chapter 2, I set the scene by describing the characteristics of natural tree cavity nests and nest boxes that are found in the study area. I compare the characteristics of the two nest types to understand what differences exist, if any, before using these data to explore their effects on breeding attempts and breeding success. I will be specifically exploring the proportion of breeding attempts that fledged a chick as a measure for breeding success. The effect of nest type on reproductive output is investigated in conjunction with environmental (rainfall and habitat) and social factors (group size). This aspect of the thesis expands on a previous investigation on factors affecting variation in reproductive success (Wilson & Hockey 2013). Their study used breeding data recorded up to 2008. I build on their study by including an additional eight years of data on breeding attempts for the 23 breeding groups in the study area. Wilson and Hockey (2013) included group size, nest type, rainfall over the breeding season and the amount of open habitat around the nest site in their study of factors associated with breeding success. This study includes additional factors that could be important in explaining variation in reproductive output that have not yet been explored for this species, such as temperature, previous breeding success and the timing of breeding. I also describe the changes in group size and the density of breeding groups that have occurred after the installation of nest boxes.

In Chapter 3, I build on from the previous chapter's findings on the effect of timing of breeding on reproductive success, by exploring the environmental and social factors that affect when groups initiate breeding. I investigate the effect of nest-type on the timing of breeding, as well the effects of group size, rainfall and temperature.

In Chapter 4, I present the first description of natal dispersal in ground hornbills using resightings of ringed individuals, since ringing began in 2005. This analysis has four objectives: 1) to assess the movement of individuals between groups within the study area and into the neighbouring Kruger National Park, 2) to understand what factors influence dispersal distances and whether there is a sex-bias in dispersal distance, 3) to investigate whether females disperse at a younger age than males, 4) to assess which factors may affect an individual's decision to move to a new group, such as group size of both the original and adopted group.

In the final synthesis, Chapter 5, I collate the results from the three data chapters to present the case for positive or negative effects of the provision of nest boxes. I also review insights into the breeding biology, timing of breeding and dispersal ecology of ground hornbills gained in an area supplemented with nest boxes. This will guide future efforts of installing nest boxes into other areas lacking natural nesting sites, and whether or not they are suitable to use as a means to solve the problem of a shortage of nest sites that is currently limiting population growth in this threatened species.

Study area

This study took place on the western boundary of the Kruger National Park (24.16° S, 31.18° E; Figure 1.5) in north-eastern South Africa. The study area encompasses four private nature reserves, Klaserie (600 km^2, Figure 1.6 and Figure 1.7), Timbavati (540 km^2), Umbabat (310 km^2) and Balule (350 km^2). Timbavati and Klaserie were established as private nature reserves in 1956 and 1969, respectively (Bornman 1995). The Associated Private Nature Reserves (hereafter study area), comprising Klaserie, Timbavati, Umbabat and Balule Reserves, was formed in 1976 when all fences between the reserves were removed. Fences between the Kruger National Park and the study area were removed during 1991–1993. Before their establishment as private nature reserves, most of the privately-owned farms within the reserves were used for hunting of wild game such as Cape Buffalo (*Syncerus caffer*) and Blue Wildebeest (*Connochaetes taurinus*) with a few used for cattle grazing and growing fruit (Bornman 1995).

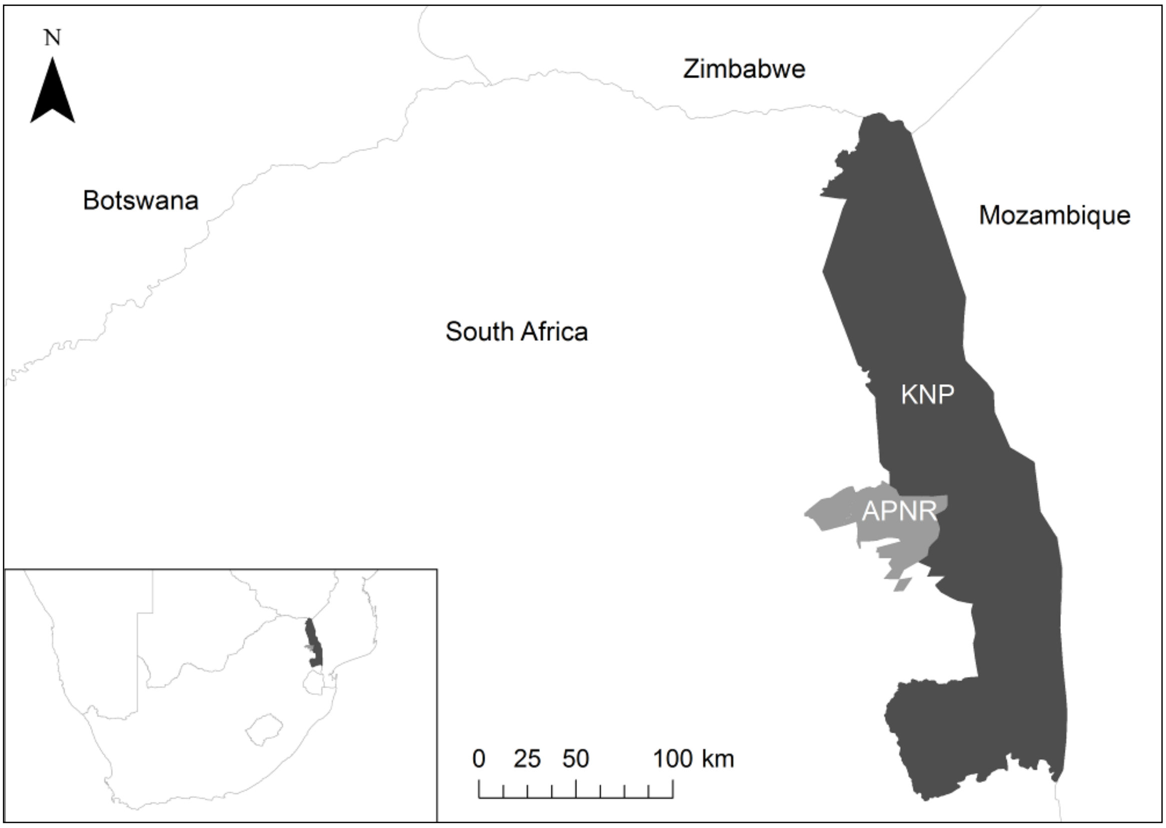


Figure 1.5. Location of the study area, the Associated Private Nature Reserves (APNR) adjacent to the Kruger National Park (KNP) in north-eastern South Africa.

Figure 1.6. Mixed woodland with a Baobab *Adensonia digitata* in the south-eastern section of Klaserie Private Nature Reserve during the dry season.

Figure 1.7. The Klaserie River in summer.

The study area has distinct wet (October–March) and dry (April–September) seasons, with a mean annual precipitation of 500 mm (van der Waal 2010). Rainfall is typically patchily distributed. Altitude ranges from 300–500 m.a.s.l. In summer, mean daily minimum and maximum temperatures are 20 °C and 33 °C, respectively. In the winter, mean daily minimum and maximum temperatures are 10 °C and 20 °C, respectively. The geomorphology is undulating over most of the area, the northern parts being particularly rugged approaching the Olifants River where rocky outcrops are common, and the south comprises flat, grassy plains. Surface stones and rocks are common in Klaserie, Balule and Umbabat, while in Timbavati soils are primarily sandy to loamy. The vegetation within the study area falls within the savannah biome. The habitat is heterogeneous, varying from open savannah to closed woodland (van der Waal 2010). Mopani *Colophospermum mopane* belts are present and dominant over large areas such as over central Klaserie and northern Timbavati, and decreases in extent over the southern areas where it is present in small, scattered pockets. Drainage is provided primarily by the Olifants river in the north and the Klaserie River that meanders through central Klaserie Reserve from south to north where it joins the Olifants (Figure 1.8). Both rivers can be reduced to a small stream during the dry winter months, particularly the Klaserie River which can cease to flow in some years. The Nhlaralumi River provides drainage to western Timbavati and Umbabat, and the Timbavati River provides drainage to southern Timbavati (Figure 1.8). The study area is covered by a network of small drainage lines that flow briefly and only during flash-flooding.

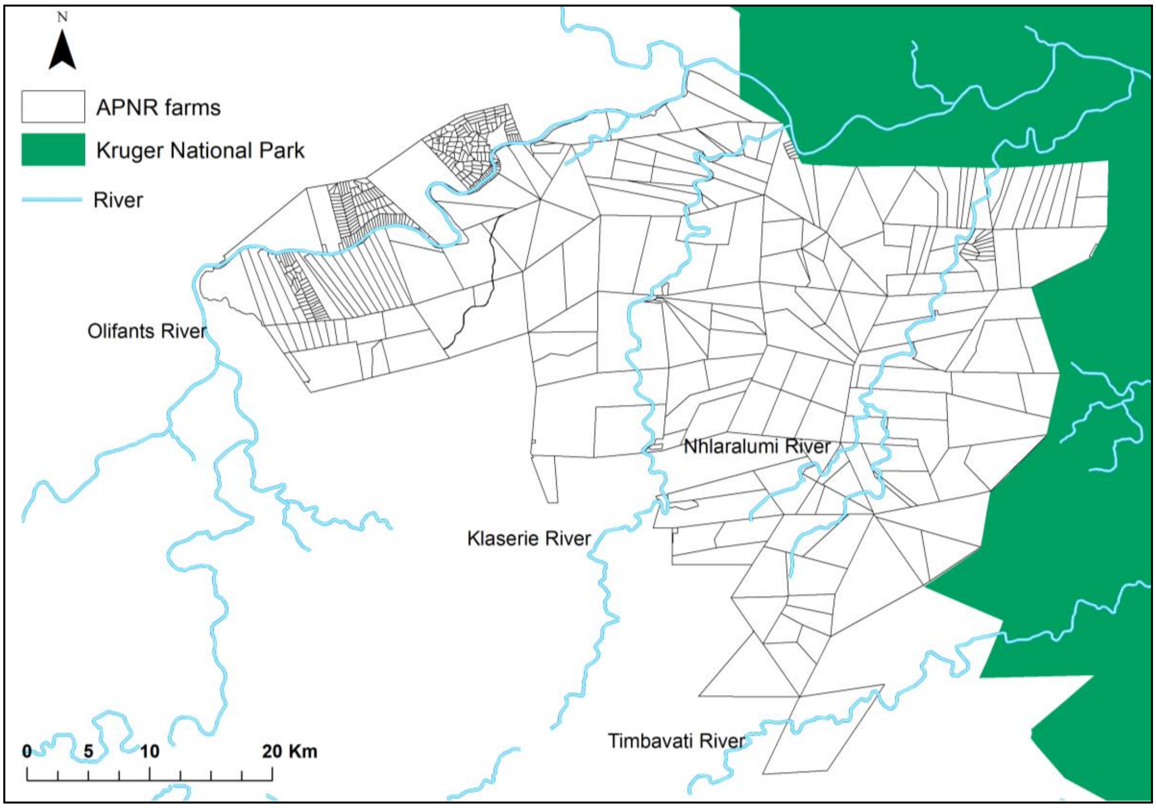


Figure 1.8. The Associated Private Nature Reserves in north-eastern South Africa, showing the four main rivers flowing through them.

Chapter 2 Reproductive productivity of Southern Ground Hornbills in an area supplemented with nest boxes

Artificial nests can improve the conservation status of threatened birds that are limited by nest-site availability. For the endangered Southern Ground Hornbill, the shortage of natural nesting sites is one factor limiting population growth. A total of 31 wooden nest boxes were installed in an 1800 km^2 study area in north-eastern South Africa during 2002–2015. The study area initially had only one known breeding group. During the 2003 breeding season, 24 % of nest boxes were occupied. By 2015, 68 % of nest boxes were occupied, representing 70 % of groups breeding in the study area. The number of breeding groups identified in the study area increased from one in 2000, to 23 by 2015. The source of individuals that formed new breeding groups appeared to be local, supported by the decrease in average group size soon after nest boxes were installed. The amount of rain that fell over the previous year came close to having a significant effect on whether a group attempted to breed in the subsequent year. However, breeding success (the proportion of breeding attempts that fledge a chick) was not associated with rainfall. In addition, breeding success was not affected by habitat, group size, orientation of the nest entrance or by removing from the nest the redundant second chick. But the thickness of the cavity walls, and the height of the nest entrance above the ground were important factors influencing breeding success. In addition, the timing of breeding had important consequences for breeding success, with nests initiated earlier in the season having a higher likelihood of fledging a chick than nests initiated later in the season. Importantly, breeding success was not associated the type of nest occupied (natural tree cavity or nest box). Furthermore, predation levels were similar between the two nest types (20 % in nest boxes and 18 % in natural nests). The only adverse effect of nest boxes was the high density at this study site: breeding success increased initially but then decreased as the number of breeding groups increased above 20 breeding groups in the study area. Nest boxes are an effective conservation tool if spaced optimally. In this study area, optimal density is one group per 90–120 km^2. Nest boxes can and should be used together with other conservation initiatives, such as removing second chicks for hand-rearing (that would naturally have died in the nest), to enhance breeding and reproductive output in areas where suitable nest sites are lacking.

Introduction

Breeding densities of birds that nest in tree cavities are often limited by the shortage of nesting sites (Newton 1994). One approach to increase the number of nest cavities available is to install artificial nest structures such as nest boxes. Providing nest boxes can decrease intra-specific competition for cavities, allowing additional pairs/groups to breed where there was previously a shortage of cavity nest sites (Newton 1994; Radford & du Plessis 2004). By providing cavities that are more suitable for nesting than natural cavities, such as offering greater protection against nest predators, reproductive output per pair/group can be increased (Korpimäki 1985; Mitrus 2003; Sherley et al. 2012; Briskie et al. 2014).

The installation of artificial nests can be used as a conservation tool to improve the population status and reproductive output of threatened birds with nest-site-limited populations. Artificial nests have assisted population increases in seabirds (Bolton et al. 2004; Morrison & Gurney 2007; Bried et al. 2009) and waterfowl (Dennis & Dow 1984; Pöysä & Pöysä 2002) as well as raptors (Schmutz et al. 1984; Toland & Elder 1987; Johnson 1994; Ewins 1996; Ramsden 1998; Fargallo et al. 2001; Catry et al. 2007) including Western Burrowing Owls *Athene cunicularia hypugaea* (Belthoff & Smith 2003). Nest boxes also have enhanced reproduction in the endangered Gouldian Finch *Erythrura gouldiae* (Brazill-Boast et al. 2013), and the Great Hornbill *Buceros bicornis* (Pasuwan 2000).

However, artificial nests can have costs, both demographic and financial. Breeding success of Northern Goshawks *Accipiter gentilis* and Common Buzzards *Buteo buteo* was reduced when these species began occupying artificial nests (although the precise reason could not be identified, Björklund et al. 2013). Nest boxes provided for Great Tits *Parus major* created ecological traps in certain habitats (Mänd et al. 2005; Demeyrier et al. 2016). Lastly, the costs of provisioning and maintaining nest boxes needs to be recognised. These costs may be high to facilitate regular maintenance to nest boxes that may be required over a long term, e.g. those species requiring a perpetual supply of nest boxes for ~ 100+ years until natural nesting develop in mature trees (Lindenmayer et al. 2009). For some species, the costs to build and maintain nest boxes are met by an annual donation fee by a nest adoptee through a nest adoption program (NCF-India, 2017). Therefore, the costs and benefits of providing artificial nest cavities vary among species, and their value as a conservation tool needs to be tested.

In north-eastern South Africa, Southern Ground Hornbills nest typically in existing hollows in mature trees. Limited availability of suitable natural cavity nests is thought to be one factor limiting population growth of the Southern Ground Hornbill in South Africa (Kemp & Begg 1996; Jordan 2011). Thus natural nesting sites in the form of natural tree cavities may be in short supply. Wind and African Elephants *Loxodonta africana* appear to be the leading causes of both the creation and loss of nesting sites in Kruger (Kemp & Begg 1996). Mature, decaying trees can fall during strong winds, and Elephants push over these trees easily. Given the scarcity of natural nesting sites, the study area in north-eastern South Africa was supplemented with wooden nest boxes to improve reproductive output of ground hornbills there (Wilson & Hockey 2013).

Reproductive performance in birds can be affected by various social and environmental factors in addition to nest site availability. Factors that potentially influence the likelihood of breeding, and breeding success in ground hornbills include group size, rainfall, laying dates, nest characteristics (such as the type of nest used, whether natural or artificial), previous breeding history, human disturbance and nest predation. Wilson & Hockey (2013) investigated the effect on reproductive output (both breeding attempts and breeding success) of a few social and environmental factors. These included: rainfall over the breeding season, group size, type of nest occupied (natural or nest box), and the amount of open woodland around the nest site. Their study identified that reproductive output was associated with group size, rainfall over the breeding season, and the amount of open area around natural nests. Their study used data collected during 2000–2008. Ongoing field work facilitated a further seven years of data to be collected. This provided an opportunity to test whether Wilson & Hockey’s (2013) findings still hold, and to identify the importance on reproductive output of several additional social and environmental factors. These include food supply, timing of breeding, previous breeding success, nest characteristics (such as their height above ground and thickness of the cavity wall), the conservation action of removing the redundant second chick for the captive breeding and wild release program, and nest predation. Each of these factors will be presented in more detail below. Arthropods and other invertebrates are an important food source for ground hornbills (Kemp 1976). In African savannahs, invertebrate abundance is closely tied with rainfall, with abundance increasing as rainfall increases (Kemp 1976; Cumming & Bernard 1997). There is also evidence that the previous-year’s rainfall influences vegetation growth, particularly by grasses (Dudney et al. 2016), which would in turn affect arthropod abundance as arthropods feed mainly on vegetative material. Rainfall can therefore be a useful proxy for prey abundance in species such as the ground hornbill, for which arthropods form a large part of their diet. A year of below-average rainfall would translate into leaner times going into the breeding season (Robb et al. 2008). If conditions are too poor (low rainfall over the season or previous season), adults may forego breeding, rather investing energy on survival or maintenance of body condition, such as moult (Perrins 1965; Magrath 1991; Langston & Rohwer 1996; Dawson et al. 2005; Dietz et al. 2013). The importance on rainfall leading up to the breeding season, as a proxy for food supply, will be tested for ground-hornbills to understand the constraints to breeding.

The timing of breeding, a decision taken by a female bird as to when to lay an egg in a season, can affect the likelihood of a successful breeding attempt. Many birds show reduced reproductive success late in the breeding season (Perrins 1970; Daan et al. 1989; Verhulst & Nilsson 2008). Although early nests may be costly to breeding females due to low food availability during egg production, they potentially benefit by having a chick(s) that hatches just before peak food availability. Late nests would hatch chicks after this peak, making food provisioning for the growing chick increasingly difficult (Siikamäki 1998). This pattern has been demonstrated in numerous studies from the northern hemisphere, chiefly from the temperate zone, with a few from the northern hemisphere subtropical and tropical species (Woolfenden & Fitzpatrick 1978; Koenig & Mumme 1987). However, there are only a few studies from the southern hemisphere, which is ocean-dominated, and where seasonality is less marked and less predictable due to the much greater buffering effect of the oceans Some southern hemisphere studies confirm the north temperate trend (Reyer 1984; Garnett et al. 2001), but one found no effect of the timing of breeding on reproductive success (Heinsohn 1992). The inclusion of the timing of breeding here can assist with understanding whether trends seen in the northern temperate regions are repeated across different latitudes. In addition, I am interested to known whether ground-hornbills, a non-passerine species, conforms to the northern hemisphere, passerine trend of early nesters showing greater breeding success. I expected ground hornbills to show reduced breeding success later in the season due to diminishing food resources.

Some birds breed every season, even raising multiple broods per season. Other species, like the ground hornbills, are constrained to raise at most one brood, and make typically only one breeding attempt per season. Some species are constrained by carry-over effects from the previous year, and may not attempt to breed if they were successful in the previous season

(Martínez et al. 2006). Breeding in some large birds, like albatrosses, is constrained by the need to moult, which is another energetically expensive and time-consuming process (Langston & Rohwer 1996), and one that may require some pairs to skip a year of breeding. Long-lived, K-selected species (such as ground hornbills), are expected to make modest reproductive attempts and favour survival as breeding adults over rapid reproductive efforts seen in species with shorter life-span such as r-selected species (Stearns 1976). Therefore, for ground hornbills, constrains by success of the previous year on breeding attempts will be investigated.

Nest box characteristics such as cavity dimensions, height and microclimate, can influence the probability of nest occupancy and breeding success (Bortolotti 1994; Smith & Belthoff 2001; Stamp et al. 2002; Bourgeois et al. 2015; Rahman et al. 2016). Tree Swallows *Tachycineta bicolor* prefer nest boxes with an entrance orientation which makes the nest warmer (Ardia et al. 2006), and American Kestrels *Falco sparverius* prefer larger nest boxes (Bortolotti 1994). Breeding in the Tengmalm's Owl *Aegolius funereus* was most successful in thick-walled nest boxes (Korpimäki 1985). And numerous species prefer higher nests and/or are more successful in them (Coleman 1974; Schmutz et al. 1984; Negro & Hiraldo 1993; Wilson & Cooper 1998; Saab et al. 2004; Desimone & DeStefano 2005). Furthermore, habitat around the nest can influence occupancy and/or breeding success (Finch 1989; Rendell & Robertson 1990; Pell & Tidemann 1997; Blakesley et al. 2005; Desimone & DeStefano 2005; Zicus et al. 2006; Wilson & Hockey 2013). Therefore, optimising the design and placement of nest boxes can further improve the likelihood of occupancy and breeding success. The effect of entrance height, orientation and thickness of the nest cavity wall on breeding success in ground-hornbills will be tested.

Removing redundant eggs and/or chicks from wild nests (hereafter harvesting) can be a useful conservation action to bolster threatened bird species (Williams et al. 2013). Some species can only raise one chick to fledging, and thus all other chicks in the nest, typically those that hatch after the first, will eventually die e.g. by starvation due to their inability to compete for food with their older sibling. Harvesting redundant chicks increased productivity in the Mauritius Kestrel *Falco punctatus* (Jones et al. 1995) and Whooping Crane *Grus americana* (Boyce et al. 2005), and had no effect on a wild Bald Eagle *Haliaeetus leucocephalus* population (Wood & Collopy 1993). Harvesting redundant, second-hatched ground hornbill chicks has been taking place in South Africa since the late 1990s. Second chicks are typically ignored by the female and succumb to dehydration within a few days of hatching. Each year, no more than 15 second-hatched chicks are harvested from wild nests by field researchers in the Associated Private Nature Reserves and Kruger National Park, north eastern South Africa. Harvested chicks are hand- or parent-reared for release either back into the wild or integrated into the captive breeding programme. The effect of harvesting on the success of wild nests has yet to be evaluated, and it’s continuation as a conservation action requires an assessment of its impact on the productivity of harvested nests.

The differences in nest predation rates between natural and artificial nest sites may be due to characteristics of the predators or the sites. Predation rates may be lower in nest boxes because nest predators may lack experience with artificial nest sites (Mitrus 2003), or because nest boxes were modified or guarded deter certain predators or prevent them from gaining access to the nest (Sutherland et al. 2004; Mainwaring & Hartley 2008; Skwarska et al. 2009; Barnett et al. 2013). Alternatively, predation rates may be higher in nest boxes due to the placement of nest boxes at conspicuous sites (Evans et al. 2002; Williams et al. 2013). Most published data on nest predation stems from north-temperate zones, and mostly from passerines, and an important gap exists in predation research outside of this zone and involving non-passerine species (Ibáñez-Álamo et al. 2015).

This chapter investigates social and environmental factors associated with breeding success, with the aim to assess the use of next boxes as a conservation tool to enhance ground hornbill population status and reproductive productivity. First, I compare characteristics of nest boxes and natural nests. Second, I describe the change in the number of breeding groups and the changes in group size over time. Third, I investigate the effects of nest boxes and other social and environmental factors on the decision to breed and resultant breeding success by groups, to understand whether nest boxes had a positive or negative effect on the population in the study area.

Methods

Nest characteristics

Natural nests were located using information on known cavities provided by reserve staff. One natural nest was located using a transmitter that was placed on a bird. A total of 31 nest boxes were built using large logs mostly from exotic trees (*Pinus* spp., n = 26; *Eucalyptus* spp., n = 1) and less often from indigenous trees (Marula, n = 1; Weeping Boer Bean, n = 3). Logs were cut in half longitudinally, hollowed using a chisel and hammer, and the two faces re-joined with metal rods. Nest entrances were cut in the upper half of the log (either rectangular or roughly oval, and approximately 30 cm wide and 40 cm high, Figure 2.1). Nest cavities were designed to be approximately 50 cm across and 80 cm high (Figure 2.1).

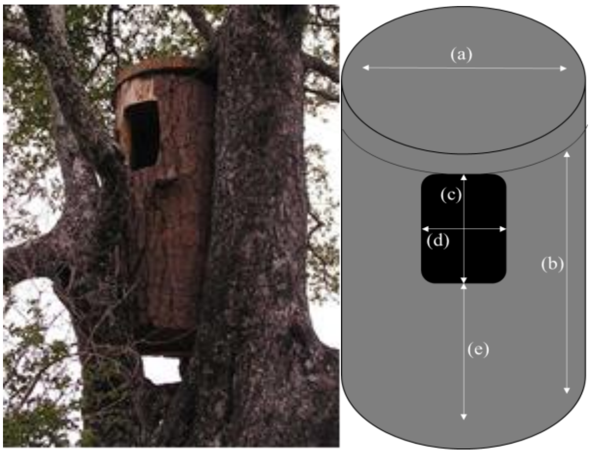


Figure 2.1. An example of the Southern Ground Hornbill nest boxes installed in the study area. Mean nest dimensions: (a) internal diameter 50 cm, (b) internal height 80 cm, (c) entrance height 40 cm, (d) entrance width 30 cm, (e) internal depth 40 cm.

Nest boxes were placed throughout the study site in trees large enough to support these heavy (~ 80 kg) structures (Wilson & Hockey 2013). Fourteen nest boxes were placed in the winter (non-breeding season) of 2002, 11 in 2003, three in 2005, one in 2009 and two in 2013. Nest boxes were placed in three of the four reserves comprising the study area: Klaserie, Timbavati and Umbabat Reserves, but not Balule (20 % of the study area). They were placed in Leadwoods *Combretum imberbe* (n = 16), Jackalberries *Diospyros mespiliformes* (n = 5) and Weeping Boer-beans *Schotia brachypetala* (n = 4), with the remaining four in a Marula *Sclerocarya birrea*, Knobthorn *Senegalia nigrescense*, Appleleaf *Philenoptera violacea* and

Brown Ivory trees *Berchemia discolor*. Most nest boxes were placed with their entrances facing north and this is taken into consideration when discussing results below. The location and orientation of each nest site was recorded with a Garmin 76CSx Map GPS. In the case of vertical, chimney-like tree cavities, orientation was scored as 'top'. Other variables recorded included: nest height (ground to the lowest lip of the nest entrance); entrance height and width; floor depth (lowest lip of the cavity entrance to the cavity floor); and floor length and width. The area for the nest floor area and oval entrance was calculated using the equation: ellipse area (m^2) = π x ½ length x ½ width. Areas for entrances that were rectangular were calculated using the equation l x b. Nest thickness was estimated by taking the average of four measurements of the thickness at the nest entrance using Vernier calipers.

The locations of nest sites were mapped using ArcMap 10.1 (ESRI, Redlands, CA). Average nearest neighbour distance (inter-nest distance) was calculated between active nests each year. Inter-nest distances between and within group territories were obtained manually using the ArcMap Measure tool.

To investigate the difference in microclimates between natural nests and nest boxes, temperature iButtons (DS1923, Fairbridge Technologies) were installed in 16 nest boxes (11 used and five that were never used) and nine used tree cavity nests. Nests that had been occupied previously were last active 1.7 ± 1.1 years (range 1–4 years) prior to the installation of iButtons (range 1–15). iButtons were set to record temperature every 15 minutes, throughout the day and night, at a sensitivity of 0.07 °C. They could not be placed in occupied nests during summer because the nesting birds destroyed or removed them, so iButtons were deployed outside of the breeding season and for 22 days (13 July–03 August 2015). iButtons were mounted inside next boxes, 10 cm below the nest entrance to avoid direct sunlight. Since natural tree cavity nests were mostly chimney nests, an iButton was mounted 10 cm below the entrance. For these chimney nests, iButtons were placed beneath a small wooden roof for shade. At all nest sites, a control iButton was placed externally on the south facing side of the nest tree at the same height as the nest iButton to record ambient temperature in the shade.

A one-way anova with a Welch correction for non-normal residuals in R (version 3.03, R Core Team 2014) was used to investigate differences in ambient temperatures at all nests. Tukey comparisons (Faria et al. 2014) were calculated in R using the 'agricolae' package (de

Mendiburu 2007) to identify significant differences in temperature variables. *P*-values were calculated by performing a Wilcoxon rank sum test. The rate of temperature increase (T_{rate}) was calculated by dividing the temperature difference between the minimum and maximum temperatures inside each nest by the number of hours between the two extremes. The difference in temperature (T_{diff}) between the nest microclimate and the control temperature was calculated over two time periods: day (07:30 to 17:30) and night (17:30 to 07:30). To obtain a temperature difference value, the ambient temperature at each nest was subtracted from the nest temperature.

Group size and density

Observations of groups took place throughout the year during 1998–2007, and again during 2011–2015. Group observation data were missing in the database for the period during 2008–2010. Groups were captured using walk-in traps (Zoghby et al. 2015) and individuals were ringed using a combination of three colour rings and one numbered metal ring. Groups were located by their duet calls at dawn, or by using telemetry devices fitted as backpacks (Zoghby et al. 2015). Groups were identified by one or more of the following criteria: (a) their composition of adults, sub-adults and juveniles and location within a known home range, (b) the presence of ringed individuals, (c) their presence at a nest site used by the group.

To determine whether there was a significant increase in the number of small (2–3 individuals) and medium-sized groups (4–6 individuals) in the years immediately following the installation of nest boxes, I performed a pairwise comparison using t-tests between the number of small groups observed in each of three time periods: up to the winter that nest boxes were installed (1998–2002), two years immediately after installation of the first nest boxes took place (2003–2004), and later (2005–2015). *P*-values were adjusted for multiple comparisons using the Bonferroni correction method (Rice 1989).

To investigate the effect of year on group sizes, I performed two generalised linear models (GLMs, package lme4) in R using group size data for 30 groups during 2000–2015 (n = 368). Data exploration, such as plotting histograms and testing for multicollinearity between variables, was carried out following the protocols described in Zuur & Ieno (2016). For the first model, I modelled *Group size small* (categorical, the number of groups that had two or three individuals) as a function of *Year* (categorical). *Year* was included as non-linear variable based on initial plots. The second model investigated the effect of year on medium-sized groups. I modelled *Group size medium* (categorical, the number of groups that had 4–6 individuals) as a function of *Year* (categorical). *Year* was included as linear variable based on initial plots. All two models used a poisson distribution with a log link function. Non-significant ($P > 0.05$) variables were sequentially removed from each model. Non-significant variables that were removed, were each added back to the reduced model one at a time, to double check that their inclusion did not contribute significantly toward the model's power. The estimates and probabilities of these non-significant terms from the full model are included in the summary table for completeness. Confidence intervals (95 %) for each parameter were obtained using Wald's approximation (Wald 1947). A Hosmer-Lemeshow Goodness of Fit (GOF) test was performed to assess model fit (Hosmer & Lemeshow 1980). A high *P*-value from this GOF test would indicate no evidence of a poor model fit. Model assumptions were verified using plots of residuals against fitted values as well as residuals versus each explanatory variable used in the model. The model's overall contribution was tested by comparing each model to a null that had only a constant (1) as an explanatory variable.

Breeding attempts and breeding success

Observations of breeding attempts took place during 2000–2007 and 2009–2015. Data for failed breeding attempts were not available during 2008–2009 due to missing data and therefore these years are excluded from analysis. Nest checks every 7–10 days commenced at the end of September each year. Once at the nest, the side of the nest was tapped to flush the incubating female. A full, fresh lining of leaves (typically the shed leaves of Mopane *Colophospermum mopane*) indicated that egg-laying was imminent. If one egg was found, the nest was revisited after five days to check for the presence of a second egg. Laying date was estimated as the middle date between the check when an egg was first discovered and the previous nest check. Each nest was visited again 40–42 days after the estimated lay-date to check for hatching of the first chick, then again after another few days to check for hatching of the second chick. When the first chick was present and healthy, the second chick or pipping egg was harvested shortly after hatching. The chick was harvested as part of a conservation action to raise redundant second-hatch chicks and incorporate them into either the wild-release or captive breeding programs, as one of several actions to slow and reverse the decline of the species in the wild. The remaining chick was checked again 40 days after hatching, and ringed and measured after 72 days. The nest was re-checked 10 days later to confirm that the chick had fledged.

Habitat and rainfall

Environmental variables included in the analysis of breeding attempts and breeding success included habitat features and rainfall. The amount of open woodland and savanna around each nest (both natural nests and nest boxes) was determined using GIS software. A circle around each with a radius of 3 km was drawn. This 3-km circle was then intercepted with a vegetation cover shape file. Habitat types used to determine the proportion of open woodland around the nest were: (a) *Senegalia nigrescens - Combretum hereroense* open woodland, (b) *C. apiculatum - Sclerocarya. birrea - Strychnos madagascariensis* open woodland, (c) disturbed areas (old fields, air fields), (d) *C. apiculatum - S. birrea* open woodland, and (e) *Terminalia sericea - C. zeyheri - Pterocarpus rotundifolius* open woodland. The amount of riparian habitat within each home range was calculated as above, but each group's entire home range was included and only the riparian-*Phragmites* habitat type was selected. Monthly rainfall data were obtained from reserve records of rainfall collected at 14 rain gauges checked daily (by reserve staff) throughout the study area. Rainfall for each group's home range was taken to be the amount of rainfall measured at the nearest rain gauge to the centre of the home range and nest for breeding attempts (since some groups had more than one nest) and breeding success analyses, respectively. Rain gauges were situated at a mean distance of 5 ± 3 km (range 1–11 km) from each nest.

Statistical modelling of environmental and social factors influencing breeding attempts

To investigate factors affecting breeding attempts (whether a female laid an egg in a given season), I performed a generalised linear mixed-effect model (GLMM, package lme4, Bates et al. 2015) in R using data for 19 groups during 2000–2015 (n = 235). Not all groups in the study area had access to a nest box, and not all groups had access to a natural nest. In addition, groups differed by how many nests they had access to. To understand how nest boxes influenced whether or not a group laid an egg, I incorporated variables that described the nesting resources that each group had access to. Data exploration, such as plotting histograms and testing for multicollinearity between variables, was carried out following the protocols described in Zuur & Ieno (2016). I modelled *breeding attempt* (binary, 1 if the alpha female of the group laid an egg, 0 if not) as a function of the *number of nest boxes* and *number of natural nests* (both discrete, the number of nest boxes and natural tree cavity nests each in a group's home range), as well as *home range size* (continuous, included as a proxy for the number of possible additional cavity nests, and determined by a polygon which included all locations of group sightings) and *the amount of riparian vegetation* (continuous, included as a proxy for the number of possible additional cavity nests), and *nest age* (discrete, the age in years of the cavity in the home range). Average natural cavity lifespan is 14 years (Kemp and Begg 1996), therefore an estimate average age for each natural cavity upon discovery at the study site was given as 7 years. If more than one previously-used nest was present, the youngest nest age was used. *Nest box* (binary, whether or not a group has access to a nest box) was not included in the model as the variation inflation factor was > 3, indicating a high level of multicollinearity between predictors (Zuur and Ieno 2016). Other variables included in the model included *raising a chick the previous season* (binary, 1 if the group fledged a chick, 0 if not), *group size* (discrete, size of the group during preceding winter), *rainfall over the previous year* (continuous, total rainfall during July–June), *dry season rainfall* (continuous, total rainfall during April–August), *spring rainfall* (continuous, total rainfall during September–November) and *breeding season rainfall* (continuous, total rainfall during September–March). *Group identity* and *year* were included as random terms. The best model was determined by eliminating all non-significant terms. These terms were later added separately to confirm their non-significance, and removed if they remained non-significant. A Hosmer-Lemeshow GOF test was performed to assess model fit (Hosmer and Lemeshow 1980). Confidence intervals (95 %) for each parameter were obtained using Wald's approximation (Wald 1947). Model assumptions were verified using plots of residuals against fitted values as well as residuals versus each explanatory variable used in the model.

Statistical modelling of environmental and social factors influencing breeding success

To investigate factors affecting breeding success, I performed a GLM (package lme4, Bates et al. 2015) in R using breeding success data for 18 groups during 2000–2015 (n = 117). This data set excluded the years 2008 and 2009 as data for unsuccessful nests were not available. The sample size for this model is smaller than the previous model since, unlike the previous model that included nests that fledged a chick and nests that failed, this model included only those nests that fledged a chick. Data exploration, such as plotting histograms and testing for multicollinearity between variables, was carried out following the protocols described in Zuur

& Ieno (2016). I modelled *breeding success* (binary, 1 if the group raised a chick to fledging, 0 if the breeding attempt failed) as a function of *nest type* (binary, natural cavity or nest box), the *number of breeding groups* (discrete, the number of groups that were known to breeding in the study area), *breeding season rainfall* (continuous, during October–March), *rainfall over the previous year* (continuous, during July–June), *group size* (discrete, group size during winter), *open woodland* around nest (continuous, the proportion of open woodland within a 3-km radius of the nest), *timing of breeding* (discrete, days after 1 September that the first egg was laid), *year* (discrete, the season in which the breeding attempt took place), *harvest* (binary, whether or not the second egg/chick was harvested from the nest), *nest height* (continuous, the height of the nest entrance above ground in meters), *orientation* (categorical, the direction of the nest entrance: N, S, E or W), *thickness* (continuous, the average thickness of the cavity wall measured at four sides of the nest entrance to the nearest 1 mm) and *nest age* (discrete, the age in years of the nest in the home range). *Nest age* was included to determine whether the state of the nest box, that generally declined with age, affected breeding success. If more than one nest was available, age was taken as the youngest nest). *Nest age* had a variance-inflation factor value > 5 and was therefore dropped prior to modelling. *Breeding season rainfall* was initially included as a non-linear term based on a previous study that showed a non-linear effect of seasonal rainfall on breeding success (Wilson 2011). However, this term was not significant, and was therefore included as a linear term in the model. *Year* was included as a fixed term based on initial plots that showed some trend with time. The model used a binomial distribution with a logistic link function. *Group identity* was initially included as a random variable (using a GLMM). The effect *group identity* was checked from the model output summary, was found to be zero, and was therefore dropped from the model (no random effects therefore continued with a GLM). The interaction between *nest type* and the *amount of open woodland* around the nest site was included as this interaction was found to be significant in a previous study (Wilson and Hockey 2013). The interaction between laying day and nest type was included to determine whether there were differences in success in late and early nesters between the two nest types. Model fit was tested as in the previous model investigating the likelihood of a group making a breeding attempt.

Nest predation

No formal study of predation in Southern Ground Hornbill nests have been undertaken, but species are assumed to include various large and small predators adept at climbing trees such as genets *Genetta* spp., Slender Mongoose *Galerella sanguine* and Leopard *Panthera pardus*. A nest was noted as being predated by the disappearance of eggs or chicks, or by the presence of broken egg shells and the remains of chicks found in or near the nest. The predator was identified at one nest by a nest camera, and twice by their physical presence at the nest when recently broken ground hornbill eggs were found on the ground beneath the two nests. In addition, any species using the nests as roosting sites were noted. Mammal scat found in the nest was also used to determine species occupancy.

To investigate the effect of nest site on the probability of nest predation, I performed a GLMM (package lme4, Bates et al. 2015) in R using predation data for 18 groups during 2000–2015 (n = 117 breeding attempts). This data sat excluded the years 2008 and 2009 as data for predated nests were not available. Breeding success and predation are inextricably linked, however in this model I wanted to distinguish nest failure from suspected or known predation, from nest failure from other causes such as nest abandonment, with the aim being to determine whether nest boxes were more susceptible to nest predation than natural nests. I modelled *predated* (binary, 1 if predation was suspected, or 0 if the nest failed for other reasons) as a function of *nest type* (binary, natural cavity or nest box), *rainfall over the previous year* (continuous, during July–June) and *nest height* (continuous, the height of the nest entrance above ground in meters). *Group identity* (categorical) and *Year* (categorical) was initially included as a random variable. *Group identity* was having no effect and was dropped. Model fit was tested as per the previous model. The explanatory power of the model was confirmed by comparing the model against a null that contained a constant fixed value (1) plus random effect *Year*. The result indicated a low explanatory power ($\chi 2$ = 4.24, df = 3, *P* = 0.23), and the results are discussed in light of this.

Results

Nest characteristics

Natural cavity entrances were on average larger than the entrances in the nest boxes provided (Table 2.1). Nineteen nest boxes were placed facing north, one east, two south and eight facing west. Natural nests typically resembled chimneys, and only one nest had a side-facing entrance (S-facing). Natural nest cavities (n = 12) were found in six tree species, mostly in Leadwoods *Combretum imberbe* (n = 4) and Appleleaf trees *Philenoptera violacea* (n = 3). Other nest trees included Weeping Boer Bean *Schotia brachypetala* (n = 2), and one nest in each of the species: Jackalberry *Diospyros mespiliformes,* Marula *Sclerocarya birrea and* Mopane tree *Colophospermum mopane.*

Table 2.1. Dimensions of natural tree cavity nests and nest boxes occupied by Southern Ground Hornbills.

	Natural nests			Nest boxes			Wilcoxon test	
Dimension	Mean ± SD (range)	Median	*N*	Mean ± SD (range)	Median	*N*	*W*	*P*
DBH (cm)	84.0 ± 27.0 (60.0–145.0)	72.0	9	78.0 ± 17.0 (53.0–125.0)	75.0	23	97	0.95
Height (m)	**3.6 ± 1.0 (2.7–6.1)**	**3.2**	**10**	**6.0 ± 1.4 (4.0–9.0)**	**6.0**	**24**	**17**	**< 0.01**
Entrance (m^2)	**0.2 ± 0.1 (0.1–0.5)**	**0.2**	**8**	**0.08 ± 0.01 (0.06–0.10)**	**0.07**	**24**	**189**	**< 0.01**
Depth (cm)	**71.2 ± 33.3 (19.0–135.0)**	**70.0**	**9**	**42.9 ± 10.3 (26.0–64.0)**	**42.5**	**24**	**161**	**< 0.01**
Floor (m^2)	**0.1 ± 0.1 (0.04–0.3)**	**0.1**	**8**	**0.20 ± 0.06 (0.06–0.31)**	**0.19**	**24**	**43**	**0.04**
Thickness (mm)	62.4 ± 44.9 (23.1–169.7)	44.1	**9**	67.3 ± 28.6 (28.4–126.8)	61.6	18	63	0.49

Nest boxes and natural nests shared similar microclimates, with the single exception being that natural nests were more buffered against cooling night temperatures (Table 2.2). When comparing nests within nest boxes that had been occupied historically at least once to nests that had never been occupied, used nest boxes also shared similar microclimates, with the single exception being that unused boxes experienced lower minimums (Figure 2.2, Table 2.2). Some of the more extreme high temperatures were recorded in frequently occupied nest boxes and natural nests. The highest maximum temperature was recorded inside a nest box that had been occupied at least once by a group (36 °C, Table 2.2). The fastest rate of temperature increase was recorded in a natural nest (4 $°C.hr^{-1}$, Table 2.2).

Table 2.2. Daily temperatures (°C) inside nest boxes that were occupied at least once (used, n = 11), nest boxes that had never been unoccupied (unused, n = 5), and natural tree cavity nests (n = 9) between 13 July 2015 and 03 August 2015. Mean ± SD (range). Comparisons of the different temperature variables between the three nest types were made using a Tukey test (Faria et al. 2014). Temperature variables with different letters assigned by the test are significantly different at the 5 % level.

Variable	Used nest boxes	Unused nest boxes	Natural nests
T_{min}	12.3 ± 3.4 (3.9–20.5)	11.4 ± 3.1 (4.9–19.1)	12.0 ± 3.0 (3.8–18.7)
Tukey	a	b	ab
T_{max}	25.9 ± 3.3 (17.6–36.0)	26.1 ± 2.8 (20.0–33.4)	25.5 ± 3.0 (18.9–35.2)
Tukey	a	a	a
T_{mean}	18.7 ± 2.3 (10.1–24.1)	18.6 ± 2.4 (10.7–23.4)	18.4 ± 2.1 (9.9–23.8)
Tukey	a	a	a
T_{rate}*	2.2 ± 0.6 (0.8–3.0)	2.4 ± 0.3 (2.0–2.7)	2.5 ± 0.7 (1.6–4.0)
Tukey	a	a	a
$T_{diff\ (day)}^{\S}$	-1.1 ± 0.3 (-1.4–0.2)	-0.7 ± 0.3 (-1.3–0.03)	-1.3 ± 1.5 (-2.0–0.4)
Tukey	ab	a	b
$T_{diff\ (night)}^{\S}$	0.5 ± 0.4 (-0.5–1.1)	0.8 ± 0.6 (-0.2–1.8)	1.5 ± 0.6 (-0.5–2.3)
Tukey	a	a	b

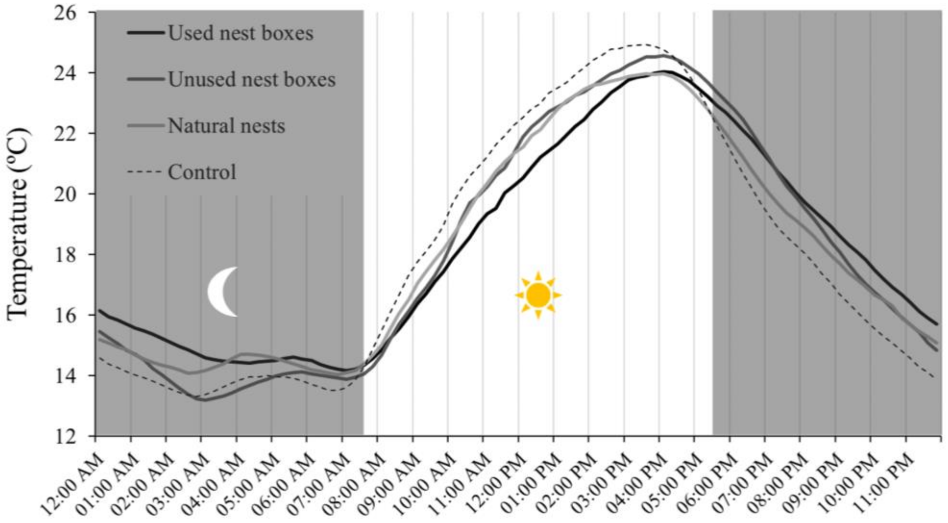


Figure 2.2. Nest temperatures and the ambient temperature in the shade (control) over a 24 hour period for 15 nest boxes and nine natural tree cavity nests. Nest boxes were divided into two categories: those that had been previously occupied at least once (used, n = 11), and those that had never been occupied (unused, n = 4).

Group size and density

A total of 1950 observations were used to estimate group size during 1998–2015. In 1998 and 1999, no groups bred and only one group bred in 2000 (Figure 2.3). In the year before nest boxes were installed (2001), five breeding groups (Figure 2.3) and an additional 10 non-breeding groups (Figure 2.4) were identified. The number of breeding groups increased sharply after nest boxes were installed from 5 in 2001 to 15 by 2004, and increased further to 23 by 2015 (Figure 2.3). When considering all the groups observed in the study area, including non-breeding groups, the number of smaller groups (2–3 individuals) increased significantly in 2003 and 2004, the two years immediately following the first installation of boxes in 2002 (t-test, $P < 0.05$, Figure 2.4), and then decreased (non-linear trend with time, model A, Table 2.3). Medium-sized groups (4–6 individuals) increased linearly over time (Figure 2.4, Table 2.3) Groups of seven or more individuals were not known before nest boxes were installed, and were first seen in the study area in two years after nest boxes were installed (Figure 2.4). These larger groups became increasingly common over time (Figure 2.4). Average group size continued to grow until 2014, after which it stabilised. Overall, average group size was 4.0 ± 1.4 individuals.

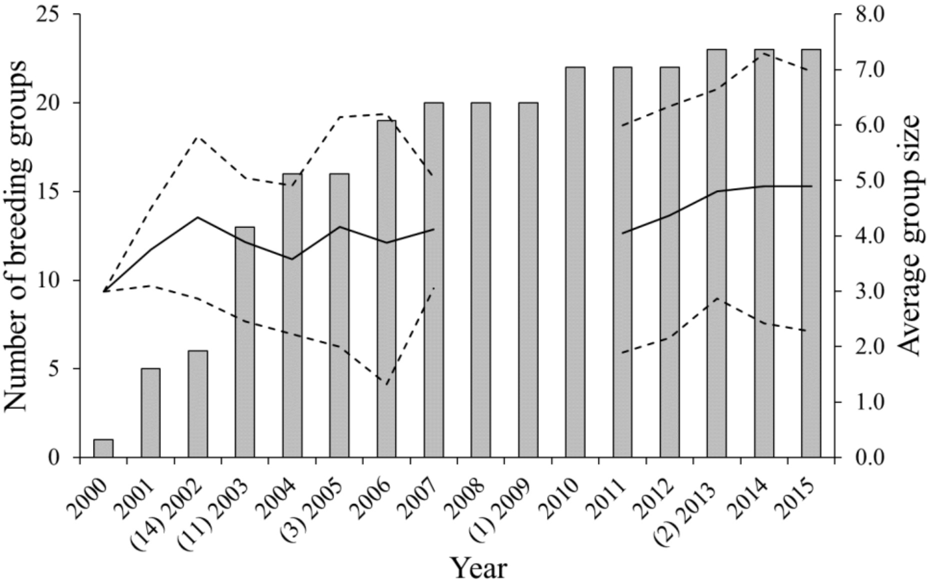


Figure 2.3. The number of breeding groups identified over time (bars) and their average group size (solid line, with variance plotted with dashed lines). The number of nest boxes installed in that particular year are provided in parentheses on the x-axis.

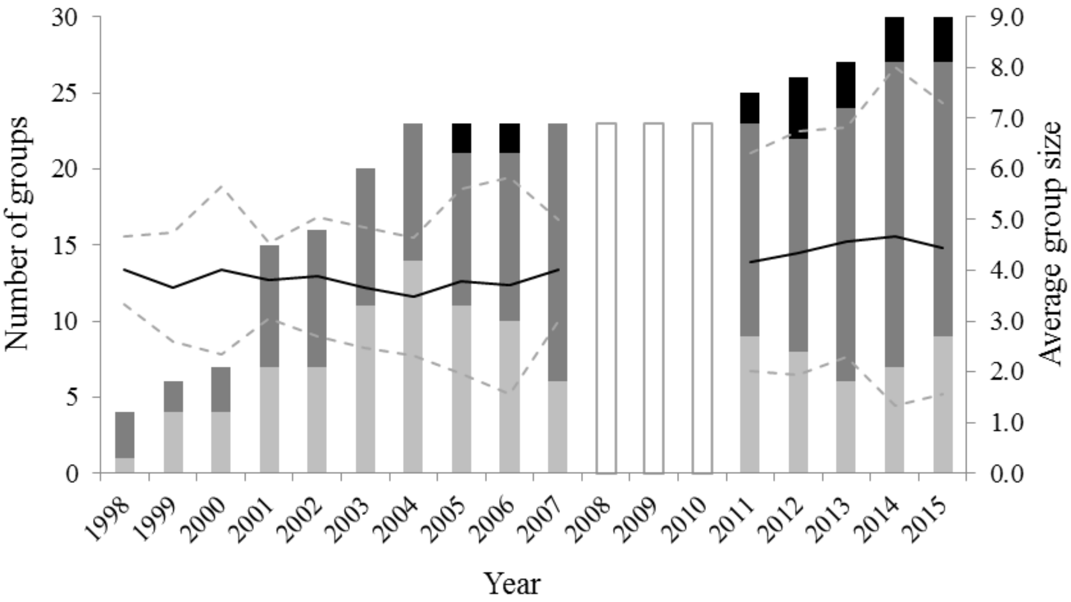


Figure 2.4. Average group size over time (solid line, with variance plotted with dashed lines) and the frequency of group sizes observed for 30 groups, including both breeding and non-breeding groups. Light grey bars show groups of 2–3 individuals, dark grey for groups 4–6 individuals, and black for groups containing > 7 individuals. Data for group sizes were lacking for 2008–2010, however the number of groups were assumed at the least to have remained unchanged, therefore the data for these years are presented as unfilled bars.

Table 2.3 Linear models to describe the changes in the frequencies of small and medium-sized groups during 1998–2015. In model A, and based on initial plots, year was included in as a cubic term (degree = 3) using beta splines (bs) to fit the trend line. The number next to year denotes the basis function, which is a measure of how flexible the curve is.

Variable	Est. (95 % CI)	SE	Z	*P*
Model A				
Group size 2–3; Model: Group size ~ bs(Year, degree=3); year as non-linear				
(Intercept)	0.49 (-0.51–1.50)	0.47	1.05	0.29
Year.1	3.73 (1.31–6.15)	1.13	3.31	< 0.05
Year.2	0.66 (-0.59–1.92)	0.59	1.13	0.26
Year.3	1.68 (0.43–2.94)	0.59	2.87	< 0.05
Model B				
Group size 4–6; Model: Group size ~ Year; year as linear				
(Intercept)	-1885 (-2258–1513)	176	-10.72	< 0.05
Year	0.95 (0.76–1.13)	0.09	10.79	< 0.05

By 2015, the study site contained a high density of breeding groups: ~6 % of South African breeding groups (23 of 417 breeding groups) on 1 % of the distribution area. The density of groups (breeding and non-breeding) in the study site was one group per 60 km^2 (30 groups in 1800 km^2). Areas of the study site lacking nest boxes had a low density of groups: Balule Reserve (20 % of the study area) contained no nest boxes and had only one historical breeding group that was not known to breed during the study period, and a second group that was never known to breed (one group per 175 km^2). Compared to Balule Reserve, the density of groups in Klaserie, Timbavati and Umbabat reserves that each contained nest boxes was three-fold higher (one group per 52 km^2 in 80 % of the study area).

Factors influencing breeding attempts

Twenty-three ground hornbill groups made 159 breeding attempts over 16 breeding seasons (2000–2015). A total of 13 natural tree cavities and 23 nest boxes were occupied. Occupancy of nest boxes increased over time (Figure 2.5). In the winter of 2002, 11 nest boxes were installed. That summer, one nest box was occupied. In the 2003/2004 breeding season, six nest boxes were occupied. By 2007, half of the nest boxes installed had been occupied, and by 2015 this had increased to 74 % (23 of 31 nest boxes), which were being used by 70 % of breeding groups. An average of nine nest boxes and two natural cavity nests were occupied per season (Figure 2.5, Appendix 2.1). The average nearest-neighbour distance varied between seasons from 6 ± 2 km (range 3–18 km, n = 23 breeding groups, Appendix 2.2). Groups using mostly nest boxes attempted nesting twice as often as groups that used only natural nests (one attempt every 1.4 years and 2.9 years, respectively, Appendix 2.3).

No factors significantly affected the probability of groups attempting to breed (Table 2.4). Rainfall over the previous year explained almost significant variation in the probability to breed, and when compared to the null model, this factor added significant value ($\chi^2 = 3.81$, df = 1, $P = 0.05$). However, the Hosmer Lemeshow GOF test identified a weak fit (Table 2.4). When plotting the data, there was evidence for non-linearity but when compared to the null, this term was not significant ($\chi^2 = 9.43$, df = 1, $P = 0.09$). Intermediate amounts of rainfall were positive for groups (80% of attempts successful if between 450 and 700 mm of rain fall over the previous year).

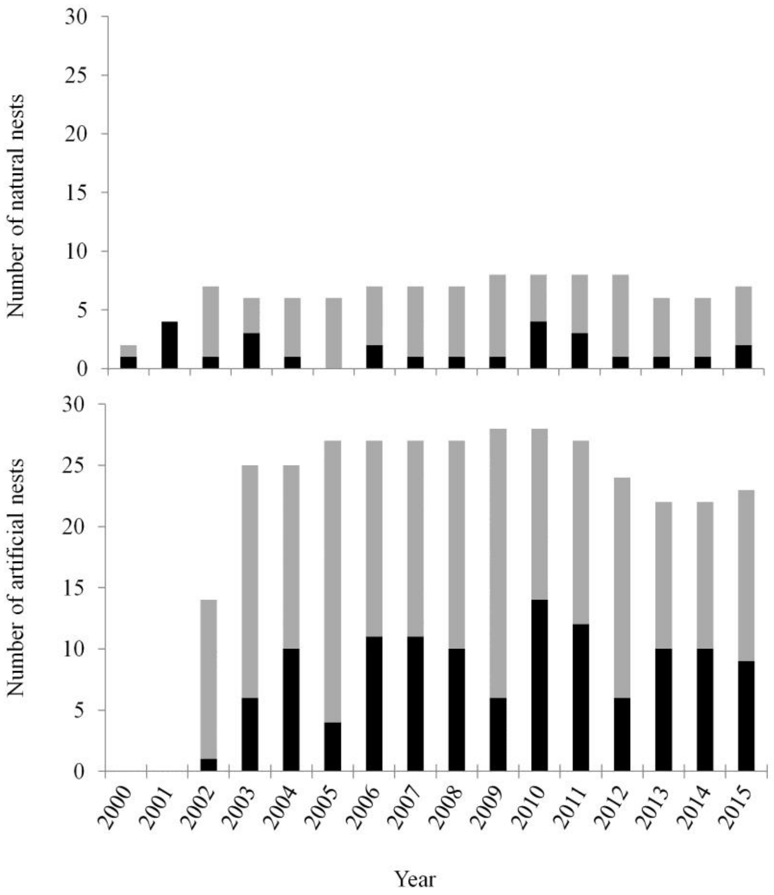


Figure 2.5. Number of breeding attempts each year in natural cavities and nest boxes available to ground hornbills in the study area.

The proportion of successful breeding attempts decreased marginally when lower or higher amounts of rain fell over the previous year (60 % attempted breeding when ≤ 450 mm of rain fell over the previous year, and 70 % when > 700 mm of rain fell over the previous year). Groups were not constrained by group size or by whether they fledged a chick during the previous season (Table 2.4). The breeding resources available to groups had no effect on the likelihood of groups attempting to breed (Table 2.4).

Table 2.4. Results of a binomial model exploring the probability of a group laying an egg(s). The model included data for 19 breeding groups over 235 group years during 2000–2015. The minimum model is shown including and above the underlined variable, and non-significant variables are shown below the underlined variable. All estimates are from the full model, and the estimates and SE's are logits. Hosmer Lemeshow GOF test of the final model: χ^2 = 15.78, df = 8, *P* = 0.05.

Variable	Est. (95 % CI)	SE	Z	*P*
(Intercept)	0.80 (-1.13–3.05)	0.42	1.92	0.06
Rainfall over the previous year	0.46 (-0.07–0.99)	0.24	1.91	0.06
Success over the previous year	0.02 (-0.74–0.78)	0.39	0.05	0.97
Group size	0.16 (-0.32–0.63)	0.24	0.64	0.53
Dry season rainfall	0.28 (-0.24–0.80)	0.27	1.06	0.29
Summer rainfall	-0.45 (-1.01–0.10)	0.28	-1.61	0.11
Spring rainfall	-0.03 (-0.52–0.46)	0.25	-0.11	0.91
Nest age	-0.02 (-0.16–0.12)	0.07	-0.28	0.78
Riparian habitat	-0.56 (-1.28–0.16)	0.37	-1.51	0.13
Home range size	0.22 (-0.35–0.80)	0.29	0.75	0.45
No. of natural nests	0.77 (-0.65–2.19)	0.72	1.06	0.29
No. of nest boxes	-0.23 (-1.39–0.92)	0.59	-0.40	0.69

Overall, 69 % of breeding attempts raised one chick to fledging (110 of 159). For each season, one fledgling was produced from breeding attempts in natural nests and six from breeding attempts in nest boxes (Appendix 2.3). Two seasons after the first nest boxes were installed, the number of chicks fledging from these nests surpassed that of natural nests (Figure 2.6), but this was not surprising given the higher number of nest boxes that were available. Groups in the study area fledged one chick every three years (Appendix 2.3).

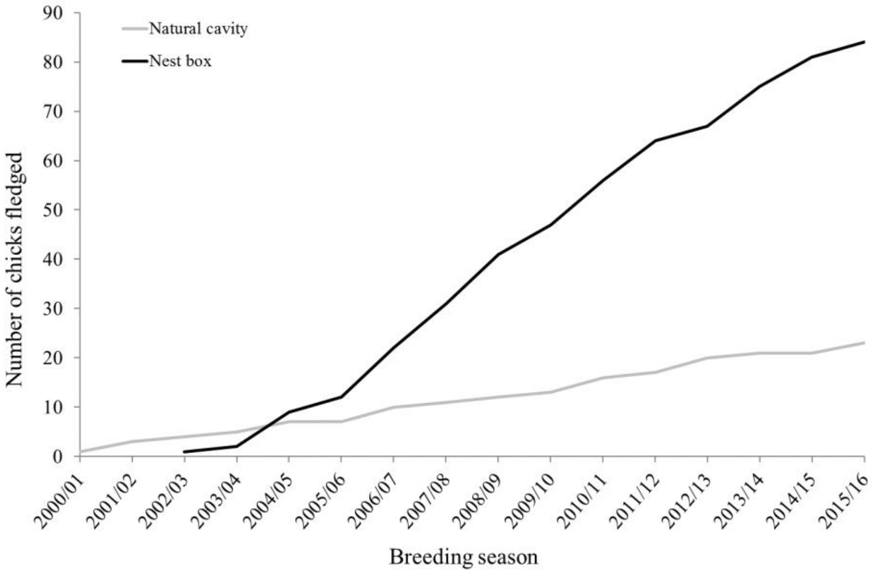


Figure 2.6. Cumulative total of chicks fledged from natural nests and nest boxes over 16 breeding seasons.

Groups rarely made a second breeding attempt in the same season if the first attempt failed. Only 3 % of breeding attempts were second attempts (four in 159 breeding attempts). Of the four groups that attempted to breed twice, the eggs in the first attempt were laid early in the season: their first attempt was initiated on average 16 ± 8 days earlier than the mean lay-date for each season (range 10–27 days). Furthermore, all four first attempts failed during incubation. Three of the four re-nesting groups had access to an alternative nest, and in all three cases they switched nests for the second attempt. Females re-laid 17 ± 5 days after the last attempt failed (range 11–23 days).

Nest boxes provided for ground hornbills were rarely occupied by other birds. Western Barn Owls *Tyto alba* were recorded nesting a total of six times and in a total of three nest boxes that had been previously occupied at least once by ground hornbills. None of these attempts by barn owls succeeded in fledging chicks, and it was suspected that ground hornbills either cracked the eggs or killed the chick. A pair of barn owls were however successful at fledging three chicks from a nest box that had never been used by ground hornbills. No natural ground hornbill cavity nests were occupied by owls.

Factors influencing breeding success

Nest type, whether a group occupied a nest box or a natural cavity, was not associated with breeding success (Table 2.5). Groups breeding in nest boxes were as successful as groups using natural nests (68 % breeding success in nest boxes, n = 95; 54 % in natural nests, n = 22). The final model that investigated factors affecting the likelihood of a successful breeding attempt in all nests (both natural and nets boxes), identified three variables associated with breeding success: year, nest height, and the thickness of the cavity wall (Table 2.5).

The variation in breeding success over time was non-linear (year was a significant term when it was included in the breeding success model as a non-linear term, Table 2.5). Overall, breeding success increased in the initial years of the study up to a maximum of 80 % in 2005, but then later decreased steadily after 2005 to only 45 % in 2015 (Figure 2.7). When the breeding group density increased to above 20 groups, average breeding success began to fall sharply (Figure 2.7). The high success in 2013 compared to previous and subsequent seasons, could not be explained by rainfall over the season or rainfall over the previous year (Figure 2.8). However, this marked increase in breeding success came two years after a season of exceptionally high rainfall caused by Tropical Cyclone Dando that made landfall on the Mozambique coast on 16 January 2012, bringing heavy rains and subsequent flooding to the study site two days later.

Two nest features were associated with breeding success: the height of the entrance above ground as well as the thickness of the cavity walls. These findings must be interpreted with caution as both *P*-values were only marginally significant (Table 2.5). Nests with entrances ≥ 6 m off the ground were more successful (75 %, n = 60) than lower nests (56 %, n = 57). Furthermore, nests with thicker cavity walls increased breeding success (Table 2.5, Figure 2.9); nests with walls > 6 cm thick were more successful (72 %, n = 65) than thinner-walled nests (58 %, n = 52).

Although laying day was identified as a non-significant term when included with the other terms in the final model (Est. = -0.42, CI = -0.87–0.02, SE = 0.22, *P* = 0.06), the removal of this term from the final model had a nearly significant effect on model power (*P* = 0.05), indicating that laying day is an important factor explaining variation in breeding success. The likelihood of a group fledging a chick marginally decreased as the breeding season progressed (Table 2.5). Attempts initiated before and during the peak laying period (56–76 days after 1 September, 49 % of nests initiated) enjoyed higher success (71 %, n = 31; 72 %, n = 56, respectively) than those nests initiated after the peak (50 %, n = 30). Harvesting the second egg or chick did not affect breeding success (Table 2.5). Nests where a chick or egg was harvested were as likely to fledge a chick (77 %, n = 26) than nests where no harvest occurred (63 %, n = 91, Table 2.5).

Table 2.5. Results of a Generalised Linear Model exploring the probability of a group fledging a chick. The model included breeding attempt outcomes (fledged a chick or not) for 18 breeding groups over 117 group years during 2000–2015. The best minimal model contained the underlined variable and those above it. All variables excluded from the minimal model are shown below the underlined variable. The estimates, standard errors (SE), Z-values and *P*-values are all from the full model. Estimates and SE's are logits. Based on initial plots, Year was included in the model as a cubic term (degree = 3) using beta splines to fit the trend line. The number next to year denotes the basis function, which is a measure of how flexible the curve is. Nest type(Natural) and Orientation(North) are included as the reference categories for the factors of nest type and nest orientation, respectively, and are therefore included within the Intercept term. Hosmer-Lemeshow goodness-of-fit test for the final model, $\chi^2 = 5.56$, df = 8, $P = 0.69$.

Variable	Est. (95 % CI)	SE	Z	*P*
(Intercept)	-0.72 (-3.41–1.98)	1.36	-0.53	0.60
Year.1	1.64 (-4.48–7.76)	3.09	0.53	0.59
Year.2	3.58 (0.66–6.49)	1.47	2.43	0.02
Year.3	0.44 (-2.65–3.54)	1.56	0.28	0.78
Nest height	0.54 (0.02–1.05)	0.26	2.07	0.04
<u>Thickness of the cavity wall</u>	0.49 (0.01–0.96)	0.24	2.02	0.04
Group size	0.36 (-0.17–0.88)	0.26	1.35	0.18
Rainfall over the previous year	-0.01 (-0.56–0.53)	0.27	-0.05	0.97
Seasonal rainfall	-0.44 (-1.00–0.13)	0.29	-1.54	0.12
Open habitat	-0.43 (-2.82–1.97)	1.20	-0.35	0.72
Nest type (Nest box)	0.66 (-2.94–4.27)	1.82	0.36	0.72
Harvesting	0.38 (-0.91–1.66)	0.65	0.58	0.56
Orientation (South)	0.07 (-3.62–3.76)	1.86	0.04	0.97
Orientation (Top)	0.95 (-2.72–4.62)	1.85	0.51	0.61
Orientation (West)	-0.78 (-2.25–0.70)	0.75	-1.04	0.30
Laying day	-0.52 (-1.02–-0.01)	0.25	-2.03	0.04
Open habitat x Nest type (Nest box)	0.01 (-2.60–2.63)	1.32	0.01	0.99

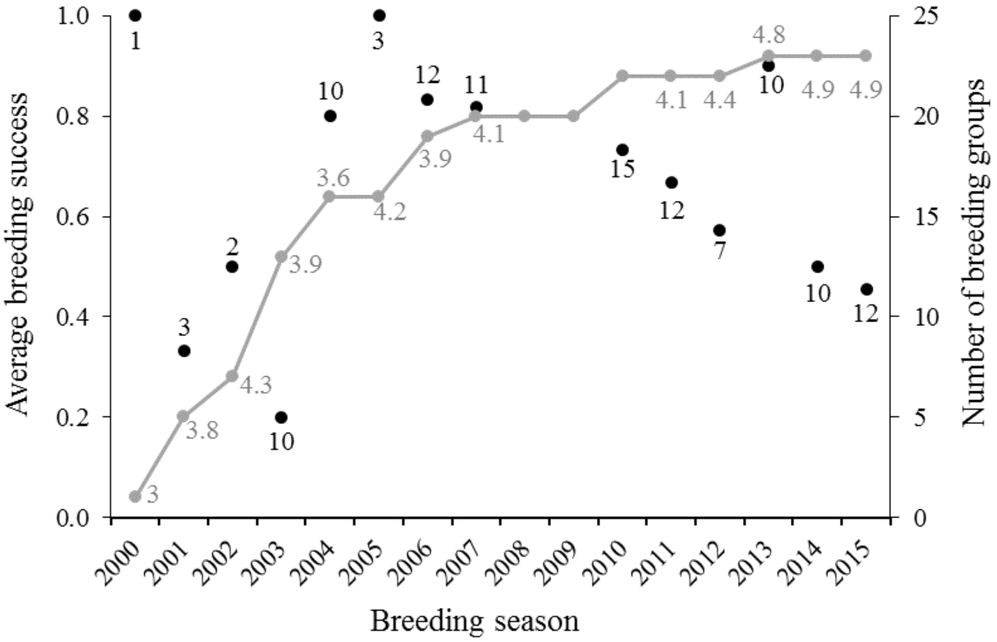


Figure 2.7. Variation in average seasonal breeding success (the proportion of breeding attempts that fledged a chick, black dots) relative to the number of breeding groups (grey line). Data for group sizes were not available during 2008–2010. Number of breeding attempts made and average group size are provided next to black and grey data points, respectively.

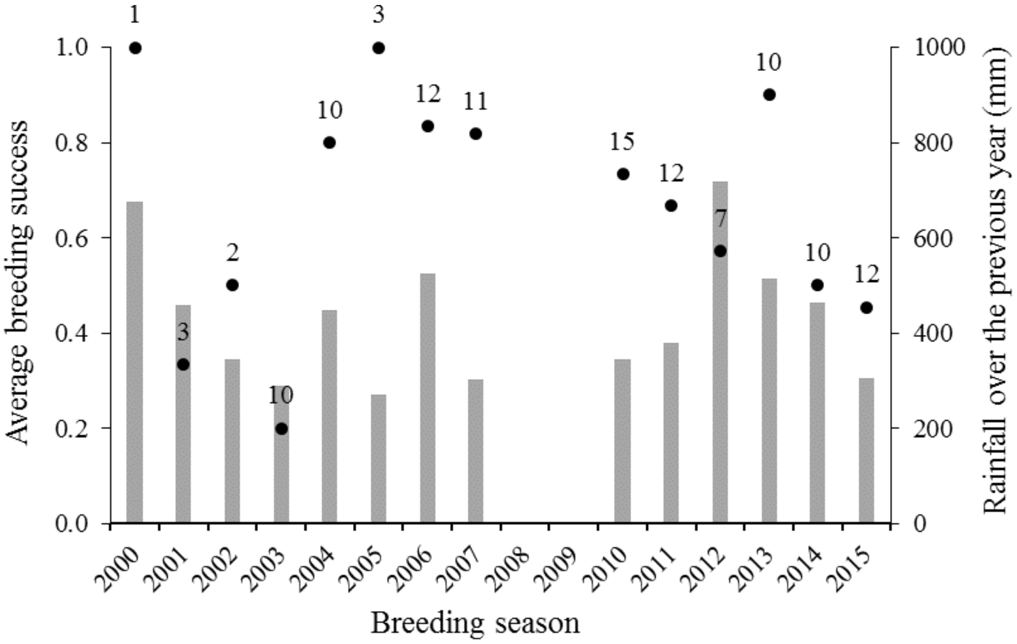


Figure 2.8. Variation in seasonal breeding success relative to rainfall over the previous year (Jul–Jun, grey bars). Breeding success is the proportion of breeding attempts that fledged a chick, indicated by black dots, with the number of breeding attempts above. Data for failed breeding attempts were not available for 2008–2010.

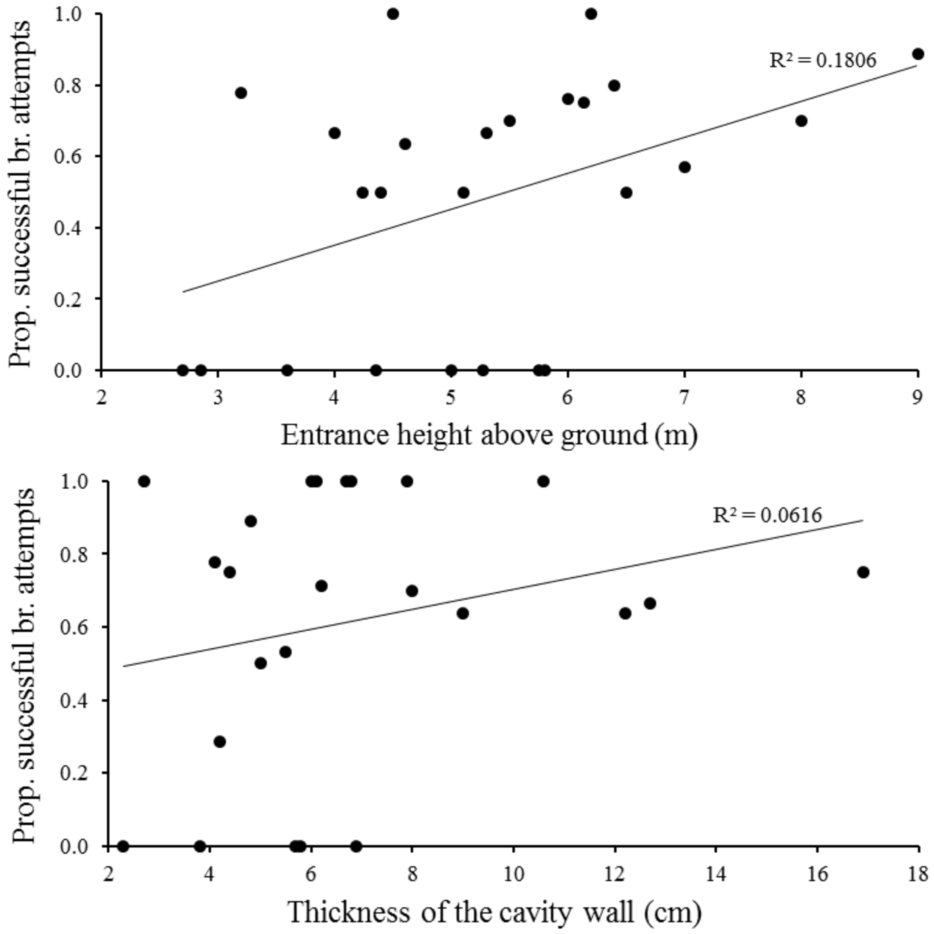


Figure 2.9. The effect on breeding success on the height of the nest entrance above ground and the thickness of the nest cavity wall.

Nest predation

Nest predation was a leading cause of nest failure in both nest boxes and natural nests (Table 2.6). Outside of the breeding season 64 % of nest boxes and 42 % of natural nests were used as sleeping sites by known or suspected nest predators: Small-spotted Genet *Genetta genetta*, Slender Mongoose *Galerella sanguine* and Rock Monitor *Varanus albigularis* and African Rock Python *Python sebae*. The type of nest did not affect the predation frequency (Table 2.7). In nest boxes, 22 predation events took place in 112 breeding attempts (predation rate of 20 %). In natural cavities, six predation events took place in 33 breeding attempts (predation rate of 18 %). In addition, there was no effect of rainfall over the previous year or the height of nest entrances on the likelihood of predation. Predation occurred more often during the incubation stage than during the chick stage (87 % and 13 %, respectively). Other causes of nest failure included nest abandonment and eggs falling through cracks in the nest floor (Table 2.6).

Table 2.6. Causes of nest failure in nest boxes and natural nests.

Cause of nest failure	Nest boxes	Natural nests
Predation	22	6
Nest abandonment	6	0
Eggs fell through the nest floor	3	0
Total	31	6

Table 2.7. Results of a binomial model exploring variation in predation levels. The model included predation events for 18 breeding groups over 117 group years during 2000–2015. Hosmer Lemeshow GOF test: $\chi^2 = 8.37$, df = 8, $P = 0.40$.

Variable	Est. (95 % CI)	SE	Z	*P*
(Intercept)	-1.57 (-2.27– -0.88)	0.36	-4.42	< 0.05
Nest type (Natural)	0.64 (-0.71–1.98)	0.69	0.93	0.35
Nest height	-0.24 (-0.81–0.33)	0.29	-0.82	0.41
Rainfall over the previous year	-0.36 (-0.90–0.18)	0.28	-1.30	0.19

The costs of building, installing and maintaining nest boxes

Logs were donated by a logging company 200 km from the study site. Logs were transported, at a cost of R 200 per log, from the Pine plantation 200 km away to the headquarters of the study site for construction. To build a nest required a day’s labour for one person. The consumables needed to construct one nest box cost R 177.10 as of 2016 (Table 2.8). The finished nest boxes could then be transported on the back of a pick-up truck, usually individually, to each site requiring a nest. Installation took two people half a day. Nests were supported and stabilised in the tree using fallen wooden logs found near the tree that were fastened to the nest and the tree using pliable metal wire.

The wooden rooves and floors of nest boxes in the APNR had a life span of 9 ± 3 years (range 3–14 years). The life-span of nests were extended by repairing holes in the roof and floor inexpensively using donated pallet wood from a local fruit packer. If a nest box collapsed to the ground and broke apart, it was replaced by another in the same position. During 2002–2015, four of the 32 nests needed replacing. Provided logs remain a free resource by donation, the cost to maintain nests over a decade will be the price to construct and install a new nest once every three years. Nests were monitored once during the breeding season and every 7-10 during the breeding season. These fuel costs for these exercises (one tank per week during the non-breeding season, two-three tanks per month during the breeding season) were covered by donations from reserves and lodges in the area.

Table 2.8. A list of consumables required to construct one nest log for Southern Ground Hornbills as of 2016. Priced in South African Rands (R 1 is roughly equivalent to US$ 0.08).

Item	Cost
750 ml two-stroke oil	R 31.50
2 litres of petrol	R 26.00
2 m binding wire	R 2.20
Two 1 m threaded metal bars	R 26.52
Four nuts	R 2.48
Four washers	R 6.60
1 m^2 plastic sheeting	R 12.60
20 nails	R 5.20
10 screws	R 4.00
Two 150x300 mm metal ‘gryptite’ plates	R 60.00
Total	R 177.10

Discussion

Nest boxes are a useful conservation tool for the Southern Ground Hornbill. Groups used nest boxes more frequently than natural nests after these were placed, and fledged chicks more often than groups occupying natural nests. Nest boxes had no adverse effect in ground hornbill breeding success, as breeding success was as high in nest boxes than in natural nests. The decrease in productivity at a time when breeding group density and average group size was high, highlighted the importance of long-term monitoring of breeding success over time, and indicates that creating densities higher than optimal, or groups sizes larger than optimal, can slow the progress toward increasing reproductive output for this species. Although the costs per nest were high, the long life-span of nests and infrequent and inexpensive maintenance to them required meant that maintaining nest site availability at the study site required only one nest replacement on average every three years.

Nest characteristics

The type of nest used, either natural or artificial, was not associated with breeding success. Therefore, although some studies on other bird species identified a negative effect of artificial nests reproductive output (Catry et al. 2011; Björklund et al. 2013; Demeyrier et al. 2016) or a positive effect (Brazill-Boast et al. 2013; Sutherland et al. 2014; Bourgeois et al. 2015), nest boxes for ground hornbills had no adverse effect on breeding success for those groups occupying them. Importantly, in this study, ground hornbill groups with access to a nest box attempted breeding more often than groups that had access to natural nests only, and fledged a chick more often than groups occupying natural tree cavity nests. Similarly, Eurasian Kestrels *Falco tinnunculus* fledged more chicks in artificial nests than in natural nests, and nest boxes were the most frequently used nest site (Fargallo 2001). For Eurasian Kestrels, nest predation was higher in natural nests than in artificial nests, and this contributed to the differences in reproductive output between pairs occupying the two nest types (Fargallo 2001). For ground hornbills, it is apparent that nest boxes are attractive nesting sites, and groups occupying them are highly productive, and predation levels in nest boxes and natural nests were similar (20 % and 18 %, respectively).

The microclimate inside nest boxes mimicked natural tree cavity nests closely. This indicated that the nest boxes provided for ground hornbills in the study area mimicked natural nest conditions closely. In cool areas, warmer nests have been associated with heavier chicks (Dawson et al. 2005; Larson et al. 2015), and heavier chicks generally have higher survival rates (Perrins 1965; Magrath 1991; Dawson et al. 2005). Warmer nests are generally favoured due to important benefits such as energy savings during incubation and/or the prevention of chilling of eggs and chicks while the female is off the nest (Ardia et al. 2006; Landler et al. 2014), which then require greater energy costs to the incubating female to bring the eggs back up to the desired temperature (Wiebe 2001). But in a hot environment such as north-eastern South Africa, avoidance of hotter nests would be expected due to the fatal effect of high temperatures (>41 °C) on eggs and chicks for birds in general (Webb 1987). Hotter nests were occupied by ground hornbills, and groups fledged chicks from these nests. Although nest temperatures were recorded out of season, during the relatively cooler months in winter, the highest temperatures were experienced inside a frequently occupied nest box (11 of 14 seasons), and the highest rate of temperature increase was recorded inside a frequently occupied natural tree cavity nest (10 of 16 seasons). Their tolerance and success in these warm nests indicated a high degree of heat tolerance. Some natural nests of ground hornbills in the study area, and some in Kruger (Kemp & Begg 1996), were chimney nests which are open to the top and thus would be exposed to the sun's direct rays during the middle part of the day. During the beeding season in the autral spring and summer months, the egg contents would be at risk of overheating, and quite possibly reaching or exceeding the thermal upper limit. The negative effect of exceptionally hot temperatures on ground hornbill egg failure was demonstrated during the 2015/2016 season at the study site, when maximum temperatures of 45 °C were reported (C Rowles pers. comm 2016) when a high proportion of eggs failed to hatch. A total of 24 % (4 of 17 eggs) of eggs failed to hatch at a site where, on average, fewer than 10 % of eggs fail to hatch (average failure rate of 7 % or 16 of 234 eggs laid between 2000/2001 and 2015/2016). In a similar scenario, 22 % of Lesser Kestrel *Falco naumanni* nests experienced hatching failures associated with atypically high temperatures (Catry et al. 2011). Given that thicker cavity walls improved breeding success for ground hornbills, this feature should be considered when designing nest boxes that will buffer the negative effects of exceptionally hot conditions during the breeding season.

The distance between active nests provides a useful demonstration of the minimum distances between nests that can be tolerated by a species. This kind of information can be important when deciding how to place nests in other areas in the future. In the study area, neighbours nested no closer than 2.7 km apart (5.7 ± 2.4 km, range 2.7–18.2 km). Available literature suggests this species can nest as close as 1.5 km apart in south-western Zimbabwe (Witteveen et al., 2013). Groups in northern South Africa, along the Limpopo River Valley, have very large home ranges (200 km^2, Theron 2011) and, not surprisingly, very large nearest neighbour distances (40 km, though this was between the nests of only two groups; Theron et al. 2013). In the Kruger National Park during 1967–78, nearest neighbouring distances between eight breeding groups was greater than in this study (8.9 ± 3.2 km, range 4.8–13.7 km, Kemp & Kemp 1980). Additional research in other parts of the species range would shed light on the minimum inter-nest distance tolerated by this species, especially in Mana Pools, Zimbabwe, where groups defend very small territories (20 km^2; Kemp, 2005).

Group size and group density

Average group size decreased immediately following the installation of nest boxes, and over time, average group size recovered and eventually surpassed the average group size for the country. The increase in density was likely balanced by the dispersal of individuals from the APNR into Kruger (Chapter 4). By 2015, the average group size had stabilised at 4.9 individuals, suggesting that the population in the study area was saturated. The number of breeding groups also increased rapidly after nest boxes were installed. The number of Red-cockaded Woodpeckers breeding groups also increased following the installation of nest boxes (Carrie et al. 2014). The rapid increase in the identification of ‘new’ breeding ground hornbill groups suggested a local source of breeding pairs, either by stimulating existing pairs to breed or stimulating the formation of new breeding pairs by the dispersal of non-breeding individuals out of existing groups. Group sizes of Green Woodhoopoes *Phoeniculus purpureus* were smaller at sites where nest sites were available in the marginal habitats, allowing for an outlet for non-breeding birds from their natal home ranges (du Plessis 1989). The dispersal of ground hornbill non-breeders into marginal habitat that, after nest box provisioning, contained suitable nesting sites. would explain the decrease in group sizes immediately following the installation of nest boxes, as well as the rapid increase in pairs and groups of three individuals observed in the initial years after nest box were installed.

Average breeding success showed a non-linear trend with time. Initially, breeding success increased, but later began to decrease. The initial improvement in breeding success over time may have been caused by increasing breeding experience (Sydeman et al. 1991, Saunders et al. 2016). In Western Gulls *Larus occidentalis*, the proportion of eggs hatching and hatched chicks fledging increased with age, and was best explained by previous breeding experience (Sydeman et al. 1991). Similarly, in Carnaby’s Cockatoo *Calyptorhynchus latirostris*, nest failure rates of inexperienced breeders in their first two seasons were four times as high as experienced breeders (Saunders et al. 2016). Assuming new ground hornbills breeding groups identified in the study site had little to no previous breeding experience, one might expect that, like the Western Gull and Carnaby’s Cockatoo, the likelihood of ground hornbill breeding success increases as pairs become more experienced, explaining the increase in breeding success over the first few years of the study.

The decrease in breeding success in later years may be explained by the high density of breeding groups and the increasing group size. In the study area, group density of both breeding and non-breeding groups was higher (1 group per 72 km^2, Wyness 2011) than in central Kruger (1 per 100 km^2, Kemp & Kemp 1980), which is a protected area immediately adjacent to the study area comprising savannah habitat and was thus considered most appropriate for comparisons. In 2005, average group size was similar to that observed before nest boxes were installed. However, after 2005 the average group size continued to increase possibly to levels above the carrying capacity of the smaller home ranges. If the carrying capacity for some territories were exceeded, this may well have resulted in resource depletion, especially during the breeding season when groups reduced their foraging range (Wyness 2011) putting additional pressure on individuals to find enough food over a reduced area. If the seasonal abundance of food during the breeding season was not high enough to provide sufficient food for all individuals, it can result in weight loss and negative effects on survival (Sorato et al. 2016). In a different study, an above-optimal breeding density was created by saturating optimal habitat with nest boxes, which caused a decline in reproductive output in territorial Great Tits *Parus major* (Mänd et al. 2005). Furthermore, efforts to improve breeding habitat for the declining Canadian Warbler resulted in a high density of birds occupying smaller territories that resulted in lower breeding success (Flockhart et al. 2016). Another important factor to consider when identifying a reason for declining reproductive productivity despite group size and the number of helpers increasing, is the possibility that conflicts between individuals in the same group may have hampered reproductive output, as seen in the Seychelles Magpie Robin *Copsychus sechellarum* (López-Sepulcre et al. 2009). Like ground hornbills, Seychelles Magpie Robins live in social groups where subordinate individuals do not breed. In that species, social conflict occurs through nest disturbance by helpers and aggressive interactions between a dominant individual and a helper during take-over attempts (López-Sepulcre et al. 2009). For ground-hornbills, nest disturbance by helpers has not yet been identified (pers. obs.), and conflict between dominant individuals and sub-ordinates is rare (pers. obs.), and thus unlikely to be an important contributor to decreasing breeding success with increased group size.

Rainfall

Rainfall over the previous year had a positive effect on whether a group attempted to breed. It is likely that rainfall itself was not the cue, but rather the lagged effect it had on vegetation growth (Dudney et al. 2017), and ultimately arthropod abundance (Kemp 1976), which is the main diet of ground hornbills. Interestingly, rainfall did not affect how likely a group was to fledge a chick. Thus, once breeding, it appears that ground hornbills are more resilient to variable rainfall conditions than previously thought (Wilson & Hockey 2013). A previous study on ground hornbills in the study area during 2000–2008 found rainfall < 300 mm or > 500 mm during the season negatively affected breeding success (Wilson & Hockey 2013). By including an additional eight years of data, this study unexpectedly found otherwise, that rainfall did not influence breeding success when included both as linear and non-linear terms. The varied diet of the ground hornbill, which includes invertebrates, reptiles, amphibians and small mammals, likely assists them to switch between prey items under varying rainfall conditions during the breeding season, ultimately facilitating breeding success during seasons of high rainfall or low rainfall. This is reassuring given the predicted changing environmental conditions in north-eastern South Africa due to climate change (Cunningham et al. 2016).

Timing of breeding

Timing of breeding had an important effect on breeding success. Groups laying earlier in the season, before the median lay date of 03 November, were more likely to raise a chick to fledging (71 %) than those laying after that date (50 %). This finding for ground hornbills is one of a few for the southern hemisphere, where studies show either a similar trend to the north-temperate zone (Reyer 1984; Garnett et al. 2001), or no effect of timing of breeding on breeding success (Heinsohn 1992). Additional contributions from the southern hemisphere, such as results from this study, will help to better understand the effect of timing of breeding on breeding success at various latitudes.

Nest predation

Comparing predation rates in this study to predation rates in ground hornbill nests in other studies, the predation rate in natural nests in the study area was similar to that in the Kruger National Park (22 %; Kemp & Kemp 1980). But given the difficulty of distinguishing predation from scavenging, this is likely to be an overestimate. Predation levels of ground hornbills are similar to nest-sealing hornbills (15 %, Poonswad et al., 1999). Bucerotid hornbills generally suffer low levels of predation due to their nest sealing behaviour (Moreau 1936; Kemp & Kemp 1980; Poonswad et al. 2013). This suggests that even without the benefit of a sealed nest entrance, ground hornbill nests in both natural nests and nest boxes suffered relatively low levels of nest predation. Since ground hornbills can likely inflict serious harm to, or even kill, most nest predators, it is likely that nest predators are understandably wary of raiding ground hornbill nests.

Recommendations

Maximising reproductive output through human interventions for threatened species is vital. My study identifies several factors which can be applied to the placement and design of nest boxes to maximise reproductive output for the ground hornbill. Nest boxes can be placed as close as 3 km apart, as this was the shortest distance recorded between two active nests in the study site. However, it would be prudent to space nest boxes adequately to facilitate home range sizes that are near to the average for the area:100 km^2 in the Kruger National Park, South Africa (Kemp et al. 1989). This will avoid any chance of creating an unsuitably high density of groups. Furthermore, providing an additional nest box for each group once their territories have been established may have positive benefits for reproductive success. Most groups that failed their first attempt switched nests before attempting again in the same season. These nests were typically < 1 km apart in the same home range. Switching nests is common in other birds following nest failure, and one explanation is that this behaviour reduces predation risk (Sonerud 1985; Lima 2009). Designs of nest box should consider the thickness of the cavity walls. Thicker cavity walls can improve breeding success. For example, nests with walls > 6 cm thick were more successful (72 %) than those with thinner cavity walls (58 %). Therefore, constructing nest boxes with a minimum wall thickness of 6 cm would be a suitable standard. Lastly, placing nest boxes at a suitable height above ground can assist with maximising reproductive output. Groups occupying nests ≥ 6 m off the ground were more successful (75 %) than lower nests (56 %), and therefore I recommend that nest boxes be placed so that nest entrances are at least 6 m off the ground.

The provision of nest boxes addresses the symptom of the loss of large trees in the landscape, which is the lack of suitable natural nesting sites for ground-hornbills. This conservation tool does not however address the cause of the loss of large trees. Humans and Elephants have been identified as the major contributors to higher than natural tree-fall rates in African savannas that occur in protected areas (Mograbi et al. in press). In communal lands, where ground-hornbills can occur (L. Kemp pers. comm.), trees > 3 m tall are scarce (Mograbi et al. in press). The loss of, or damage to, large trees in the landscape places higher pressure on the classes of woody vegetation at the lower height classes, thereby compromising ecosystem resilience (Mograbi et al. in press). If nest boxes are to be considered a tool to bridge the gap until new suitable tree cavities are formed, then an important conservation action for the species is promoting and protecting the growth and persistence of large, mature trees into the future.

Appendix 2.1. Breeding success of 23 Southern Ground Hornbills *Bucorvus leadbeateri* breeding groups in north-eastern South Africa occupying natural nest cavities and nest boxes. Data were available for successful breeding attempts only for seasons 2008/09 ans 2009/10.

	Natural cavities		Nest boxes		
Season	Attempts	Fledged (%)	Attempts	Fledged (%)	% Nest boxes
2000/01	1	1 (100)	-	-	-
2001/02	5	2 (40)	-	-	-
2002/03	2	1 (50)	1	1 (100)	33
2003/04	4	1 (25)	8	1 (13)	67
2004/05	2	2 (100)	10	7 (70)	83
2005/06	0	0	4	3 (75)	100
2006/07	4	3 (75)	11	10 (91)	73
2007/08	1	1 (100)	11	9 (82)	92
2008/09	≥ 1	1	≥ 10	10	91
2009/10	≥ 1	1	≥ 6	6	86
2010/11	4	3 (75)	14	9 (64)	78
2011/12	3	1 (33)	12	8 (67)	80
2012/13	3	3 (100)	6	3 (50)	67
2013/14	1	1 (100)	10	8 (80)	91
2014/15	1	0	10	6 (60)	91
2015/16	2	2 (100)	10	3 (30)	83
Total	35	23 (66)	123	84 (68)	
Average	2.2	1.4 (66)	8.8	6.0 (68)	80

Appendix 2.2 Average nearest-neighbour distance (km) between active ground hornbill nests in three areas of southern Africa: Associated Private Nature Reserves (APNR), north-eastern South Africa (this study); Kruger National Park (KNP), north-eastern South Africa (Kemp & Kemp 1980); and the communal areas surrounding the Motobo National Park, southern Zimbabwe (sZim, Witteveen et al., 2013).

Location	Breeding season	No. breeding groups	Mean distance ± SD	Distance range
APNR	2001/02	3	6.3 ± 0.0	5.7–7.6
	2002/03	2	12.7	-
	2003/04	9	6.2 ± 1.9	3.7–8.0
	2004/05	11	6.3 ± 1.3	4.6–8.3
	2005/06	4	12.1 ± 5.5	6.8–18.2
	2006/07	13	7.1 ± 1.4	5.0–9.6
	2007/08	12	5.4 ± 2.3	2.7–8.1
	2008/09	11	7.8 ± 1.1	5.8–9.6
	2009/10	7	9.4 ± 4.1	4.6–16.1
	2010/11	18	6.3 ± 1.5	4.6–9.6
	2011/12	15	6.6 ± 2.7	3.5–14.4
	2012/13	9	11.8 ± 2.4	8.0–14.4
	2013/14	11	7.7 ± 4.4	4.7–15.9
	2014/15	11	7.3 ± 4.3	3.9–15.9
	2015/16	11	8.6 ± 3.6	5.1–15.9
All APNR		23	5.7 ± 2.4	2.7–18.2
KNP	1967–78	8	8.9 ± 3.2	4.8–13.7
sZIM	2008/09	18	6.0 ± 1.7	1.6–32.2
	2009/10	27	3.5 ± 0.3	3.5–4.4

Appendix 2.3. Breeding histories for 23 Southern Ground Hornbill *Bucorvus leadbeateri* groups during 2000–2015 in north-eastern South Africa.

Group name	No. years observed	Min. no. of br. attempts	No. chicks fledged	Years per chick fledged
Rhino Road$	15	12	11[a]	1.3
Keer Keer*	16	10	8	1.3
Addger	17	13	9	1.3
Goedehoop*	4	4	3	1.3
Karan Khaya	14	12	9	1.6
Copenhagen	13	9	9	1.9
Johnniesdale$	15	13	8[b]	1.9
Ntsiri	13	10	6	2.0
Janovsky	14	9	8	2.1
Caroline	14	7	5	2.2
Senalala	15	12	7	2.3
Pitlochry	14	9	7	2.5
Hermansburg	14	9	5	2.5
Naylor$	9	5	4[c]	3.0
De Luca$	11	8	3[b]	3.7
Giraffe*	13	6	3	4.0
Java	5	1	1	5.0
Ntoma*	5	2	2	5.5
Strydom	11	4	2	9.0
Mandavan*	13	1	0	> 12.0
Hancock*	12	1	0	> 12.0
Mananga*	15	1	0	> 14.0
Charloscar	11	1	0	> 11.0
Total	283	159	110	**2.6**

*Used natural nest only; $ Used natural cavities and nest boxes; [a] One chick fledged from a natural nest; [b] No chicks fledged from a natural nest; [c] All chicks fledged from a natural nest

Chapter 3 Variation in the timing of egg-laying

The timing of breeding in birds has important consequences for the likelihood of a successful nesting attempt. Timing of breeding to coincide peaks in food available with the most energetically demanding stage of nesting can increase the likelihood of a successful breeding attempt. There are costs and benefits associated with both early and late breeding. For example, early breeders may have a higher likelihood of success but producing eggs early for some bird species can be costly to females. Late breeders may enjoy the benefit of higher food supply during egg production and incubation, but their offspring will likely hatch after the peak in food availability if food availability is non-uniform through the season. Weighing up these costs and benefits is important for a species such as the Southern Ground Hornbill that typically produces only a single brood, and at best, a single fledgling, per breeding season. In the previous chapter, I found that ground hornbill groups that lay earlier are more likely to fledge a chick than groups that lay late in a breeding season. In this chapter, I investigate how laying dates vary among and within seasons, and whether rainfall, temperature, group identity, group size are associated with the variation in laying dates in a study site supplemented with nest boxes. In addition, I explore whether the timing of breeding varies between nests in nest boxes and natural tree cavities. Ground hornbills in the study area laid from 9 September–13 January, with a median laying date of 3 November, but there was considerable variation in the timing and distribution of laying dates. Egg laying commenced in different seasons from 9 September to 14 November. Laying dates were not significantly different between groups that occupied nest boxes and natural tree cavity nests. Laying was delayed during warmer springs, particularly under dry conditions, and large groups were more likely to lay later in the season than small groups.

Introduction

Timing of breeding has important consequences for the likelihood of a successful nesting attempt (Daan et al. 1989) and survival to breeding age of offspring (Perrins 1970). For most bird species that live in seasonal environments, nests initiated in the first half of the season are more likely to fledge a chick and have offspring that survive to the next season than breeding attempts in the latter part of the breeding season (Perrins 1970; Daan et al. 1989; Verhulst & Nilsson 2008). Indeed, changes in environmental conditions due to climate change has affected the timing of breeding in many bird species with mostly negative consequences (Dunn & Winkler 2010). Since most studies emanate from the northern temperate regions, there is a need to better understand the effects of environmental conditions on avian phenology across a wider geographic scale (Dunn & Winkler 2010), and in bird species other than passerines, such as Hornbills.

There are costs and benefits to both early and late breeders, where early breeders have a higher likelihood of success but producing eggs early can be costly to females (Perrins 1970; Williams 2005). In areas where food supplies peak during the breeding season, late breeders enjoy the benefit of higher food supply during egg production and incubation, but their offspring will likely hatch after the peak in food availability. This has even been found in environments such as the tropics that show little seasonality (Poulin et al. 1992). Costs and benefits become increasingly important for species that typically produce only a single brood during a breeding season. Each nesting attempt in such cases, whether they can only produce a single-brood or are limited to typically only produce a single brood, represents the total seasonal reproductive success, making the investment in each clutch and brood particularly valuable (Svensson 1995). Adjusting the timing of breeding (laying date) could mean the difference between a successful and a failed breeding attempt, and the cues that birds use are discussed below.

The timing of the onset of breeding in birds has been linked to triggers such as changes in photoperiod (Wikelski et al. 2000; Hau 2001; Trivedi et al. 2006), ambient temperature (Visser et al. 2009), rainfall (Zann et al. 1995; Lloyd 1999; Hau 2001), and the combined effects of temperature and rainfall on food availability (Sinclair 1978; Turner 1982; Perrins 1991; Sydeman et al. 1991; Meijer et al. 1999; Eeva et al. 2000; Pasinelli 2001; Townsend et al. 2013; Shiao et al. 2015). For most species, these factors act in a hierarchy (Dunn & Winkler 2010), with photoperiod as the primary cue setting off the "neuroendocrine cascade" (Hau 2001 and references therein), even in the tropics where there is little variation in day-length between seasons (Hau 2001). Additional cues used to determine the timing of egg-laying are largely secondary to photoperiod, such as environmental conditions like rainfall, temperature, food availability, or combinations thereof.

In addition to cues, there are other factors that influence the timing of breeding in birds. The type of nest used can affect the timing of breeding (Brazill-Boast et al. 2013), for example by making available suitable nesting sites in better habitat quality allowing for earlier nesting due to better food supplies (Fargallo et al. 2001) In addition, female-specific qualities can be associated with timing of breeding, such as age, breeding experience and condition (Amininasab et al. In press; Sydeman et al. 1991; McCleery et al. 2008; Low et al. 2015). Furthermore, for cooperatively breeding species, the size of breeding group (the number of helpers at the nest to provision chicks) can also influence the timing of breeding by facilitating later breeding by larger groups due to reduced starvation risk of later fledging chicks (Heinsohn & Cunningham 1992 in Heinsohn 1992). Different factors, specific to each species under varying conditions, are likely provide the stimulus to breeding, and effect the timing of breeding, depending on the species-specific requirements for nesting (Thomson 1950).

Proximate and ultimate factors influencing the timing of breeding are well recognised for northern hemisphere, temperate bird species (Perrins 1970; Daan et al. 1989; Perrins 1991). In the tropics and southern hemisphere temperate regions however, such as southern Africa and Australia with its wide-ranging conditions, the matter is more intricate (Thomson 1950; Ford 1989). In Australia, most bird species time their breeding to fall within Spring and within the period of highest plant growth (Nix 1976 in Ford 1989), but with exceptions arising due to differences in feeding strategies, the risk of predation, heavy rainfall inhibiting breeding, less seasonal environments resulting in irregular rainfall, and extreme temperatures. In southern Africa, insectivorous species adjust the timing of breeding from late in the winter rainy season in south-western areas, to well in advance of the summer rainy season in northern parts of the southern African region (Thomson 1950). Some breeding birds time their nesting phase during the periods of vegetation flush and thus insect abundance (Thomson 1950). In the ‘intermediate types of country’ in the southern African region described by Moreau (1950), which include the savannah habitats relevant to this study, the author notes how “in all areas, breeding begins on rising temperature and ceases before there is an important fall in temperature”, supporting photoperiod as a proximate stimulus. While food supply is important for the timing of breeding, there have been numerous cases where other, more important factors controlling the timing of breeding, have been identified (Brown & Brown 1984). In the southern African context (and globally), factors controlling the timing of breeding may include, day-length, temperature, rainfall and its effect on food supply, as well as the appearance of grass fires and green vegetation (Moreau 1950; Lloyd 1999). But importantly, there is no single important factor influencing the timing of breeding in southern Africa's birds (Moreau 1950).

The breeding season of the Southern Ground Hornbill in South Africa occurs during the wet, austral spring and summer months (September–March) and typically only a single breeding attempt is made per season. Breeding females generally lay two eggs. At most, one chick, usually the first-hatched, is raised to fledging. With time and energy focussed on only a single breeding attempt per season (attempting again after a failed first attempt is rare), timing the onset of egg-laying to maximise the likelihood of success would be crucial to achieve maximum fitness benefits. The previous chapter identified that breeding success was associated with the timing of breeding. In this chapter, I build on that finding and explore what factors are associated with the timing of breeding. In a study in the Kruger National Park, South Africa, timing of breeding generally coincides with spring rains, and food supply was considered an important factor (Kemp & Kemp 1991). It however remains to be determined how the timing of breeding is associated with other climatic factors (rainfall before the breeding season and temperature) and social factors (group size, group identity), and what the effect of nest type is on timing of breeding in a study population of ground hornbill supplemented with nest boxes. Here, I investigate how winter and spring rainfall, winter and spring temperatures, group size, female identity and the type of nest used, affect the onset of breeding in an area supplemented with nest boxes.

Methods

During the spring and summer months of 2000–2015, 31 nest boxes and 13 natural tree cavity nests were checked every 7–10 days for signs of nesting activity, but laying dates were not available for the years 2008 and 2009. A full, fresh lining of leaves (typically the shed leaves of Mopane *Colophospermum mopane*) indicated that egg-laying was imminent. If one egg was found, the nest was revisited after five days to check for the presence of a second egg. Laying date was estimated as the middle date between the check when an egg was first discovered and the previous nest check. Laying date was scored as the number of days after 1 September when the first egg was laid.

Daily temperatures were available from the town Hoedspruit, 20 km west of the study site. Mean temperatures were the average of a maximum and minimum for each day, averaged over the season. Rainfall was available from 14 rain gauges scattered throughout the study site that were each checked daily. Rainfall estimates for each group were taken from the nearest raingauge to their nest, which were situated 5 ± 3 km (SD; range 1–11 km) from each nest.

Statistical analyses

To investigate factors influencing the timing of egg laying, I performed a generalised linear mixed effect model (GLMM, package lme4, Bates et al. 2015) using laying date data for 23 groups over 134 group-years from 2000–2015. A mixed effect model includes both fixed effects (those effects that are constant across individuals, Gelman 2005) and random effects (those that vary across individuals, Gelman 2005). The program R (version 3.03, R Development Core Team 2009) was used for all statistical analyses. Data exploration was carried out following the protocols described in Zuur & Ieno (2016). I modelled *laying day* (continuous, the number of days after 1 September that the first egg was laid) as a function of *nest type* (binary, natural tree cavity nest or artificial nest box), *group size* (discrete, sizes of groups ranged from 2–8 individuals), *rainfall over the previous year* (continuous, over the months July–June), *rainfall over winter* (continuous, over the months Jun–Aug), *rainfall over spring* (continuous, over the months September–November), *temperature over winter* (continuous, mean temperature recorded during June–August), *temperature over spring* (continuous, mean temperature recorded during September–November), as well as the *number of hot spring days* (discrete, the number of days in spring where the maximum daily temperature was above 30 °C). We included a random intercept for *Group identity* (categorical). Three biologically relevant interactions were considered: (a) '*group size* x *nest type'* to investigate whether large groups occupying natural nests were more likely to initiate egg laying later (and potentially the reason why larger groups occupying natural nests fledged fewer chicks than smaller groups occupying natural nests, Carstens unpubl. data), (b) '*spring rainfall* x *spring temperature'* to investigate whether warm, wet springs affect the timing of egg laying, and (c) '*winter rainfall* x *winter temperatures'*, to investigate whether warm, wet winters affect egg laying. The response variable was continuous and normally distributed. Variables were checked for collinearity using a matrix of scatterplots. A global model was created using all terms of interest, as well as the three biologically relevant interactions. Variables with p-values < 0.05 were sequentially removed from each model, and were each added back to the reduced model one at a time, to double check that their inclusion did not contribute significantly toward the model's power. The estimates of these non-significant terms from the full model are included in the results for completeness. Model fit was verified using plots of residuals against fitted values as well as residuals versus each explanatory variable used in the full model. A histogram of residuals was created to confirm a normal distribution. Confidence intervals (95 %) for each parameter were obtained using Wald's approximation (Wald 1947). The marginal and conditional R^2 values for mixed-effect models (R^2_m and R^2_c), as described by Nakagawa & Schielzeth (2013), were computed using 'piecewiseSEM'. These two estimates measure the percentage of variation in the model explained by fixed effects (R^2_m) and both random and fixed effects (R^2_c). We used a likelihood ratio test whether fixed effects collectively explained variation in laying dates.

To investigate the possible role of female-specific or group-specific differences in laying date, we performed a GLMM using data for six groups where females were individually recognisable (n = 56 breeding attempts over 14 seasons during 2000–2015). Females were identifiable by leg bands or unique differences in their physical appearance (e.g. hind toe of left foot without a nail; very large, swollen facial skin under the bill, unusual habit of not flushing during nest checks). I modelled *laying date* as a function of *group identity* (as a proxy for female identity), with *year* as a random term to account for repeated laying dates by the same groups over multiple years. Model validation procedures were as in the previous model.

For all boxplots, the bottom and top of each box indicate lower and upper quartiles, and the solid bar within each box indicates the median. Upper and lower whiskers mark 1.5 times the interquartile range above the upper quartile and below and lower quartile. Open circles indicate data points that lie outside the limits of the whiskers and are thus outliers.

Results

Laying dates were recorded for 23 groups across 14 breeding seasons during 2000–2015, for a total of 134 group years. During this time, groups contained 4 ± 1 individuals (mean ± SD, range 2–8 individuals). Rainfall over the previous year for each of 14 seasons was 487 ± 147 mm (range 237-948 mm), over the dry season was 73 ± 45 mm (range 0–173 mm), and over spring was 101 ± 54 (range 28–277). The mean temperature in winter was 18 ± 1 °C (range 16–20 °C) and during spring was 23 ± 0 °C (range 22–24 °C).

Median laying date was 3 November. Ground hornbills displayed considerable variation in the timing and distribution of laying dates between seasons (Figure 3.1): in 2014, the first egg of the season was laid on 9 September, but in 2002 the first egg was laid on 14 Nov (2002), and groups were recorded as initiating clutches up to 13 January (2003, Figure 3.1). The mean length of the breeding season (number of days between first and last egg laying) was 55 ± 30 days (SD; range 10–101 days; Figure 3.1). Peak egg laying took place during October (39 %) and November (47 %), with 49 % of clutches initiated between 27 October and 16 November. Laying dates were advancing with time, although not significantly (r = -0.11, *P* = 0.18).

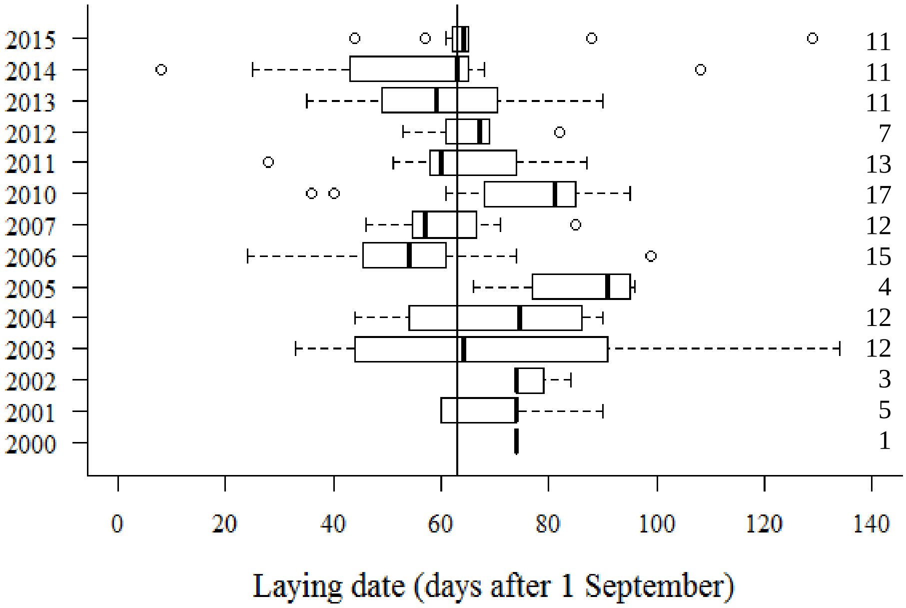


Figure 3.1. Timing of egg-laying by Southern Ground Hornbill groups across 14 breeding seasons in north-eastern South Africa. Verticle line at day 63 is the median lay date. Sample sizes are provided in the right column.

Overall variation in laying date was explained by mean spring temperature and the interaction between spring temperature and spring rainfall, as well as group size and the interaction between group size and nest type used (Table 3.1). Egg-laying was delayed when mean spring temperatures were elevated (Table 3.1), and this effect became more pronounced under lower rainfall conditions (Figure 3.2). Hot springs were not always indicative of dry conditions, as spring temperatures and spring rainfall were weakly but positively correlated (R^2 = 0.11). Larger groups initiated egg laying later than smaller groups (Table 3.1, Figure 3.3). There was a marginal effect on the interaction between group size and nest type, that suggested that laying date was more delayed in larger groups that occupied natural nests than nest boxes, but the P-value of 0.05 suggests this result should be interpreted with caution (Table 3.1, Figure 3.4). Overall, groups using nest boxes initiated egg-laying at a similar time to groups using natural tree cavity nests (Table 3.1, Figure 3.5). Variation in laying dates was not explained by the number of hot spring days (temperatures above 30 °C), the amount of spring rainfall nor rainfall and mean temperatures during the dry, cold winter months.

Table 3.1 Results of a GLMM investigating the effects of social and environmental variables on laying dates. Data included lay dates (continuous) for 23 breeding groups over 134 group years during 2000–2015. The minimum model is shown including and above the underlined variable, and non-significant variables are shown below the underlined variable. All estimates are from the full model. R^2 estimates of the model fit were calculated following Nakagawa & Schielzeth (2013). R^2(marginal) = 0.10, R^2(conditional) = 0.16.

Variable	Est. (95 % CI)	SE	t	*P*
(Intercept)	70.03 (62.41 – 77.64)	3.89	18.03	< 0.01
Group size	11.84 (1.71 – 21.97)	5.17	2.29	0.02
Nest type	-7.15 (-15.69 – 1.40)	4.36	-1.64	0.10
Spring rainfall	0.19 (-3.32 – 3.69)	1.79	0.10	0.92
Spring temp.	3.63 (0.11 – 7.15)	1.80	2.02	0.04
Group size x nest type	-10.98 (-21.73 – -0.23)	5.49	-2.00	0.05
Spring rainfall x spring temp	-3.35 (-6.62 – -0.08)	1.67	-2.01	0.04
Rainfall over the previous year	-2.26 (-6.09–1.36)	1.89	-1.19	0.23
Dry season rainfall	1.31 (-2.95–5.57)	2.17	0.60	0.55
Winter temp	0.47 (-4.20–5.15)	2.38	0.20	0.84
No spring days > 30 °C	-0.71 (-6.51– 5.10)	2.96	-0.24	0.81
Dry season rainfall x winter temp	-1.52 (-5.12–2.076)	1.83	0.83	0.41

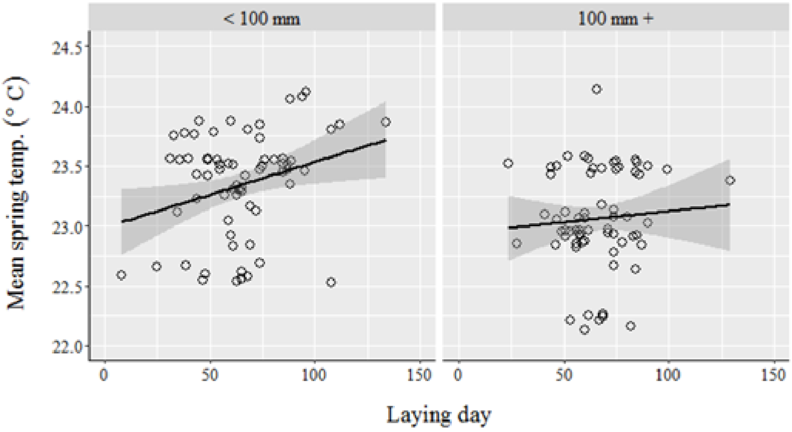


Figure 3.2. Timing of laying for Southern Ground Hornbill groups in relation to spring rainfall and mean spring temperatures. Nearly half (66 of 134 group years) experienced < 100 mm of spring rainfall. Laying day is given as the number of days after 1 Sept that the first egg was estimated to have been laid. A generalized additive model smoothing line was fitted showing 95 % confidence intervals.

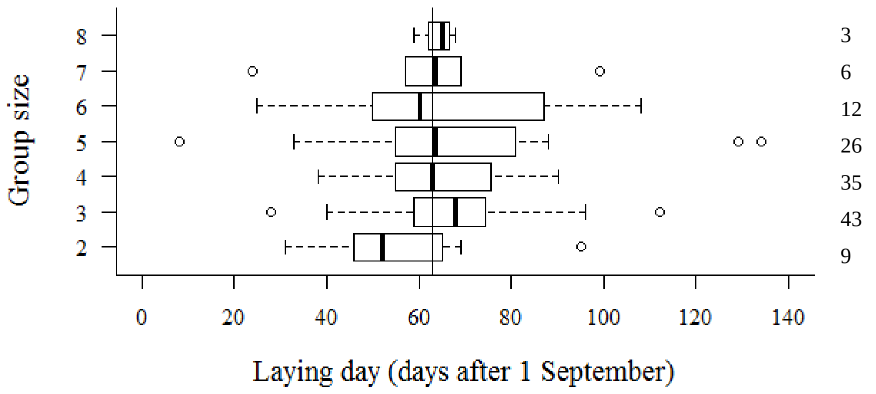


Figure 3.3 Variation in laying date between Southern Ground Hornbills groups comprising 2–8 individuals across 14 breeding seasons in north-eastern South Africa. The vertical line indicates the median laying day. Sample sizes provided on the right of the figure.

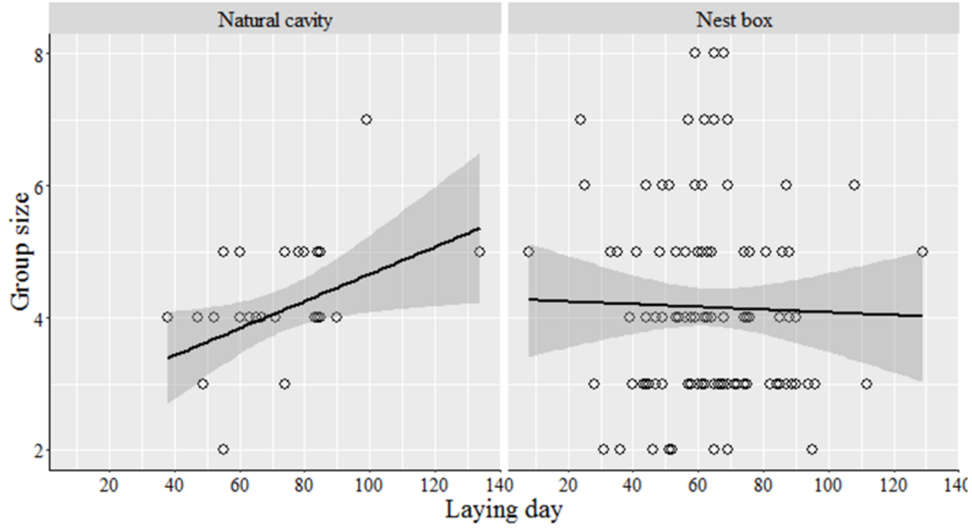


Figure 3.4. A comparison in the variation in the initiation of laying between Southern Ground Hornbill groups occupying natural tree cavity nests and nest boxes across 14 breeding seasons in north-eastern South Africa. Laying day is given as the number of days after 1 Sept that the first egg was laid. A generalized additive model smoothing line was fitted showing 95 % confidence intervals.

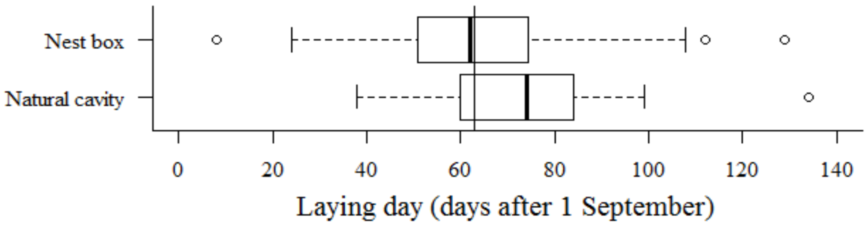


Figure 3.5. The variation of laying date for Southern Ground Hornbill individuals laying dates in nest boxes (n = 104) and natural tree cavity nests (n = 30) across 14 breeding seasons in north-eastern South Africa. The vertical line indicates the overall median lay date of 03 November, or 63 days after 01 September.

Peak hatching occurred in December before the peak rains in January (Figure 3.6, Appendix 3.1). The peak in hatching each season mostly occurred either before (64 % of seasons), during (22 %), or one month after (14 %) the peak in rainfall for each year. However, the average peak in rainfall was less pronounced than the average peak in hatching (Figure 3.6). On average, peak rain occurred in December and January (46 % of seasonal rain each year, respectively; 2564 of 5634 mm over 14 breeding seasons), whereas a sharp peak in hatching occurred in December (59 %, 69 of 114 chicks).

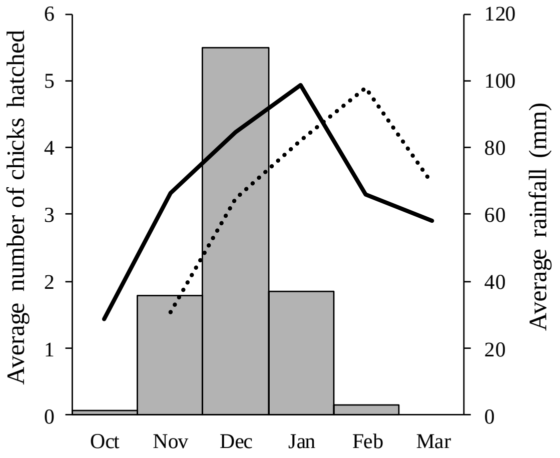


Figure 3.6 Average number of ground hornbill chicks that hatched each month (grey bars) relative to rainfall (solid line) across 14 breeding seasons in north-eastern South Africa. An arbitrary insect abundance trend was added (dashed line) to visualise the delay, of approximately one month, in peak insect abundance after peak rainfall (Cumming & Bernard 1997).

Second attempts were never made if the attempt failed at the chick stage, and the probability of a no reattempt were made later than 80 days after the start of spring (Figure 3.7).

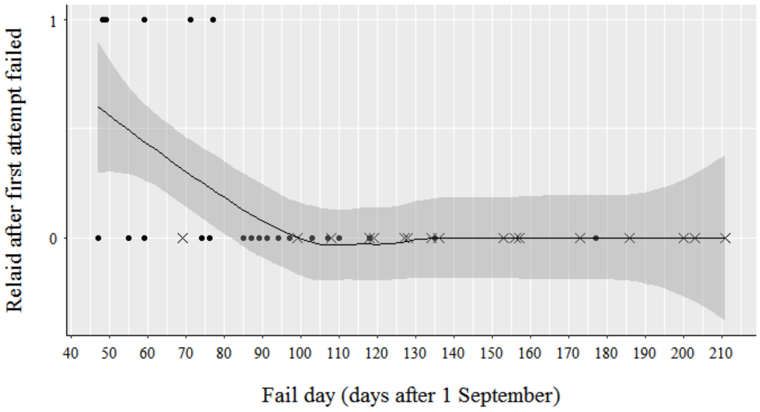


Figure 3.7 Days that nests failed and whether or not groups made a second breeding attempt. A LOESS regression line is plotted with 95 % CI's. Circles, failed at the incubation stage; crosses, failed at the chick stage.

A preliminary investigation into individual differences in laying dates

Individual differences among females may explain some variation in laying dates. Of the six groups with identifiable females (Figure 3.8), the female / group identity significantly explained variation in lay dates for the Keer Keer group (Table 3.2). The variable *group identity*, as a proxy for female identity for those groups with identifiable females, added significant value to the model when compared to a null (χ^2 = 12.95, df = 5, P = 0.02).

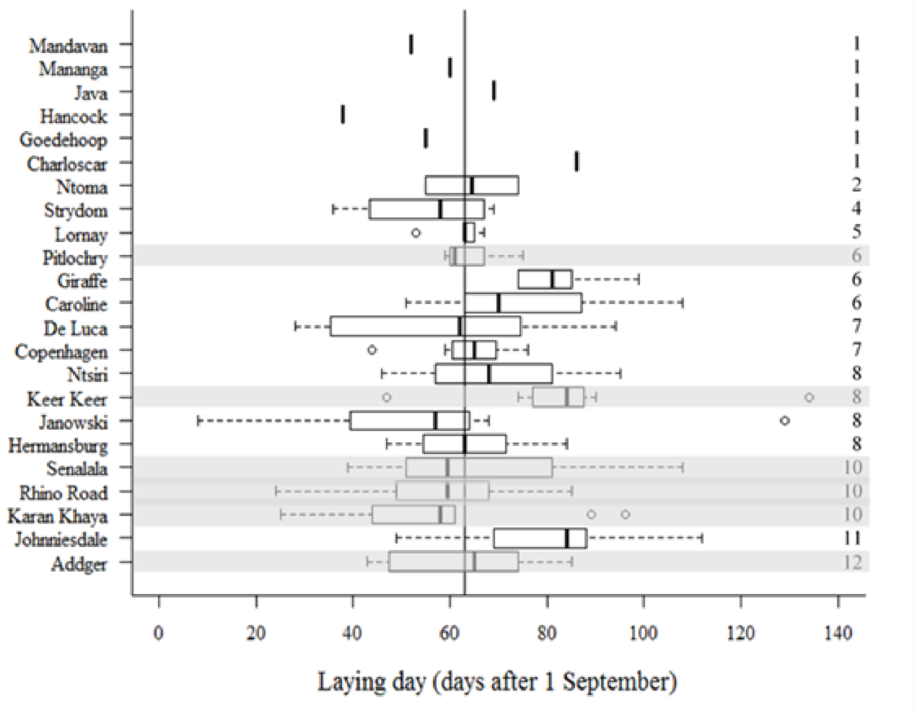


Figure 3.8. Variation in laying dates across 23 ground hornbill groups. Group names are provided on the left axis, and sample sizes for each group are provided to the right of each box plot. Grey shading indicates those groups with a known breeding female present throughout the study period during 2000–2015. The solid vertical line represents the median lay day.

Table 3.2 Results of a GLMM investigating the effect of group identitiy, as a proxy for female identity, to explain the variation in laying dates by ground hornbills. Data included laying date data (continuous) for six groups for which the individual females were known, which included laying dates for 56 breeding attempts over 16 years during 2000–2015. Estimates R^2 estimates of model fit were calculated following Nakagawa & Schielzeth (2013). R^2 (marginal) = 0.18, R^2(conditional) = 0.26. Addger group is listed first alphabetically, it is therefore incorporated within the intercept term.

Variable	Factor	Est. (95 % CI)	SE	t	*P*
(Intercept)		61.00 (50.27 – 71.74)	5.48	11.14	< 0.01
Group	Karan Khaya	-2.05 (-17.32 – 13.22)	7.79	-0.26	0.79
	Keer Keer	23.54 (7.34 – 39.73)	8.26	2.85	< 0.01
	Pitlochry	2.38 (-15.33 – 20.10)	9.04	0.26	0.79
	Rhino Road	-4.29 (-19.43 – 10.85)	7.72	-0.56	0.58
	Senalala	3.79 (-11.41 – 18.98)	7.75	0.49	0.63

Discussion

Compared to the northern hemisphere temperate bird species, there is a scarcity of data describing cues and factors that affect the timing of breeding in species inhabiting other geographical zones. Studies from southern Africa identified day-length, temperature, rainfall and its effect on food supply, as well as the appearance of grass fires and green vegetation as factors controlling the timing of breeding (Moreau 1950; Lloyd 1999). For ground hornbills in the Kruger National Park, South Africa, timing of egg-laying by was not affected by rainfall over the dry season or previous wet season (Kemp & Kemp 1991). My results from this study corroborated this finding, as the timing of egg laying by ground hornbills in the APNR was not explained by previous rainfall events either during the dry season leading up to the breeding season, or during the previous year. Rather, this study found that the timing of breeding was affected by both group size and spring weather conditions. For groups using both nest boxes and natural nests, larger groups laid later. In addition, the timing of breeding was delayed during dry, hot spring weather conditions. Groups were shown to initiate breeding despite little to no rainfall before the breeding season, indicating that cues other than early spring rainfall were important in explaining the variation in the timing of breeding observed. This variation was not explained by the type of nest alone, since groups using nest boxes and natural nests did not differ significantly in the timing of the onset of breeding.

Ground hornbills delayed egg laying during warmer springs, going against the general trend in birds (studies dominated by northern temperate species) that mostly show advancing laying dates with warmer spring temperatures (Dunn 2004). Studies of the effect on temperature in the southern temperate region remain sparse. One study supports the northern hemisphere trend in a southern hemisphere species: warm temperatures advance laying in the cooperatively breeding Sociable Weaver *Philetairus socius* that are present in the South African arid zone (Mares et al. unpubl. data). But one species was shown to delay breeding in hotter conditions. For captive Houbara bustards *Chlamydotis undulata*, warmer temperatures at the start of their breeding season (winter months in Saudi Arabia), resulted in delayed egg-laying, possibly due to the poorer body condition of females under hot conditions caused by reduced foraging and decreased body mass (van Heezik et al. 2002). One reason why laying in ground hornbills was delayed by warmer temperatures may be due to food supply. In the savannahs, hotter springs could limit food availability, for example, if higher temperatures cause the vegetation to dry out, resulting in a swift rapid decline in insect abundance (Koenig & Mumme 1987), especially in the phytophagous insect groups (Denlinger 1980) which form a large part of the ground hornbill diet (Kemp 1976). This idea was supported by laying dates being particularly delayed under the combined conditions of warmer, drier springs. Not that warmer springs were always drier, since spring temperatures and spring rainfall showed a weak, positive correlation. However, any decline in insect abundance during conditions of warmer, drier springs remains to be tested, since arthropods are a key food item provided to young chicks, and arthropods of the main sources of food for adults (Kemp 1976). Furthermore, to limit food availability, one would also require a similar decline in the abundance/activity/detectability of other prey items of ground hornbills such as amphibians, reptiles and other small vertebrates (Kemp 2005) during hotter, drier spring conditions. It seems more likely that any decline in, or low levels of, food availability experienced by ground hornbills, or low levels of food intake due to hot, dry conditions, might act as a cue to delay breeding more due to the anticipation of harsher conditions to raise chicks than due to costs of egg production, which for ground hornbills is relatively small (A. Kemp pers. comm.). This is supported by some groups laying despite no spring rainfall prior to laying (e.g. 2004, 2010 and 2013, Appendix 3.2), which would have been expected to delay egg production if eggs were costly to produce.

Laying date was more delayed in larger groups. Ground hornbill breeding seasons typically exhibited declining breeding success as the season progressed (Chapter 2), likely due to difficulties in finding food for the growing chick in each nest as food supplies diminish towards the end of the breeding season. This would be especially difficult for smaller groups where all the effort in providing for the chick would be divided only between the breeding pair. Larger groups benefit from non-breeding helpers assisting the pair to provide food items for the chick (Kemp & Kemp 1980). Therefore, although raising chicks may be more difficult later in the season, larger groups appeared less constrained to breed later. It might be that females in larger groups develop eggs later in the season when food is more readily available, knowing that the additional helper(s) will assist with raising the chick later in the season when food diminishes. The question remains of why larger groups don't attempt earlier if they can. Each season, at least one smaller group (3 or less individuals) was known to attempt breeding. The possibility, therefore, of larger groups laying later because they were too constrained to lay earlier by conditions that would have prevented smaller groups from attempting, is not a plausible explanation of the delay in egg laying by larger groups.

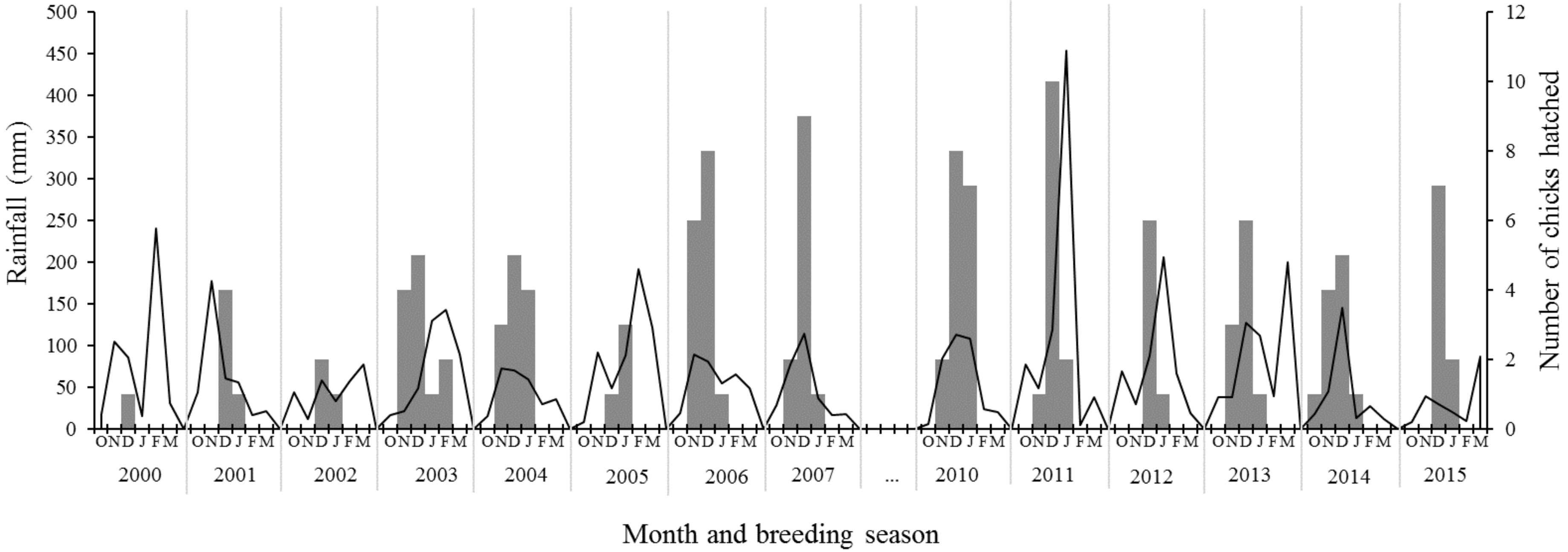
Two findings suggest the importance of rainfall as a trigger for food availability, and hence the timing of breeding. First, there is a correlation between ground hornbill laying date and the start of the rainy season at various latitudes (0–32 °S; Kemp 1976). Second, captive ground hornbills, who enjoy stable food supplies, lay out of season in the cold, dry winter months (D. Gunn & J. Meyer pers. comm.). Declines in food availability toward the end of summer places a constraint on laying dates. The ground hornbill breeding cycle is comparatively long (four months), more than half of the seven-month population breeding season (September–March). Therefore, unlike species that have short individual breeding cycles relative to the population's breeding season, and that can wait until various conditions are met before laying, or even have multiple broods if time and resources allow, ground hornbills are constrained by the length of their individual breeding cycle to produce a single brood and ensure that their chick fledges before the commencement of the dry season. If the first breeding attempt failed, second attempts were rare, even early in the breeding season. None of the attempts that failed beyond 80 days after the start of spring made and second attempt at breeding, suggesting some constraints exist to limit relaying late in the season. If attempting too late, a group with a chick that only fledges well into autumn would find it harder to provision the fledgling as feeding resources diminish (Kemp 1976). Therefore, like north-temperate insectivorous species, food supply is an important consideration for ground-hornbills in the southern sub-tropics.

The relatively low explanatory power of the best-fit model suggests that other factors may explain the observed variation in laying date. Possible factors may relate to individual variation in breeding females such as condition (Low et al. 2015), age and breeding experience (Amininasab et al. In press; Sydeman et al. 1991; Saunders et al. 2016), foraging ability (Goutte et al. 2010), or her need to avoid bad weather during incubation (such as storms; Turner 1982). My preliminary investigation of individual differences in laying dates suggests that there is some group specific or female-specific effect on laying dates. Although not currently available, data on the age of breeding females, their condition, and the foraging ability or provisioning ability of her entourage (females cease foraging themselves prior to egg-laying, augmented with courtship feeding by the males, Kemp 1976) might further link variation in the timing of breeding to the abilities and condition of individual alpha female and her group.

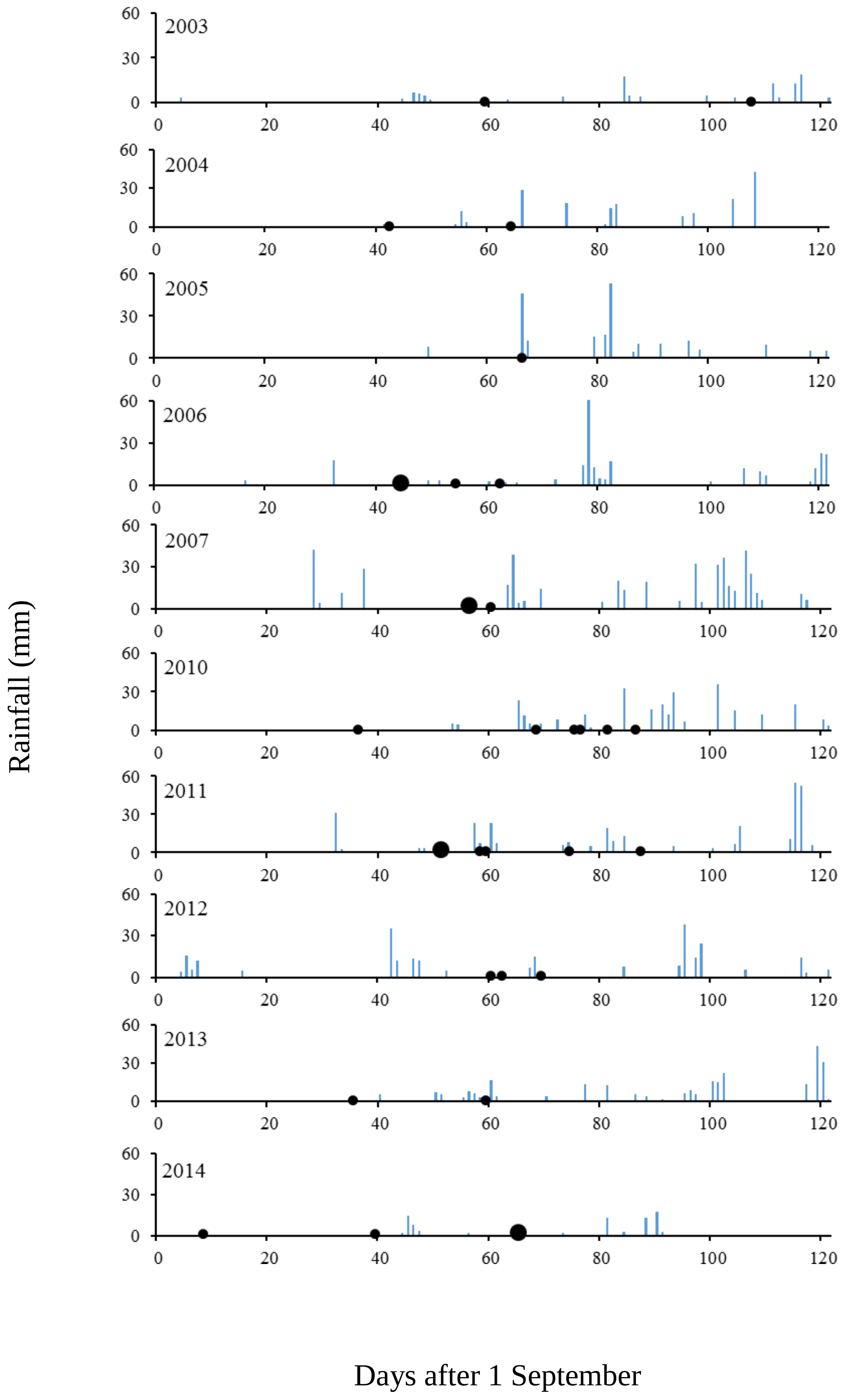
Further research

North-eastern South Africa has been experiencing a cooling trend since 2000, with reduced precipitation (Cunningham et al. 2016). If the trend continues, can ground hornbills track the cooling conditions by laying earlier or, alternatively, track the drier conditions by laying later? And what might the long-term implications of this be in light of climate-change and potentially mis-timing avian reproduction and peaks in food supplies (Both et al. 2004; Visser et al. 2009; Møller et al. 2010)? To answer this for ground hornbills, future research would require that food availability be investigated in the presence of continued data collection on breeding for several decades, to be able to fully track whether or not ground hornbills adapt to changing climatic conditions over time, and if so how.

Appendix 3.1.Timing of hatching of the first laid egg relative to rainfall over 13 Southern Ground Hornbill breeding seasons during 2000–2007 and 2010–2015 in north-eastern South Africa. Average monthly rainfall figures (line) were from 14 raingauges in the study area. The number of chicks hatching each month is shown by grey bars.



Appendix 3.2. Timing of egg-laying (black dots) of Southern Ground Hornbills in relation to rainfall (blue columns) in the Klaserie Private Nature Reserve. Larger dots indicate instances when two groups laid on the same day. Daily rainfall estimates for Klaserie were available for 2003–2014.



Chapter 4 Natal dispersal in the Southern Ground Hornbill

Dispersal is of critical ecological and evolutionary importance for population biology because it affects a species' ability to expand its range, to colonise new favourable habitat and the likelihood of population persistence. In birds, and with a few exceptions, males are philopatric, delaying dispersal or dispersing closer to their natal territories. Females tend to disperse further than their male siblings to reduce the chances for inbreeding. Dispersal in the endangered, cooperatively breeding Southern Ground Hornbill is poorly understood. It is not known how far individuals can disperse, or what the difference in dispersal age and distance is between males and females. I investigate dispersal events using field observations of banded individuals within groups in a study population and resightings in surrounding areas. A total of 113 individuals from 19 groups were ringed during 2005–2015 (86 chicks, 12 sub-adults, 15 adults). A total of 73 individuals dispersed (disappeared from their group; 25 females, 25 males, 23 unknowns), of which 18 were resighted post-dispersal (seven females, nine males, and two gender unknowns). There was no evidence for sex-biased dispersal, based on similar numbers of males and females dispersing. Dispersal distance was explained by rainfall over the previous year, with individuals dispersing further following a year of low rainfall. This may act as a push factor for non-breeders, to disperse from territories were foraging demands are not being met or where the competition for feeding resources among group members is too great. Dispersal was not associated with gender or age of the individual. Median dispersal distance was similar for females and males. Females dispersed at a similar range of ages to males. Males delayed dispersal beyond nine years, and all but one female dispersed before two years of age. These data provide insights into the dispersal dynamics and dispersal propensity of this endangered species. The relatively small sample size generated from a long-term study highlights the importance of long-term research in this long-lived species, and the need for even longer-term studies if breeding dispersal using ringing and resightings is to be observed.

Introduction

Natal dispersal in animals is the permanent movement of individuals away from their natal site to the first site where they attempt to breed, and breeding dispersal is the movement of individuals among breeding sites (Greenwood & Harvey 1982). The movement of individuals away from their place of hatching or first breeding to new areas affects the potential for colonisation of new and favourable habitat (Brotons et al. 2005), range expansion (Walters et al. 2002; Duckworth & Badyaev 2007; Armstrong et al. 2015), as well as gene flow (Double et al. 2005; Temple et al. 2006; Woxvold et al. 2006; Rollins et al. 2012; Ponnikas et al. 2013; Kurvers et al. 2014).

Why do individuals disperse? Several ultimate and proximate factors drive the decision to disperse. Ultimate factors include kin interactions, inbreeding avoidance and habitat variability (Bowler & Benton 2005). Dispersal can act to reduce the level of competition between close relatives for a breeding opportunity at the natal site, since dispersing individuals will then be competing with non-kin (Hamilton & May 1977). Dispersal can also act to lower the chances for breeding with close relatives (Howard 1960; Woxvold et al. 2006; Ortego et al. 2008; Nelson-Flower et al. 2012) and the costs of breeding between close relatives are widely recognised, such as reduced hatch rate, brood size and survival (Keller & Waller 2002). At the proximate level, dispersal decisions may be influenced by the need to avoid crowded areas or those lacking in food supply (Howard 1960). Therefore, dispersal is governed by a suite of ultimate and proximate factors. Understanding a species ability to disperse and what conditions favour or limit dispersal, is important to understand the species' ability to track environmental shifts and thus the likelihood of a species persistence (Ferriere et al. 2000).

Avian families mostly exhibit male philopatry and female-biased dispersal (Greenwood & Harvey 1982; Williams & Rabenold 2005; Temple et al. 2006). In most bird species, males defend resources to attract females. This type of mating system is called 'resource defence' (Greenwood 1980). The resources that individuals defend may include access to a nest site or high quality foraging areas or both. Therefore, securing access to these resources is of fundamental importance to future breeding opportunities. Increasing the chances of gaining access to scarce resources required for breeding would increase overall individual fitness. This type of mating system is tied to male philopatry on the assumption that a male will have greater ease of acquiring a territory closer to home than further away (Greenwood 1980). This may occur either by greater familiarity with the surrounding habitat or knowledge of potential breeding gaps (Greenwood & Harvey 1982; Zack & Stutchbury 1992). In addition, it may occur through benefits associated with nepotism, whereby increased survival or securing a resource could be enhanced by the presence of relatives (Greenwood 1980; Koenig

& Dickinson 2004). Under these scenarios, it may benefit a male to delay dispersal rather than disperse (Koenig et al. 1992).

If male offspring delay dispersal, then any female siblings remaining and hoping to breed near the natal site would run the risk of pairing with close relatives. Dispersing further than male relatives can assist in reducing inbreeding if inbreeding is costly, and thus helps individuals to escape the negative effects associated with inbreeding depression. But not all species show this difference in dispersal distances between the sexes, with some studies revealing systems where males and females disperse equally far (Blackmore et al. 2011; Nelson-Flower et al. 2012; Engler et al. 2014). In some cases, the dispersal distances are similar because of a distance limitation, such as on relatively small islands (Engler et al. 2014). In another case, females may not have to disperse far to avoid pairing with close relatives, due to their ability to recognise and avoid familiar group members as mates (Nelson-Flower et al. 2012).

Studies have investigated not only when and how far individuals disperse, but also investigated the question of ‘where to?’: decisions involved in immigration. Ideally, individuals would disperse along a territory gradient, immigrating into territories of higher quality (Korpimaki 1988; Komdeur 1992; Forero et al. 1999). Within territories of higher quality, the fitness benefits of breeding independently can be higher than remaining as a helper on their natal territory (Komdeur 1992). However, good quality territories become quickly saturated, and individuals may be constrained to settle in territories of equal or lower quality (Zack & Stutchbury 1992). Like the fitness consequences for immigrating into territories of different qualities, there are also fitness consequences for immigrating into groups of different sizes. Resource depletion caused by breeding individuals foraging in a restricted area near the nest during the breeding season is exacerbated by increasing group size, which could result in significant weight loss and may ultimately affect survival (Sorato et al. 2016). Similarly, groups that are too small (such as pairs only), may be limited by the lack of helpers to assist with chick-rearing, territory defence or the detection of predators. However, smaller groups typically have fewer non-breeding individuals queuing for future breeding opportunities (Pasinelli & Walters 2002), so smaller groups can be beneficial for immigrating individuals.

Southern Ground Hornbill groups typically comprise a breeding pair and a variable number of mostly male non-breeding helpers (Kemp 1990). From a previous study that used observations of unringed (but individually identifiable individuals) in the Kruger National Park (hereafter Kruger) suggested that males and females appeared to have different dispersal strategies (Kemp 1990). In that study, Kemp (1990) found young females were indistinguishable from young males, until females develop a blue throat colour when mature (Kemp 1990). Young females were thought to disperse once mature, and non-breeding females ‘floated’ between home ranges, alone, or in all-female groups of up to three birds (Kemp 1990). Female sub-adults seldom undertook any helper roles, and presumably gained greater protection from being in a group than floating alone (Kemp 1990). Males delayed dispersal and assisted with territory defence, predator detection, and rearing the next generation (Kemp 1990). They remained in their natal territories for at least six years, after which they presumably inherited the natal or a neighbouring territory (Kemp 1990).

In this chapter, I test the generality of Kemp’s (1990) inference of male philopatry and female dispersal. This study describes dispersal events of ringed individuals, the first for ground hornbills, and investigates factors influencing dispersal distance and age at dispersal. I also compare group size between natal groups and those into which individuals immigrated, to understand individual immigration decisions. Because dispersal in birds is costly (Kingma et al. 2016), I predict that individuals should disperse farther in a year when food availability is high thus following a year of good rainfall. I predict that dispersing individuals should select to join smaller groups rather than larger groups, because there is a greater chance of inheriting a breeding opportunity in smaller groups (Pasinelli & Walters 2002), and because the costs for individuals in large groups are comparatively higher (Sorato et al. 2016).

Methods

Individual ground hornbills were banded with a unique combination of three plastic colour rings and one, metal, numbered ring. Most individuals were banded as chicks a few days before fledging. Smaller numbers of sub-adults and adults were captured using walk-in traps at dawn, making use of call-up recordings and life-size, fibreglass, ground hornbill decoys in the trap to attract groups to the capture site. The ages of immature individuals were estimated using throat patch colour (Kemp & Kemp 1980). The colour of the throat patch gradually transitions from pale yellow to red if male or to red and blue if female. The gender of each ringed individual was determined by the colour of the facial skin where possible or using genetic markers (see Theron et al. 2013).

To obtain resightings of ringed individuals, groups were located by their duet calls at dawn. For each resighting, the location was recorded using a Garmin 76CSx Map GPS, as well as the group size and demographic composition. Estimating the precise timing of dispersal is possible in studies where regular monitoring of banded individuals is conducted (Nilsson & Smith 1985; Altwegg et al. 2000; Woxvold et al. 2006; Sharp et al. 2008; Blackmore et al. 2011; Nelson-Flower et al. 2012; Engler et al. 2014). Although every attempt was made to make regular contact with groups, resightings of ringed individuals were irregular and infrequent due to the large territory sizes (± 70 km^2), the wary nature of individuals and the dense habitat in the study area. Groups were observed on average 8 ± 10 (mean ± SD) times a year (range 1–71 times a year, n = 1972 group observations). In each group contact, 75 % of the individuals on average could be checked for rings. Opportunistic sightings of ringed individuals were available from neighbouring Kruger. These sightings, typically with photographs to confirm ring combinations, were largely provided by tourists as part of a ground hornbill sighting programme.

Dispersal date was taken as the midway between successive sightings. Estimates were excluded for birds where the interval between relevant sightings was greater than six months. Dispersal distance was calculated as the straight-line distance between the nest sites of the natal group and the new group. If the location of the new nest site was not known, the distance from the natal nest to where the individual was seen with the new group was used. When investigating emigration decisions, I used data from four males and six females for which age at dispersal was accurately known (less than six months between sightings) and the group sizes of natal and new groups were known.

Territory quality was used as one factor to compare natal and new groups of dispersing individuals. Two estimates of territory quality were used: the reproductive productivity of the group and the proportion of favourable habitat in each group’s home range (each defined below). Reproductive output was defined as the number of fledged chicks divided by the number of breeding attempts over the entire study period. Thus, each group had one productivity estimate. Favourable habitat was defined as the riparian and disturbed areas. Groups in the study area preferred riparian habitats in summer and disturbed areas (air fields, old agricultural fields, old home steads) during winter (Wyness 2011). Because groups occupy home ranges year-round, higher quality territories were identified as those with a higher percentage of both habitat types. Comparisons of territory quality between natal and new groups was only possible for those individuals that dispersed within the study area (n = 10), as home ranges of groups outside of the study area were not known. Areas for each habitat type were calculated by clipping home range polygons and vegetation shape files (defined by Van Rooyen 2005) in ArcMap 10.2, exporting the attribute tables to MS Excel and calculating the proportion of the riparian and disturbed habitat types in each home range polygon. For one group, the vegetation shape file did not cover the full extent of the home range, so the amounts of riparian and disturbed habitats in areas lacking vegetation data were estimated from orthophotographs. Groups with higher reproductive output (Forero et al. 1999) or that occupy a territory with a higher proportion of favourable habitat were assumed to occupy territories of high quality.

Statistical analyses

The programme R (version 3.03, R Core Team 2014) was used for all statistical analyses. Wilcoxon's rank-sum test was used to analyse differences in dispersal age and distance between females and males.

To investigate factors explaining variation in natal dispersal distances, I used a linear model in R (version 3.03, R Development Core Team 2014), with the package 'nlme' (Pinheiro et al. 2017), using data for 16 individuals from eight groups for which both gender and dispersal distances were known**Error! Reference source not found.**. Data exploration, such as checking variables for multicollinearity, was carried out following the protocols described in Zuur & Ieno (2016). I modelled the log of *dispersal distance* (continuous, the distance in kms between the natal nest site and the nest site of the new group) as a function of *age* (discrete, age at dispersal in months), *gender* (binary, male or female) and *rainfall of the previous year* (continuous, July–June, Chapter 2). The response variable, dispersal distance, was log-transformed to bring in the outlier dispersal distance that was greater than 100 km. Where the new nest site was not known, dispersal distance was calculated to where the individual was last seen with the new group. Dispersal age was taken as the midway between the date it was last seen in the group, and the day it was reported as absent. *Group identity* was included as a random variable, but the output summary identified this variable as having no effect on the model and was therefore removed. Non-significant (*P* > 0.05) variables were sequentially removed from each model. Non-significant variables that were removed, were each added back to the reduced model one at a time, to double check that their inclusion did not contribute significantly toward the model's power. The estimates and probabilities of these non-significant terms from the full model are included in the summary table in the results for completeness. The explanatory power of the final model was confirmed by performing a likelihood ratio test between the final model and a null model that contained constant explanatory variable '1'. Confidence intervals (95 %) for each parameter were obtained using Wald's approximation (Wald 1947). Model assumptions were verified using plots of residuals against fitted values as well as residuals versus each explanatory variable used in the model. The marginal and conditional R^2 values for mixed-effect models (R^2_m and R^2_c), as described by Nakagawa & Schielzeth (2013), were computed for the final model using the package 'piecewiseSEM'. These two estimates measure the percentage of variation in the final model explained by fixed effects (R^2_m), and both random and fixed effects (R^2_c).

Results

A total of 113 individuals were ringed from 19 groups during 2005–2015. Of these, 15 were ringed as adults, 12 as sub-adults (1–6 years) and 86 were ringed as chicks. Of the 86 ringed as chicks, 74 were ringed from nest boxes, and 12 from natural nests. A total of 35 ringed individuals are still present in the study site and five deaths were recorded (three males, one female, one unknown). A total of 73 individuals dispersed (disappeared from their group; 25 females, 25 males, 23 unknowns), of which 18 were resighted post-dispersal (seven females, nine males, and two gender unknowns, Figure 4.1). All 18 individuals re-sighted post-dispersal fledged from nest boxes. Individuals were observed dispersing into groups within the study site (n = 10, Figure 4.1) and into neighbouring Kruger National Park (n = 8, Figure 4.1). The average number of months (mean ± SD) between when an individual was last seen in the natal group and when it was first seen in the new group was 40 ± 27 months (range 2–88 months). No breeding adults were observed to switch groups.

Figure 4.1. Natal dispersal of 18 individuals within and outside the study area. Polygons are home ranges of ground hornbill groups. Solid line = females; dashed line = males; grey line = unknown gender.

Dispersal distance

There was no significant difference in dispersal distances between females and males (W = 35, *P* = 0.76, Figure 4.2). Median dispersal distance was 22 km for females and 29 km for males. All but one female dispersed at least four home ranges away from their natal groups, whereas most males dispersed into groups 1–2 home ranges away (Figure 4.2). Dispersal distance was inversely proportional to the amount of rainfall over the previous year (Table 4.1, Figure 4.3). For every 50 mm increase in rainfall over the previous year, dispersal distance decreased by 18 % (0.996^50 = 0.82 = 18 % reduction, Table 4.1). There was no support for an effect of either individual gender or age on dispersal distance (Table 4.1).

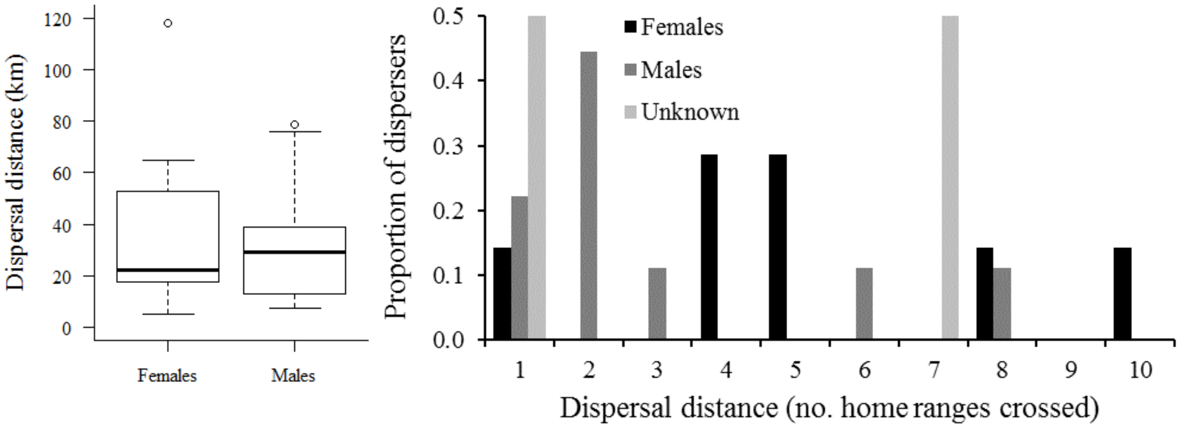


Figure 4.2 Natal dispersal distances for seven females, nine males and two gender unknowns. Box plot: dark bars indicate median dispersal distance, error bars indicate 95 % CI's, and dots show outliers.

Table 4.1. Factors explaining variation in the dispersal distances of 18 ground hornbill individuals. R^2_c = 0.25. Model compared to a null: F = 2.03, df = 12, *P* = 0.16.

Variable	Est. (95 % CI)	SE	t	*P*	Ratio change (95 % CI)
(Intercept)	2.26 (1.47–3.05)	0.36	6.23	< 0.05	
Rainfall	-0.002 (-0.003–0.0002)	0.0007	-2.46	0.03	0.996 (0.992–0.999)
Gender	0.0008 (-0.43–0.43)	0.20	0.004	0.99	1.002 (0.370–2.714)
Age	-0.002 (-0.01–0.007)	0.004	-0.40	0.70	0.996 (0.976–1.017)

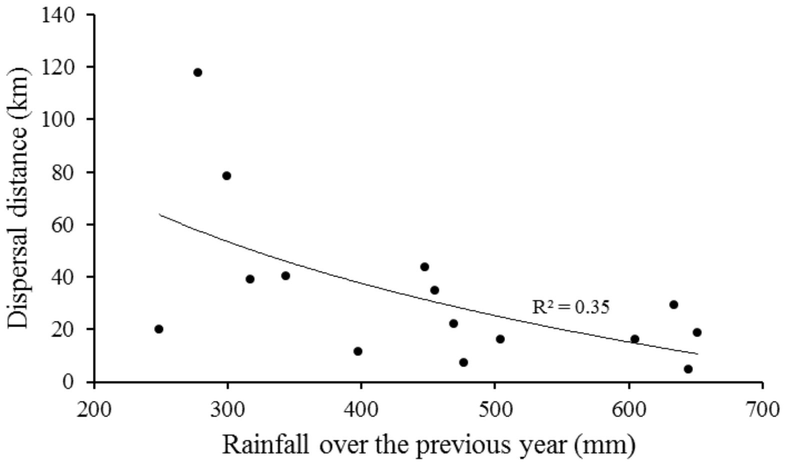


Figure 4.3. Influence of previous years rainfall on dispersal distances of individual ground hornbills.

Age at dispersal

When investigating age of dispersal for all individuals that disappeared from their groups, including those individuals that left the group but were not resighted, females and males left the group at similar ages (11 months for females and 43 months for males, W = 75, *P* = 0.06). Males delayed dispersal up to eight years, but all females except one dispersed before the age of two years (Figure 4.4). One female delayed dispersal for up to five years. One male that was still present with the natal group at the end of 2016, has remained as helper with the natal group for nine years.

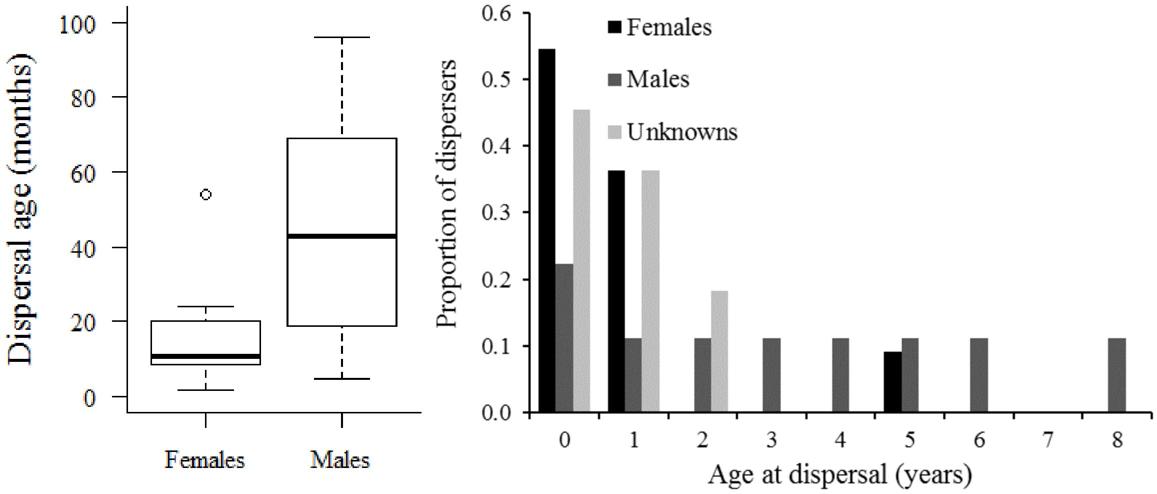


Figure 4.4. Age of natal dispersal for 11 females, nine males and 11 unknowns.

Four dispersing individuals became alpha individuals in a new group (two males, two females). One male dispersed from his natal group after five years, but was only observed with the neighbouring group one year later as the new breeding male after the death of the previous breeding male. A second male dispersed at 10 months and was only resighted six years later together with an adult female, 76 km from his natal nest site. A female who dispersed at nine months was resighted seven years later as the only female in a group of four, 118 km from her natal nest site. A second female who also dispersed at 11 months was resighted eight years later with an adult male, 40 km from her natal nest site. No males or females that remained in their natal groups have inherited their natal territory and acquired breeding status (two females, 12 males and six unknowns fledged during 2006–2015).

Two sub-adult siblings were resighted together in a non-natal group outside of the study site in western Kruger, eight territories from their natal nest site. Interestingly, the older male dispersed the season before his younger sibling fledged. The older male fledged in March 2009 and dispersed 22 months later. Its sibling fledged in March 2012 (gender unknown) and dispersed nine months later. The older sibling was seen in the new group two years later, and five months before the younger sibling arrived.

The formation of two new groups were observed over the course of this study. In 2013, a new pair occupied a small territory between the home ranges of two larger groups (Double Highway pair, Figure 4.5). The pair comprised an adult male and female. Both birds were unringed and their origins were unknown. No nest was known in the area and there appeared to be considerable overlap between this pair and the groups to the north and south. In 2014, another unringed pair was observed occupying a small area between the larger groups (Rothsay pair, Figure 4.5). The pair responded to call-ups but paid only casual attention to the decoys and made no attempt to enter the walk-in trap. The pair was territorial, with morning duets given when neighbouring groups were near. Both pairs remained holding small territories in 2016, but no nests are presently known in their territories.

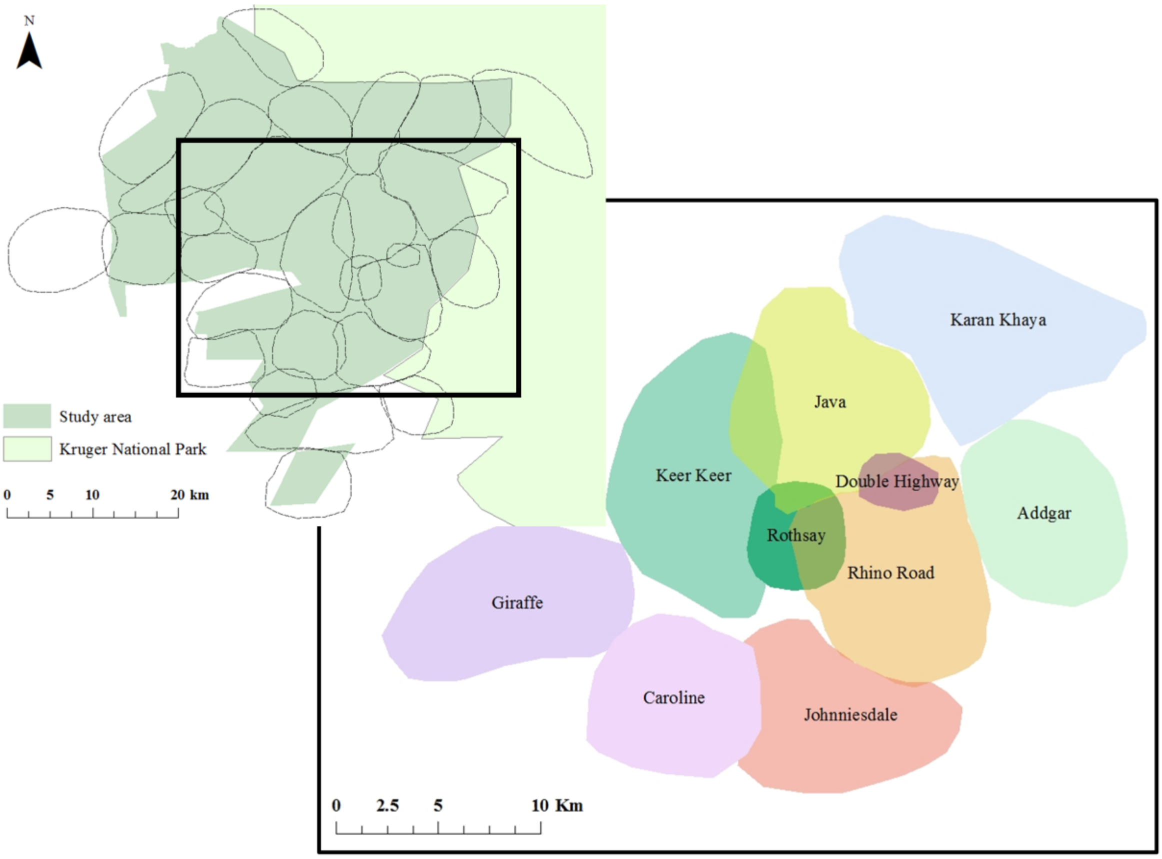


Figure 4.5. Home-range polygons of nine Southern Ground Hornbill groups, showing the location of two newly-established groups: Rothsay and Double Highway.

Comparisons between natal and non-natal groups

When investigating the difference in group size between natal and new groups, there did appear to be a difference in the selection of new groups based on group size by females and males. All four males dispersed into new groups that had fewer non-breeding individuals than in their natal group (Table 4.2). For females, this trend was less clear, with three dispersing into smaller groups and three into larger groups (Table 4.2). When investigating immigration decisions for individuals for which dispersal date was accurately known, and the group size and area of the new group was known (n = 10), three of 10 individuals immigrated into groups that were more productive than their natal groups. In addition, three of 10 individuals immigrated into groups that contained higher quality habitat. Neither of these findings differed significantly from random ($\chi^2 = 0.21$, df = 1, $P = 0.65$).

Table 4.2. Ages of dispersing males (n = 4) and females (n = 6), and the differences in the number of non-breeding individuals in their natal and new groups. Immature males were ≤ 3 years of age (males reach maturity at four years, Kemp 1995). Immature females were ≤ 5 years of age (females reach maturity at six years, Kemp 1995).

	Age	Year		# sub-ordinates		
Gender	dispersed	fledged	dispersed	Natal	New	Outcome by 2016
Male	Immature	2007	2007	2	0	Presumably acquired breeding status, paired with adult female
	Mature	2000	2008	3	2	Breeding status unconfirmed
	Mature	2006	2011	4	2	Became breeder in neighbouring territory
	Immature	2011	2012	4	3	Sub-ordinate
Female	Immature	2007	2007	1	0	Presumably acquired breeding status, paired with adult male
	Immature	2012	2013	0	1	Not breeding
	Immature	2007	2007	2	1	Presumably acquired breeding status, only adult female in group
	Immature	2010	2012	3	1	Not breeding
	Immature	2007	2007	0	2	Not breeding
	Immature	2009	2009	1	2	Not breeding

Discussion

This is the first time that resightings data have been presented for the Southern Ground Hornbill. Ringing of ground hornbill individuals has been ongoing since 2005, and the data are not yet appropriate for robust modelling of factors influencing dispersal distances or age the findings yield some interesting and unexpected results.

Ground Hornbills in the APNR showed a lack of sex-biased dispersal. Males and females dispersed at similar ages and at similar distances from their natal group. During the 10-year study period during 2005-2015, only natal dispersal and no breeding dispersal was recorded. The small data set acquired emphasises the importance of long-term studies, especially for long-lived species where dispersal is an uncommon event. The small amount of data also required caution when interpreting the results.

There appears to be a lack of sex-biased dispersal in this species, indicated by the similar number of males and females observed dispersing. This result is unusual in that most bird species show female-biased dispersal (Greenwood & Harvey 1982). Kemp (1990) studied 12 groups over 20 years, where there appeared to be a sex-bias in dispersal. Furthermore, in Kemp’s (1990) study, males appeared to remain in parental territories, with females dispersing and probably breeding far from the territory. However, Kemp’s (1990) followed unmarked individuals. To date, no males in the APNR study site that have delayed dispersal have acquired their natal home range. Only one male acquired breeding status in a neighbouring territory. Of those individuals that have not dispersed and are still present in the study area, it is possible that they may in the future inherit the parental territory but not enough study time has elapsed to observe this: the ringing of chicks began in 2005, and the age at first breeding is suspected to be 10 years old for males (Spear et al. 2005). Therefore, realistically, the likelihood of observing a male inheriting the natal territory began in 2015. Ongoing group sightings over the next few years from 2015 onwards may yield records of breeding dispersal.

Ground Hornbills showed an absence of sex-biased dispersal. For birds in general, an absence of sex-biased dispersal has been attributed to limited space to move such is the case on islands (Engler et al. 2014), or constraints on independent breeding (Beck et al. 2008; Blackmore et al. 2011). Natal dispersal may be constrained by a lengthy dependence on the group by juveniles, or a lack of breeding opportunities for mature individuals, which may lead both sexes to remain in their natal groups resulting in an absence of sex-biased dispersal (Beck et al. 2008). Alternatively, high rates of dispersal by both sexes, such as what is seen in ground hornbills, may be caused by incest avoidance (Blackmore et al. 2011). It would be reasonable to assume that breeding opportunities for ground hornbills arise only rarely, supported by the low turnover of pairs in the study area (pers. obs.), and the low number of individuals that were known to acquire breeding status. Given the difficulty and length of time required to acquire breeding status, once a breeding position is acquired, it would presumably not be relinquished soon or easily. Therefore, individuals waiting for a breeding opportunity in their natal group could run the risk of pairing with a parent individual if they delay dispersal in the hopes of inheriting their natal territory. Dispersing of non-breeding individuals would be a strategy that would avoid incest, and could explain why non-breeding male and female ground hornbills dispersed from their natal groups in equal frequency.

Males and females dispersed at similar ages. But these results should be interpreted with caution, as imprecise data on dispersal date may have obscured sex-specific differences. Although females and males tended to disperse young, males appeared more likely to delay dispersal longer than females. One male remained in the natal group up to eight years before dispersing, and one male has remained a helper within his natal group for nine years and has not dispersed as of 2016. Contrastingly, all but one female dispersed before two years of age. This suggests that females are not inclined to wait until they are mature before dispersing, as suggested by Kemp (1990), but appear to do so long before they reach maturity.

Males and females disperse equally far from their natal group, which raises some questions on how ground hornbills avoid inbreeding. Most other studies of dispersal in birds found that females disperse farther than males, largely to reduce the risk of inbreeding. However, some studies have found that males and females disperse equally far (Nelson-Flower et al. 2012; Engler et al. 2014; van Dijk et al. 2015). In the Southern Pied Babbler *Turdoides bicolor*, a cooperative breeder like the Southern Ground Hornbill, inbreeding avoidance was facilitated by females moving beyond the range of genetically similar individuals, and by recognising and avoiding familiar group members as mates (Nelson-Flower et al. 2012). It remains unclear how ground hornbills avoid inbreeding. Since breeding vacancies arise only rarely, it seems reasonable to speculate that finding a genetically compatible, unrelated mate may take a relatively long time. But given their average life-span, waiting years for a breeding gap, or for a more suitable partner, is unlikely to pose a major setback.

Southern Ground Hornbill groups comprised a breeding pair and mostly male helpers. Groups containing more than one adult female were rare (2 of 31 groups). In one instance when an adult female dispersed into a neighbouring group with a breeding female present, she was clearly subordinate to the alpha female, a finding shared with observations of beta-females in Kruger (Kemp 1990). This female remained on the periphery of the group and maintained a hunched appearance, seldom raising her head fully to reveal her throat patch. Short-distance dispersal was, in this case, unlikely to be an inbreeding risk since this young female was not involved in breeding (assuming submissive beta-females are not involved in breeding), but possibly the result of the female choosing to remain temporarily with a group willing to tolerate the presence of a second mature female, and in a familiar area. The tolerance of additional females is not always the case, with released females known to be chased relentlessly out of surrogate groups (L. Kemp pers. comm.). It may also explain why females showed no tendency to select smaller groups after dispersing. In other species, site unfamiliarity has been shown to have negative effects on mate attraction and territory acquisition (Greenwood 1980; Pärt 1990), thus females can potentially benefit from dispersing into familiar areas near to their natal home range, which could explain the high number of young females observed dispersing close to their natal territories.

Remaining with a group is safer than floating alone (Kemp 1990), since in a group there is a greater chance of detecting predators. This is probably why I only encountered one female floater during the study period. She remained in the peripheral area of the natal home range for a few weeks and then disappeared. Although few female floaters were detected, females, either alone or in groups, do prospect widely and wander unseen in the study area, monitoring for vacancies. This supposition is supported by the sudden appearance of a ringed female with an adult male on a peripheral territory west of the study site, despite not having been seen for eight years after her dispersal at a young age from her natal group. It is also supported by the replacement of a breeding female shortly after her death in July 2010. Her position was filled by an unringed female within two months, and, in October 2010 (4 months after the vacancy occurred), the new female laid an egg. Although the first breeding attempt was unsuccessful, the pair succeeded in fledging a chick the following season.

Field studies investigating dispersal are typically limited both spatially and temporally, which could lead to underestimates of dispersal distances and abilities (Koenig et al. 1996). Despite observations of ringed individuals took place over a relatively long period of time (10 years), relatively few dispersal events of ringed individuals were identified, highlighting the need for and importance of long-term studies in long-lived species such as ground hornbills. Although the small sample size limits the conclusions taken from the results, an additional decade of direct observation would assist with verifying these findings, which will depend on continued financial support for the existing project A worthwhile future study would combine direct observations of ringed individuals with fine-scale genetic structure of study groups, and determining the relatedness of individuals within social groups as seen in numerous cooperative species (Double et al. 2005; Temple et al. 2006; Woxvold et al. 2006; Nelson-Flower et al. 2012; Vangestel et al. 2013).

Chapter 5 Synthesis

The key aims of my thesis were to assess the role of nest boxes as a conservation tool for ground hornbills and to explore three aspects of the species' biology in a population supplemented with nest boxes. The three aspects included an assessment of productivity, timing of breeding, and dispersal.

Nest boxes can provide a tool with which to increase the amenability and efficiency with which a species can be studied (Griffith et al. 2008). A study site without nest boxes would have resulted in 77 % fewer breeding attempts with which to investigate breeding success (Chapter 2) and timing of breeding (Chapter 3). Regarding dispersal of ringed individuals, chicks fledged from nest boxes accounted for 100 % of the dispersal data from individuals resighted post-dispersal (n = 18 individuals). None of the 18 individuals resighted post dispersal fledged from natural nests, but rather from nest boxes (74 were ringed from nest boxes, and 12 from natural nests, Chapter 4).

Did nest boxes improve reproductive output?

For the ground hornbill, nest boxes in the study area enhanced reproduction, mostly by providing suitable nesting cavities in an area where few natural tree cavity nests exist. Breeding success was similar for breeding attempts in nest boxes and natural cavities (Chapter 2), and those with access to a nest box attempting breeding twice as often as those with access to natural nests only (Chapter 2). Furthermore, breeding attempts initiated earlier in the season were more likely to succeed (Chapter 2), and breeding attempts in nest boxes were initiated at a similar time to breeding attempts in natural nests (Chapter 3), again confirming that groups provided with nest boxes were not prevented from laying early for reasons such as food limitations due to nests being placed in poorer habitat, and so nest provisioning had no adverse effect on the timing of breeding (Chapter 3). This study therefore supports the general findings on the effects of artificial nests in birds, where the number of cases showing similar or higher levels of productivity and breeding success in artificial nests are three times higher than those reporting lower productivity or success (Williams et al. 2013). But the density-dependence of breeding success discovered in my study highlights the importance of ensuring suitable spacing between nest boxes to support suitable densities and thus maximise reproductive output. Such findings in the literature are scarce, with only two studies reporting that the installation of artificial nests created a supra-optimal density (Pöysä & Pöysä 2002; Mänd et al. 2005), and one other study highlighting the need for continuous monitoring to detect possible problems associated with high densities (Libois et al. 2012). The possibility that providing a high density of nest boxes may negate any conservation actions aimed at slowing and ultimately reversing the decline in the wild ground hornbill population should be carefully considered before installing nest boxes elsewhere in South Africa. In the APNR, one nest should be placed every 90–120 km^2, or at least 10 km apart.

Was there any indication that nest boxes could be having a subtle negative effect?

Providing artificial nests to improve the status of threatened bird populations has been largely positive (Dennis & Dow 1984; Toland & Elder 1987; Walters et al. 1991; Franzreb 1997; Fargallo et al. 2001; Pöysä & Pöysä 2002; Catry et al. 2007; Williams et al. 2013) but some studies have reported negative effects (Finch 1990, 1990; Feekes 1991; Botelho & Arrowood 1998; Brightsmith & Figari 2003; Dailey 2003; Sanz et al. 2003; Mänd et al. 2005; Smallwood & Collopy 2009; Briceño-Linares et al. 2011; Demeyrier et al. 2016). One maladaptive outcome of artificial nests is decreased breeding success. This can be due to several reasons including: (a) increased competition for nesting sites (Finch 1990), (b) supra-optimal breeding densities (Mänd et al. 2005), (c) nests that were placed in sub-optimal habitats (Mänd et al. 2005; Smallwood & Collopy 2009; Demeyrier et al. 2016), (d) increased harvesting of eggs or poaching by humans due to increased nest conspicuousness or easier access to artificial sites (Feekes 1991; Sanz et al. 2003; Briceño-Linares et al. 2011), (e) higher temperature fluctuations inside the artificial nests (Brightsmith & Figari 2003; Pichegru 2013), or (f) higher levels of predation in artificial nests (Finch 1990; Botelho & Arrowood 1998; Dailey 2003). The relative success of providing artificial nests can therefore be species-specific, and the levels of success should be tested. Each of the above possible negative outcomes will be discussed below to identify the overall effect of provisioning nest boxes for ground hornbills.

There was no evidence that providing nest boxes caused increased competition for nesting sites. The increase in nesting sites probably decreased competition immediately after nest boxes were installed, due to a surplus of nesting sites within the population, allowing an outlet for non-breeding individuals in the area. There was also no evidence that nest boxes caused increased levels of inter-specific competition for nesting sites. During the breeding season, only one ground hornbill nest (a nest box) was used as a nesting site by another species: a pair of Western Barn Owl *Tyto alba*, nested on two occasions in a nest box. Owls nested only rarely in the nest boxes (Chapter 2), and they were not considered to be competitors for nesting sites since they never prevented ground-hornbills from nesting. The two breeding attempts by owls both failed shortly before the ground hornbills began to occupy the nests, and it is quite likely that the ground hornbills destroyed the eggs or killed the nestlings as seen at another study site (L. Kemp pers. comm.). Outside of the breeding season, nest boxes were frequented by a diversity of small to medium-sized mammals, birds and reptiles (Chapter 2, Figure 5.1).

Figure 5.1. Other occupants of known Southern Ground Hornbill nesting sites Left: Small-spotted Genet *Genetta genetta*. Right: Western Barn Owl *Tyto alba*.

The installation of nest boxes resulted in a high breeding density. Ground hornbill breeding success was non-linear over time. Breeding success increased up to a maximum of 100 % during 2000–2005, but thereafter decreased steadily to 45 % breeding success in 2015. High breeding success was achieved during 2005–2007, when the average breeding success was > 80 % and the number of breeding groups in the study area was between 15–20. The average group size fluctuated throughout the study period, but remained consistently above 4 individuals per group after 2011, at a time when breeding success was already decreasing. Therefore, the relationship between breeding success and the number of breeding groups appears to be clearer than breeding success and average group size. Therefore, the increase in the number of breeding groups may have had an important negative effect on the likelihood of a group fledging a chick. When comparing the sizes of hornbill home ranges in the study area to those in the adjacent Kruger National Park, those in the study site were 70 % of the size of the home ranges in Kruger (100 km^2 in KNP, Kemp et al. 1989; 70 km^2, Wyness

2011). Furthermore, although the average group size decreased in the study site soon after nest boxes were installed, it later increased above previous levels and even surpassed the average for groups across the entire country (average group size for SA = 3.5 individuals, Kemp & Webster 2008; average for APNR = 4.0 individuals, this study). Therefore, groups in the study area were getting bigger, but inhabiting smaller than average territories. This could have either caused increased competition for feeding resources, or increased social conflict among group members, which can both have negative effects on breeding success in birds (Mänd et al. 2005, López-Sepulcre et al. 2009).

An ecological trap can be created when artificial nests attract nesting birds to sites that ultimately result in them having lower reproductive output than if they had settled in other more suitable habitat. For example, artificial nests attracted American Kestrel *Falco sparverius* pairs to occupying territories in sub-optimal foraging habitats that resulted in lower breeding success (Smallwood & Collopy 2009). For the ground hornbill, there was no indication that territory habitat attributes, such as the amount of riparian habitat, influenced breeding success (Chapter 2). The habitats in the study area are heterogeneous, varying from open savannah to closed woodland (van der Waal 2010). Open areas are considered to provide superior foraging habitat due to the increased detection of natural ground hornbill predators, and the increased detection of their prey items (Wyness 2011; Wilson & Hockey 2013). Wilson & Hockey (2013) found a significantly positive effect of more open habitats on the breeding success in natural nests, but the amount of open woodland around nests (natural and artificial) did not have a significant effect on breeding success when additional eight years of data were included (Chapter 2).

For ground hornbills, removing the second chick from the nest (harvesting) has been a conservation action that forms part of the implementation of the Species Recovery Plan. The second chick, that would die in the nest from starvation and dehydration, are removed from the nest soon after hatching and hand-reared for the captive breeding or wild-release programmes (Jordan 2011). This action of harvesting the second egg or chick had no negative effect on breeding success (Chapter 2). In some species, the installation of artificial nests resulted in the increased harvesting of eggs for human consumption, or the increased poaching of chicks by humans due to increased nest conspicuousness or easier access to artificial sites compared to natural nests sites (Feekes 1991; Sanz et al. 2003; Briceño-Linares et al. 2011). The study area for ground hornbills is a protected area with restricted access, and nests were only accessed by researchers to monitor breeding activity. Thirty-five chicks were harvested from the study area up to 2015, and the study area is the most important source of harvested chicks for this conservation initiative. Results from this study provide support that this practice can continue without hindering the success of wild groups.

Providing nest boxes with micro-climates that are too extreme can create an ecological trap if individuals are attracted to occupy nest boxes despite their unsuitable microclimate. A short-coming of the microclimate and orientation study was that most nest boxes had been placed with their entrances facing north, and thus did not provide a suitable opportunity to empirically test nest choice with respect to variation in entrance orientation and micro-climates. Despite this issue, my results suggest that ground hornbills can buffer fluctuations in nest temperature. This is not surprising given that natural cavities are often chimney nests, exposing the incubating female and chick to the sun during midday, suggesting that ground hornbills are well adapted to breeding successfully in hot environments. However, prolonged exposure of bird eggs to high temperatures (> 43 °C, Grant 1982) is more detrimental to embryo development than cold temperatures (Webb 1987). This is because exposure to high temperatures causes the embryo or chick to die, whereas cold temperatures effect embryo development but not necessarily death. Therefore, future nest boxes should be designed or placed to buffer nest temperatures from reaching 43 °C where possible, such as placing nest boxes in shady locations, and designing nest boxes with thick cavity walls (> 6 cm) to help buffer against extreme ambient temperatures.

In conclusion, nest boxes are a marginally effective conservation tool. Given the similarity in breeding success and the timing of breeding between groups using natural nests and nest boxes, as well as the similarity in micro-climate and predation levels between nest boxes and natural nests, suggest that these structures can provide suitable nesting sites. The installation of nest boxes appeared to have a potential negative effect only through creating a supra-optimal breeding density which may have resulted in a decrease in breeding success. One way to prevent this would be to place nest boxes that promote territory sizes closer to the average for the area. In the Kruger National Park, average territory size was 100 km^2 (Kemp et al. 1989), compared to 70 km^2 in the study area following the installation of nest boxes (Wyness 2011). The density of natural nests is low in the Kruger National Park, which results in a low density of groups and hence the large home range sizes. However, at higher densities the decline in breeding success indicates that the lower density enhances reproductive output.

One shortcoming of my study was the short period spent monitoring groups prior to the installation of nest boxes. When field work in the APNR study area began in 1998 and 1999, field visits were brief. More intensive field work to identify groups only began in 2000, two years prior to the first batch of nest boxes that were installed in 2002. The priority at the time was to provide suitable nest sites as soon as possible since these were presumed to have been in short supply. The lack of a robust study-area-wide investigation into the number of natural nests was a second-short coming, as it is not known from where the evidence came that there was a shortage of nesting sites, or whether it was presumed to be so because of the lack of nesting sites identified in neighbouring Kruger National Park (Kemp & Begg 1996). Furthermore, nest boxes were not specifically installed to test whether they would be more suitable than natural cavities, nor to assess what effect they would have on the population in the study area. However, offsetting the paucity of data prior to the installation of nest boxes is the quantity of data in the years thereafter, which allowed me to draw some conclusions with regards to trends in the population over time (the simultaneous decrease in group size immediately following nest box installation and increase in the number of pairs, followed by a steady increase in group size) after nest boxes were installed.

Natal dispersal inferred from direct observations

New insights gained from the ringing and resightings study included the unexpected similarity between males and females in dispersal age and dispersal distances. Males were expected to delay dispersal and possibly inherit the natal territory, as suggested by Kemp (1990). However, my study found no evidence for male philopatry, based on the similar numbers of females and males that dispersed from their natal groups. Among cooperative breeders, the absence of sex-biased dispersal is extremely rare (Blackmore et al. 2011). A lack of sex-biased dispersal has only been found in two other cooperatively breeding birds: the White-winged Chough *Corcorax melanorhamphos* (Beck et al. 2008) and the Australian Grey-crowned Babbler *Pomatostomus temporalis* (Blackmore et al. 2011). High rates of dispersal by both sexes, such as what is seen in ground hornbills, may be caused by incest avoidance (Blackmore et al. 2011): as seen in the Grey-crowned Babbler, helpers only stand to inherit a territory if they are unrelated to the dominant opposite sex (Blackmore & Heinsohn 2007).

There was no sex-bias in dispersal distances in the ground hornbill, and females and males both dispersed into new groups both close to their natal territories and further away. Dispersal is one way that individuals can avoid inbreeding, such as when females disperse beyond the range of related males. The lack of a sex-bias in dispersal distances indicates that incest avoidance does not occur through the separation of sexes by dispersal distance, but by other means such as individual recognition of close-kin (Nelson-Flower et al. 2012). However, these results should be interpreted with caution, given the higher density of groups in the study area compared with the average for adjacent Kruger National Park, which may have resulted in atypical dispersal patterns than what would happen under conditions of average group density.

How important was rainfall?

I found that above-average rainfall during the previous year resulted in more groups attempting to breed, whereas a drier season resulted in fewer groups attempting to breed. Rainfall affects food availability in the savannas, and too little rain would result in low insect abundance (Denlinger 1980, Koenig & Mumme 1987), which form a large part of the ground hornbill diet (Kemp 1976). Dry conditions and low food availability leading up to the breeding season could dissuade groups from attempting to breed if the conditions are too poor. This would be not unexpected for this long-lived ‘K-selected’ species where individuals should favour survival over reproductive efforts (Stearns 1976). Rainfall has been shown in other studies on ground hornbills to have an important effect on the timing and the success of breeding attempts (Kemp 1976; Kemp & Kemp 1991; Wilson & Hockey 2013). However, the effect of rainfall during the previous year had not previously been incorporated into studies of the decision by ground hornbills whether to undertake a breeding attempt. This was the first study to show the importance of rainfall events during the previous year on breeding decisions by ground hornbills (Chapter 2). By comparison, I found that more recent rainfall events had no marked effect on breeding decisions; neither the dry season (winter) nor spring rainfall were significant factors influencing the occurrence of breeding attempts (Chapter 2). Thus, it appears that ground hornbills base their decision to breed on environmental signals, such as food availability, that are triggered by rainfall six or more months prior to the start of the breeding season, rather than during the few weeks or months leading up to the breeding season.

In contrast to the effect of rainfall on whether a group attempted breeding, rainfall was not associated with breeding success (Chapter 2). Neither rainfall during the previous year, nor during the breeding season effected breeding success (Chapter 2). This result is contrary to a previous study on ground hornbills that indicated the importance of rainfall over the breeding season on breeding success (Wilson & Hockey 2013). In their study, Wilson and Hockey (2013), identified that breeding success was highest in years when 300–500 mm of rain fell over the breeding season, and that productivity declined when breeding season rainfall was either above 500 mm or below 300 mm. My finding that success was not associated with rainfall, suggests that ground hornbills are more resilient to varying rainfall conditions during the specific breeding season than previously thought. But importantly, rainfall prior to the breeding season is important to presumably increase food availability to thus influence breeding decisions in ground hornbills.

There was no indication that the first spring rains influence the timing of breeding in the study area (Chapter 3). The importance of first spring rains for the initiation of egg laying in ground hornbills was previously identified as being important for groups in the Kruger National Park (Kemp & Kemp 1991). The combined effects of temperature and rainfall affected the timing of breeding, which ultimately affected breeding success: groups initiated egg-laying later in the breeding season under hot, dry weather conditions (Chapter 3), and were less likely to fledge a chick than groups that initiated early in the season (Chapter 2). This is likely linked to reduced food supplies when the vegetation dries out (Koenig & Mumme 1987). Drier, hotter seasons ultimately have a negative effect on breeding success, whereas cooler, wetter seasons have a positive effect on breeding success. This is one of a few studies that shows how warmer temperatures delay, rather than advance, the timing of breeding in birds. For captive Houbara bustards *Chlamydotis undulata*, warmer temperatures at the start of their breeding season (winter months in Saudi Arabia), resulted in delayed egg-laying, possibly due to the poorer body condition of females under hot conditions caused by reduced foraging and decreased body mass (van Heezik et al. 2002).

The north-eastern parts of South Africa have become cooler but also drier over the past few decades (Cunningham et al. 2016). It remains to be determined whether ground hornbills will track the cooler conditions by laying earlier, or respond to the drier conditions by laying later. I suspect that ground hornbills are more responsive to rainfall, and that the drier conditions will cause them to lay later. Precipitation has a more marked effect on vegetation growth than does temperature in north-eastern South Africa (Fritz & Duncan 1994). Drier conditions may affect not only arthropod abundance adversely, which is a main food source of ground hornbills (Kemp 1976), but also ultimately the timing of breeding (Chapter 3). Continued data collection at the study site, if possible, could investigate whether laying dates become increasingly delayed with the predicted drier conditions, and whether this may result in lower breeding success and thus lower productivity levels.

Recommendations for the future use of nest boxes for ground hornbills

In areas that are devoid of natural nesting sites, nest boxes can be used as a tool to increase the reproductive output of groups. I provide guidelines below that will assist landowners, reserve managers or conservation organisations that are interested to install nest boxes on properties where natural nesting sites are thought to be scarce or absent.

In South Africa, an appropriate average home range size is 100 km^2, based on home range sizes for KNP (Kemp & Webster 2008), and that higher densities are sub-optimal (this study). Therefore, nest boxes should be spaced 10 km apart, or one box every ~100 km^2. This will assist in spacing nest boxes to create a natural density of groups that will maximise reproductive output. Once territories have been established at a suitable density, a second box can be provided for groups based on the evidence that switching nest boxes after a predation event increased the likelihood of the second attempt fledging a chick (three of four groups switched nests and fledged a chick, one group did not switch and failed to fledge a chick).

Nest boxes can be built from Pine logs need to be a minimum of 1 m tall and 80 cm in diameter. This is to create a cavity within the log that has walls 6 cm thick, a circular cavity floor of 50 cm in diameter, and internal height of 80 cm. Nest entrances should be cut in the upper half of the log (either rectangular or roughly oval, and approximately 30 cm wide and 40 cm high. Nests should be placed so that the entrances are situated > 6 m above the ground. Nests should not be placed in a dense canopy as it makes nest access hard by these large birds. Ideally, nests should be placed in the fork of a large tree that is easily accessible for them. If a natural perch is present, place the nest so that individuals that are arriving at the nest can land here and have the nest entrance within easy reach. This is more important than ensuring the nest faces a certain direction. A small but important consideration for placing nests that will be monitored in future: place nests that are not too difficult to reach by ladder if they are to be monitored by researchers. Being able to access a nest box quickly and safely means less time required near the nest and thus less disturbance to the birds. It will also mean a lower risk of injury by field workers. Think twice before installing a nest box close to a house or school. Ground hornbills break windows as they see their reflection in the window as another ground hornbill and break glass trying to eliminate the supposed ‘intruder’. Place nests > 500 m away from a house or any building, or further where possible.

Given the few advantages of nest boxes over natural cavities, nest boxes should not be viewed as the best long-term solution to providing nesting sites in areas were natural tree cavity nests are in short supply. Nest boxes should be viewed only as a short-term solution. One critical factor needing addressing is the future supply of natural tree cavity nests in areas where ground hornbills typically nest in tree cavities. Long-term conservation action should be directed at protecting large trees in the landscape, and mitigating the factors that are causing the loss of large trees and negatively affecting seedling growth, to allow for the potential for large tree cavities to develop in the future, and for nest boxes to therefore be used now only to bridge the gap until natural tree cavity nests are no longer scarce or lacking.

References

Altwegg R, Ringsby TH, Sæther B-E. 2000. Phenotypic correlates and consequences of dispersal in a metapopulation of House Sparrows *Passer domesticus*. Journal of Animal Ecology **69**:762–770.

Amininasab SM, Hammers M, Vedder O, Komdeur J, Korsten P. In press. No effect of partner age and lifespan on female age-specific reproductive performance in Blue Tits. Journal of Avian Biology.

Anderson MD, Anderson T. 2010. A breeding island for Lesser Flamingos *Phoeniconaias minor* at Kamfers Dam, Kimberley, South Africa. Bulletin of the African Bird Club **17**:225–228.

Ardia DR, Pérez JH, Clotfelter ED. 2006. Nest box orientation affects internal temperature and nest site selection by Tree Swallows *Tachycineta bicolor*. Journal of Field Ornithology **77**:339–344.

Armstrong D, Hayward M, Moro D, Seddon P. 2015. Advances in Reintroduction Biology of Australian and New Zealand Fauna. CSIRO Publishing, Australia. 320 p.

Barnett CA, Sugita N, Suzuki TN. 2013. Observations of predation attempts on avian nest boxes by Japanese Martens (*Martes melampus*). Mammal Study **38**:269–274.

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

Beck NR, Peakall R, Heinsohn R. 2008. Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in White-winged Choughs. Molecular Ecology **17**:4346–4358.

Belthoff JR, Smith BW. 2003. Patterns of artificial burrow occupancy and reuse by Burrowing Owls in Idaho. Wildlife Society Bulletin **31**:138–144.

Berthier K, Leippert F, Fumagalli L, Arlettaz R. 2012. Massive nest-box supplementation boosts fecundity, survival and even immigration without altering mating and reproductive behaviour in a rapidly recovered bird population. PLoS ONE **7**:e36028.

Beyer GL, Goldingay RL. 2006. The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. Wildlife Research **33**:161

Björklund H, Valkama J, Saurola P, Laaksonen T. 2013. Evaluation of artificial nests as a conservation tool for three forest-dwelling raptors. Animal Conservation **16**:546–555.

Blackmore CJ, Heinsohn R. 2007. Reproductive success and helper effects in the cooperatively breeding Grey-crowned Babbler. Journal of Zoology **273**:326–332.

Blackmore CJ, Peakall R, Heinsohn R. 2011. The absence of sex-biased dispersal in the cooperatively breeding Grey-crowned Babbler. Journal of Animal Ecology **80**:69–78.

Blakesley JA, Noon BR, Anderson DR. 2005. Site occupancy, apparent survival, and reproduction of California Spotted Owls in relation to forest stand characteristics. Journal of Wildlife Management **69**:1554–1564.

Bolton M, Medeiros R, Hothersall B, Campos A. 2004. The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran Storm Petrel *Oceanodroma castro*. Biological Conservation **116**:73–80.

Bornman H. 1995. Klaserie Private Nature Reserve. Klaserie Private Nature Reserve, Hoedspruit. 84 p.

Bortolotti GR. 1994. Effect of nest-box size on nest-site preference and reproduction in American Kestrels. Journal of Raptor Research **28**:127–133.

Botelho E, Arrowood P. 1998. The effect of burrow site use on the reproductive success of a partially migratory population of Western Burrowing Owls. Journal of Raptor Research **32**:233–240.

Both C, Artemyev AV, Blaauw B, Cowie RJ, Dekhuijzen AJ, Eeva T, Enemar A, Gustafsson L, Ivankina EV, Järvinen A, Metcalfe NB, Nyholm NEI, Potti J, Ravussin P-A, Sanzi JJ, Silverin B, Slater FM, Sokolov LV, Török J, Winkel W, Wright J, Zang H, Visser ME. 2004. Large–scale geographical variation confirms that climate change causes birds to lay earlier. Proceedings of the Royal Society of London B **271**:1657–1662.

Bourgeois K, Dromzée S, Vidal E. 2015. Are artificial burrows efficient conservation tools for seabirds? A case study of two sympatric shearwaters on neighbouring islands and guidelines for improvement. Biological Conservation **191**:282–290.

Bowler DE, Benton TG. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews **80**:205–225.

Boyce M, Lele S, Johns B. 2005. Whooping Crane recruitment enhanced by egg removal. Biological Conservation **126**:395–401.

Brazill-Boast J, Pryke SR, Griffith SC. 2013. Provisioning habitat with custom-designed nest boxes increases reproductive success in an endangered finch. Austral Ecology **38**:405–412.

Briceño-Linares JM, Rodríguez JP, Rodríguez-Clark KM, Rojas-Suárez F, Millán PA, Vittori EG, Carrasco-Muñoz M. 2011. Adapting to changing poaching intensity of Yellow-shouldered Parrot (*Amazona barbadensis*) nestlings in Margarita Island, Venezuela. Biological Conservation **144**:1188–1193.

Bried J, Magalhães MC, Bolton M, Neves VC, Bell E, Pereira JC, Aguiar L, Monteiro LR, Santos RS. 2009. Seabird habitat restoration on Praia Islet, Azores Archipelago. Ecological Restoration **27**:27–36.

Brightsmith D, Figari A. 2003. Breeding ecology and clay bank usage by macaws from Madre de Dios. National Institute of Natural Resources (IRENA), Arequipa, Peru.

Briskie J, Shorey L, Massaro M. 2014. Nest boxes increase fledging success in the declining Rifleman *Acanthisitta chloris*, New Zealand. Conservation Evidence **11**:12–15.

Brotons L, Pons P, Herrando S. 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? Journal of Biogeography **32**:789–798.

Brown L, Brown C. 1984. Is food supply the main determinant of African bird breeding seasons? Proceedings of the Pan-African Ornithological Congress **5**:753–761.

Bruyns RK, Williams VL, Cunningham AB. 2013. Finely Ground-Hornbill: the sale of *Bucorvus cafer* in a traditional medicine market in Bulawayo, Zimbabwe. In: RRN Alves and IL Rosa (Eds). Animals in Traditional Folk Medicine. Springer, Berlin. pp. 475–486

Butler D, Merton D. 1993. The Black Robin: Saving the World's Most Endangered Bird. Oxford University Press, Auckland. 308 p.

Bux M, Giglio G, Gustin M. 2008. Nest box provision for Lesser Kestrel *Falco naumanni* populations in the Apulia region of southern Italy. Conservation Evidence **5**:58–61.

Cade TJ, Temple SA. 1995. Management of threatened bird species: evaluation of the hands-on approach. Ibis **137**:161–172.

Carrie NR, Moore KR, Stephens SA, Keith EL. 2014. Influence of cavity availability on Red-cockaded Woodpecker group size. Wilson Bulletin **110**:93–99.

Catry I, Alcazar R, Henriques I. 2007. The role of nest-site provisioning in increasing Lesser Kestrel *Falco naumanni* numbers in Castro Verde Special Protection Area, southern Portugal. Conservation Evidence **4**:54–57.

Catry I, Franco AMA, Sutherland WJ. 2011. Adapting conservation efforts to face climate change: modifying nest-site provisioning for Lesser Kestrels. Biological Conservation **144**:1111–1119.

CITES, CBD COP. 2011. Strategic Vision: 2008–2020 Objectives and the Aichi Targets. Page Strategic Plan for Biodiversity 2010-2020 (CBD COP 10 decision X/2). 7 p.

Coetzee H, Nell W, van Rensburg L. 2014. An exploration of cultural beliefs and practices across the Southern Ground Hornbill's range in Africa. Journal of Ethnobiology and Ethnomedicine **10**:28.

Coleman JD. 1974. The use of artificial nest sites erected for starlings in Canterbury, New Zealand. New Zealand Journal of Zoology **1**:349–354.

Cousins J, Sadler J, Evans J. 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: stakeholder perspectives. Ecology and Society **13**:e4.

Cruz JB, Cruz F. 1996. Conservation of the Dark-rumped Petrel *Pterodroma Phaeopygia* of the Galápagos Islands, 1982–1991. Bird Conservation International **6**:23–32.

Cumming GS, Bernard RTF. 1997. Rainfall, food abundance and timing of parturition in African bats. Oecologia **111**:309–317.

Cunningham S, Madden C, Barnard P, Amar A. 2016. Electric crows: powerlines, climate change and the emergence of a native invader. Diversity and Distributions **22**:17–29.

Daan S, Dijkstra C, Drent R, Meijer T. 1989. Food supply and the annual timing of avian reproduction. In: H Ouellet (Ed). Proceedings of the 19th International Ornithological Congress, 1986. University of Ottawa Press, Ottawa. pp. 392–407.

Dailey T. 2003. Nest box use and nesting success of House Wrens *Troglodytes aedon* in a mid-western wetland park. Ohio Journal of Science **103**:25–28.

Dawson RD, Lawrie CC, O'Brien EL. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. Oecologia **144**:499–507.

De León A, Mínguez E. 2003. Occupancy rates and nesting success of European Storm Petrels breeding inside artificial nest boxes. Scientia Marina **67**:109–112.

de Mendiburu F. 2007. Statistical procedures for agricultural research. Unpublished Masters dissertation. National Engineering University, Lima.

Demeyrier V, Lambrechts MM, Perret P, Grégoire A. 2016. Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. Animal Behaviour **118**:181–190.

Denlinger DL. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. Biotropica **12**:100–106.

Dennis RH, Dow H. 1984. The establishment of a population of Goldeneyes *Bucephala clangula* breeding in Scotland. Bird Study **31**:217–222.

Desimone SM, DeStefano S. 2005. Temporal patterns of Northern Goshawk nest area occupancy and habitat: a retrospective analysis. Journal of Raptor Research **39**:310–323.

Dietz MW, Rogers KG, Piersma T. 2013. When the seasons don't fit: speedy moult as a routine carry-over cost of reproduction. PLoS ONE **8**:e53890.

Doerr E, Doerr VJ. 2007. Positive effects of helpers on reproductive success in the Brown Treecreeper and the general importance of future benefits. Journal of Animal Ecology **76**:966–976.

Double MC, Peakall R, Beck NR, Cockburn A. 2005. Dispersal, philopatry, and infidelity: dissecting local genetic structure in Superb Fairywrens (*Malurs cyaneus*). Evolution **59**:625–635.

du Plessis MA. 1989. The influence of roost-cavity availability on flock size in the Red-billed Woodhoopoe *Phoeniculus Purpureus*. Ostrich **60**: 97–103.

du Plessis M. 1991. The role of helpers in feeding chicks in cooperatively breeding Green (Red-billed) Woodhoopoes. Behavioral Ecology and Sociobiology **28**:291–295.

du Plessis M. 1995. The effects of fuelwood removal on the diversity of some cavity-using birds and mammals in South Africa. Biological Conservation **74**:77–82.

Duckworth RA, Badyaev AV. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. Proceedings of the National Academy of Sciences **104**:15017–15022.

Dudney J, Hallett LM, Larios L, Farrer EC, Spotswood EN, Stein C, Suding KN. 2017. Lagging behind: have we overlooked previous-year rainfall effects in annual grasslands? Journal of Ecology **105**:484–495.

Dunn P. 2004. Breeding Dates and Reproductive Performance. In: AP Møller, W Fiedler, and P Berthold (Eds). Birds and Climate Change. Elsevier, San Diego. pp. 67–85.

Dunn P, Winkler D. 2010. Effects of climate change on timing of breeding and reproductive success in birds. In: AP Møller, W Fielder, and P Berthold (Eds). Effects of Climate Change on Birds. Oxford University Press, Oxford. pp. 113–128.

Eeva T, Veistola S, Lehikoinen E. 2000. Timing of breeding in subarctic passerines in relation to food availability. Canadian Journal of Zoology **78**:67–78.

Engler JO, Sacher T, Elle O, Coppack T, Bairlein F. 2014. No evidence of sex-biased dispersal in an island population of Common Blackbirds *Turdus merula*. Ibis **156**:885–891.

Evans KL, Rodrigues ASL, Chown SL, Gaston KJ. 2006. Protected areas and regional avian species richness in South Africa. Biology Letters **2**:184–188.

Evans MR, Lank DB, Boyd WS, Cooke F. 2002. A comparison of the characteristics and fate of Barrow’s Goldeneye and Bufflehead nests in nest boxes and natural cavities. Condor **104**:610–619.

Ewins P. 1996. The use of artificial nest sites by an increasing population of Ospreys in the Canadian Great Lakes basin. In: DM Bird, DE Varland, and JJ Negro (Eds). Raptors in Human Landscapes: Adaptation to Built and Cultivated Environments. Academic Press, San Diego. pp. 109–123.

Fargallo JA, Blanco G, Potti J, Viñuela J. 2001. Nest box provisioning in a rural population of Eurasian Kestrels: breeding performance, nest predation and parasitism. Bird Study **48**:236–244.

Faria J, Jelihovshi E, Allaman J. 2014. Conventional Tukey Test. Universidade Estadual de Santa Cruz, Ilhéus, Brazil.

Feekes F. 1991. The Black-bellied Whistling Duck in Mexico - from traditional use to sustainable management? Biological Conservation **56**:123–131.

Ferriere R, Belthoff JR, Olivieri I, Krackow S. 2000. Evolving dispersal: where to go next? Trends in Ecology & Evolution **15**:5–7.

Finch DM. 1989. Relationships of surrounding riparian habitat to nest-box use and reproductive outcome in House Wrens. Condor **91**:848–859.

Finch DM. 1990. Effects of predation and competitor interference on nesting success of House Wrens and Tree Swallows. Condor **92**:674–687.

Flockhart DT, Mitchell G, Krikun R, Bayne E. 2016. Factors driving territory size and breeding success in a threatened migratory songbird, the Canada Warbler. Avian Conservation and Ecology **11**:4.

Ford HA. 1989. Ecology of Birds: an Australian Perspective. Surrey Beatty & Sons, Chipping Norton. 288 p.

Forero MG, Donázar JA, Blas J, Hiraldo F. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. Ecology **80**:1298–1310.

Franzreb KE. 1997. Success of intensive management of a critically imperilled population of Red-cockaded Woodpeckers in South Carolina. Journal of Field Ornithology **68**:458–470.

Fritz H, Duncan P. 1994. On the carrying capacity for large ungulates of African savanna ecosystems. Proceedings of the Royal Society B: Biological Sciences 256: 77–82.

Garnett ST, Pedler LP, Crowley GM, Garnett ST, Pedler LP, Crowley GM. 2001. The breeding biology of the Glossy Black Cockatoo *Calyptorhynchus lathami* on Kangaroo Island, South Australia. Emu **99**:262–279.

Gibbons P, Lindenmayer DB, Fischer J, Manning AD, Weinberg A, Seddon J, Ryan P, Barrett G. 2008. The future of scattered trees in agricultural landscapes. Conservation Biology **22**:1309–19.

Goutte A, Antoine E, Weimerskirch H, Chastel O. 2010. Age and the timing of breeding in a long-lived bird: a role for stress hormones? Functional Ecology **24**:1007–1016.

Grant GS. 1982. Avian Incubation: Egg Temperature, Nest Humidity, and Behavioral Thermoregulation in a Hot Environment. Ornithological Monographs. American Ornithologists Union, Washington, D.C. 75 p.

Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140–1162.

Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics **13**:1–21.

Griffith SC, Owens IPF, Burke T. 1999. Environmental determination of a sexually selected trait. Nature **400**:358–360.

Griffith SC, Pryke SR, Mariette M. 2008. Use of nest-boxes by the Zebra Finch (*Taeniopygia guttata*): implications for reproductive success and research. Emu **108**:311–319.

Hamilton WD, May RM. 1977. Dispersal in stable habitats. Nature **269**:578–581.

Hau M. 2001. Timing of breeding in variable environments: tropical birds as model systems. Hormones and Behavior **40**:281–290.

Heinsohn R. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding White-winged Choughs. American Naturalist **137**:864–881.

Heinsohn RG. 1992. Cooperative enhancement of reproductive success in White-winged Choughs. Evolutionary Ecology **6**:97–114.

Hosmer DW, Lemeshow S. 1980. Goodness of fit tests for the multiple logistic regression model. Communications in Statistics - Theory and Methods **9**:1043–1069.

Howald G, Donlan CJ, Galván JP, Russel JC, Parkes J, Samaniego A, Wang Y, Veitch D, Genovesi P, Pascal M, Saunders A, Tershy B. 2007. Invasive rodent eradication on islands. Conservation Biology **21**:1258–1268.

Howard WE. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist **63**:152-161.

Hoyo JD, Elliott A, Sargatal J (Eds). 2001. Handbook of the Birds of the World, Volume 6: Mousebirds to Hornbills. Lynx Edicions, Barcelona. 589 p.

Ibáñez-Álamo JD, Magrath RD, Oteyza JC, Chalfoun AD, Haff TM, Schmidt KA, Thomson RL, Martin TE. 2015. Nest predation research: recent findings and future perspectives. Journal of Ornithology **156**:247.

IUCN. 2016. The IUCN Red List of Threatened Species. Version 2016-2.

IUCN, UNEP-WCMC. 2014. Global Statistics from the World Database on Protected Areas. UNEP World Conservation Monitoring Centre, Cambridge, UK. Available at: www.protectedplanet.net.

Johnson P. 1994. Selection and use of nest sites by Barn Owls in Norfolk, England. Journal of Raptor Research **28**:149–153.

Jones C, Heck W, Lewis R, Mungroo Y, Cade T. 1995. The restoration of the Mauritius Kestrel *Falco punctatus* population. Ibis **137**:173–180.

Jones C, Merton D. 2012. A tale of two islands: the rescue and recovery of endemic birds in New Zealand and Mauritius. In: JG Ewen, D Armstrong, K Parker, and P Seddon, (Eds). Reintroduction Biology: Integrating Science and Management. John Wiley & Sons, Ltd, Chichester. pp. 33–70.

Jordan M. 2011. Southern Ground Hornbill (*Bucorvus leadbeateri*) Species Recovery Plan for South Africa. Johannesburg Zoo/Endangered Wildlife Trust, Johannesburg. 29 p.

Keller LF, Waller DM. 2002. Inbreeding effects in wild populations. Trends in Ecology & Evolution **17**:230–241.

Kemp AC. 1976. Environmental factors affecting the onset of breeding in some southern African hornbills, *Tockus* spp. Journal of Reproduction and Fertility. **19**:319–331.

Kemp AC. 1990. The behavioural ecology of the Southern Ground Hornbill: are competitive offspring at a premium? Proceedings of the 100th Meeting of the German Ornithological Society. Bonn. pp. 267–271.

Kemp AC. 1995. The Hornbills, Bucerotiformes. Oxford University Press, Oxford. 302 p.

Kemp AC. 2005. Southern Ground Hornbill. In: PAR Hockey, WAJ Dean, and PG Ryan (Eds). Roberts Birds of Southern Africa, 7th edition. John Voelcker Bird Book Fund, Cape Town. pp. 158–159

Kemp AC, Begg KS. 1996. Nest sites of the Southern Ground Hornbill *Bucorvus leadbeateri* in the Kruger National Park, South Africa, and conservation implications. Ostrich **67**:9–14.

Kemp AC, Joubert SCJ, Kemp MI. 1989. Distribution of Southern Ground Hornbills in the Kruger National Park in relation to some environmental features. South African Journal of Wildlife Research **19**:93–98.

Kemp AC, Kemp LV, Nienaber N, Weprin NE. 2013. Use of Artificial Nest Cavities in Southern Ground-Hornbill Conservation: Preparing a National Strategy. Mabula Ground Hornbill Project, Limpopo. 39 p.

Kemp AC, Kemp MI. 1980. The biology of the Southern Ground Hornbill *Bucorvus leadbeateri* (Vigors) (Aves: Bucerotidae). Annals of the Transvaal Museum **32**:65–100.

Kemp AC, Kemp MI. 1991. Timing of egg-laying by Southern Ground Hornbills *Bucorvus leadbeateri* in the central Kruger National Park. Ostrich **62**:80–82.

King LE., Lawrence A, Douglas-Hamilton I, Vollrath F. 2009. Beehive fence deters crop-raiding Elephants. African Journal of Ecology 47:131–37

Kingma SA, Komdeur J, Hammers M, Richardson DS. 2016. The cost of prospecting for dispersal opportunities in a social bird. Biology Letters **12**:e20160316.

Knight GM. 1990. Status, distribution and foraging ecology of the Southern Ground Hornbill (*Bucorvus cafer*) in Natal. Unpublished Masters dissertation. University of Natal, Pietermaritzburg. 202 p.

Koenig WD, Dickinson JL. 2004. Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, UK. 308 p.

Koenig WD, Mumme RL. 1987. Population Ecology of the Cooperatively Breeding Acorn Woodpecker. Princeton University Press, Princeton. 460 p.

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT. 1992. The evolution of delayed dispersal in cooperative breeders. Quarterly Review of Biology **67**:111–150.

Koenig WD, van Vuren D, Hooge PN. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution **11**:514–517.

Koenig WD, Walters EL, Haydock J. 2011. Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the Acorn Woodpecker. American Naturalist **178**:145–158.

Koeppel KN, Kemp LV. 2015. Lead toxicosis in a Southern Ground Hornbill *Bucorvus leadbeateri* in South Africa. Journal of Avian Medicine and Surgery **29**:340–344.

Komdeur J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles Warbler. Nature **358**:493–495.

Korpimäki E. 1985. Clutch size and breeding success in relation to nest-box size in Tengmalm’s Owl *Aegolius funereus*. Ecography **8**:175–180.

Korpimaki E. 1988. Effects of territory quality on occupancy, breeding performance and breeding dispersal in Tengmalm’s Owl. Journal of Animal Ecology **57**:97–108.

Kurvers RHJM, Krause J, Croft DP, Wilson ADM, Wolf M. 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. Trends in Ecology & Evolution **29**:326–335.

Landler L, Jusino MA, Skelton J, Walters JR. 2014. Global trends in woodpecker cavity entrance orientation: latitudinal and continental effects suggest regional climate influence. Acta Ornithologica **49**:257–266.

Langston NE, Rohwer S. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. Oikos **76**:498–510.

Larson ER, Eastwood JR, Buchanan KL, Bennett ATD, Berg ML. 2015. How does nest box temperature affect nestling growth rate and breeding success in a parrot? Emu **115**:247–255.

Libois E, Gimenez O, Oro D, Mínguez E, Pradel R, Sanz-Aguilar A. 2012. Nest boxes: a successful management tool for the conservation of an endangered seabird. Biological Conservation **155**:39–43.

Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biological Reviews **84**:485–513.

Lindenmayer DB, Laurance WF, Franklin JF, Likens GE, Banks SC, Blanchard W, Gibbons P, Ikin K, Blair D, McBurney L, Manning AD, Stein JAR. 2014. New policies for old trees: averting a global crisis in a keystone ecological structure. Conservation Letters **7**:61–69.

Lindenmayer DB, Welsh A, Donnelly C, Crane M, Michael D, Macgregor C, McBurney L, Montague-Drake R, Gibbons P. 2009. Are nest boxes a viable alternative source of cavities for hollow-dependent animals? Long-term monitoring of nest box occupancy, pest use and attrition. Biological Conservation. **142**, 33-42.

Lindenmayer DB, Laurance WF, Franklin JF. 2012. Global decline in large old trees. Science **338**:1305–1306.

Lloyd B, Powlesland R. 1994. The decline of Kakapo *Strigops habroptilus* and attempts at conservation by translocation. Biological Conservation **69**:75–85.

Lloyd P. 1999. Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. Ibis **141**:637–643.

López-Sepulcre A, Norris K, Kokko H. 2009. Reproductive conflict delays the recovery of an endangered social species. Journal of Animal Ecology **78**: 219–25.

Lopez-Vaamonde C, Koning JW, Brown RM, Jordan WC, Bourke AFG. 2004. Social parasitism by male-producing reproductive workers in a eusocial insect. Nature **430**: 557–60.

Low M, Arlt D, Pärt T, Öberg M. 2015. Delayed timing of breeding as a cost of reproduction. Journal of Avian Biology **46**:325–331.

Lundberg A, Alatalo RV. 1997. The Pied Flycatcher. T&AD Poyser, London.

Magrath RD. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. Journal of Animal Ecology **60**:335–351.

Mainwaring MC, Hartley IR. 2008. Covering nest boxes with wire mesh reduces Great Spotted Woodpecker *Dendrocopos major* predation of Blue Tit *Cyanistes caeruleus* nestlings, Lancashire, England. Conservation Evidence **5**:45–46.

Mainwaring MC. 2015. The use of man-made structures as nesting sites by birds: a review of the costs and benefits. Journal for Nature Conservation **25**:17–22.

Major RE, Kendal CE. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis **138**:298–307.

Mänd R, Tilgar V, Lõhmus A, Leivits A. 2005. Providing nest boxes for hole-nesting birds – does habitat matter? Biodiversity & Conservation **14**:1823–1840.

Martínez JE, Pagán I, Calvo JF. 2006. Factors influencing territorial occupancy and reproductive output in the Booted Eagle *Hieraaetus pennatus*. Ibis **148**:807–819.

McCleery RH, Perrins CM, Sheldon BC, Charmantier A. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. Proceedings of the Royal Society of London B **275**:963–970.

Meijer T, Nienaber U, Langer U, Trillmich F. 1999. Temperature and timing of egg-laying of European Starlings. Condor **101**:124–132.

Mezquida ET, Marone L. 2003. Are results of artificial nest experiments a valid indicator of success of natural nests? Wilson Bulletin **115**:270–276.

Miller KE. 2002. Nesting success of the Great Crested Flycatcher in nest boxes and in tree cavities: are nest boxes safer from nest predation? Wilson Bulletin **114**:179–185.

Mitrus C. 2003. A comparison of the breeding ecology of Collared Flycatchers nesting in boxes and natural cavities. Journal of Field Ornithology **74**:293–299.

Mograbi P, Asner G, Witkowski E, Erasmus B, Wessels K, Mathieu R, Vaughn N. In press. Humans and elephants as treefall drivers in African savannas. Ecography.

Møller AP. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos **56**:421–423.

Møller AP, Fiedler W, Berthold P (eds). 2010. Effects of Climate Change on Birds. Oxford University Press, Oxford. 332 p.

Moreau R. 1936. The breeding biology of certain East African hornbills (Bucerotidae). Journal of the East Africa and Uganda Natural History Society **13**:1–28.

Moreau RE. 1950. The breeding seasons of African birds— 1. Land birds. Ibis **92**:223–267.

Morrison K, Daly B, Burden D, Engelbrecht D, Jordan M, Kemp AC, Kemp MI, Potgieter C, Turner A, Friedmann Y. 2005. Southern Ground Hornbill Population and Habitat Viability Assessment (PHVA) (*Bucorvus leadbeateri*) - Final Report. Conservation Breeding Specialist Group; Endangered Wildlife Trust, Johannesburg. 109 p.

Morrison P, Gurney M. 2007. Nest boxes for Roseate Terns *Sterna dougallii* on Coquet Island RSPB reserve, Northumberland, England. Conservation Evidence **4**:1–3.

Nadeau CP, Conway CJ, Rathbun N. 2015. Depth of artificial Burrowing Owl burrows affects thermal suitability and occupancy. Journal of Field Ornithology **86**:288–297.

Nakagawa S, Lee JW, Woodward BK, Hatchwell BJ, Burke T. 2008. Differential selection according to the degree of cheating in a status signal. Biology Letters **4**:667–669.

Nakagawa S, Ockendon N, Gillespie DOS, Hatchwell BJ, Burke T. 2007. Assessing the function of House Sparrows' bib size using a flexible meta-analysis method. Behavioral Ecology **18**:831–840.

Nakagawa S, Schielzeth H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution **4**:133–142.

Nana ED, Sedláček O, Vokurková J, Hořák D. 2014. Nest position and type affect predation rates of artificial avian nests in the tropical lowland forest on Mount Cameroon. Ostrich **85**:93–96.

NCF-India. 2017. Hornbill Nest Adoption Program: Saving Hornbill Homes with Communities. Available at: http://ncf-india.org/projects/hornbill-nest-adoption-program.

Negro JJ, Hiraldo F. 1993. Nest-site selection and breeding success in the Lesser Kestrel *Falco naumanni*. Bird Study **40**:115–119.

Nelson-Flower MJ, Hockey PAR, O'Ryan C, Ridley AR. 2012. Inbreeding avoidance mechanisms: dispersal dynamics in cooperatively breeding Southern Pied Babblers. Journal of Animal Ecology **81**:876–883.

Newton I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation **70**:265–276.

Nilsson J-Å, Smith HG. 1985. Early fledgling mortality and the timing of juvenile dispersal in the Marsh Tit *Parus palustris*. Ornis Scandinavica **16**:293–298.

Nix HA. 1976. Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. In: Proceedings of the 16th International Ornithological Congress. Australian Academy of Science, Canberra. pp. 272–305.

Nogales M, Martín A, Tershy BR, Donlan CJ, Veitch D, Puerta N, Wood B, Alonso J. 2004. A review of feral cat eradication on islands. Conservation Biology **18**:310–319.

Oritz-Catedral L, Brunton D. 2010. Success of translocations of Red-fronted Parakeets *Cyanoramphus novaezelandiae* from Little Barrier Island (Hauturu) to Motuihe Island, Auckland, New Zealand. Conservation Evidence **7**:21–26.

Ortego J, Calabuig G, Aparicio JM, Cordero PJ. 2008. Genetic consequences of natal dispersal in the colonial Lesser Kestrel. Molecular Ecology **17**:2051–2059.

Pärt T. 1990. Natal dispersal in the Collared Flycatcher: possible causes and reproductive consequences. Ornis Scandinavica **21**:83–88.

Pasinelli G. 2001. Breeding performance of the Middle Spotted Woodpecker *Dendrocopos medius* in relation to weather and territory quality. Ardea **89**:353–361.

Pasinelli G, Walters JL. 2002. Social and environmental factors affect natal dispersal and philopatry of male Red-cockaded Woodpeckers. Ecology **83**:2229–2239.

Pasuwan C. 2000. Appropriate technology for artificial nest construction based on hornbill perception in Budo-Sungai Padee National Park, Narathivat Province, Thailand. Unpublished Masters dissertation. Mahidol University, Bangkok.

Pell AS, Tidemann CR. 1997. The impact of two exotic hollow-nesting birds on two native parrots in savannah and woodland in eastern Australia. Biological Conservation **79**:145–153.

Perrins CM. 1965. Population fluctuations and clutch-size in the Great Tit *Parus major*. Journal of Animal Ecology **34**:601–647.

Perrins CM. 1970. The timing of birds' breeding seasons. Ibis **112**:242–255.

Perrins CM. 1991. Tits and their caterpillar food supply. Ibis **133**:49–54.

Pichegru L. 2013. Increasing breeding success of an endangered penguin: artificial nests or culling predatory gulls? Bird Conservation International **23**:296–308.

Pinheiro J, Bates D, DebRoy S, Sakar D, R Core Team. 2017. Nlme: Linear and Nonlinear Mixed Effects Models.

Ponnikas S, Kvist L, Ollila T, Stjernberg T, Orell M. 2013. Genetic structure of an endangered raptor at individual and population levels. Conservation Genetics **14**:1135–1147.

Poonswad P, Chinchome V, Plongmai K, Chuilua P. 1999. Factors influencing the reproduction of Asian hornbills. In: NJ Adams, RH Slotow (Eds). Proceedings of the 22nd International Ornithological Congress. BirdLife South Africa, Johannesburg. pp 1740–1755.

Poonswad P, Kemp AC, Strange M. 2013. Hornbills of the World: A Photographic Guide. Draco Publishing, Singapore. 212 p.

Poulin B, Lefebvre G, McNeil R. 1992. Tropical avian phenology in relation to abundance and exploitation of food resources. Ecology **73**:2295–2309.

Pöysä H, Pöysä S. 2002. Nest-site limitation and density dependence of reproductive output in the Common Goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. Journal of Applied Ecology **39**:502–510.

Purcell KL, Verner J, Oring LW. 1997. A comparison of the breeding ecology of birds nesting in boxes and tree cavities. Auk **114**:646–656.

R Development Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Radford AN, du Plessis MA. 2004. Green Woodhoopoe *Phoeniculus purpureus* territories remain stable despite group-size fluctuations. Journal of Avian Biology **35**:262–268.

Rahman M, Purev-ochir G, Batbayar N, Dixon A. 2016. Influence of nest box design on occupancy and breeding success of predatory birds utilizing artificial nests in the Mongolian steppe. Conservation Evidence **13**:21–26.

Ramsden DJ. 1998. Effect of barn conversions on local populations of Barn Owl (*Tyto alba*). Bird Study **45**:68–76.

Rangen SA, Clark RG, Hobson KA. 2000. Visual and olfactory attributes of artificial nests. Auk **117**:136–146.

Ratcliffe N, Bell M, Pelembe T, Boyle D, Benjamin R, White R, Godley B, Stevenson J, Sanders S. 2010. The eradication of feral cats from Ascension Island and its subsequent recolonization by seabirds. Oryx **44**:20–29.

Rendell WB, Robertson RJ. 1990. Influence of forest edge on nest-site selection by Tree Swallows. Wilson Bulletin **102**:634–644.

Reyer HU. 1984. Investment and relatedness: A cost/benefit analysis of breeding and helping in the Pied Kingfisher (*Ceryle rudis*). Animal Behaviour **32**:1163–1178.

Rice WR. 1989. Analyzing tables of statistical tests. Evolution **43**:223–225.

Robb GN, McDonald RA, Chamberlain DE, Reynolds SJ, Harrison TJE, Bearhop S. 2008. Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters **4**:220–223.

Robertson RJ, Rendell WB. 1990. A comparison of the breeding ecology of a secondary cavity nesting bird, the Tree Swallow (*Tachycineta bicolor*), in nest boxes and natural cavities. Canadian Journal of Zoology **68**:1046–1052.

Rollins L, Browning L, Holleley C, Savage J, Russell AF, Griffith S. 2012. Building genetic networks using relatedness information: a novel approach for the estimation of dispersal and characterization of group structure in social animals. Molecular Ecology **21**:1727–1740.

Saab VA, Dudley J, Thompson WL. 2004. Factors influencing occupancy of nest cavities in recently burned forests. Condor **106**:20–36.

Sanz V, Rodriguez-Ferraro A, Albornoz M, Bertsch C. 2003. Use of artificial nests by the Yellow-shouldered Parrot *Amazona barbadensis*. Ornitologê Neotropical **14**:345–351.

Saunders DA, Dawson R, Nicholls A. 2016. Breeding failure and nestling body mass as a function of age of breeding females in the endangered Carnaby’s Cockatoo, *Calyptorhynchus latirostris*. Australian Zoologist **38**:171–182.

Schmutz JK, Fyfe RW, Moore DA, Smith AR. 1984. Artificial nests for Ferruginous and Swainson’s Hawks. Journal of Wildlife Management **48**:1009–1013.

Seddon N, Mace GM, Naeem S, Tobias JA, Pigot AL, Cavanagh R, Mouillot D, Vause J, Walpole M. 2016. Biodiversity in the Anthropocene: prospects and policy. Proceedings of the Royal Society of London B **283**:e2016.2094.

Sharp SP, Baker MB, Hadfield JD, Simeoni M, Hatchwell BJ. 2008. Natal dispersal and recruitment in a cooperatively breeding bird. Oikos **117**:1371–1379.

Sherley RB, Barham BJ, Barham PJ, Leshoro TM, Underhill LG. 2012. Artificial nests enhance the breeding productivity of African Penguins *Spheniscus demersus* on Robben Island, South Africa. Emu **112**:97–106.

Shiao MT, Chuang MC, Yuan HW, Wang Y. 2015. Effects of weather variation on the timing and success of breeding in two cavity-nesting species in a subtropical montane forest in Taiwan. Auk **132**:671–684.

Siikamäki P. 1998. Limitation of reproductive success by food availability and breeding time in Pied Flycatchers. Ecology **79**:1789–1796.

Sinclair ARE. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palaearctic migrants in a tropical African savannah. Ibis **120**:480–497.

Skwarska JA, Kalinski A, Wawrzyniak J, Banbura J. 2009. Opportunity makes a predator: Great Spotted Woodpecker predation on tit broods depends on nest box design. Ornis Fennica **86**:109–112.

Smallwood J, Collopy M. 2009. South-eastern American Kestrels respond to an increase in the availability of nest cavities in north-central Florida. Journal of Raptor Research **43**:291–300.

Smith BW, Belthoff JR. 2001. Effects of nest dimensions on use of artificial burrow systems by Burrowing Owls. Journal of Wildlife Management **65**:318–326.

Sonerud GA. 1985. Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. Journal of Animal Ecology **54**:179–192.

Sorato E, Griffith SC, Russell A. 2016. The price of associating with breeders in the cooperatively breeding Chestnut-crowned Babbler: foraging constraints, survival and sociality. Journal of Animal Ecology **85**:1340–1351.

Spear D, Morrison K, Daly B, du Plessis M, Turner A, Friedmann Y. 2005. Southern Ground Hornbill (*Bucorvus leadbeateri*) Population and Habitat Viability Assessment. South African Wildlife College, Hoedspruit. 114 p.

Stamp RK, Brunton DH, Walter B. 2002. Artificial nest box use by the North Island Saddleback: effects of nest box design and mite infestations on nest site selection and reproductive success. New Zealand Journal of Zoology **29**:285–292.

Stearns SC. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology **51**:3–47.

Storaas T. 1988. A comparison of losses in artificial and naturally occurring Capercaillie nests. Journal of Wildlife Management **52**:123–126.

Sutherland DR, Dann P, Jessop RE. 2014. Evaluation of artificial nest sites for long-term conservation of a burrow-nesting seabird. Journal of Wildlife Management **78**:1415–1424.

Sutherland WJ, Newton I, Green RE. 2004. Bird ecology and conservation: a handbook of techniques. Oxford University Press, Oxford. 386 p.

Svensson E. 1995. Avian reproductive timing: when should parents be prudent? Animal Behaviour **49**:1569–1575.

Sydeman WJ, Penniman JF, Penniman TM, Pyle P, Ainley DG. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relation to food availability. Journal of Animal Ecology **60**:135-149.

Taylor MR, Kemp LV. 2015. Southern Ground Hornbill. In: MR Taylor, F Peacock, and RM Wanless (Eds). The 2015 Eskom Red Data Book of Birds of South Africa, Lesotho and Swaziland. BirdLife South Africa, Johannesburg. pp. 119–121.

Temple HJ, Hoffman JI, Amos W. 2006. Dispersal, philopatry and intergroup relatedness: fine-scale genetic structure in the White-breasted Thrasher, *Ramphocinclus brachyurus*. Molecular Ecology **15**:3449–3458.

Theron N. 2011. Genetic connectivity, population dynamics and habitat selection of the Southern Ground-Hornbill (*Bucorvus leadbeateri*) in the Limpopo Province. Unpublished Masters dissertation. University of the Free State, Bloemfontein.

Theron N, Dalton D, Grobler JP, Jansen R, Kotze A. 2013a. Molecular insights on the re-colonization of the Limpopo Valley, South Africa, by Southern Ground Hornbills. Journal of Ornithology **154**:727–737.

Theron N, Jansen R, Grobler P, Kotze A. 2013b. The home range of a recently established group of Southern Ground Hornbill (*Bucorvus leadbeateri*) in the Limpopo Valley, South Africa. Koedoe **55**: [online article no. 1135].

Thompson CF, Neill AJ. 1991. House Wrens do not prefer clean nest boxes. Animal Behaviour **42**:1022–1024.

Thomson AL. 1950. Factors determining the breeding seasons of birds: an introductory review. Ibis **92**:173–184.

Tittensor DP et al. 2014. A mid-term analysis of progress toward international biodiversity targets. Science **346**:241–244.

Toland BR, Elder WH. 1987. Influence of nest box placement and density on abundance and productivity of American Kestrels in central Missouri. Wilson Bulletin **99**:712–717.

Townsend AK, Sillett TS, Lany NK, Kaiser SA, Rodenhouse NL, Webster MS, Holmes RT. 2013. Warm springs, early lay dates, and double brooding in a North American migratory songbird, the Black-throated Blue Warbler. PLoS ONE **8**:e59467.

Trivedi AK, Rani S, Kumar V. 2006. Control of annual reproductive cycle in the subtropical House Sparrow (*Passer domesticus*): evidence for conservation of photoperiodic control mechanisms in birds. Frontiers in Zoology **3**:12.

Turner AK. 1982. Timing of laying by Barn Swallows (*Hirundo rustica*) and Sand Martins (*Riparia riparia*). Journal of Animal Ecology **51**:29–46.

van de Pol M, Bailey LD, McLean N, Rijsdijk L, Lawson CR, Brouwer L. 2016. Identifying the best climatic predictors in ecology and evolution. Methods in Ecology and Evolution **7**:1246–1257.

van der Waal C. 2010. Nutrients in an African savanna: the consequences of supply heterogeneity for plants and animals. PhD Thesis, University of Wageningen, Wageningen.

van Dijk RE, Covas R, Doutrelant C, Spottiswoode CN, Hatchwell BJ. 2015. Fine-scale genetic structure reflects sex-specific dispersal strategies in a population of Sociable Weavers (*Philetairus socius*). Molecular Ecology **24**:4296–4311.

van Heezik Y, Jalme MS, Hémon S, Seddon P. 2002. Temperature and egg-laying experience influence breeding performance of captive female Houbara Bustards. Journal of Avian Biology **33**:63–70.

van Rooyen N. 2005. Vegetation types of the Timbavati, Klaserie and Umbabat Private Nature Reserves. Unpublished report. Centre for Wildlife Management. University of Pretoria, Pretoria.

Vangestel C, Callens T, Vandomme V, Lens L. 2013. Sex-biased dispersal at different geographical scales in a cooperative breeder from fragmented rainforest. PLoS ONE **8**:1–11.

Verhulst S, Nilsson J-Å. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society of London B **363**:399–410.

Vernon CJ. 1986. The Ground Hornbill at the southern extremity of its range. Ostrich **57**: 16–24.

Visser ME, Holleman LJM, Caro SP. 2009. Temperature has a causal effect on avian timing of reproduction. Proceedings of the Royal Society of London B **276**:2323–2331.

Visser ME, van Noordwijk A, Tinbergen JM, Lessells CM. 1998. Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). Proceedings of the Royal Society of London B **265**:1867–1870.

Wald A. 1947. Sequential Analysis. J. Wiley & Sons, New York. 232 p.

Walters JR, Copeyon CK, Carter JH. 1991. Induction of Red-cockaded Woodpecker group formation by artificial cavity construction. Journal of Wildlife Management **55**:549–556.

Walters JR, Crowder LB, Priddy JA. 2002. Population viability analysis for Red-cockaded Woodpeckers using an individual-based model. Ecological Applications **12**:249–260.

Watson JEM, Jones KR, Fuller RA, Marco MD, Segan DB, Butchart SHM, Allan JR, McDonald-Madden E, Venter O. 2016. Persistent disparities between recent rates of habitat conversion and protection and implications for future global conservation targets. Conservation Letters **9**:413–421.

Webb DR. 1987. Thermal tolerance of avian embryos: a review. Condor **89**:874–898.

Wesołowski T, Stańska M. 2001. High ectoparasite loads in hole-nesting birds – a nest box bias? Journal of Avian Biology **32**:281–285.

Wiebe KL. 2001. Microclimate of tree cavity nests: is it important for reproductive success in Northern Flickers? Auk **118**:412–421.

Wiebe KL. 2011. Nest sites as limiting resources for cavity-nesting birds in mature forest ecosystems: a review of the evidence. Journal of Field Ornithology **82**:239–48.

Wikelski M, Hau M, Wingfield JC. 2000. Seasonality of reproduction in a Neotropical rain forest bird. Ecology **81**:2458–2472.

Williams DA, Rabenold KN. 2005. Male-biased dispersal, female philopatry, and routes to fitness in a social corvid. Journal of Animal Ecology **74**:150–159.

Williams DR, Pople RG, Showler DA, Dicks LV, Child MF, zu Ermgassen EKHJ, Sutherland WJ. 2013. Bird Conservation: Global Evidence for the Effects of Interventions. Pelagic Publishing, Exeter. 593 p.

Williams TD. 2005. Mechanisms underlying the costs of egg production. BioScience **55**:39–48.

Wilson G. 2011. What causes variation in the reproductive performance of groups of Southern Ground-Hornbills *Bucorvus leadbeateri*? BSc Honours project. University of Cape Town, Cape Town.

Wilson G, Hockey PAR. 2013. Causes of variable reproductive performance by Southern Ground Hornbill *Bucorvus leadbeateri* and implications for management. Ibis **155**:476–484.

Wilson RR, Cooper RJ. 1998. Acadian Flycatcher nest placement: does placement influence reproductive success? Condor **100**:673–679.

Witteveen M, Parry E, Norris-Rogers M, Brown M. 2013. Breeding density of the Southern Ground Hornbill, *Bucorvus leadbeateri*, in the communal areas surrounding the Matobo National Park, Zimbabwe. African Zoology **48**:274–278.

Wood P., Collopy M. 1993. Effects of egg removal on Bald Eagle productivity in northern Florida. Journal of Wildlife Management **57**:1–9.

Woolfenden GE, Fitzpatrick JW. 1978. The inheritance of territory in group-breeding birds. BioScience **28**:104–108.

Woxvold IA, Magrath ML. 2005. Helping enhances multiple components of reproductive success in the cooperatively breeding Apostlebird. Journal of Animal Ecology **74**:1039–1050.

Woxvold IA, Adcock GJ, Mulder RA. 2006. Fine-scale genetic structure and dispersal in cooperatively breeding Apostlebirds. Molecular Ecology **15**:3139–3146.

Wyness W. 2011. Home range use by Southern Ground Hornbills (*Bucorvus leadbeateri*) - quantifying seasonal habitat selection and vegetation characteristics. Unpublished Honours dissertation. University of Cape Town, Cape Town.

Zack S, Stutchbury BJ. 1992. Delayed breeding in avian social systems: the role of territory quality and “floater” tactics. Behaviour **123**:194–219.

Zann R, Morton S, Jones K, Burley N. 1995. The timing of breeding by Zebra Finches in relation to rainfall in central Australia. Emu **95**:208–222.

Zicus MC, Rave DP, Das A, Riggs MR, Buitenwerf ML. 2006. Influence of land use on Mallard nest-structure occupancy. Journal of Wildlife Management **70**:1325–1333.

Zoghby BA, Ryan PG, Little RM, Reid T, Hockey PAR. 2015. Seasonal changes in movement and habitat use by Southern Ground Hornbills in the South African lowveld. Ostrich **86**:87–96.

Zuur AF, Ieno EN. 2016. A protocol for conducting and presenting results of regression-type analyses. Methods in Ecology and Evolution **7**:636–645.