INDIVIDUAL CONTRIBUTIONS TO GROUP BEHAVIOUR IN THE COOPERATIVELY BREEDING SOUTHERN GROUND-HORNBILL *BUCORVUS LEADBEATERI*

Kyle-Mark Middleton

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Supervised by Dr Rita Covas, Dr Fanny Rybak, and Prof. Claire Spottiswoode

Declaration

This thesis reports original research that I conducted under the auspices of the FitzPatrick Institute of African Ornithology, 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.

Signed by candidate

Kyle-Mark Middleton

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Permits

Data were collected under the animal ethics permit 2020/2019/V5/RC/A1, University of Cape Town. I ringed southern ground-hornbills under a single-species ringing licence issued by SAFRING (Ringer number: 18249), Limpopo Economic Development, Environment and Tourism (LEDET), and Mpumalanga Tourism and Parks Agency (MTPA). All of this work was conducted within the Associated Private Nature Reserves (APNR) under the APNR Ground-Hornbill Project research agreement. Additionally, yearly research permits were acquired from the provincial entities LEDET and MTPA.

Fieldwork insight 1. Handling 75-day old chicks like this to weigh, measure, and ring them was always a highlight of the field season and provided the perfect opportunity to closely observe their incredible biology.

Abstract

Cooperative breeding, in which individuals other than breeders contribute to raising offspring, has been the focus of much scientific research over the past decades. Why do some individuals help to raise offspring that are not their own? In birds, cooperative breeding is found mainly in harsh regions with greater environmental variability, such that individuals might do better to help relatives than attempt to breed themselves. However, in some bird families cooperative breeding is instead associated with stable and benign environments, suggesting that species may form cooperative groups for different reasons. Most studies have focused on the benefits that additional group members bring to offspring, by increasing provisioning rates, nestling survival, and overall reproductive output. These benefits have been suggested to mitigate the effects of harsh climatic conditions and to be particularly important in the face of anthropogenic climate change, during which increases in temperature extremes and interannual rainfall variability are expected to push species' tolerance to the limit. However, other advantages of group living have been less often considered; for example, collective territory defence is common in cooperative breeders and ensures exclusive access to crucial resources such as food, nesting sites, and mates. A better understanding of the diverse factors favouring cooperative behaviour can offer insights as to why, and in what environmental conditions, social behaviour has evolved, and whether and how it might help animal populations to cope with environmental change.

Therefore, the aims of this thesis were to investigate how individuals within cooperative groups contribute to reproduction and territory defence in a cooperative breeder with an atypical life-history, the southern ground-hornbill *Bucorvus leadbeateri*. The large body size and exceptionally long lifespan of ground-hornbills leads to a "slow" life-history strategy, providing a striking contrast to most well-studied avian cooperative breeders, which tend to be small, relatively short-lived passerines. Furthermore, while the hornbill family is usually associated with mesic, stable environments, ground-hornbills inhabit semi-arid, fluctuating environments. Studying them thus may shed light on why cooperative breeding might be favoured in both harsh, fluctuating environments, as well as benign, stable environments. I use a combination of my own data collected over five years (2017–2022) and long-term data collected from the APNR Southern Ground-Hornbill Project (2000–2022) to test the

effects of environmental and social factors (climatic conditions, group size and composition, and age structure of group members) on reproductive and territorial cooperative behaviour.

The first two data chapters focus on how group members influence provisioning efforts and reproductive outcomes, and whether group members of different ages can mitigate the effects of harsh climatic conditions. My results showed that high temperatures and low rainfall had generally negative effects on reproduction, and that cooperative breeding provided some reproductive benefits, but did not act as a buffer to provisioning rates or reproductive outputs. Specifically, we showed that adult males had the highest provisioning rates and provisioned larger items, but the additive care they provided did not buffer the negative effects of high temperatures on group feeding rates. Additionally, we showed that hot and dry conditions were associated with decreased breeding probability, later laying dates, and decreased nestling body mass, and that group composition did not significantly mitigate these negative effects. Instead, our results suggested that group or territory quality may be a more important factor in determining reproductive success.

The second two data chapters focus on territory defence. Specifically, I asked how different group members contributed to the species’ characteristic deep booming chorus vocalisations used to advertise territories, and how responses to territorial intrusions were mediated by caller identity and group size. I showed that calls were significantly different between the sexes, and that females produced sequences of calls that formed unique melodies that could be automatically assigned to the correct individual with a 94% success rate. Melodies are an effective way of signalling individual identity in long distance communication, as this acoustic information travels well when composed of low-pitched sounds. Therefore, since each group generally contains only one adult female, groups can be identified by the female’s signature. Next, I showed that there were no clear effects of intruder group identity on the responses of territory holders, but found that group size was positively associated with aggressive responses, indicating that group living may provide resource defence benefits.

Overall, the findings in this thesis indicated that group living provided benefits for territory defence and to a lesser extent, reproduction, and that individual contributions of different group members varied between different cooperative behaviours. Despite ground-hornbills inhabiting semi-

arid regions with harsh climatic conditions, the presence of additional group members of different ages during reproduction were insufficient to mitigate the negative effects of high temperature and low rainfall. However, the likely benefits provided by additional helpers to territory defence suggest that the ecology, longevity, and slow-development of ground-hornbills may render the presence of additional helpers less critical for reproduction, but more important for resource defence. Further research into other group behaviours such as predator vigilance, foraging and hunting, and energy conservation would provide additional insights into other benefits that cooperative breeding might provide. This study implies that a species' life-history strategy may be an important mechanism determining the benefits individuals receive from breeding cooperatively, and so help to explain the ecological correlates and diversity of forms taken by cooperative breeding, including the remarkable biology of the southern ground-hornbill.

Keywords: cooperative breeding, reproduction, offspring provisioning, climate, temperature, rainfall, territory defence, chorus vocalisations, signatures of identity, life-history strategy, southern ground-hornbill

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Chapter 1

General introduction

A typical sighting of a southern ground-hornbill group. *As seen here, their large size, characteristic bills, black plumage, and red facial skin make them easily identifiable in their diverse habitat. Photo: Cassie Carstens*

Introduction

Sociality and cooperation

Darwin's theory of evolution by natural selection is based on the existence of genetic variation, expressed as phenotypic traits, with some variants, relative to others, increasing the chances of an individual to survive and reproduce under given external conditions with certain constraints (Darwin, 1859). Consequently, individuals possessing these variants are more likely to pass them on to the next generation. Over time, this can result in a larger proportion of individuals within a population possessing those heritable traits. At first glance, one could think that natural selection should always favour competition among members of the same species, as selfish behaviours should provide survival and reproductive benefits favoured by selection. Yet, sociality and cooperation, in which individuals form conspecific groups and contribute to the benefit of other individuals, occur in a wide variety of species (Alexander, 1974; West, Griffin & Gardner, 2007a; van Veelen, García & Avilés, 2010). Given the benefits of selfishness, how do cooperative traits emerge and persist?

One of the first fundamental insights to explain the evolution of social behaviour was provided by Hamilton's theory of inclusive fitness (Hamilton, 1964). It offered a theoretical framework to explain the benefits individuals receive from cooperative social behaviour, by partitioning them into direct and indirect fitness components (Pizzari & Gardner, 2012). Direct fitness benefits occur when social behaviour allows individuals to increase their own reproductive success. Indirect fitness benefits occur when social behaviour allows individuals to help close relatives to reproduce successfully, allowing them to pass on copies of their genes indirectly to the next generation, otherwise known as kin selection (Hamilton, 1964; West, Griffin & Gardner, 2007b; Pizzari & Gardner, 2012; Bourke, 2014). This was formalised in a simple formula, known as Hamilton's Rule, where in order for altruistic social behaviour to be evolutionarily favoured (i.e. where individuals provide costly help for the benefit of others; West, Griffin & Gardner, 2007a), the sum of the indirect fitness benefits (through kin selection; rb) and direct fitness costs (c) should be greater than zero, where r is the relatedness between the recipient and actor, b is the direct fitness benefit to the recipient, and c is the direct fitness cost for the actor (Hamilton, 1964; West, Griffin & Gardner, 2007b; Bourke, 2014). Empirical evidence has provided support for

this theory by showing that related individuals form the basis of many social groups and that relatedness is often associated with increased investment in cooperation (Hatchwell, 2009; Browning et al., 2012; Riehl, 2017; Robertson et al., 2018). However, relatedness does not always provide an explanation for social behaviour, as many social groups also contain unrelated individuals, suggesting that direct benefits may also play an important role (Magrath & Whittingham, 1997; Riehl, 2013; Koenig, 2017).

Cooperative breeding

Cooperative breeding is a particular form of sociality in which certain individuals (generally known as 'helpers') forego their own reproduction to help others in the caring and rearing of offspring (Cockburn, 1998). These helpers (who are often offspring from the breeding pair; Riehl, 2013) also engage in various other group tasks, such as constructing or maintaining breeding sites, detecting and deterring predators, and contributing to territorial defence (Emlen, 1982; Brockmann, 1997; Heinsohn, 1997; Cockburn, 1998; Cant, Otali & Mwanguhya, 2002; Cant, 2012; Golabek, Ridley & Radford, 2012a; Jungwirth et al., 2015; Groenewoud et al., 2016; Koenig, Dickinson & Emlen, 2016; Zöttl et al., 2016; Josi, Taborsky & Frommen, 2020).

Cooperative breeding occurs in approximately 9% of birds (and more commonly in passerines than in non-passerines; Cockburn, 2006; Jetz & Rubenstein, 2011), 1% of mammals (primarily in rodents, carnivores, and primates; Lukas & Clutton-Brock, 2017), and less than 0.1% of fish (Taborsky, Frommen & Riehl, 2016), primitively social insects, and spiders (Brockmann, 1997; Crespi & Choe, 1997; Cant, 2012). In the general pursuit to understand the evolution of cooperative breeding, much attention has been given to its ecological correlates (Cockburn & Russell, 2011). Comparative analyses in birds and mammals showed that cooperatively breeding species occur predominantly in regions with lower rainfall and greater environmental variability (Figure 1.1; Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011). Since climatic conditions influence the reproductive decisions and outputs of species (Drent & Daan, 1980; Cruz-McDonnell & Wolf, 2016; Legagneux et al., 2016; Jean-Gagnon et al., 2018; Wise & Lensing, 2019; Bourne, Ridley, Spottiswoode, et al., 2021), this distributional observation led to the suggestion that cooperative breeding might facilitate successful reproduction

when environmental conditions are difficult (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011; Lukas & Clutton-Brock, 2017).

However, in some taxa, stable and benign environments have also been shown to favour this social system (Ford et al., 1988; Avilés et al., 2007; Gonzalez, Sheldon & Tobias, 2013). Specifically, comparative analyses focusing on the hornbill family (Bucerotidae) showed that cooperative breeding was associated with inter- and intra-annual climatic stability (Gonzalez, Sheldon & Tobias, 2013). These authors suggested that the family's life-history strategy (typically involving large body size, high survival, low fecundity, and stable food sources) made the presence of helpers less relevant for reproduction, although still potentially important for other group tasks such as territory defence (Gonzalez, Sheldon & Tobias, 2013). In addition, across most bird species, climatic stability was also found to be associated with the evolution of family formation from solitary living (Griesser, Drobniak, et al., 2017; Koenig, 2017). This might be specifically expected because, under these conditions, environments are likely to be productive and lead to habitat saturation where offspring delay dispersal to form family groups (especially in long-lived species with high survival), which in turn facilitates the evolution of helping at the nest (Emlen, 1982; Cockburn & Russell, 2011; Rubenstein, 2011; Gonzalez, Sheldon & Tobias, 2013).

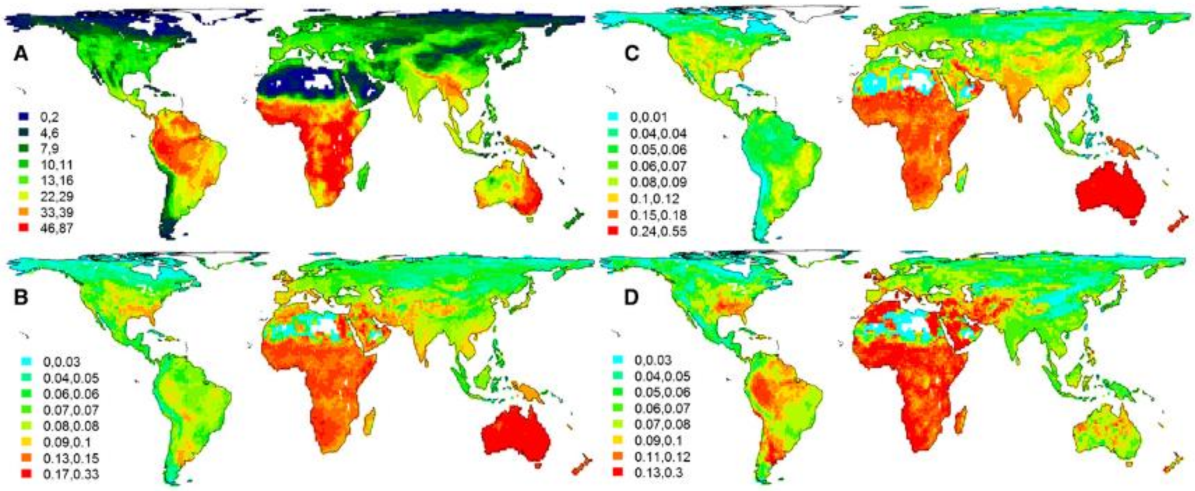


Figure 1.1. Biogeographic distribution of cooperatively breeding birds. A) Total richness of 9310 nonmarine cooperative breeders, B) proportional richness of all birds, C) proportional richness of passerines, and D) proportional richness of non-passerines. The proportions are represented by colour categories with red representing the highest proportions, and light blue representing the lowest proportions. Source: Jetz & Rubenstein, 2011.

By remaining in their natal groups, and subsequently helping relatives, offspring can gain indirect fitness benefits through kin selection (Stacey & Ligon, 1991), while avoiding the costs associated with dispersing and floating on their own when resources are scarce (Emlen, 1982; Ridley, Raihani & Nelson-Flower, 2008; Cockburn & Russell, 2011; Rubenstein, 2011; Groenewoud et al., 2016). They may also gain direct fitness benefits by increasing future breeding opportunities and enhancing survival through increased access to high quality territories or mates, and practicing parenting skills (Stacey & Ligon, 1991; Komdeur, 1996; Cockburn, 1998; Hinde, 2008; Ridley, Nelson-Flower & Thompson, 2013; Kingma et al., 2014; Downing, Griffin & Cornwallis, 2018; Nelson-Flower et al., 2018). Direct benefits such as these are likely to be more important than previously thought, as they can help explain why unrelated immigrant individuals sometimes also occur in cooperative groups (Koenig & Dickinson, 2004; Riehl, 2013; Taborsky, Frommen & Riehl, 2016; Kingma, 2017). Moreover, as stated by the group augmentation hypothesis, helpers (related and unrelated) and breeders alike may benefit by increasing their group size if it improves the effectiveness and efficiency of behaviours such as predator vigilance, territory defence, foraging and hunting, energy conservation, and offspring provisioning (Kokko, Johnstone & Wright, 2002; Gusset & Macdonald, 2010; van Dijk et al., 2013; Kingma et al., 2014; Shen et al., 2017; Ostreiher & Heifetz, 2020; Humphries et al., 2021; Sheppard et al., 2021).

Recent studies attempting to explain the evolution of cooperative breeding have begun to pay more attention towards understanding these direct benefits of group living. It has been suggested that the benefits provided by different group behaviours (such as offspring provisioning and territory defence) vary in importance depending on the environmental conditions that a species inhabits (Shen et al., 2017; Nelson-Flower et al., 2018; Lin (林宇恒) et al., 2019; Liu (劉彥廷) et al., 2020). Previous studies have focussed mostly on behaviours directed towards offspring provisioning, expecting that additional group members increase offspring and group member survival, and overall reproductive success (Browning et al., 2012; Zöttl, Fischer & Taborsky, 2013; Tanaka, Kohda & Frommen, 2018; van Boheemen et al., 2019; Josi, Taborsky & Frommen, 2020). Group members maintaining their provisioning efforts despite additional help leads to ‘additive’ care that can increase offspring condition

and survival, and therefore result in higher reproductive success during that breeding event (Hatchwell, 1999; Meade et al., 2010; Johnstone, 2011; Tanaka, Kohda & Frommen, 2018; van Boheemen et al., 2019). Alternatively, group members may reduce their provisioning effort when there is additional help in order to 'load-lighten' and maintain their own body condition, which can improve survival and lifetime reproductive success (Hatchwell, 1999; Kingma et al., 2010; Paquet et al., 2015). However, these two strategies are not mutually exclusive, and research has shown that additional helpers may reduce the provisioning burden of carers, while simultaneously increasing the total number of provisions to offspring (Covas, Du Plessis & Doutrelant, 2008; Kingma et al., 2010; van Boheemen et al., 2019). Group members can also have flexible strategies in relation to environmental conditions and work harder when necessary, such that helpers can reduce nestling starvation and improve reproductive output during adverse conditions (Covas, Du Plessis & Doutrelant, 2008; Rubenstein, 2011; Groenewoud & Clutton-Brock, 2021). For example, high temperatures and low rainfall can reduce foraging efficiency through its influence on body condition, which can subsequently reduce provisioning efforts (Chesson et al., 2004; Bolger, Patten & Bostock, 2005; du Plessis et al., 2012; Iknayan & Beissinger, 2018; van de Ven et al., 2020; Barras et al., 2021; Cunningham, Gardner & Martin, 2021). It has been suggested that, in these circumstances, additional helpers providing additive care can mitigate these negative effects and ensure that adequate provisioning rates can be maintained (Rubenstein & Lovette, 2007; Covas, Du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011).

However, the empirical evidence that cooperation helps to buffer against the effects of adverse climatic conditions is conflicting (Covas, Du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Bourne et al., 2020a; D'Amelio et al., 2022) and inconsistent across taxa (Gonzalez, Sheldon & Tobias, 2013; Lin (林宇恆) et al., 2019). Gonzalez et al. (2013) suggested that this could be linked to the species' life-history strategy. The authors mentioned that in long-lived species inhabiting stable environments, long territory occupancy should lead to habitat saturation, and this may be the primary mechanism linking cooperative breeding to climate. In addition, individuals of long-lived species are expected to invest less in current breeding activities and more into self-maintenance, in order to

maximise survival and lifetime breeding success through maximising the number of breeding events over their lifetime (Clutton-Brock, 1988; Covas & Griesser, 2007). This can lead to lower reproductive investment and/or to intermittent breeding in which individuals skip breeding opportunities, particularly when conditions are adverse (Hamel et al., 2010; Shaw & Levin, 2013; Griesser, Wagner, et al., 2017).

The trade-off between survival and reproduction can also apply to helpers, which have been shown to balance their investment decisions according to the cost of helping (Mendonça et al., 2020; Covas et al., 2022). This means that during harsh environmental conditions when the costs of helping are high, individuals are more likely to reduce than increase their investment. Furthermore, in slow developing species, groups may contain members of varying ages and experience, which may influence their contributions to provisioning, and so to reproductive output (Covas & Griesser, 2007; Browning et al., 2012). For example, younger individuals may lack mature foraging skills and still rely on older, more experienced individuals for food and protection (Rowley, 1976; Woxvold, 2004; Woxvold, Mulder & Magrath, 2006; Gunst, Boinski & Fragaszy, 2008a; Maynard et al., 2021). Therefore, the costs and benefits associated with the age structure of group members might lead to different investment strategies, and so modulate the effects of group size on reproductive behaviours. However, so far this has received relatively little research attention.

While reproductive benefits are expected to play a role in the evolution of cooperative breeding, other group behaviours can be equally important, but are less often considered (Gonzalez, Sheldon & Tobias, 2013; Josi, Taborsky & Frommen, 2020). One such behaviour common in cooperatively breeding species is territory defence, whereby groups defend a spatial area against conspecific groups to ensure access to limited and crucial resources such as food, breeding sites, and mates (Brown & Orians, 1970; Cockburn, 1998; Cant, Otali & Mwanguhya, 2002; Golabek, Ridley & Radford, 2012a; Christensen & Radford, 2018).

In many species, group territories are not only physically defended from conspecific groups, but are also advertised through group behaviours involving olfactory, visual, or acoustic signals (Palphramand & White, 2007; Christensen & Radford, 2018), depending on the environmental constraints on the communication system and the purpose of the signals exchanged (Boncoraglio &

Saino, 2007; Laiolo, 2010; Keen, Meliza & Rubenstein, 2013; Witzany, 2014; Tanimoto et al., 2017; Christensen & Radford, 2018; Wu et al., 2021). For example, in dense environments where visual channels are limited, acoustic communication is often the primary sensory channel used, particularly when long-distance communication is required (Boncoraglio & Saino, 2007; Benti, Curé & Dufour, 2019). Territory advertisement can serve to convey group identity and facilitate inter-group relationships, which can be an important factor in determining the responses of individuals to territorial intrusions (Radford, 2005; Mares, Young & Clutton-Brock, 2012; Christensen & Radford, 2018). As demonstrated in numerous territorial solitary species, in cooperatively breeding species the responses of territory holding groups towards neighbour groups (groups occupying adjacent territories who are likely to be familiar to the territory holders) and stranger groups (groups occupying territories further adrift who are likely to be unfamiliar to the territory holders), can differ depending on the level of threat they pose (Temeles, 1994; Radford, 2005; Christensen & Radford, 2018). However, only a handful of studies have shown this in cooperative breeders, and further research is needed to understand how group identity is conveyed, as well as the benefits it provides.

The collective actions of individuals during physical territory defence have also been shown in many species to provide a numerical advantage needed to deter intruders and win territorial conflicts (Cant, Otali & Mwanguhya, 2002; Radford, 2003; Seddon & Tobias, 2003; Mosser & Packer, 2009; Cassidy et al., 2015). Additionally, larger groups can be more likely than smaller groups to initiate territorial encounters with rivals, suggesting that groups assess whether they have a numerical advantage over intruders (Seddon & Tobias, 2003; Benson-Amram et al., 2011; Cassidy et al., 2015). Grouping benefits also help to explain the occurrence of kidnapping youngsters, which has been reported from at least three cooperatively breeding species, the southern ground-hornbill *Bucorvus leadbeateri*, the white-winged choughs *Corcorax melanorhamphos*, and the southern pied babbler *Turdoides bicolor* (Heinsohn, 1991; Kemp & Ezzey, 2020; Ridley et al., 2022). The existence of kidnapping suggests that groups benefit from recruiting new members to enlarge their own groups, perhaps to contribute towards cooperative group tasks or the mutualistic benefits of group living. The kidnapping risks that youngsters face in joining a non-natal group, as well as their smaller body sizes

and inexperience, suggests that age may modulate the effect of group size on territorial responses. Similarly, this should also influence reproductive investment, yet both have received limited attention. Taken together, these lines of evidence suggest that territory defence is an important behaviour to consider when investigating the benefits associated with group formation.

Aims and objectives

The broad aims of this thesis are to understand the grouping benefits that cooperative breeding provides not only to reproductive behaviours, but also to the less-considered group task of territory defence, and how investments in both are influenced by environmental factors. In achieving this, I hope to contribute to our understanding of how life-history strategy might influence individual investment decisions into vital group behaviours, and how this can affect the outcomes of these behaviours.

To do this, I investigate how individuals in groups of the world's largest and longest-lived cooperatively-breeding bird, the southern ground-hornbill (*Bucorvus leadbeateri*), contribute to reproduction and territory defence, and how group living improves the efficiency of these group behaviours. I used a combination of data that I collected over five years (2017–2022) and long-term data (2000–2022), and divided this thesis into two parts, each focussing on one form of group behaviour and investigating the different components that individuals contribute towards. Within each part, stand-alone chapters are presented to facilitate publication, so there is repetition of information within the introductions, methods, and discussions.

Part I: Reproduction

This first part consists of two data chapters (Chapters 2 & 3) that investigate how climatic factors (temperature and rainfall), social factors (group size and composition) and life-history factors (group member age) influence provisioning efforts (provisioning rates, food size, and food type) and reproductive outcomes (probability of breeding, reproductive timing, fledging success, and nestling condition), and whether group members of different ages can mitigate the effects of harsh climatic conditions.

Part II: Territory defence

The second part consists of two data chapters (Chapters 4 & 5) that investigate territorial acoustic signalling and group territory defence. The first of these chapters investigates the remarkable chorus vocalisations used to advertise territories, which have never been studied in detail before. Specifically, I investigated whether calls comprising these choruses contained consistent and repeatable sexual differences in their acoustic parameters, and whether the choruses conveyed individual and thus group identity, which should allow recognition between groups.

The second of these chapters investigates how the chorus calls are involved in group territorial interrelations, by testing how territorial responses are affected by social factors (group size), life-history factors (group composition), and the identity of an intruding group. I did so by testing the responses of groups to simulated territorial intrusions, through playback experiments simulating the chorus vocalisations of neighbours and strangers.

Study species

Southern ground-hornbills

Southern ground-hornbills (*Burcorvus leadbeateri*) are one of only two ground-hornbill species, with the other being the largely allopatric Abyssinian ground-hornbill *Bucorvus abyssinicus* (Figure 1.2). The ground-hornbills are most often considered to be a highly divergent sister clade within the hornbill family (Bucerotidae), although they are also commonly placed in a separate family (Bucorvidae; Gonzalez et al., 2013). Ground-hornbills are endemic to Africa and, unlike other hornbills, do not seal themselves in nests during breeding, and have other interesting biological differences such as a limb structure that allows them to walk efficiently rather than hop (Kemp & Kemp, 1980; Gonzalez et al., 2013; Kemp, 2017).

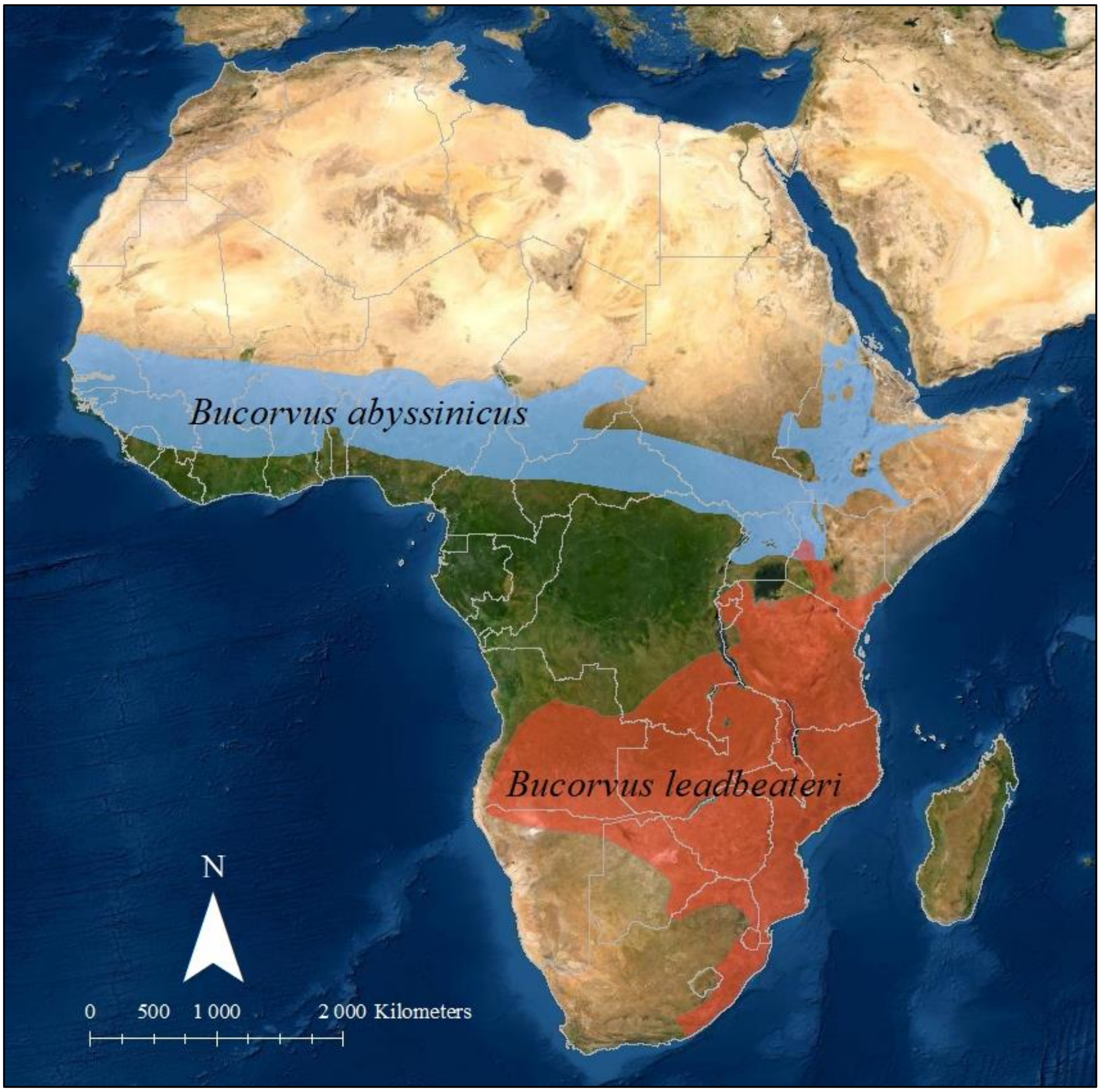


Figure 1.2. Distribution map of southern ground-hornbills Bucorvus leadbeateri *(red) and Abyssinian ground-hornbills* Bucorvus abyssinicus *(blue).*

Southern ground-hornbills are the largest and longest-lived cooperatively breeding birds (and the largest hornbills) in the world, with a height of approximately 1 m and a mass of 3.3–4.4 kg. They occur across a wide landscape of semi-arid savanna habitats (unlike most other cooperatively breeding hornbills) with woody cover percentages of up to 60%, ranging from Kenya to South Africa (Figure 1.2; Taylor & Kemp, 2015; Loftie-Eaton, 2017). They live for up to 60 years in the wild and develop slowly, reaching adulthood from around 6–8 years old (Kemp & Kemp, 1980; Kemp, 2017). Groups consist of 2–12 individuals and comprise a breeding pair and offspring (mostly males) from previous broods, and sometimes unrelated immigrant males (Carstens et al., 2019a). As such, most group

members likely receive benefits associated with helping or being helped by relatives (e.g. nepotistic benefits and kin-selected benefits), either in the short- or long-term. Additional adult or sub-adult females may also be present, but this is rare (as females generally disperse 2–24 months after fledging; Carstens et al., 2019a), and they contribute little towards group activities (Kemp & Kemp, 1980). Individuals are usually classified into three age categories according to the development of their plumage, bare facial skin, and beak colouration (Kemp & Kemp, 1980; Carstens, 2017): 1) juveniles from 0–2 years old, 2) sub-adults from 2–8 years old and, 3) adults from 8 years up (Figure 1.3). These individuals of different ages contribute to different degrees to group behaviours such as territory defence and provisioning (Kemp & Kemp, 1980; Kemp, 1988). The sex of individuals can be determined only from the sub-adult stage onwards, when facial colouration begins to develop. Males are slightly bigger and have throats that are entirely red, whereas the females have a patch of violet blue just below the bill (Figure 1.3). They are generalist feeders and spend an average of 70% of their day walking and foraging for prey (Kemp & Kemp, 1980), where they consume anything which they can overpower with their disproportionately large beaks, including arthropods, amphibians, reptiles, birds, and small mammals (Combrink, 2016). Common vertebrate prey species in my study site include flap-necked chameleons (*Chamaeleo dilepis*), scrub hares (*Lepus saxatilis*), and puff-adders (*Bitis arietans*). Predation on southern ground-hornbills has been recorded to occur from several felid species, genets (*Genetta* spp.), chacma baboons (*Papio ursinus*), and large raptorial birds such as martial eagles (*Polemaetus bellicosus*) and crowned eagles (*Stephanoaetus coronatus*) (Kemp, 2017). Most predation is on young individuals (Kemp, 2017).

Figure 1.3. Southern ground-hornbill age and sex differences. Top left: juvenile (0–2 years old) with pale throat skin, blue eyes, and dark brown feathers. Top right: sub-adult (2–5 years old) with blotchy red throat skin and white on bill. Bottom left: adult female (8+ years old) with blue patch under bill, black feathers, and little to no white on bill. Bottom right: adult male with solid red throat skin, black feathers, and little to no white on bill. Photos were taken by Kate and Cassie Carstens.

Nests are found several meters above ground, mostly within large tree cavities but sometimes in cliff faces or earth banks. Hence the species requires a landscape that includes large trees (Kemp, 1988; Wilson & Hockey, 2013; Loftie-Eaton, 2017). Breeding occurs during the summer rainfall season (usually from September to March) and a breeding cycle usually lasts up to 130 days from egg laying to fledging (Kemp & Kemp, 1980; Wilson & Hockey, 2013). Nests are reused from season to season and are lined with leaves and grass by the members of the group prior to egg laying, and throughout the breeding period. Clutches comprise 1–2 eggs (rarely 3) and are laid asynchronously about 5 days apart. Hatching is also asynchronous and the second-hatched chicks are consequently smaller and always

succumb to starvation (except when the first-laid eggs fail to hatch), resulting in a lone survivor (Kemp, 1988, 2017). Incubation of eggs occurs solely by the female and lasts for ca. 40 days before the eggs hatch, and the surviving nestlings fledge after 80–90 days (Carstens, 2017; Kemp, 2017). During incubation, and during the first few weeks after hatching when the female is brooding, the rest of the group provides food and nest lining to the female. During the nestling growth period, the whole group (including the female) provides for the surviving nestling (Kemp, 1988). Once fledged, offspring delay dispersal, although the nestling age at which this dispersal occurs is sex dependent. Males remain in groups for up to 11 years (KMM, unpublished data), while females disperse 2–24 months after fledging from the nest when the dominant males eject them from the group (Kemp & Kemp, 1980; Carstens et al., 2019a; Kemp, Kotze, et al., 2020). They then mostly float on their own until a breeding vacancy appears in another group, or occasionally join all-female groups (Kemp & Kemp, 1980; Carstens et al., 2019a; Kemp, Kotze, et al., 2020).

Groups occupy large year-round territories which range from 50–200 km^2. These are actively advertised using low frequency vocalisations, or physically defended if intrusion occurs (Kemp & Kemp, 1980; Theron et al., 2013; Zoghby et al., 2015, pers. obs.). Vocalisations are usually performed simultaneously by adult group members (and occasionally sub-adults), and comprise a chorus given at dawn each day from a perch, audible to humans from several kilometers away (Kemp & Kemp, 1980). During the incubation stage, members of the group return to the nesting site each morning, where the incubating female briefly joins the rest of the group to contribute towards chorus vocalisations and to forage. After incubation, these territorial vocalisations are less confined to around the nesting site and may occur anywhere within the territory (pers. obs.). Physical defence of territories is uncommon but used when necessary, and involves aerial displays, chasing and bill grappling (Kemp & Kemp, 1980). Juvenile birds are also subject to kidnapping by other groups (Kemp & Ezzey, 2020) and have been observed to play no part in territorial defence, instead taking refuge out of sight from intruders (Kemp, 1988).

Conservation status

Southern ground-hornbills are listed as Vulnerable throughout their range but are regionally Endangered within South Africa, having lost up to 70% of their historic range in the past century, and with populations continuing to decline (Taylor & Kemp, 2015; Kemp, 2017). Some of the immediate anthropogenic threats identified include: 1) land-use change/habitat loss, which usually involves the loss of nesting sites which are often scarce to begin with and are considered a factor limiting reproduction (particularly outside of protected areas); 2) secondary poisoning as a result of carcasses deliberately laced with poisons targeted towards carnivores, and as a result of lead toxicosis from hunting practices; and 3) persecution for breaking windows of buildings, as ground-hornbills are territorial and can be aggressive when seeing their reflections (Taylor & Kemp, 2015; Kemp, 2017).

Together with these threats, the low density and restricted range of southern ground-hornbills are thought to make them particularly vulnerable to the effects of climate change. Temperatures are increasing at unprecedented rates worldwide due to anthropogenic climate change (IPCC, 2021). The intensity, frequency, and duration of heat waves (Meehl & Tebaldi, 2004; van Wilgen et al., 2016; Stillman, 2019), as well as changes in the timing, frequency, and intensity of rainfall (van Wilgen et al., 2016; Wise & Lensing, 2019) have increased over the past decades, and are predicted to continue to increase. These changes are expected to be particularly important in arid and semi-arid environments where temperatures are already high and rainfall is variable, and where species' thermal tolerance are already close to their limits (Huang, Guan & Ji, 2012; Ji et al., 2014; Huang et al., 2016; van Wilgen et al., 2016; Dube & Nhamo, 2020; Mbokodo et al., 2020). Ground-hornbills may be vulnerable to these changes because they begin costly heat dissipation behaviours at relatively low temperatures, around 26 °C, and because their breeding period is restricted to the hottest time of the year when prey abundance is highest (Kemp, 2017; Janse van Vuuren, Kemp & McKechnie, 2020a).

In other species, the adverse effects of climate change have already been shown to reduce adult and offspring body condition and survival (du Plessis et al., 2012; Wingfield et al., 2017; Bourne et al., 2020a,b; Bourne, Ridley, Spottiswoode, et al., 2021), reduce foraging efficiency (Goldstein, 1984; du Plessis et al., 2012; Cunningham, Martin & Hockey, 2015), reduce provisioning rates and breeding

success (Cunningham, Kruger, et al., 2013; Cruz-McDonnell & Wolf, 2016; Wiley & Ridley, 2016; van de Ven et al., 2020; Pattinson et al., 2022), alter reproductive timing (McNamara et al., 2011; Aranzamendi et al., 2019), increase hyperthermic mortality (McKechnie & Wolf, 2010; McKechnie, Hockey & Wolf, 2012), shift and reduce species ranges (Chen et al., 2011; Stewart et al., 2022) and alter migration patterns (Samplonius et al., 2018; Bauer, McNamara & Barta, 2020). Therefore, understanding the effects of climate change on ground-hornbill reproduction, and whether their cooperative behaviour can buffer periods of high temperatures and low rainfall, can help inform conservation efforts on the species, as well as provide insights as to how they might cope under these conditions.

Current conservation efforts for the species are focussed on education, habitat preservation, installing artificial nests, and the artificial formation and reintroduction of groups back into their historical range (Botha et al., 2011; Cilliers et al., 2013; Kemp, 2017). For the latter, individuals for reintroductions are sourced from wild populations (including from my study population) by ‘harvesting’ the second-hatched chicks, otherwise doomed to die, before they starve. This effectively doubles the breeding success, without having any effect on the source population dynamics. ‘Harvested’ chicks are sent to the Mabula Ground-Hornbill Project (https://ground-hornbill.org.za) where they are placed with captive ground-hornbills (individuals which cannot be released) in a rearing facility before being strategically placed in groups for release. Therefore, knowledge of social and climatic effects on reproduction can help identify individuals vital for group success, and the characteristics of suitable release sites.

Study site

We worked in a 2000 km^2 area of the Greater Kruger National Park on the Associated Private Nature Reserves (APNR, centred on 24.16˚S, 31.18˚E; Figure 1.4), South Africa. The APNR comprises five private nature reserves: Klaserie (600 km^2), Timbavati (540 km^2), Umbabat (310 km^2), Balule (350 km^2) and Thornybush (140 km^2). The area has distinct wet (October–March) and dry seasons (April–September) with an annual rainfall range of 450–600 mm (Figure 1.5). Dry seasons coincide with the

winter months, although the relatively hot conditions during this period do not fit the conventional idea of winter conditions: mean minimum and maximum temperatures for dry seasons are 12˚C/26˚C, and 20˚C/33˚C for wet seasons, respectively. During the wet (summer) season, daily maximum temperatures sometimes exceed 40˚C. The vegetation throughout the study area consists of heterogeneous savannah habitat, varying from open savannah to closed woodland, over undulating hills in the north that transition to flat grasslands in the south (Carstens, 2017). The fauna of the area consists of a wide variety of species as it is connected to the Kruger National Park, including larger mammals comprising the ‘big five’ (elephant *Loxodonta africana*, rhinoceros *Ceratotherium simum*, buffalo *Syncerus caffer*, leopard *Panthera pardus*, and lion *Panthera leo;* Figure 1.6).

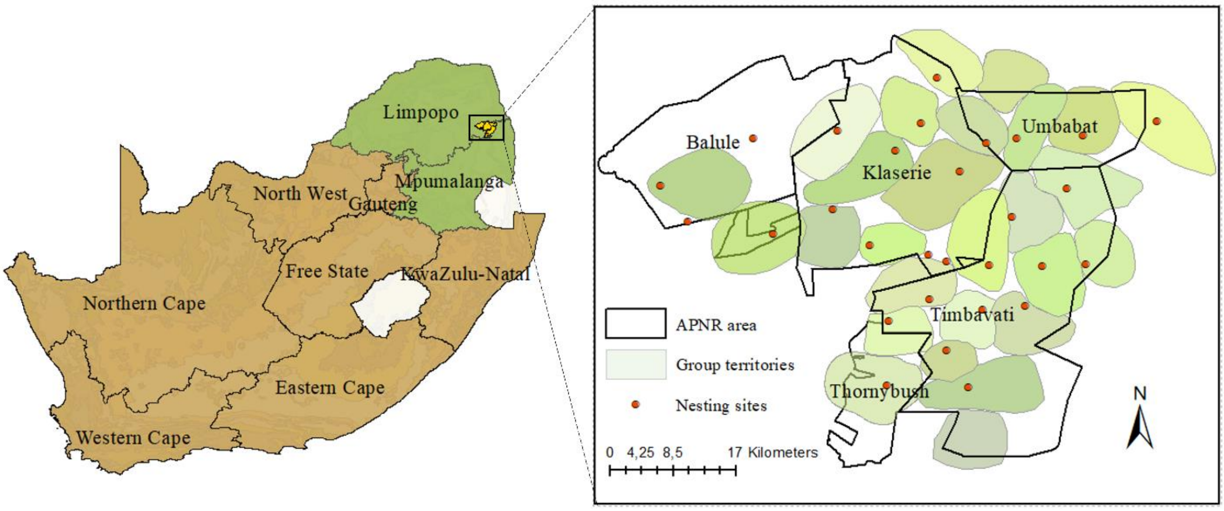


Figure 1.4. Map of the study site. Left: The study site is located across the border of the Mpumalanga and Limpopo Provinces of South Africa (highlighted in green on the map of South Africa). Right: a larger scale map showing the five private nature reserves that comprise the APNR study site, as well as the southern ground-hornbill group territories we monitored, and the location of their nesting sites.

Figure 1.5. Photographs taken from the same point in our study area during the dry (top) and wet (bottom) seasons. Photos: Chad Cocking

Figure 1.6. A rare sighting of a group of ground-hornbills and a lion coalition within the study site. Photo: Chad Cocking

APNR Ground-Hornbill Project

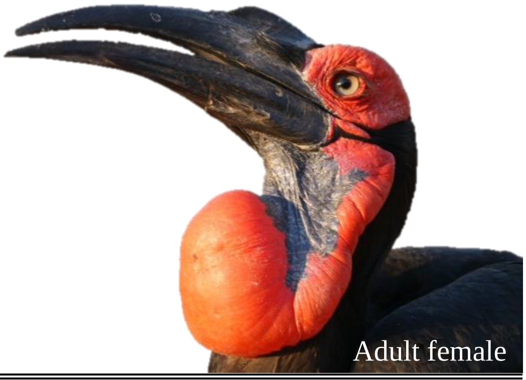
This study site has been the location of a long-term project on the species since 2000, where the original motivation was to monitor group distribution, composition, and breeding performance of southern ground-hornbills given that they are the world's largest cooperative breeder. Groups (approximately 23 per year) are monitored through opportunistic sightings, active efforts by researchers to re-sight groups, trail camera footage at nesting sites, aerial censuses, and through citizen science (involving nature guides scattered throughout the reserves). As a result, the group sizes, group compositions, and general territories are known (Figure 1.4).

The rarity of natural breeding cavities led to the first artificial nests being installed in 2002 to increase breeding productivity in the area and to allow for the monitoring (Carstens et al., 2019b). Each group typically has one nest within their home-range, and the majority of these are artificial (i.e. nest boxes), with only three viable natural nests (across three territories) currently available to birds. It is likely that the density of natural nests in the study site is lower now than historically for anthropogenic reasons (mainly land-use change), such that artificial nests are making up for a relatively recent change. Nests are monitored to determine the breeding status, lay dates, and reproductive success of the different groups in the study site. If breeding occurs, eggs and nestling are weighed and measured. Additionally, prior to fledging, nestlings are ringed for identification in the field. Colour rings have also previously

been used for easier identification, but we have not used them in recent years because they lose their colour over time and cannot be changed. Most ringed individuals within the study site were ringed as nestlings, and only a few were ringed as adults. Catching adult birds or entire groups in their enormous territories is extremely difficult as well as stressful for birds, making it time-consuming and near impossible. Furthermore, recapture rates are very low as birds become extremely nervous after being caught, making them even harder to find. The difficulty of thus obtaining DNA samples makes studying genetic relatedness incredibly challenging, which is why in this study we used a more passive approach and did not consider relatedness. Fortunately, individual birds can be reliably identified in the field and on images through specific facial features (sideburns, shape and colouration of red throat pouch and scars; see examples in Figure 2.1 in Chapter 2).

Part I: Reproduction

Chapter 2



High temperatures and carers' age influence nest attendance in a slow-developing cooperative breeder, the southern ground-hornbill *Bucorvus leadbeateri*

Trail camera footage from the Strydom group nest site in November 2017. *This photo shows a female (left) and a ringed male (right) visiting an artificial nest prior to breeding. Unfortunately, this breeding attempt failed because of genet (Genetta genetta) predation. Photo: Kyle-Mark Middleton*

Abstract

1. During avian reproduction, offspring and incubating individuals usually rely on carers for food and resources, and the quality and quantity provisioned can have important impacts on survival and reproductive success. Increases in temperatures and extreme weather events through anthropogenic climate change is likely to affect these provisioning efforts, making it vitally important to understand how species might respond. Cooperative breeders are commonest in harsh climates and such cooperation has been suggested to mitigate adverse environmental conditions, but results have been inconsistent and differ across taxa, perhaps because variation in life-history strategy influences breeders' and helpers' investment decisions. In addition, long-lived, slow-developing species can contain group members of varying age and experience which might modulate any effects of group size on provisioning efforts.
2. Here, we examined how social, life-history (group member age and number of individuals of each age), and climatic factors affected provisioning efforts in a large, long-lived, slow-developing cooperative breeder, the southern ground-hornbill *Bucorvus leadbeateri*. Groups in this species contain mostly males (and typically only a single adult female in groups ranging from 2–12 individuals) and can be morphologically classified into four age-sex categories (adult female, adult male, sub-adult male, and juvenile), allowing us to examine their individual contributions and their effects on provisioning efforts, and whether they mitigate the effects of environmental conditions.
3. We used three years of data collected from trail cameras placed at the nesting sites of 15 different territorial groups (comprising 53 different individuals) within the Associated Private Nature Reserves, South Africa, to investigate how temperature, age-sex category, group size, and group composition were associated with provisioning rates, prey types (vertebrates/invertebrates) and prey sizes.
4. We found that individual contributions varied with age, with older individuals having higher provisioning rates and provisioning larger prey, including more vertebrates, than younger individuals. In general, larger groups and groups with more adult males provisioned at the highest rates (i.e. "additive care"), but individuals reduced their own provisioning efforts in the presence of

additional helpers (i.e. “load-lightening”). High temperatures were associated with lower provisioning rates and smaller prey provisioned, and there was no evidence that these costs of high temperatures were mitigated by groups with more helpers.

5. We conclude that provisioning decisions in southern ground-hornbills differ between individuals of different ages, and that group living provides both additive and load-lightening benefits. These benefits, however, do not meaningfully mitigate the negative effects of high temperatures. As such, this study is consistent with the expectation that long-lived, slow-developing species maximise survival and lifetime reproductive success by favouring self-maintenance over current reproduction.

Keywords: Cooperative breeding, provisioning, prey size, age, temperature

Introduction

In species where young rely on carers to obtain food and protection, the quality of care provided (e.g. quantity of food or quality of the shelter) can influence body condition, survival, and future reproductive opportunities (Cunningham, Martin, et al., 2013; Dubiec, Góźdź & Mazgajski, 2013; Senécal et al., 2021). Thus, the provisioning behaviour of carers plays an important role in the productivity and population persistence of populations/species (Maness & Anderson, 2013; Perrig et al., 2017). However, parental care is costly, as the need to provision offspring in addition to self-maintenance results in increased energetic expenditures that have been shown to be associated with reduced body condition and survival (Ridley & Raihani, 2008; Wiebe & Slagsvold, 2015; Wiley & Ridley, 2016; Mendonça et al., 2020; Covas et al., 2022). Therefore, carers face a trade-off and are required to decide on how much to invest in provisioning and self-maintenance. This balance is further influenced by environmental conditions that affect carer body condition, and by life-history strategy, as long-lived species typically reduce investment in current breeding events to maximise lifetime breeding success (Stearns, 1992).

One of the environmental factors imposing an energetic cost on animals, through its influence on food availability and adult condition, is temperature (Drent & Daan, 1980; Cruz-McDonnell & Wolf, 2016; Bourne, Ridley, Spottiswoode, et al., 2021). Thus, in the context of anthropogenic climate change

in which temperatures will continue to increase, the energetic demands of parents during reproduction are likely to be intensified. This might be particularly important in arid and semi-arid habitats where predicted temperature increases are likely to have both direct and indirect effects on species (Donnelly et al., 2012; Cahill et al., 2013; Cunningham, Martin, et al., 2013; Dybala et al., 2013; Winkler, Luo & Rakhimberdiev, 2013; Bourne et al., 2020c). For example, studies have shown that temperature extremes may directly affect the thermoregulatory requirements of individuals and alter their behaviour to favour self-maintenance (e.g. shade seeking), subsequently leading to missed foraging opportunities and reduced body condition (du Plessis et al., 2012; Conradie et al., 2019; Bourne, Ridley, McKechnie, et al., 2021; Cunningham, Gardner & Martin, 2021). Furthermore, high temperatures, by reducing primary production and food availability across the trophic levels, should compound indirect effects of decreasing foraging efficiency and reduce individual investment into reproductive behaviours such as provisioning (Chesson et al., 2004; Bolger, Patten & Bostock, 2005; du Plessis et al., 2012; Iknayan & Beissinger, 2018; van de Ven et al., 2020; Barras et al., 2021; Cunningham, Gardner & Martin, 2021).

In cooperatively breeding species, individuals (generally known as ‘helpers’) other than the parents contribute towards offspring provisioning (Cockburn, 1998), and other group tasks (see Ridley & Raihani, 2008; Golabek, Ridley & Radford, 2012; Jungwirth et al., 2015; Groenewoud et al., 2016). When parents (and helpers) maintain their own provisioning effort despite additional help, an increase in the overall provisioning rate results. Such ‘additive’ care is expected to improve offspring condition and survival (Hatchwell, 1999; Meade et al., 2010; Johnstone, 2011; van Boheemen et al., 2019). Alternatively, they can also adopt a ‘load-lightening’ strategy when there is additional help, by reducing their provisioning effort to offspring and thus improving their own survival and lifetime reproductive success (Hatchwell, 1999; Kingma et al., 2010; Paquet et al., 2015; van Boheemen et al., 2019). These two strategies are not mutually exclusive, however, and studies have shown that additional helpers may lighten the provisioning load of individual group members, while simultaneously increasing the total quantity of provisions to nestlings (Covas, Du Plessis & Doutrelant, 2008; Kingma et al., 2010; van Boheemen et al., 2019). Carers can also have flexible strategies in relation to environmental conditions and work harder when needed, leading to mitigating effects of helpers specifically under adverse

environmental conditions (Rubenstein & Lovette, 2007; Covas, Du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). As a result, while we would expect a general negative effect of high temperature on provisioning effort and reproductive success, overall provisioning rates might be maintained when additional group members are present, leading to sustained juvenile survival or condition. As such, having additional group members present suggests that cooperative breeding may buffer the effects of adverse breeding conditions, such as high temperatures, on provisioning efforts (Covas, Du Plessis & Doutrelant, 2008; Rubenstein, 2011; Groenewoud & Clutton-Brock, 2021), thereby potentially increasing the resilience of species to climate change via improved reproductive output.

The potential for helpers to buffer the effects of adverse environmental conditions is consistent with comparative phylogenetic research on the distribution of cooperative breeding, which was found to be more common in harsh, fluctuating environments (Cornwallis et al., 2017; Firman et al., 2020). However, recent studies on two cooperatively breeding species, the sociable weaver *Philetairus socius* and the southern pied babbler *Turdoides bicolor,* found no support for these buffering effects (Bourne et al., 2020a; D'Amelio et al., 2022). Moreover, the evidence that cooperative breeding is more common in certain environmental conditions is somewhat inconsistent across taxa (Shen et al., 2017; Lin (林宇恒) et al., 2019). A striking example is the hornbill family (Bucerotidae), in which cooperative breeding is instead associated with stable, benign environments (Gonzalez, Sheldon & Tobias, 2013; Lin (林宇恒) et al., 2019). This was suggested to be as a result of the hornbill family's slow life-history strategy in which, unlike most cooperatively breeding passerines, high survival, large body size, low fecundity, and stable year-round food supplies were suggested to make the presence of helpers less critical for reproductive behaviours (Gonzalez, Sheldon & Tobias, 2013). Since long-lived species are expected to invest less in current breeding events and more into self-maintenance (Clutton-Brock, 1988; Hamel et al., 2010), longevity might be particularly important under adverse conditions when reproductive costs are high and benefits potentially lower. Such a trade-off should not only apply to parents, but also to helpers, which have been shown to balance their investment between self-maintenance and helping (Mendonça et al., 2020; Covas et al., 2022). However, helpers that are not the offspring of both breeders

are expected to invest less than parents as they benefit less from providing costly help towards offspring to which they are more distantly related (Komdeur, 2006; Koenig, Dickinson & Emlen, 2016). Furthermore, long-lived species usually have slower development, and in cooperative breeders this can translate to group members of varying ages and experience, which may influence the quality of care provided to young (Covas & Griesser, 2007; Browning et al., 2012). For example, younger individuals may provision less if they lack foraging skills and still depend on adults for food and protection (Rowley, 1976; Langen, 1996; Woxvold, 2004; Woxvold, Mulder & Magrath, 2006). Additionally, foraging skills of younger individuals may also develop slowly, meaning that costs to provisioning are higher, and that when they do provision, the items brought might differ in type and size from those brought by adults (Gunst, Boinski & Fragaszy, 2008b; Maynard et al., 2021). Thus, in long-lived, slow-developing species, load-lightening may be particularly expected in larger groups and more pronounced in younger individuals, subsequently diminishing the positive effects of group size on reproductive outcomes and provisioning rates. Yet, this has received limited attention so far.

In this study, we aimed to understand the effects of climatic, social, and life-history factors on offspring provisioning, and whether group members can mitigate the effects of adverse conditions in arguably the longest-lived, slowest-developing cooperative breeder ever studied, the southern ground-hornbill *Bucorvus leadbeateri* (hereafter ‘ground-hornbills’). Ground-hornbills are large, generalist top predators which are very long-lived (up to 60 years in the wild) and prey on animals ranging from invertebrates to small mammals (Kemp & Kemp, 1980; Kemp, 2017). Individuals develop slowly, reaching adulthood from around 6–8 years old. Juveniles have extended dependency periods of up to 3 years and seem not to contribute towards group tasks such as territory defence and provisioning (Kemp & Kemp, 1980; Kemp, 1988, 2017). Cooperatively breeding groups consist of 2–12 individuals which comprise a breeding pair, and mostly sons from previous broods (and occasionally immigrant males). These distinct age structures are readily detectible from characteristics of the un-feathered throat, feather and beak colouration (Kemp & Kemp, 1980; Kemp, 1988). Group members provide food (often as multi-prey loads) and “parcels” (containing nest lining and occasionally food items) to both the incubating female and subsequently to the nestling, over a long nesting period that takes approximately

five months (Kemp & Kemp, 1980). Nest lining consists mostly of fallen leaves (Kemp & Kemp, 1980), which studies of other avian species have suggested can help provide cushioning, maintain nest microclimates, reduce nest parasites and pathogens, or directly benefit nestling health and development (Wimberger, 1984; Gwinner et al., 2000; Mennerat et al., 2009; Dubiec, Góźdź & Mazgajski, 2013; Mainwaring et al., 2014; Polo, Rubalcaba & Veiga, 2015).

Ground-hornbills are obligate cavity nesters and their large size require that they use large territories (> 200 km^2). These ecological requirements and their slow life-history are implicated in their marked population decline over the last decades (Kemp, 2017; IUCN, 2021). Conservation concerns are further intensified by the current threat of climate change. Ground hornbills begin heat dissipation behaviours at relatively low temperatures (26˚C; Janse van Vuuren, Kemp & McKechnie, 2020), and high temperatures are negatively associated with nestling mass (Chapter 3). Therefore, understanding whether high temperatures impact provisioning behaviour in this species (as has been recently found in arid region species; van de Ven et al., 2020; Bourne et al., 2021) is an important requirement for current conservation efforts, particularly efforts to artificially form groups for release back into their historic range (Kemp, 2017). Understanding how individuals of different ages contribute towards provisioning, and whether they mitigate harsh conditions, will directly aid these reintroduction efforts by providing valuable information on which age classes are vital for success.

We used data from the incubation and nestling stages from three consecutive breeding seasons to examine the effects of temperature, group member age, group structure, and group size on individual and group provisioning behaviour. Specifically, we investigated how temperature, life-history, and social factors were associated with: 1) prey provisioning rates, 2) parcel provisioning rates (i.e. supply of predominantly nesting material), 3) prey type, and 4) prey size. Given that ground-hornbills show signs of heat sensitivity at relatively low temperatures (26ºC; Janse van Vuuren, Kemp & McKechnie, 2020), and given that their prey species likely face similar challenges (McMaster & Downs, 2013; Garcia-Heras et al., 2017), we hypothesised that high temperatures would have negative effects on provisioning rates, and be associated with smaller prey sizes (since individuals will likely forage less and be less selective), and a higher frequency of invertebrates in relation to vertebrates (since insects

and other arthropods are more abundant than vertebrates and therefore might be generally easier to find) being provisioned. Considering the longevity and slow development of ground-hornbills, we hypothesised that group member age would be associated with individual provisioning efforts and, specifically, that the parents and most experienced helpers (i.e. adults) would contribute the most, and provision larger prey than younger individuals with less experience. We then tested whether the provisioning rates of these differently aged individuals were associated with increases in group size. Specifically, given the slow life-history of southern ground-hornbills, we predicted that the number of adult males within groups should have mainly positive effects on group provisioning rates, but that adult males in larger groups should reduce their individual contributions (i.e. load-lighten) to favour self-maintenance. Moreover, we predicted that younger individuals should reduce their individual contributions even more than adults since the costs of provisioning are predicted to be higher. Finally, given that ground-hornbills inhabit mainly semi-arid habitats, the negative effects of temperature on provisioning may be mitigated by the presence of additional helpers, particularly adults, so that we specifically predict an interactive effect of temperature and group size. However, given the life-history strategy of the hornbill family and the suggestion that it makes the presence of helpers generally less relevant for reproduction (Gonzalez, Sheldon & Tobias, 2013), we expected that any mitigating effects would be weak or even absent.

Methods

Data collection

Southern ground-hornbills have been monitored at the study site since 2000. Throughout this period, artificial nests have been used to compensate for a lack of natural sites, and therefore there is typically one nest per territorial group. This monitoring led to nestlings (and some adults) throughout the area being ringed and monitored each year. Nests were on average 8042 ± 2053 m apart.

During breeding seasons 2018/2019 to 2020/2021, nests were visited every 7–10 days from mid-September to determine the breeding status of groups. Once breeding was initiated and the first-laid eggs were found (average lay date within the study site was 8 November ± 21 days), the nests were

visited 5 days later to check for the second-laid egg. The next two visits occurred 40 and 45 days after the laying of the first egg to check for the hatching of each egg. Hatched chicks could be aged based on their size and skin colouration as they hatch small and pink, but quickly grow and turn dark grey after 2–3 days. The nests were then visited twice more, usually when the surviving nestling was approximately 40 days old and 75 days old, although this sometimes varied depending on weather conditions. We installed trail cameras facing the nest entrances to video record provisions made to the incubating female and resulting nestling. The cameras used were Browning Spec Ops Advantage, Browning Spec Ops Edge, and Browning Patriot trail cameras (Browning Trail Cameras, Alabama, USA). The only difference between these cameras was the field of view and so were unlikely to influence the results. Camouflaged housings were installed 2–5 m from the nests prior to the breeding season to minimise any possible disturbance created when installing new objects in the vicinity of the nest during the breeding season. Cameras were then installed inside the boxes for a minimum of 5 days (and nights) during three stages of the breeding process: incubation (from when eggs were found), early nestling (after finding first hatched egg), and middle-to-late nestling (when surviving nestlings were 34–86 days old). During each period, the cameras were set to take 20 second videos with an inter-video period of 5 seconds. Feeding events were slow enough that the 5-second inter-video period did not miss individuals coming to feed. These high-resolution videos allowed us to visually identify each individual within the respective groups based on specific facial features (sideburns, shape and colouration of red throat pouch and scars; Figure 2.1), as well as the colour rings previously placed on the birds. We collected on average (± SD) 97.4 ± 34.3 daylight hours of footage per nest stage and analysed 6441 nest visits from 63 individual birds in 15 different groups. Nine of these groups were monitored for more than one breeding season. Group structures between years varied slightly, usually only with the addition or loss of juveniles from previous years.

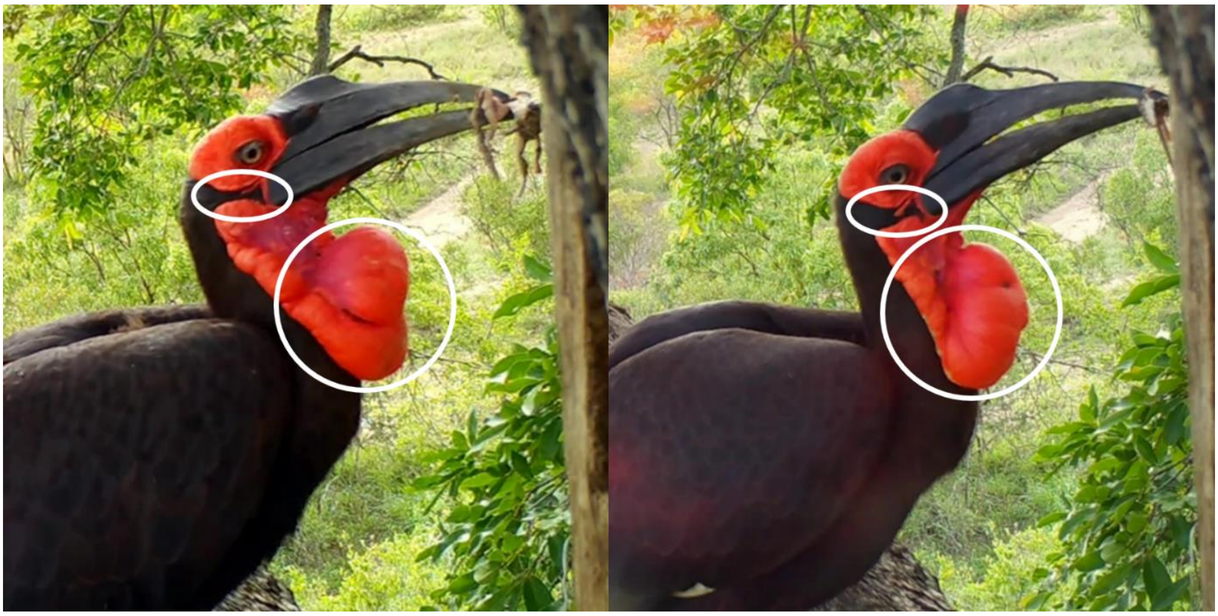


Figure 2.1. An image from the trail camera footage showing how two different male ground-hornbills from the same group are identified. The small white circles show the different patterns of sideburns, and the large white circles show the different throat shapes with different scars.

Video recordings were viewed using VLC media player and Windows Media Player. For each nest visit, we recorded the individual ID, arrival and departure times, sex, age class, stage of breeding, age of nestling (for nestling stages), contributions brought (Y/N), whether a parcel was brought (i.e. a bundle of leaves, or leaves and prey items; Y/N), delivery to incubating female or nestling (Y/N), type of prey item (vertebrate or invertebrate), and size of prey (small/medium/large). The size of food provisioned was classified by comparing the food to the bill depth of the birds. Prey was considered small if the collective size of all items in the bill was smaller than the bill depth, medium if it was about the same, and large if it was bigger. Camera observation days which contained camera malfunctions (8 days in total) or were mistimed with breeding stages were removed from the data.

Hourly maximum temperatures were obtained from a Vantage Pro2 weather station (Davis Instruments, USA) located within the study site (maximum distance from weather station to furthest nest was 28.5 km).

Statistical analyses

We investigated how life-history (group member age and number of individuals per age class), social (group size), and climatic (maximum temperatures) factors were associated with *individual* and *group* provisioning efforts. We focused on four response variables: 1) prey provisioning rates (as the total number of provisions delivered per day, including prey items that were delivered together with parcels; continuous), 2) parcel provisioning rates (as the total number of parcels provisioned per day; continuous), 3) prey type (invertebrate/vertebrate; binary), and 4) prey size (small/medium/large; ordinal). Prey size was considered separately to prey type since ground-hornbills often provision more than one item at a time, especially with smaller prey items, making them largely independent of each other. Each of these variables was examined separately during three stages of the nesting period: incubation stage (where only the incubating female is fed); early nestling stage (where the incubating female and nestling are fed); and middle-to-late nestling stage (where only the nestling is fed).

To investigate the *individual* provisioning rates of different group members and how these varied with group size, we used the total number of food and parcel provisions per day, per individual (with repeated provisioning observations from 63 individuals across an average of 5.4 ± 2.0 days per stage) as the dependent variable (daily individual food provisions: n [incubation stage] = 282, n [early stage] = 236, n [middle-to-late stage] = 564; daily individual parcel provisions: n [incubation stage] = 187, n [early stage] = 172, n [middle-to-late stage] = 230). Member age was combined with member sex into a categorical age-sex variable, and given that groups typically contain a single adult female, this contained four levels: adult male (31 individuals), adult female (15 individuals), sub-adult male (11 individuals), and juvenile (of either sex; 11 individuals). This was included as an explanatory variable in all analyses for individual provisioning rates. Nestling age was included during the middle-to-late nestling stage to account for the variation in observation days within the nestling period (variation = 52 days). The interaction between age-sex and nestling age variables was also tested since provisioning rates may be influenced by how they each vary. As larger groups often included sub-adults and/or juveniles, the variables of age-sex and group size were correlated, and so group size was not included in these first models. However, since our analyses revealed that juveniles contributed very little towards provisioning and were also associated with larger group sizes, we subsequently removed juveniles as focal individuals and repeated the analyses. This resulted in the variables of age-sex and group size no longer being correlated, allowing us to investigate how the daily individual provisioning rates of adults

and sub-adults varied with group size (daily individual food provisions: n [incubation stage] = 279, n [early stage] = 221, n [middle-to-late stage] = 548). Group size, and the quadratic term for group size were included in these analyses since we expected that there may be an optimal group size. Interactions between these group size variables and age-sex category were also tested since the provisioning behaviour of individuals of different ages may respond differently to the presence of additional group members.

To investigate associations of temperature and group composition on *group* provisioning rates, we used the total number of prey and parcel provisions per day, per group (with repeated provisioning observations from 15 groups across an average of 5.4 ± 2.0 days per stage) as the dependent variable (daily group food provisions: n [incubation stage] = 132, n [early stage] = 104, n [middle-to-late stage] = 173; daily group parcel provisions: n [early stage] = 96, n [early stage] = 91, n [middle-to-late stage] = 96). All analyses included the daily mean maximum temperature, as well as the quadratic term since we expected that there may be an optimal temperature for provisioning (where both cold and hot temperatures may have similar negative effects). Daily mean maximum temperatures were obtained by averaging the hourly maximum temperatures between 05:00 and 19:00 (the time between the earliest and latest recorded provisioning events) for each day. Group size and group composition (i.e. number of adults, sub-adults, and juveniles), as well as the quadratic terms for these variables, were also included to examine the associations between social and life-history effects on group daily provisioning rates under different weather conditions. Hence, in each of the models we considered as explanatory variables temperature, group size, group composition (comprising separate variables of number of adults, sub-adults, and juveniles), and included interactions between group size/group composition (since these were not included in the same models) and temperature variables, as specifically predicted by the hypothesis that cooperative breeding mitigates harsh conditions. Additionally, as above, nestling age was also included for the middle-to-late nesting stage.

Finally, to investigate how prey type and prey size were associated with the climatic, social, and life-history variables described above, we used the prey type (vertebrate/invertebrate) and prey size (small/medium/large) brought during individual provisioning events as the dependent variables.

Independent variables were the individual's age-sex category, group composition (i.e. number of adults, sub-adults, and juveniles), group size, hourly maximum temperature (during the nearest hour in which the feed took place), and nestling age (for the middle-to-late stage). A quadratic term was included for hourly maximum temperatures since we expected prey to vary at different temperatures and different times of day. Interactions between hourly maximum temperatures and age-sex category were also included since individuals of different ages may differ in their foraging abilities and respond differently to increasing temperatures.

Statistical analyses were conducted in R version 4.0.4. Core Team (R Development Core Team 2021) using packages glmmTMB version 1.1.2.3, Ordinal version 2019.12-10, and MuMIn version 1.43.17. Data exploration was carried out following the protocol described in Zuur, Ieno and Elphick (2010). General and Generalised Linear Mixed Models (GLMMs), and Cumulative Linked Mixed Models (CLMMs) were used to investigate the potential predictors of prey provisioning rates (truncated-Poisson, GLMMs), parcel provisioning rates (truncated-Poisson, GLMMs), prey type (binary, GLMMs), and prey size (ordinal, CLMMs). All continuous variables were scaled by centering and standardising by the mean (Schielzeth, 2010). Year and group identity were included as random terms in all the analyses. Individual identity (nested within group identity) was also included as a random term for analyses on the *individual* prey and parcel provisioning rates, as well as prey type and prey size analyses. Incubating females did not contribute towards provisioning during the early nestling and incubation stages and so were removed from analyses for these periods. Strongly correlated variables ($r > 0.30$) were not included in the same models. Group size was correlated with the group composition (i.e. number of adults, sub-adults and juveniles) variables and so these were not included together. Similarly, the group composition variables of number of adult males and number of sub-adults were also strongly correlated for all analyses and so separate models were run for each and then compared. Residuals of the final models were visually inspected to ensure that the model assumptions were met. Models were then compared using Akaike's Information Criteria (AICc) and were considered better when the AICc values reduced by more than 2. When competing models had ΔAICc < 2, the simpler model with fewer parameters was used for further inference (Richards, 2008; Richards,

Whittingham & Stephens, 2011). Akaike's model weights were also calculated to determine the likelihood of models relative to the other models.

Results

Individual prey provisioning rates

How individuals in the different age-sex categories contributed towards prey provisioning rates was analysed using GLMMs with Truncated-Poisson error structures. During the incubation (n = 282 daily individual provisions) and early nestling stages (n = 236 daily individual provisions), the best-fit models for the *individual* contributions both contained the variable of age-sex category (excluding females; see above and Table S2.2). During the middle-to-late nestling stage (n = 564 daily individual provisions), there were two nested best-fit models (AICc < 2). Both models included the variable of age-sex category and differed only by the inclusion of nestling age. The simpler model, containing only the variable of age-sex category, with the larger model weight (0.57 compared to 0.26) was used for further inference (Table S2.2). All these models for the different stages indicated that provisioning rates differed among individuals of different ages. For all stages, adult males (the reference category) and females (during the middle-to-late nestling stage only) were associated with the highest provisioning rates, followed by sub-adults, and then juveniles with the lowest provisioning rates (Table 2.2; Figure 2.2).

Table 2.1. Summary of variable means (±SE) and ranges from 2018–2021

Variable	**Mean (± SE) from 2018–2021**		
Group size	4.04 ± 0.18 (range: 2–6 individuals)		
Number of adult males per group	1.81 ± 0.12 (range: 1–3 individuals)		
Number of sub-adults per group	0.59 ± 0.10 (range: 0–1 individuals)		
Number of juveniles per group	0.59 ± 0.13 (range: 0–2 individuals)		
	Incubation stage	**Early nestling stage**	**Middle-to-late nestling stage**
Daily mean maximum temperature (˚C)	27.53 ± 0.40 (Range: 18.27–36.32)	28.06 ± 0.33 (Range: 21.65–34.53)	27.03 ± 0.20 (Range: 21.73–32.95)
Hourly maximum temperature (˚C)	24.98 ± 0.24 (Range: 13.4–39.9)	26.39 ± 0.16 (Range: 17.9–39.1)	26.25 ± 0.11 (Range: 16.1–37.3)
Nestling age	N/A	N/A	Range: 34–86
Total individual provisions per day	3.35 ± 1.91 (Range: 1–10)	4.60 ± 2.16 (Range: 1–10)	2.74 ± 1.46 (Range: 1–12)
Total group provisions per day	7.17 ± 3.47 (Range: 1–15)	10.71 ± 3.45 (Range: 2–18)	8.94 ± 4.02 (Range: 1–28)
Total individual parcel provisions per day	2.25 ± 1.21 (Range: 1–6)	1.95 ± 0.95 (Range: 1–5)	1.58 ± 0.79 (Range: 1–6)
Total group parcel provisions per day	4.38 ± 2.22 (Range: 1–11)	3.68 ± 1.94 (Range: 1–9)	3.79 ± 2.39 (Range: 1–11)

Table 2.2. Age-sex factors predicting daily individual provisioning rates for all stages, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Categorical variables of females, sub-adult males and juveniles were compared to the reference category of adult males. Variables highlighted in bold have 95% CI which do not cross zero. Incubation stage: n = 282 from 3 years, 14 groups and 40 individuals. Early nestling stage: n = 236 from 3 years, 11 groups and 32 individuals. Middle-to-late nestling stage: n = 564 from 3 years, 12 groups and 46 individuals.

Variable	**Estimate**	**SE**	**95% CI**
Incubation stage			
Sub-adults	**-0.56**	**0.15**	**-0.86 – -0.26**
Juveniles	**-1.62**	**0.59**	**-2.77 – -0.46**
Early nestling stage			
Sub-adults	**-0.39**	**0.16**	**-0.70 – -0.08**
Juveniles	**-0.98**	**0.25**	**-1.46 – -0.50**
Middle-to-late nestling stage			
Females	-0.18	0.13	-0.41 – 0.04
Sub-adults	**-0.33**	**0.16**	**-0.65 – -0.01**
Juveniles	**-0.75**	**0.30**	**-1.34 – -0.16**

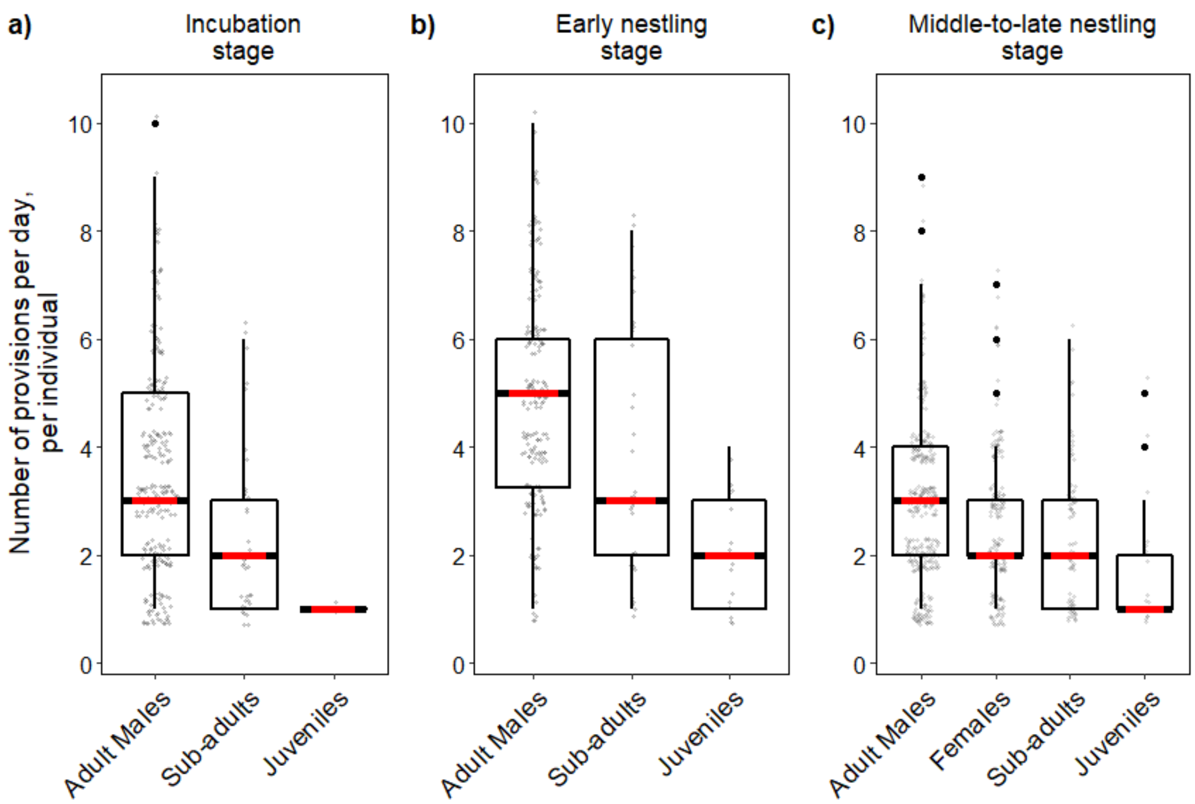


Figure 2.2. Number of daily provisions per individual in relation to their age-sex category for a) incubation, b) early nestling, and c) middle-to-late nestling stage. Boxplots show median values (red lines), first and third quartiles (box) and interquartile range (whiskers). Points represent individual provisions per day (where there are several points per individual) and are jittered for improved visibility.

Analyses of load-lightening effects were analysed using GLMMs with Truncated-Poisson error structures. During the incubation stage (n = 279 daily individual provisions), there were two nested best-fit models (ΔAICc < 2), indistinguishable from each other. Both models contained interactions between variables of age-sex category and group size, and differed only by the addition of a quadratic effect for group size. We used the simpler model without a quadratic term for further inference (Table 2.3). In this model, there was no clear relationship between provisioning rates and group size for adult males, although there was a negative tendency (estimate = -0.10 ± 0.07, 95% CI = [-0.23 – 0.03]; Figure 2.3a). There was, however, a clear negative relationship between provisioning rates and group size for sub-adults (estimate = -0.24 ± 0.07, 95% CI = [-0.38 – -0.10]; Figure 2.3a), indicating load-lightening effects for sub-adults during the incubation stage.

During the early nestling stage (n = 221 daily individual provisions), there were two nested best-fit models (ΔAICc < 2) indistinguishable from each other. Similar to the incubation stage, both models contained an interaction with the age-sex variable and group size, with the difference occurring only from the addition of a quadratic term for group size. Again, the simpler model was used for further inference (Table 2.3). Within this model, there were strong negative relationships between provisioning rates and group size for both adult males (estimate = -0.20 ± 0.05, 95% CI = [-0.30 – -0.10]; Figure 2.3b) and sub-adults (estimate = -0.28 ± 0.06, 95% CI = [-0.39 – -0.17]; Figure 2.3b), indicating load-lightening effects for both adult males and sub-adults during the early chick stage.

During the middle-to-late nestling stage (n = 548 daily individual provisions), the best-fit model with the highest model weight (0.59) was the null model, indicating that there were no clear load-lightening effects for individuals in any age-sex class during this stage (Table 2.3).

Table 2.3. Top five models for group size effects on the individual daily provisioning rate for all stages. Dev = model deviance.. Random terms: year, group identity. Models highlighted in bold were the models used for inference.

Model	k	Dev	AICc	∆AICc	Model Weight
Incubation stage					
Age-sex : Group size^2	6	1013.2	1025.56	0	0.60
Age-sex : Group size	**6**	**1014.1**	**1026.38**	**0.81**	**0.40**
Group size + Group size^2	6	1025.4	1037.76	12.20	0
Group size	5	1027.8	1038.01	12.45	0
Null model	4	1031.9	1040.08	14.52	0
Early nestling stage					
Age-sex : Group size	**6**	**881.0**	**893.42**	**0**	**0.51**
Age-sex : Group size^2	6	882.7	895.11	1.69	0.22
Group size + Group size^2	6	883.3	895.66	2.23	0.16
Group size	5	886.2	896.49	3.07	0.11
Null model	4	896.8	904.99	11.57	0
Middle-to-late nestling stage					
Null model	**4**	**1784.0**	**1792.03**	**0**	**0.59**
Group size	5	1784.0	1794.07	2.04	0.21
Age-sex : Group size	7	1781.8	1795.98	3.95	0.08
Age-sex : Group size^2	7	1782.0	1796.20	4.17	0.07
Group size + Group size^2	6	1784.9	1797.01	4.98	0.05

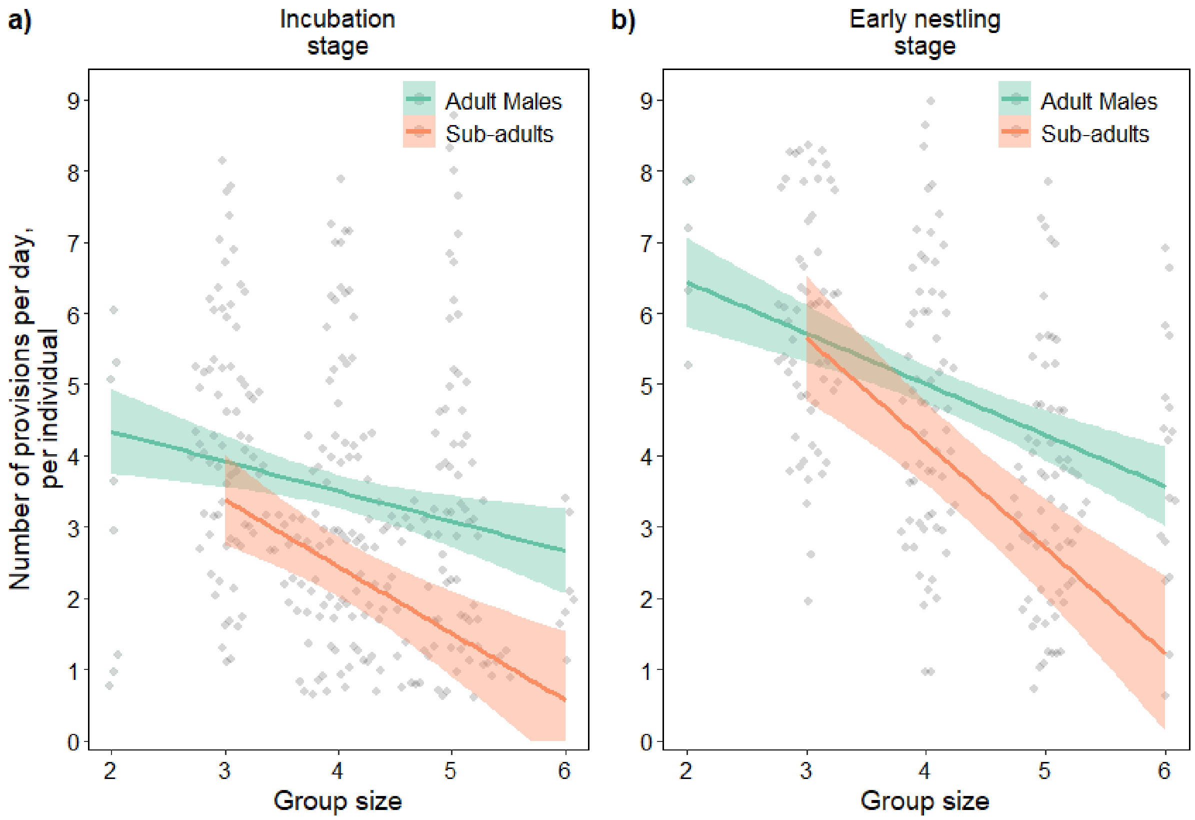


Figure 2.3. The interaction effect of age-sex category and group size on the number of provisions per day, per individual. Although the interaction for adult males during the incubation stage appears negative, it was not significant in our model. Data points are jittered for improved visibility and lines represent the relationship with 95% confidence intervals.

Group prey provisioning rates

The prey provisioning rates for groups were analysed using GLMMs with Truncated-Poisson error structures. During the incubation stage (n = 132 daily group provisions), there was one best-fit model with a model weight of 0.84 which included the variables of number of adult males (with a quadratic term), number of juveniles, and daily mean maximum temperature (with a quadratic term; Table 2.4). There was no clear association between daily prey provisioning rate and the number of juveniles (estimate = -0.11 ± 0.07, 95% CI = [-0.24 – 0.02]) as it had 95% confidence intervals which overlapped zero. There was, however, support for clearer associations between prey provisioning rates and increases in the number of adult males (estimate = 0.12 ± 0.05, 95% CI = [0.02 – 0.22]), as well as a quadratic term for this variable (estimate = -0.15 ± 0.04, 95% CI = [-0.23 – -0.07]; Figure 2.4a). Increases in daily mean maximum temperature were associated with decreased daily provisioning rates (estimate = -0.15 ± 0.04, 95% CI = [-0.23 – -0.07]), and there was a negative association for the

quadratic term for daily mean maximum temperatures (estimate = 0.12 ± 0.03, 95% CI = [-0.19 – -0.06]; Figure 2.5a).

During the early nestling stage (n = 104 daily group provisions), there were two nested best-fit models (ΔAICc < 2) with similar model weights (0.31 and 0.28), making them indistinguishable from each other. Both models included the variables of daily mean maximum temperature and group size, differing only by the addition of a quadratic term for the daily mean maximum temperature. The simpler of the two models, which excluded the quadratic term, was used for further inference (Table 2.4). Within this model, group size had no clear effect on the daily prey provisioning rate (estimate = 0.12 ± 0.10, 95% CI = [-0.06 – 0.31]) as 95% confidence intervals broadly overlapped zero. There was, however, a strong negative relationship between the daily prey provisioning rate and daily mean maximum temperature (estimate = 0.12 ± 0.03, 95% CI = [-0.19 – -0.06]; Figure 2.5b).

During the middle-to-late nestling stage (n = 173 daily group provisions), there was one best-fit model with a model weight of 0.99. This model included daily mean maximum temperature and group size, as well as a quadratic term for group size (Table 2.4). The birds did not feed more or less when days were hotter or colder (estimate = -0.03 ± 0.05, 95% CI = [-0.12 – 0.06]) as 95% confidence intervals broadly overlapped zero. However, there was a clear positive relationship with group size (estimate = 0.14 ± 0.05, 95% CI = [0.05 – 0.23]), as well as a clear negative relationship for the quadratic term of group size (estimate = -0.12 ± 0.03, 95% CI = [-0.19 – -0.06]; Figure 2.4b), indicating an initial increase in daily provisions with increasing group size, but a gradual decrease as groups became larger.

Table 2.4. Top five models for the temperature, social, and life-history effects on the daily prey provisioning rate per group for all stages. Dev = model deviance, Dtmax = daily mean maximum temperature, AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles. Random terms: year, group identity. Models highlighted in bold were the models used for inference.

Model	k	Dev	AICc	∆AICc	Model Weight
Incubation stage					
Dtmax + Dtmax^2 + AM + AM^2 + Juv	**8**	**656.7**	**673.90**	**0**	**0.84**
Dtmax + Dtmax^2 + Group size + Group size ^2	7	663.3	678.21	4.31	0.10
Dtmax + Dtmax^2 + AM + Juv	7	666.7	681.56	7.66	0.02
Dtmax + Dtmax^2 + SA + Juv	7	666.9	681.77	7.87	0.02
Dtmax + Dtmax^2 + AM + Juv + Dtmax^2 * AM	8	665.1	682.32	8.42	0.01
Early nestling stage					
Dtmax + Group size	**6**	**510.9**	**521.50**	**0**	**0.31**
Dtmax + Dtmax^2 + Group size	5	508.9	521.74	0.24	0.28
Dtmax + Dtmax^2 + Group size + Dtmax^2 * Group size	7	509.1	524.30	2.79	0.08
Dtmax + SA + Juv	6	511.5	524.34	2.83	0.07
Dtmax + Dtmax^2 + Group size + Group size^2	7	509.3	524.44	2.93	0.07
Middle-to-late nestling stage					
Dtmax + Group size + Group size^2	**6**	**926.3**	**941.02**	**0**	**0.99**
Null model	3	954.7	960.83	19.80	0.001
Dtmax + Group size + Nestling age	6	948.5	961.06	20.03	0.001
Dtmax + AM + Juv	6	949.2	961.74	20.72	0.001
Dtmax + AM + Nestling age	6	951.4	963.87	22.85	0.001

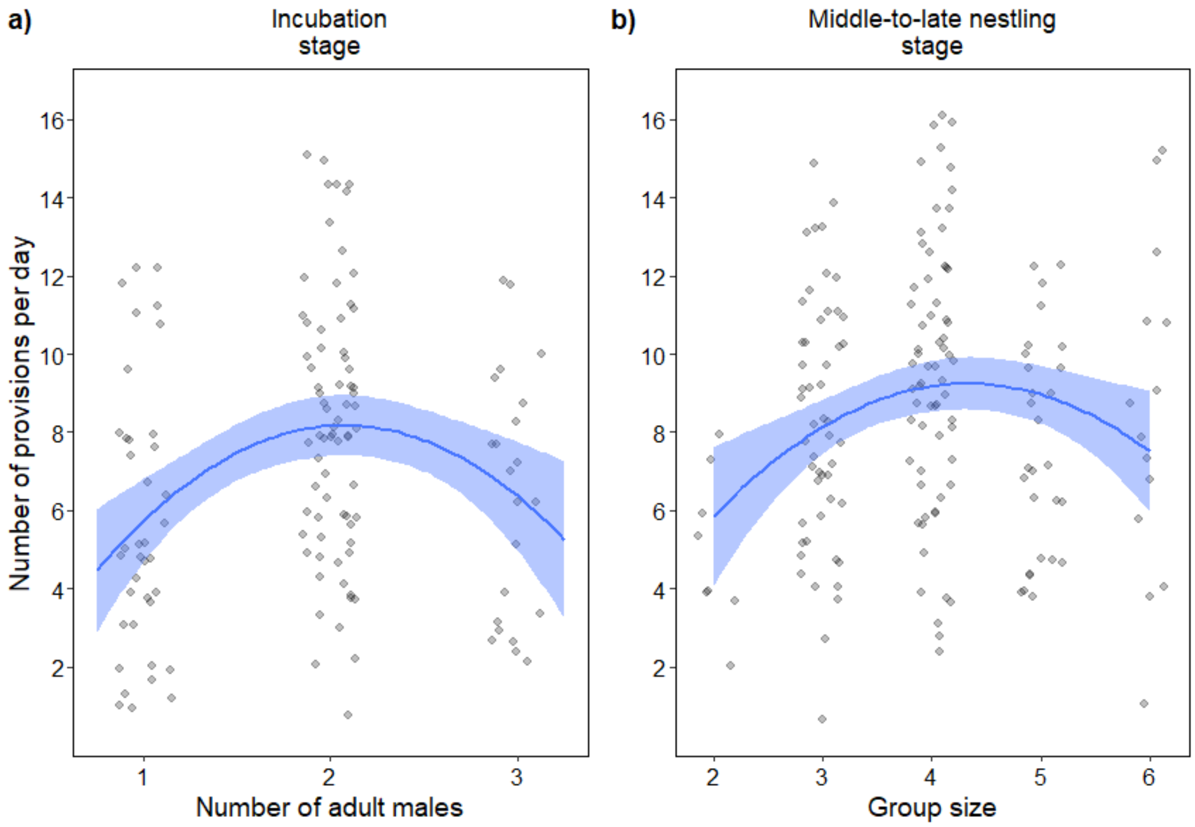


Figure 2.4. Relationship between social factors and the number of daily provisions per group for the incubation and middle-to-late nestling stages. Points represent different groups and are jittered for improved visibility. a) represents the best-fit model from the incubation stage which had the quadratic term for number of adult males as an explanatory variable, and b) represents the best-fit model for the middle-to-late nestling stage which had the quadratic term for group size and an explanatory variable. Blue lines with shaded areas represent the relationship with 95% confidence intervals.

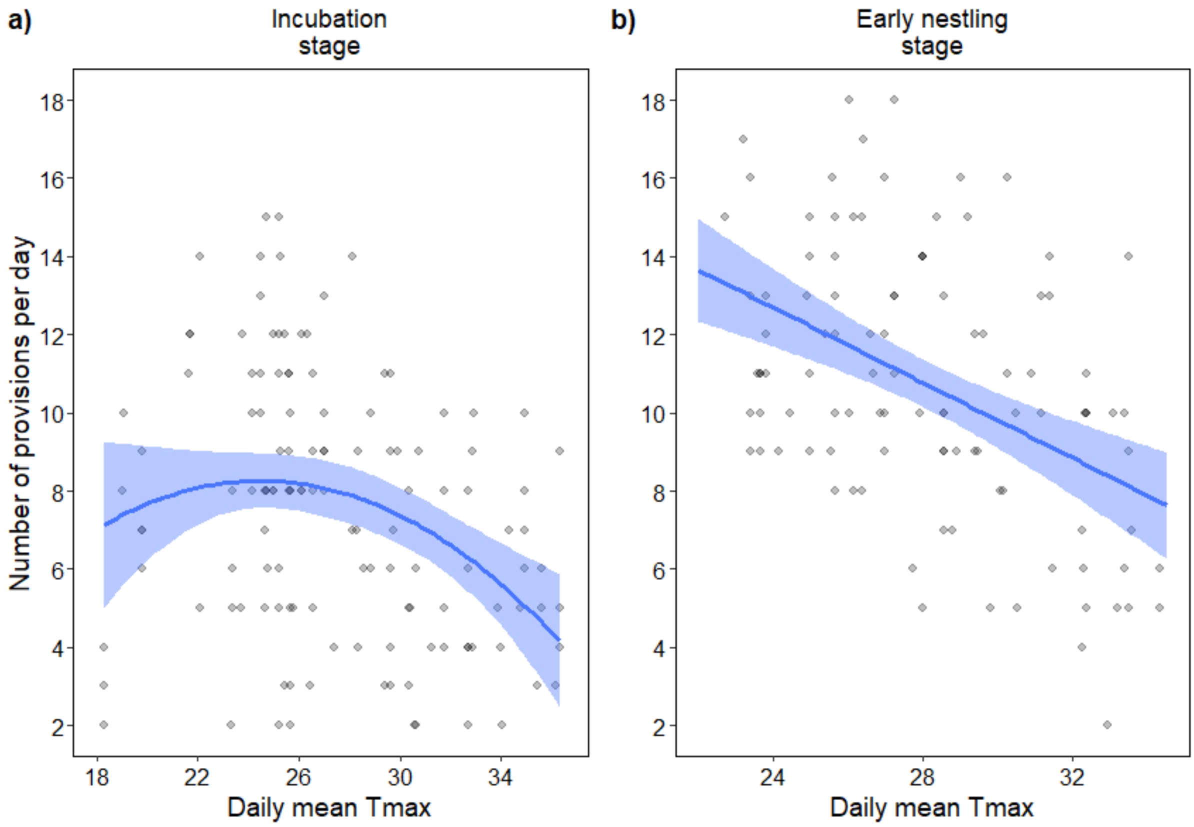


Figure 2.5. The relationship of daily mean maximum temperatures on the number of daily provisions per group for the incubation and early nestling stages. A) represents the best-fit model of the incubation stage which had a quadratic term for daily mean maximum temperature, and b) represents the best-fit model for the early nestling stage which had daily mean maximum temperature as an explanatory variable. Blue lines with shaded areas represent the relationship with 95% confidence intervals.

Individual parcel provisioning rates

The individual parcel provisioning rates were analysed using GLMMs with Truncated-Poisson error structures. During the incubation stage (n = 187 daily individual provisions), juveniles were excluded from the analyses since they did not provision any parcels. The best-fit model for this stage, as well as for the early nestling stage (n = 172 daily individual provisions) where juveniles were included and did provision parcels, both contained the variable of age-sex category (Table S2.6). This indicated that the parcel provisioning rates were associated with the individuals' ages. Adult males had the highest parcel provisioning rates, followed by sub-adults, and then juveniles (during the early nestling stage; Table 2.5; Figure 2.6). During the middle-to-late nestling stage (n = 230 daily individual provisions), however, this was not the case and there were two nested best-fit models. The simpler of the two was the null

model (Table S2.6), indicating that parcel provisioning rate was not associated with age-sex (or nestling age) for this stage.

Table 2.5. Age-sex factors predicting daily individual parcel provisioning rates for all stages, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Categorical variables of females, sub-adult males and juveniles were compared to the reference category of adult males. Variables highlighted in bold have 95% CI which do not cross zero. Incubation stage: n = 282 from 3 years, 14 groups and 40 individuals. Early nestling stage: n = 236 from 3 years, 11 groups and 32 individuals. Middle-to-late nestling stage: n = 564 from 3 years, 12 groups and 46 individuals.

Variable	**Estimate**	**SE**	**95% CI**
Incubation stage			
Sub-adults	**-1.66**	**0.23**	**-2.12 – 1.20**
Early nestling stage			
Sub-adults	**-0.65**	**0.30**	**-1.23 – -0.07**
Juveniles	**-1.03**	**0.41**	**-1.83 – -0.24**

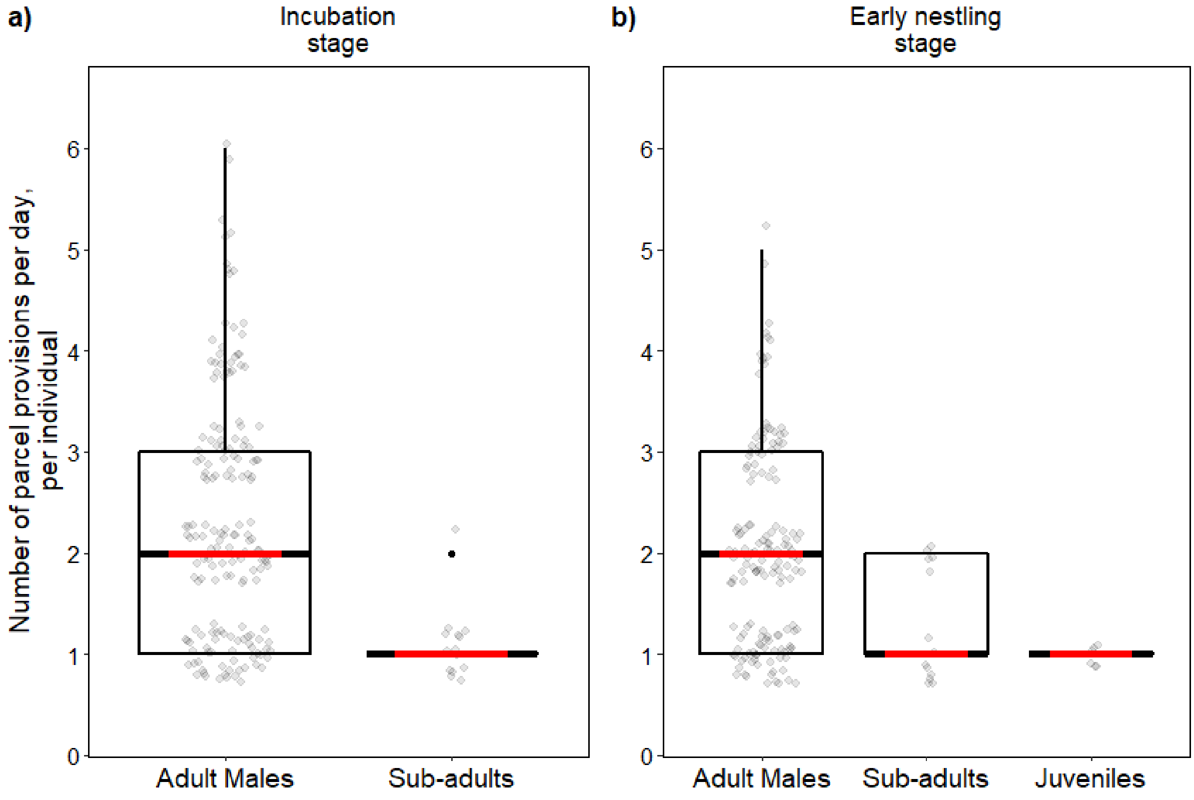


Figure 2.6. Number of daily parcel provisions per individual in relation to their age-sex category for a) incubation, and b) early nestling stages. Boxplots show median values (red lines), first and third quartiles (box) and interquartile range (whiskers). Points are jittered for improved visibility.

Group parcel provisioning rates

The daily parcel provisioning rates for groups were analysed using GLMMs with Truncated-Poisson error structures. During the incubation stage (n = 96 daily group provisions), there was one best-fit model, with a model weight of 0.51, that included the variables of daily mean maximum temperature, number of juveniles, and number of adult males, as well as the quadratic term for number of adult males (Table 2.6). Neither the number of juveniles (estimate = -0.07 ± 0.16, 95% CI = [-0.39 – 0.25]), nor the number of adult males had any clear association with the daily parcel provisioning rate (estimate = 0.08 ± 0.08, 95% CI = [-0.08 – 0.23]) since confidence intervals broadly overlapped zero. However, there was a negative relationship with the quadratic term for the number of adult males (estimate = -0.19 ± 0.06, 95% CI = [-0.31 – -0.07]; Figure 2.7a), indicating that the number of parcel provisions per day initially increased with additional adult males, but this decreased again when numbers were higher. Higher daily mean maximum temperatures were also associated with lower parcel provisioning rates (estimate = -0.14 ± 0.06, 95% CI = [-0.27 – -0.01]; Figure 2.8).

During the early nestling stage (n = 91 daily group provisions), there was one best-fit model with a model weight of 0.83. This model contained the same variables as the incubation stage (daily mean maximum temperature, number of juveniles, number of males, and the quadratic term for number of adult males; Table 2.6), although their relationship with parcel provisioning rates differed slightly. Neither the daily mean maximum temperature (estimate = -0.07 ± 0.06, 95% CI = [-0.19 – 0.05]), nor the number of juveniles (estimate = -0.11 ± 0.09, 95% CI = [-0.06 – 0.28]) had any clear effects on the parcel provisioning rates. However, the number of adult males (estimate = -0.43 ± 0.08, 95% CI = [0.27 – 0.58]), and the quadratic term (estimate = -0.17 ± 0.06, 95% CI = [-0.28 – -0.05]) both had clear associations with the parcel provisioning rates (Figure 2.7b).

During the middle-to-late nestling stage (n = 96 daily group provisions), there was one best-fit model with a model weight of 0.70, that contained the variables of daily mean maximum temperature, number of adult males, and number of juveniles (Table 2.6). Within this model, there were clear positive relationships between the daily parcel provisioning rate and the number of adult males (estimate = 0.39 ± 0.11, 95% CI = [0.17 – 0.61]; Figure 2.7c), as well as the number of juveniles (estimate = 0.23 ± 0.08,

95% CI = [0.07 – 0.39]; Figure 2.9). Daily mean maximum temperatures, however, had no clear effect on the provisioning rate (estimate = 0.02 ± 0.06, 95% CI = [-0.09 – 0.13]) as confidence intervals broadly overlapped zero.

Table 2.6. Top five models for the temperature, social, and life-history effects on the daily parcel provisioning rate per group for all stages. Dev = model deviance, Dtmax = daily mean maximum temperature, AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles. Random terms: year, group identity. Models highlighted in bold were the models used for inference.

Model	k	Dev	AICc	ΔAICc	Model Weight
Incubation stage					
Dtmax + AM + AM^2 + Juv	**7**	**388.8**	**404.10**	**0**	**0.51**
Dtmax + SA	5	396.0	406.63	2.53	0.14
Dtmax + Dtmax ^2 + SA + Juv	7	392.4	407.66	3.57	0.09
Dtmax + SA + Dtmax^2 + Dtmax * SA	7	392.5	407.78	3.68	0.08
Dtmax + AM	5	398.9	409.58	5.49	0.03
Early nestling stage					
Dtmax + AM + AM^2 + Juv	**7**	**325.9**	**341.30**	**0**	**0.83**
Dtmax + AM	5	335.2	345.88	4.58	0.08
Dtmax + AM + Juv + Dtmax * AM	7	331.2	346.52	5.23	0.06
Dtmax + Dtmax^2 + Group size	6	337.4	350.36	9.06	0.01
Dtmax + Group size	5	341.2	351.63	10.63	0.004
Middle-to-late nestling stage					
Dtmax + AM + Juv	**6**	**406.4**	**419.34**	**0**	**0.70**
Dtmax + Group size + Nestling age	6	410.2	423.12	3.78	0.11
Dtmax + Group size + Group size^2	6	410.2	423.13	3.79	0.11
Dtmax + Group size + Nestling age + Dtmax * Group size	7	409.7	424.98	5.64	0.04
Null model	3	420.9	427.13	7.79	0.01

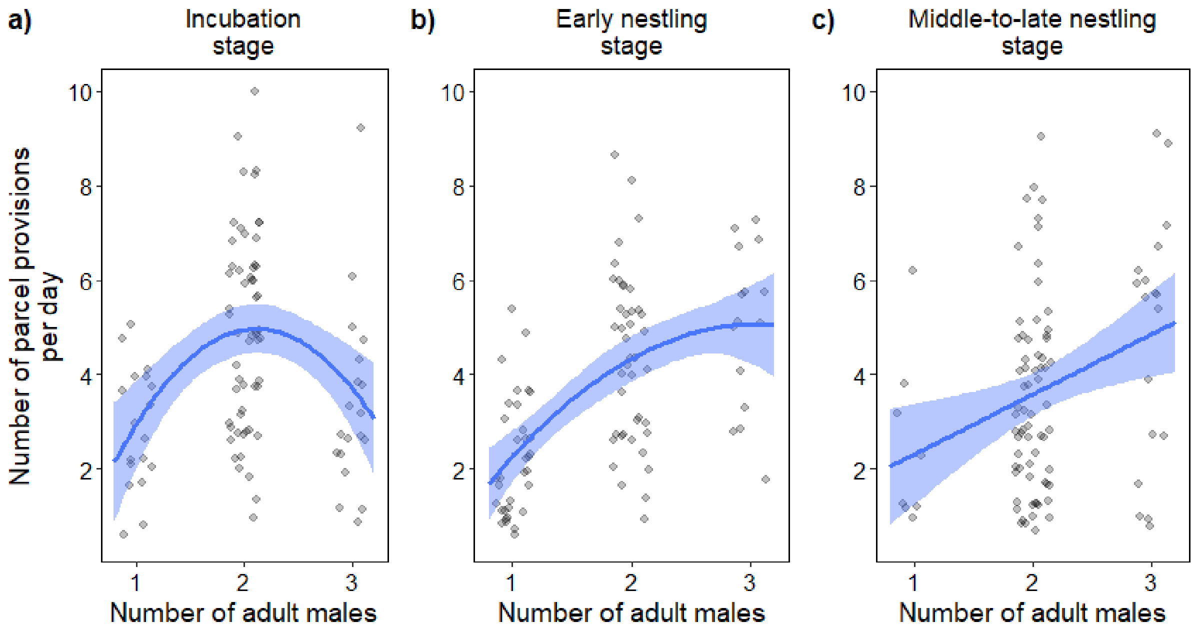


Figure 2.7. Social relationship between the number of adult males and the number of daily provisions per group for all stages. Points are jittered for improved visibility. Blue lines and shaded areas represent the relationship with 95% confidence intervals.

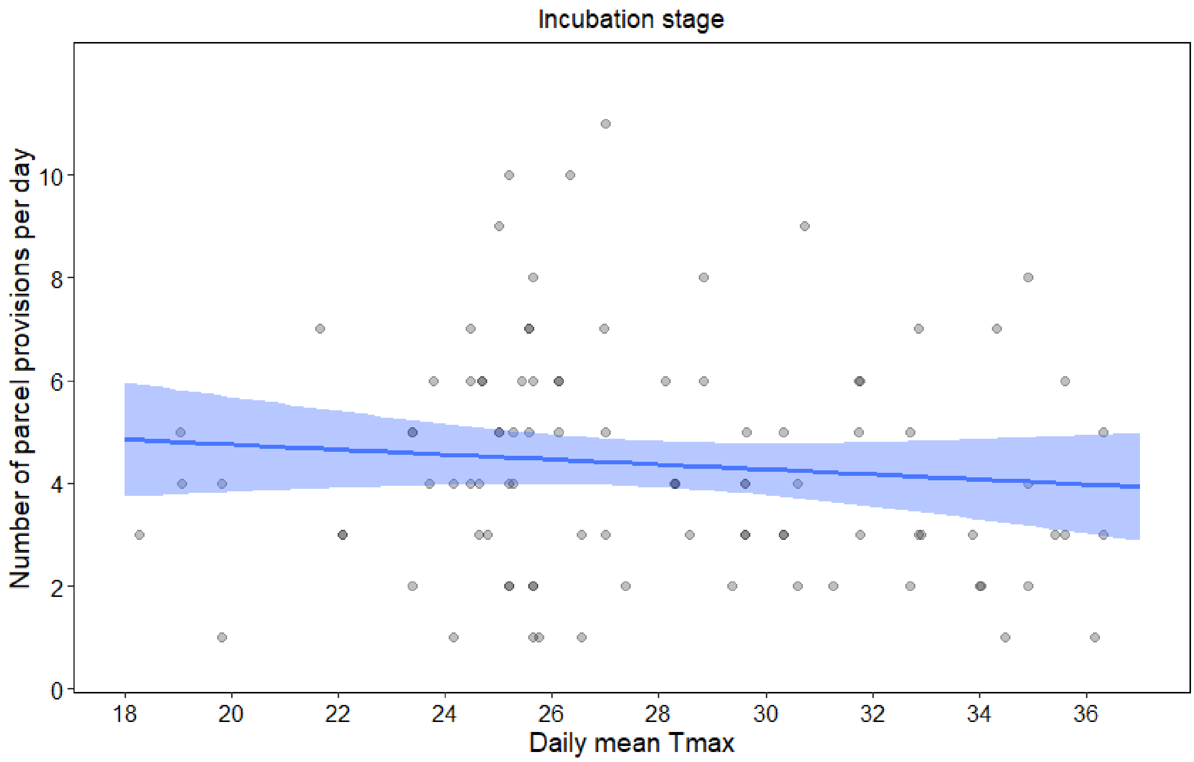


Figure 2.8. The relationship between the daily maximum temperature and the number of daily parcel provisions per group for the incubation stage. Blue line and shaded area represent the relationship with 95% confidence intervals.

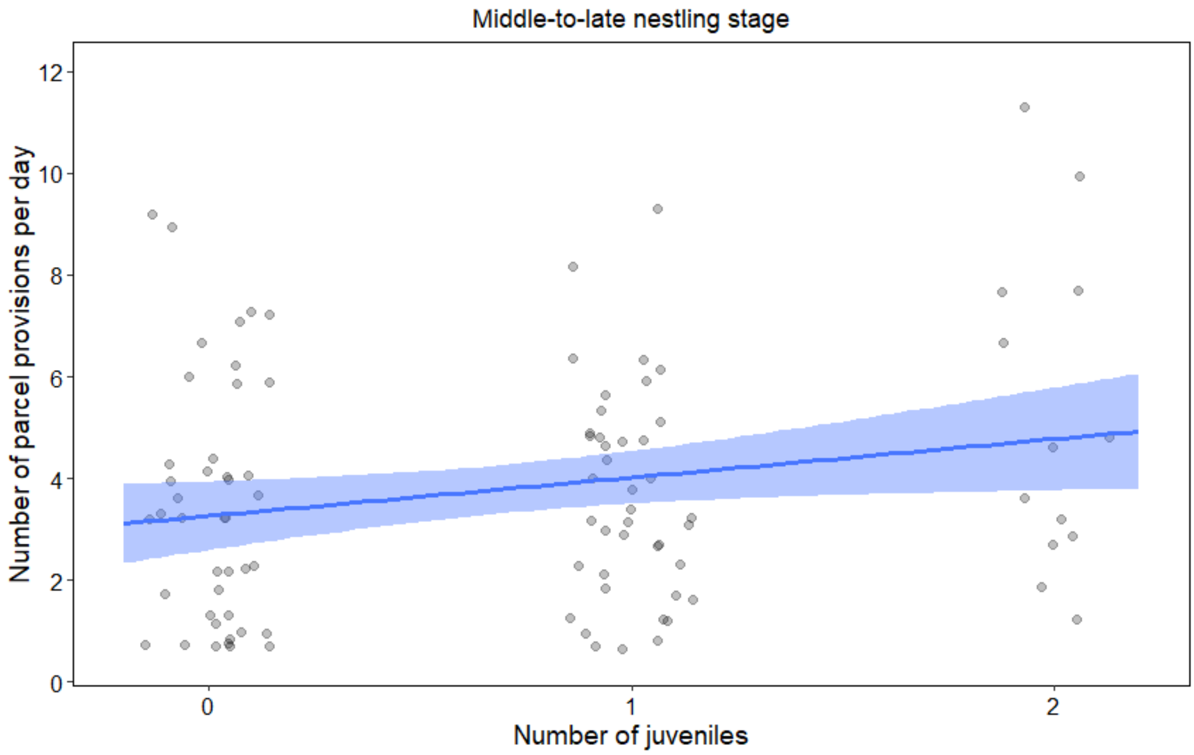


Figure 2.9. The relationship between the number of juveniles and the number of daily parcels provisioned per group during the middle-to-late nestling stage. Points are jittered for improved visibility. Blue line and shaded area represent the relationship with 95% confidence intervals.

Prey type

The prey types provisioned were analysed using GLMMs with binomial (binary) error structures. During the incubation stage (n = 488 individual visits), there were several best-fit models with ΔAICc < 2, including the null model, making them indistinguishable from each other (Table 2.7). This indicated that there were no clear climatic or social predictors for the type of prey provisioned during the incubation stage.

During the early nestling stage (n = 689 individual visits), there was one best-fit model with a model weight of 0.62. This model contained the explanatory variables of age-sex category and hourly maximum temperature, as well as an interaction between the two (Table 2.7). No clear effects were detected for the hourly maximum temperature (estimate = -0.11 ± 0.09, 95% CI = [-0.29 – 0.07]) or for the interactions between age-sex categories and hourly maximum temperature (Sub-adults*Htmax: estimate = -0.62 ± 0.36, 95% CI = [-1.32 – 0.08]; Juveniles*Htmax: estimate = -2.11 ± 1.37, 95% CI = [-4.79 – 0.56]), as they had 95% confidence intervals which broadly overlapped zero. Prey type

provisioned was associated with the age-sex category. Adult males (reference category) were more likely to bring vertebrates compared to that of sub-adults (estimate = -0.92 ± 0.37, 95% CI = [-1.64 – -0.20]; Figure S2.1) and juveniles (estimate = -2.44 ± 1.07, 95% CI = [-4.53 – -0.35]; Figure S2.1).

During the middle-to-late nestling stage (n = 978 individual visits), there were two best-fit models (ΔAICc < 2) with similar weights (0.26 and 0.19), making them indistinguishable from each other. Both models contained the variable of nestling age and differed only by the addition of group size. Therefore, the simpler model was used for further inference (Table 2.7). Within this model, there was a clear negative association of prey type with nestling age (estimate = -0.03 ± 0.004, 95% CI = [-0.04 – -0.02]; Figure 2.10), indicating that as the nestling aged, more invertebrates were provisioned.

Table 2.7. Top five models for the temperature, social, and life-history effects on the type of prey provisioned for all stages. Dev = model deviance, HTmax = daily mean maximum temperature, AM = number of adult males, Juv = number of juveniles. Random terms: year, group identity. Models highlighted in bold were the models used for inference.

Model	k	Dev	AICc	∆AICc	Model Weight
Incubation stage					
Null model	**4**	**660.6**	**668.72**	**0**	**0.24**
Htmax + Htmax^2	6	656.8	669.02	0.30	0.20
Age-sex	5	660.2	670.35	1.63	0.10
Group size	5	660.3	670.39	1.67	0.10
AM	5	660.4	670.56	1.84	0.09
Early nestling stage					
Age-sex + Htmax + Age-sex * Htmax	**9**	**800.1**	**818.35**	**0**	**0.62**
Age-sex + Htmax	7	806.9	821.10	2.76	0.16
Age-sex	6	811.0	823.12	4.77	0.06
Htmax	5	814.0	824.04	5.69	0.04
Htmax + AM + Htmax * AM	7	810.6	824.73	6.38	0.03
Middle-to-late nestling stage					
Nestling age	**5**	**1253.9**	**1263.97**	**0**	**0.26**
Nestling age + Group size	6	1252.5	1264.61	0.64	0.19
Nestling age + Juv	6	1253.2	1265.32	1.35	0.13
Nestling age + Group size + Htmax	7	1251.7	1265.82	1.85	0.10
Nestling age + AM + Htmax	7	1252.3	1266.40	2.43	0.08

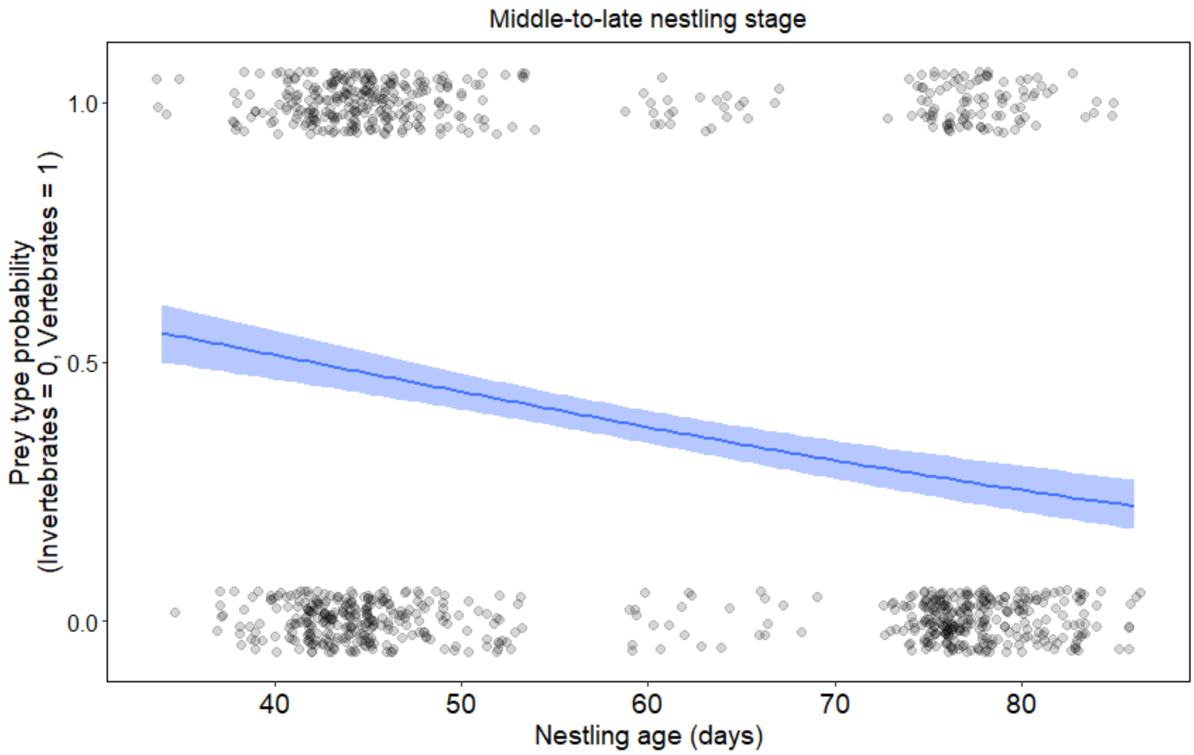


Figure 2.10. Prey type probability (invertebrates = 0, vertebrates = 1) of vertebrates to invertebrates in relation to the nestling age for the middle-to-late nestling stage. Points are jittered for improved visibility. Blue line and shaded area represent the relationship with 95% confidence intervals.

Prey size

The prey sizes provisioned were analysed using CLMMs with ordinal error structures. During the incubation stage (n = 650 individual visits), there were two nested best-fit models (ΔAICc < 2), making them indistinguishable from each other. Both models contained the variables of age-sex category, hourly maximum temperature, and a quadratic term for hourly maximum temperature. They differed only by an interaction between the variables of age-sex category and the quadratic term for hourly maximum temperature, and so the simpler model was used for further inference (Table 2.8). Within this model, there was a clear association between prey size and the age-sex variable. Adult males (reference category), in general, brought prey of greater sizes than sub-adults (estimate = -0.90 ± 0.26, 95% CI = [-1.41 – -0.39]; Figure 2.12a), and juveniles (estimate = -2.07 ± 1.02, 95% CI = [-4.06 – -0.07]; Figure 2.12a). Larger prey items were associated with increasing hourly temperatures (estimate = 0.13 ± 0.06, 95% CI = [0.02 – 0.25]) and there was a clear negative relationship with the quadratic term for hourly maximum temperatures (estimate = -0.14 ± 0.05, 95% CI = [-0.23 – -0.04]; Figure 2.11a).

During the early nestling stage (n = 889 individual visits), there was one best-fit model which contained the same variables as the incubation stage (age-sex category, hourly maximum temperature, and a quadratic term for hourly maximum temperature). There were no clear effects for the hourly maximum temperature (estimate = -0.01 ± 0.05, 95% CI = [-0.12 – 0.09]) as the 95% confidence intervals broadly overlapped zero. There was a clear association between the variable of age-sex category and the prey size provisioned, with adult males (the reference category) provisioning the larger items compared to sub-adults (estimate = -0.79 ± 0.26, 95% CI = [-1.31 – -0.28]; Figure 2.12b) and juveniles (estimate = -1.49 ± 0.51, 95% CI = [-2.48 – -0.50]; Figure 2.12b). There was also a clear negative relationship between the prey size provisioned and the quadratic term for hourly maximum temperature (estimate = -0.10 ± 0.04, 95% CI = [-0.18 – -0.02]; Figure 2.11b).

During the middle-to-late nestling stage (n = 1303 individual visits), we had two nested best-fit models (ΔAICc < 2) with similar model weights (0.41 and 0.24). Both models contained the variables of nestling age, with the more complex of the two containing the group composition variables of number of adult males and number of juveniles. We used the simpler model for further inference (Table 2.8) which indicated a clear negative relationship between nestling age and prey size (estimate = -0.02 ± 0.002, 95% CI = [-0.02 – -0.01]; Figure 2.13).

Table 2.8. Top five models for the temperature, social, and life-history effects on the prey size provisioned for all stages. Dev = model deviance, HTmax = daily mean maximum temperature, AM = number of adult males, Juv = number of juveniles. Random terms: year, group identity. Models highlighted in bold were the models used for inference.

Model	k	AICc	∆AICc	Model Weight
Incubation stage				
Age-sex + Htmax + Htmax^2	**9**	**1354.97**	**0**	**0.64**
Age-sex + Htmax + Htmax^2 + Age-sex * Htmax^2	11	1356.39	1.42	0.31
Age-sex	7	1361.31	6.35	0.03
Age-sex + Htmax	8	1361.65	6.69	0.02
AM + Htmax + Htmax^2	8	1366.96	11.99	0.001
Early nestling stage				
Age-sex + Htmax + Htmax^2	**9**	**1660.56**	**0**	**0.53**
Age-sex + Htmax + Htmax^2 + Age-sex * Htmax^2	11	1662.74	2.18	0.18
Htmax + Htmax^2 + AM + Htmax * AM	9	1663.70	3.14	0.11
Age-sex + Htmax + Htmax^2 + Age-sex * Htmax	11	1664.44	3.88	0.08
Age-sex	7	1665.66	5.10	0.04
Middle-to-late nestling stage				
Nestling age	**6**	**2674.00**	**0**	**0.44**
Nestling age + AM + Juv	8	2675.09	1.09	0.25
Nestling age + Htmax	7	2676.02	2.02	0.16
Nestling age + Group size + Htmax	8	2677.74	3.74	0.07
Nestling age + Htmax + Htmax^2	8	2678.04	4.04	0.06

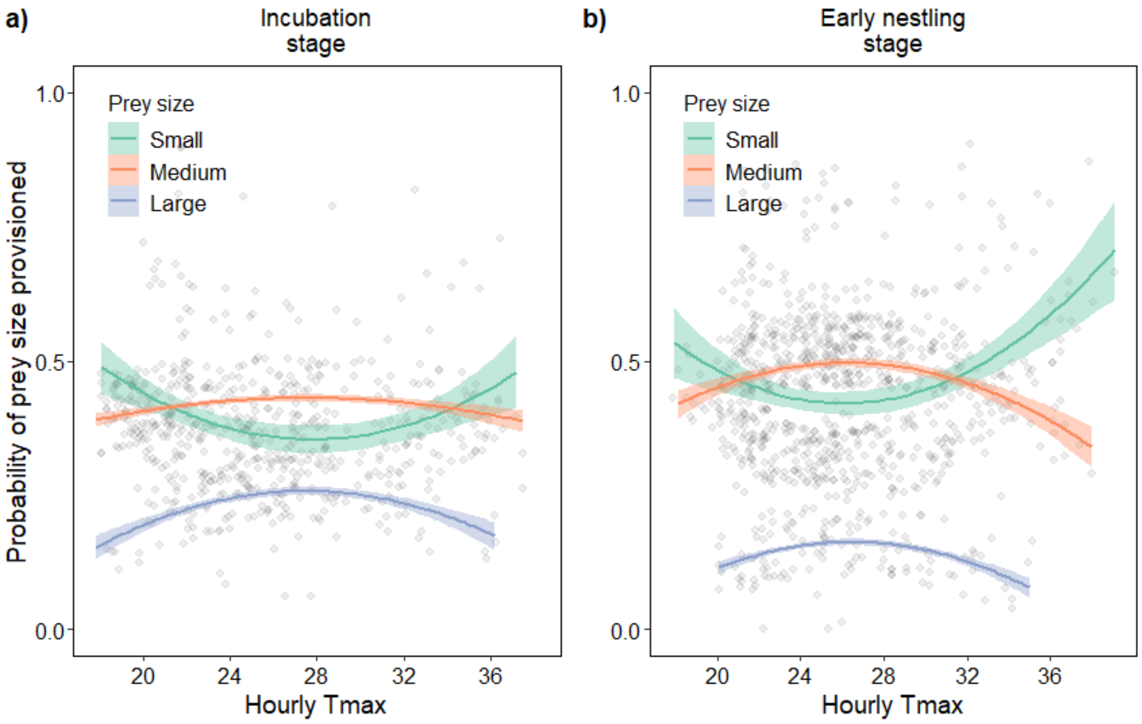


Figure 2.11. The predicted relationship between hourly maximum temperature and the probability of each prey size category being provisioned for the incubation and early nestling stages. Points represent predicted probability and are jittered for improved visibility. Lines represent predicted relationship with 95% confidence intervals.

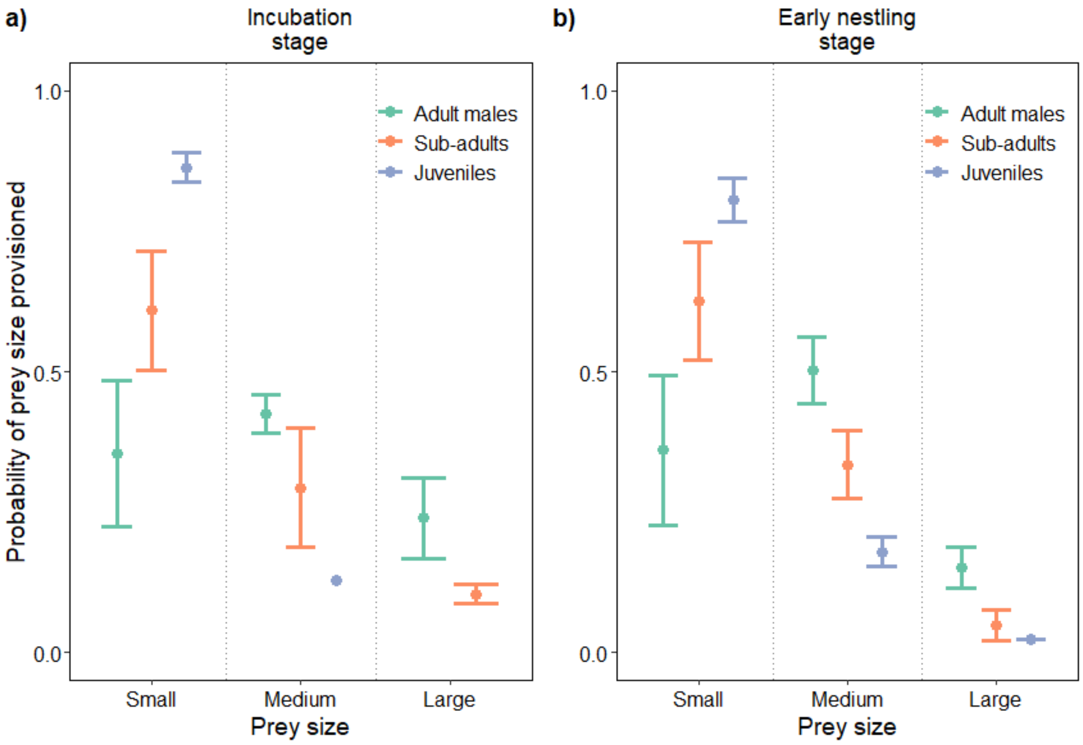


Figure 2.12. Probability of different food sizes being brought for each age-sex category during the incubation and early nestling stages. Points represent mean predicted values and bars represent the 95% confidence intervals.

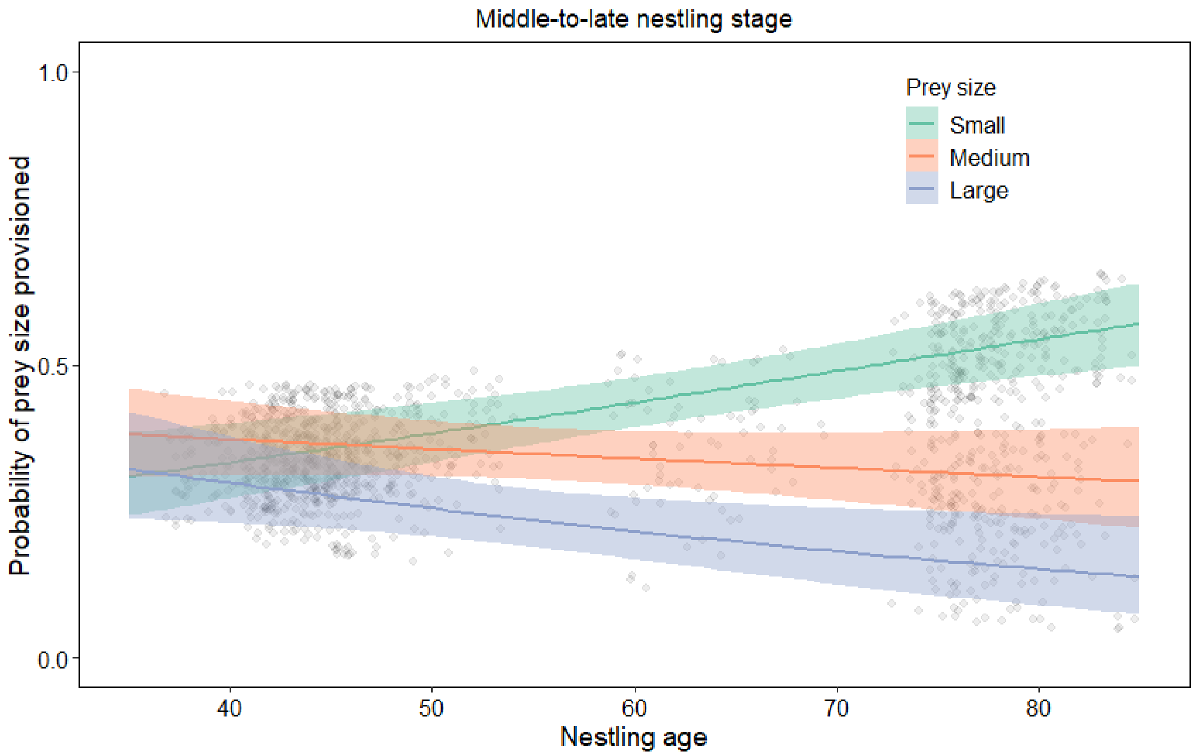


Figure 2.13. The predicted relationship between nestling age and prey size for the middle-to-late nestling stage. Points represent predicted probability and lines represent predicted relationship with 95% confidence intervals.

Discussion

We investigated how group member age, group size, group composition and air temperature influenced the individual and group provisioning efforts of a long-lived cooperative breeder, the southern ground-hornbill, and whether social factors could mitigate the adverse effects of high temperatures. Our data showed that, as predicted, larger group sizes were in general associated with higher group provisioning rates. In addition, group member age was associated with higher provisioning effort, with older birds having both higher rates of provisioning, and provisioning more vertebrates and larger prey items than younger individuals. However, individual carers decrease their workloads when there are additional helpers (i.e. load-lightening). High temperatures were associated with reduced provisioning rates and smaller prey items, supporting the expectation that increased temperatures would reduce nest attendance. However, there was no evidence to suggest that having additional group members can mitigate these adverse temperature effects.

Member age, group size and group composition

In most cooperative breeders, a significant number of group members are retained offspring from previous broods (Riehl, 2017). This means that groups can contain members of different ages and experience, which may contribute varying amounts. Our results confirmed this expectation, and showed that group member age was a strong predictor of individual food and parcel (i.e. nest material) provisioning rates, and of the prey type and prey size provisioned to the nest. Adults provisioned the most food and parcels during all nesting stages (except during the middle-to-late nestling stage for parcel provisions where we found no difference) and were also more likely to provision larger prey items and more vertebrates (particularly during the early nestling stage) than sub-adults and juveniles. A higher provisioning rate by adults could be explained by one of the adult males and the female being the breeders, and hence being expected to have the highest fitness gains from provisioning and successfully reproducing (Komdeur, 2006; Barati et al., 2018). Additionally, although ground-hornbills are generalist feeders (Combrink, 2016), finding and catching larger prey items (often vertebrates such as scrub hares, tortoises, and venomous snakes) may require skills that are acquired with age and experience, or learnt from other individuals (Thornton, 2008; Maynard et al., 2021). Further detailed research into what prey species is disproportionately provided by adults versus younger birds would provide an interesting insight into which species require the most experience to find, catch and handle.

We found that daily provisioning rates per individual were negatively associated with group size. This suggests a load-lightening strategy, where individual nest provisioning decreases with additional help. In long-lived cooperative breeders, individuals are expected to shift their investment towards self-maintenance over helping when the risk of nestling starvation is low, such as when there are additional group members to contribute (Johnstone, 2011; Savage et al., 2017; MacLeod & Brouwer, 2018; van Boheemen et al., 2019). However, the load-lightening effects found here were stronger for sub-adults than adults males. Sub-adults do not parent offspring, so their fitness gains are consistently lower than adult males, one of which is guaranteed to be the father and who therefore likely contributes the most due to the high fitness benefits gained (Komdeur, 2006; Barati et al., 2018). Like juveniles, sub-adults may also lack mature foraging skills, meaning that provisioning comes at a high cost as well

as providing fewer benefits; therefore, reducing provisioning rates in the presence of additional group members may allow sub-adults to improve their own body condition (Woxvold, 2004; Woxvold, Mulder & Magrath, 2006; Pike et al., 2019).

As a result of these varying individual contributions, we found evidence that both prey and parcel provisioning rates increased with the number of adult males and with overall group size. However, significant quadratic terms indicated that with more than two adult males present and in larger groups, the total prey and parcel provisions peaked and reduced. This might arise from intra-group conflict where the breeding male attempts to keep other adult males away from the incubating and brooding female (see Lardy et al., 2012; Paquet et al., 2015). Mating opportunities are scarce for male ground-hornbills (since each group generally only has a single female), therefore warranting female protection, and our trail camera footage provided some evidence for this as aggression was occasionally observed between males around the nest (KMM, pers. obs.). Alternatively, it may also arise from the poorer coordination that can occur from additional members attempting to balance self-investment vs provisioning efforts during group behaviours (Dostálková & Špinka, 2007; Raihani et al., 2010). For example, if an individual has collected a prey item but waits for the rest of the group to provision, that individual may be required to eat it themselves to maintain their own body condition before they have the opportunity to provision it to the nest. Regardless, the additive effects of prey and parcel provisions suggest that nestlings do benefit from the presence of additional group members, particularly during the middle-to-late nestling stage, where the relationship was strongest and also when avian growth rates are considered most rapid (Gebhardt-Henrich & Richner, 1998; Cunningham, Martin, et al., 2013). This is consistent with Chapter 3 which showed that increases in the number of adult males and juveniles were associated with longer nestling tarsus lengths; however, considering that juveniles contribute less, it is likely that they are causally associated with group and/or territory quality.

In summary, we found support that ground-hornbills are using both load-lightening and additive provisioning strategies simultaneously. This is consistent with the growing evidence from other studies on avian cooperative breeders that found similar results, suggesting that there are both individual and group benefits to cooperative breeding (Kingma et al., 2010; van Boheemen et al., 2019). However, our

results demonstrate that these strategies are not fixed throughout the breeding period (as we found no load-lightening during the middle-to-late nestling stage, and different levels of additive care during different stages). This might arise from the variable demands of offspring at different stages (e.g. the late nestling stage might be a time when demand is at its peak and thus carers cannot flexibly adjust the amount of care provided). Regardless, these results suggest that ground-hornbills use flexible provisioning strategies.

Temperature

As expected, increasing temperatures were negatively associated with prey and parcel provisioning rates, and reductions in the size of prey provisioned to the nest. However, this effect was only found during the incubation and early nestling stages. These stages coincided with the hottest periods where the daily mean maximum temperatures were 27.53°C and 28.06°C, respectively. The increased thermoregulatory requirement associated with high temperatures likely led birds to spend more time seeking shade and engaging in heat dissipation behaviours rather than foraging, probably driving the reduced provisioning rates we observed (Kemp & Kemp, 1980; Wolf, 2000; Wiley & Ridley, 2016; Conradie et al., 2019; Nord & Nilsson, 2019; Cunningham, Gardner & Martin, 2021). In southern pied babblers *Turdoides bicolor*, foraging efficiency is lower at higher temperatures, suggested to be as a result of birds being unable to pant and forage at the same time (du Plessis et al., 2012). This may also be the case for ground-hornbills, as they begin heat dissipation behaviours at around 26°C (see Janse van Vuuren, Kemp & McKechnie, 2020), which is lower than the mean maximum temperatures mentioned above (Table 2.1). Our results on the size of prey provisioned are consistent with this suggestion, showing that smaller prey items, which are presumably more abundant and easier to catch, were more likely to be provisioned at higher temperatures (Figure 2.11). Larger prey items, such as reptiles and mammals, may retreat to microsites such as subterranean burrows during high temperatures, making them inaccessible and so reducing their availability (McMaster & Downs, 2013; Martin, Cunningham & Hockey, 2015). The negative association between parcel provisioning rates and increasing temperatures was weaker than prey provisioning rates, and only occurred during the incubation stage. This is likely explained by nest lining being easier and less costly than food collection

during periods of high temperatures, since ground-hornbills typically collect fallen leaves from mopane *Colophospermum mopane* and apple-leaf *Philenoptera violacea* trees to line nests, which are usually abundant in shady areas near nesting sites, making them easily accessible at all times of day and at all temperatures.

We found no clear evidence to support the hypothesis that helpers buffer against the effects of high temperature. Cooperative breeding has been suggested to be a mechanism to facilitate successful reproduction in harsh climates, whereby additional group members particularly help to maintain adequate feeding rates during difficult conditions (Rubenstein & Lovette, 2007; Covas, Du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). Despite cooperation in hornbills being thought to have evolved in relatively mesic environments (Gonzalez, Sheldon & Tobias, 2013), ground-hornbills inhabit mainly semi-arid regions. We suggest that the absence we observed of any buffering effects may result from the slow life-history and longevity of ground-hornbills, leading to individuals reducing the energetic costs involved with helping in order to favour self-maintenance and survival. This trade-off may be further compounded by reduced coordination from the synchronous provisioning behaviours of ground-hornbills, where individuals move together as a group and wait for other group members to catch up with them before provisioning (Dostálková & Špinka, 2007; Raihani et al., 2010). This may be particularly difficult to coordinate during high temperatures, as individuals each have their own thermoregulatory requirements and optimal activity schedules, which may not align with those of other individuals (Raihani et al., 2010; Cunningham, Thompson & McKechnie, 2017).

During the middle-to-late nestling stage, we found that the strongest predictor of the type and size of prey was nestling age, whereas temperature did not predict any metrics of provisioning efforts. This was unexpected, and we suspect it may be due to the milder ‘autumn’ temperatures associated with this late stage of the breeding season (see Table 2.1). Surprisingly, the association with prey type and size was for more invertebrates and smaller prey items to be provisioned with increasing nestling age, despite the increased demands of larger nestlings. Studies on other bird species have found that prior to fledging, carers decrease their provisioning rates to encourage nestlings to fledge (Morbey et al., 1999; Gray & Hamer, 2001), and to reduce mass to optimise wing loading in newly fledged chicks (Shultz &

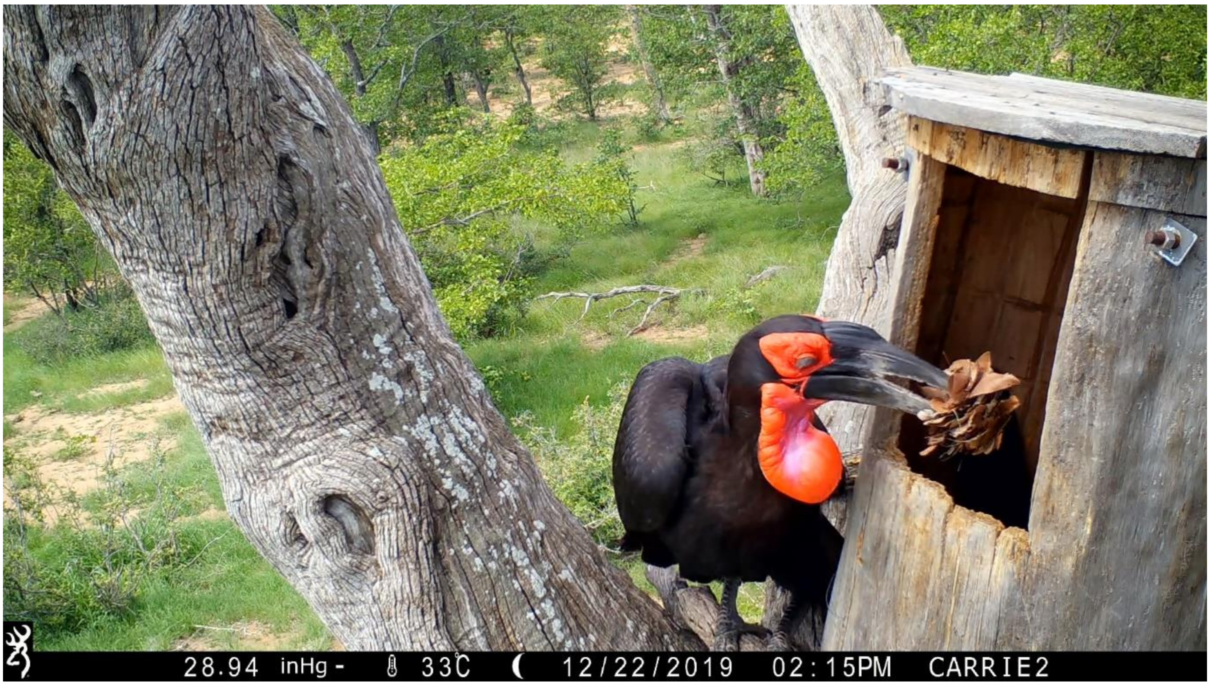
Sydeman, 1997; Morbey et al., 1999; Moeller & Ritchison, 2019). This may explain the pattern we observed of smaller prey being fed to larger chicks; anecdotal evidence from our trail cameras supports this suggestion, as adults were sometimes observed arriving at nests containing a larger chick but rather than feeding nestlings immediately, would stand nearby and produce contact calls, delaying and sometimes entirely foregoing feeding the chick (KMM, pers. obs.).

Conclusion

Our study provides evidence that provisioning decisions towards reproduction differ between southern ground-hornbill individuals of different ages, and reveals that load-lightening and additive provisioning strategies occur simultaneously in this species. We found that high temperatures were generally negatively associated with provisioning rates and the size of prey provisioned to the nest. This highlights the sensitivity of this vulnerable species to the predicted temperature increases associated with climate change (IPCC, 2021). Our results showed that adult males are important for provisioning, but that the additive effects they provided were not enough to buffer the reduction in provisioning associated with high temperatures. Hence, a species' life-history strategy, as well as other factors involved in offspring provisioning (such as prey type and size, and nestling age), should be collectively considered when predicting contributions to provisioning, as well as the responses of helpers to environmental conditions. These results are nonetheless consistent with other recent studies that found a similar absence of buffering effects of additional group members in two other South African bird species (Bourne, Ridley, Spottiswoode, et al., 2021; D'Amelio et al., 2022), and agrees with the suggestion that the benefits of cooperative breeding in hornbills may be less relevant for reproduction, particularly under harsh conditions (while they still may provide benefits to other group behaviours; Gonzalez, Sheldon & Tobias, 2013). However, when conditions are ideal, social factors can contribute to improving the growth and condition of nestlings. Additional studies on cooperative provisioning under varying climatic conditions in other long-lived cooperative breeders are needed to broaden our understanding of the association between climate and cooperative breeding.

Appendix

Fieldwork insight 2. Trail camera footage from one of the nests showing an adult male provisioning a chick during the middle-to-late nestling stage



Fieldwork insight 3. Trail camera footage showing an adult male provisioning a parcel to the nest

Fieldwork insight 4. Checking nests and installing cameras high up in the trees to get a better insight into the private lives of the birds.

Table S2.1. A description of the different analyses conducted, and explanatory variables used within the different models

Type	**Variable**	**Explanation**
Response	Prey daily provisioning rate	The number of prey provisions per full day (Truncated-Poisson)
	Parcel daily delivery rate	The number of parcel provisions per full day (Truncated-Poisson)
	Prey type (1/0)	The type of prey item provisioned – vertebrate (1) or invertebrate (0; Binary)
	Prey size	The size of prey provisioned – small, medium, or large (Ordinal)
Explanatory Question i) only	Age-sex	The combination of age and sex of individuals within the groups (Categorical): Breeding female, adult male, sub-adult male and juvenile.
Question i) and ii)	Nestling age	The age of the nestling during the middle-to-late-stage time-period (Continuous)
Question ii) only	Number of adult males + quadratic effect	The number of adult males within the group during breeding (Discrete)
	Number of sub-adults + quadratic effect	The number of sub-adults within the group during breeding (Discrete)
	Number of juveniles + quadratic effect	The number of juveniles within the group during breeding (Discrete)
	Group size + quadratic effect	The number of individuals within each group (Discrete)
	Daily maximum temperatures + quadratic effect	The daily maximum temperatures used to investigate the effects on prey and parcel daily provisioning rates (Continuous)
	Hourly maximum temperatures + quadratic effect	The hourly maximum temperatures used to investigate the temperature effects on prey type and prey size (Continuous)
Interactions	Maximum temperatures * Group size and composition	The interaction between the maximum temperatures (daily and hourly) with the group size, and the number of adult males, sub-adults and juveniles.

Random	Year	The year in which the breeding attempt occurred
	Group	The name/identity of the group
	ID	The name/identity of the individual (nested within Group)

Individual prey provisioning rates

Table S2.2. Top models for individual contributions to prey provisioning rate, for all stages. Dev = model deviance. Random terms: year, group identity and individual identity. Models highlighted in bold were models used for interpretation.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
			Incubation stage		
Age-sex	**6**	**1020.3**	**1032.56**	**0**	**0.99**
Null model	4	1037.7	1045.83	13.27	0.01
			Early nestling stage		
Age-sex	**6**	**928.8**	**941.18**	**0**	**0.99**
Null model	4	944.8	953.02	11.84	0.01
			Middle-to-late nestling stage		
Age-sex	**7**	**1819.9**	**1834.13**	**0**	**0.57**
Age-sex + Nestling age	8	1819.5	1835.71	1.58	0.26
Null model	4	1829.3	1837.41	3.28	0.11
Age-sex + Nestling age + Age-sex * Nestling age	11	1816.3	1838.82	4.68	0.06

Group prey provisioning rates

Incubation stage:

Table S2.3. Factors predicting the group prey daily provisioning rate for the incubation stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 132 from 3 years and 14 groups. Model was run with a log link function. Dtmax = daily maximum temperature, AM = number of adult males, Juv = number of juveniles, ^2 = quadratic term.

Variable	**Estimate**	**SE**	**95% CI**
Dtmax	**-0.15**	**0.04**	**-0.23 – -0.07**
Dtmax^2	**-0.12**	**0.03**	**-0.19 – -0.06**
AM	**0.12**	**0.05**	**0.02 – 0.22**
AM^2	**-0.15**	**0.04**	**-0.23 – -0.07**
Juv	-0.11	0.07	-0.24 – 0.02

Early nestling stage:

Table S2.4. Factors affecting the group daily prey provisioning rate for the early nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 104 from 3 years and 11 groups. Model was run with a sqrt link function. Dtmax = daily mean maximum temperature.

Variable	**Estimate**	**SE**	**95% CI**
Dtmax	**-0.23**	**0.05**	**-0.34 – -0.13**
Group size	0.12	0.10	-0.06 – 0.31

Middle-to-late nestling stage:

Table S2.5. Factors predicting the group daily prey provisioning rate for the middle-to-late nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 173 from 3 years and 12 groups. Model was run with a log link function. Dtmax = daily mean maximum temperature, ^2 = quadratic term.

Variable	Estimate	SE	95% CI
Dtmax	-0.03	0.05	-0.12 – 0.06
Group size	**0.14**	**0.05**	**0.05 – 0.23**
Group size^2	**-0.12**	**0.03**	**-0.19 – -0.06**

Individual parcel provisioning rates

Table S2.6. Top models for individual contributions to parcel provisioning rate, for all stages. Dev = model deviance. Random terms: year, group identity and individual identity. Models highlighted in bold were models used for interpretation.

Model	k	Dev	AICc	∆AICc	Model Weight
Incubation stage					
Age-sex	**5**	**513.2**	**523.55**	**0**	**0.99**
Null model	4	530.8	538.98	15.42	0.01
Early nestling stage					
Age-sex	**7**	**459.8**	**474.52**	**0**	**0.91**
Null model	5	468.7	479.10	4.58	0.09
Middle-to-late nestling stage					
Null model	**5**	**540.7**	**550.99**	**0**	**0.58**
Age-sex + Nestling age	9	534.1	552.90	1.91	0.23
Age-sex	8	536.7	553.37	2.38	0.18
Age-sex + Nestling age + Age-sex * Nestling age	12	533.2	558.66	7.67	0.01

Group parcel provisioning rates

Incubation stage:

Table S2.7. Factors predicting the group daily parcel provisioning rate for the incubation stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 96 from 3 years and 11 groups. Model was run with a log link function. Dtmax = daily mean maximum temperature, AM = number of adult males, Juv = number of juveniles, ^2 = quadratic term.

Variable	**Estimate**	**SE**	**95% CI**
Dtmax	**-0.14**	**0.06**	**-0.27 – -0.01**
AM	0.08	0.08	-0.08 – 0.23
AM^2	**-0.19**	**0.06**	**-0.31 – -0.07**
Juv	-0.07	0.16	-0.39 – 0.25

Early nestling stage:

Table S2.8. Factors predicting the group daily parcel provisioning rate for the early nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 91 from 3 years and 11 groups. Model was run with a log link function. Dtmax = daily mean maximum temperature, AM = number of adult males, Juv = number of juveniles, ^2 = quadratic term.

Variable	**Estimate**	**SE**	**95% CI**
Dtmax	-0.07	0.06	-0.19 – 0.05
AM	**0.43**	**0.08**	**0.27 – 0.58**
AM^2	**-0.17**	**0.06**	**-0.28 – -0.05**
Juv	0.11	0.09	-0.06 – 0.28

Middle-to-late nestling stage:

Table S2.9. Factors predicting the group daily parcel provisioning rate for the middle-to-late nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 96 from 3 years and 8 groups. Model was run with a log link function. Dtmax = daily maximum temperature, AM = number of adult males, Juv = number of juveniles.

Variable	**Estimate**	**SE**	**95% CI**
Dtmax	0.02	0.06	-0.09 – 0.13
AM	**0.39**	**0.11**	**0.17 – 0.61**
Juv	**0.23**	**0.08**	**0.07 – 0.39**

Prey type

Early nestling stage:

Table S2.10. Factors predicting the prey type during the early nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 978 from 3 years, 12 groups and 45 individuals. Model was run with a log link function. Htmax = hourly maximum temperature, AM = number of adult males.

Variable	**Estimate**	**SE**	**95% CI**
Sub-adults	**-0.92**	**0.37**	**-1.64 – -0.20**
Juveniles	**-2.44**	**1.07**	**-4.53 – -0.35**
Htmax	-0.11	0.09	-0.29 – 0.07
Sub-adults * Htmax	-0.62	0.36	-1.32 – 0.08
Juveniles * Htmax	-2.11	1.37	-4.79 – 0.56

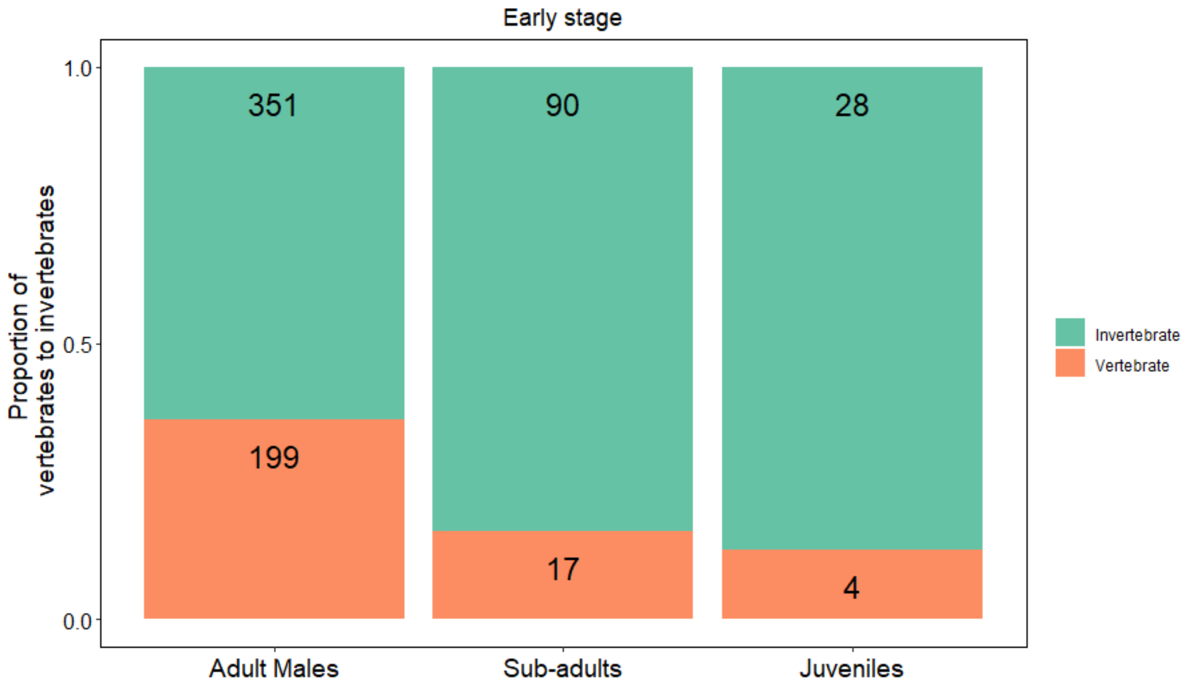


Figure S2.1. Proportion of vertebrates to invertebrates for each age-sex category for the early stage. Values represent the number of vertebrate and invertebrate observations.

Middle-to-late nestling stage:

Table S2.11. Factors predicting the prey type during the middle-to-late nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 978 from 3 years, 12 groups and 45 individuals. Model was run with a log link function. Htmax = hourly maximum temperature, AM = number of adult males.

Variable	**Estimate**	**SE**	**95% CI**
Nestling age	**-0.03**	**0.004**	**-0.04 – -0.02**
Group size	-0.13	0.10	-0.32 – 0.07
Htmax	0.06	0.07	-0.07 – 0.20

Prey size

Incubation stage:

Table S2.12. Factors predicting the prey size for the incubation stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. Htmax = hourly maximum temperature. N = 650 from 3 years, 15 groups and 41 individuals. Model was run with a loglog link function.

Variable	**Estimate**	**SE**	**95% CI**
Sub-adults	**-0.90**	**0.26**	**-1.41 – -0.39**
Juveniles	**-2.07**	**1.02**	**-4.06 – -0.07**
Htmax	**0.13**	**0.06**	**0.02 – 0.25**
Htmax^2	**-0.14**	**0.05**	**-0.23 – -0.04**
Small | Medium (threshold)	-0.17	0.15	-0.46 – 0.11
Medium | Large (threshold)	1.29	0.16	0.97 – 1.61

Early nestling stage:

Table S2.13. Factors predicting the prey size for the early nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. Htmax = hourly maximum temperature. N = 889 from 3 years, 11 groups and 33 individuals. Model was run with a loglog link function.

Variable	**Estimate**	**SE**	**95% CI**
Sub-adults	**-0.79**	**0.26**	**-1.31 – 0.28**
Juveniles	**-1.49**	**0.51**	**-2.48 – -0.50**
Htmax	-0.01	0.05	-0.12 – 0.09
Htmax^2	**-0.10**	**0.04**	**-0.18 – -0.02**
Small | Medium (threshold)	-0.16	0.26	-0.67 – 0.35
Medium | Large (threshold)	**1.82**	**0.27**	**1.29 – 2.56**

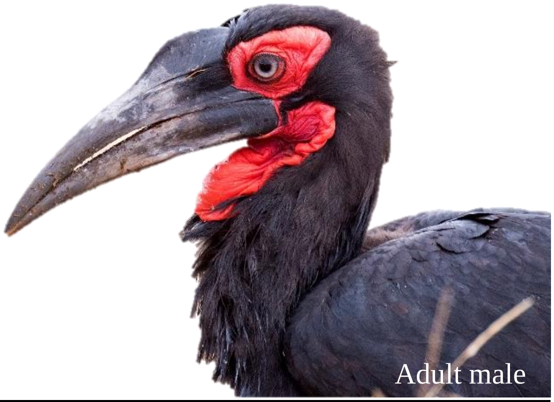
Middle-to-late nestling stage:

Table S2.14. Factors predicting the prey size for the middle-to-late nestling stage, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). N = 1303 from 3 years, 13 groups and 50 individuals. Model was run with a loglog link function.

Variable	**Estimate**	**SE**	**95% CI**
Nestling age	**-0.02**	**0.002**	**-0.02 – -0.01**
Small | Medium (threshold)	**-0.80**	**0.20**	**-1.20 – -0.41**
Medium | Large (threshold)	**0.46**	**0.21**	**0.05 – 0.86**

Part I: Reproduction

Chapter 3



Hot-dry weather is associated with poorer reproductive outcomes regardless of group composition in the long-lived, cooperatively breeding southern ground-hornbill *Bucorvus leadbeateri*

An example of what we found during a routine nest check for Thornybush group in April 2019. *This is one of the only natural nests used throughout the study site. This nestling was 75 days old and almost ready to fledge. It was temporarily removed from the nest to be measured, weighed, and ringed. Photo: Kyle-Mark Middleton*

Abstract

1. Anthropogenic climate change is driving increases in temperature and extreme weather events, and understanding how species respond to these conditions has become of major importance. Cooperative breeding is common in regions experiencing higher environmental variation and has been suggested to mitigate harsh climatic conditions, but results have been inconsistent and differ across taxa, perhaps because variation in life-history strategy influences breeders' and helpers' investment decisions and so the effect of helpers. In addition, long-lived, slow-developing species can contain group members of varying age and experience which might modulate group size effects.
2. Here, we examined how different reproductive parameters are associated with climatic, social, and life-history factors in a large, slow-developing, and long-lived cooperative breeder, the southern ground-hornbill (*Bucorvus leadbeateri*). Groups in this species typically contain members that can be morphologically classified into distinct age classes (adult, sub-adult, and juvenile), allowing us to examine the effects of members of different ages on reproduction, and whether they modulate the effects of environmental conditions.
3. We used 17 years of breeding data collected from 23 territorial groups within the Greater Kruger National Park, South Africa, to test for associations between climate and group composition and breeding probability, laying date, fledging success, and nestling growth.
4. We found that, regardless of group composition, higher winter and breeding season temperatures were associated with later laying dates and declines in nestling body mass, while low winter rainfall was associated with decreased breeding probability. There was no clear association between group composition and fledging probability. The number of adult helpers was associated with longer nestling tarsi, while the number of juvenile group members (and, to a lesser extent, sub-adults) was associated with higher breeding probability, earlier laying, and longer nestling tarsi. However, we suggest that the associations with number of juveniles and sub-adults more likely reflect group or territory quality than contributions by these younger individuals.
5. We conclude that hot and dry conditions are associated with poorer breeding performance in southern ground-hornbills, and that this negative association is not meaningfully mitigated by the

composition of cooperative groups. We expect that further research on other long-lived species will produce similar findings and contribute to broaden our understanding of this social system and its biogeography.

Keywords: Cooperative breeding, reproduction, age, temperature, rainfall, climate mitigation

Introduction

Anthropogenic climate change is leading to an increase in global temperatures and weather extremes, such as droughts and hot spells (IPCC, 2021). This is expected to be particularly important in arid and semi-arid environments, as climate change exacerbates the already high temperatures and variable rainfall characteristics of those habitats (Huang, Guan & Ji, 2012; Ji et al., 2014; Huang et al., 2016; van Wilgen et al., 2016; Dube & Nhamo, 2020; Mbokodo et al., 2020). Understanding how the biological processes of species inhabiting these areas might be affected by climate change is crucial to predict their future vulnerability (Cahill et al., 2013; Cunningham, Martin, et al., 2013; Camacho et al., 2018; Bourne et al., 2020a). We therefore need to understand how temperature and rainfall affect breeding decisions and output for different species.

Climatic variation is known to influence the decisions of whether or not to breed and how much to invest in reproduction, through its influence on food availability and adult condition (Drent & Daan, 1980; Legagneux et al., 2016; Jean-Gagnon et al., 2018; Bourne, Ridley, Spottiswoode, et al., 2021; Cruz-McDonnell & Wolf, 2016). However, current increases in temperature extremes and inter-annual variability in rainfall are now expected to push species' tolerance to the limit (Donnelly et al., 2012; Cahill et al., 2013; Cunningham, Martin, et al., 2013; Bourne et al., 2020a). For example, studies in vertebrates have shown that droughts and extreme temperatures can reduce body condition through declines in primary production and food abundance, requiring increased foraging effort (Bolger et al., 2005; Iknayan & Beissinger, 2018; Bourne et al., 2020; van de Ven et al., 2020). Extreme temperatures further intensify this effect by increasing the thermoregulatory demands of individuals, particularly in many low-latitude climates where high maximum temperatures can persist throughout the year (du Plessis et al., 2012; Kruuk, Osmond & Cockburn, 2015; Noakes, Wolf & McKechnie, 2016; Conradie

et al., 2019; Bourne et al., 2020a; Dube & Nhamo, 2020; van de Ven et al., 2020). These additional impacts on adult condition (Jean-Gagnon et al., 2018) should further influence reproductive timing (via food abundance), offspring growth rates and body mass (Cunningham et al., 2013; Catry et al., 2015; Conradie et al., 2019; Cook et al., 2020; Wong & Forrest, 2021), and hence reproductive output (van de Ven et al., 2020; Bourne, Ridley, McKechnie, et al., 2021; D'Amelio et al., 2022).

The adverse effects of climatic variation on reproduction have been suggested to be mitigated by the presence of helpers in cooperatively breeding species (Rubenstein & Lovette, 2007; Covas, Du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). In these species, non-breeding individuals contribute towards feeding the offspring of breeding pairs (Cockburn, 1998) and to other activities, including territory defence (Golabek, Ridley & Radford, 2012b) or increased predator vigilance (Jungwirth et al., 2015; Groenewoud et al., 2016). Parents assisted by helpers may reduce their workload, in order to invest in self-maintenance and survival (known as 'load-lightening'; Hatchwell, 1999). Alternatively, they may maintain their feeding rates in response to additional help, leading to 'additive' care, which can increase nestling condition and survival during the current reproductive attempt (Hatchwell, 1999; Meade et al., 2010; Johnstone, 2011; van Boheemen et al., 2019). Breeding groups may also have flexible strategies according to breeding conditions, such that the presence of helpers leads to improved breeding output when conditions are adverse, but go unnoticed when conditions are good (Covas, Du Plessis & Doutrelant, 2008; Rubenstein, 2011; Groenewoud & Clutton-Brock, 2021). These possible mitigating effects of helpers could contribute to explaining the geographical distribution of cooperative breeding, which has been found to be more common in areas with lower rainfall and greater environmental variation (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011).

However, the empirical evidence that cooperation helps to buffer adverse climatic conditions is conflicting (Covas, Du Plessis & Doutrelant, 2008; Rubenstein, 2011; Bourne et al., 2020a; D'Amelio et al., 2022), and the pattern is also inconsistent across taxa. For example, comparative analyses focusing on the hornbill family (Bucerotidae) found that the occurrence of cooperative breeding was instead positively associated with more humid environments and climatic stability (Gonzalez, Sheldon

& Tobias, 2013). The authors suggested this family's life-history, typically with larger body sizes, high survival, low fecundity, and stable year-round food supply (which is less affected by climatic fluctuations) made the presence of helpers less relevant for reproduction, while still potentially important for other group functions such as territory defence. The life-history decision of how to balance investment in self-maintenance versus reproduction is strongly influenced by adult survival prospects and the probability of successful reproduction (Stearns, 1992), as long-lived species typically maximise their lifetime reproductive success through maximising the number of breeding events over their lifetimes (Clutton-Brock, 1988). This can lead to lower reproductive investment per event, and/or intermittent breeding (Hamel et al., 2010; Shaw & Levin, 2013). These survival vs reproduction trade-offs also apply to helpers, which have been shown to balance their decisions of how much to help according to the cost of helping (Mendonça et al., 2020; Covas et al., 2022). Furthermore, costs and benefits of helping should be influenced by the age and experience of helpers (Covas & Griesser, 2007). In long-lived, slow-developing group-living species, members will typically have different ages and experience, which might influence group reproductive performance in different ways. For example, some younger individuals may lack the foraging skills to efficiently feed themselves and the offspring of others, or may even still depend on the older, more experienced birds for food and protection (Rowley, 1976; Woxvold, 2004; Woxvold, Mulder & Magrath, 2006). This means that the costs and benefits associated with the age structure of group members might lead to different investment strategies, and so modulate the effect of group size on reproductive outcomes. Hence, the life-history strategies of helpers and breeders should play a key role in determining how the contributions of different group members translate into reproductive outcomes, making it crucial to conduct studies on a diverse array of species with different life-histories. Despite this, most studies on the effects of helpers on reproduction have focused on small, insectivorous passerines with relatively short lifespans.

In this study, we aimed to understand how climatic, social, and life-history factors associate with reproductive outcomes in a cooperative breeder with an atypical life-history, the southern ground-hornbill *Bucorvus leadbeateri*, and whether group members help to mitigate the effects of adverse weather. Southern ground-hornbills (hereafter 'ground-hornbills') are large, top predators associated

with semi-arid habitats. They are very long-lived (up to 60 years in the wild) and develop slowly, reaching adulthood from around 6–8 years old (Kemp & Kemp, 1980; Kemp, 2017). They are also relatively heat intolerant, and begin heat dissipation behaviours at around 26˚C (Kemp, 2017; Janse van Vuuren, Kemp & McKechnie, 2020b). Groups consist of 2–11 individuals, comprising of one breeding pair assisted usually by sons from previous broods (and, in some cases, immigrant males). These distinct age structures are readily identifiable from the un-feathered throat, feather and beak colouration of sub-adult and juvenile birds (Kemp & Kemp, 1980; Kemp, 1988; Kemp, Joubert & Kemp, 1989). Ground-hornbills require large territories (up to 200 km^2), resulting in low population densities (Carstens, 2017; Kemp, 2017; Theron et al., 2013). Throughout their range, ground-hornbills are listed as Vulnerable, which is attributed mainly to land use change and habitat loss (Kemp, 2017). Conservation of the species is currently focussed primarily on habitat preservation, installing artificial nests, and the artificial formation and reintroduction of groups back into their historic range (Botha et al., 2011; Cilliers et al., 2013). Hence, insights about the effects of group size and composition on reproduction will be also useful to aid reintroduction efforts to ensure group success and persistence.

We used a 17-year dataset to examine the effects of temperature, rainfall, group size and group member age on 1) breeding probability, 2) laying date, 3) fledging success, and 4) nestling condition. Given that ground-hornbills show behavioural evidence of heat sensitivity, and given their size and longevity, we hypothesised that high temperatures and low rainfall would have detrimental effects on their propensity to reproduce, as well as on their reproductive output. In addition, large body size generally translates into greater food and thermoregulatory requirements (Weathers, 1981; Smit et al., 2016), and so adverse conditions may further tilt the trade-off towards self-maintenance over reproductive tasks. Hence, we predicted that hot and dry conditions would lead to intermittent breeding, delayed laying dates, and reduced nestling condition. We also expected that reproductive outcomes should depend on group composition, because adult, sub-adult and juvenile birds should differ in their contributions and costs of helping. We therefore tested for associations between reproductive parameters and each age class separately, rather than pooling this potentially relevant biological variation into a single measure of group size. Specifically, we predicted that adult and sub-adult birds

should have mainly positive effects, as they are known to contribute towards several reproductive tasks such nest lining, provisioning, and defence (Kemp, 1988; Chapters 2 & 5). By contrast, juveniles have extended dependence on older individuals for both food and protection, and so should contribute less towards the benefit of the group. We therefore expected the presence of juveniles to have a negative effect on reproductive outcomes. Finally, given that ground-hornbills inhabit a highly variable environment, there is ample scope for group members to mitigate the effects of adverse breeding condition (Jetz & Rubenstein, 2011). However, given their size, longevity, and stable, generalist diet (Gonzalez, Sheldon & Tobias, 2013), we expected that any mitigating effects could be weak or even absent.

Methods

Data collection

Long-term research on the southern ground-hornbill has been conducted at our study site since 2000. The rarity of natural breeding cavities within the study site led to artificial nests being used to increase breeding productivity in the area and to allow for monitoring (Carstens et al., 2019b). Each group typically has one nest within their home-range (Carstens, 2017).

Nests were visited once every 7–10 days from 2000–2019 to ascertain the breeding status of groups by observing lining material inside the nests. Once breeding was initiated and first-laid eggs were found, the nests were visited 5 days later to check for the laying of the second egg. The next two visits only occurred 40 and 45 days later, to check for hatching of each egg. More accurate lay dates (to within a day or two) could then be determined by back-dating based on the age of the first hatched chick. The final nest visit occurred at between 53 and 81 days, when the nestlings were ringed with a uniquely numbered aluminium ring and measurements taken for commonly used proxies of nestling condition (mass and tarsus length). Nestling mass was measured using a hanging scale and tarsus length was measured using Vernier callipers. Group sizes and compositions were compiled and recorded manually during 1998–2019, except for 2008–2010 when no recording took place. They were obtained from a combination of opportunistic sightings, active efforts by researchers to re-sight groups, trail

camera footage from nest sites, and aerial censuses. Sightings from local wildlife guides and other citizen scientists were also added to the database. Birds seen were linked to specific group areas based on the proximity of the sighting to the nearest nesting sites and from pre-recorded group home-ranges. Since group size and composition may vary depending on the time of the year, only sighting data from within and just prior to the breeding season (July–April) were used. Data collection sought to balance effective monitoring with the impact of human presence.

Maximum daily temperatures were obtained from weather stations for the towns of Hoedspruit (20 km west of study site and maintained by the Hoedspruit Air Force Base) and Phalaborwa (20 km north of study site and maintained by the Kruger National Park Gate). Temperatures were taken from the nearest weather station to each nest. Rainfall was available from 16 rain gauges scattered throughout the study site. Estimates were taken from the rain gauges nearest to each nest (distance range: 0.97–14.66 km).

Statistical analyses

We aimed to investigate how climatic (rainfall and maximum temperatures) and social and life-history factors (number of group members of different ages) were associated with reproductive parameters, while accounting for other factors likely to influence reproduction (see below). We focused on four breeding variables: 1) breeding probability – whether groups attempted to breed (binary), 2) laying date – the number of days after 1 September when the first egg was laid (discrete), 3) fledging success – whether the group raised a nestling to fledging (binary), and 4) nestling condition – the mass and tarsus length of nestlings prior to fledging (continuous; Table S3.).

To investigate associations with climate, all analyses, except for fledging success (see below), included the mean daily maximum temperature and rainfall (continuous variables), although the period captured by these variables varied for each analysis depending on what was considered biologically meaningful (Table S3.). For breeding probability and lay date, winter and spring mean maximum temperatures and rainfall were used, as well as the previous year's rainfall. For nestling condition, mean maximum temperatures and rainfall for the period from hatching to measurement were used. Analyses

of fledging success did not include climate variables due to statistical limitations, since the duration of the nestling period (and hence the amount of rainfall received and average maximum temperature) was very different for nests that succeeded from nests that failed at different stages. In addition, we never obtained any indication of nestlings dying of starvation (or even losing condition between visits), and trail camera footage strongly indicates that predation is the main factor leading to breeding failure (KMM, unpublished data). Nest height and lay date were also included in the analyses for fledging success following Carstens et al. (2019) which suggested that groups were more successful in nests higher off the ground (presumably due to reduced predation) and when laying earlier in the season (presumably due to better synchrony with food abundances and reduced overlap of incubation periods with the hottest months). Interactions between temperature and rainfall variables were also tested, since changes in one variable may influence any effect from the other. For example, hot and humid conditions are expected to be more detrimental due to increased thermoregulatory constraints (Powers, 1992; Gerson et al., 2014).

To investigate effects of social and life history factors, we examined associations between the number of group members of different age classes and reproductive outcome under different climatic conditions. Hence, in each of the models we considered as explanatory variables the number of adult males, sub-adults, and juveniles in the group, and included the interactions between climate and group composition variables.

All statistical analyses were conducted in R v 4.0.1 (R Core Team 2020) using packages lme4 version 1.1.23 and MuMIn version 1.43.17. Data exploration was carried out following the protocol described in Zuur, Ieno and Elphick (2010). Potential predictors of breeding probability, lay date, fledging success, and nestling condition were investigated by fitting General and Generalized Linear Mixed Models (GLMMs). Continuous variables were scaled by centring and standardising by the mean (Schielzeth, 2010). Strongly correlated variables ($r > 0.30$) were not included in the same models (see below for each analysis). Group identity was included as a random term in all the analyses. Year was only included as a random term in analyses of fledging success and nestling condition and not included in breeding probability and lay date analyses, because for the latter two all observations within each

year had climate values from the same temporal period. Some groups initially included in our dataset only bred in the study area once or twice, resulting in the models failing to converge, and so were removed from the analyses. This resulted in 22 groups being monitored over 17 years, although sample sizes varied between the breeding variables analysed (due to missing parameters such as group composition during breeding attempts). Residuals of the final models were visually inspected to ensure that model assumptions were met. The different link functions were compared using AICc (Akaike's Information Criteria) and models were considered better when the AICc values reduced by more than 2. The likelihoods of the models relative to the other models tested were also checked using Akaike's model weights. When models had similar weights and ΔAICc < 2, the simpler model with fewer parameters was used for further inference (Richards, 2008; Richards, Whittingham & Stephens, 2011). Random effects were tested using Likelihood Ratio Tests and were considered significant when *p* values were less than 0.05. Marginal and conditional R^2 values were also calculated to show the variance explained by fixed effects and by both fixed and random effects respectively.

Results

The mean (± SE) group size within the study site from 2002–2021 (with each group being re-counted each year) was 3.98 ± 0.07 individuals (range: 2–7 individuals). These groups contained a mean (± SE) of 1.84 ± 0.05 adult males (range: 1–4 individuals), 0.60 ± 0.05 sub-adults (range: 0–3 individuals) and 0.50 ± 0.04 juveniles (range: 0–2 individuals). Winter rainfall ranged from 0–46 mm (average: 8.59 ± 0.58 mm) and winter mean maximum temperatures ranged from 24.85–27.55 ˚C (average: 25.97 ± 0.36 ˚C. Spring rainfall ranged from 17–317 mm (average: 107.13 ± 3.45 mm) and spring mean maximum temperatures ranged from 28.04–31.09 ˚C (average: 29.79 ± 0.04 ˚C). Rainfall for specific nestling condition periods ranged from 30–542 mm (average: 202.64 ± 14.31 mm) and mean maximum temperatures ranged from 29.06–34.71 ˚C (average: 31.50 ± 0.14 ˚C).

Probability of breeding

The breeding probability of groups was analysed using a GLMM with binomial (binary) error structure and a logit-link function, using breeding data from 22 different groups from 2000–2007 and 2011–2021

(n = 244 group-years). Table S3.2 in the supplementary materials shows number of groups analysed per year. Mean maximum winter temperatures and previous year's rainfall were strongly correlated ($r > 0.45$) and so were not included within the same models.

There were two nested best-fit models for the probability of breeding (ΔAICc < 2) and similar model weights (0.46 and 0.19), making them indistinguishable from each other (Table 3.1). Both models included the different variables of group composition (see below), winter mean maximum temperature and winter rainfall. They differed only by the addition of an interaction between the winter climate mean maximum temperature and rainfall variables, and the simpler model was used for further inference (Table S3.3). Within this model, neither the number of adult males (estimate = -0.12 ± 0.18, 95% CI = [-0.47 – 0.23], Table S3.3) nor the mean maximum winter temperature (estimate = -0.12 ± 0.16, 95% CI = [-0.21 – 0.44], Table S3.3) had any clear effects, with both having 95% confidence intervals which broadly overlapped zero (Table S3.3). There was, however, support for clearer associations between breeding probabilities and increases in the number of sub-adults (estimate = 0.38 ± 0.19, 95% CI = [0.02 – 0.78], Table S3.3, Figure 3.1a) and juveniles (estimate = 0.58 ± 0.18, 95% CI = [0.23 – 0.95], Table S3.3, Figure 3.1b) within the groups. There was also a strong positive relationship between the probability of breeding and the amount of winter rainfall (estimate = 0.47 ± 0.18, 95% CI = [0.14 – 0.84], Table S3.3, Figure 3.1c). Breeding probability was also related to 'group identity' (variance = 0.92, p = <0.001, Table S3.4), and although most of the variation in the model was unexplained (66.6%), the random effect of 'group identity' explained a greater proportion of the variation than the fixed effects. This was indicated by a conditional R^2 (explaining both fixed and random effects) of 33.3%, compared to the 14.6% marginal R^2 (explaining the fixed effects only).

Table 3.1. Top five models for breeding probability. AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles, Winter Tmax = mean maximum winter temperature, Winter rain = total rainfall over winter, Spring Tmax = mean maximum spring temperature, Spring rain = total rainfall over spring months & Dev = model deviance. The random term of group identity was included in all models. Displayed model highlighted in bold was used for inference.

Model	**k**	**Dev**	**AICc**	**∆AICc**	**Model Weight**
AM + SA + Juv + Winter Tmax + Winter rain	**7**	**279.5**	**293.99**	**0**	**0.46**
AM + SA + Juv + Winter Tmax*Winter rain	8	279.1	295.72	1.74	0.19
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain	9	278.4	297.14	3.16	0.10
AM + SA + Juv + Spring Tmax + Spring rain + Previous years rainfall	9	278.4	297.15	3.16	0.10
AM*Winter rain + SA*Winter rain + Juv*Winter rain + Winter Tmax	10	276.9	297.82	3.83	0.07

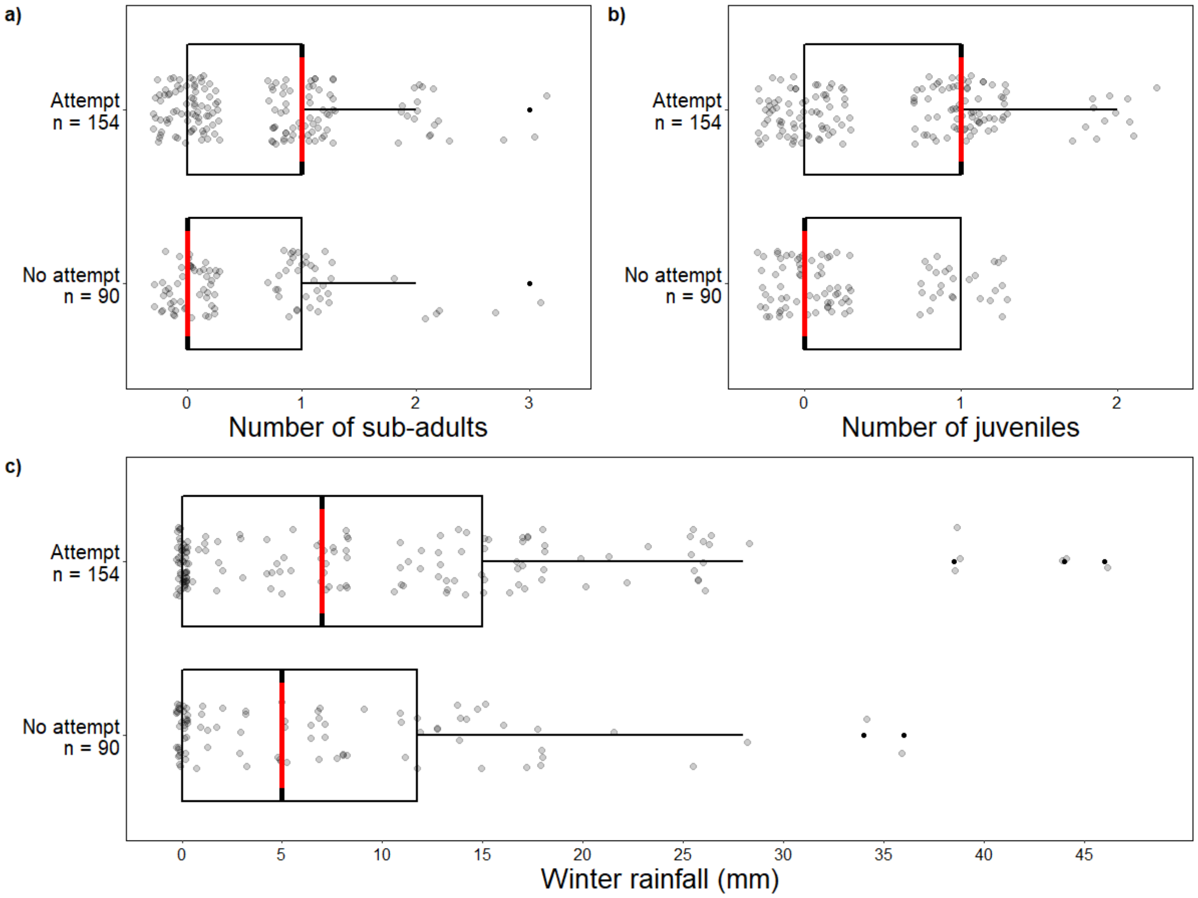


Figure 3.1. Breeding probability in relation to a) the number of sub-adults, b) the number of juveniles, and c) winter rainfall (in mm). Boxplots show median values (red lines), first and third quartiles (box) and interquartile range (whiskers). Data points are jittered for improved visibility.

Lay date

The timing of egg laying was analysed using a LMM with Gaussian error structure, maximum likelihoods, and logit-link function for 23 groups over 14 years (n = 153 group-years; Table S3.5). Mean maximum winter temperatures and previous year’s rainfall were strongly correlated ($r > 0.45$) and so were run separately in different models.

There were two nested best-fit models for lay date, where ΔAICc < 2 and the model weights were close (0.48 and 0.32), and so the simpler of the two models, which excluded the interaction terms between group composition and rainfall, was used for further inference (Table 3.2). This model included the variables of group composition, winter and spring rainfall, winter and spring mean maximum temperatures, and interactions between winter and spring mean maximum temperatures and rainfall

(Table 3.2). No clear effects were detected for the number of adult males (estimate = 1.30 ± 1.69, 95% CI = [-2.03 – 4.63], Table S3.6), number of sub-adults (estimate = -0.78 ± 1.69, 95% CI = [-4.12 – 2.57], Table S3.6), winter rainfall (estimate = 0.17 ± 1.70, 95% CI = [-3.20 – 3.53], Table S3.6) and spring rainfall (estimate = -0.62 ± 1.73, 95% CI = [-4.06 – 2.83], Table S3.6), spring mean maximum temperatures (estimate = 2.71 ± 1.73, 95% CI = [-0.70 – 6.11], Table S3.6), and the interaction between spring mean maximum temperatures and spring rainfall (estimate = -3.00 ± 1.89, 95% CI = [-6.74 – 0.74], Table S3.6) as they all had 95% confidence intervals which broadly overlapped with zero. Earlier laying dates were associated with the number of juveniles present in the group (estimate = -3.89 ± 1.69, 95% CI = [-7.23 – -0.52], Table S3.6, Figure 3.2). Increases in the mean maximum winter temperature were associated with delayed laying dates (estimate = 3.90 ± 1.80, 95% CI = [0.36 – 7.44], Table S3.6), and there was an interaction between winter mean maximum temperature and winter rainfall (estimate = 4.66 ± 1.94, 95% CI = [0.82 – 8.49], Table S3.6). This interaction suggests that when there was less rain over the winter period, the lay date was not predicted by temperature, whereas when there was more rain over the winter period, lay date was positively associated with temperature; in other words, hot and wet winters were associated with laying later in the season (Figure 3.3). Most of the variation within the model was unexplained (80.9%) and the random effect of 'group identity' (variance = 17.57, $p = 0.22$, Table S3.7) showed no relation with lay date and explained very little of the model's variation (conditional R^2 = 19.1%, marginal R^2 = 15.1%).

Table 3.2. Top five models predicting lay date. AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles, Winter Tmax = mean maximum winter temperature, Winter rain = total rainfall over winter, Spring Tmax = mean maximum spring temperature, Spring rain = total rainfall over spring months & Dev = model deviance. The random term of group identity was included in all models. Displayed model highlighted in bold was used for inference.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain + AM*Spring rain + SA*Spring rain + Juv*Spring rain + Winter Tmax*Winter rain + Spring Tmax*Spring rain	15	1328.7	1366.55	0	0.48
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain + Winter Tmax*Winter rain + Spring Tmax*Spring rain	**12**	**1338.6**	**1367.36**	**0.78**	**0.32**
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain + AM*Winter Tmax + SA*Winter Tmax + Juv*Winter Tmax + Winter Tmax*Winter rain + Spring Tmax*Spring rain	15	1369.9	1366.80	3.34	0.09
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain	10	1370.3	1369.66	3.81	0.07
AM + SA + Juv + Winter Tmax + Winter rain + Spring Tmax + Spring rain + AM* Winter rain + SA* Winter rain + Juv* Winter rain + Winter Tmax*Winter rain + Spring Tmax*Spring rain	15	1372.8	1369.86	6.34	0.02

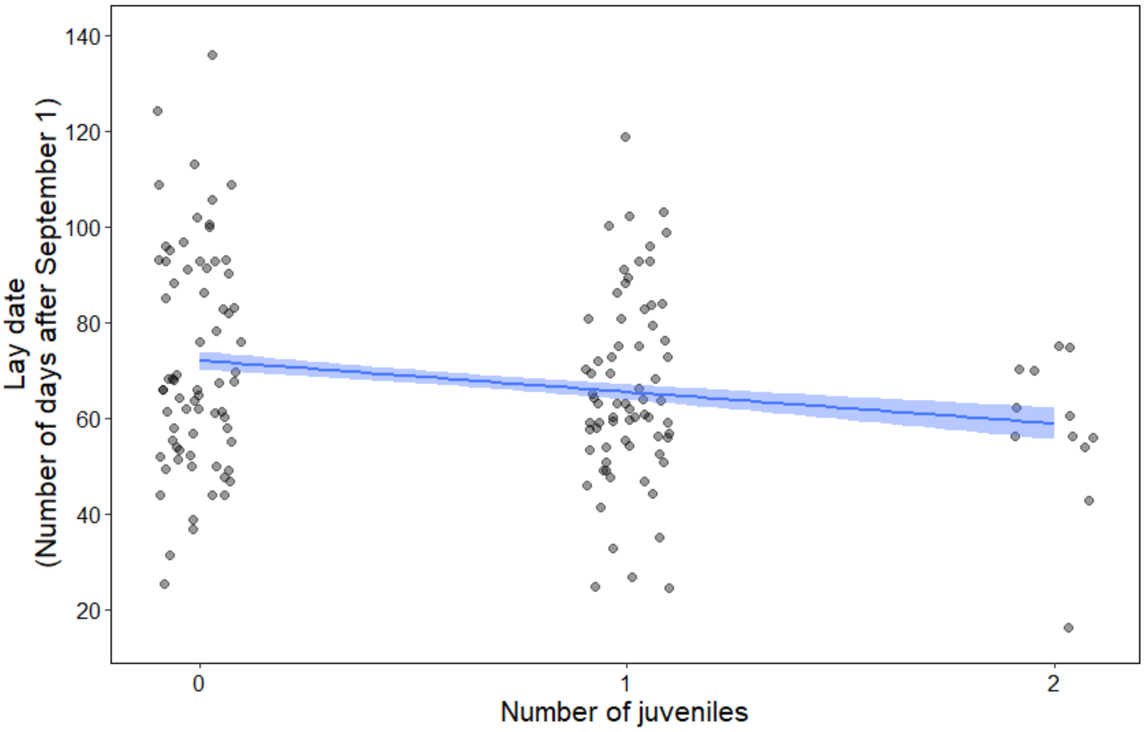


Figure 3.2. Lay date in relation to the number of juvenile group members. Lay date measured as the number of days after 1 September. Data points represent different nests, and blue line and confidence intervals represent the model predicted relationship.

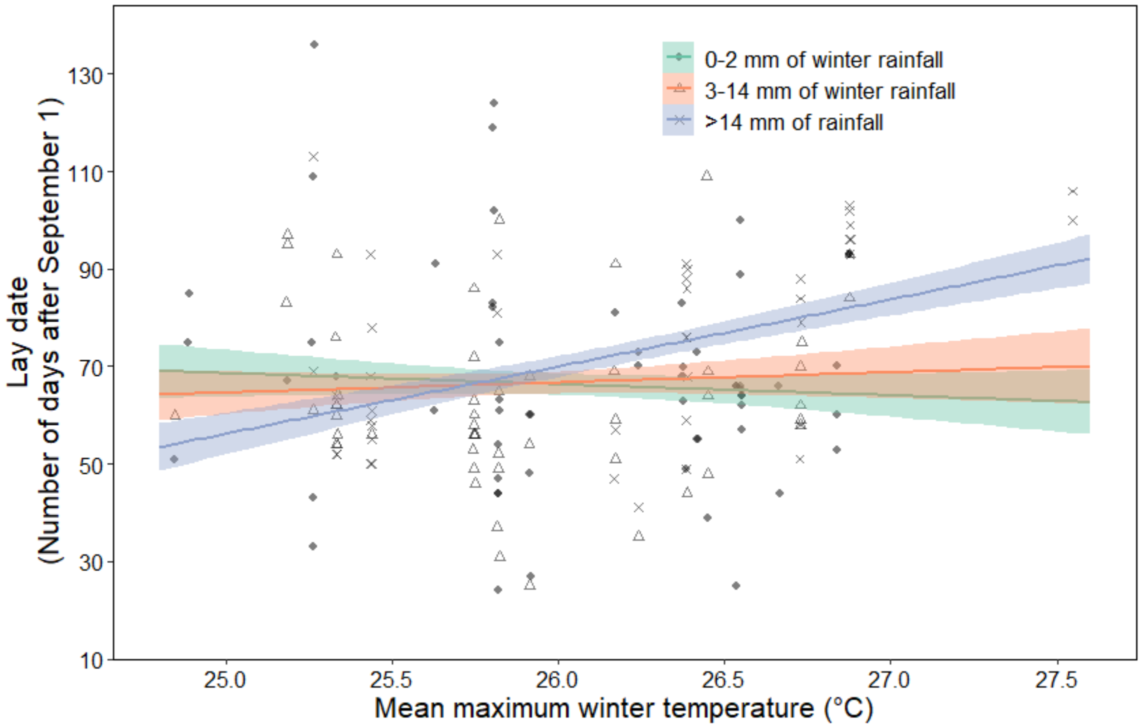


Figure 3.3. The interaction effect of mean maximum winter temperature and rainfall on the lay date. Lay date measured as the number of days after 1 September. For ease of visualisation, rainfall is separated into three categories, but was continuous in the main analysis. Lines represent the model predicted relationship with 95% confidence intervals.

Fledging success

The probability of successfully fledging the single nestling was analysed using a GLMM with a binomial (binary) error structure and a probit-link function, in 18 groups from 2002–2007 and 2011–2021 (n = 142 group-years; Table S3.8). Previous studies on this species found that reproductive success was associated with lay date (measured as the number of days after 1 September) and nest height, and so these covariates were included in the analyses (Carstens et al., 2019b).

The best-fit model was the null model with a model weight of 0.78, indicating that none of the variables clearly predicted fledging probability in our data set (Table 3.3). There was also no relation between fledging success and the random variables of 'group identity' (variance = <0.001, *p* = 1, Table S3.9) and 'year' (variance = 0.08, *p* = 0.29, Table S3.9).

Table 3.3. Top five models for nestling fledging success. AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles & Dev = model deviance. Random terms: group identity and year. Model in bold was the model used for inference.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
Null model	**3**	**181.9**	**188.06**	**0**	**0.78**
AM + SA + Juv + Lay date	7	177.4	192.20	4.14	0.10
AM + SA + Juv	6	180.5	193.14	5.08	0.06
AM + SA + Juv + Lay date + AM*Lay date	8	177.3	194.36	6.31	0.03
AM + SA + Juv + Lay date + Nest height	8	177.3	194.43	6.37	0.03

Nestling condition

We analysed body mass and tarsus length at fledging using LMMs with Gaussian error structure, maximum likelihoods, and logit-link function, for a total of 18 groups from 2004–2008 and 2011–2021 (nestling mass: n = 79, tarsus length: n = 80, Table S3.10). The age at which nestlings were ringed and measured varied from 53 to 81 days in 2005–2021 (mostly because of difficulties in accessing the nests on the right date). To account for this variation, nestling age was included in the models. Temperature

and rainfall variables were highly correlated (r > 0.30) and so were not included in the same models. Tarsus length was also included as a covariate to nestling mass to account for the structural growth of the individuals.

Nestling mass: Mean nestling mass (± SD) at ringing was 3050 ± 374 g (range: 2150–4150 g). There was one best-fit model, with a model weight of 0.78 (Table 3.4). This model contained the explanatory variables of group composition, mean maximum temperature for the nestling growth period, and tarsus length, with no interactions among them. The model parameters, however, did not indicate a clear association between nestling mass and the number of adult males (estimate = 5.70 ± 38.59, 95% CI = [-72.36 – 83.78], Table S3.11), number of sub-adults (estimate = 54.20 ± 41.48, 95% CI = [-29.36 – 137.28], Table S3.11), or number of juveniles (estimate = -62.75 ± 39.89, 95% CI = [-144.84 – 20.19], Table S3.11) as they all had confidence intervals which broadly overlapped zero. Increasing mean maximum temperature was associated with decreases in nestling mass (1˚C increase in mean maximum temperatures was estimated to be associated with a 88.5 g decrease in nestling mass: estimate = -107.50 ± 47.90, 95% CI = [-213.18 – -11.89], Table S3.11, Figure 3.4). There was also a positive association between tarsus length and nestling mass (estimate = 172.01 ± 41.46, 95% CI = [86.01 – 256.58], Table S3.11). The fixed and random effects explained 37.1% of the variation (conditional R^2) and the fixed effects alone explained 25.1% of the variation (marginal R^2). 'Year' explained most of the variation from the random effects (variance = 17729, *p* = 0.10, Table S3.12), but a large proportion of the model's variation was unexplained (62.9%).

Table 3.4. Top five models for nestling mass. AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles, Mean Tmax = mean maximum temperature for nestling period, Rainfall = total rainfall over nestling period & Dev = model deviance. Random terms: group identity and year. Model in bold was the model used for inference.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
AM + SA + Juv + Mean Tmax + Tarsus length	**9**	**1138.9**	**1159.53**	**0**	**0.78**
AM + SA + Juv + Rainfall + Tarsus length	9	1143.1	1163.73	4.20	0.09
AM + SA + Juv + Mean Tmax + Tarsus length* Age	11	1138.0	1163.97	4.45	0.08
AM + SA + Juv + Tarsus length*Age + Rainfall + Rainfall^2	12	1138.7	1167.42	7.89	0.02
AM + SA + Juv + Rainfall + Tarsus length* Age	11	1142.3	1168.23	8.70	0.01

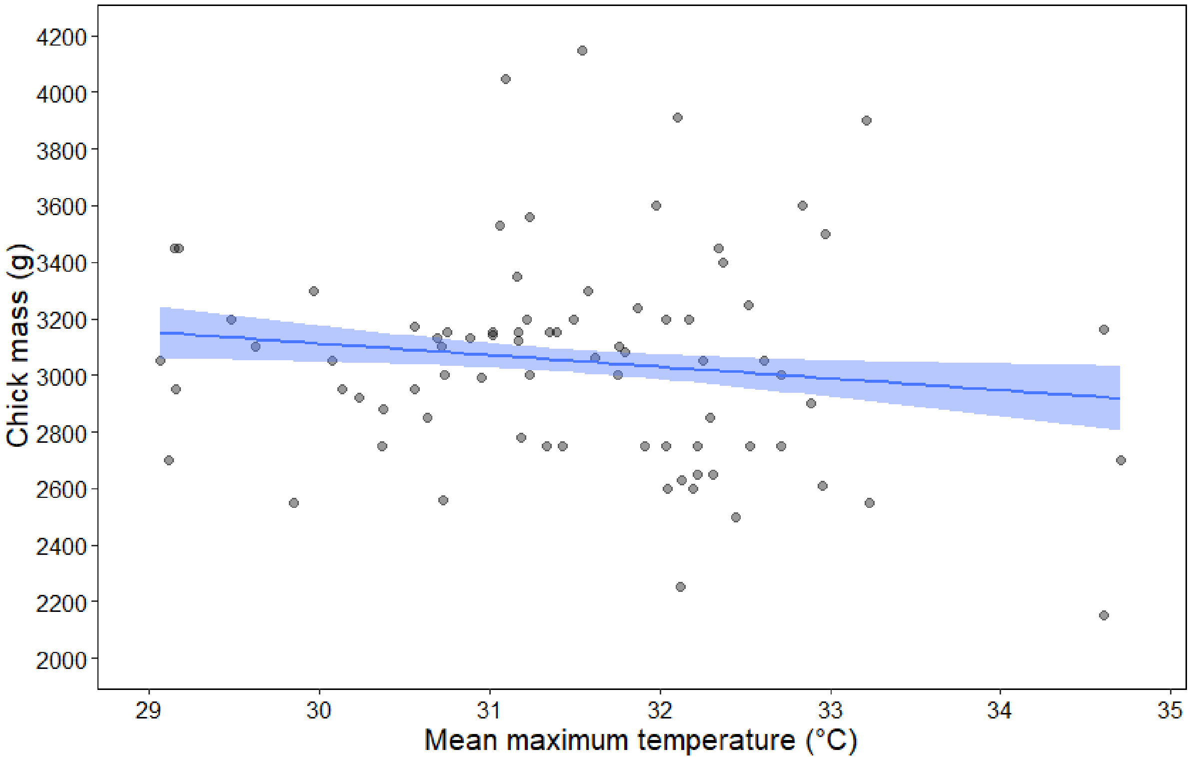


Figure 3.4. The relationship between mean maximum temperature (measured during the nestling period) and nestling mass. Data points represent different nests, and the blue line and confidence interval represents the model predicted relationship.

Nestling tarsus length: Mean tarsus length (± SD) was 150.85 ± 10.07 mm (range: 128–179 mm). There were two best-fit models with ΔAICc < 2 and similar model weights (0.52 and 0.31), differing only in the replacement of variable Mean maximum temperature with rainfall (Table 3.5). These two variables were correlated; therefore, we present the top model only. This model contained the explanatory variables of group composition, mean maximum temperature for the nestling growth period, nestling mass, and nestling age, with no interactions among them. No clear effects were detected for the number of sub-adults (estimate = 0.65 ± 1.11, 95% CI = [-1.66 – 2.96], Table S3.13) and the mean maximum temperature (estimate = 1.42 ± 1.27, 95% CI = [-1.28 – 3.95], Table S3.13) with both having 95% confidence intervals that broadly overlap zero. Tarsus length was positively associated with the number of adult males (estimate = 2.58 ± 0.98, 95% CI = [0.59 – 4.55], Table S3.13), with the addition of a single adult male resulting in an estimated increase of 3.75 mm in nestling tarsus length (Figure 3.5a). The number of juveniles had a similar effect (estimate = 2.90 ± 1.07, 95% CI = [0.62 – 5.20], Table S3.13), in this case leading to an estimated increase of 4.83 mm per juvenile (Figure 3.5b). As expected, increases in the age of the chick were positively associated with tarsus length (estimate = 2.30 ± 1.13, 95% CI = [0.01 – 4.62], Table S3.13, Figure 3.5c). The fixed and random effects explained 37.2% of the variation (conditional R^2) and the fixed effects alone explained 18.1% of the variation (marginal R^2). ‘Year’ explained most of the variation from the random effects (variance = 13.56, p = 0.04, Table S3.14), however, a large proportion of the model’s variation was unexplained (62.8%).

Table 3.5. Top five models for tarsus length. AM = number of adult males, SA = number of sub-adults, Juv = number of juveniles, Mean Tmax = mean maximum temperature for nestling period, Rainfall = total rainfall over nestling period & Dev = model deviance. Random term: group identity and year. Model in bold was the model used for inference.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
AM + SA + Juv + Mean Tmax + Age	**9**	**572.1**	**592.70**	**0**	**0.52**
AM + SA + Juv + Rainfall + Age	9	573.2	593.74	1.04	0.31
AM + SA + Juv + Rainfall + Rainfall^2 + Age	10	573.0	596.16	3.46	0.09
AM + SA + Juv + AM*Mean Tmax + SA*Mean Tmax + Juv*Mean Tmax + Age	12	569.8	598.46	5.76	0.03
AM + SA + Juv + AM*Mean Tmax + SA*Mean Tmax + Juv*Mean Tmax + Mean Tmax^2 + Age	13	567.1	598.61	5.91	0.03

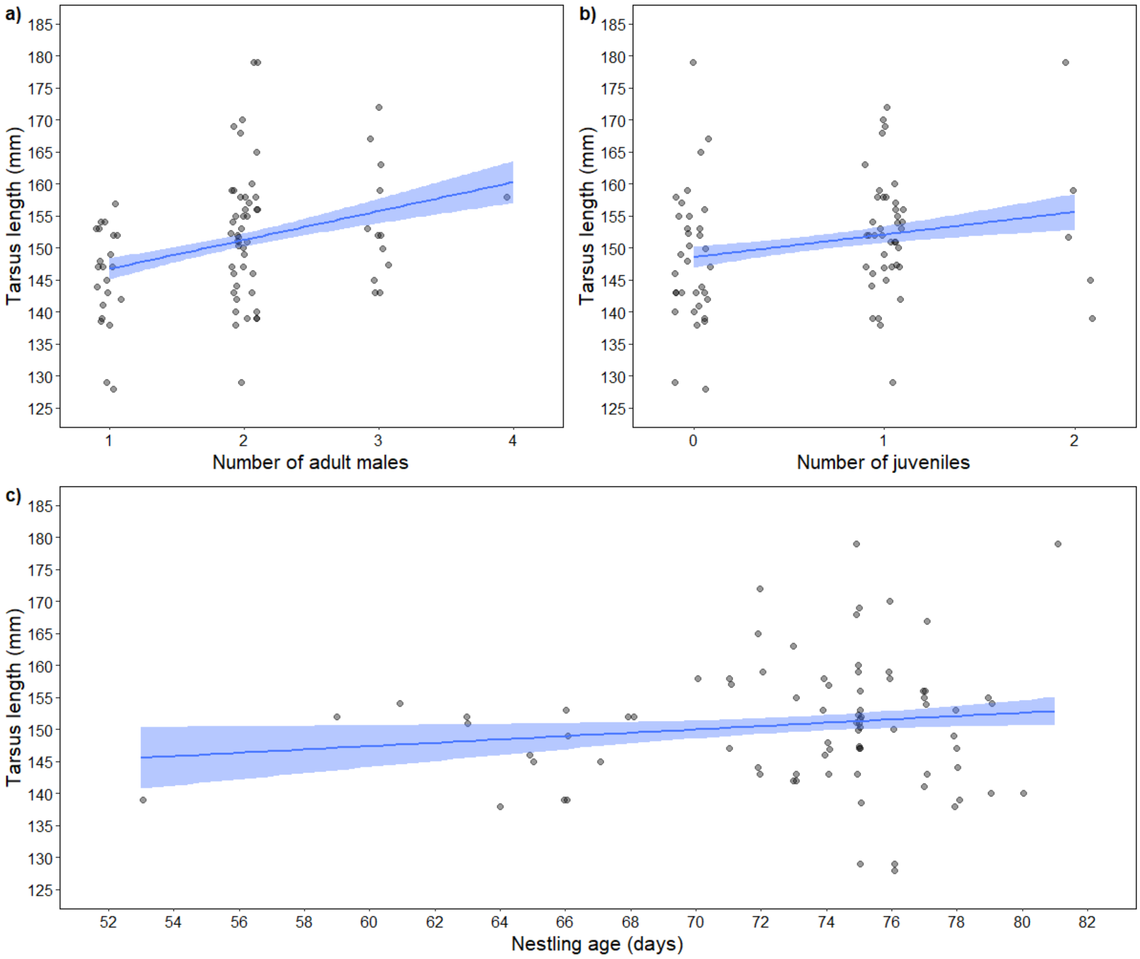


Figure 3.5. Tarsus length of nestlings in relation to a) the number of adult males in the group, b) the number of juveniles in the group, and c) nestling age when it was measured. Data points represent individual nests, and blue lines and confidence intervals represent the model predicted relationship.

Discussion

We investigated how climatic factors and group composition influenced reproductive outcomes of a long-lived cooperative breeder, the southern ground hornbill, and whether social factors could mitigate the effects of unfavourable breeding conditions (or compound them, through the extended parental dependency of juveniles). Our data showed that, as expected, high temperatures and low rainfall were usually negatively associated with reproductive outcomes. The number of adults, sub-adults and juveniles were, in general, positively associated with the reproductive parameters we analysed, but the effects were often unclear and lacked significance, and there was no evidence to suggest that having more group members mitigates (or, for juveniles, exacerbates) the adverse effects of high temperatures and low rainfall. Hence, even though ground-hornbills are associated with semi-arid environments,

having more group members does not appear to improve reproduction under adverse conditions. Our results are instead consistent with comparative analyses on the hornbill family (Gonzalez, Sheldon & Tobias, 2013), suggesting that the family's typically slow life-history, low fecundity, large body size, and access to relatively stable food resources makes the presence of additional group members less relevant for reproductive outcomes, including under adverse conditions.

Temperature and rainfall

As expected, high mean maximum temperatures were negatively associated with reproduction and were the strongest predictors of laying date and nestling mass at fledging. Higher winter temperatures were followed by delayed laying dates, but this effect was modulated by the quantity of winter rainfall, indicating that it was specifically warm and wet (rather than warm and dry) conditions that were negatively associated with reproduction. The negative effects of high temperatures on bird reproduction have mostly been studied during warmer summer months (e.g. McKechnie, Hockey & Wolf, 2012; Kemp et al., 2020). However, in our study area, like in many tropical and sub-tropical regions, maximum winter temperatures can reach levels that might also become detrimental. In this study, winter mean maximum temperature was 26˚C, which is the temperature at which southern ground-hornbills commence heat dissipation behaviours (see Janse van Vuuren et al., 2020). Therefore, thermoregulatory difficulties may continue throughout the winter period, and additional rainfall may increase humidity, consequently reducing the potential for evaporative heat loss (Gerson et al., 2014; van Dyk, Noakes & McKechnie, 2019). Any such compromised evaporative heat loss may be further compounded by the lack of shade and increase in bare ground solar radiation exposure associated with the lack of foliage characteristic of the dry season, and which have been shown to have an effect on thermoregulation in other bird species (Abdu et al., 2018; Pattinson et al., 2020). A greater need for thermoregulation leads to birds spending more time seeking shade and performing heat dissipation behaviours rather than foraging for food, and so to a trade-off between these two vital behaviours (Conradie et al., 2019; Cunningham, Gardner & Martin, 2021). Previous studies of arid zone species have shown that under high temperatures, foraging may either become less efficient or cease entirely (Goldstein, 1984), both of which have negative impacts on body condition (du Plessis et al., 2012; van de Ven et al., 2020).

Therefore, the delay in laying dates could arise from a reduction in body condition of the breeders during the winter, as extra time is needed to recover prior to laying.

We also found that high mean maximum temperatures were strongly associated with reduced nestling body masses at fledging. Our results are consistent with similar studies showing the adverse effects of high temperatures on offspring development (Cunningham, Martin, et al., 2013; Andreasson, Nord & Nilsson, 2018; Bourne, Ridley, Spottiswoode, et al., 2021), although we do not currently know the exact mechanisms involved. Nestlings are likely to be subjected to the effects of increased temperature both directly, through increased thermoregulatory demands, and indirectly through the possible effects of reduced provisioning rates from the carers (Cunningham, Martin, et al., 2013; Bourne et al., 2020a; van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021; Corregidor-Castro & Jones, 2021). However, our results also suggest a lack of any group member mitigation effects on the negative effects of temperature. The detrimental effects of high temperatures on nestlings might not only reflect lack of food, which could be compensated for in groups with more carers, but other possible stressors acting on the nestlings or on the carers, such as difficulty in maintaining an adequate body temperature, leading to physiological stress, poorer condition and (for carers) lower foraging efficiency. Given that ground-hornbills have an exceptionally slow life-history and high longevity, it is expected that carers should not risk incurring higher costs in order to increase nestling provisioning under adverse conditions (e.g. Ghalambor & Martin, 2001). Since fledging mass is expected to impact post-fledging survival (Clutton-Brock, 1988; Greño, Belda & Barba, 2008; Maness & Anderson, 2013; Perrig et al., 2017; Bourne et al., 2020a), and given the predicted increases in temperature under current climate change scenarios, this result raises concerns about how recruitment in this species might be affected and how that will impact its conservation status.

Although rainfall was, as expected, positively associated with breeding probability, and lay date, the effect was not as strong and prevalent as expected, especially considering that rainfall is usually a key factor for breeding (but see D’Amelio et al., 2021 for a similar result in an arid region passerine). Increased rainfall over winter led to more groups attempting to breed, as also reported in other arid- and semi-arid zone birds (Grant et al., 2000; Bolger, Patten & Bostock, 2005; Mares et al., 2017;

Aranzamendi et al., 2019). This is likely due to the increase in phytophagous insects (e.g. grasshoppers) which comprise an important part of southern ground-hornbill diet (Kemp, 1976), and whose abundance correlates with rainfall (Bolger, Patten & Bostock, 2005; Jamieson et al., 2012), presumably leading to improved body condition.

Group composition

In the majority of cooperative breeders, a significant number of group members are retained young from previous broods, that help for one or two years before dispersing to breed independently (Riehl, 2013). This leads to a long-established difficulty in separating the effects of breeder and territory quality (which should be associated with higher reproductive success) from the effects of helper presence (i.e., retained young). Given the slow development of southern ground-hornbills and their distinct age-related appearance, we were able to separately analyse the effects of group members of different ages. We found that groups with juvenile members were more likely to breed, and bred earlier in the season. However, it is very unlikely that this association arises from any direct contributions of juvenile group members to reproduction, as these individuals have extended dependency periods on adult birds and continue to beg for food from other group members for at least two years after leaving the nest (Kemp, 1988). Moreover, these young birds provide little to no contribution towards the provisioning of new offspring and have even been seen stealing food from the nestlings (Chapter 2). Therefore, the association between number of juveniles and reproductive success is more likely to have arisen from a positive association with parental (or territory) quality or experience. The importance of the random effect of group identity on the probability of breeding further supports this idea.

The effect of number of sub-adults on a group's breeding probability followed the same direction as that of the number of juveniles, but was weaker and less clear. Sub-adult birds are more experienced than juveniles, mostly forage independently, and are known to contribute to feed the incubating female and developing nestling (Kemp, 1988), although to a lesser extent than that of adults (Chapter 2). Younger sub-adults can also still occasionally be seen begging for food from the adults (pers. obs.). In our dataset, many sub-adults were retained offspring, and hence the positive association

between the number of sub-adults and breeding probability is likely due to similar variables to those underlying the association between the number of juveniles and breeding probability.

The only clear positive association between number of group members and reproductive parameters was that between the number of adult members and nestling tarsus length. Adult group members provision most of the food to the nestling, and this effect suggests that the adults' provisioning efforts are additive and have a positive effect on the structural development of the nestling. On the other hand, there was no positive association between number of adult birds and nestling mass. However, our data show that southern ground-hornbill nestlings tend to reach peak mass inside the nest at about 50–60 days old, just past the halfway point of the nestling period, whereas nestling tarsus lengths continue to grow throughout that period. This difference in development is also illustrated by our results showing that nestling age is associated with tarsus lengths but not mass. Hence, any possible effects of the number of adult males on body mass might be more important during earlier developmental stages, and additional research during this early-life period is currently ongoing.

Surprisingly, we found no association between group composition variables and fledging probability, despite our expectation of a positive effect from increasing numbers of adult and sub-adult members, due to increased provisioning rates and nest protection. This lack of association is likely due to the main reason for nesting failure after hatching being predation. Trail cameras used in ground-hornbill research over the past 4 years have indicated that about 60% of failed breeding attempts were from confirmed or inferred predation, occurring from opportunistic species adept at climbing such as genets *Genetta* spp., leopards *Panthera pardus*, and chacma baboons *Papio ursinus* (Carstens et al., 2019b). Studies on other vertebrates have shown that larger group sizes can decrease (through increased surveillance and defence; Clutton-Brock et al., 1999; Santema & Clutton-Brock, 2013; Ausband & Mitchell, 2021), or increase (through increased activity around nesting site; Martin, Scott & Menge, 2000) nest predation, depending on the species and their respective breeding behaviours. For ground-hornbills, however, it is unknown how effective group members are at preventing nest predation, but given their large body size and energy requirements, much of their time is spent away from the nest foraging as a group (Zoghby et al., 2015), leaving nestlings vulnerable to predation. This may explain the lack of evidence for any group composition associations with fledging success.

Hence, we did not find clear indication that group members contribute to improve the overall reproductive outcome in this species, apart from the association between the number of adult males and tarsus length. Our results also do not support the hypothesis that members buffer against the effects of adverse breeding conditions. It has been suggested that cooperative breeders are more common in areas that experience greater climatic variation, such as arid and semi-arid regions, because the presence of group members provides additional food that allows sustained reproduction under adverse breeding conditions, which are more common in these unpredictable regions (Rubenstein & Lovette, 2007; Covas et al., 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). While most hornbill species are associated with relatively mesic environments (Gonzalez, Sheldon & Tobias, 2013), ground-hornbills (both the southern and its congener the Abyssinian) are mainly associated with semi-arid regions. As expected, southern ground-hornbill reproduction was negatively associated with hotter and drier conditions, but their social structure did not have any clear effect on how these conditions influenced reproductive outcomes. This suggests that group members do not flexibly adjust their investment in reproduction when needed. This is consistent with the hypothesis that the physiological costs (Covas et al., 2022) and general risk-taking associated with nestling care should be minimised in species with high life expectancy and slow life-history strategy (Ghalambor & Martin, 2001). Hence, a species' life-history strategy should be considered when predicting whether helpers will respond flexibly to environmental conditions such that they could have a mitigating effect when conditions are poor.

Conclusion

Our study provides evidence that high temperatures and low rainfall are detrimental to breeding propensity and offspring quality in southern ground-hornbills, and that these associations are largely independent of the presence of cooperative members in a breeding group. Climate predictions suggest that temperatures will become increasingly hot and rainfall increasingly variable (IPCC, 2021). In southern ground-hornbills, our results show that this might lead to decreases in reproductive productivity, and considering the Vulnerable status of the species, this is a worrying but important result in understanding the impacts climate change might have on population persistence. As expected, these detrimental effects appear not to be buffered by larger group sizes, adding to previous studies on

cooperative breeders that obtained similar results (Bourne, Ridley, Spottiswoode, et al., 2021; D’Amelio et al., 2022). They are also in agreement with the suggestions that the life-history characteristics and more stable food resources of hornbills render the number of helpers less relevant for reproductive output (while helpers could be important for other group functions such as territory defence; Gonzalez, Sheldon & Tobias, 2013). Additional studies on other long-lived social breeders are needed to broaden our understanding of whether and how reproduction is influenced by the interaction of social and climactic factors, and how this relates to the biogeography and taxonomic distribution of cooperative breeding.

Appendix

Fieldwork insight 5. Carrying the ladder was an important part of the job as nests were sometimes a few hundred meters from the nearest road.

Fieldwork insight 6. Brooding females had to be flushed out of the nest so that we can monitor the chicks. They would return a few minutes after we left.

Table S3.1. Description of the different variables used within the different models of the breeding stages.

Type	**Variable**	**Explanation**
Response	Breeding probability (1/0)	Whether the group attempted to breed (Binary)
	Fledging success (1/0)	Whether the group raised a nestling to fledging (Binary)
	Nestling condition (Nestling mass and tarsus length)	The mass and tarsus length of the nestlings at measurement (Continuous)
	Lay date	Days after 1 September when the first egg was laid (Discrete)
Explanatory	Number of adult males	The number of adult males within the group during breeding (Discrete)
	Number of sub-adults	The number of sub-adults within the group during breeding (Discrete)
	Number of juveniles	The number of juveniles within the group during breeding (Discrete)
	Mean maximum temperature	The mean maximum temperatures for different periods. Winter: June–August, spring: September–November, or specific nestling period from hatching to measurement (Continuous)
	Rainfall	The quantity of rainfall for different periods. Winter: June–August, spring: September–November, or specific nestling period from hatching to measurement (Continuous)
	Nest height	The height of the nest from the ground (Continuous)
	Nestling age	The age of the nestlings during measurements, in days (Discrete)

	Lay date	Days after 1 September when the first egg was laid (Discrete)
Interactions	Rainfall*Tmax	The interaction between the amount of rainfall and mean maximum temperatures for different periods (when not correlated). Winter: June – August, Spring: September – November, or specific nestling period from hatching to measurement (Continuous)
	Amal/SA/Juv*Rainfall	The interaction between the number of adults/sub-adults/juveniles and the amount of rainfall for different periods. Winter: June – August, Spring: September – November, specific nestling period from hatching to measurement (Continuous)
	Amal/SA/Juv*Tmax	The interaction between the number of adults/sub-adults/juveniles and the mean maximum temperatures for different periods. Winter: June – August, Spring: September – November, specific nestling period from hatching to measurement (Continuous)
Random	Group identity	The name/identity of the group
	Year	The year in which the breeding attempt occurred

Breeding probability

Table S3.2. Number of groups analysed per year for breeding probability analyses.

Year	Breeding probability: No. of Groups
2001/2002	4
2002/2003	5
2003/2004	14
2004/2005	17
2005/2006	16
2006/2007	18
2007/2008	18
2011/2012	16
2012/2013	14
2013/2014	16
2014/2015	13
2015/2016	15
2016/2017	16
2017/2018	16
2018/2019	14
2019/2020	17
2020/2021	15

Table S3.3. Factors predicting breeding probability, with estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 244 from 22 groups. The model was run with binomial (binary) error structure with a logit link function.

Variable	**Estimate**	**SE**	**95% CI**
Number of adult males	-0.12	0.18	-0.47 – 0.23
Number of sub-adults	**0.38**	**0.19**	**0.02 – 0.78**
Number of juveniles	**0.58**	**0.18**	**0.23 – 0.95**
Mean maximum winter temperature	0.12	0.16	-0.21 – 0.44
Winter rainfall	**0.47**	**0.18**	**0.14 – 0.84**

Table S3.4. Random effects variance and significance in relation to the probability of breeding estimated by likelihood ratio test. Random effects highlighted in bold show significance.

Random effect	**Variance**	**df**	**LogLik**	**Chi-squared**	***P***
(None)	-	-	-145.93	-	-
Group identity (n = 22)	**0.92**	**1**	**-139.76**	**12.35**	**<0.001**

Lay date

Table S3.5. Number of egg-laying dates analysed per year for lay date analyses.

Year	No. of Breeding Attempts
2001/2002	2
2002/2003	2
2003/2004	8
2004/2005	11
2005/2006	4
2006/2007	13
2007/2008	11
2011/2012	12
2012/2013	7
2013/2014	11
2014/2015	8
2015/2016	10
2016/2017	13
2017/2018	11
2018/2019	5
2019/2020	12
2020/2021	13

Table S3.6. Factors predicting laying date, with estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 153 from 23 groups. The model was run with a Gaussian error structure and a logit link function. Winter Tmax = mean maximum winter temperature, Spring Tmax = mean maximum spring temperature.

Variable	**Estimate**	**SE**	**95% CI**
Number of adult males	1.30	1.69	-2.03 – 4.63
Number of sub-adults	-0.78	1.69	-4.12 – 2.57
Number of juveniles	**-3.89**	**1.69**	**-7.23 – -0.52**
Mean maximum winter temperature	**3.90**	**1.80**	**0.36 – 7.44**
Winter rainfall	0.17	1.70	-3.20 – 3.53
Mean maximum spring temperature	2.71	1.73	-0.70 – 6.11
Spring rainfall	-0.62	1.73	-4.06 – 2.83
Winter Tmax*Winter rainfall	**4.66**	**1.94**	**0.82 – 8.49**
Spring Tmax*Spring rainfall	-3.00	1.89	-6.74 – 0.74

Table S3.7. Random effects variance and significance in relation to the lay date estimated by likelihood ratio test.

Random effect	**Variance**	**df**	**LogLik**	**Chi-squared**	***P***
(None)	-	-	-670.55	-	-
Group identity (n = 23)	17.57	1	-671.29	1.48	0.22
Residual	360.38	-	-	-	-

Fledging success

Table S3.8. Number of breeding attempts analysed per year for fledging success analyses.

Year	No. of Breeding Attempts
2001/2002	0
2002/2003	0
2003/2004	8
2004/2005	11
2005/2006	4
2006/2007	13
2007/2008	11
2011/2012	12
2012/2013	7
2013/2014	11
2014/2015	8
2015/2016	10
2016/2017	12
2017/2018	9
2018/2019	5
2019/2020	11
2020/2021	10

Table S3.9. Random effects variance and significance in relation to the fledging success estimated by likelihood ratio test.

Random effect	**Variance**	**df**	**LogLik**	**Chi-squared**	***P***
(None)	-	-	-91.50	-	-
Group identity (n = 18)	<0.001	1	-91.50	0	1
Year (n = 15)	0.08	1	-91.50	1.11	0.29

Nestling condition

Table S3.10. Number of nestlings measured per year for nestling condition analyses.

Year	No. of Nestlings measured	
	Mass	Tarsus length
2001/2002	0	0
2002/2003	0	0
2003/2004	0	0
2004/2005	6	6
2005/2006	3	3
2006/2007	11	11
2007/2008	7	8
2011/2012	4	4
2012/2013	4	4
2013/2014	9	9
2014/2015	4	4
2015/2016	3	3
2016/2017	4	4
2017/2018	7	7
2018/2019	5	5
2019/2020	6	6
2020/2021	6	6

Table S3.11. Predictors of nestling mass, estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). N = 79 from 20 groups over 14 years. Variables highlighted in bold have 95% CI which do not cross zero. The model was run with a Gaussian error structure and a logit link function.

Variable	**Estimate**	**SE**	**95% CI**
Number of adult males	5.70	38.59	-72.36 – 83.78
Number of sub-adults	54.20	41.84	-29.36 – 137.28
Number of juveniles	-62.75	39.89	-144.84 – 20.19
Mean maximum temperature	**-107.50**	**47.90**	**-213.18 – -11.89**
Tarsus length	**172.01**	**41.46**	**86.01 – 256.58**

Table S3.12. Random effects variance and significance in relation to nestling mass estimated by likelihood ratio test.

Random effect	**Variance**	**df**	**LogLik**	**Chi-squared**	***P***
(None)	-	-	-570.82	-	-
Group identity (n = 20)	153	1	-570.82	0	1
Year (n = 14)	17729	1	-569.46	2.71	0.10
Residual	94128	-	-	-	-

Table S3.13. Predictors of tarsus length, with estimates of effect sizes, standard errors (SE), and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% CI which do not cross zero. N = 80 from 20 groups over 14 years. The model was run with a Gaussian error structure and a logit link function.

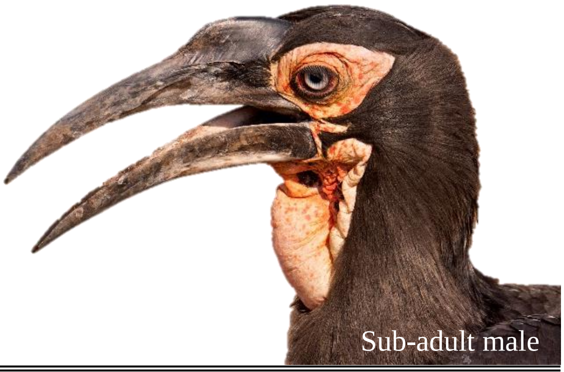
Variable	**Estimate**	**SE**	**95% CI**
Number of adult males	**2.58**	**0.98**	**0.59 – 4.55**
Number of sub-adults	0.65	1.11	-1.66 – 2.96
Number of juveniles	**2.90**	**1.07**	**0.62 – 5.20**
Mean maximum temperature	1.42	1.27	-1.28 – 3.95
Nestling age	**2.30**	**1.13**	**0.01 – 4.62**

Table S3.14. Random effects variance and significance in relation to nestling tarsus length estimated by likelihood ratio test. Random effects highlighted in bold show significance.

Random effect	**Variance**	**df**	**LogLik**	**Chi-squared**	***P***
(None)	-	-	-288.41	-	-
Group identity (n = 20)	5.03	1	-288.41	0	1
Year (n = 14)	**13.56**	**1**	**-286.29**	**4.23**	**0.04**
Residual	61.08	-	-	-	-

Part II: Territory defence

Chapter 4



Sub-adult male

Group signatures carried by melodies of female territorial calls in the cooperatively breeding southern ground-hornbill *Bucorvus leadbeateri*

***A typical dawn sighting when birds begin their territorial chorus vocalisations**. Ground-hornbills do not have specific roost sites, but usually find dead trees at the end of the day to spend the night. This constant movement can make them incredible challenging to locate in their vast territories. Photo: Kevin MacLaughlin*

Abstract

1. In solitary species, vocalisations used to advertise and defend territories often convey information about individual identity, which facilitates relationships between neighbours. However, in group-living species, where individuals contribute collectively to territorial chorus vocalisations, delivering a vocal group signature is likely more challenging, as several individuals vocalise at the same time. As such, this also makes it more challenging to investigate.
2. The cooperatively breeding southern ground-hornbill (*Bucorvus leadbeateri*) is an ideal species to investigate this question. Within each group, individuals produce low frequency booming chorus vocalisations while gathered close to the nest, to assert group presence in their territory. As each group consists of a single female occupying a dominant reproductive position, we were able to avoid the difficulties associated with analysing group vocalisations by investigating whether the calls of males and females could be distinguished, and whether the sole female calls could be individually distinct and so constitute a signature of the group.
3. Since southern ground-hornbills are difficult to approach in the field, we collected data using a combination of trail camera videos and audio recordings. These were analysed through manual labelling, semi-automated acoustic analyses, and machine learning techniques to test whether females could be distinguished from males and individually identified through their vocalisations.
4. We found that the male and female vocalisations contained consistent and repeatable sexual differences in the fundamental frequency. Female calls contained individual signatures within their vocalisations that could be automatically assigned to the correct individual with 93.6% success rate.
5. We conclude that the lone female's highly reproducible melody of calls is an ideal platform to convey information about group identity, which suggests a central role of females during territorial disputes and inter-group conflict. The acoustic characteristics of these low frequency calls also make them well suited for long range transmission; however, it is not yet known whether this information is indeed decoded by receivers in other groups. Further research on the species is needed to clarify this, and to test the function of female melodies in inter-group conflict.

Keywords: Chorus vocalisations, territory advertisement, signatures of identity, melody

Introduction

Animal communication plays a fundamental role in allowing conspecifics to exchange vital information during territorial conflicts, reproduction, foraging, predator defence, and resource competition. Information can be conveyed through one or more sensory channels, depending on the environmental and (sometimes) phylogenetic constraints on the communication system, and on the function of the signals exchanged (Boncoraglio & Saino, 2007; Laiolo, 2010; Keen, Meliza & Rubenstein, 2013; Witzany, 2014; Tanimoto et al., 2017; Wu et al., 2021). The form and extent of communication may also be determined by the constraints related to the social system. For example, solitary species predominantly communicate and interact with solitary mates and competitors, compared to social species that interact with numerous individuals within their own groups and from other groups. Therefore, solitary individuals may have different communication requirements to those of individuals living in social groups (Freeberg, Dunbar & Ord, 2012; Leighton, 2017; Wittwer et al., 2017).

In cooperatively breeding species where individuals live in groups, some individuals, considered as helpers, forego their own reproduction, and contribute to several group tasks (e.g., provisioning young, predator vigilance, and territory defence; Emlen, 1982; Kingma et al., 2014; Koenig, Dickinson & Emlen, 2016). This results in complex social environments in which multiple interactions occur within and between groups (Sewall, 2015; Leighton, 2017). Interactions between groups often involve coordination within groups to act as a collective to advertise and defend resources from conspecifics (McDonald & Wright, 2011; Keen, Meliza & Rubenstein, 2013; Benti, Curé & Dufour, 2019). These interactions increase the demand for intra- and inter-group discrimination and recognition. Acoustic communication is often the primary sensory channel used, particularly in dense environments where visual channels are limited and long-distance communication is required (Boncoraglio & Saino, 2007; Benti, Curé & Dufour, 2019).

In many territorial group-living species, groups specifically use chorus calls as a means of between-group communication to advertise and defend their established territories (Reyer & Schmidl, 1988; McComb, Packer & Pusey, 1994; Seddon & Tobias, 2003; Radford, 2005; Baker, 2009). Chorus

calls within cooperative groups are collective calls formed from the simultaneous vocalisations of more than two individual group members, and are sometimes accompanied by a visual display (Radford, 2003). These group territorial chorus calls have been shown to have similar functions to the territorial calls of individuals or mated pairs, allowing for territory advertisement and acting as the medium through which inter-group discrimination and recognition occurs (Seddon & Tobias, 2003; Bradley & Mennill, 2009; Zaccaroni et al., 2012; Christensen & Radford, 2018). Groups, mated pairs, and individuals alike benefit from the ability to recognise the calls of potential territorial intruders, as it allows them to decide how to respond. Responses to intruder vocalisations can vary depending on the relative level of threat they pose to the group (Christensen & Radford, 2018). For example, in the 'dear-enemy' phenomenon, neighbours are likely to pose less of a threat to defended resources than strangers, as they are familiar and already maintain a territory, making them more predictable and less likely to intrude (Temeles, 1994). Therefore, territory holders may respond less aggressively when recognising the vocalisations of neighbours (Radford, 2005; Christensen & Radford, 2018).

Yet, for any acoustic recognition and discrimination to occur, the signals produced must contain signatures that are unique to the individual, sex, or group (Baker, 2009). Signatures arise from differences in the acoustic characteristics (frequency or temporal parameters, or both) of calls between individuals and between certain categories of individuals. Attempting to identify these differences is a key step in investigating whether individuals are able to discriminate and recognise one another through their vocalisations (Keen, Meliza & Rubenstein, 2013; Budka & Osiejuk, 2014; Mumm & Knörnschild, 2017). Furthermore, species that produce vocalisations for the purpose of long-distance communication in cluttered environments may only have available to them a fraction of the potential acoustic characteristics that could encode signatures (Wiley & Richards, 1978; Seifart et al., 2018). This is due to high frequency sounds attenuating and degrading to a greater extent over long distances compared with lower frequency sounds, which often constrains vocalisations to lower frequencies (Forrest, 1994; Cornec et al., 2017).

Group chorus calls might encode group identity information through two mechanisms. Firstly, the calls of the different individuals participating in the chorus may share the same group-specific

acoustic characteristics. In groups consisting predominantly of family members (most likely retained offspring), these shared characteristics may be as a result of inheritance from breeders whose calls may differ genetically from the breeders of other groups (Radford, 2005; Payne, 2016; Mumm & Knörnschild, 2017). For example, in bell miners, acoustic similarity of provisioning calls increased with increased genetic relatedness, particularly when comparing helpers and breeders (McDonald & Wright, 2011). In cooperative groups consisting of both related and unrelated individuals (Kingma, 2017), shared acoustic characteristics can be the result of convergence or imitation by the other members of the group on the acoustic parameters of a particular individual’s call (Mammen & Nowicki, 1981; WallØe et al., 2015; Evans & Kleindorfer, 2016; Mumm & Knörnschild, 2017). These particular individuals may occupy a central place and function in the group, such as the breeders/dominant individuals, and are often responsible for the initiation of chorus calls (Immelmann, 1960; Reyer & Schmidl, 1988; Radford, 2005). Secondly, the calls of the different individuals within the groups may not share any vocal parameters, but instead all group members simultaneously produce their own individual signatures repeatedly at their own pace. Through each individual repetitively following his/her own vocal pace during each chorus, chorus calls may convey information about the group and individual identity simultaneously. Radford (2005) provided evidence of this latter mechanism, showing that the chorus calls of green woodhoopoes *Phoeniculus purpureus*, resulting from different individuals contributing separately of their own accord, were significantly distinct between groups and allowed for discrimination between groups. Breeders/dominant individuals are also expected to play a central role in this mechanism since they are the most consistently present individuals in the group over time and are often the most vocal (Golabek & Radford, 2013). Yet, the central role of these individuals in conveying group signatures has received limited attention.

The southern ground-hornbill, *Bucorvus leadbeateri*, is an ideal species in which to investigate how long-distance chorus vocalisations might carry group signatures. In this African cooperatively breeding bird, groups occupy year-round territories of up to 200 km^2 (Kemp & Kemp, 1980; Theron et al., 2013; Zoghby et al., 2015) in savannah habitats with woody cover percentages of up to 60% (Loftie-Eaton, 2017). These large territories within relatively cluttered environments suggest that vocalisations

may be particularly useful to advertise and defend territories. Groups range from 2–11 individuals and are comprised of a dominant breeding pair, and mostly subordinate males of various ages (Kemp & Kemp, 1980; Kemp, 1988; Kemp, Kotze, et al., 2020). Each morning, the lone adult female and adult males (with the occasional sub-adult males) of the group perform deep booming chorus vocalisations from within their territory, which can be heard over large distances (Kemp & Kemp, 1980; Kemp, 1988). This means that chorus vocalisations contain calls produced by several males and by a single female. Their acoustic structure has never been studied, and nor has the information potentially conveyed. Considering the central role of females in the reproductive success of the group, we hypothesised that their territorial calls could play a central role in the chorus, and could convey information about group identity that could be used across territorial boundaries. Studying an elusive species which occupies such large territories is a challenge. The extensive daily movements of southern ground-hornbills through cluttered environments makes them difficult to approach and observe visually. We therefore took advantage of the opportunity to record and film birds when nesting to develop a semi-automated tool for assigning calls to sex, enabling further analyses of audio-recordings acquired from a distance. In this study, we first investigated whether the territorial calls of males and females contained consistent and repeatable differences in their acoustic parameters, to confirm that their vocalisations are sexually dimorphic. Second, we asked whether female calls contained individual signatures that could convey individual identity, and so group identity too given the consistent presence of a single female in any one group.

Methods

Recording procedure

Audio and video recordings were collected over the course of three breeding seasons (2016–2018 and 2021) using two different methods, passive and active. Vocalisations on passive recordings were extracted from videos and so involved known individuals, whereas for active recordings, birds were mostly out of sight and so only group identity was known. Therefore, passive recordings were used to

train a model of group identification based on female identity, and active recordings were used to test this model.

Passive video and audio recordings were performed using high-definition trail cameras (Browning Spec Ops Advantage, no-glow IR flash, 20 MP resolution and Browning Spec Ops Elite HP4, no-glow IR flash, 22 MP, Browning Trail Cameras, Alabama, USA) placed at the nesting sites of several breeding groups. These are ideal locations because all individual group members visit regularly during breeding and trail cameras allow for close-up recordings of the birds with no disturbance to their behaviour, an otherwise difficult task for wild birds. Cameras were set up facing nest entrances 2–10 m away for 5-day periods during four different stages of breeding: stage 1 – incubation (where eggs were inside the nest); stage 2 – early nestling (where the nestling was 0–10 days old); stage 3 – middle nestling (where the nestling was 35–50 days old), and 4 – late nestling (where the nestling was 75–85 days old). Audio-video recordings lasted for 20 s with between-video intervals of 5 s, and were triggered by movement and temperature variance (using a passive infrared detector). Nine groups were recorded this way.

Many of the audio-video footage only contained a single bird vocalising per video and these videos were separated into folders according to the individual in the frame (identified through unique facial features; Figure 1.3). The audio from each of the videos was then extracted as a .wav file using VLC media player version 3.0.14 (VideoLAN, France) and stored for further analysis (see Acoustic Analyses, below). Videos which contained more than one individual vocalising were still separated into different folders where audio was then extracted, and audio analyses were conducted simultaneously with video analyses to ensure the individuals were matched with the corresponding audio. Birds in the videos were considered to be vocalising if they showed the following distinctive behaviour: a characteristic down-tilted bill, arched neck, neck inflation, and body contraction (Kemp & Kemp, 1980). Only files containing territorial vocalisations, identified as several very loud calls emitted in series by an individual during early mornings (Kemp & Kemp, 1980, KMM pers. obs.), were further analysed. The total amount and duration of the passive data analysed differed from individual to individual, depending on the footage captured (see Results).

Active audio recordings of territorial vocalisations emitted each morning were performed during the incubation stage of breeding using a directional shotgun Sennheiser ME67 microphone (frequency response: 40–20 000 Hz ± 2.5 dB), equipped with a windshield, and connected to a Marantz PMD661 recorder (frequency response: 40–24 000 Hz, sampling frequency: 44.1 kHz, uncompressed wave format). The best opportunity to record territorial vocalisations and to avoid any disturbance to the birds while recording was to arrive in the nest vicinity before dawn, hide in a suitable location out of sight of the birds, approximately 100 m from the nest, and wait until the birds began calling. The birds produce their choruses in the vicinity of the nest, although in unpredictable precise locations. Consequently, the recording distance varied from 50–300 m, and visual individual identification was not always possible. Eleven different groups were recorded (five of which were also recorded in the passive audio recordings), and each group was recorded on several occasions when possible (with a maximum of 4 days between recordings). Recordings ranged from 90 s to 1020 s (depending on the location of the birds and the signal-to-noise ratio) and were ended after 30 s of silence from the birds. In total, for each group, 360 s of the best signal-to-noise ratio files were analysed.

Acoustic analyses

Chorus calls consist of several individuals vocalising simultaneously, where each individual produces a series of calls termed a sequence. Therefore, chorus calls contain several individuals producing sequences of individual calls (Figure 4.1). Each call had a harmonic structure which was more apparent in calls recorded at closer distances. All calls were analysed using Avisoft-SASLab Pro 5.2.12 sound analysis software (Avisoft Bioacoustics, Berlin, Germany), and MATLAB. Prior to analyses, recording files were band-pass filtered (bandpass = 0–2.0 kHz) to remove background noise, and down-sampled at Fe = 2756 Hz.

Passive audio recordings were manually labelled with a code specific to the group, individual, and sex of the individuals identified in the corresponding videos. Preliminary analyses of these recordings clearly showed that the distribution of inter-call intervals produced by a given individual was bimodal, with one mode inferior to 1 s, and one mode superior to 1 s (Figure S4.2). Thus, sequences of calls were distinguished and labelled accordingly when separated by more than 1 s of silence. Then

within each sequence, calls were manually numbered. For example, an individual’s call labelled A1Fcall1 = group A, individual number 1, female, call number 1 (Figure 4.1).

Active audio recordings were manually labelled to identify calls. As no video was available, calls were not assigned to any individual at this stage. The only purpose of the manual labelling of the active audio set was to allow automatic computations on each call and avoid errors related to automatic call detection.

From each labelled call in both audio sets, the following acoustic parameters were automatically extracted (using a homemade MATLAB script):

- Fundamental frequency F0 of each call (in Hz, which corresponded to the frequency of maximum amplitude computed on the Fourier spectrum of the whole call, except for a few exceptions that were manually corrected).
- Duration of each labelled call (in s, computed as the length of time from the start of the call to the end of the call)
- Duration of the inter-call interval (in s, computed as the length of time between two consecutive calls)

When necessary, for recordings with higher background noise or suspected outliers, measurements were double-checked by manual analysis.

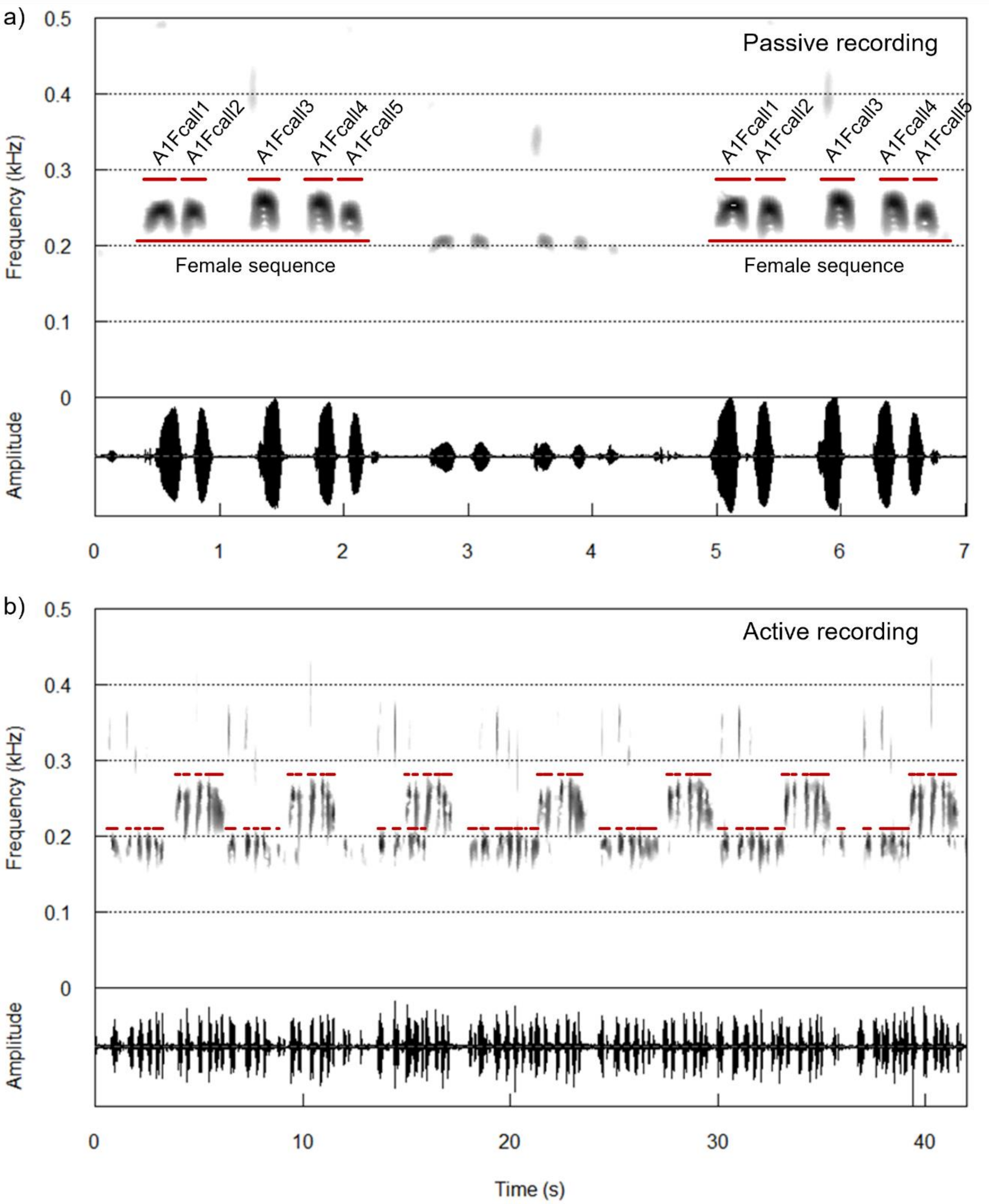


Figure 4.1. Southern ground-hornbill territorial vocalisations: a) spectrogram (top) and oscillogram (bottom) of a 7 s extract of a passive recording acquired from the trail camera footage of a female. Sequences (long red lines) were separated by more than 1 s of silence and the calls within each sequence were manually labelled (short red lines) with codes specific to the group, individual, sex, and call number. For example, A1Fcall1 = group A, individual number 1, female, call number 1. Between the female sequences is a male sequence that was labelled in a separate file. b) Spectrogram (top) and oscillogram (bottom) of a 42 s extract of an active recording. Calls were manually labelled (short red lines) but were not assigned to individuals at this stage.

Data and statistical analysis

Our data analyses had two aims. First, the passive audio recordings were used to analyse differences between sexes and to train a linear discriminant analysis classification between males and females. Second, the active audio recordings, owing to the large amount of data, were used to test whether it was possible to automatically identify individually each female, using a machine learning algorithm after automatic classification of female and male calls.

In the passive audio recordings, differences between sexes were analysed using a linear mixed-effect model (R package lme4, Bates et al., 2015). The model goal was to determine whether the call fundamental frequency (F0) and duration (both considered as response variables) were consistently different between sexes and positions in the sequence (considered as fixed effects). Individual and group identity were included as putative random effects. The models were followed by Tukey's post-hoc multiple comparison tests using the R package emmeans (Lenth et al., 2018). Statistical significance level was set to 0.05.

Calls were automatically classified between male and female calls using a linear discriminant analysis (LDA) trained on a passive acoustic recording set. Each call was represented as a vector of two features (call duration and call F0), and its class corresponded to the sex of the emitter. The LDA was trained using a 5-fold cross-validation process to avoid overfitting. As the LDA classification performance was very high for the first four calls (91.4% accuracy, see Figure S4.3), the learned classification line was further used to classify the calls from the active acoustic recordings set. It is important to note that the performances of automatic sex identification strongly dropped after the 4th call position within the sequence (Figure S4.4), and therefore we only used the first four calls.

Semi-automatic labelling of the active audio recordings

The active audio recordings were semi-automatically treated for clustering sequences of calls, using a two-step process. First, in each recording, calls were manually marked using Avisoft SASLab Pro. Then, each recording was further processed in MATLAB by an automatic labelling algorithm using the same code as for the passive audio set. Sex identification was performed by applying the classification

line learned from the LDA on passive recordings. This allowed drawing inter-call interval distributions for males and for females separately (Figure S4.5). Given the bimodality of the female inter-call interval distribution, sequences were defined as series of calls whose inter-call intervals were below 1 s. Then, within each female sequence, calls were automatically numbered. All the first 4 calls of females were automatically labelled. Further calls (5th and 6th) were not labelled as the LDA's performances dropped after the fourth call (Figure S4.4).

Female/Group signature

The active audio dataset was used to investigate whether each group could be identified by the individual signature in the calls produced by the lone female of the group. To do so, each sequence was formatted into a feature vector containing 12 features and 1 class. The class corresponded to the group identity (11 possible classes corresponding to *Addger, Caroline, Hermansburg, Copenhagen, Java, Lillydale, Ntsiri, Rhino Road, Senalala, Thornybush* and *Johnniesdale*). The features included fundamental frequency (F0) of the first four calls of the sequence, the duration of each call, each inter-call interval and the sequence duration. The goal of the machine learning algorithm was to correctly identify the female/group identity (the class) from the 12 features of a given call sequence.

In order to define an appropriate classification model, several algorithms were tested using the MATLAB toolbox Statistics and Machine Learning. Preliminary model selection and hyperparameter tuning for each model type was performed using a Bayesian Optimization approach following the workflow described in https://fr.mathworks.com/help/stats/bayesian-optimization-workflow. Holdout training-testing splits were performed on the data by randomly assigning each call to either the training or the test set. Both sets had approximately the same class proportions as in the original data. The 80% training set was used for training the model, and the model's efficiency was evaluated on the remaining unseen 20%. Model efficiency was estimated using the test global accuracy (percentage of correct classifications in the test set).

The retained model was an AdaboostM2 learning algorithm, which is an ensemble boosting method adapted for multiclass classification (Freund & Schapire, 1997), with a deviance split criterion, a learning rate of 0.55, and a mean leaf size of 3.

Results

Identifying sexual differences in passive recordings

8 females and 18 males from 7 different groups were recorded by trail cameras, and 1119 female calls, with an average of 140 (range: 44–379) calls per female, and 1384 male calls with an average of 81 (range: 24–174) calls per male, were analysed (Table 4.1).

Female calls had higher F0 at 228 ± 23 Hz when compared to males calls at 195 ± 47 Hz (Figure 4.2a, linear mixed effect $R^2 = 0.8$, $p < 0.001$), and this held true for all call positions in the sequence (post-hoc comparisons, all $p < 0.001$). However, call durations were not significantly different between females and males (Figure 4.2b, linear mixed effect $R^2 = 0.74$, $p = 0.187$).

Table 4.1. Number of calls recorded and analysed for each individual within each geographically distinct group using trail cameras.

Group names	Group members					
	Alpha female	**Sub-adult female**	**Male 1**	**Male 2**	**Male 3**	**Male 4**
Addger	379		174	62	25	
Camp George			32			
Janovsky	44	50	123			
Karan Khaya	118		24	163	99	30
Ntsiri			41			
Johnniesdale	52		53	150	84	
Copenhagen	176		156	88	24	
Hermansburg	165		56			
Senalala	135					

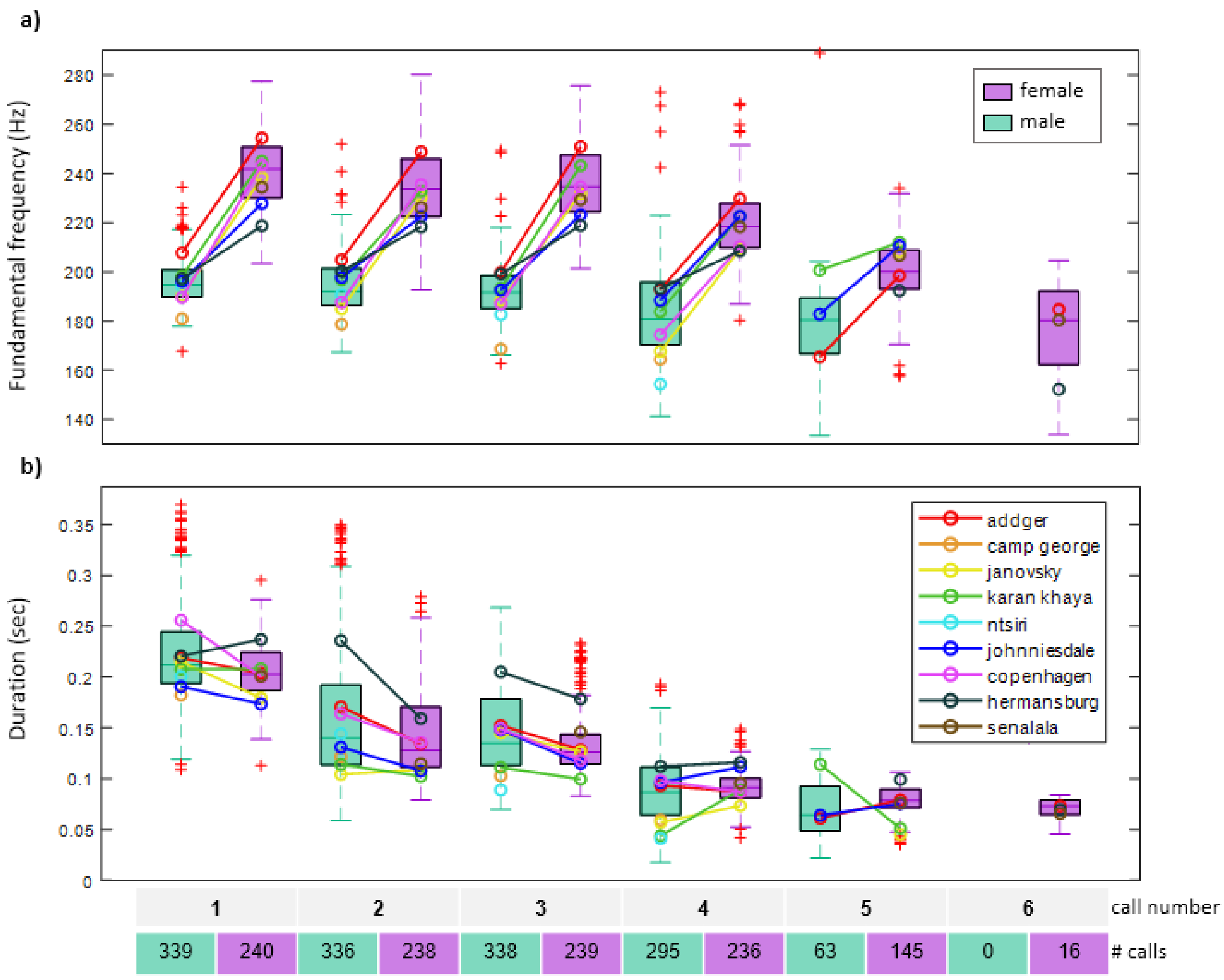


Figure 4.2. Acoustic parameters of calls within sequences of males and females. a) Fundamental frequency of each call within sequence, and b) Duration of each call within sequence. On each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles respectively. The whiskers extend to the most extreme data points not considered as outliers, which are plotted individually with the + symbol. Open circles indicate mean values per group and connection lines show the differences between sexes.

Individual signatures

The active audio dataset comprised the vocalisations from 11 females and numerous males in 11 different groups. A total of 9034 calls was analysed. Linear Discriminant Analysis resulted in 3831 calls being automatically assigned to females, and 5203 calls to males. Considering that 2–3 males were vocalising per group, each female produced more calls (mean: 348.2 calls) than each of the males (mean: 203.4 calls) within the chorus (Table 4.2). Since each group consisted of several males with a single female, automatic individual identification could only be performed on females. And, as LDA classification performances dropped after the fourth call (see Methods), only the first four calls per sequence produced by females were analysed (N=3259, Table 4.2).

Table 4.2. Number of calls recorded, analysed, and automatically assigned in each geographically distinct group using active audio recordings.

Group names	Group members		
	Female	**Males (no. of males in group)**	**Female first four calls**
Addger	326	515 (3)	264
Caroline	352	459 (2)	261
Hermansburg	392	502 (2)	323
Copenhagen	395	598 (2)	378
Java	360	420 (2)	308
Lillydale	160	604 (2)	160
Ntsiri	430	436 (2)	344
Rhino Road	416	615 (3)	387
Senalala	378	449 (3)	318
Thornybush	339	339 (3)	300
Johnniesdale	283	266 (3)	216

Following the classification of calls according to the caller's sex, automatic numbering of call positions within a sequence were performed for female calls. This allowed the building of sequences of calls consisting of the duration of the first four calls, together with their fundamental frequency and their inter-call intervals. Examples of such sequences are provided in Figure 4.3 for the Hermansburg and Senalala groups. For both groups, the figures show the mean sequence (mean frequency, mean duration and mean inter-call interval of the four calls), alongside the standard deviation of frequency and duration across all female sequences recorded in each group. The Hermansburg and Senalala females produced very different sequences, with Hermansburg's female producing more consistent sequences (i.e. all lines overlap) than Senalala's (i.e. two separate groups of orange lines represent the second call in the sequence). As shown in Figure 4.3, each female produced calls that created a mostly

unique melody (with slight variations), where each call within the sequence had a specific F0 and duration, and were followed by specific inter-call durations.

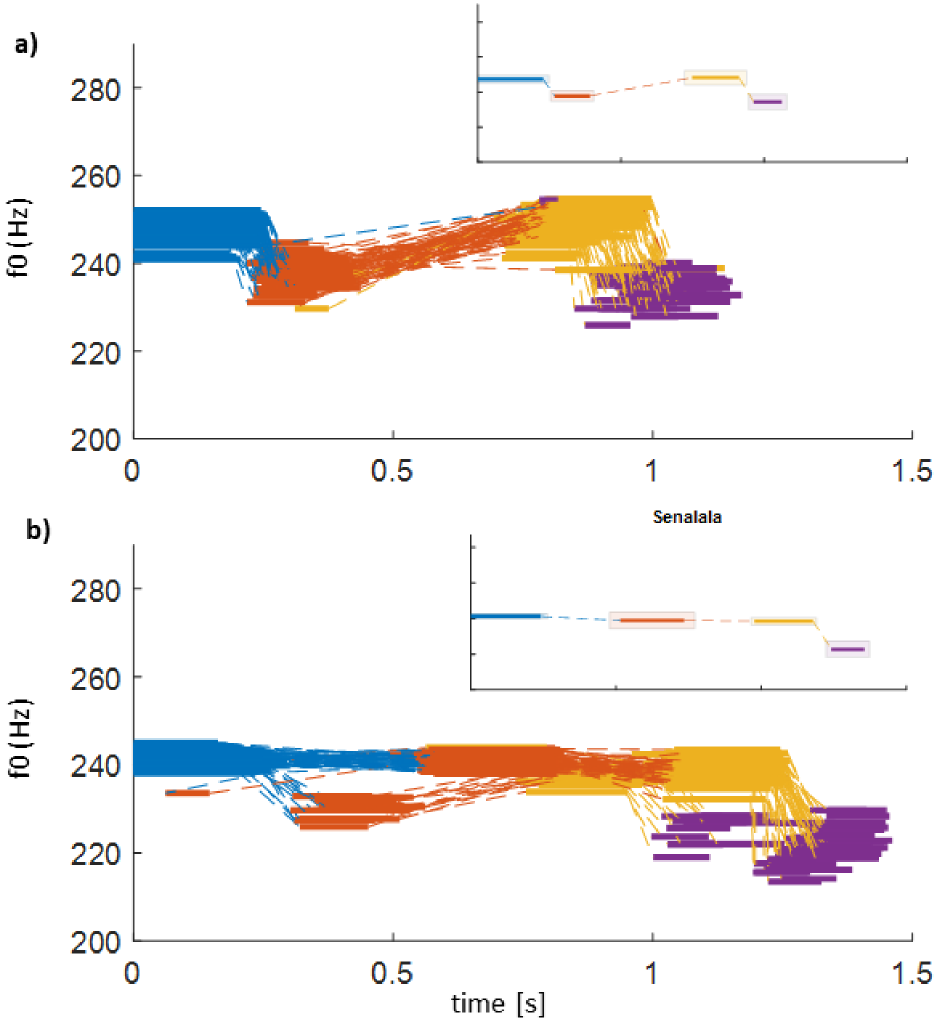


Figure 4.3. Female melodies. Examples of all sequences for a) the Hermansburg female, and b) the Senalala female. Call 1 (and respectively calls 2, 3 and 4) is represented by a blue line (and respectively orange, yellow and purple lines). The length of the line corresponds to the call's duration, and its vertical position to its fundamental frequency. Dotted lines represent the inter-call intervals, and link each call to the following call in a given sequence. Insets in the top right corners show the 'mean sequence' for each female. The mean F0 and duration of each call are represented by a thick line (following the same colour coding as above for different positions), and the standard deviations are represented by the shaded area around the means. For 'mean sequences', the inter-call intervals are also represented by dotted lines.

In order to assess whether this held true for all groups, a machine learning algorithm was trained to classify sequences according to their group. The AdaboostM2 learning algorithm had a high level of classification, showing that sequences do carry the information necessary to differentiate groups. As shown in Figure 4.4, the machine learning performances surpassed 90% (93.64%), which is far above

chance level (9%), indicating that female sequence information (call frequency, duration and inter-call intervals) not only differed among groups, but was stable enough within groups to carry a group/individual signature (Figure 4.4).

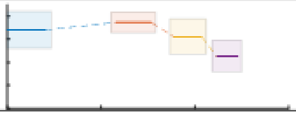
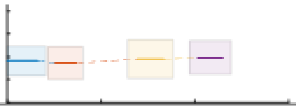
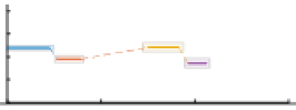
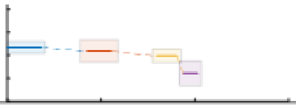
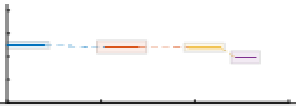
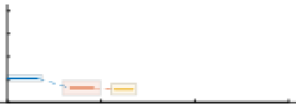
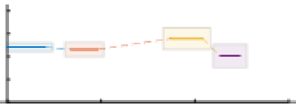
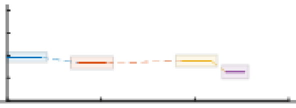
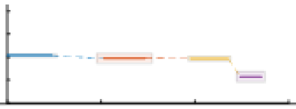
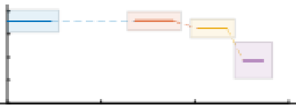
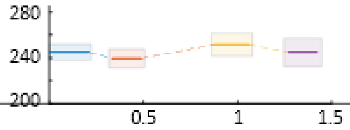
Group	Mean sequence	N	Training	Correctly classified
Addger		68	55	92,3%
Caroline		73	59	100%
Hermansburg		81	65	100%
Hull		97	77	100%
Java		77	62	93,3%
Lillydale		74	60	100%
Ntsiri		86	68	77,8%
Rhino Road		100	80	95%
Senalala		80	63	94,1%
Thornybush		76	61	86,7%
Johnniesdale		54	43	90,9%

Figure 4.4. Female melodies as potential group signatures. For each group, the first column represents the 'mean sequence' with the same representation as in the Figure 4.3 inserts. The second column (N) shows the total number of sequences. The third column (Training) indicates how many sequences were used for machine learning training (80%). The last column shows the percentage of correct classifications of each group using the female's melody as an identification criterion, as measured on the test dataset. Total test accuracy was 93.64%.

Discussion

In this study, the iconic deep booming chorus calls produced each morning by the lone female and adult males of southern ground-hornbill groups from their nest sites were extensively recorded and analysed in detail for the first time. We set out to investigate whether the territorial vocalisations of males and females contained consistent and repeatable sexual differences in their acoustic parameters, and whether the female vocalisations could be individually distinguished, and so encode a detectible signature of group identity. We took advantage of passive audio-video recordings to set up a semi-automated method of call and sequence identification, allowing us to use and successfully analyse long-range recordings of streams of chorus vocalisations produced by 11 different groups of these secretive and difficult to approach birds. Our data showed that adults of both sexes produce low frequency calls given in sequences during choruses, that these calls are sexually dimorphic, and that female chorus vocalisations are sequences of calls with individually distinctive melodies.

Each individual in the group produced sequences of calls of very low fundamental frequency. In birds, at an interspecific level, larger species tend to produce lower pitched songs (doves: Tubaro & Mahler, 1998; woodcreepers: Palacios & Tubaro, 2000; tinamous: Bertelli & Tubaro, 2002; songbirds: Badyaev & Leaf, 1997; Derryberry et al., 2018), following the morphological constraints hypothesis which proposes that the body size of a species limits the range of sound frequencies an animal can produce (Ryan & Brenowitz, 1985). The production of very low frequencies, such as those produced by southern ground-hornbills, is rare in birds and often associated with larger body sizes (see review Hart et al., 2020), sometimes combined with a particular way of sound production with the beak closed and the throat inflated (Riede et al., 2016). In our study, calls were sexually dimorphic, with females producing higher F0 values than males. This may be explained by differences in body size. This is consistent with studies of other species showing that body size has a negative relationship with vocalisation frequencies between individuals of the same species (e.g., in passerines: Wallschläger, 1980; in non-passerines: Cornec et al., 2015). This is presumably because the fundamental frequency of vocalisations is determined by the vibrating frequency of the syringeal membrane (Nowicki & Marler, 1988). Larger and stronger birds are expected to have larger vibratory structures and to make

them vibrate with more energy, which can subsequently produce lower frequency sounds (Ryan & Brenowitz, 1985; Tubaro & Mahler, 1998; Palacios & Tubaro, 2000). In the southern ground-hornbill, we do not have exact body sizes for the recorded individuals, but females are generally smaller and lighter (mean: 3.7 kg) than males (mean: 4.5 kg; KMM, unpublished data) which is consistent with this expectation.

As predicted, we found that the females' contributions to the chorus calls were individually distinctive, which in turn likely encode a distinct group identity, since each group contains only one female. Within choruses, female calls were clearly distinguishable and more abundant than each of the individual male calls, and had sequences combining the use of both frequency and temporal parameters to create signatures unique to the individual. These unique parameter combinations within the sequences can be described as melodies, since they consist of rhythmically ordered movement from frequency to frequency (Nowicki & Marler, 1988; Nooteboom, 1997; Richner, 2016). Investigating the structure and information encoded in acoustic sequences is a growing field of research in animal communication (e.g. Kershenbaum et al., 2014). In particular, recent developments in computational analyses allowed investigation of the temporal structures and rhythms in zebra finch *Taeniopygia guttata* song sequences (Norton & Scharff, 2016), and in the multisyllabic vocalisations of neotropical bats *Saccopteryx bilineata* (Burchardt et al., 2019) and humpback whales *Megaptera novaeangliae* (Schneider & Mercado, 2019), using similar techniques to those with which human language and music are investigated (Ravignani & Norton, 2017; Burchardt & Knörnschild, 2020). In birds, the temporal structures of acoustically complex zebra finch vocalisations (Norton & Scharff, 2016) and simple, disyllabic monotonous corncrake *Crex crex* vocalisations (Rek & Osiejuk, 2011) were both shown to be individually distinctive. Another study on the latter species also demonstrated that the rhythm and temporal structure of a specific call encoded information about aggressiveness (Ręk & Osiejuk, 2010). Our results show that female melodies, when considered as a whole object (i.e. the combined temporal structure and frequency of each call), do carry enough information to be distinguishable between individuals. However, it remains to be tested whether this information is used by neighbouring groups.

We suggest further playback experiments specifically addressing this by modifying the female melodies used in the chorus stimuli played to focal groups.

The use of melodies to encode information about individual identity overcomes some of the constraints of using low-frequency calls for long-distance communication. Low-frequency calls propagate well in natural environments and so are probably an adaptation to maximise the effectiveness of sound transmission over long distances (following the acoustic adaptation hypothesis; Morton, 2002; Padgham, 2004; Mikula et al., 2021). However, using low frequencies for long-distance communication comes with the trade-off of only using a small proportion of the frequency range (Forrest, 1994; Seifart et al., 2018). Therefore, the acoustic features available for encoding information in these low-frequency calls are limited. The additional use of rhythm together with frequency variations to create the sequences of melodies may counteract this limitation, and provide the means to effectively convey group and individual identity, as shown here in the southern ground-hornbill. This is the first demonstration of long-range communication using melodies in birds, but similar techniques have been used historically by human cultures around the world which used drums to play different rhythms to convey different messages over distances where verbal communication was not possible (Stern, 1957; Fuchs & Robert, 1999; Seifart et al., 2018).

For southern ground-hornbills, conveying identity information effectively over large distances to conspecific groups using chorus vocalisations may provide several benefits to individuals. On a group level, conveying group identity allows territory ownership to be advertised, which can reduce intrusions by conspecific groups and ensure that territory holders maintain access to vital resources (Nowicki, Searcy & Hughes, 1998; Siracusa et al., 2017). Such deterrence may be particularly important for ground-hornbills, as recent field observations have found intruding groups usurping nesting sites (KMM, unpublished data), which are a primary resource within territories and which limit reproductive success (Kemp, 1988; Carstens, 2017). Similarly, daily chorus vocalisations can increase the familiarity of neighbouring groups with the calling group’s identity and, in turn, reduce the frequency and intensity of territorial conflicts (following the 'dear-enemy' effect; Temeles, 1994; Christensen & Radford, 2018).

Our results highlight the potentially key role of females in chorus vocalisations, since female melodies provide a detectibly group-specific acoustic signature. However, males may also play an important role, regardless of whether their calls convey identity or not. This is because the presence of chorusing males may contribute not only towards the advertisement of resources and territory ownership, but may also deter other males in search of mating opportunities. Given that the adult sex ratio is male-biased in this species, sexually mature females are a scarce resource that males are likely to actively defend. Moreover, male calls may also convey general information on the size of the group by ‘filling up’ the acoustic space, which can deter intruding groups. Group size effects have been shown to mediate and affect the outcomes of conflict in other cooperatively breeding birds (e.g., green woodhoopoes *Phoeniculus purpureus* (Radford, 2003); and subdesert mesites *Monias benschi* (Seddon & Tobias, 2003)). More research is needed on the role of male calls in the chorus vocalisations of ground-hornbill groups. We suggest a starting point with the further use of trail cameras to investigate whether the territorial vocalisations of males are also individually distinctive.

Finally, our use of machine learning algorithms in this study showed that the chorus vocalisations of ground-hornbills could be automatically classified with a very high success rate. These algorithms are analogous to the present-day use of similar algorithms designed to identify unknown music using mobile applications such as ‘Shazam’ (https://www.shazam.com/, Shazam Entertainment, United Kingdom). This passive method for group identification could provide a useful conservation tool to survey ground-hornbill groups over large distances in difficult terrain, particularly since they occur in such low densities and tracking their movements is difficult.

Conclusion

Our study provides evidence that the territorial vocalisations of southern ground-hornbills contain consistent and repeatable sexual differences, and that the melodic female signatures within the choruses appear to be well-adapted to convey individual and group identity information over large distances, yet the latter still requires further detailed testing. This highlights the potentially central role of females within groups of this species. This study represents the first step in understanding the information

encoded in southern ground-hornbill territorial vocalisations, and so their potential function in territorial disputes between neighbours. We expect that further experimental research on this species will demonstrate that information can be accurately decoded over large distances in their natural habitat, since female- and so group-specific melodies are expected to propagate well over long distances. Future work should also aim to investigate the role of males in these chorus vocalisations, and specifically to test whether and how male calls may help to encode information about group size in the chorus. This would provide deeper insights into how these choruses are constructed and the selection pressures placed on the species, sexes, and individuals.

Appendix

Fieldwork insight 7. Early morning recordings often required us leaving home at 2am, but the sunrises made it worth it.

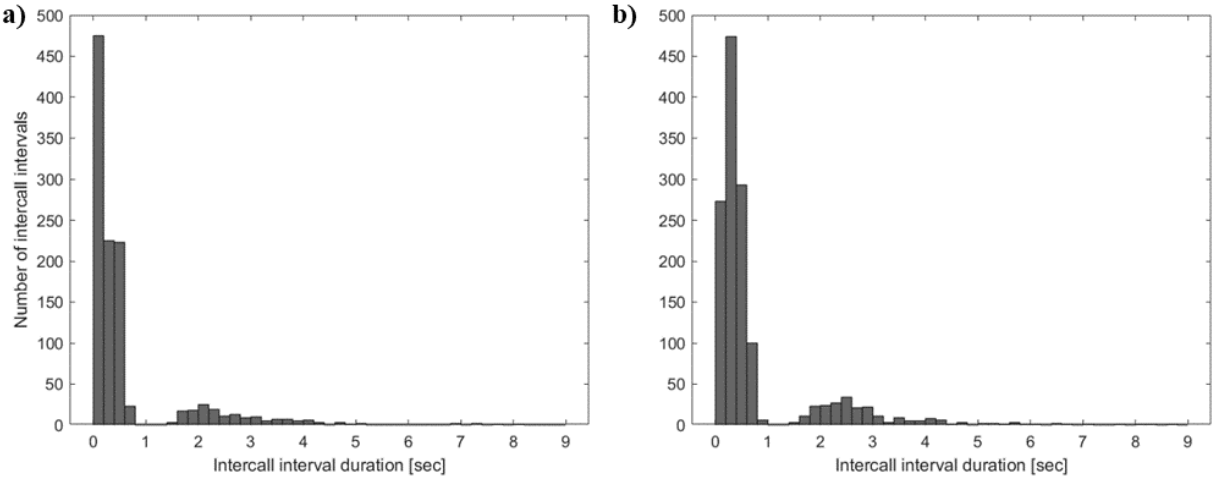


Figure S4.2. Frequency distribution of inter-call interval values for calls produced by a) females and b) males. Calls are from the passive audio recordings, n = 8 females, n = 15 males

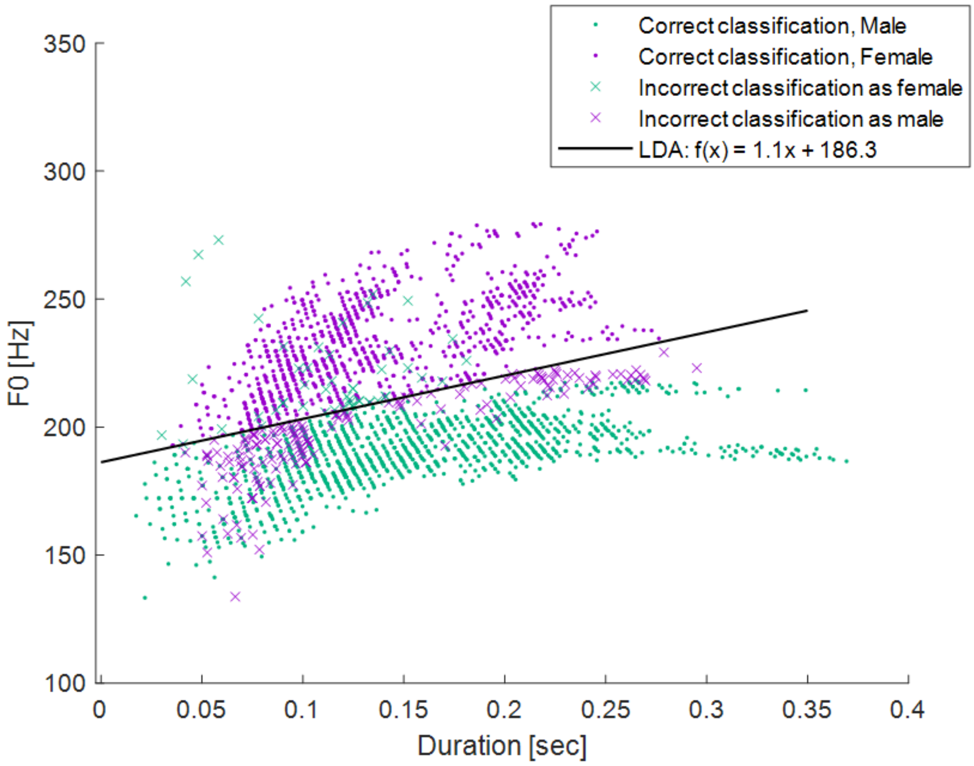


Figure S4.3. Fundamental frequency as a function of duration of all calls produced by males and females in the passive audio recordings. Male calls are green, female calls are purple. Correct classifications are represented by dots, incorrect ones by crosses. LDA classification appears as black line

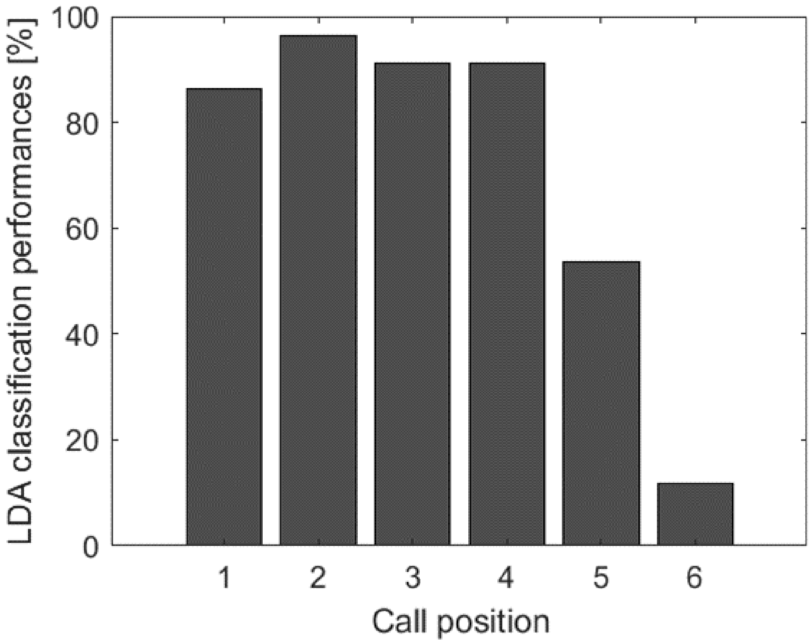


Figure S4.4. Percentage of correct LDA classification of female calls as a function of their position in the sequence in the passive audio recordings. The performance of classification is very high for the first four calls, and decreases from the 5th call.

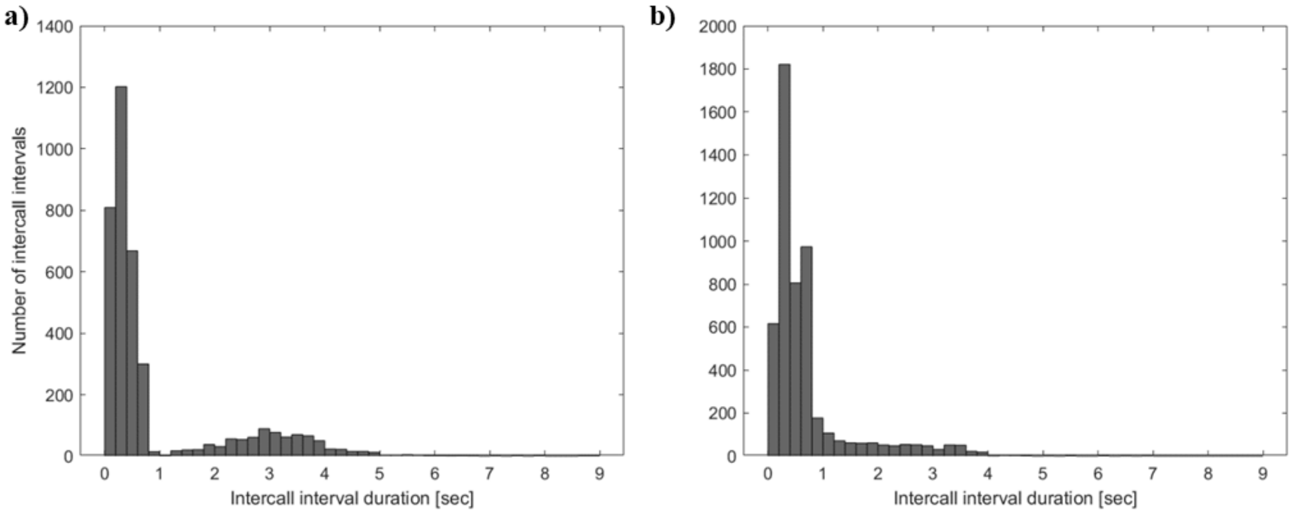


Figure S4.5. Frequency distribution of inter-call interval values for calls produced by a) females and b) males. Calls are from the active recordings. N = 3831 calls classified as female calls; n = 5203 calls classified as male calls.

Part II: Territory defence

Chapter 5

Group responses to simulated territory intrusions in the cooperatively breeding southern ground-hornbill *Bucorvus leadbeateri*

***Pitlochry group of birds**. Ground-hornbills spend most of their time walking and foraging on the ground, but when they do take flight, their white primary feathers flash and make them easily distinguishable. Photo: Kevin MacDonald*

Abstract

1. Territory advertisement and defence is common throughout the animal kingdom and ensures access to crucial resources vital for survival and reproduction. However, defence can be a costly behaviour, and studies in solitary species have shown that responses to intruders depend on the level of threat posed. In group-living territorial species, where several individuals cooperate in territory defence, the responses of groups should depend on the level of threat posed, the number and ‘quality’ of the individuals taking part in the collective response, and the reproductive value of any vulnerable offspring on the territory they are defending.
2. Here, we examined how territorial chorus vocalisations are involved in inter-group communication in a long-lived, territorial cooperative breeder, the southern ground-hornbill (*Bucorvus leadbeateri*). Specifically, we performed a propagation experiment to investigate the potential active space of the vocalisations, and exposed groups to playbacks of the chorus vocalisations of neighbour and stranger groups. We tested whether these responses depended on the identity of the simulated intruding groups, and on the group size and composition of the receiver groups being tested.
3. We found that vocalisation parameters important to group identity propagated effectively at least over a distance of 1 km. Larger groups responded more often and more quickly to simulated threats, regardless of the age structure of the group. Contrary to expectations, we did not detect any significant difference in response to simulated intrusions by groups of different identities (i.e. neighbour vs stranger).
4. We conclude that vocalisations play an important role in territory defence by southern ground-hornbills, and that group size is a key factor in mediating the responses of groups to conspecific territorial intrusions. Our results also suggest either that intruders of different identities represent an equal threat in this species, or that identities are not always distinguishable in the group chorus. This study provides evidence of the non-breeding benefits associated with group formation and so helps broaden our understanding of the evolution of cooperative breeding.

Keywords: Territory defence, simulated intrusion, group size, intruder identity

Introduction

Cooperative breeding occurs across diverse taxa and involves the contributions of non-reproductive members to raising the offspring of others (Cockburn, 1998). Such “helping” behaviour in this social system has evolved because its fitness benefits to breeders and their helpers outweighs its costs (Hamilton, 1964; Hatchwell, 1999; Wright & Russell, 2008). To date, most studies investigating these benefits of sociality have focused on helping behaviours associated with reproduction, such as offspring provisioning and care (Josi, Taborsky & Frommen, 2020). Yet, cooperative behaviours can also be directed towards other group tasks such as territory defence (Heinsohn, 1997; Golabek, Ridley & Radford, 2012b) or predator vigilance (Jungwirth et al., 2015; Groenewoud et al., 2016), amongst others, which can be equally, if not more, important for group success and persistence (Gonzalez, Sheldon & Tobias, 2013; Josi, Taborsky & Frommen, 2020). However, while these non-reproductive benefits are often invoked as drivers for general sociality and group formation, they have received far less attention in the context of cooperative breeding and further research is needed to understand their contribution to the overall benefits of sociality, and so their importance for the evolution of cooperative breeding.

Contributions of helpers to territorial behaviour may be important because territory defence ensures the benefits of exclusive access to limited and in-demand resources such as food, mates and breeding sites, which are all vital for survival and reproductive success (Hinde, 2008; Humphries et al., 2021). Group territoriality is common in cooperative breeders, and is associated with the collaboration of helpers and breeders in defending a spatial area against conspecific groups (Brown & Orians, 1970; Cockburn, 1998; Christensen & Radford, 2018). Territorial defence is often considered one of the most important cooperative tasks in this social system (Heinsohn, 1997), and understanding how territory holders respond to intrusion, and the factors that influence them, can provide insights into the benefits and maintenance of sociality (Hinde, 2008; Almstead et al., 2021). Much research on this topic has focussed on social carnivores or primates (Kitchen & Beehner, 2007; Müller & Manser, 2007; Mosser & Packer, 2009; Benson-Amram et al., 2011; Crofoot & Gilby, 2012; Cassidy et al., 2015; Majolo et al., 2020), although a few studies have focussed on cooperatively breeding birds (Radford, 2005;

Strong, Sherman & Riehl, 2018; Almstead et al., 2021; Humphries et al., 2021). Cooperative breeding is found in only approximately 1% of mammal species (Lukas & Clutton-Brock, 2017) but in approximately 9% of bird species (Riehl, 2013; Kingma, 2017). Therefore, investigating the benefits of cooperation for territory defence in cooperatively breeding birds is needed to provide a broader understanding of the advantages of this social system.

While territory defence protects the crucial resources contained in a territory against intruders, it may also come with costs in terms of energy, injury, or even death. Consequently, the decision of individuals group members on whether and how to respond depends on the level of threat posed by the intruders (Cant, Otali & Mwanguhya, 2002; Mosser & Packer, 2009; Mares, Young & Clutton-Brock, 2012; Arseneau-Robar et al., 2017). For example, rival groups looking to take over a territory, or intruding into the centre of a territory near valuable resources, pose a high level of threat to the entire group, creating the incentive for members to cooperate and respond equally (Radford, 2003, 2005; Kitchen & Beehner, 2007; Furrer et al., 2011; Werba et al., 2022). In these situations where all members contribute, group size has been shown to provide the numerical advantage needed to deter intruders and win territorial conflicts (Cant, Otali & Mwanguhya, 2002; Radford, 2003; Seddon & Tobias, 2003; Mosser & Packer, 2009; Cassidy et al., 2015). Additionally, groups with numerical advantages have also been shown to initiate encounters with rivals, suggesting that individuals assess the size of intruder groups when deciding whether or how to respond to a territorial intrusion (Seddon & Tobias, 2003; Benson-Amram et al., 2011; Cassidy et al., 2015).

However, group size alone does not always predict the responses and outcomes of territorial intrusions. In long-lived, slow-developing species, members of the same group typically have different ages and levels of experience (Covas & Griesser, 2007). Therefore, the costs and benefits of territory defence are expected to differ between individuals, influencing their contributions and the overall output of group defence (Crofoot & Gilby, 2012; Cassidy et al., 2015; Gavrilets, 2015; Van Belle & Scarry, 2015). For instance, Cassidy et al. (2015) showed that gray wolf *Canis lupus* packs with more adult males had higher odds of winning an inter-pack interaction during territorial disputes, even when they had a numerical disadvantage. It is less clear whether young or inexperienced individuals may also be

important for territorial defence. For example, recent studies have shown that some cooperatively breeding species engage in “kidnapping”, in which young individuals are taken from their natal groups and incorporated into intruder groups (Müller & Bell, 2009; Kemp & Ezzey, 2020; Ridley et al., 2022). This increases the intruder group’s size, and suggests that groups benefit from having more members, perhaps to aid breeding attempts and other group tasks (Heinsohn, 1991; Riehl, 2013). However, the contribution of youngsters to group defence may be relatively small given that youngsters tend to be inexperienced, to be smaller in body size, and risk being kidnapped (Ridley, 2016). This means that the costs and benefits associated with the age structure of groups might lead to different investment strategies by different age classes of individuals, and so modulate the effect of group size on territorial responses, but this is poorly understood.

The identity of intruders may also affect the relative level of threat posed to territory holders (Temeles, 1994). This has been shown extensively in studies demonstrating the different responses of territory holders to neighbours (individuals and groups occupying adjacent territories and who are likely to be familiar to the territory holders) and strangers (individuals and groups occupying territories further away and who are likely to be less familiar to the territory holders; Christensen & Radford, 2018). For example, the ‘dear-enemy’ hypothesis suggests that neighbours pose less of a threat to defended resources than strangers, since they are predictably present and less likely to intrude into a territory. Therefore, year-round territorial individuals or groups are expected to respond less aggressively to neighbours than to strangers (Fisher, 1954; Christensen & Radford, 2018; Humphries et al., 2021; Werba et al., 2022). Conversely, the ‘nasty-neighbour’ hypothesis suggests that neighbours are likely to pose the greater threat since they may be in better condition or have larger group sizes, resulting in a more aggressive response towards them than strangers (Botero, Riveros & Vehrencamp, 2007; Müller & Manser, 2007; Courvoisier, Camacho-Schlenker & Aubin, 2014). Evidence has been found for both hypotheses, but it has been suggested that the ‘nasty-neighbour’ phenomenon may be more prevalent in social species (Temeles, 1994; Müller & Manser, 2007; Newey, Robson & Crozier, 2010) since in these systems, encounters with strangers are typically the result of individuals (or small groups) dispersing and under these circumstances, territory holders are likely to have a numerical advantage

during conflict. Neighbours, on the other hand, may be in search of territory expansion in the search for crucial food and resources, therefore posing a greater threat and eliciting a stronger response (Müller & Manser, 2007; Newey, Robson & Crozier, 2010).

The ability of territory holders to distinguish neighbours from strangers requires intruders to convey their identity through one or more sensory modalities (Brown & Orians, 1970; Christensen & Radford, 2018). For many cooperative breeders occupying large territories or dense environments, advertising presence and conveying messages over large distances is often done using chorus vocalisations, which involve the simultaneous vocalisations of more than two group members, sometimes accompanied by a group visual display (Radford, 2003; Boncoraglio & Saino, 2007). Studies have shown that these chorus vocalisations allow for group and individual identity to be conveyed across territorial boundaries (Baker, 2004; Radford, 2005; Benti, Curé & Dufour, 2019), much like the territorial vocalisations of solitary (Mathevon et al., 2008; Budka & Osiejuk, 2014; Charrier et al., 2017) and pair-bonded species (Hall, 2004; Dahlin & Benedict, 2014; Kovach et al., 2014). Therefore they potentially facilitate the recognition of intruders and mediate competitive interactions to reduce the need for physical defence (Hopkins, 2013). Few studies have investigated group identity effects in cooperatively breeding birds, and most of these have only considered small, short-lived passerines with relatively small territories (but see Almstead et al., 2021). The benefits of group territorial defence may be especially important when territory sizes are large, meaning that further research is needed into the responses of long-lived, non-passerine birds (which occupy large territories) to fully understand how important group defence may be as a benefit of sociality.

We studied southern ground-hornbills *Bucorvus leadbeateri* to investigate how social (group size and intruder identity) and life-history (group age structure) factors affect territorial responses. Southern ground-hornbills (hereafter ‘ground-hornbills’) are large, top predators, which are very long-lived (up to 60 years in the wild) and develop slowly, reaching adulthood from around 6–8 years old (Kemp & Kemp, 1980; Kemp, 2017). Groups range from 2–11 individuals, with distinct age structures that are detectible from characteristics of the un-feathered throat, feather, and beak colouration (Kemp & Kemp, 1980; Kemp, 1988; Kemp, Kotze, et al., 2020). This African endemic species occupies large

year-round territories of up to 200 km^2 which are advertised and defended through the use of low frequency chorus vocalisations, and occasionally through physical defence (Chapter 4, Kemp & Kemp, 1980; Theron et al., 2013; Zoghby et al., 2015). Chorus vocalisations are performed by adults of both sexes, and occasionally sub-adults, and can be heard from several kilometers away, although to date no detailed analyses have been done on their propagation. The calls of the sole females in these groups contain individual signatures that could allow for group recognition (Chapter 4). Ground-hornbills are classified as Vulnerable throughout their range, attributable mainly to land-use change and habitat loss (Kemp, 2017). Conservation of the species is currently focussed on habitat preservation, provision of artificial nests, and the artificial formation and reintroduction of groups back into their historic range. Hence, understanding the effects of group size and composition on territory defence, and the importance of neighbour recognition, can provide novel insights to aid conservation and ensure group success and persistence.

In this study, we first conducted a propagation experiment to assess how chorus calls are acoustically modified as they propagate through the species’ natural habitat, to determine the ability of these calls to encode group identity over long distances. Second, we simulated territorial intrusions by playing back the chorus vocalisations of neighbour and stranger groups to 12 different ground-hornbill groups, and recorded their vocal and non-vocal behavioural responses. This allowed us to investigate 1) whether territorial responses differed according to whether the simulated intruders were neighbours or strangers, and 2) whether the group size and composition of the receiver groups influenced their responses. Studying such an elusive species which occupies such large territories is a challenge, and it is particularly difficult to test groups when they are gathered and likely to defend a crucial resource. Therefore, to enable this study, we conducted experiments exclusively on breeding groups and in the vicinity of occupied nests. Ground-hornbill groups in this study site only have a single nest per territory, and recent unpublished observations from a long-term project on the species (FitzPatrick Institute of African Ornithology’s APNR Ground-Hornbill Project) has found evidence of nests being usurped and used by neighbouring groups (KMM, personal observation). Given this threat from neighbours, we hypothesised that the responses to neighbours and strangers should differ and be more aggressive

towards neighbours than to strangers, since they likely pose a greater threat to breeding opportunities. We expected that the responses to intrusion should further depend on the composition of the group being intruded upon, because adult, sub-adult, and juvenile birds should differ in their experience and therefore in their contributions to territory defence. Specifically, we expected that groups with additional adult and sub-adult birds should respond more quickly, and by means of direct aggression rather than responding vocally. Juveniles, on the other hand, have extended dependence on older individuals for food and protection and have been shown to contribute less to other group tasks such as offspring provisioning (Chapter 4), as well as being susceptible to kidnapping (Kemp & Ezzey, 2020). We therefore predicted that the presence of juveniles within groups would make groups more susceptible to successful intrusion, and so be associated with increased vocal responses rather than direct aggression.

Methods

Call stimuli and equipment

To prepare call stimuli for playback and propagation experiments, we recorded the territorial vocalisations of 13 wild ground-hornbill groups during the breeding seasons of 2016, 2017, 2018 and 2021. Recordings were all made during the incubation stage of breeding, using a directional shotgun Sennheiser ME67 microphone (frequency response: 40–20 000 Hz ± 2.5 dB), equipped with a windshield, and connected to a Marantz PMD661 recorder (frequency response: 40–24 000 Hz, sampling frequency: 44.1 kHz, uncompressed WAV format). The best way to record territorial vocalisations and to avoid any disturbance to the birds while recording was to arrive in the nest vicinity before dawn, hide in a suitable location out of sight of the birds, approximately 100 m from the nest, and wait until the birds began calling. During the incubation stage the birds produce their choruses in the vicinity of the nest, although the exact location is unpredictable. Recordings ranged from 90 s to 1020 s (depending on the location of the birds and the signal-to-noise ratio) and groups were recorded on several occasions when possible. Two minutes of high-quality extracts were selected from these recordings, and were bandpass filtered using Avisoft SASLab Pro 5.2.12, using the frequency domain

transformation function ([100–800] Hz) to remove background noise and keep the low-frequency chorus vocalisations at a high signal-to-noise ratio. In total, 14 exemplar recordings of 2 minutes were prepared for subsequent broadcast as neighbour or stranger calls. Some of the stimulus recordings were used in multiple playbacks (e.g. as a stranger and a neighbour for different focal groups).

Chorus calls were played in both the playback and propagation experiments using a custom-made two-way speaker (made specifically to reduce distortion from high amplitude, low frequency sounds), connected to a FOXPRO Fury TX500 (FOXPRO Inc. USA) which allowed for remote control of playback calls on the speaker. Signals were played at an amplitude level estimated to be slightly higher than the measured maximum amplitude level of a captive southern ground-hornbills territorial call (90–95 dB at 1 m, using a Bioblock Scientific Sound Level Meter, C-weighting).

Propagation experiment

To assess the modification of chorus calls during sound propagation, we selected from our previous recordings an extract of recorded territorial calls including one female sequence of four calls, and one male sequence of three calls (Thornybush group). This groups recording was used because of its high quality. We then built a series of calls by repeating the extract and a synthetic sound placed prior to the extract 10 times. The synthetic sound showed an inverted V-shape frequency modulation (0.2–2.0 kHz) which helped the synchronisation in time of the different recordings at the different distances. The series was broadcast at a mean intensity of 90 dB, and re-recorded twice (using the same equipment described above) over six distances along a single transect line: 1 m (control sequence), 62.5 m, 125 m, 250 m, 500 m, and 1000 m. The speaker and microphone were positioned 1 m above the ground, which is the typical height of an adult ground-hornbill, and distances were measured using a Nikon Forestry Pro Laser Rangefinder (for distances up to 125 m) and using a GPS (for distances further than 125 m). The experiment was carried out in August 2020 in an area without any ground-hornbill groups and which best represented the surrounding habitat, while still allowing for a clear view over the full 1000 m distance. A maximum distance of 1000 m was chosen because maintaining a clear line-of-sight over larger distances was not possible in the habitat.

To characterise the change in acoustic pattern of the calls during propagation, we used Avisoft Correlator based on the digital spectrographic cross-correlation (SPCC) method. This method, described in detail by Clark et al. (1987) and Khanna et al. (1997), simultaneously analyses the frequency, amplitude, and time components of a signal by sliding the averaged spectrograms (FFT size 1024, overlap 87.5%) of the propagated signal at each distance along the time axis of the averaged spectrogram of the non-propagated control signal. The degree of correlation between the spectrogram of the sound at a given distance and the sound at source (i.e. 1 m) gives an indication of how much the sound has been acoustically modified as it travels. Of the 10 repetitions of each call sequence, all the 4th calls of the female sequence, and all the 3rd calls of the male sequence were analysed (due to being the highest quality with no saturation), except for calls not retained due to interruption by external noise (e.g. bird calls) during broadcast (1 female call at 1000 m, 3 male calls at 1000 m, and 2 male calls at 500 m), making a total of 490 spectrographic correlations for female calls and 450 for male calls. Each of these spectrogram correlations was averaged for each propagation distance.

Playback experiment

The protocol used for the experiment was based on our previous experience of working with the species. Considering the relatively small group sizes, large territories and relatively cluttered environment, birds can be difficult to find and responses difficult to observe. Therefore, experiments were conducted exclusively on breeding groups near the nesting sites where all group members are likely to be gathered in the mornings to provision offspring, making this the best time to test them. We limited the period of testing to when nestlings were 30–65 days old, to ensure no disruption to incubation or fledging behaviour. The experiment consisted of two playback trials per group, performed during mornings several days apart (range: 2–5 days depending on the weather conditions) to avoid habituation and allow groups to return to their natural behaviour after the first trial. In each trial, one of two treatments (i.e. a neighbour or a stranger vocalisation) was played, simulating a territorial intrusion from a familiar and or an unfamiliar group. A neighbour was defined as a group which shared a territorial boundary with the target group, usually occupying the nearest nest. A stranger was defined as a group which did not share a territorial boundary, and which occupied a territory more than 10 km away. The order of the

neighbour vs. stranger vocalisations played was randomised and blind to the observers; this was done by randomising the order several months in advance and using a coded system whereby the neighbour/stranger status was undetectable from the sound file name.

Prior to each test, the speaker was set up at dawn under a camouflage net, 184–202 m from the nest site. A pop-up hide for the observers was then set up at a location from which the nest and the speaker were both visible. Experiments were started once birds were observed at the nesting site to feed the nestling, and start times ranged from 07:10 to 10:25. Observers remained silently in the hide from set-up until the experiment was completed and the birds were no longer visible. Playbacks were conducted on 12 different groups, and each trial consisted of a 2 min playback period, followed by 38 minutes of observations, totalling 40 min.

Response measures

For each playback trial, the vocal and behavioural responses of the group were measured for the entire experiment length of 40 min. Group behaviours were filmed for post-experiment analyses when possible, using a Panasonic Lumix FZ80 camera. Any vocal responses by group members were also recorded using the equipment described above.

All birds responded detectibly to the playback. The following responses were scored/measured: 1) type of first response (approach/vocalisation, binary), with ‘approach’ corresponding to the movement (whether flying or walking) of focal groups towards the speaker, 2) latency to first response (continuous), corresponding to the time between the onset of the first signal played and the time of initiating either a vocal or approach response, 3) the latency to approach (continuous), corresponding to the to the time between the onset of the first signal played and the time of initiating an approach towards the speaker, 4) the latency to first vocal response (continuous), corresponding to the time between the onset of the first signal played and the time of initiating a vocal response, 5) total amount of time spent vocalising during the experiment (continuous), 6) closest distance to speaker (continuous) and, 7) duration of time spent near the speaker, corresponding to the amount of time any individual was within 50 m of the speaker (continuous).

Statistical analyses

All data were analysed in R version 4.0.4. Core Team (2021) using packages lme4 version 1.1.23 and MuMIn version 1.43.17. Data exploration was carried out following the protocol described in Zuur, Ieno and Elphick (2010).

The aim of the playback experiment was to investigate the effects of social factors (territory holder group size and intruder identity) and life-history factors (territory holder group composition) on the different response parameters, while accounting for other factors likely to influence responses. Potential predictors of the response variables (see above) were investigated by fitting General and Generalised Linear Models (GLMMs). In each response model, we included the playback treatment (neighbour/stranger) and either the group size or a single age structure variable of the focal group. The age structure variables considered were 1) number of adults and sub-adults combined, and 2) presence/absence of juveniles. Group size and age structure variables were analysed separately in different models since they were highly correlated with $r > 0.3$. Model comparisons were conducted using AICc (Akaike's Information Criteria), and we present the models with the lowest AICc values and highest model weights. Group identity of the focal group was included as a random term in all models to account for any other sources of variation between groups. Residuals of the best-fit models were visually inspected to ensure that all model assumptions were met. Models for response variables 'latency to first response', 'latency of approach', 'latency to vocal response' and 'closest distance to speaker' all had residuals that were not normally distributed, and therefore these variables were log-transformed which improved normality. Wilcoxon matched-pairs signed-rank tests were also used for each continuous response variable to determine whether there was any ordinal effect of playback trial on the responses. Similarly, for the categorical response variable of 'type of first response', we used a Fisher's exact test. These statistical tests were considered significant when $p < 0.05$. These ordinal tests were done separately from the models due to the small sample size and in order to preserve degrees of freedom for the main effects.

Results

Propagation experiment

The correlations between the control (1 m) and propagated spectrograms were high and steadily constant between 62.5 m and 500 m, and decreased at 1000 m, but were higher than 0.5 for both female and male calls (Table 5.1). This indicates that calls propagate well through the environment over this distance.

Table 5.1. Correlation for averaged spectrograms between the reference signal (1 m) and the propagated signal at different distances (from 62.5 m to 1000 m) for both female and male chorus calls. All values are mean ± SD (N)

Propagation distance	**62.5 m**	**125 m**	**250 m**	**500 m**	**1000 m**
Female	0.87 ± 0.01 (100)	0.86 ± 0.01 (100)	0.86 ± 0.01 (100)	0.84 ± 0.02 (100)	0.64 ± 0.07 (90)
Male	0.97 ± 0.01 (100)	0.97 ± 0.01 (100)	0.97 ± 0.01 (100)	0.95 ± 0.01 (80)	0.64 ± 0.10 (70)

Playback experiment

The mean (± SE) group size for the 12 groups tested in this study was 3.83 ± 0.14 individuals (range: 3–5 individuals). These groups contained a mean (± SE) of 3 ± 0.08 adults (range: 2–4 adults), 0.42 ± 0.10 sub-adults (range: 0–1 sub-adults) and 0.42 ± 0.10 juveniles (range: 0–1 juveniles). Means, standard errors and ranges for continuous response variables were: latency to first response = 135 ± 27.08 s (range: 15–591 s), latency to approach = 361 ± 108.37 s (range: 15–2105 s), latency to first vocal response = 243 ± 49.19 s (range: 65–900 s), total time vocalising = 830 ± 88.91 s (range: 0–1539 s), closest distance to speaker = 40 ± 12.47 m (range: 5–200 m), and duration near speaker = 193 ± 74.70 s (range: 0–1430 s). Groups which responded by approaching the speaker usually included the adults and sub-adults only, who collectively approached the speaker at the same time. Juveniles, on the other hand, tended to remain behind and only re-join the group at a later stage.

The best-fit models for the response variables of ‘type of first response’, ‘latency to approach’, and ‘latency to first vocal response’ all contained playback treatment and the social variable of group size (Table S5.1, Table S5.3, Table S5.4). The playback treatment (neighbour/stranger) had no clear effects on ‘latency to approach’ or ‘latency of first vocal response’, as 95% confidence intervals for both broadly overlapped zero (Table 5.2). For ‘type of response’, the effect of playback treatment could be considered as potentially relevant given that the 95% confidence intervals only marginally overlapped zero (Table 5.2) and the sample size was relatively small. Although not fully clear, these results suggested that groups may react differently according to the type of playback treatment, with a trend towards groups being more likely to respond to a stranger treatment by approaching it, but to a neighbour treatment by vocalising (Figure 5.1).

Group size was clearly associated with all the response variables, with 95% confidence intervals not including zero (Table 5.2). Larger groups were more likely to initially approach the simulated intrusion than to vocalise (‘type of first response’; Figure 5.2), and vocalise later (‘latency to first vocal response; Figure 5.3a) but approach sooner (‘latency to approach; Figure 5.3b).

The best fit models for the response variables ‘latency to first response’, ‘total time vocalising’, and ‘duration near speaker’ all contained playback treatment and the age structure variable of the presence/absence of juveniles (Table S5.2, Table S5.5, Table S5.7). However, none of the variables within these models had any clear effects, with all the 95% confidence intervals broadly overlapping zero. Similar results were found for the response variable ‘closest distance to speaker’ which had a best-fit model that included the playback treatment and the age structure variable of the number of adults and sub-adults (Table S5.6).

Finally, we found an ordinal effect of the playback trial on the ‘latency to approach’ ($p = 0.05$), suggesting that groups approached faster during the second trial than the first trial (Table S5.8). However, none of the other response variables provided any further evidence for this effect (Table S5.8, Figure S5.2).

Table 5.2. Results of best-fit models showing the effects of playback treatment (neighbour/stranger) and group composition (group size, number of adults and sub-adults combined, and presence/absence of juveniles) variables on the seven response variables, with estimates, standard errors (SE) and 95% confidence intervals (95% CI). Variables highlighted in bold have 95% confidence intervals which do not cross zero.

Variable	Estimate	SE	95% CI
1. Type of first response			
Intercept	-4.99	3.09	-15.40 – 0.60
Playback treatment	-1.82	1.05	-4.64 – 0.09
Group size	**1.67**	**0.86**	**0.19 – 4.71**
2. Latency to first response (log transformed)			
Intercept	4.76	0.30	4.19 – 5.33
Playback treatment	-0.07	0.36	-0.76 – 0.62
Presence/absence of juveniles	-0.46	0.37	-1.15 – 0.24
3. Latency to approach (log transformed)			
Intercept	8.51	1.48	5.68 – 11.34
Playback treatment	0.02	0.55	-1.03 – 1.07
Group size	**-0.91**	**0.38**	**-1.63 – -0.20**
4. Latency to vocal response (log transformed)			
Intercept	2.98	0.96	1.09 – 4.82
Playback treatment	-0.35	0.30	-0.93 – 0.24
Group size	**0.63**	**0.26**	**0.14 – 1.14**
5. Total time vocalising			
Intercept	868.27	154.13	574.98 – 1161.56
Playback treatment	97.75	171.87	-248.68 – 444.18
Presence/absence of juveniles	-209.04	198.22	-594.07 – 175.98
6. Closest distance to speaker (log transformed)			
Intercept	-0.24	2.11	-4.34 – 3.85
Playback treatment	0.04	0.26	-0.48 – 0.56
Number of adults and sub-adults	0.92	0.61	-0.26 – 2.11
7. Duration near speaker			
Intercept	43.05	138.37	-224.69 – 310.80
Playback treatment	82.75	54.67	-28.63 – 194.13
Presence/absence of juveniles	261.87	210.13	-146.29 – 670.04

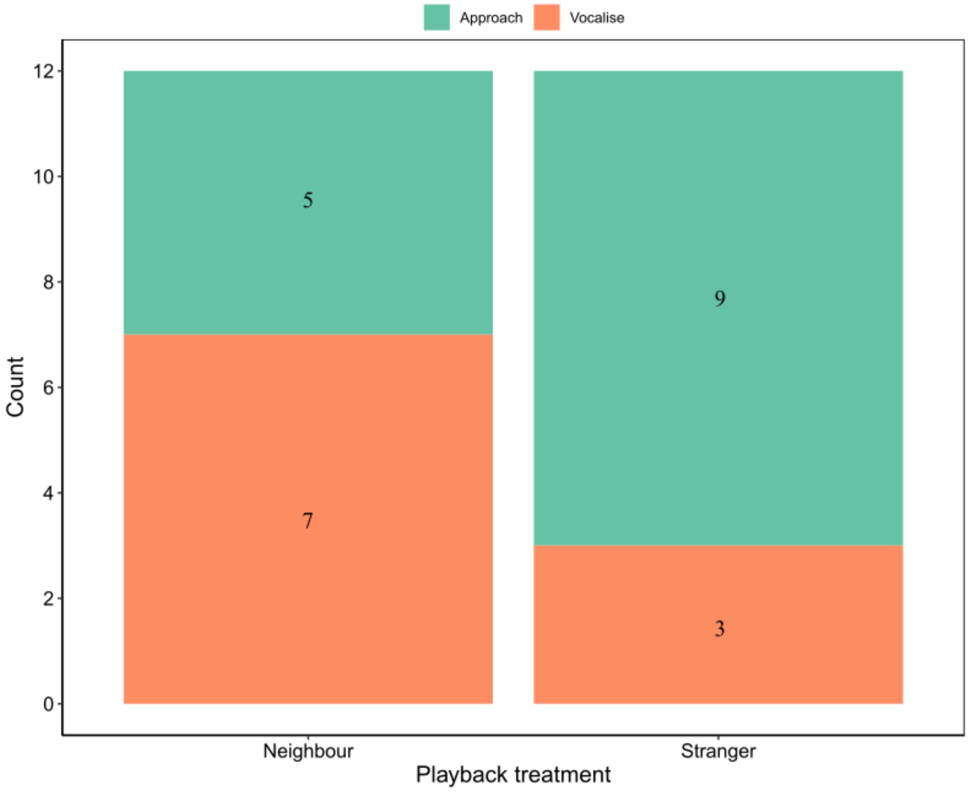


Figure 5.1. Count proportions of first response types (approach/vocalisation) to the different playback treatments. Values represent the number of playback trials for each response per treatment.

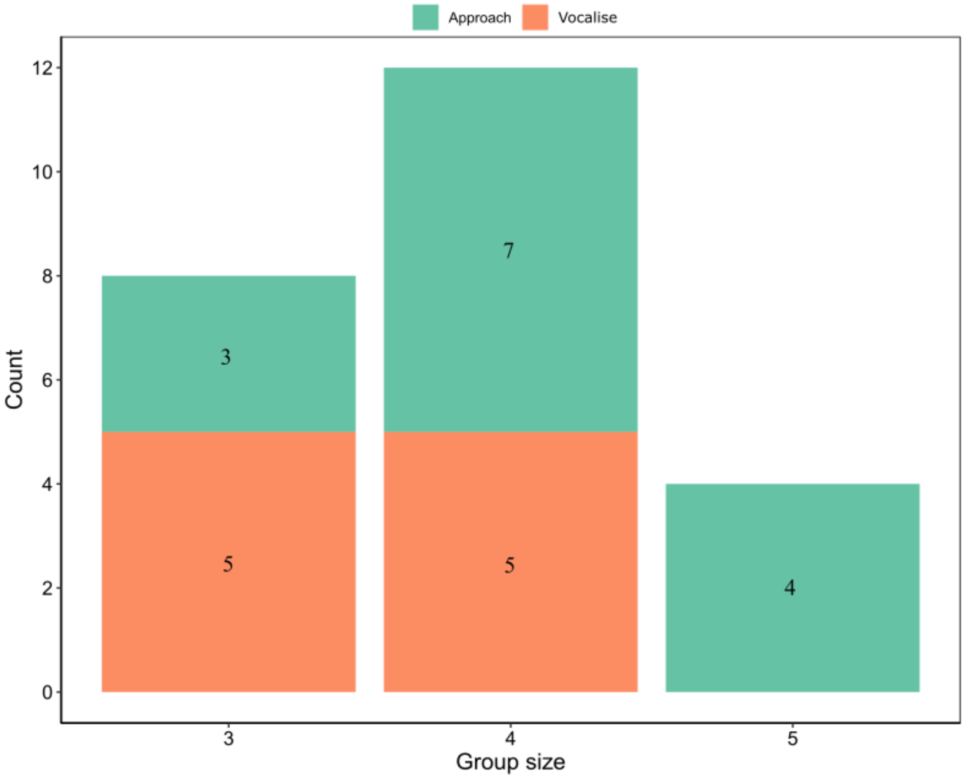


Figure 5.2. Count proportions of first response types (approach/vocalisation) for focal groups of different sizes. Values represent the number of playback trials for each response per focal group size.

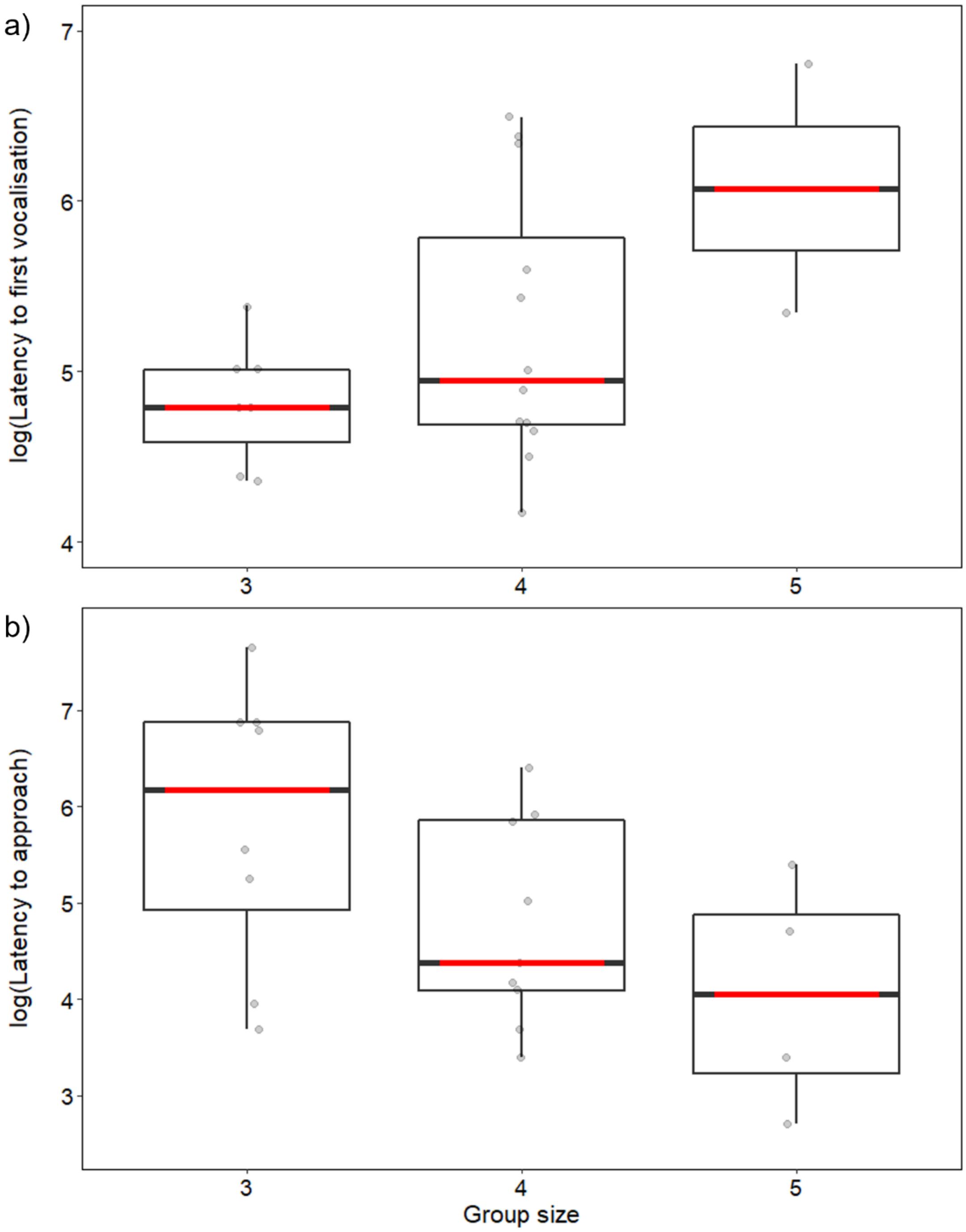


Figure 5.3. a) Latency to first vocal response (log-transformed), and b) latency to approach (log-transformed) as a function of focal group size. Boxplots show median values (red lines), first and third quartiles (box) and interquartile range (whiskers). Data points are jittered for improved visibility.

Discussion

We investigated which social (group size and intruder identity) and life-history (group's age structure) factors may influence the territorial responses of a large, long-lived cooperative breeder, the southern ground-hornbill. Our propagation experiment showed that the low frequency chorus vocalisations of

ground-hornbills are well adapted for long-range inter-group communication, which suggests that group-specific acoustic signatures (Chapter 4) are likely to be detectible by receivers at long range. However, our playback experiment suggested that ground hornbill territory owners reacted in the same way to the chorus vocalisations of intruding groups, regardless of the intruding group's identity (i.e., neighbour or stranger), though there was a trend for groups to be more likely to produce chorus vocalisations rather than approach the simulated intrusion of a neighbour, and vice versa for strangers. We found stronger evidence that focal group size is positively associated with the strength of responses to simulated territorial intrusions, with larger groups being quicker to approach but slower to vocalise, whereas there were no clear associations between a group's age structure and our response variables.

As expected, our propagation results showed that the call parameters of southern ground-hornbill vocalisations were effectively transmitted over long distances, and suggest that they provide the ideal platform to advertise territories and convey identity to conspecific groups (which can often be several kilometers away through relatively cluttered environments). The strong responses of groups to these vocalisations during our intrusion experiment highlight the importance of vocal communication in territory defence. This was further supported by our results showing that the 'latency to approach' was negatively associated with the playback order. As the playback order was randomised to avoid any ordinal effect, this unexpected result suggests the absence of habituation and further highlights the importance of vocalisations in everyday interactions. However, contrary to our expectations, whether a neighbour or a stranger group's vocalisations were played back to a group did not clearly predict any of the responses that we measured, except for perhaps the type of response. Similar responses to neighbours and strangers have been shown to occur both in solitary and group-living species (Stoddard et al., 1991; Schibler & Manser, 2007; Christensen et al., 2016; McGregor & Bee, 2018; Ferrandiz-Rovira et al., 2020), but such findings do not necessarily mean that discrimination does not occur. Rather, they could also be due to neighbours and strangers posing similar levels of threat, requiring similar responses. This is likely the case for ground-hornbills, since their chorus vocalisations contain individually distinct signatures that allow for recognition (Chapter 4), and we suspect that our

acoustically simulated intrusions of neighbours and strangers posed a similar level of threat for two main reasons that are artefacts of our experimental design.

First, the location of playback experiments might have generated non-specific responses by the birds. We conducted these experiments towards the centre of the territory, close to the nest, due to the practical constraints of working with a species that is extremely difficult to find and observe in their vast territories. However, a simulated intrusion near a critical resource like the nesting site may constitute a high level of threat to members, resulting in highly aggressive group responses regardless of the identity of the intruder (Carazo, Font & Desfilis, 2008; Furrer et al., 2011; Brown, 2013; Werba et al., 2022). Second, the stage of the breeding season may have influenced the responses of groups to neighbours and strangers. For instance, studies on skylarks *Alauda arvensis* (Briefer et al., 2008) and great tits *Parus major* (Jin et al., 2021) both found that individuals respond flexibly depending on the stage of the breeding season. In the great tit study, non-specific physical responses to neighbours and strangers were found during the nestling stage (Jin et al., 2021), which is also the stage at which our experiments were conducted. Increased nest defence during the nestling period has been shown to occur in several other bird species, and has been suggested to result from the high reproductive value of offspring that are close to fledging after high investment from carers. Strong territorial responses at this stage would be adaptive to preserve this investment and its fitness benefits to carers (Johnston, 2011; Jukkala & Piper, 2015; Tseng et al., 2017). Our system involves a species with high adult survival and low fecundity, such that chicks close to fledging are of particularly high reproductive value; this could again have favoured highly aggressive group responses regardless of the identity of the intruding group.

A hint that the typical responses towards neighbours and strangers may in fact differ was provided by our finding that ‘type of first response’ had a 95% confidence interval that only marginally overlapped zero. This could be suggestive of a real difference between how groups usually respond to the chorus vocalisations of neighbours (a weaker response: vocalisations) and how they respond to those of strangers (a stronger response: approaching the speaker), which would likely have become more evident with additional trials and so more statistical power. If so, this would at first sight suggest a response consistent with the ‘dear-enemy’ effect, and so that stranger groups pose a greater threat to

territory holders than neighbouring groups (Fisher, 1954). Alternatively, it may be incorrect to assume that approaching the speaker is the stronger response. Instead, remaining near the nest to vocalise may be a means to ensure the protection of the chick inside the nest, particularly if neighbours are able to recognise the territory holders by the vocalisations that they produce. This may be the case for ground-hornbills considering recent field observations of neighbour groups evicting incubating females and destroying eggs (KMM, unpublished data). This highlights a need to better understand the different threats posed by neighbours and strangers, to better predict the responses of groups to these threats.

In ground-hornbills, like most other cooperative breeders, a significant number of group members are retained young from previous broods that contribute to group tasks before dispersing to breed independently (Riehl, 2013; Carstens, 2017). These differences in age mean that not all group members are equally helpful for different tasks, potentially offsetting any positive effects of group size. Given that ground-hornbills are slow-developing and can be classified into distinct age categories, we were able to separately analyse these life-history effects of the group members' ages on territorial responses. Contrary to our expectation that the group composition should be important in determining a group's response to territorial contribution, our results suggested that a group's size (regardless of its composition) was the main factor predicting the nature of their response. Even though group sizes only ranged from 3–5 individuals, there was a clear relationship with the type of first response, with smaller groups responding more frequently using vocalisations, while larger groups instead more frequently approached the simulated threat. Latency to approach was also negatively associated with group size, such that larger groups were also slower to start vocalising. These results suggest that there may be a benefit to having a numerical advantage during territorial conflicts, regardless of group composition, and that groups take their resource-holding potential into account when deciding how to respond to a threat. Additionally, this suggests that group interactions could be influenced by differences between group sizes, if birds are able to estimate the group size in the vocal responses. Yet, this requires further investigation.

For many of the groups tested in this study, a larger group often meant the presence of a juvenile in the group (since these two variables were correlated). The response of these juveniles to our

experimentally simulated territorial intrusions were consistent with observations of real territorial intrusions in previous studies, which reported that juveniles remained hidden during territorial conflicts (Kemp, 1988; Kemp & Ezzey, 2020). For example, in one of our experiments, the juvenile disappeared out of sight shortly after beginning playback of the simulated intrusion, while the rest of the group responded by approaching the sound. After some time, the group eventually perched in a tree and began their territorial vocalisations, at which point the juvenile appeared and re-joined them. Considering that kidnapping has been documented in ground-hornbills (Kemp & Ezzey, 2020), aggressive responses may serve to protect not only the nest site but also fledged offspring. This further highlights the importance of group size in the context of not only territorial defence as investigated here, but also other group tasks such as protecting fledged young from kidnapping.

Conclusion

Our study highlights the importance of vocalisations in territory defence and provides evidence that group size is a key factor in mediating the responses of groups to territorial intrusions, irrespective of the group composition. This shows that group living provides individuals with benefits that go beyond helping at the nest, by helping individuals secure resources vital for survival and reproduction. This is also in agreement with the suggestion that, in the hornbill family (Bucerotidae), the presence of helpers in cooperatively breeding species may be more relevant for group behaviours other than those related to reproduction (Gonzalez, Sheldon & Tobias, 2013). Such findings may help to explain the inconsistent effects of helpers seen on the reproductive outcomes of other cooperatively-breeding species (Hatchwell, 1999), and to explain why individuals unrelated to the breeding pair could nonetheless also experience benefits from group living such as the ability to retain a territory. This helps to broaden our understanding of the evolution of cooperative breeding across a range of avian life histories and ecological settings.

Appendix

Fieldwork insight 8. Some of the views from within the pop-up hide while we waited for the birds to arrive to start the playback experiments.

Table S5.1. Exploratory model comparisons for group composition variables on the type of first response. Playback treatment = neighbour or stranger binary variable. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	**k**	**Dev**	**AICc**	**ΔAICc**	**Model Weight**
Playback treatment + Group size	**4**	**24.8**	**34.88**	**0**	**0.58**
Playback treatment + Presence/absence of juveniles	4	25.8	35.92	1.04	0.34
Playback treatment + Number of adults and sub-adults combined	4	28.7	38.77	3.89	0.08

Table S5.2. Exploratory model comparisons for group composition variables on the latency to the first response. Playback treatment = neighbour or stranger binary variables. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	**k**	**AICc**	**ΔAICc**	**Model Weight**
Playback treatment + Presence/absence of juveniles	**5**	**74.40**	**0**	**0.52**
Playback treatment + Number of adults and sub-adults combined	5	75.85	1.46	0.25
Playback treatment + Group size	5	76.07	1.68	0.23

Table S5.3. Exploratory model comparisons for group composition variables on the latency to approach. Playback treatment = neighbour or stranger binary variable. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	**k**	**AICc**	**ΔAICc**	**Model Weight**
Playback treatment + Group size	**5**	**80.64**	**0**	**0.51**
Playback treatment + Presence/absence of juveniles	5	81.83	1.19	0.28
Playback treatment + Number of adults and sub-adults combined	5	82.44	1.80	0.21

Table S5.4. Exploratory model comparisons for group composition variables on the latency to the first vocal response. Playback treatment = neighbour or stranger binary variable. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	k	AICc	ΔAICc	Model Weight
Playback treatment + Group size	**5**	**58.14**	**0**	**0.65**
Playback treatment + Number of adults and sub-adults combined	5	60.24	2.10	0.23
Playback treatment + Presence/absence of juveniles	5	61.44	3.30	0.12

Table S5.5. Exploratory model comparisons for group composition variables on the total time vocalising. Playback treatment = neighbour or stranger binary variabls. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	k	AICc	ΔAICc	Model Weight
Playback treatment + Presence/absence of juveniles	**5**	**336.02**	**0**	**0.38**
Playback treatment + Number of adults and sub-adults combined	5	336.25	0.22	0.34
Playback treatment + Group size	5	336.66	0.63	0.28

Table S5.6. Exploratory model comparisons for group composition variables on the closest distance to the speaker. Playback treatment = neighbour or stranger binary variable. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	**k**	**AICc**	**ΔAICc**	**Model Weight**
Playback treatment + Number of adults and sub-adults combined	**5**	**77.15**	**0**	**0.48**
Playback treatment + Presence/absence of juveniles	5	77.52	0.37	0.40
Playback treatment + Group size	5	79.88	2.72	0.12

Table S5.7. Exploratory model comparisons for group composition variables on the duration spent near the speaker. Playback treatment = neighbour or stranger binary variable. Random term = Group identity. Model in bold was the best model, which is presented in the Results.

Model	**k**	**AICc**	**ΔAICc**	**Model Weight**
Playback treatment + Presence/absence of juveniles	**5**	**311.99**	**0**	**0.47**
Playback treatment + Number of adults and sub-adults combined	5	312.54	0.55	0.36
Playback treatment + Group size	5	314.07	2.08	0.17

Table S5.8. Chi-squared test and Wilcoxon matched pairs sign-ranked tests investigating the possible effect of trial order on the seven response variables.

Response variable	**X²**	**p-value**
1. Type of first response (Chi-squared test)	1.54	0.21
2. Latency to first response	N/A	0.34
3. Latency to first approach	**N/A**	**0.05**
4. Latency to first vocal response	N/A	1.00
5. Total time vocalising	N/A	0.73
6. Closest distance to speaker	N/A	0.10
7.Duration near speaker	N/A	0.48

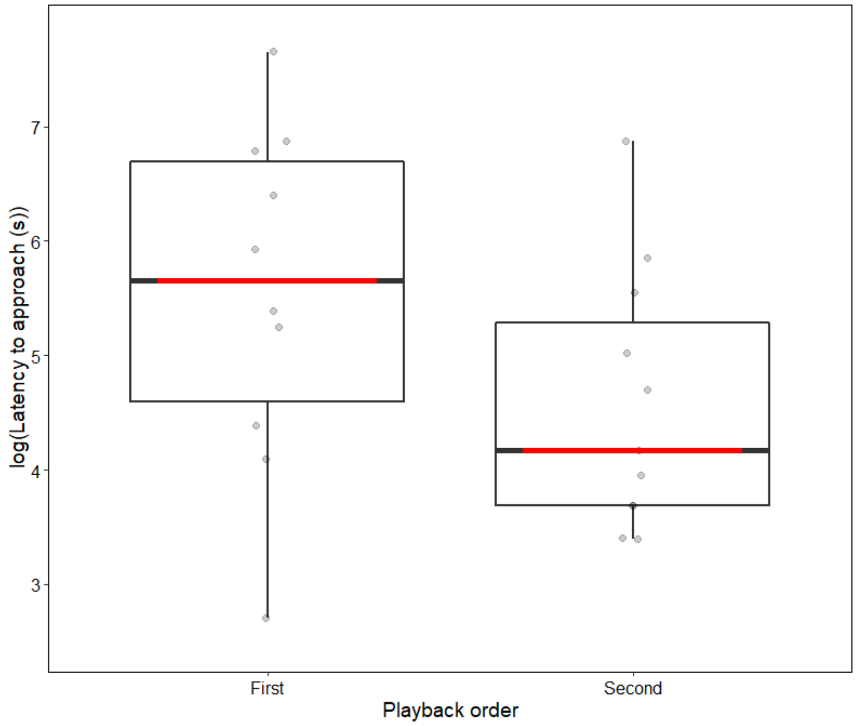


Figure S5.1. Log-transformed latency to approach in relation to the playback order (p = 0.05). Boxplots show median values (red lines), first and third quartiles (box) and interquartile range (whiskers). Data points are jittered for improved visibility.

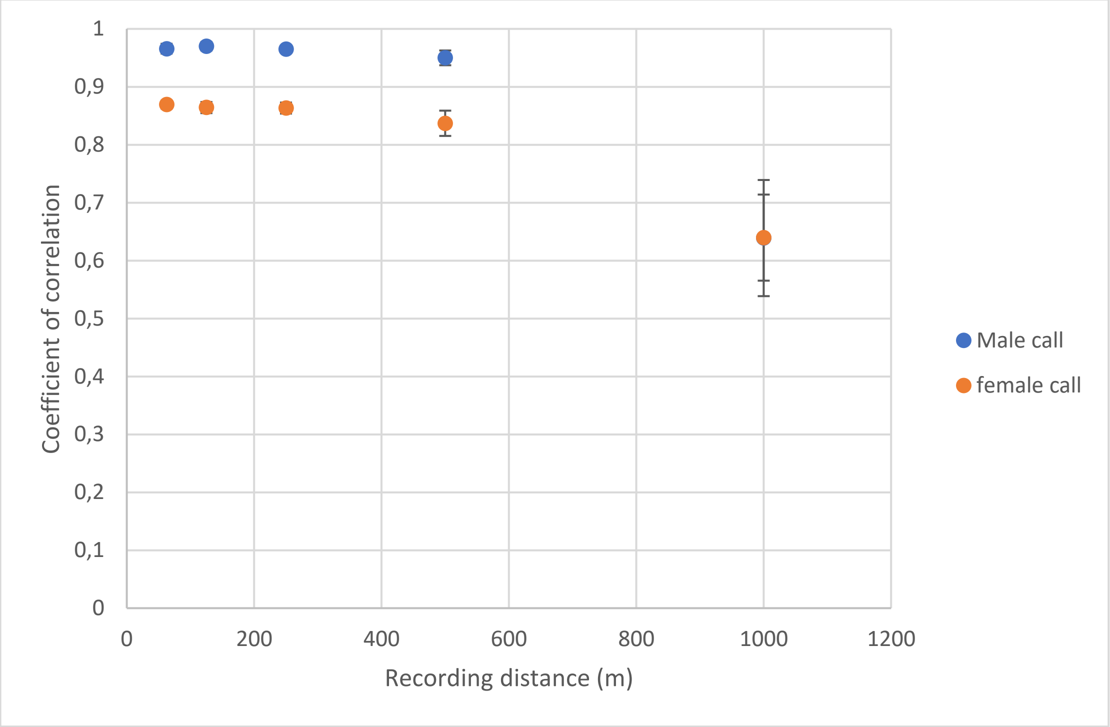


Figure S5.2. Correlation (mean ± sd) between spectrograms of female and male calls at different distances and control spectrograms (1m)

Chapter 6

Synthesis and conclusions

A photograph of a female (top bird) with her offspring (bottom birds) from the previous two breeding seasons. *Juveniles can continue to beg older individuals for several years after fledging. Photo: Jonathan Cooper*

General discussion

Cooperative breeding involves group members (helpers) contributing to the reproduction of a dominant breeding pair. These helpers usually also contribute to other group tasks besides breeding, but such other behaviours, and how they might vary among individuals with different investment strategies, have received less attention than helping at the nest. This study aimed to understand how individuals in cooperatively breeding southern ground-hornbill groups contribute to two vital group behaviours, reproduction and territory defence, and whether and how the presence of additional group members improves the outcomes of these group behaviours. In addition, I was specifically interested in whether individuals at different developmental stages might contribute differently to group tasks, and whether these contributions are modulated by environmental and social factors (specifically, climate and 'intruder' group identity). To do so, I focused on a southern ground-hornbill population that has been part of a long-term study since 2000 in north-eastern South Africa. In the first part of the thesis, I investigated the social, life-history, and climatic factors associated with cooperative provisioning and reproductive outputs. In the second part, I investigated the functions of territorial chorus vocalisations and how these, along with social and life-history factors, influenced territorial responses.

Summary of key findings

For part one, focusing on reproduction, I set out with the expectation that due to their longevity and slow development, older individuals would play a larger role than younger individuals in nest provisioning and in determining the reproductive outcomes of groups. I also expected that the low rainfall and high temperatures associated with the semi-arid regions inhabited by this species would have negative effects on reproductive behaviours. In addition, it has been suggested that the presence of helpers mitigates the effects of adverse environmental conditions on cooperatively breeding species, and I also investigated this hypothesis. As expected, in Chapter 2 I found that adults contributed the most towards nest provisioning, and that larger groups with more adult males had higher provisioning rates. Furthermore, in Chapter 3 I found that the number of adult males in a group was positively associated with nestling tarsus lengths prior to fledging, perhaps due to the additive care provided by additional adult male helpers (Chapter 2). However, provisioning rates per individual (for both adults

and sub-adults) were lower in larger groups, suggesting that larger groups allow individuals to lower their own costs by sharing care (“load-lightening”). Juveniles contributed the least to provisioning. A correlation between the number of juveniles and the probability and timing of breeding was more likely explained by high-quality groups and/or groups in high-quality territories both breeding more often/earlier, and producing more young. Apart from this likely indirect correlation with the number of juveniles, there was little evidence to suggest that any social or life-history factors increased the probability or breeding, advanced lay dates, or increased fledging success of southern ground-hornbills. I also showed that, as expected, high temperatures and low rainfall were in general negatively associated with reproductive behaviour and output of this species. Specifically, I found that high temperatures were associated with decreased provisioning rates and food sizes brought to the nest (Chapter 2). Moreover, high temperatures and low rainfall were associated with reduced probability of breeding, delayed laying dates, and reduced nestling mass (Chapter 3). However, these negative effects on provisioning efforts and reproductive outcomes were not buffered by increases in the numbers of group members of different ages.

In part two where I focus on territory advertisement and defence, I expected that the lone females’ contributions to the chorus vocalisations would contain sexual and individual signatures that could also be considered as group signatures. I expected that ground hornbill groups would defend their territories from other groups and that these responses would be more aggressive in groups with a larger number of adult and sub-adult individuals. Finally, I expected that intruder identity would mediate the responses of groups to territorial intrusions; specifically, that territory holders would respond more aggressively to neighbour groups (groups occupying adjacent territories and who are likely to be more familiar to territory holders), than to stranger groups (groups occupying territories further adrift and who are likely to be less familiar to territory holders), since neighbours pose a more serious threat to breeding opportunities. I found that predominantly adults contribute to territorial vocalisations and defence, consistent with previous studies on this species. As expected, there were consistent and repeatable differences between the sexes in the fundamental frequency parameters of their vocalisations, with females producing higher pitched calls. I found that the vocal contribution of the

lone female in each group consisted of individually distinctive melodies that could be correctly classified to the right individual with a 94% success rate (Chapter 4), and that these melodies were well suited to propagate long distances in the environment. This supports the hypothesis that female vocalisations in the chorus allow for individual and group identity to be conveyed over large distances to conspecifics, and highlights the central role of females within groups. Surprisingly, though, my simulated territorial intrusion experiments showed that caller identity only had a marginal influence in determining the responses of groups, and that group composition also had little effect on their responses. I found instead that group size alone was the best predictor of how groups responded to simulated intrusion, with larger groups responding faster and more aggressively than smaller groups (Chapter 5).

In the next section, I consider the wider implications of each of these main findings in more detail.

Group size and cooperative behaviours: Investment increases with age

In the majority of cooperative breeders, a significant number of group members are retained offspring from previous broods, that help for one or two years before dispersing to breed independently (Riehl, 2013). In ground-hornbills, males may delay dispersal for up to 11 years (KMM, unpublished data), whereas females disperse 2–24 months post fledging, when dominant males eject them from the group (Kemp & Kemp, 1980; Carstens et al., 2019a; Kemp, Kotze, et al., 2020). This results in male-biased groups consisting mostly of offspring from previous broods, along with the occasional immigrant male (as immigrant females are rare and contribute little to group tasks; Kemp & Kemp, 1980; Carstens et al., 2019). As such, relatedness likely plays an important role in mediating individual investment to group behaviours. However, genetic studies in southern ground-hornbills remain incredibly challenging as the adult birds are difficult to catch, and captures are extremely stressful for these Vulnerable birds, which can alter their behaviour and make them harder to study afterwards. Yet, given their longevity, slow development, and therefore their distinct age-related appearance, I was still able to investigate the contributions and effects of differently aged group members towards reproduction and territory defence. My results showed that individuals of different ages varied in their investment strategies to group

behaviours. This indicates that the group size effects usually associated with cooperative breeding can be contingent on the group members' ages.

In general, my results showed that younger individuals contributed less to provisioning efforts (since they provisioned fewer items and smaller prey; Chapter 2) and territory defence (since we observed them delaying their responses and even hiding from conflicts; Chapter 5). Furthermore, although not the primary aim of chapter 4, we did not observe any of the younger birds (juveniles in particular) taking part in territorial chorus vocalisations. These findings are consistent with earlier studies on southern ground-hornbills (Kemp & Kemp, 1980; Kemp, 1988; Kemp & Ezzey, 2020) and other avian cooperative breeders which have shown similar patterns for younger individuals (e.g., provisioning rates in apostlebirds *Struthidea cinerea*: Woxvold, Mulder & Magrath, 2006; and chorus contributions in green woodhoopoes *Phoeniculus purpureus*; Radford, 2003).

Age effects in cooperative tasks are likely due to the balance between costs and benefits differing between individuals. Specifically, the costs for individuals of different ages likely arise from different levels of experience, and the benefits from direct and indirect fitness gains. Breeders (which often make up most of the adult contingent within groups) gain the most from contributing to group behaviours, as successful reproduction provides them with high direct fitness gains, and successful territory defence ensures access to breeding opportunities. By contrast, sub-adults and juveniles are younger individuals, likely consisting of full siblings or half siblings to the offspring, or even unrelated individuals. These individuals are expected to benefit less than breeders from behaviour that help the group, as they receive fewer fitness gains from raising offspring that are not their own, and do not gain immediate access to breeding opportunities. Costs of contributing to group behaviours are likely also higher for sub-adults, and to an even greater extent for juveniles, which probably also explains their reduced investment. This is because particularly in long-lived, slower-developing species, younger individuals may have extended dependence on older individuals for food and protection (Rowley, 1976; Langen, 1996; Woxvold, 2004; Woxvold, Mulder & Magrath, 2006), and lack the experience needed to be effective in inter-group conflict, foraging, and particularly in catching larger (and often more dangerous) prey (Gunst, Boinski & Fragaszy, 2008b; Maynard et al., 2021). Foraging ability plays an

important role in survival, and a recent study has even proposed that an important benefit of group living is to allow individuals to learn different foraging specialisations from a number of different individuals (Sheppard et al., 2021). Therefore, by delaying dispersal, ground-hornbill offspring could gain not only some indirect kin selection benefits, but crucially also several direct benefits such as access to a territory and extended care from other group members. A mix of indirect and direct benefits of group living therefore likely explains the evolution of sociality in southern ground-hornbills.

Larger groups are better, no matter the weather

There has been a healthy debate as to why cooperative breeding has been found to be more prevalent in both harsh and unpredictable environments (Jetz & Rubenstein, 2011; Rubenstein, 2011), and in benign and stable environments (Avilés et al., 2007; Gonzalez, Sheldon & Tobias, 2013). Recent work suggests that individuals within groups gain benefits from improving the efficiency of group behaviours, and that different group behaviours (such as offspring provisioning and territory defence investigated in this thesis) become more important under different climatic conditions (Shen et al., 2017; Lin (林宇恒) et al., 2019; Liu (劉彥廷) et al., 2020). Specifically, group behaviours that improve reproductive success have been suggested to provide greater benefits in harsh and unpredictable environments where breeding may not be possible without the additional help. Additional help to territorial behaviours, on the other hand, may provide greater benefits in benign and stable environments, as these habitats are likely to be saturated with intense intraspecific competition for resources (Hinde, 2008; Shen et al., 2017; Nelson-Flower et al., 2018; Lin (林宇恒) et al., 2019; Humphries et al., 2021).

This thesis provided an ideal system to investigate these hypotheses, as the southern ground-hornbill (as well as the congener species, the Abyssinian ground-hornbill) occurs in semi-arid regions with harsh climatic conditions, whereas comparative analyses on the hornbill family (Bucerotidae) found that cooperative breeding was favoured in more mesic environments (Gonzalez, Sheldon & Tobias, 2013). This makes the southern ground-hornbill an interesting exception to the rule in its family: a long-lived species in a saturated habitat, but living in a semi-arid environment. This makes it a good

candidate to test the relative importance of the two alternative hypotheses above, involving different classes of benefits to group living in different climatic conditions.

From their occurrence in semi-arid regions, there is ample scope to think that the benefits of group formation would be primarily directed towards reproduction in southern ground-hornbills, where additional group members can mitigate the effects of adverse environmental conditions. My results do show that there are direct benefits of group living associated with provisioning behaviours and, to a lesser extent, reproductive outcomes, but these benefits did not mitigate the negative effects of high temperatures and low rainfall (Chapters 2 & 3). This adds to the growing evidence from other bird species that also seem to experience no buffering effects from breeding cooperatively in harsh conditions (Bourne, Ridley, Spottiswoode, et al., 2021; D’Amelio et al., 2022). My results on provisioning behaviours provide evidence that additional group members lead to simultaneous additive and load-lightening benefits that likely promote cooperative breeding (Chapter 2). The positive association between nestling tarsus lengths and group size (likely due to each being associated with provisioning rates), suggest that perhaps offspring gain survival benefits from additive care particularly when conditions are ideal for breeding (Chapter 3). This has been shown in several other bird species with altricial young, in which increases in provisioning rates were associated with enhanced nestling body condition and post-fledging survival (Maness & Anderson, 2013; Naef-Daenzer & Grüebler, 2016). As their name suggests, ground-hornbills spend a large amount of time walking and foraging on the ground, travelling on average 7.4 km per day (Kemp & Kemp, 1980; Zoghby et al., 2015). Enhanced body condition after fledging, and particularly when it relates to structural growth involved with walking (i.e., such as tarsus length), may provide important survival benefits by ensuring that fledglings are better able to keep up with the rest of the group (see Alatalo & Lundberg, 1986). Therefore, additive care is likely important for ensuring success of offspring post-fledging.

At the same time, the evidence for load-lightening found here also suggests that carers might be better able to maintain body condition and gain survival benefits when group size increases and they have additional help. Individuals are then able to invest more in self-maintenance and their own survival, while still maintaining adequate provisioning rates to the incubating females and resulting

nestlings (Chapter 2; Hatchwell, 1999; van Boheemen et al., 2019). This is consistent with the hypothesis that long-lived species with low mortality rates should maximise their survival by reducing the physiological costs (Covas et al., 2022) and general risk-taking associated with nestling care (Clutton-Brock, 1988; Ghalambor & Martin, 2001). Hence, a species' life-history strategy should be considered when predicting the contributions of helpers to group behaviours.

These results are consistent with the suggestion that the hornbill family's life-history strategy, involving larger body sizes, high survival, low fecundity, and stable year-round food supply make successful reproduction less reliant on the presence of helpers, although helpers could still be relevant for other group functions (Gonzalez, Sheldon & Tobias, 2013). My results support this at least in part by showing that benefits of group living also arise through enhanced territory defence. Territory defence has been suggested to be an especially important factor in promoting cooperative breeding in benign and stable environments, but it can also be important in harsh and unpredictable environments when limited resources need to be defended year-round (Koenig, 2017; Shen et al., 2017; Lin (林宇恒) et al., 2019). This is likely the case for ground-hornbills, as nesting sites remain temporally fixed, are frequently reused, and are considered as a primary factor that restricts breeding in the species (Kemp, 1988, 2017; Carstens, 2017).

My results showed that group chorus vocalisations play a key role in maintaining access to these critical resources, particularly during reproduction. I showed that group choruses convey individual and group identity (through the dominant females' melodic contribution; Chapter 4) over large distances (Chapter 5). Ground-hornbill territories are vast, and this group advertisement may act as a means to convey territory ownership to several competing individuals and groups simultaneously. Consequently, group members may benefit by deterring any prospecting groups, and by increasing familiarity with neighbours (through vocalising frequently within their territory) to reduce the risks associated with inter-group conflict (Chapter 5). I also showed that larger groups were more aggressive in their responses to simulated intrusions (Chapter 5), presumably to defend nesting sites and to defend juveniles who may be susceptible to kidnapping (Kemp & Ezzey, 2020). Similar results have been

found in other cooperatively breeding species (e.g., green woodhoopoes Radford, 2008), supporting the hypothesis that there is a direct benefit to having a numerical advantage during disputes.

Conservation outputs

Although not the primary aim of this thesis, the results I found here contribute to the conservation efforts of the species by contributing to our understanding of two vital group behaviours, reproduction and territory defence. Southern ground-hornbills are listed as globally Vulnerable by IUCN (IUCN, 2021) and regionally Endangered within South Africa, mainly as a result of habitat alteration (leading to loss of nesting sites), poisoning, and persecution of groups for breaking windows when they see their reflection (Taylor & Kemp, 2015; Carstens, 2017; Kemp, 2017). Currently, most of the conservation efforts addressing these issues are based on education, habitat preservation, installing artificial nesting sites, and the reintroduction of artificially formed groups back into their historic range (Taylor & Kemp, 2015; Kemp, Kotze, et al., 2020). This thesis provides valuable information for these reintroduction efforts, as it informs us about which individuals are contributing the most to the group behaviours which are important for group success and persistence. Reintroductions have represented a successful conservation measure for ground hornbills, albeit a slow one, as groups typically take several years before attempting to breed. I hope that the demonstration of the importance of experienced individuals within groups can be applied to the artificial formation of groups, and help accelerate the reproductive success of released groups. Furthermore, my results showing negative effects of high temperatures and low rainfall on the provisioning efforts and overall reproductive success, and the lack of any buffering effects of group size, suggest that ground-hornbills are likely susceptible to anthropogenic climate change. Considering their longevity and high survival, the population consequences of these effects may be slow to be observed, as successful breeding slowly decreases. This is a worrying but important result, as it provides much-needed evidence to aid release site decisions. Additionally, my results suggest that high temperatures are associated with reduced nestling mass, which is a strong motivation for increasing efforts to provide more thermally buffered artificial nests, as these may help to improve chick condition.

Future research

Through the course of this research, new questions became apparent. Below, I present a few possible directions for future research.

1. Research into the climatic, social, and life-history factors affecting other group behaviours (analogous to my research on reproductive and territorial behaviour) such as foraging, and predator vigilance has been missing in studies on cooperative breeders. This would provide a more complete understanding of the benefits that individuals receive from breeding cooperatively in a variety of different conditions.
2. Investigating the influence of nest predation on the reproductive success of ground-hornbills has been a difficult task in the past, particularly as their breeding cycles are extended and sites are far apart. However, using trail cameras, this may now be possible to investigate and may provide additional information on whether there are any benefits of group-living associated with predator deterrence at the nests. For example, the trail camera footage from this study recorded nest predation occurring from leopards (Figure 6.1) and genets. However, ground-hornbill groups were also recorded deterring chacma baboons (Figure 6.2) and genets attempting to predate.
3. Although ground-hornbill groups appear to mostly consist of kin, genetic studies to determine exact relatedness between individuals would be crucial to provide further insights into the investment decisions of individuals by shedding light on the indirect benefits they receive by contributing to cooperative tasks. This is something that I was unable to measure in this study, and remains a difficult task in this species. However, I am confident that the further development of non-invasive techniques such as feather and faecal sampling can address this problem.
4. Dominance hierarchies can play an important role in determining the individual contributions to group behaviour, as lower ranked individuals are likely to benefit the least from these behaviours, as well as paying the highest costs since they should be last in line to gain immediate access to resources such as food and shade. Therefore, determining the hierarchies within ground-hornbill groups (and groups of other cooperatively breeding species), and how they are determined, could help further our understanding of the trade-offs determining individual investment decisions.

5. A better understanding is needed of the mechanisms involved in nestling growth rates, and particularly whether changes in growth rates are influenced mainly by provisioning rates or by climatic conditions. This will help to shed further light on the vulnerability of ground-hornbills to climate change.
6. We need further investigation into the role of males in the chorus vocalisations, and specifically whether, like females, they also convey individual identity using melodies, and whether all the individual vocal contributions to the chorus can be perceived by receivers and so convey information about group size. This would help clarify the role of chorus vocalisations in mediating territorial responses to intrusions.
7. Conveying individual identity in chorus vocalisations could also theoretically aid individuals in search of potential mating opportunities by acting as a form of long-distance self-advertisement. This could reduce the risks involved with departing from the group and prospecting on their own. Investigation into the roles of these individual signatures may therefore help provide valuable insights into the constraints that individuals face when making dispersal decisions.
8. Finding and identifying ground-hornbill groups in their vast territories can be difficult, so further research into the field applications of our classification results on group signatures could allow groups to be remotely identified and so aid population surveys and long-term monitoring.

Figure 6.1. An image from a trail camera showing a leopard predation event when the nestling was 20 days old.

Figure 6.2. An image from the trail camera at the same nest showing an adult bird chasing a baboon away from the nest.

Conclusion

This thesis substantially improves our understanding of the social structure of the southern ground-hornbill, and provides the first detailed description of the individual contributions to female and nestling care during reproduction, and to territory advertisement and defence. These findings in a species with exceptionally slow life-history have wider implications for understanding of the evolution of cooperation. Despite ground-hornbills inhabiting semi-arid regions with harsh climatic conditions, the benefits of additional group members of different ages on reproduction were insufficient to mitigate the negative effects of high temperature and low rainfall. This bolsters and generalises evidence from other recent studies in short-lived passerines showing that the presence of additional helpers might not effectively buffer against reproductive failure (Bourne, Ridley, Spottiswoode, et al., 2021; D'Amelio et al., 2022). This has important implications for both the validity of the buffering mechanism proposed to explain the association between cooperative breeding and environmental variability, and the expectation that social species may be more resilient in the face of anthropogenic climate change. However, while the ecology and life-history characteristics of ground-hornbills may render the presence of additional helpers less relevant for reproduction in harsh conditions, additional group members do appear to be important for resource defence, as also suggested by Gonzalez et al. (2013). Hence, this thesis highlights the importance of studying group behaviours that take place away from the nest. The apparent importance of group size away from the nest may also help explain intriguing observations, such as the acceptance of unrelated individuals into groups or the kidnapping of young individuals, which therefore likely function to increase resource holding potential. Hence, a broader approach to the study of cooperative breeding, integrating life-history strategy and examining different cooperative behaviours, may be fundamental to determining the benefits individuals receive from breeding cooperatively. This will help us to explain the environmental correlates of cooperative breeding and the diversity of forms that it can take, including the remarkable biology of the southern ground-hornbill.

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Each step that we make in the more intimate knowledge of nature leads us to the entrance of new labyrinths ~ Alexander von Humboldt, 1845

The End