What causes variation in the reproductive performance of groups of Southern Ground-Hornbills *Bucorvus leadbeateri*?

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Acknowledgements

Abstract

Cooperatively breeding birds live in stable, social groups within which individuals help to raise offspring that are not their own. Most studies of cooperatively breeding species have focused on group size and helper effects to explain all aspects of breeding, and the ways in which these influence the evolution of cooperative breeding behaviour amongst birds. Of central importance to understanding complex, cooperatively breeding societies is recognising which factors cause variation in reproductive performance amongst groups of the same species. Variation in reproductive success can be influenced by many factors and characteristics. I examined the influence of social and environmental factors on reproductive success in the cooperatively breeding Southern Ground-Hornbill *Bucorvus leadbeateri* using data gathered over eight breeding seasons (23 groups, 184 group years). The conservation status of Southern Ground-Hornbills in South Africa is poor, and the effective management of the remaining populations is hampered by a lack of fundamental understanding of the factors determining reproductive performance. Reproductive success in ground-hornbills was influenced primarily by rainfall, the interaction of nest type with the amount of open woodland in the vicinity of the nest, and group size. Groups breeding in natural nests were successful only when the proportion of open woodland surrounding the nest site was high. Those that bred in artificial nests, where overall breeding success was higher, were less dependent on the amount of open woodland available to them. High rainfall (>500 mm) over the breeding season resulted in a decrease in reproductive success, with groups being most successful in years when rainfall ranged from 300-500 mm. Large groups (> 3 birds) bred more successfully than groups comprising only 2-3 individuals. Group size, helper effects and rainfall cannot be managed to increase the productivity of ground-hornbills. However, the fact that the availability of artificial nest sites and the amount of open woodland around the nest site both contribute positively to breeding performance identify two possible management options (nest boxes and bush clearance) for increasing the reproductive output of ground-hornbill populations in South Africa.

Key words: Southern Ground-Hornbill, *Bucorvus leadbeateri*, reproductive success, environmental effects, social effects, management.

Chapter 1: Introduction

Understanding the factors and mechanisms that influence and regulate population numbers is fundamental to population ecology (Brouwer *et al*., 2006; Carrete *et al*., 2006). It is only relatively recently, as a result of long-term studies of marked individuals, that monitoring the performance of individual birds throughout their lives has become possible, enabling the measurement of lifetime reproductive success (LRS – Newton, 1989; Korpimaki, 1992). Lifetime reproductive success is related to the number and the condition of offspring that an individual rears to independence (Clutton-Brock, 1988; Newton, 1989; Russell *et al*., 2002) and is one of the most complete measures of fitness currently available (Newton, 1989; Russell *et al*., 2002). Lifetime reproductive rates can provide good approximations for individual biological fitness; i.e. genetic contributions that individuals make towards future generations, and LRS studies facilitate investigation into which components of life history, environment, phenotype and genotype contribute the most to variation in reproductive performance (Newton, 1989). What causes intra-specific variation in the partitioning of reproduction is an intriguing problem, and understanding the factors that cause this variability is of central importance to understanding complex animal societies (Keller & Reeve, 1994).

Variation in reproductive success can be influenced by a multitude of factors and characteristics, both individual and environmental. The LRS of an individual could be the result of chance events, environmental factors, social factors, phenotype or any combination of these (Newton, 1989; Partridge, 1989). There is a large body of literature that has focused on studies of factors that influence LRS, survival and dispersal in cooperatively breeding birds (Newton, 1989; Stacey & Koenig, 1990). In cooperatively breeding birds, it is the combination of group living, dispersal and territoriality (Newton, 1989), as well as environmental and phenotypic factors, that can potentially affect reproductive success.

Cooperatively breeding birds are species which live in stable social groups within which one, dominant pair breeds and other group members exhibit alloparental behaviour (Stacey & Koenig, 1990) and cooperate in rearing the young (Cockburn, 1998; Hatchwell & Komdeur, 2000; Dickinson & Hatchwell, 2004; Clutton-Brock, 2002), providing care and protection to offspring that are not their own. Cooperative breeding is a relatively rare and specialised reproductive system that has been estimated to occur in approximately 9% of all avian species (Cockburn, 2006): it has been suggested to occur most frequently in tropical and warm-

temperate habitats (Stacey & Koenig, 1990). The most common form of cooperative breeding involves a single pair of birds breeding on an all-purpose territory within which they retain offspring from previous broods who assist in the current breeding effort (Magrath & Yezerinac, 1997). Because most cooperatively breeding birds live in groups comprising relatives (Brown, 1987), kin selection (Hamilton, 1964) could therefore be important in some species and essential in others for explaining why individuals stay on natal territories and assist in raising young (Emlen, 1991; Hatchwell & Komdeur, 2000). Individual birds can benefit from group living through increased reproduction and survival, and coping more effectively with ecological constraints (e.g. thermoregulation). Young birds living within a supportive group environment may learn effective foraging and breeding skills through alloparental care (Brown, 1987; Legge, 2000a). Parental 'support' and other benefits of group living are thus powerful selective forces that maintain cooperative breeding amongst birds (Legge, 2000a).

Factors affecting reproductive success

Several studies have investigated the effects that certain factors, environmental and social, have on reproductive success in cooperatively breeding birds (Table 1). Most of these studies have focused on group size and helper effects to explain all aspects of breeding, and the ways in which these influence the evolution of cooperative breeding amongst birds. Most of what is known about variation in reproductive success comes from studies of this kind and there is relatively little understanding of how different factors (e.g. environmental, social and phenotypic) interact and possibly influence intra-specific variation in breeding success amongst cooperatively breeding species.

The most common and fundamental hypotheses that have attempted to explain the occurrence of cooperative breeding in birds have been those that focus on the effects of supernumerary birds ('helpers') and ways in which their presence on territories influences the reproductive success of the dominant pair they assist (Cockburn, 1998; Hatchwell & Komdeur, 2000; Woxwold & Magrath, 2005; Cockburn *et al.*, 2008). There are many potential direct benefits to helpers that remain with their natal groups (Emlen & Wregge, 1991; Heinsohn & Legge, 1999; Magrath, 2001). These include having better opportunities to acquire high-quality territories (Komdeur, 1992); increased survival and enhanced foraging efficiency (Emlen & Wregge, 1989; Koenig *et al.*, 1992); increased indirect fitness through increasing the survival and reproductive success of relatives (Stacey & Ligon, 1991; Mumme, 1992); and acquiring mates

(Reyer, 1990). Individuals that help to raise related offspring are gaining indirect fitness benefits by furthering the spread of genes shared between relatives (Nelson-Flower, 2009). Although there are a variety of possible benefits to be gained by helpers, the most significant and commonly cited is that helpers increase the reproductive success of relatives by increasing the reproductive output of the group (Brown, 1987; Mumme, 1992), through increasing the number of breeding attempts in a season (Innes & Johnston, 1996), or by increasing the survivorship and reproductive life span of the breeders by reducing parental workloads (Crick, 1992; Ridley, 2007; Covas et al., 2008). Several studies have shown strong support for these effects (Emlen & Wregge, 1991; Heinsohn, 1992; Restrepo & Mondragon, 1998; Conner et al., 2004; Lloyd et al., 2009). However, the evidence is inconsistent with some studies concluding that helpers have no measurable effect on reproductive success (Magrath &Yezerinac, 1997; Eguchi et al., 2002) or even have a negative effect (e.g. Laughing Kookaburra *Dacelo novaeguineae* – Legge, 2000a, b).

A correlation between reproductive success and presence/numbers of helpers does not necessarily mean that increased reproductive success is a result of helper presence (because such an argument is circular - Magrath & Yezerinac, 1997; Woxvold & Magrath, 2005; Cockburn et al., 2008). Previously successful reproduction results in larger number of helpers within a group and is therefore a consequence but not necessarily a cause of high reproductive success (Cockburn, 1998; Dickinson & Hatchwell, 2004) – "larger groups could be both the cause and the result of greater production of philopatric young" (Woxvold & Magrath, 2005). Positive correlations between helper numbers and reproductive output could simply be a result of the confounding effects of breeder and territory quality (Cockburn, 1998; Legge, 2000; Eguchi et al., 2002). Ongoing successful breeding could thus be incorrectly credited to the effects of group size (Magrath & Yezerinac, 1997; Legge, 2000). Another reason for the discrepancy in helper effects, as found in Sociable Weavers *Philetarius socius*, is that helpers could have a positive influence on success when breeding conditions are unfavourable but confer no measurable benefit when conditions are good, therefore improving reproductive performance only under adverse environmental conditions (Covas et al., 2008). The lack of a convincing paradigm regarding helper benefits could also stem from difficulties of trying to separate social effects from environmental and maternal effects (Ridley, 2007).

Another common focus of research on cooperative breeding has been exploring reasons for differences in reproductive skew (Clutton-Brock, 1998), which can manifest itself in

differences in reproductive success between groups. Many cooperatively breeding bird species are characterised by high reproductive skew, whereby only a few females within the population produce most or all of the young (Keller & Reeve, 1994; Clutton-Brock, 1998; Cockburn, 2004). In the Florida Scrub-Jay *Aphelocoma coerulescens*, reproductive success is highly skewed with nearly half of all scrub-jays failing to produce a single surviving offspring throughout their reproductive lives (Fitzpatrick & Woolfenden, 1989). Approximately 20 percent of females produce about 65 percent of the new recruits into the breeding population (Woolfenden & Fitzpatrick, 1990). A large body of literature focuses on the reproductive strategies of dominants and subordinates under a range of different social and ecological conditions, making the assumption that the dominants in the group can control subordinate reproduction (Keller & Reeve, 1994; Clutton-Brock, 1998). In the Southern Pied Babbler *Turdoides bicolor*, there is reproductive suppression but conflict between dominants and competitive subordinates occurs in such a way that neither is completely in control of the subordinate's reproduction (Nelson-Flower, 2009). Reproductive skew theory encompasses a series of models which attempt to predict the degree to which same-sex group members share reproduction based on their relatedness, status, control on dispersal, and the effect of individuals on group reproductive success (Keller & Reeve, 1994; Clutton-Brock, 1998; Johnstone, 2000). The application of these models to group-living animals has had mixed success (Williams, 2004), because some of the assumptions (such as dominants having complete control over subordinate reproduction) are unrealistic (reviewed by Johnstone, 2000). Recently, alternative models that take into account incomplete control of subordinates by dominants have been developed (Williams, 2004), and these address both intra-group conflict and its effect on group stability (Nelson-Flower, 2009). Although it is doubtful that any single model will predict reproductive skew in all group-living animals (Johnstone, 2000), these models can still be useful for identifying factors that may be important for explaining broad patterns of reproductive skew in cooperative breeders (Williams, 2004).

Variation in individual survival is also a major source of individual variation in lifetime reproductive success (Clutton-Brock, 1988; Brouwer *et al*., 2006). This is particularly true for long-lived species where small differences in survival can have large evolutionary effects and extensive consequences for population dynamics (Newton, 1989; Brouwer *et al*., 2006). Years of comprehensive data are needed in order to analyse the reproductive traits and breeding performance of K-selected species, making it difficult to formulate and implement conservation management plans for long-lived species. Survival and breeding success may be

influenced by individual differences in both genotype and phenotype (Brouwer *et al.*, 2006), and may vary over time as a function of age (Clutton-Brock, 1988; Newton, 1989; Komdeur, 1996). Individual reproductive success may improve with age due to improved foraging skills, breeding experience, and the duration of the pair-bond (Clutton-Brock, 1988; Newton, 1989; Cockburn *et al.*, 2008) or, beyond a certain point, may decrease with age because of senescence (Komdeur, 1996).

Environmental factors also influence survival and therefore affect the reproductive success of individuals (Russell *et al.,* 2002; Brouwer *et al.*, 2006). Food availability, which is mediated by rainfall and temperature, can influence survival and reproductive success directly (Clutton-Brock, 1988; Newman, 1989). In addition, differences in weather patterns can cause pronounced fluctuations in breeding success between years (Clutton-Brock, 1988; Brouwer *et al.*, 2006). Food availability has significant effects on productivity in White-fronted Bee-eaters *Merops bullockoides* (Emlen & Wrege, 1991), and successful breeding by Arabian Babblers *Turdoides squamiceps* is dependent on food availability as a result of rainfall (Zahavi, 1989). High spring rainfall also significantly and positively influences reproductive success in Splendid Fairy-Wrens *Malurus splendens*, whilst drought conditions have the opposite effect (Cockburn *et al.*, 2008).

A major determinant of reproductive success for many birds is the ability to protect their offspring from predation (Hatchwell *et al.*, 1999). A variety of strategies have evolved amongst birds to reduce nest predation, including dispersed breeding, use of cavities, camouflage and elaborate nest designs (Hatchwell *et al.*, 1999). Long-tailed Tits *Aegithalos caudatus* suffer frequent reproductive failure, largely as a result of predation: consequently, nest placement and nest characteristics play important roles in determining breeding success (Hatchwell *et al.*, 1999). Nest positioning is the most important factor, with breeding success decreasing with increasing height of the nest above ground (Hatchwell *et al.*, *op. cit.*). Among White-throated Magpie-Jays *Calocitta formosa* the strongest overall predictor of nesting success is the rate at which chicks are lost to predation (Innes & Johnston, 1996). Among Rufous Vangas *Schetba rufa*, one of the major causes of poor breeding performance is the total loss of clutches or broods as a result of predation (Eguchi *et al.,* 2002).

Food availability, territory size, nest sites, refuges and types of vegetation are all variables that have been used as measures of territory quality and have been shown to influence reproductive

success in cooperatively breeding birds (Table 1). Studies that have focused on cavity-nesting birds have shown that territory quality is an important cause of variation in reproductive success. Adequate cavities and large trees are often scarce resources and therefore play an important role in the ability of groups to become established and to persist in a particular territory (Stacey & Ligon, 1987; Restrepo & Mondragon, 1998). In Green Wood-Hoopoes *Phoeniculus purpureus* the most critical factor affecting reproductive success is territory quality, determined primarily by the availability of safe roosting and nesting cavities (wood-hoopoes roost in cavities at night - Ligon & Ligon, 1989; 1990). Overall, annual survival and reproductive success is significantly higher amongst groups in high-quality territories (Ligon & Ligon, 1989). For both Acorn Woodpeckers *Melanerpes formicivorus* and Red-cockaded Woodpeckers *Picoides borealis*, large trees with safe cavities have a significant, positive effect on the survival and reproductive success of the individuals that occupy that territory (Stacey & Ligon, 1987; Walters, 1990). For Acorn Woodpeckers, which cache their food, availability of food storage trees determines territory quality. The birds depend on these caches as primary winter food sources, and the amount of food that can be stored depends on the number of cavities available for storage (Stacey & Ligon, 1987). Birds that occupy territories with many 'larders' fledge more young and have higher survival rates than birds living in territories with only a few storage cavities (Stacey & Ligon, 1987). Adequate trunks also represent a limiting resource for cavity-nesting Toucan Barbets *Semnornis ramphastinus*, with the availability of suitable cavities affecting group nesting success (Restrepo & Mondragon, 1998).

Although many studies have attempted to explain patterns of reproductive success among cooperative breeders, few have focused on the possible combined influences of environmental and social factors in influencing such success. In this study, I interrogate both social (group demographics) and environmental factors (rain, nest site availability, vegetation, grass biomass) using multivariate analyses to investigate variation in reproductive performance in groups of cooperatively breeding Southern Ground-Hornbills *Bucorvus leadbeateri*. The study aims to evaluate which factor(s) influence variation in reproductive success amongst groups as a contribution towards a conservation-management plan for the species. Specifically, I ask (1) which groups are the most reproductively successful; (2) does the position of the territory influence group reproductive success through variation in vegetation structure and rainfall; (3) is group size correlated with group success; (4) does the use of artificial nest boxes facilitate more successful breeding; and (5) how can these analyses contribute towards an adaptive conservation-management plan for this species?

Table 1: A summary of the studies that have focused on factors affecting reproductive success in cooperatively breeding birds. In the table (+) indicates a positive effect, (-) indicates a negative effect and (0) indicates that no effect was found on reproductive success. All body mass values were taken from Dunning, 2008.

Species	Mean Body mass (g)	Territory quality	Food availability	Rainfall	Presence of helpers	Group size	Nest site availability	Age at 1st breeding	Predation	Reference
Groove-billed Ani (Central America) *Crotophaga sulcirostris*	87.3	+[1]			0		+		-	Koford *et al.* 1986, 1990
Laughing Kookaburra (Australia) *Dacelo novaeguineae*	313	+[2]	+		- / 0	- / 0				Legge 2000a, b
Pied Kingfisher (sub-Saharan Africa) *Ceryle rudis*	82.4				+	+				Reyer 1984, 1986, 1990
White-fronted Bee-eater (sub-equatorial Africa) *Merops bullockoides*	34.8		+		+	+			-	Emlen & Wrege 1991
Green Wood-Hoopoe (sub-Saharan Africa) *Phoeniculus purpureus*	86.6	+[3]	+	+	0				-	Ligon & Ligon 1989
Toucan Barbet (Columbia & Ecuador) *Semnornis ramphastinus*	97.7				+	+	+			Restrepo & Mondragon 1998
Acorn Woodpecker (USA) *Melanerpes formicivorus*	81.8	+[4]			+ / 0		+			Stacey & Ligon 1987
Red-cockaded Woodpecker (USA) *Picoides borealis*	48.6				+	+	+			Conner *et al.* 2004
Superb Fairy-Wren (Australia) *Malurus cyaneus cyaneus*	11.3			+	+ / 0	+				Cockburn *et al.* 2008
Splendid Fairy-Wren (Australia) *Malurus splendens splendens*	10.6	+[5]	0		+				-	Rowley & Russell 1989
White-browed Scrub-Wren (Australia) *Sericornis frontalis frontalis*	13.3				0	0			-	Magrath & Yezerinac 1997
Bell Miner (Australia) *Manorina melanophrys*	32.3	0[6]	0		0	-			-	Poiani 1993
Grey-crowned Babbler (Australia, Indonesia) *Pomatostomus temporalis*	75	0[7]			+	0				Brown *et al.* 1982
White-winged Chough (Australia) *Corcorax melanorhamphos*	364		+		+	+				Heinsohn 1992
Apostlebird (Australia) *Struthidea cinerea*	132				+	0				Woxvold & Magrath 2005

Species	Mean Body mass (g)	Territory quality	Food availability	Rainfall	Presence of helpers	Group size	Nest site availability	Age at 1st breeding	Predation	Reference
Florida Scrub-Jay (North America) *Aphelocoma coerulescens*	79.3	+[8]			+			-	-	Fitzpatrick & Woolfenden 1989,
		0			+			-		Burt & Peterson 1993
Brown Jay (North & central America) *Cyanocorax morio*	204				+	+			-	Lawton & Guindon 1981, Williams & Hale 2006
White-throated Magpie-Jay (central America) *Calocitta Formosa*	210	0[9]			+	0			-	Innes & Johnston 1996,Langen & Vehrencamp 1999
Siberian Jay (Eurasia) *Perisoreus infaustus*	84.4	+[10]				+			-	Ekman *et al.* 2001
Rufous Vanga (Madagascar) *Schetba rufa*	37.3				0	0			-	Eguchi *et al.* 2002
Western Bluebird (North America) *Sialia mexicana*	25.8				+					Dickinson *et al.* 1996
Galapogas Mockingbird (Galapagos Islands) *Nesomimus parvulus*	56.2		+		+					Curry & Grant 1989
Karoo Scrub-Robin (Southern Africa) *Cercotrichas coryphaeus*	20.4				+	+				Lloyd *et al.* 2009
Stripe-backed Wren (Columbia & Venezuela) *Campylorhynchus nuchalis*	23.2				+	+			-	Rabenold 1984
Long-tailed Tit (Europe & Asia) *Aegithalos caudatus*	8.6				+		+		-	Hatchwell *et al.* 1999, Maccoll & Hatchwell 2004
Seychelles Brush-Warbler (Seychelles) *Acrocephalus sechellensis*	16.8	+[11]	+	+	+ / -					Brouwer *et sel.* 2006, Komdeur 1992
Arabian Babbler (Arabia) *Turdoides squamiceps*	64 - 83		+	+	+	+			-	Zahavi 1989
		+[12]			+	0			-	Ridley 2007
Southern Pied Babbler (Southern Africa) *Turdoides bicolor*	78.3		+	+	+	+		0	-	Nelson-Flower 2009 Ridley (pers. comm.)

1. Territory size, tree density; 2. territory size; 3. tree size, cavity quality; 4. storage facilities; 5. vegetation type, fire; 6. Habitat quality; 7: vegetation type; 8: habitat variation, fire; 9: food resources, suitable nests; 10. distance from human settlement, amount of dense forest; 11. insect prey available, territory size, foliage cover; 12. plant diversity, habitat type.

Study site

The Ground-Hornbill Research and Conservation Project was initiated in 2001, is run by the Percy FitzPatrick Institute of African Ornithology, and is based in the Associated Private Nature Reserves (APNR) in the Limpopo and Mpumalanga Provinces of South Africa. The APNR is located on the western boundary of the Kruger National Park and encompasses an area of 180 000 ha, forming one of the largest private nature reserves in the world (Greyling *et al.* 2004). Both the Klaserie and Timbavati Private Nature Reserves were officially proclaimed in 1972 and as time progressed, neighbouring farms became incorporated into the reserve (Greyling *et al.*, 2004). To date, the APNR consists of the Klaserie, Timbavati, Umbabat and Balule Private Nature Reserves (24º 02'- 24º 33' S; 31º 02' – 31º 29'E).

Prior to proclamation as a nature reserve, some areas now incorporated within the reserve were subjected to cattle ranching, heavy and selective hunting, excessive development of artificial water points, artificial control of veld fires and animal populations which were either over-protected or over-hunted (Bornman, 1995; Greyling *et al.*, 2004; Stauth & Grindley, 2004). All four reserves have now adopted the management principles and policies of the Kruger National Park and form part of the greater Kruger National Park Biosphere Reserve (Greyling, 2004). The western boundary fence, which separated Kruger from the APNR, Sabi-Sand Game Reserve and other provincial nature reserves, was removed in 1993. The APNR is characterized by a highly seasonal, sub-tropical climate of hot, humid summers and warm, dry winters. Mean annual rainfall over the study site ranges from *ca* 375 – 625 mm and there is a pronounced rainfall gradient, with rainfall increasing along a north-west/south-east gradient. The summer rains fall between October and March and account for approximately 90 percent of the annual rainfall. The ground-hornbills breed during the wet season, with the first eggs being laid in October and the last chicks fledging in March/April (Kemp & Kemp, 1991, this study). The dominant vegetation types are lowland savanna, open tree savanna, mixed and open woodland, low thicket and shrubveld (Venter & Gertenbach, 1986; Bornman, 1995). The dominant tree species are the Red Bushwillow *Combretum apiculatum*, Acacia spp. (*Acacia nigrescens, A. tortilis*), Marula *Sclerocarya birrea* and Mopane *Colophospermum mopane* scrub. The smaller shrub layer commonly contains Roundleaf Teak *Pterocarpus rotundifolius*, Scented Thorn *Acacia nilotica*, Red Thorn *A. gerrardii*, and False Thorn *Albizia harveyi*. The grass layer is moderately developed, with Redgrass *Themeda triandra* and Small Buffalograss *Panicum coloratum* being dominant (Venter & Gertenbach, 1986; Bornman, 1995).

Study species: the Southern Ground-Hornbill

The Southern Ground-Hornbill *Bucorvus* leadbeateri is a large, carnivorous bird, weighing 3.5 - 5 kg (Kemp, 1995): it is one of only two members in the family Bucorvidae. It is the largest bird species known to breed cooperatively, and is one of only five African hornbills thought to display this social organisation (Kemp, 1995). Ground-hornbills are facultative cooperative breeders, living in cohesive groups of 2-11 individuals (Kemp, 1995). They are found at low densities, occupying exclusive, year-round territories of approximately 80-100 km^2 in South Africa (Kemp *et al*., 1989). The highest recorded density of Southern Ground-Hornbills is one group per 20 km^2 at Mana Pools, Zimbabwe (Begg, 1996 in Kemp & Begg, 1996). Groups consist of a dominant breeding pair: all juveniles and virtually all the non-breeding adult members of the population are included within groups (i.e. there are very few singletons - Kemp *et al*., 1989). These non-breeding group members are subordinate helpers, which are generally retained offspring of the dominant pair (Kemp, 1995). Groups roost overnight in large trees, leaving at sunrise to forage, which they do together as a group (Vernon, 1986; Kemp & Begg, 1996). Their diet comprises mostly insects, reptiles, amphibians, small mammals and birds (Vernon, 1986).

Southern Ground-Hornbills nest in natural cavities in large trees, laying a clutch of 1-2 (very rarely 3) eggs (Kemp & Begg, 1996). Because the birds are so large, nest sites are considered to be a limiting resource due to the scarcity of large trees in the landscape (Kemp *et al*., 1989). It has been hypothesised that the shortage of large trees reflects the impacts of increasing numbers of African Elephants *Loxodonta africana* across the ground-hornbill's range (Owen-Smith *et al*., 2006; Shannon *et al*., 2008). The availability of suitable nesting sites may be a critical determinant of territory quality and has been hypothesised to influence ground-hornbill reproductive success (Kemp & Begg, 1996; Henley & Henley, 2005). Starting in 2002, artificial nest-boxes were placed throughout the APNR. Many of these were occupied rapidly and used successfully by some ground-hornbill groups, apparently supporting the hypothesis of nest-site limitation.

Within a group, only the dominant pair breeds and no more than one chick is fledged per group per breeding season (Kemp *et al*., 1989). The alpha male lines the nest with dry foliage and all group members deliver food to the alpha female and chick during the incubation and nestling

periods (Kemp, 1987; Kemp & Begg, 1996). The same nest sites are used over successive breeding seasons, but breeding is erratic (Kemp & Begg, 1996): ground-hornbill groups in the Kruger National Park fledge on average only one chick every nine years (Kemp & Begg, 1996).

Southern Ground-Hornbills have experienced a 65% reduction in range, and probably in numbers, over the past three generations (100 years) (Kemp & Webster, 2008). It has been estimated that fewer than 1500 ground-hornbills remain in South Africa, most of which are in protected areas (Kemp & Webster, 2008). As a result, the species is listed as *Vulnerable* on the Red List in South Africa (Barnes, 2000). Community expansion and agricultural practices such as forestry have reduced the natural habitat available to ground-hornbills, and changing distribution patterns for the species show a direct correlation with habitat loss (Kemp & Webster, 2008). Its naturally low density, large territory size, high predicted lifespan, and the fact that not all groups breed every year makes ground-hornbills difficult to survey and generating sufficient data a protracted process. However, the data collected over the past eight years through continuous monitoring by the Ground-Hornbill Research Project offers some consistency and the opportunity to understand the factors affecting the reproductive performance of ground-hornbills. If it can be determined why certain groups are more successful than others, then it may be possible to introduce an adaptive conservation-management plan for the species.

Comprehensive data and observations of nest sites, breeding attempts, reproductive success and group size have been collected over the eight years for 23 groups. Many of the adults and almost all the chicks fledged since 2002/2003 have been ringed, making identification and re-sighting in the field easier. Dispersal by juveniles or subordinates, although very limited, does occur, and unique individual rings allow for positive disperser identification. There are dramatic differences in reproductive success amongst the 23 groups of ground-hornbills, but the reasons for these differences remain unresolved. Nonetheless, understanding the causes of this variation is clearly of fundamental importance in formulating a conservation-management plan for this species. Social factors such as group size and helper effects cannot be managed to increase the ground-hornbills productivity, but if environmental factors are contributing to reproductive performance, then environmental management, such as erection of the artificial nest-boxes that are already in use, becomes a conservation option.

Using both intrinsic (group size) and extrinsic (rainfall, vegetation, nest site availability, grass biomass) factors, this study seeks to investigate and understand reproductive performance amongst groups of Southern Ground-Hornbills. Specifically, the study addresses the following questions:

1. Which factor(s) influence variation in reproductive success amongst groups of ground-hornbills?

2. Do the most successful groups occupy more favourable territories in terms of environmental variables such as rainfall and vegetation types?

3. Do artificial nest boxes facilitate more successful breeding?

4. Using the results, can a successful adaptive habitat-management plan be introduced for the ground-hornbill?

Chapter 2: Materials and Methods

Data collection

The Ground-Hornbill Research Project has monitored the population of Southern Ground-Hornbills in the APNR since 2001. During the eight breeding seasons included in the study, 23 groups have been consistently monitored and 184 group-years of data have been collected. All nest sites were visited before, during and after the breeding season, for each of the eight breeding seasons, to record nesting activity, breeding attempts, breeding success and durability of the nests. At the start of the breeding season (September/October), all nests were checked on a weekly basis until a breeding attempt was discovered, after which the nest was checked every 4-5 days until hatching occurred. The chicks were monitored closely until fledging occurred (in March/April). When no breeding was recorded for a ground-hornbill group an effort was made to try locate any alternative natural nest sites possibly used by the group and, subsequently, any evidence of a chick having been raised during the season (at an undiscovered nest).

The first set of artificial nest boxes were constructed and erected throughout the APNR in 2002. The location (GPS) of each nest-box and the dimensions of the trees used to hold the boxes were recorded. All other nests in natural cavities as well as potential nesting sites were recorded using GPS. The type and location of the nest for each breeding year was recorded for each group. When groups bred successfully but the nest site could not be found, the successful breeding attempt was recorded as being in a natural, but unknown nest (because all nest boxes within the territory had been checked).

Social factors

Group size was recorded as the number of individuals present in each group at the start of each breeding season. The large territory size and dense vegetation make observing the birds and determining the true group size very difficult. Sightings of the birds by land owners and tourist lodges and knowledge of each group's previous breeding attempts gives an indication of group demographics, but in years when sightings were few and breeding sites unknown or uncertain for some of the ground-hornbill groups, group size could not be determined accurately and was left out of the analysis.

Environmental factors

The average monthly rainfall data for the years 2000-2009 were collated from 16 sites spread throughout the APNR (seven from Klaserie, six from Timbavati and three from within Umbabat). Each ground-hornbill group was then linked to the rainfall station closest to its territory. In ground-hornbills, laying date is correlated with rainfall, and the onset of laying coincides with the first rains of summer (Kemp & Kemp, 1991). It is doubtful that rainfall *per se* influences the laying date, but it is assumed to influence the availability of food for the dominant female and chick (Kemp & Kemp, 1991). Rainfall over the six-month breeding season (October–March) for each year was used in the analyses.

Vegetation characteristics for each group's territory were determined using ArcView GIS 3.3. A detailed vegetation map of the APNR was used to calculate the proportion of each vegetation type within a 3 km radius of each group's nest. There is no record of how far ground-hornbills move during the breeding season in order to forage and to provision the dominant female and chick at the nest. However, from field observations outside the breeding season, it is known that they can travel large distances (~8-10 km) in a single day and therefore a distance of 3 km around the nest was considered realistic. The proportion of different vegetation types within this radius was then used to calculate vegetation diversity associated with each nest using the Shannon-Wiener Diversity Index. Ground-hornbills often forage in open areas, where prey are easily found and caught (Kemp *et al*., 1989). In Kruger National Park, most nests are in areas with bare ground or with grass of short to medium height (Kemp & Begg, 1996). Using the same vegetation map, the proportion of open woodland within a 3 km radius of each nest was calculated.

The nature of the terrain and habitat made it impossible to quantify rates of food acquisition. Grass biomass data were collected for the APNR over the eight-year period. Grass biomass is assumed to represent a reasonable surrogate for food availability and was incorporated in analyses. The grass fuel load was estimated annually in March/April at 103 sites across the APNR using a disc pasture meter (Trollope & Potgieter, 1986; Zambatis *et al*., 2006). The biomass values of the five closest sites to each nest were used to calculate the average grass biomass for each ground-hornbill group in each year.

Statistical analyses

A Generalized Linear Mixed Model (GLMM) was used to investigate the factors affecting overall breeding success. Ground-hornbills only ever fledge one chick per breeding season so they are either successful or they fail at breeding in that year. Two dependent variables were analysed; breeding success (where 0 = failed and 1 = success) and breeding attempts (where 0 = no attempt and 1 = attempt) in GLMMs using a binomial distribution and logit link function in Program R (version 2.10.0, The R Foundation for Statistical Computing, Ihaka & Gentleman, 1996). The same breeding pairs were present in the study for more than one year resulting in the potential for non-independence in the data. Mixed models are necessary to analyse such data correctly, because random as well as fixed effects can both be included (Bennington & Thayne, 1994; Johnson & Omland, 2004). To control for pair identity, I included the random factor 'group identity' in all analyses of breeding success. The random term was never dropped from the analyses, even when insignificant, because this would ultimately inflate the degrees of freedom and would therefore regress to pseudo-replication. All relevant two-way interactions were tested but only those that were significant are presented. The methods described by Burnham & Anderson (2002) were used for the GLMMs. Akaike's Information Criterion (AIC) was used to select the most parsimonious model (Akaike, 1973). This approach compares the fits of a suite of candidate models using the AIC. AIC allows models with different numbers of parameters to be directly compared with each other. AIC is calculated for a suite of models and the best-fitting model is the one with the lowest AIC value (termed AIC_{min}). AIC differences are calculated relative to the minimum, so therefore the model difference is calculated as:

$$\Delta_i = AIC_i - AIC_{min}$$

The difference in AIC between models indicates the relative support for the models. The potential explanatory variables fitted to the model included: (1) availability and type of nest sites (i.e. whether an artificial nest was or was not available to the group); (2) environmental factors (rainfall over the breeding season, grass biomass, vegetation diversity, proportion of open woodland); and (3) group size.

Because the inclusion of strongly associated variables into a GLMM analysis can lead to false estimates of significance, the association between all potential explanatory variables was verified prior to analysis using linear regression methods. There was no relationship between the environmental and social factors incorporated in the analysis and therefore all terms could

be included simultaneously. However, within the category of environmental factors there were some strong autocorrelations. Rainfall and grass biomass were highly correlated, as were vegetation diversity and the proportion of open woodland. The terms that contributed the most to the model power and had the lowest AIC values were retained and used in the models. This was determined by adding each term separately to the full model, comparing the AIC values generated from their inclusion, and dropping the one contributing to the higher AIC value from the model. The proportion of open woodland and rainfall generated the lowest AIC values and were retained; vegetation diversity and grass biomass were removed.

Chapter 3: Results

Reproductive success

There were major differences in reproductive success amongst the 23 ground-hornbill groups within the APNR. Over the period 2001-2008 there were some highly successful groups that bred and fledged a chick almost every year, whereas other groups either did not breed or did not rear a single chick over the same period. During 2001–2008 (184 possible group breeding years) there were a total of 67 breeding attempts by 17 groups. Six groups did not attempt to breed at all. Of the 67 breeding attempts, 51 (76%) were successful, with seven of the groups (30%) collectively contributing 60% of this reproductive output (Table 2). These seven groups all bred in artificial nests: only 5 of the 23 groups bred in natural cavities. Of these latter groups, three groups did not fledge a single chick over the eight years. Turnover of the dominant pair in ground-hornbills is not common, and all but one group retained the same breeding pair for the duration of the study.

Table 2: Breeding attempts and reproductive success for the 23 ground-hornbill groups.

No.	Group name	Breeding attempts	Chicks reared	No.	Group name	Breeding attempts	Chicks reared
1	Rhino Road	6	6	13	Caroline	3	2
2	Johnniesdale	7	5	14	Copenhagen	2	2
3	Karan Khaya	5	4	15	Ntoma	2	2
4	Senalala	5	4	16	Lornay	1	0
5	Addger	5	4	17	Mananga	1	0
6	Pitlochry	4	4	18	Ross	0	0
7	Von Tonder	4	4	19	Yankee Dam	0	0
8	De Luca	6	3	20	Roussow	0	0
9	Keer Keer	5	3	21	Strydom	0	0
10	Giraffe	4	3	22	Charloscar	0	0
11	Janowski	3	3	23	Chimani	0	0
12	Ntsiri	4	2				

The best-supported model identified the amount of rainfall over the breeding season, group size and the interaction of artificial nests with the amount of open woodland as the terms best explaining the variation in reproductive success (Model 1 - Table 3). Both social (group size) and environmental factors (rainfall, proportion of open woodland, nest type) thus contribute to explaining variation in breeding success.

When analysing variation in the frequency of breeding attempts among groups the best-supported model was the same as the minimum adequate model for reproductive success. The same terms that best explained reproductive success were identified by the model to best explain breeding attempts amongst the groups of ground-hornbills. The difference between the best and second-best model (ΔAIC) in both analyses was similar (Model 1 - Appendix 1). Therefore the same environmental and social parameters that influence reproductive success, affect whether or not a group attempts to breed. This suggests that the factors causing breeding attempts to fail are the same factors that cause some groups not to attempt breeding.

Table 3: Output of GLMM model selection statistics investigating causes of variation in reproductive success in Southern Ground-Hornbills. Reproductive success (0 or 1) was set as the response term and group identity as a random term. Deviance = -2 log-likelihood; K = total number of parameters (explanatory terms + random term + residual variance); AIC = Akaike's Information Criterion; and ΔAIC = difference between the AIC value for that model and the best model. Analysis is based on 23 groups monitored over an eight-year period. (x) indicates an interaction term.

No.	Model	K	AIC	ΔAIC	Deviance
1	Nest type x open woodland + group size + rain	7	165.6	0	151.6
2	Nest type x open woodland + group size	6	170.7	5.1	158.7
3	Nest type + group size + rain + open woodland	6	173.4	7.8	161.4
4	Nest type x rain + group size + open woodland	7	175.3	9.7	161.3
5	Nest type + group size + rain	5	175.8	10.2	165.8
6	Nest type + group size + woodland	5	177.1	11.5	167.1
7	Nest type + group size	4	178.9	13.3	170.9
8	Group size + rain + open woodland	5	179.3	13.7	169.3
9	Nest type x open woodland + rain	6	192.7	27.1	180.7
10	Nest type x woodland	5	195.6	30.0	185.6
11	Nest type x rain + open woodland	6	198.1	32.5	186.1
12	Rain + open woodland	4	208.0	42.4	200.0

Significant explanatory terms (minimal model)	Effect	s.e.
Intercept	-7.312	1.926
Group size	0.971	0.202
Rain	-0.005	0.002
Nest type x Open woodland		
- Artificial nest	1.222	4.558
- Natural nest	13.642	4.558

Effects of environmental factors

When rainfall over the breeding season exceeded 500 mm, breeding success decreased (Table 3). Breeding success was highest in years when rainfall over the six months of the breeding season ranged from 300–500 mm (Figure 1). Sixteen of the 67 breeding attempts failed. Of the 51 successful breeding attempts, 36 (71%) occurred when rainfall was between 300–500 mm and only 13 (25%) when rainfall was less than 300 mm. In years when rainfall exceeded 500 mm only two attempts were successful, both in artificial nests (Figure 1).
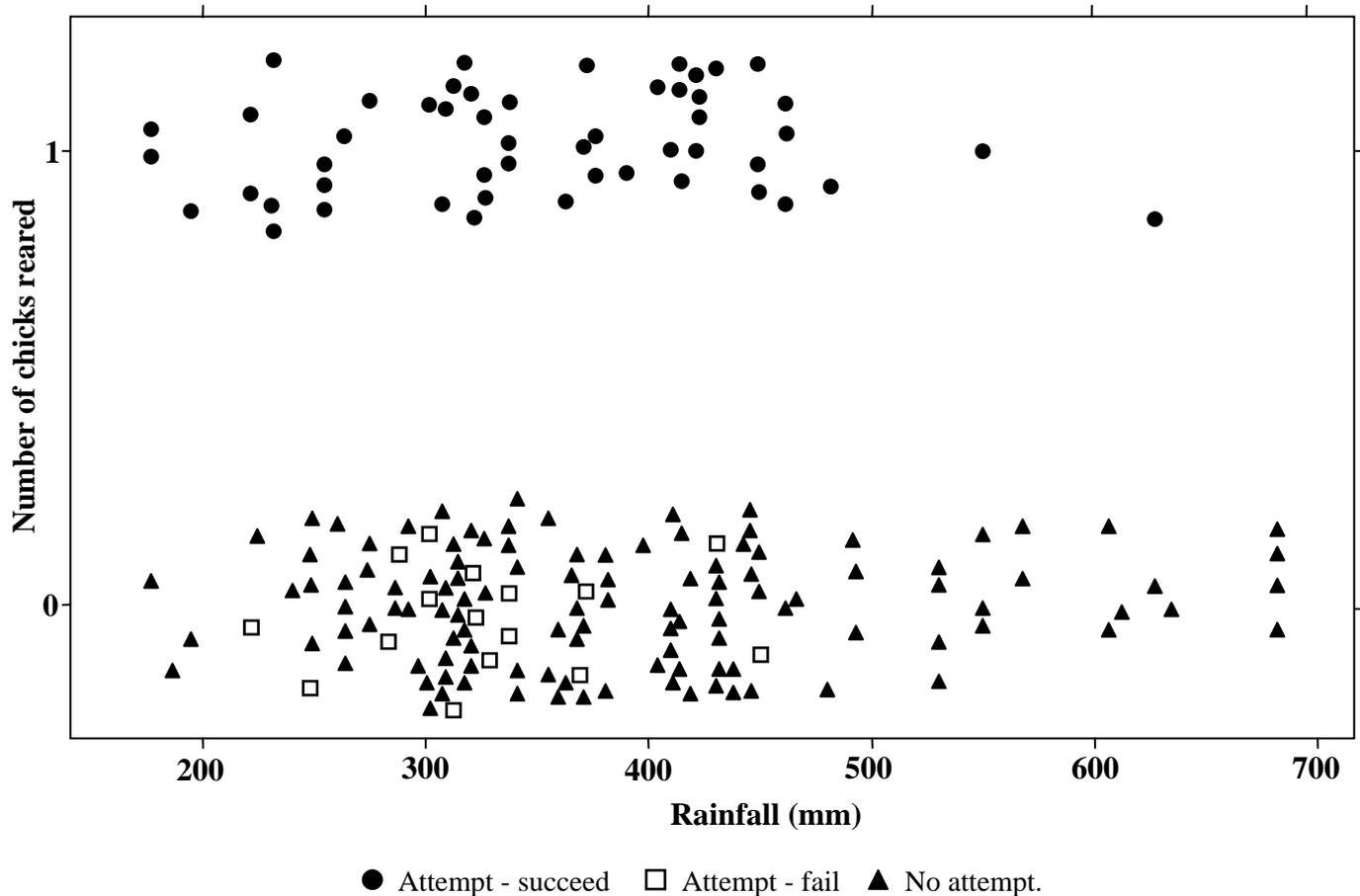

Figure 1: Rainfall over the breeding season and reproductive performance for each group and each year (184 breeding years).

The inclusion of a significant interaction term linking nest type with the proportion of open woodland within 3 km of the nest site suggests that groups that have artificial nests available to them as well as a relatively large area of open woodland close to the nest are more successful

breeders (Table 3). In support of this interaction, groups that bred in natural cavities were most successful when they also had access to extensive areas of open woodland (Table 3, Figure 2). When the surrounding proportion of open woodland was low, groups that used artificial nests had higher reproductive success than those in natural nests. The combination of an artificial nest and large open areas therefore contributed positively towards reproductive success.
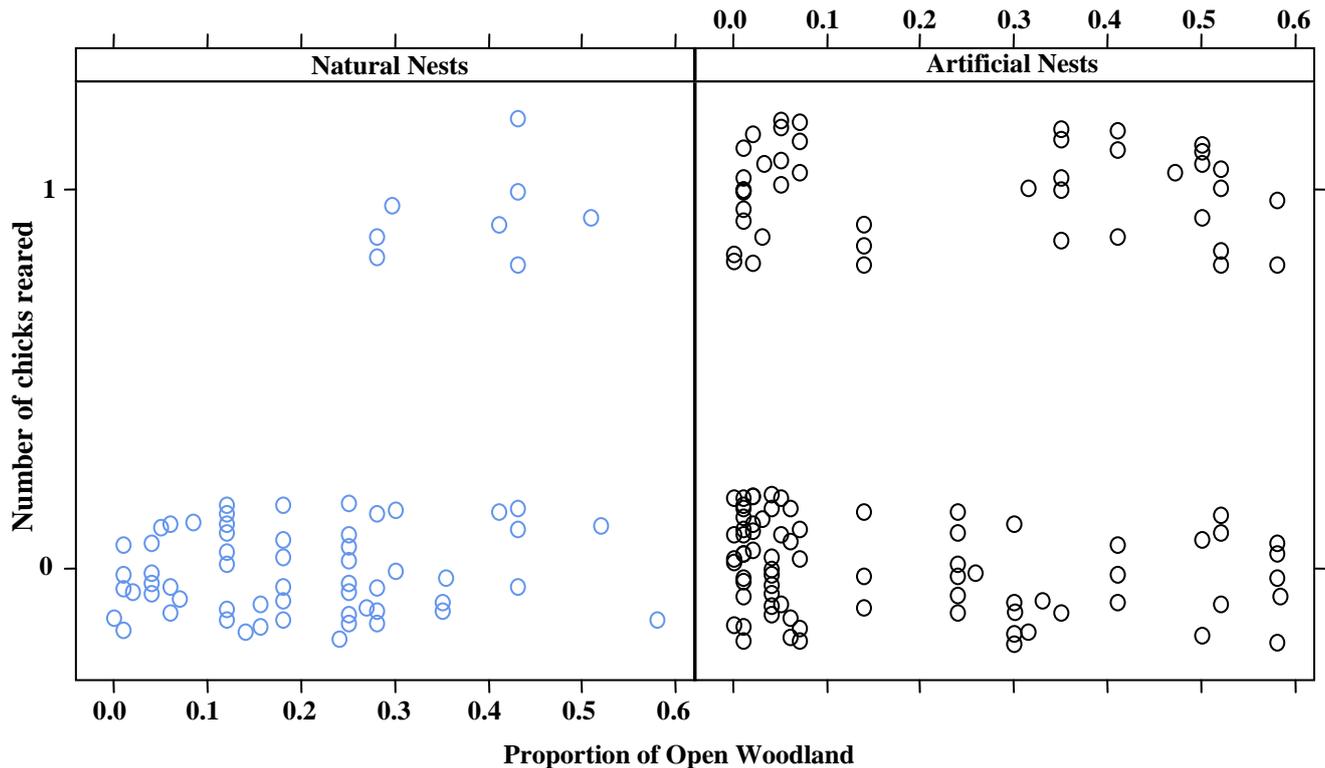

Figure 2: The proportion of open woodland within 3 km of each group's nest in relation to breeding success.

Effects of group size

Group size and reproductive success were correlated. Average group size over the study period was 3.4 ± 1.2 birds, with the largest group comprising seven individuals. Models that excluded group size as an explanatory variable had significantly higher AIC values than did models which included group size (Table 3, Models 9-12). Larger groups (> 3 birds) bred more successfully than did groups comprising only 2-3 individuals (Figure 3).
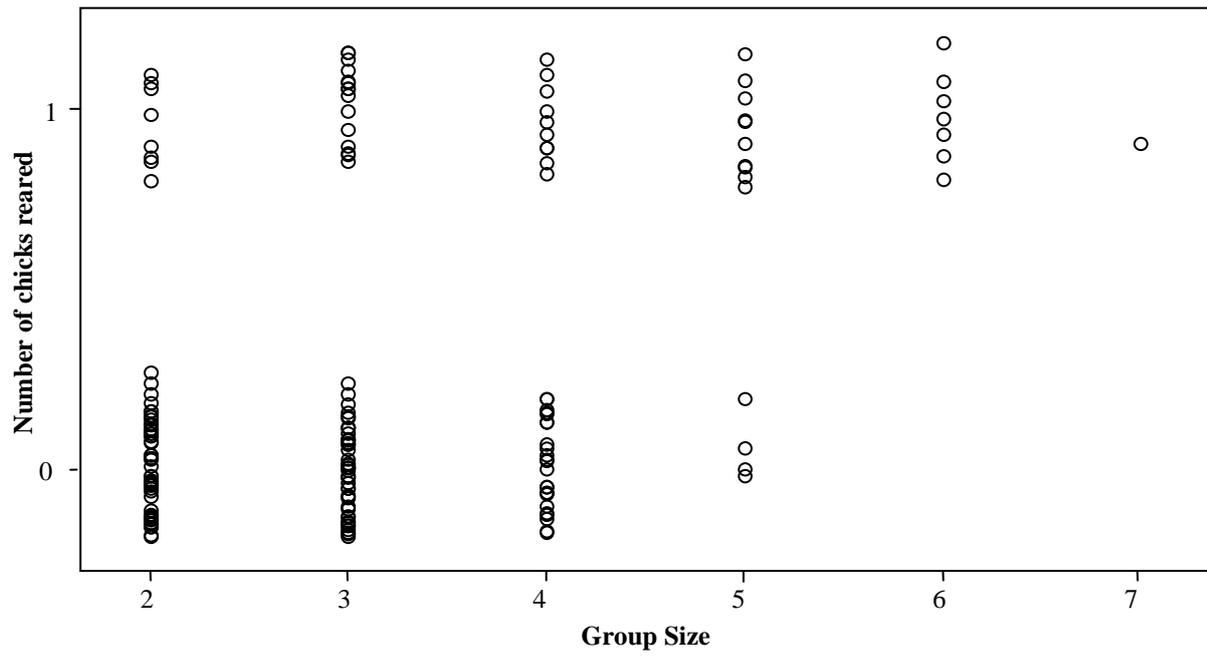
Figure 3: Breeding success in relation to group size in Southern Ground-Hornbills.

Chapter 4: Discussion

Understanding the various factors and mechanisms that influence reproductive performance and cause intra-specific variation amongst groups of cooperatively breeding species is important for understanding complex societies and is key to the population ecology of such species (Keller & Reeve, 1994; Brouwer *et al*., 2006). Over the past few decades there has been considerable concern surrounding the decline in the distribution and numbers of ground-hornbills in South Africa (Kemp, 1980, 1987; Kemp & Begg, 1996; Kemp & Webster, 2008). For the management of these birds to be effective a fundamental understanding of the factors influencing their reproductive performance is essential. Knowing which individuals succeed in breeding and what factors influence this success can provide insights into how best to manage and conserve the ground-hornbills. Statistical models of reproductive performance of Southern Ground-Hornbills identified three strong positive correlates: rainfall over the breeding season, the interaction of nest type with the amount of open woodland available in the nest vicinity, and group size.

Determinants of reproductive success

Reproductive success was determined primarily by environmental factors. The amount of rainfall over the breeding season significantly influenced the reproductive performance of ground-hornbills. In years when rainfall exceeded 500 mm reproductive success decreased dramatically. Of the 21 group-years that experienced breeding-season rainfall > 500mm, only two breeding attempts were successful. When rainfall was in the range 300-500 mm breeding success was highest, with up to twelve groups being successful in one breeding season. Reproductive success was also lower when rainfall was below 300 mm over the breeding season and, during the eight years, only 13 attempts were successful in low-rainfall years. Rainfall is one of the main determinants of food availability (Cockburn *et al*., 2008; Covas *et al*., 2008) and in ground-hornbills precipitates egg laying (Kemp & Kemp, 1991), which could explain why breeding performance was highest in years of constant, steady rainfall. High rainfall may have restricted other aspects of the ground-hornbills reproduction, for example by flooding of nests: several of the natural nests are open to the sky. Flooding of eggs and small chicks has been recorded elsewhere (Kemp & Begg, 1996). The design and position of the nest could therefore play an important role in facilitating successful breeding, with some nests being more suitable for breeding under adverse conditions such as heavy rainfall events and

excessive heat. In support of this hypothesis, both the successful breeding attempts during high rainfall years occurred in artificial nests, which are more protected from the elements than are most natural nests.

Understanding the effects of helpers on reproductive success can be complicated because it is often difficult to separate the true effects of helpers from effects of territory or parental quality (Legge, 2000a, b; Cockburn *et al.*, 2008; Covas *et al.*, 2008). High-quality parents and parents inhabiting high-quality territories may be the most successful breeders, with large group size being a consequence rather than a cause of this success (Cockburn, 1998; Magrath, 2001; Cockburn *et al.*, 2008). This conundrum is unlikely to have confounded the conclusions of this study because group identity was controlled for statistically in all models, therefore accounting for inter-group variation that may be associated with parental quality. Female quality (identity) did not confound the relationship between group size and reproductive success. Larger groups (>3 individuals) were more successful compared to groups consisting of only 2-3 individuals. This positive correlation suggests that larger groups may be more efficient at provisioning the dominant female and her chick during the breeding season (i.e. it is a genuine social effect of group size). Among birds, the effects of helpers are usually related to the extra food that they bring to the nest (Legge, 2000a, b; Canestrari *et al.*, 2008; Covas *et al.*, 2008). Ground-hornbills are large, carnivorous birds that require large amounts of prey, especially when feeding a chick. Larger groups with more helpers would therefore increase the combined foraging rate and decrease the individual workload of the group. Load lightening may also contribute to improved survival of the dominant pair, although there was no evidence of differential mortality rates between dominant birds in large groups and those in small groups.

Since the artificial nest boxes were first placed in the APNR in 2002 they have facilitated successful breeding. Only five groups nest in natural nests and of these only two groups have been successful at rearing chicks. The seven most successful groups that have contributed 60% of the reproductive output all breed in artificial nests. In 2001, before the erection of artificial nests, only three of these seven groups even attempted to breed (in natural nests), with only one group being successful. Since 2002 all three groups that attempted to breed in 2001 have moved from natural nests and now breed successfully in artificial nests. This suggests that the artificial nests are favoured by the ground-hornbills and are clearly more conducive to successful breeding. There are various possible explanations as to why the ground-hornbills prefer the artificial nests to natural nests: 1) artificial nests are better protected from both rain

and direct sunshine, reducing the risks of nest flooding or overheating; 2) because of their positioning and construction, they are less accessible to arboreal predators (one natural nest, when not occupied by ground-hornbills, is occasionally used as a roost site by a Leopard *Panthera pardus*); and 3) they are more spacious for the developing chick. Kemp & Begg (1996) found that nest attractiveness was correlated with features of the nest (nest height and cavity depth) and suggested that the structural arrangement of the entrance or gradient and texture of the inner walls as well as the topography of the nest floor may all influence breeding success.

The interaction of nest type with the proportion of open woodland in the nest vicinity had a positive influence on reproductive performance. Groups nesting in natural cavities are most successful when there are extensive areas of open woodland nearby. The amount of open woodland also had a positive influence on groups nesting in artificial nest boxes, but the effect was not as strong. This suggests that having an artificial nest is the more important of the two variables but if groups are nesting in natural cavities then the amount of nearby open woodland is extremely important for successful reproduction. Therefore the most successful combination involves both an artificial nest and extensive open woodland surrounding the nest site. The reason for the positive effect of open woodland is probably food-related. Ground-hornbill prey items such as snakes, lizards, small mammals and insects are presumably much easier to find and catch in open areas than in dense, shrubby habitats where the mobility of the birds and detectability of prey would both be constrained to some degree by habitat architecture. Proximity of prime foraging habitat to the nest would therefore reduce travel costs during the breeding season when the birds are effectively central place foragers. In a study of ground-hornbill nest sites in the Kruger National Park, Kemp & Begg (1996) found that most nests were located in trees in open areas with bare ground, or with grass of short to medium height and that the nest was placed among only a few other prominent, large or dead trees. In combination, therefore, these results strongly suggest that the sitting of artificial nests within territories could be optimised by placing them close to areas of open woodland.

Implications for conservation and management

The fact that the availability and position of artificial nest sites and the amount of open woodland surrounding the nest site both contribute positively to breeding performance identify possible management options for increasing the reproductive output of ground-hornbill

populations in South Africa. Social factors such as group size and helper effects cannot be managed, but manipulating environmental factors such as nest boxes and the amount of open woodland are conservation options. Areas of open woodland need to be identified within the territories and the nest boxes deployed within or close to these areas. In situations where groups breed in natural nests and erection of artificial nests is not an option, then bush clearance (a management tool used for other reasons in the APNR) becomes a potential management tool to increase the amount of open woodland surrounding the nests.

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Appendix 1

Output of GLMM model selection statistics investigating causes of variation in breeding attempts in Southern Ground-Hornbills. Breeding attempts (0 or 1) were set as the response term and group identity as a random term. Deviance = -2 log-likelihood; K = total number of parameters (explanatory terms + random term + residual variance); AIC = Akaike's Information Criterion; and ΔAIC = difference between the AIC value for that model and the best model. Analysis is based on 23 groups monitored over an eight-year period. (x) indicates an interaction term.

No.	Model	K	AIC	ΔAIC	Deviance
1	Nest type x open woodland + group size + rain	7	184.4	0	170.4
2	Nest type + group size + rain + open woodland	6	187.7	3.3	175.7
3	Nest type x rain + group size + open woodland	7	188.3	3.9	174.3
4	Nest type + group size + rain	5	190.1	5.7	180.1
5	Group size + rain + open woodland	5	192.9	8.5	182.9
6	Nest type x open woodland + group size	6	196	11.6	184
7	Nest type + group size + woodland	5	197.8	13.4	187.8
8	Nest type + group size	4	199.5	15.1	191.5
9	Nest type x open woodland + rain	6	204.8	20.4	192.8
10	Nest type x rain + open woodland	6	206.6	22.2	194.6
11	Nest type x woodland	5	213.5	29.1	203.5
12	Rain + open woodland	4	216.7	32.3	208.7

Significant explanatory terms (minimal model)	Effect	s.e.
Intercept	-4.23	1.399
Group size	0.947	0.235
Rain	-0.007	0.002
Nest type x Open woodland		
- Artificial nest	1.985	3.394
- Natural nest	9.421	3.394