

Impacts of hot weather on behaviour and reproduction in a long-lived cooperative breeder

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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.

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Abstract

Rapid anthropogenic climate warming is altering ecosystems globally, impacting species distributions, population trends, and overall fitness. Animals in subtropical regions can experience high air temperatures year-round, creating trade-offs between thermoregulation, self-maintenance and reproduction. Offspring are particularly vulnerable to high temperatures because rapid growth is energetically demanding, and increased thermoregulation costs together with reduced parental provisioning, can constrain energy available for growth, increase physiological stress, and negatively affect survival. In cooperatively breeding species, helpers (non-breeding individuals) bring food to offspring, which may improve breeding conditions. Therefore, the challenges associated with harsh environments may be buffered in group-living species, potentially reducing the energetic costs of reproduction for adults and mitigating the negative impacts of heat on developing young. Understanding how high temperatures influence behaviour, reproductive decisions, and offspring development and survival is essential for predicting population resilience under current and future climate warming. However, the impacts on large, long-lived, cooperatively breeding species remain understudied, particularly in the subtropics.

This thesis investigated how environmental conditions (high temperatures, rainfall and sociality) affected adult behaviour, maternal investment in egg size, offspring growth and physiology in a large, exceptionally long-lived and slow developing cooperative breeder, the southern ground-hornbill *Bucorvus leadbeateri*. This species breeds during the hot summer months and offers a distinct contrast to most avian studies on the impacts of heat, which are typically of small, relatively short-lived birds. I collected six years (2019-2025) of field data on adult behaviour, nestling growth, physiology (using telomere dynamics as a biomarker of physiological stress) and post-fledging survival, and further used long-term data from the

APNR Southern Ground-Hornbill Project (2012–2025) on egg size. The influence of social factors (i.e. the number of helpers and juveniles within a group), was investigated to determine their effect on maternal investment in eggs and whether they buffered any adverse effects of heat exposure on the growth and physiology of nestlings.

The first data chapter examined the thermal landscape in summer and winter in two savanna habitat types (open woodland and riparian) and southern ground-hornbills' seasonal behavioural responses to high temperatures. I found that operative temperatures at landscape scale were hotter in winter than in summer at the same air temperature, which was attributed to less shade in winter. Ground-hornbills increased their heat dissipation behaviours (e.g. panting and wing drooping) at high air temperatures year-round, but reduced foraging and sought shade at high air temperatures only during summer. I also investigated humidity which showed no significant effects on most behaviours; however, panting decreased slightly with increasing humidity and birds perched off ground more at higher humidity in summer.

The second chapter investigated female investment in egg size, revealing that female southern ground-hornbills maintained consistent investment in first-laid eggs, whereas second-laid 'insurance' eggs were smaller, decreased in size when laid later in the season, and may be more flexibly adjusted in response to environmental conditions. There was no evidence that helper presence influenced the size of either first or second eggs.

The third and fourth chapters focused on nestling growth and physiology (by assessing telomere length and dynamics) in response to high temperatures. High temperatures were associated with reduced nestling growth rates but not with final fledging size and condition. Post-fledging survival was negatively associated with high nest temperatures experienced during development and high air temperatures post-fledging during winter. Nestling telomere length at fledging age was positively associated with higher nest temperatures during the incubation stage (during embryo development) but this was linked to faster telomere shortening

during later development. The number of helpers in a group did not mediate the effects of heat on chick growth, physiology, or survival.

Overall, the findings of this thesis reveal that rising summer temperatures negatively affect reproductive outcomes in southern ground-hornbills via impacts on nestling development and survival. However, my work also revealed the lesser-known impacts of rising winter temperatures. These are equally concerning, as high operative temperatures during this period impose unexpected thermal challenges on adults and fledglings during a time when food resources are limited. Despite the ground-hornbills' cooperative breeding system, helpers did not mitigate the negative effects of heat on nestlings. These results align with recent findings in other cooperative breeders raising questions about the resilience of these species under climate change. They also raise questions about the benefits of helpers in ground-hornbills, and whether they may be more relevant for other group functions, such as maintaining nests and territories, than for reproductive outcomes. Together, these results reveal that increasing heat across seasons has significant implications for ground-hornbills and likely for many other savanna-dwelling species. Conservation measures in subtropical semi-arid and arid regions should target the protection of large trees and woody vegetation to provide necessary thermal buffering to support animal thermoregulation and reproduction in a rapidly warming world.

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CHAPTER 1

General Introduction



The southern ground-hornbill, known as the “thunderbird” or “rainbird”

A cultural belief tied to their seasonal rhythm, with their booming calls coinciding with the first summer rains and the onset of breeding

1.1. General introduction

1.1.1. Climate change

Anthropogenic climate change is causing global weather extremes, leading to extensive ecological disruption and biodiversity decline (Parmesan, 2006; Nunez et al., 2019; IPCC, 2023). Global mean temperatures are likely to exceed 1.5 °C above pre-industrial levels before 2040 (IPCC, 2023) and heatwaves and droughts are becoming more frequent, pervasive and severe (Coumou & Rahmstorf, 2012; Perkins-Kirkpatrick & Lewis, 2020; IPCC, 2023; Wang et al., 2024). Many taxa may be unable to adapt or undergo climatic niche shifts rapidly enough to keep pace with the current rate of climate change (Jezkova & Wiens, 2016; Wiens, 2016), and climate-related local extinctions of animals and plants are already widespread (Wiens, 2016). Species may respond by shifting their geographical ranges poleward or to higher elevations, although such movements are often constrained by dispersal limitations and habitat availability (Parmesan, 2006; Bladon et al., 2021; Rubenstein et al., 2023). Therefore, understanding how habitats and wildlife respond to climate change is urgently needed to identify the mechanisms driving population vulnerability, form predictions, and inform conservation strategies.

Among the many climate-driven pressures on wildlife, heat exposure can strongly influence survival and reproductive success. There are now many recorded cases of catastrophic heatwaves causing mass die-offs in endotherms as a result of animals being unable to prevent lethal hyperthermia or dehydration (Welbergen et al., 2007; Pruvot et al., 2019; McKechnie et al., 2021; Holt & Boersma, 2022). Of equal concern, are the sub-lethal impacts of high environmental temperatures and droughts on reproductive outcomes, such as reduced offspring condition and fitness (van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021; Fuller et al., 2021; Khera et al., 2023), egg investment (birds and reptiles) (Lepage &

Lloyd, 2004; Potti, 2008; Wu et al., 2025), and delayed or missed breeding attempts (Moreno & Møller, 2011; Carstens et al., 2019a; Pattinson et al., 2022).

1.1.2. Thermal landscapes

Most terrestrial landscapes are characterised by spatial variation in vegetation structure and cover, and hence how they support flora and fauna (Tews et al., 2004; Turner & Gardner, 2015). Vegetation structure and heterogeneity play a key role in how animals are exposed to heat (Carroll et al., 2016; van de Ven, McKechnie & Cunningham, 2019; Mitchell et al., 2024). Leaf cover offers shade and cooling through evapotranspiration (Tabacchi et al., 1998; Catterall, Lynch, & Jansen, 2012), reducing the operative temperature of that specific small-scale location within the habitat, referred to as a microsite. Operative temperature is an integrated temperature measure incorporating radiative, convective, and conductive heat exchange (Bakken, Santee & Erskine, 1985). Considering the operative temperatures in microsites across a landscape gives a more accurate reflection of the thermal conditions experienced by animals than air temperature alone (Bakken, Santee & Erskine, 1985; Cunningham, Martin & Hockey, 2015). Consequently, if shade is well distributed in the landscape, the trade-offs animals face in heat avoidance can be minimised. An important trade-off is between thermoregulation and foraging, as time spent seeking cooler microsites can reduce foraging effort (Martin, Cunningham & Hockey, 2015; Roberts et al., 2016; Alston et al., 2020; Cook et al., 2020; Whyte et al., 2026) and body condition (Reiner et al., 2021).

However, vegetation cover is not always consistent year-round and, in deciduous systems, the loss of leaf cover in winter can elevate heat radiation in the landscape (Massetti et al., 2019). Deciduous systems occur in many environments globally, from the forests and woodlands of temperate zones (Loidi & Marcenò, 2022) to subtropical savannas (Singh & Kushwaha, 2016). Savanna ecosystems in subtropical semi-arid regions are under pressure due to prolonged periods of drought, altered rainfall patterns, increased fire frequency, and bush

encroachment, that are intensified by climate change, altering landscape heterogeneity (Whitehead, Russell-Smith & Woinarski, 2005; Smit & Prins, 2015; Case et al., 2019; Wigley et al., 2024). In many of these regions, summers are hot and coincide with seasonal rainfall, while winters are warm and dry (Scholes, 2020). Habitat fluctuations, together with rising air temperatures, create a thermally challenging environment for wildlife in these regions, with potential cascading impacts on behaviour, reproduction and survival, and even ecosystem function. In many parts of Africa, mean temperatures have been rising at double the global rate (Engelbrecht et al., 2015), and in South Africa, heatwaves are projected to become far more frequent and intense, exceeding 45–47 °C, by late century (Mbokodo et al., 2020). Such unprecedented warming makes it crucial to understand heat exposure at a landscape scale to predict species vulnerability (Strydom et al., 2025). However, how seasonal variation affects the availability of shaded microsites, particularly for larger animals in savanna landscapes, remains poorly understood.

1.1.3. Animals and heat

For animals that occupy these hot environments, maintaining a safe body temperature in extreme heat is physiologically challenging. When environmental temperatures exceed body temperature animals must engage in evaporative cooling (e.g. by panting, gular flutter, sweating, cutaneous evaporative heat loss), to maintain a body temperature within safe physiological limits (Smit, 2013; Whitfield et al., 2015; McKechnie & Wolf, 2019; Cook et al., 2020). However, these processes are energetically and water costly, increasing the risk of dehydration and thereby creating a fundamental trade-off between conserving water and avoiding lethal hyperthermia (Smit et al., 2013; Albright et al., 2017; O'Connor et al., 2017; McKechnie & Wolf, 2019; Cook et al., 2020; McKechnie, Gerson & Wolf, 2021).

Birds are particularly vulnerable to rising temperatures because they are usually small bodied (compared to large mammals), mostly diurnal, and have high mass-specific metabolic

and evaporative water loss rates, while operating within a narrow optimal body temperature range (Wolf, 2000; Angilletta et al., 2010; Albright et al., 2017). To reduce the physiological costs of dissipating heat, birds can alter their behaviour by seeking shade, reducing activity, or shifting activity to cooler periods of the day (Carroll, Davis, Elmore, Fuhlendorf, et al., 2015; Martin, Cunningham & Hockey, 2015; Bladon et al., 2019; van de Ven, McKechnie & Cunningham, 2019; Pattinson et al., 2020). However, these behavioural adjustments may incur other costs such as reduced foraging efficiency and lower provisioning rates to offspring (van de Ven, McKechnie & Cunningham, 2019; Cunningham, Gardner & Martin, 2021). Chronic exposure to high temperatures can therefore reduce adult and offspring body condition (du Plessis et al., 2012; van de Ven, McKechnie & Cunningham, 2019).

During early-life, chicks undergo rapid energetically demanding growth (Olson, 1992) and, in altricial species, are reliant on adults for food and are confined to the nest, unable to evade high nest temperatures. As a result, heat can negatively affect growth rates and physiology, both directly via high nest temperatures and indirectly via reduced provisions, compromising survival and fitness (du Plessis et al., 2012; Oswald, Lee & Smit, 2018; Nord & Giroud, 2020; van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021; Pattinson et al., 2022). An increase in the frequency of hot days over the breeding period is likely to elevate energy and water costs for nestlings, ultimately lowering reproductive outcomes.

Much of the current understanding of how adults and nestlings respond to high temperatures comes from semi-arid and arid-zone systems studied during summer, where temperatures reach extreme highs and water can be limited (Smit et al., 2013; Cunningham, Martin & Hockey, 2015; Whitfield et al., 2015; Albright et al., 2017; van de Ven, McKechnie & Cunningham, 2019; Bourne, Ridley, Spottiswoode, et al., 2021; McKechnie, Gerson & Wolf, 2021). Among arid-adapted species, heat tolerance and evaporative cooling capacity vary between drinking and non-drinking species, with drinking species able to tolerate higher

environmental temperatures (Czenze et al., 2020). Less is known about the response and heat tolerance limits of birds in more mesic semi-arid systems, particularly how these responses vary seasonally between hot, humid summers and warm, dry winters. Investigating year-round effects of heat exposure is important as negative effects from one season can carry over and influence fitness and survival in subsequent seasons (Harrison et al., 2011; Gardner et al., 2016; Lv et al., 2023). In addition, recent work emerging from humid environments shows that humidity adds an additional thermal constraint by reducing the effectiveness of evaporative cooling (Freeman et al., 2022; Coulson et al., 2025; Liddle et al., 2025). Furthermore, most studies have focused on relatively small, short-lived birds, apart from research on the world's largest bird the common ostrich *Struthio camelus* (Schou et al., 2021; Svensson et al., 2024). This leaves a gap in our understanding of how large, long-lived species, across the range of avian body sizes, between small birds and the largest species, respond to high temperatures particularly given that larger body size and lower surface-area-to-volume ratios of large birds may result in slower rates of heat exchange with the environment (Tabh et al., 2025).

1.1.4. Cooperative breeding

Cooperative breeding is a social system where more than two individuals help to raise offspring, and occurs in ~9% of bird species globally (Cockburn, 2006; Jetz & Rubenstein, 2011; Rubenstein, 2011; Riehl, 2013). In these systems, non-breeding individuals, known as helpers, assist in raising offspring that are not their own (Cockburn, 2006) and contribute to predator defence and territory protection. By defending territories, groups can secure access to vital resources like food, safe breeding sites, and mates (Brockmann, 1997; Cockburn, 1998; Cant, Otali & Mwanguhya, 2002; Golabek, Ridley & Radford, 2012; Humphries et al., 2021). In most cooperative breeders, helpers are closely related to the offspring and gain indirect fitness benefits by contributing to the survival and reproductive output of closely related individuals, thus contributing to increase the frequency of shared genes in the population

(Cockburn, 1998). However, helpers can also be non-related individuals (Riehl, 2013), that may gain direct benefits such as increased survival prospects, access to and eventual inheritance of high-quality territories, or the opportunity to develop parental skills (Cockburn, 1998; Clutton-Brock, 2002; Akinwande, Dikko & Samson, 2015; Kingma, 2017; Nelson-Flower et al., 2018).

During reproduction, helpers can improve breeding conditions, by increasing provisions (te Marvelde et al., 2009; Van Boheemen et al., 2019), enhancing predator vigilance and protection (Francis, Hailman & Woolfenden, 1989; Teunissen et al., 2021), and improving offspring survival (Brouwer, Richardson & Komdeur, 2012; D'Amelio et al., 2022). Other benefits to reproduction include increased egg investment (Lejeune et al., 2016; Valencia et al., 2017; Fortuna et al., 2023; Van de Loock et al., 2023), earlier offspring fledging (Ridley & Heuvel, 2012), and increased recruitment to adult population (Meade et al., 2010). Helpers have also been associated with reduced costs of reproduction for breeding females. Specifically, during reproduction, the investment provided by helpers can be additive, where the overall amount of care to offspring is increased (Kingma et al., 2010; Pike et al., 2019), or compensatory, where breeders can reduce their investment in care, but offspring still receive similar amount of care overall (Crick, 1992). The latter is known as load-lightening, where helpers can reduce the energetic costs of producing or raising offspring (Crick, 1992; Hatchwell, 1999). Empirical support for load-lightening has been found in species where breeders reduce workloads (Hatchwell & Russell, 1996; Meade et al., 2010; Brouwer, Pol & Cockburn, 2014; Teunissen et al., 2023) or females reduce investment in eggs in the presence of helpers (Russell et al., 2007; Canestrari, Marcos & Baglione, 2011; Santos & Macedo, 2011). In some species, this has been associated with improved survival rates, especially for females (Cockburn et al., 2008; Paquet et al., 2015; Langmore et al., 2016). Load-lightening is hypothesised to be prevalent in long-lived species, where maximising survival, and hence

breeding attempts in life, are important to maximise lifetime fitness, leading breeders to prioritise their own survival over current reproductive investment (Crick, 1992; Dixit, English & Lukas, 2017; Van Boheemen et al., 2019). Consequently, breeders' overall reproductive effort is often lower, but investment per offspring is expected to increase, ensuring that offspring quality and survival prospects are not compromised (Stearns, 1992; Griesser et al., 2017).

1.1.5. Cooperative breeding in challenging climates

Cooperative breeding is more common in birds that inhabit low-rainfall and temporally-variable environments (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011). Consequently, it has been suggested that this breeding strategy may facilitate successful reproduction where conditions are harsh, such as arid and semi-arid systems (Jetz & Rubenstein, 2011; Cornwallis et al., 2017). Specifically, it has been proposed that helpers can buffer the negative effects of adverse conditions, by providing additive care, ensuring adequate provisioning to offspring (Rubenstein & Lovette, 2007; Covas, du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). Therefore, under challenging conditions of low rainfall or heat, offspring growth and survival could be maintained when there are more helpers. In addition, helpers may also reduce the physiological costs of reproduction to group members through load-lightening, allowing individuals to allocate more time to self-maintenance behaviour during high temperatures (e.g. shade-seeking). If breeders benefit by retaining better body condition and future reproductive potential (Bourne, Ridley & Cunningham, 2023), this improved condition, may in turn influence maternal investment, for example through adjustments to egg size, number or composition (Lepage & Lloyd, 2004; Groothuis et al., 2005; Russell et al., 2007; Canestrari, Marcos & Baglione, 2011; Fortuna et al., 2021; Capilla-Lasheras, Wilson & Young, 2023; Montesana et al., 2025).

However, evidence that helpers buffer the effects of adverse conditions on breeding outcomes is mixed and varies across taxa. Buffering effects have been found in meerkats *Suricatta suricatta* where larger groups improved offspring survival in dry conditions (Groenewoud & Clutton-Brock, 2021), and in superb starlings *Lamprotornis superbus*, where helpers buffered the negative effects of low rainfall on fledging success (Rubenstein, 2011). Conversely, larger group size did not mitigate the effects of high temperature on nest attendance, chick mass or fledging success in southern pied babblers *Turdoides bicolor* (Bourne, Ridley, Spottiswoode, et al., 2021; Bourne, Ridley & Cunningham, 2023). Similarly, in sociable weavers *Philetairus socius* high temperatures and low rainfall reduced nestling survival regardless of helper number (D’Amelio et al., 2022). These contrasting results suggest that the potential for helpers to buffer adverse conditions may depend on species-specific traits and for species with low fecundity, large body size, and high survival, it has been suggested that helpers may contribute more to territory defence or predator protection than to reproduction (Gonzalez, Sheldon & Tobias, 2013; Middleton et al., 2026).

1.2. Aims and Objectives

The main objective of this research was to extend the current understanding of how animals respond to high temperatures, and to determine if these responses may be influenced by social factors.

I address this broad objective by investigating behaviour, maternal investment, offspring growth and physiology in a large, long-lived, cooperatively breeding bird, with low reproductive rates, the southern ground-hornbill *Bucorvus leadbeateri*, that inhabits hot semi-arid regions with pronounced dry and wet seasons. Studies on how animals respond to high temperatures have been mostly conducted on relatively short-lived, small birds in arid

environments, and hence the results from this thesis provide insight into the vulnerability to climate warming of larger animals inhabiting semi-arid savannas.

The specific objectives are addressed through four data chapters, each structured to support publication, therefore some information is repeated in the introductions, methods, and discussions. The aims for each chapter are outlined below:

Chapter 2: investigates how seasonal and long-term climate warming affects the thermal landscape in a semi-arid savanna habitat, and how southern ground-hornbills respond behaviourally to seasonal temperature variation within this landscape.

Chapter 3: investigates how varying social (helper presence) and environmental (weather) conditions influence maternal investment in first- and second-laid eggs of southern ground-hornbills, with the second egg functioning as an “insurance egg” with lower survival prospects.

Chapter 4: investigates how high temperatures influence nestling growth trajectories and post-fledging survival in southern ground-hornbills, and whether the presence of helpers can mitigate the negative effects of heat.

Chapter 5: investigates how early-life exposure to high temperatures and social conditions, influences physiology in southern ground-hornbill nestlings, using telomere length and dynamics as biomarkers of physiological stress.

1.2.1. Study site

Fieldwork was conducted in the Associated Private Nature Reserves (APNR; -24.255, 31.304, which comprises five reserves: Balule (510 km²), Klaserie (600 km²), Thornybush (140 km²), Timbavati (550 km²) and Umbabat (310 km²) in the northeast of South Africa (Figure 1.1). The APNR (~2,100 km²) now forms a continuous conservation landscape with Kruger National Park (KNP; -24.263, 31.735; ~20,000 km²), following the removal of boundary fences in 1993. This integration allows free movement of large predators such as lion *Panthera leo*, leopard

Panthera pardus, African wild dog *Lycaon pictus*, and megaherbivores which are important to maintain the vegetation structure such as rhinoceros *Ceratotherium simum*; *Diceros bicornis*, elephant *Loxodonta africana*, buffalo *Syncerus caffer*, giraffe *Giraffa camelopardalis* (Figure 1.2), and numerous antelope species. Historically the APNR was used for livestock farming but shifted to wildlife-based land use in the 1970s (Van Der Waal, 2010).

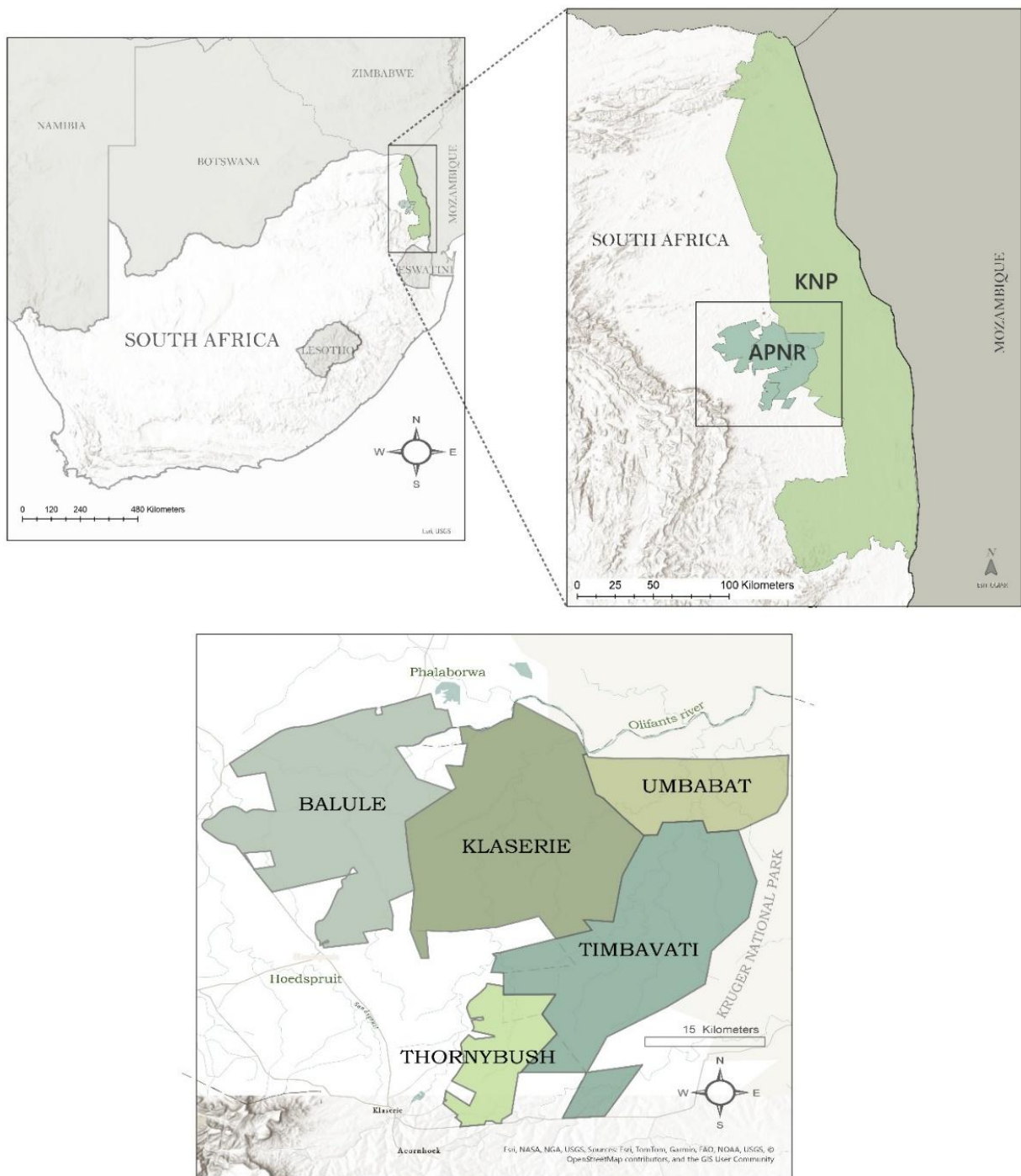


Figure 1.1. Map of the study site. The study site is located in the northeast of South Africa in the Associated Private Nature Reserves (APNR) which shares an open unfenced boundary to Kruger National Park (KNP). Maps were created using ArcGIS® software by Esri.



Figure 1.2. Study site: the Associated Private Nature Reserves fall within the savanna biome in a heterogenous landscape that supports a diverse range of wildlife, from predators such as African wild dog, lion and leopard, megaherbivores such as rhino, giraffe and elephant, antelope species, and many bird and reptile species. Photo: Chad Cocking.

This region has hot wet summers (October – March), and dry warm winters (April–September). The mean annual summer rainfall is ~430 mm (range 210–890 mm; based on data from rain gauges distributed throughout the study site; Figure 1.3). In summer, mean daily minimum and maximum temperatures are 20 °C and 32 °C, respectively, and in winter are 10 °C and 27 °C, based on data collected from 2018–2025 at the onsite Vantage Pro2 weather station (Davis Instruments, USA; location: -24.199, 31.153) in Klaserie Private Nature Reserve. Mean daily maximum air temperatures are increasing during summer and winter at the study site (Figure 1.4). The APNR falls within the savanna biome with a highly seasonal heterogenous landscape including open tree savanna, mixed and open woodland, low thicket, shrubveld and riparian habitats (Gertenbach, 1983; Peel, Kruger & MacFadyen, 2007; Van Der Waal, 2010; Zoghby et al., 2015) (Figure 1.5). Common tree species include mopane *Colophospermum mopane*, appleleaf *Philenoptera violacea*, knob thorn *Senegalia nigrescens*, leadwood *Combretum imberbe*, jackalberry *Diospyros mespiliformis*, Marula *Sclerocarya birrea* and Red Bushwillow *Combretum apiculatum*.

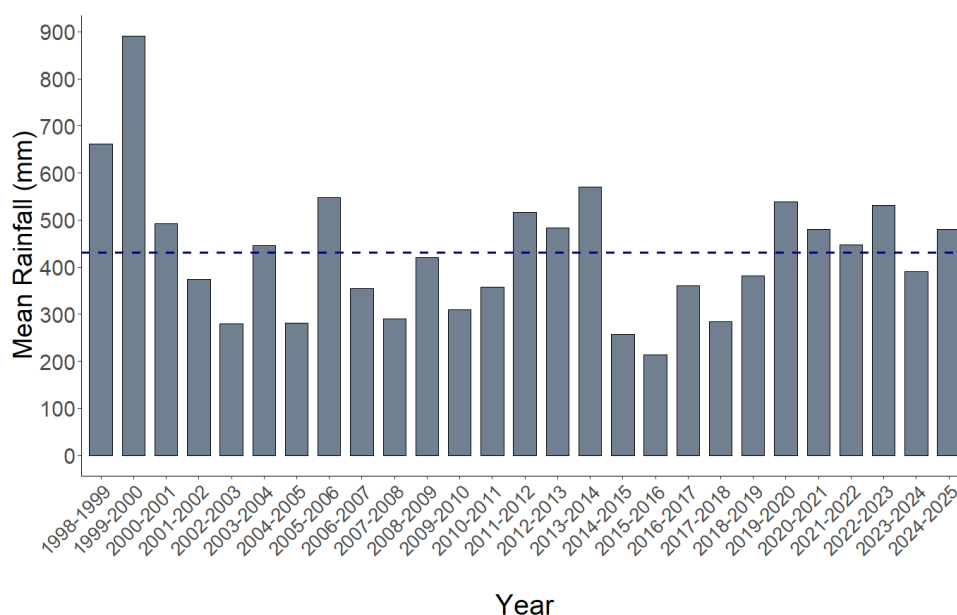


Figure 1.3. Yearly total summer rainfall (October–March) per year (1998–2025), averaged across all rain gauges within the study site. Bars show yearly total rainfall, and the blue dotted line indicates the long-term average (~430 mm, range 210–890 mm).

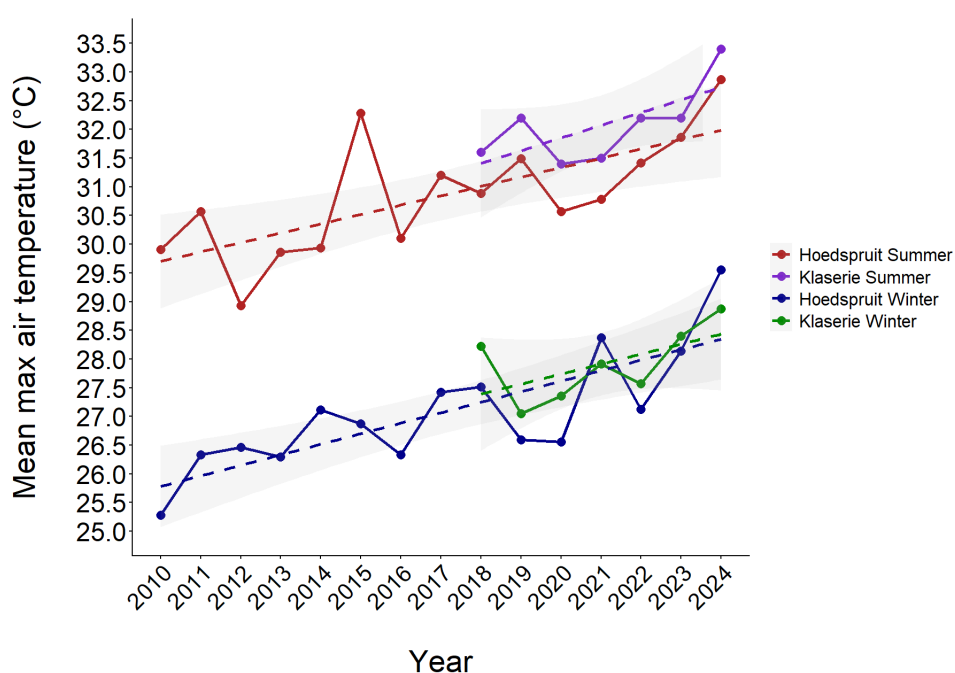


Figure 1.4. Annual trends in mean daily maximum air temperature (°C) during summer (October–March; Hoedspruit = red, Klaserie = purple) and winter (April–September; Hoedspruit = blue, Klaserie = green). Data were obtained from the Hoedspruit Airforce Base weather station (2010–2024) and the Klaserie weather station (2018–2024). Summer seasons are labelled by their starting year (e.g. 2010 = October 2010–March 2011). Points represent annual seasonal means, solid lines connect yearly means, and dashed lines indicate linear model fits with 95% confidence intervals. Temperatures increased significantly in Hoedspruit during both summer (0.16 ± 0.05 °C per year, $p = 0.003$) and winter (0.18 ± 0.04 °C per year, $p < 0.001$), whereas trends in Klaserie were positive but not statistically significant.



Figure 1.5. A marula tree *Sclerocarya birrea* in an open woodland habitat in the study site, pictured in summer (left) and in winter (right). Photos: Chad Cocking.

1.2.2. Study species

Southern ground-hornbills *Bucorvus leadbeateri* are endemic to Africa and are one of only two species of ground-hornbill, occurring across sub-Saharan semi-arid savanna and grassland habitats from Kenya south to South Africa. Another species, the largely allopatric Abyssinian ground-hornbill *Bucorvus abyssinicus* occurs north of the equator from Ethiopia and Kenya west to Senegal (IUCN, 2025). Southern ground-hornbills (hereafter ground-hornbills) are the largest and longest-living cooperatively breeding bird in the world weighing 3.3–4.4 kg, with a height of around 1 m, and can live for up to 60 years in the wild (Kemp, 1980). Groups of 2 to 11 individuals include a breeding pair and non-breeding helpers, typically male offspring from previous broods and sometimes immigrant males (Carstens et al., 2019b). Usually only one adult female is present in a group, with females dispersing earlier (average 12 months old) than males (average 48 months old) (Carstens et al., 2019b), although breeding groups with two adult females have been observed in the study site (N = 2 groups, pers.obs.). Males have been documented staying with their natal group for more than 16 years, and females for more than 7 years (pers.obs.). Sexual dimorphism is visible after 3–4 years of age when facial

colouration develops; males have an entirely red throat pouch and are larger than females, while females have a patch of violet blue under the bill (Figure 1.6). Groups occupy large territories, from 50–200 km², which they advertise with deep loud booming calls each morning, and will physically defend if another group intrudes (Kemp, 1980; Zoghby et al., 2015; Middleton, 2022; Theron et al., 2013).



Figure 1.6. Adult female with blue patch under throat (left), adult male with entirely red throat (middle), juvenile (1 years old) with pale facial features (right). Photo: Chad Cocking.

Unlike all other hornbill species, ground-hornbills do not seal their nests during breeding (Gonzalez, Sheldon & Tobias, 2013), and females leave the nest to vocalise and forage with the group for short periods during incubation and brooding (Middleton, 2022). They nest several meters above the ground, mostly in large tree cavities but occasionally use cliff faces or earth banks (Kemp & Begg, 1996; Carstens, 2017). The breeding season occurs during the summer rainfall season, from September to March in this study site (Wilson & Hockey, 2013; Middleton et al., 2026). Females lay 1–2 eggs (rarely 3), asynchronously 3–5 days apart, which are incubated solely by the female for ~42 days (Kemp, 1988; Carstens et al., 2019a). Only one chick is raised, and the second egg serves as an insurance egg; the chick

from this egg is raised only if the first egg fails to hatch or is lost to predation. Chicks hatch asynchronously, with the second hatched chick unable to compete for food from its larger sibling and succumbs to starvation within a few days (Kemp, 1988). Leopards *Panthera pardus*, genets *Genetta genetta* and *Genetta tigris* and chacma baboons *Papio ursinus* are the most common predators for nestlings (Figure 1.7).



Figure 1.7. Camera trap images capturing baboons (top), a genet (bottom left) and leopard (right) investigating nest boxes. The chick was big enough to scare away the baboons in this case, and the genet was using the box as a roost site prior to ground-hornbills taking occupancy. Here only the leopard preyed a chick which was unable to defend itself.

The group provides food and nest-lining to the incubating female. Once the chick has hatched, the female typically stays in the nest for roughly three weeks, after which she joins the group for foraging and returns with them to feed the nestling (pers.obs.). Nestlings are slow to develop and usually fledge between 80–90 days old (Carstens et al., 2019c). Once fledged,

juveniles remain dependent on adults and will continue to receive care and food from parents and helpers for several months, as it takes time for them to learn how to hunt and catch prey items successfully for themselves (Carstens et al., 2019a; Kemp, 1980; pers.obs.) (Figure 1.8).



Figure 1.8. A family group of ground-hornbills foraging with a newly fledged chick. It takes time for juveniles to learn how to hunt and catch prey and they therefore depend on adults for care for several months after fledging. Photo: Simon Price.

Ground-hornbills are non-drinking birds, obtaining all their water requirements from food. They consume anything they can overpower, including arthropods, reptiles, birds, amphibians and small mammals (Combrink, 2016; Middleton, 2022). Some common vertebrate prey species they are observed consuming include puff-adders *Bitis arietans*, scrub hares *Lepus saxatilis*, flap-necked chameleons *Chamaeleo dilepis* and leopard tortoises *Stigmochelys pardalis*. They are terrestrial foragers (Figure 1.9) and will often gather and carry multiple prey items in their large strong bill for long periods of time before consuming, or gifting to another group member (usually to the adult female or a juvenile), or provisioning to a nestling. While breeding, the group will hunt, gather prey items and return to the nest site as a collective group (Kemp, 1980; pers.obs.). They will also gather fallen leaves for nest lining throughout the entire breeding period and bring to the nest in large ‘parcels’ which usually contain food items amongst the leaves. Usually, the female will not provision parcels to offspring, this appears to be mainly a male or helper contribution to the nest (Middleton, 2022; pers.obs.).



Figure 1.9. A family group of ground-hornbills foraging through the long grass in Kruger National Park. Groups include a breeding pair and non-breeding helpers, typically male offspring from previous broods and sometimes immigrant males. Ground-hornbills are terrestrial foragers. Photo: Papa Bravo.

In South Africa, ground-hornbills are listed as Endangered, having lost up to 70% of their historic range in the past century. Current threats include human expansion, habitat alteration such as bush encroachment in savannas, the loss of large trees for nesting sites, secondary poisoning and persecution, often in retaliation for the birds' habit of pecking at reflections and shattering windows (Kemp & Rose, 2025). They do not always breed annually, often skipping multiple consecutive breeding seasons. At this study site, groups typically breed once every 2–3 years on average. Their slow life history and inherently low reproductive rates make them particularly vulnerable to the impacts of a rapidly changing climate. Recent studies show that hot winters with more rainfall can delay breeding attempts, perhaps because elevated temperatures and greater humidity, coupled with low food availability in winter, make it harder for adults to attain the body condition needed for reproduction (Carstens et al., 2019a; Middleton et al., 2026). Conservation efforts for this species have focused on several strategies, including the provision of artificial nest boxes, habitat restoration, educational outreach, and

the reintroduction of groups into their historical range (Cilliers et al., 2013; Carstens et al., 2019c; Kemp et al., 2020).

1.2.3. Nest boxes as a conservation tool

The APNR is home to a long-term research project on southern ground-hornbills that began in 2000. A lack of natural nesting sites in the area, mainly due to land-use change, led to the first artificial nest boxes being installed in 2002. Each group typically has one nest box placed within their home-range, if they do not have a viable natural nest. Nest boxes are placed 4–6 metres high in the fork or arm of a secure branch in a tree (Figure 1.10, Figure 1.12). Typically, tree species such as Leadwoods *Combretum imberbe* and Jackalberry *Diospyros mespiliformis* are chosen for nest box sites. These species have dense wood and strong branches and are comparatively resistant to elephant damage, resulting in longer-lived nesting sites. In contrast, more vulnerable species such as Knobthorn *Senegalia nigrescens* and Marula *Sclerocarya birrea* are frequently pushed over, debarked, or broken by elephants, reducing their suitability and longevity as nest trees. Nest installations have enhanced the birds' breeding productivity, contributed to population growth, and facilitated the monitoring of their reproductive behaviour and outputs (Wilson & Hockey, 2013; Carstens, 2017; Carstens et al., 2019c; Middleton, 2022; Middleton et al., 2026). Nest boxes over the years were made from several different materials, including hollowed-out tree stumps, wooden boxes made from double-layered hardwood planks, and artificial M1 composite nest structures (Figure 1.10). Currently 35 nests are monitored, of which only 5 are natural nests.



Figure 1.10. Nest boxes used in the study site have varied over the years. From hollowed out tree stumps (top), wooden boxes made from double-layered hardwood planks (bottom left), and artificial M1 composite nest box (bottom right).

1.3. General methods

1.3.1. Nest monitoring

To determine breeding activity, nests were visited every 7–10 days from the beginning of October each year. Nest checks involved climbing to the nest entrance using a ladder and gently tapping on the side of the nest box to flush the female (if present) from the nest (Figure 1.11, Figure 1.12). Camera traps placed at nests (see below) show that females typically return to the nest within 20 minutes after being flushed. Because ground-hornbills are long-lived, many breeding females in this study population have been monitored repeatedly across years, with some individuals monitored for more than 15–20 years. These experienced females are accustomed to routine nest checks and typically return to the nest quickly (< 5 mins) after

monitoring. Some females do not flush; for these nests only, we waited before dawn until the female departed naturally to vocalise with the group. This could not be done at all nests because of the large distances and the travel time required between each nest (~45 minutes). Ground-hornbills line nests with leaves and grass prior to egg laying, and usually clear out previous years' old lining, therefore, the freshness of the lining gives an indication of the group's interest in breeding. Once first eggs are found, they are measured and weighed (details in Chapter 3), and the nest is revisited 5 days later to check for a second laid egg. This visiting schedule allows for estimation of hatching dates (~42 days after laying). If two eggs are found on the first visit, both eggs are candled, a process where a light is shone through the egg to assess embryo development and estimate embryo age (Resendiz et al., 2024), allowing prediction of the hatching date. The first method is more accurate in predicting hatching dates, while candling is used when frequent visits are not possible, for example due to weather constraints such as rain or cold temperatures, to reduce the risk of exposing embryos when females are temporarily flushed from the nest. Chicks that hatch are then monitored, weighed, and measured on days 1, 8, 20, 40, 60, and 75 (details in Chapter 4).



Figure 1.11. Female flushed from the nest (top). Females typically return within 20 minutes. A one-day old hatchling in the nest next to the second later laid egg that will hatch 3 – 5 days after the first hatched (bottom). Photo: Jannie Nikola (top), Carrie Hickman (bottom).



Figure 1.12. Nests are placed at least 4–6 meters high in the fork of a large tree. These two nests are placed in leadwood trees *Combretum imberbe*, selected for their strength, and relative resistance to damage by elephants compared to other tree species. To access the nests during nest monitoring, long extension ladders are used by researchers. Photo: Kevin MacLaughlin (left), Carrie Hickman (right).

1.3.2. Sexing

Blood samples ($< 500 \mu\text{L}$) were collected from nestlings by brachial venipuncture using a 26-gauge needle and a non-heparinised 1 ml syringe and whole blood was stored in alcohol. Nuclear DNA was extracted from blood samples using a DNA extraction kit from Bio Basic (Canada), and sex was determined by amplification of chromo-helicase-DNA-binding genes located on the W and Z sex chromosomes using the P2 and P8 universal primers (Griffiths et al., 1998).

1.3.3. Weather and nest temperature data

Daily maximum air temperature ($^{\circ}\text{C}$) and rainfall (mm) data were obtained from the onsite weather station (Klaserie Private Nature Reserve), which recorded data every 30 minutes with

a resolution of 0.1 °C for air temperature and 0.2 mm for rainfall. These data were used in analyses presented in Chapters 4 and 5. All nest sites were located within a 30-km radius of the onsite weather station. As data were only available from 2018, when the onsite weather station was installed, longer-term data for 2010–2025 were obtained from the South African Weather Service (SAWS) station at Hoedspruit Airforce Base (-24.331, 31.050; 18 km from onsite station) for use in Chapter 3. Additionally, historical climate data from 1960–2023 were obtained from the SAWS weather station at Skukuza, Kruger National Park (-24.989, 31.586 ~60 km from study site) to analyse historic climate trends (details in Chapter 2).

Thermochron iButtons (DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C) were used to record internal nest temperatures at 60-min intervals in all active nests. iButtons were attached to the inside roof of nest boxes with wall holders, or out of direct sunlight on the inside wall of natural nests above where the female and nestling sit, to avoid interference by the birds.

1.3.4. Camera traps

Prior to the breeding season, camouflaged metal security cases to house camera traps were placed at nests, approximately 1–3 metres from the nest entrance. These cases allow groups to get used to a new object at the nest site prior to breeding and provides some protection to the camera from weathering and wildlife interference. Camera traps (brand: Browning Trail Cameras, type: Patriot, Spec Ops Elite) were deployed inside the security cases when nests became active, and batteries and memory cards were changed during the scheduled nest visits. This allowed for group and individual identity to be determined as well as juvenile survival from previous breeding attempts. Cameras were set to record high resolution 20 second videos, with inter-video period of 5 seconds, and are triggered by movement. Where possible, cameras were positioned to capture a side profile of the entrance rather than directly facing it, to avoid constant triggering by the incubating female or nestling.

1.3.5. Individual ID

Individuals are identified by their unique facial features, such as shape of the throat and sideburns under the eye (Figure 1.13). Females can be identified by the size and shape of their blue patch under the bill (Figure 1.13). Rings are placed on all chicks prior to fledging and historically some adult birds were caught and ringed in the study site, including some with colour ring combinations. Therefore, most birds in the study populations have unique ID rings. However, ring codes can be difficult to read, and rings usually only remain on the birds for ~10–15 years (probably due to weathering and wear and tear from them walking through long grass) therefore, some adults are now without rings. Since the birds are so long-lived, facial feature identification is therefore more reliable in the long term. The project now maintains a database of images of each individual that is updated every year. Juveniles are documented the same way, but as groups only raise a single chick each year, and not always annually, it is usually easy to record juvenile age from throat colouration. Juveniles' throats remain pale for the first 2 years before transitioning from around 3 years to yellow/red as a subadult (Figure 1.14).



Figure 1.13. Images from camera trap footage, documenting individual ID. Females (top left and right) can usually be identified by the size and shape of the blue patch under the bill as it varies significantly between individuals (images are of two different adult females). Adult males (bottom left and right) can be identified by the throat (arrow) and sideburns (circled). Pictured are two different adult males; the male on the left has a longer throat and broader sideburns (when looking at the black feathered area between the eye and throat skin patches) than male on the right.



Figure 1.14. A young individual transitioning from a juvenile to sub-adult (from one to four years old).

1.3.6. Statistical analyses

Statistical analyses were conducted in R v 4.4.1 (R core Team 2024), using the RStudio platform (RStudio Team 2024).

Throughout this thesis:

1. All continuous predictor variables were scaled by centering and standardising the mean and tested for correlation with one another (Harrison et al., 2018)
2. Variance inflation factors (VIF) in the *car* package (Fox, Weisberg & Price, 2025) were used to test for collinearity between explanatory variables, and variables were not included in same model if $VIF > 2$. The only exception was for specified interaction terms, which include their component main effects even if collinearity is present (Harrison et al., 2018).

3. I assessed whether model assumptions were met by examining residual plots with the *performance* package (Lüdtke et al., 2021).
4. Models were selected by comparing candidate model sets using `model.sel` function in the *MuMIn* package, based on Akaike's information criterion corrected for small sample size (AICc) and top models were those $\Delta\text{AICc} < 2$.
5. Effect sizes, standard errors ($\pm$), 95% confidence intervals, were reported in text and in tables from all top models within $\Delta\text{AICc} < 2$. Effects were reported as significant if confidence intervals did not overlap zero. P-values were also presented in tables.
6. Plots were created using the *ggplot2* package (Wickham, 2016) and unscaled values were used in plots for easier interpretation.

Selecting environmental variables

For Chapter 2, no prior selection of weather variables was necessary because the research question specifically addressed the effects of air temperature, humidity, and their interaction at the time of observation on behaviour. However, for Chapters 3–5, there was limited prior knowledge regarding which environmental variables, and over what timeframes, influence reproductive outcomes in this species. I initially explored *climwin* (Bailey & van de Pol, 2016) to attempt to evaluate specific time windows of relevance, using a sliding window approach. However, *climwin* did not provide biologically meaningful results. Consequently, alternative selection methods were applied to identify the best predictor variables, including air temperature, nest temperature (Chapters 4 and 5) and rainfall. For these chapters, all candidate temperature and rainfall variables across multiple time windows were first compared to identify the top-supported weather predictor(s), with candidate predictors defined *a priori* based on their expected biological relevance to the question addressed in each chapter. These were then included in the final model sets alongside social predictors (e.g. helpers and juveniles) to assess whether helpers mediated weather effects on reproductive outcomes.

CHAPTER 2

More Heat, Less Shade: rising winter temperatures, animal behaviour and thermal vulnerability under climate change



2.1. Abstract

Understanding how thermal landscapes impact animal behaviour and fitness is increasingly important under climate warming. Most studies focus on the hottest times of year, with limited insight into winter warming, but in seasonal subtropical regions high air temperatures can occur year-round. I examined the thermal landscape of a subtropical semi-arid savanna in summer and winter and assessed long-term temperature trends. I also investigated seasonal thermoregulatory behaviours of the southern ground-hornbill *Bucorvus leadbeateri*, a large, ground-foraging bird resident in this savanna. I measured operative temperatures (an integrated temperature measure incorporating radiative, convective, and conductive heat exchange) in four microsites (ground in sun/shade, off-ground in sun/shade) used by ground-hornbills, and quantified shade availability in open woodland and riparian habitats within this landscape. Landscape operative temperatures in both habitats were almost 5 °C higher in winter than summer at the same air temperature, associated with reduced shade in winter. Furthermore, long-term data (~63 years) revealed that winter temperatures have increased more rapidly than summer temperatures in open woodland areas. Riparian habitats provide thermal refuges in this landscape, especially in winter when they are on average 3.2 °C cooler than surrounding open woodlands. However, winter operative temperatures in riparian habitats are now approaching historic summer conditions. Ground-hornbills engaged in panting (evaporative cooling) at lower air temperatures in winter (31.8 °C) than summer (36.1 °C), likely in response to hotter landscape operative temperatures. In summer they also reduced foraging and sought shade as air temperature increased, but did not do so in winter, perhaps due to lower food and shade availability. Humidity was higher in summer (17.0 g m⁻³) than winter (11.1 g m⁻³), but effects on ground-hornbill behaviour were weak: birds panted slightly less and perched off-ground slightly more at higher humidity in summer but showed no other behavioural responses. Hence, rising temperatures intensify thermal challenges for savanna animals year-round, with winter

emerging as a critical period due to reduced shade and high operative temperatures. Wildlife may increasingly rely on cooler riparian habitats for thermal refuge in winter, highlighting the importance of conserving cooler habitats within landscapes in a warming climate.

2.2. Introduction

Rising temperatures and escalating frequency and intensity of heatwaves are reshaping ecosystems, impacting species distributions, population dynamics and individual fitness (Scheffers et al., 2016; Spooner, Pearson & Freeman, 2018), and even leading to mass mortalities (McKechnie & Wolf, 2010; McKechnie et al., 2021). Understanding species' behavioural and physiological responses to climate warming is essential for predicting ecological change and assessing fitness consequences in wildlife (Fuller et al., 2010; Conradie et al., 2019; van de Ven, McKechnie & Cunningham, 2019; Cunningham, Gardner & Martin, 2021). However, while an increasing number of studies address individual responses to high temperatures, most focus on the hottest periods of the year when air temperature is highest (Mason et al., 2017; van de Ven, McKechnie & Cunningham, 2019; Bourne, Ridley, Spottiswoode, et al., 2021; Cunningham, Gardner & Martin, 2021), leaving critical gaps in our understanding of the impacts of warming in winter.

Winter presents challenges including plant dormancy, food scarcity, low temperatures, and reduced daylight hours (Williams, Henry & Sinclair, 2015; Santangeli & Lehtikoinen, 2017), with animal responses varying across latitudes. Globally, winter temperatures are increasing at a faster rate than summer temperatures (IPCC, 2023) and in temperate regions, warmer winters may alleviate cold stresses for some species, offering thermoregulatory relief (Gardner et al., 2017; Chukwuka et al., 2021), increased food availability and extended growing seasons (Ozgul et al., 2010; Zeng, Jia & Epstein, 2011). These favourable conditions

could contribute to improved fitness, aiding population growth (Loe et al., 2021) and range expansion (Gardner et al., 2017, 2022; Osland et al., 2021).

Conversely, at lower latitudes, species face year-round high daily maximum temperatures. For example, in arid and semi-arid subtropical regions that experience hot summers and warm winters, daytime temperatures in winter can still be high (Scholes, 2020; Lv et al., 2023). In many eastern subtropical regions globally, rainfall is summer dominant (Peel, Finlayson & McMahon, 2007), resulting in a greater abundance of food, water, and shade in summer (Dean & Milton, 2001), but greater humidity adds to thermoregulatory demands (Freeman et al., 2022; Coulson et al., 2025). During winter, however, food and water become scarce, and animals may have to allocate more time to seeking these limited resources. Despite winter air temperatures being generally cooler because the sun is lower in the sky, and daylight hours are shorter, the loss of thermal refuges due to the shedding of leaves by deciduous trees (Singh & Kushwaha, 2016) can elevate heat radiation in the environment (Massetti et al., 2019). This potentially increases the need for heat dissipation; however, the implications of this for behaviour and physiology of animals facing warming winters in the subtropics remains poorly understood.

When exposed to high environmental temperatures (e.g. temperatures that prompt heat dissipation behaviours in animals), endotherms (birds and mammals) can dissipate heat through evaporative cooling (Tieleman & Williams, 2002a; Whitfield et al., 2015; Smit et al., 2016; O'Connor et al., 2017; Cook et al., 2020). Evaporative cooling mechanisms effectively lower body temperature, but can carry dehydration risk (Albright et al., 2017; McKechnie & Wolf, 2019) and may lose effectiveness in environments with high humidity (van Dyk, Noakes & McKechnie, 2019; Freeman et al., 2022; Coulson, 2023). To avoid physiological costs of heat exposure, animals can alternatively seek cooler locations (e.g. in shade, underground) and reduce activity (van Beest & Milner, 2013; Briscoe et al., 2014; Carroll, Davis, Elmore &

Fuhlendorf, 2015; Martin, Cunningham & Hockey, 2015; Mole et al., 2016; Bladon et al., 2019; Sharpe, Prober & Gardner, 2022) or shift activity to cooler times of day (Berry et al., 2024; Brivio et al., 2024). However, such behavioural adjustments may also carry costs such as missed foraging opportunities, reduced parental care, and reduced territory defence (du Plessis et al., 2012; Martin, Cunningham & Hockey, 2015; Woodroffe, Groom & McNutt, 2017; van de Ven, McKechnie & Cunningham, 2019; Cunningham, Gardner & Martin, 2021; Sharpe, Bayter & Gardner, 2021) which can lead to reduced body condition in both adults and offspring (du Plessis et al., 2012; van de Ven et al., 2020). Furthermore, sub-lethal effects associated with heat exposure in one season can carry over and influence fitness in subsequent seasons (Harrison et al., 2011; Gardner et al., 2016, 2017). Such carry-over impacts have been seen in superb fairy-wrens *Malurus cyaneus* and white-plumed honeyeaters *Ptilotula penicillatus*, in which exposure to high temperatures leads to lower survival later in the annual cycle (Gardner et al., 2016; Lv et al., 2023). Altogether, these patterns highlight the importance of considering the impacts of high temperatures in more than one part of the year.

The behavioural and physiological costs of keeping cool may be buffered by landscape thermal heterogeneity. Features such as topography, woody vegetation, and burrows provide critical microsites for thermoregulation by reducing sun exposure (Sears, Raskin & Angilletta, 2011; Carroll et al., 2016; van de Ven, McKechnie & Cunningham, 2019; Mitchell et al., 2024). Abundant and well-distributed shade from woody vegetation can minimise trade-offs animals face in heat avoidance, helping them maintain foraging efficiency (Martin, Cunningham & Hockey, 2015; Roberts et al., 2016; Alston et al., 2020; Cook et al., 2020; Whyte et al., 2026) and body condition (Reiner et al., 2021). However, there has been limited research on how the availability and use of shaded habitats varies seasonally, and studies that only consider air temperature may miss important variation in the thermal environments actually experienced by animals, as these are often better captured by operative temperature, which integrates air

temperature, solar radiation, wind, and conductive and convective heat exchange (Bakken, Santee & Erskine, 1985).

Here, I compared the summer and winter thermal landscapes of open woodland and riparian habitats within a subtropical, semi-arid African savanna ecosystem with deciduous vegetation, and assessed how these have changed during a prolonged (63 years) period of climate warming. Using the southern ground-hornbill *Bucorvus leadbeateri* (hereafter ground-hornbill) as a model species, I investigated how warming has affected landscape microclimate temperatures in summer and winter, and how ground-hornbills adapt their behaviour to seasonal temperature variation in this landscape. Ground-hornbills are large (2.2–6.2 kg), resident, ground-foraging birds that inhabit semi-arid savannas in southern Africa. Ground-foragers are frequently exposed to high heat, as heat radiation is highest on the ground surface (Carroll, Davis, Elmore & Fuhlendorf, 2015; van de Ven, McKechnie & Cunningham, 2019), and although ground-hornbills prefer open habitats to forage (Zoghby et al., 2015; Combrink et al., 2020) they retreat to shade (Kemp, 1980) and move to riparian or denser wooded habitats during high temperatures (Zoghby et al., 2015). Research has shown that ground-hornbills delay the onset of breeding attempts in summer after particularly hot and wet winters (Carstens et al., 2019a; Middleton et al., 2026). One possible explanation for this pattern could be that increased thermoregulatory requirements in winter, associated with high temperatures and humidity that limit effective evaporative cooling, constrain hornbills' capacity to reach ideal breeding condition before the breeding season starts. I hypothesised firstly, that the thermal landscape is influenced by the availability of shade, predicting that higher shade availability in summer should provide ground-hornbills with greater access to cooler microsites compared to in winter. Despite lower average air temperatures during winter, I predicted that decreased shade availability could make the overall landscape warmer in winter than in summer; and riparian areas that support some evergreen vegetation might provide cooler habitat than open

woodland especially in winter. Secondly, I hypothesised that ground-hornbills would display temperature-sensitive behaviours and predicted that high temperatures should influence their thermoregulatory and foraging patterns. However, I predicted that these behavioural responses could be less pronounced in winter, when food and shade availability are lower and humidity is reduced, which should influence the cost/benefit ratio of reducing foraging and seeking shade.

2.3. Methods

2.3.1. Study site

Data were collected from January 2021 to August 2023 in the Associated Private Nature Reserves (APNR, 2100 km², -24.255, 31.304) and Kruger National Park (KNP, 20,000 km², 24.263, 31.735), in northeastern South Africa (Figure A2.1). These areas feature a diverse mosaic of deciduous vegetation, including savanna, woodland, thicket, shrubveld, and riparian habitats (Gertenbach, 1983; Zoghby et al., 2015; Carstens et al., 2019a). The subtropical climate has hot, wet summers (October–March) and warm, dry winters (April–September). During winter, deciduous trees lose their leaves; however, patches of evergreen vegetation persist in riparian habitats where groundwater is present year-round. The annual rainfall is 200–900 mm, falling mainly during summer. This study considers November, December, January, February as summer, and May, June, July, August as winter. March, April, September, and October were excluded from the analysis, as these months may not fully represent distinct summer or winter conditions and may have affected the representation of seasonality in the data. In summer, the mean daily maximum air temperature is 32.1 °C, and in winter it is 27.2 °C (data from 1960–2023, South African Weather Service, SAWS).

2.3.2. Study species

The southern ground-hornbill *Bucorvus leadbeateri* is a large cooperatively breeding bird (2.2 – 6.2 kg) found throughout southern Africa (Wilson & Hockey, 2013). Groups, consisting of 2–11 birds, defend territories of 80–200 km² (typically 80–100 km² in the study site). They nest in large tree cavities several metres off the ground (Kemp & Begg, 1996) and prefer open areas with some woody cover for foraging (Zoghby et al., 2015; Loftie-Eaton, 2018; Combrink et al., 2020). As faunivorous ground foragers, they prey on invertebrates, small mammals, reptiles, amphibians, and birds (Kemp, 1974; Middleton et al., 2026) occupying a mesocarnivore-like niche in savanna systems. Reproduction occurs in summer when food availability increases (Kemp, 1974; Wilson & Hockey, 2013; Middleton et al., 2026). Ground-hornbills' reproduction rate is slow: they raise no more than one offspring per year and on average fledge one chick every 2 to 9 years (Carstens et al., 2019a; Middleton et al., 2026). They live 50–60 years, reaching sexual maturity after five years (Kemp, 1980; Middleton, 2022). They are classified as Vulnerable globally (IUCN, 2024) and Endangered in South Africa, where numbers are declining mainly due to habitat loss and persecution (Kemp & Rose, 2025).

2.3.3. Weather data

Air temperature (°C; T_{air}) and absolute humidity (g m^{-3}) data were collected from an on-site weather station (Davis Vantage Pro 2) within the APNR (-24.263, 31.735), which recorded data at 30-minute intervals. In KNP data were obtained from iLeaf, an online weather service platform (iLeaf, 2021), with 13 weather stations (Stratus 200) located throughout KNP, recording data at 60-minute intervals. To analyse long-term T_{air} trends, daily maximum T_{air} data were obtained from the South African Weather Services (SAWS) weather station at Skukuza, KNP (-24.989, 31.586, data available 1960–2023, Figure 2.2) as historic climate data were not available from the APNR.

2.3.4. Microsite availability

I conducted surveys to estimate the availability of potential ground-hornbill standing/walking or perching sites (hereafter microsites), defined as locations which could support the birds' body size and weight, both on the ground and in trees, at height intervals of two-meters. Microsite surveys were carried out in two distinct 1 km² plots: one within an open woodland habitat, and one within a riparian habitat, as ground-hornbills most frequently used these two habitat types during this study, consistent with previous GPS tracking research showing a preference for these habitats (Zoghby et al., 2015). The representative nature of these plots was confirmed by comparing grayscale and NDVI satellite imagery of each plot, processed using Google Earth Engine, with 110 additional randomly selected plots, using ArcGIS (version Pro 3.0.3), in both open woodland and riparian habitats (220 plots total) across the study area (see details in Appendix; Figure A2.2). Surveys were carried out in summer (February) and repeated in winter (July). I used ArcGIS Pro to overlay a 50m x 50m grid in each selected 1 km² area. I visited each grid point on foot and recorded all available microsites within a 1 m radius of the grid point for each height category (ground, 2 m, 4 m, 6 m, 8 m). If no microsite was present at a particular height, none was recorded for that category. For each microsite identified, I assessed exposure to the sun at midday when the sun is directly overhead (two categories: 'sun' and 'shade'), and whether it was on the ground or in a tree. I collected a total of 1600 grid points overall (400 grid points per habitat per season). Data were recorded into the ArcGIS Field Maps app (version 24.2.2), using a custom-built database.

2.3.5. Operative temperatures

Operative temperatures (T_e) were recorded using black bulb (black globe) thermometers, following Bakken, 1985. Black bulbs were constructed from 125 mm diameter hollow copper spheres, painted matt black. This diameter approximated the mean thoracic depth of an adult ground-hornbill, based on museum specimens (mean 126.7 ± 15.9 mm, $N = 4$). IButtons

(Thermochron iButton, DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C) were suspended inside each black bulb to record temperature at 30-min intervals. Black bulb thermometers measure T_e that are particular to the location in which they are placed. They consolidate the effects of radiation, convection, and T_{air} , into a single number measurement: an estimate of dry “heat load”, which can be used to approximate T_e differences between locations relevant to study species of interest, which T_{air} alone cannot do (Bakken, Santee & Erskine, 1985). Black bulbs, however, cannot account for the influence of humidity and evaporation or physical features of the bird such as plumage structure and colour, exact body size, and posture (Bakken, Santee & Erskine, 1985; Cunningham, Martin & Hockey, 2015). I deployed two replicate black bulbs per habitat type (open woodland, riparian) in each of four microsites representative of locations used by ground-hornbills: on ground in sun and shade, and in trees (approx. 4–5 metres high) in sun and shade. Black bulbs were installed sequentially, due to equipment constraints, first in the open woodland habitat for ± 25 days and then in the riparian habitat for ± 25 days, during 2023 in the summer months (January-March) and repeated in the winter months (June-August).

2.3.6. Behavioural data collection

Behavioural observations of ground-hornbills were conducted in the APNR from January 2021 to October 2023. Observations used a “scan sampling” method, in which birds were observed for < 30 s (‘instantaneous observations’) following Smit et al. (2016) and Pattinson et al. (2020), by researchers in the APNR, between the hours of 5:00–18:00 ($N = 270$). In KNP, photographs and videos were collected from citizen science contributions, primarily from tourists via direct email or the *Latest Sightings* app (Latest Sightings, 2025) between January 2021 and October 2023 ($N = 746$). Each photograph or video clip (< 30 seconds) was screened and analysed as a scan sample if the bird was fully visible with no obstructions, within close

range ($\pm < 100$ meters), and if the media contained embedded metadata: time, date, and GPS location, or if this information was available from the contributor. Citizen science observations may be influenced by variation in tourist activity across the day, potentially resulting in reduced observations during the hottest periods; however, targeted observations were undertaken by researchers to ensure observations were well distributed across the full range of air temperatures.

Binary information on foraging (0 = not foraging, 1 = foraging), shade-seeking (0 = in sun, 1 = in shade), and location (0 = on ground, 1 = off ground (perched)), and the absence (0) or presence (1) of heat dissipation behaviours (HDB); panting, wing drooping, and ptiloerection were recorded per scan sample, for each individual observed (Table A2.4). Panting occurs when a bird gapes while breathing (promoting evaporative cooling). Wing drooping occurs when a bird holds its wings away from its body, increasing surface area, exposing the area to air circulation (promoting non-evaporative heat dissipation). Ptiloerection occurs when feathers are spread and raised from the skin, exposing it to air flow (non-evaporative) (Bartholomew & Dawson, 1979; Smit et al., 2016) (Figure 2.1). The identity of ground-hornbill groups in the APNR were established through visual recognition and comparison of unique facial features from photographs of known individuals (Middleton, 2022; also see Chapter 1: General methods; Figure 1.13). In the KNP sightings were mapped and assumed to be of the same group of birds when within a 5.5 km radius of each other, based on typical territory size of 80–100 km² in study site.



Figure 2.1. Behavioural responses to high temperatures in southern ground-hornbills, photos illustrate heat dissipation (panting, wing drooping, ptiloerection; *top left*) and heat avoidance (shade seeking; *bottom left*) behaviours. Top right and bottom right images show a female who was reported to be panting heavily and slumped on the ground during a hot summer's day (~40 °C). Photos were submitted by citizen scientists. Photos: Jannie Nikola, Quim Agell, Susan Lawrence.

2.3.7. Statistical analyses

All statistical analyses were performed in the R statistical environment, v 4.4.1 (R Core Team, 2024), using the R Studio platform (R Studio Team, 2024). Model assumptions were validated by examining residual plots using the *performance* package (Lüdecke et al., 2021). Estimates and standard errors are presented, and effects are reported as significant when 95 % confidence intervals do not overlap zero.

Air temperature trends

Weather station data from Skukuza, KNP (spanning 1960–2023) were used to assess the frequency and distribution of daily maximum T_{air} in summer and winter, using kernel density

estimation to compare seasonal temperature distributions and quantify their overlap. Simple linear regression models in the stats package (R Core Team, 2020) were used to assess the relationship between year and mean daily maximum and minimum T_{air} for each season.

Landscape shade availability

I used chi-squared tests on microsite count data to assess differences in shade availability by season and habitat. To compare shade between seasons, I combined season and habitat into a single variable. Differences between open woodland and riparian habitats were tested separately for summer and winter.

Operative temperatures

I averaged T_e across replicate black bulbs, for each 30-minute time stamp in each microsite for each habitat and season. The sample size for these analyses varied due to logistical constraints; in the open woodland habitat, I recorded 22 days (1008 recorded temperatures per microsite) in summer and 25 days (1140 recorded temperatures per microsite) in winter. In the riparian habitat I recorded 29 days (1418 recorded temperatures per microsite) in summer and 26 days (1197 recorded temperatures per microsite) in winter. Welch's two-sampled t-test was used to compare T_e between seasons within each habitat and microsite for midday conditions (11:00 – 14:00; corresponding to period when T_e was hottest, Figure A2.6) and at matching T_{air} (i.e. where overlap in T_{air} occurred at midday during both summer and winter; *open woodland*: 23.2–30.8 °C, *riparian*: 21.2–32.2 °C). To calculate the overall midday landscape operative temperature ($LandT_e$), I weighted each microsite's mean midday temperature by its availability in the landscape (from the microsite availability survey), and summed the contributions as follows:

$$LandT_e = \sum_{i=1}^4 p_i \cdot T_{e,i}$$

Where p_i is the proportion of microsite type i , $T_{e,i}$ is the mean midday operative temperature for microsite i , and $i = 1$ (Sun ground), $i = 2$ (Sun tree), $i = 3$ (Shade ground), $i = 4$ (Shade tree).

To test whether midday LandT_e differed between seasons at matched T_{air}, I fitted a multiple linear regression model with LandT_e as the response and an interaction between T_{air} and season as predictors. Separate models were run for open woodland and riparian habitats, each including T_{air}, season, and their interaction as predictors of LandT_e.

Landscape operative temperature trends

To calculate the historical mean LandT_e in each season and habitat for each year, simple linear regression models were used to analyse the relationship between T_e in each microsite type (ground sun, ground shade, tree sun, tree shade) and T_{air} (from on-site weather station). Models were fitted separately for each microsite type, habitat, and season, using data collected during the midday period.

The outputs from these models were then used to predict T_e values for each microsite type by applying the annual mean daily maximum T_{air} (1960–2023 dataset) using the following equation:

$$\hat{T}_{e,i} = \beta_0 + \beta_1 \cdot \text{Mean}T_{\max}$$

Where $\hat{T}_{e,i}$ is the predicted T_e for microsite i , and $i = 1$ (Sun ground), $i = 2$ (Sun tree), $i = 3$ (Shade ground), $i = 4$ (Shade tree); β_0 is the intercept, β_1 is the coefficient estimated from the linear regression, and MeanT_{max} is the annual mean daily maximum T_{air}.

Finally, the predicted values for each microsite ($\hat{T}_{e,i}$) were weighted by their proportion (p_i) in the landscape and combined to calculate the predicted landscape operative temperature as:

$$\widehat{LandT_e} = \sum_{i=1}^4 p_i \cdot \hat{T}_{e,i}$$

As above, p_i is the proportion of microsite type i , $\hat{T}_{e,i}$ is the predicted T_e for microsite i , and $i = 1$ (Sun ground), $i = 2$ (Sun tree), $i = 3$ (Shade ground), $i = 4$ (Shade tree). This calculation allowed us to estimate the historic mean annual $LandT_e$ for each habitat and season between 1960 and 2023, assuming no substantial change in vegetation structure in either habitat over this time (a complex assumption as changes in land use, bush encroachment, and elephant population pressure have each had opposing impacts on vegetation structure in the APNR and KNP over the 63 years included in the analyses, but directional trends are not clear (Peel, Kruger & MacFadyen, 2007; Louw et al., 2021)).

Behaviour

Scan samples were subset to include observations of ground-hornbills made during summer (November, December, January, February) and winter (May, June, July, August). T_{air} and absolute humidity data were obtained from the nearest weather station (range 1km–39 km), and matched to bird observations by time, date, and GPS location. Summer and winter data were analysed using Generalised Linear Mixed Models (GLMMs) with binomial error distribution in the *glmmTMB* package (Brooks et al., 2017). Response variables panting, foraging, shade-seeking, wing drooping, ptiloerection, and location (perched off-ground or on ground) were modelled as a function of air temperature (T_{air}), absolute humidity (humidity) and the interaction between the two. Continuous explanatory variables, T_{air} and humidity were centred and scaled and tested for correlations prior to model fitting, to avoid multicollinearity. Group identity and year were included as random effects. Models including the interaction between air temperature and humidity were compared with all possible nested models, including the null model (random effects only) using Akaike's Information Criteria (AICc) in

the *MuMIn* package (Bartoń, 2020). Models with lowest AICc values were selected as the top models (Harrison et al., 2018) while results from competing models with $\Delta\text{AICc} < 2$ are also reported. Plots were based on the single model with the lowest AICc (Wickham, 2016).

Threshold T_{air} values above which heat avoidance (shade-seeking - *Shade*₅₀), heat dissipation behaviours (Panting - *Pant*₅₀, Wing drooping - *Wing*₅₀, and Ptiloerection - *Ptilo*₅₀) and other behaviours (Foraging - *Forage*₅₀, Off-ground - *Off-ground*₅₀) occurred in more than 50% of observations (*HD*₅₀) were estimated from the coefficients of binomial GLMMs using the *glmmTMB* package (Brooks et al., 2017). This method estimates the T_{air} value at which the response probability reaches 0.5 (50%), holding humidity at its mean when it appeared in the top model. Standard errors for thresholds were obtained using the delta method implemented in the *deltaMethod()* function of the *car* package (Fox, Weisberg & Price, 2025). *HD*₅₀ results are only presented if they fall within the T_{air} range of data collected.

2.4. Results

2.4.1. Long term temperature trends

From 1960 to 2023 annual mean daily maximum T_{air} ranged from 30.1–34.7 °C (mean 32.2 °C) in summer, and from 25.4–29.7 °C (mean 27.2 °C) in winter. There was a 52 % overlap between the distributions of daily maximum T_{air} recorded in summer and winter (Figure 2.2) and this overlap was annually consistent over the six decades of data (Figure A2.4).

Mean daily maximum T_{air} increased significantly in the study site from 1960 to 2023, by 0.03 °C per year in summer (estimate = 0.03 ± 0.007 °C, 95 % CI = [0.01 / 0.04], $r^2 = 0.18$; Figure 2.2) and 0.03 °C per year in winter (estimate = 0.03 ± 0.005 °C, 95 % CI = [0.02 / 0.04], $r^2 = 0.32$; Figure 2.2). No significant trends were apparent in mean daily minimum T_{air} from 1960 to 2023 in summer or winter (Figure A2.5).

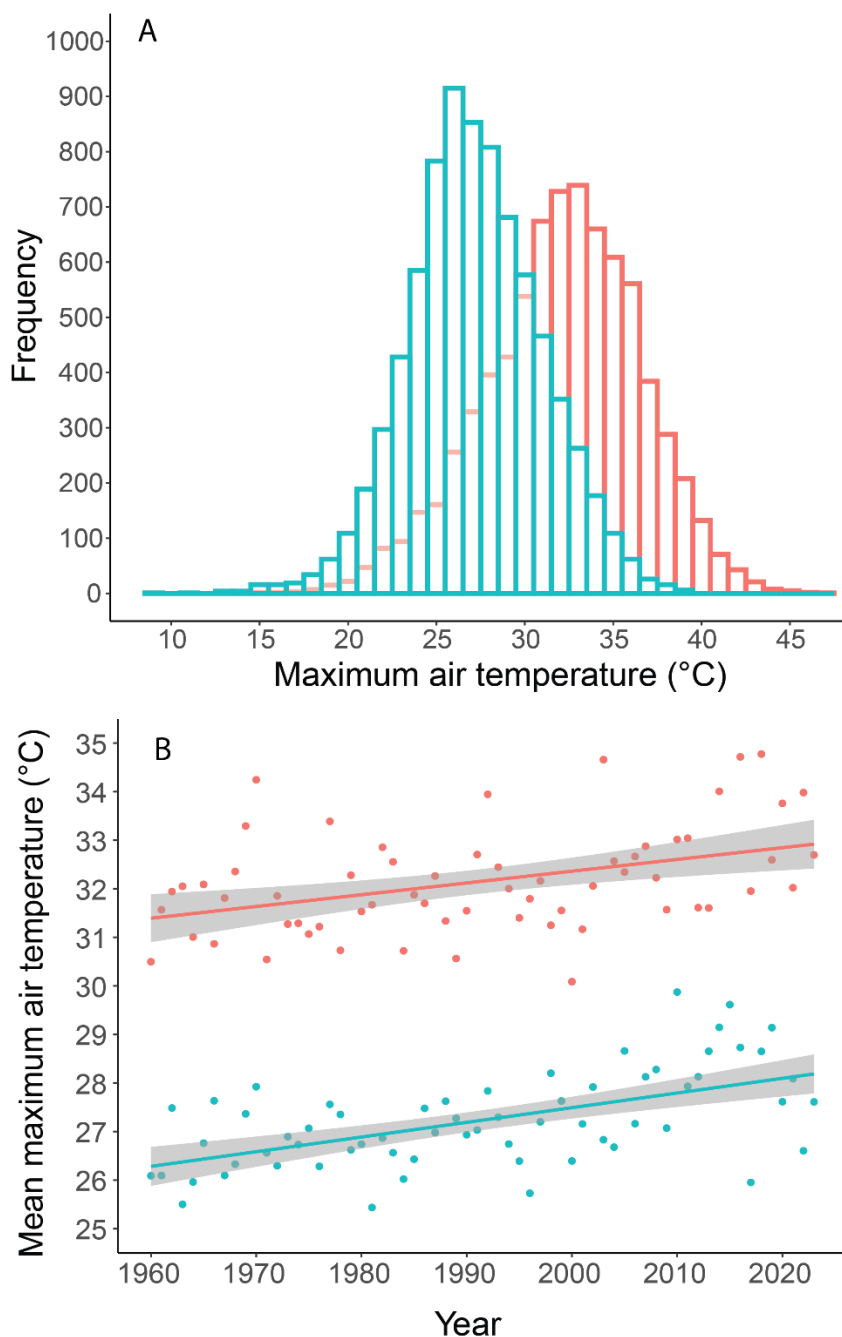


Figure 2.2. (A) Frequency distribution of daily maximum air temperatures (°C) recorded at the Skukuza Weather Station in KNP between 1960 to 2023. The blue bars represent the frequency of recorded daily maximum air temperatures on winter days, while the red bars indicate the frequencies observed during summer, with a 52 % overlap in daily maximum air temperatures between the seasons. (B) Trend in mean daily maximum air temperature over the summer and winter months each year from 1960 to 2023, Skukuza weather station in KNP. Summer data are shown in red and winter data in blue. Observed values are represented by dots, while lines are model predictions with shaded 95% confidence intervals.

2.4.2. Microsites and seasons

During the summer survey, 496 microsites, including ground and tree sites, were identified at the open woodland site and 542 at the riparian site. During winter, 509 microsites were identified at the open woodland site, and 521 identified at the riparian site. GPS accuracy was ± 3 meters, preventing the exact same sampling points being surveyed in both seasons, and resulting in slightly different numbers of potential ground or perch sites for ground-hornbills being recorded.

During midday in summer, 59.8 % of microsites in the open woodland habitat were shaded, while in winter only 28.7 % were shaded. In the riparian habitat, in summer, 63.1 % of microsites were shaded, and 45.4 % in winter. Shade availability was significantly lower in winter than in summer across both habitats ($\chi^2 = 121.17$, $df = 3$, $p < 0.001$). In winter, riparian habitats provided significantly more shade than open woodlands ($\chi^2 = 17.92$, $df = 1$, $p < 0.001$), whereas in summer, shade did not differ significantly between habitats ($\chi^2 = 0.02$, $df = 1$, $p = 0.888$) (Figure 2.3).

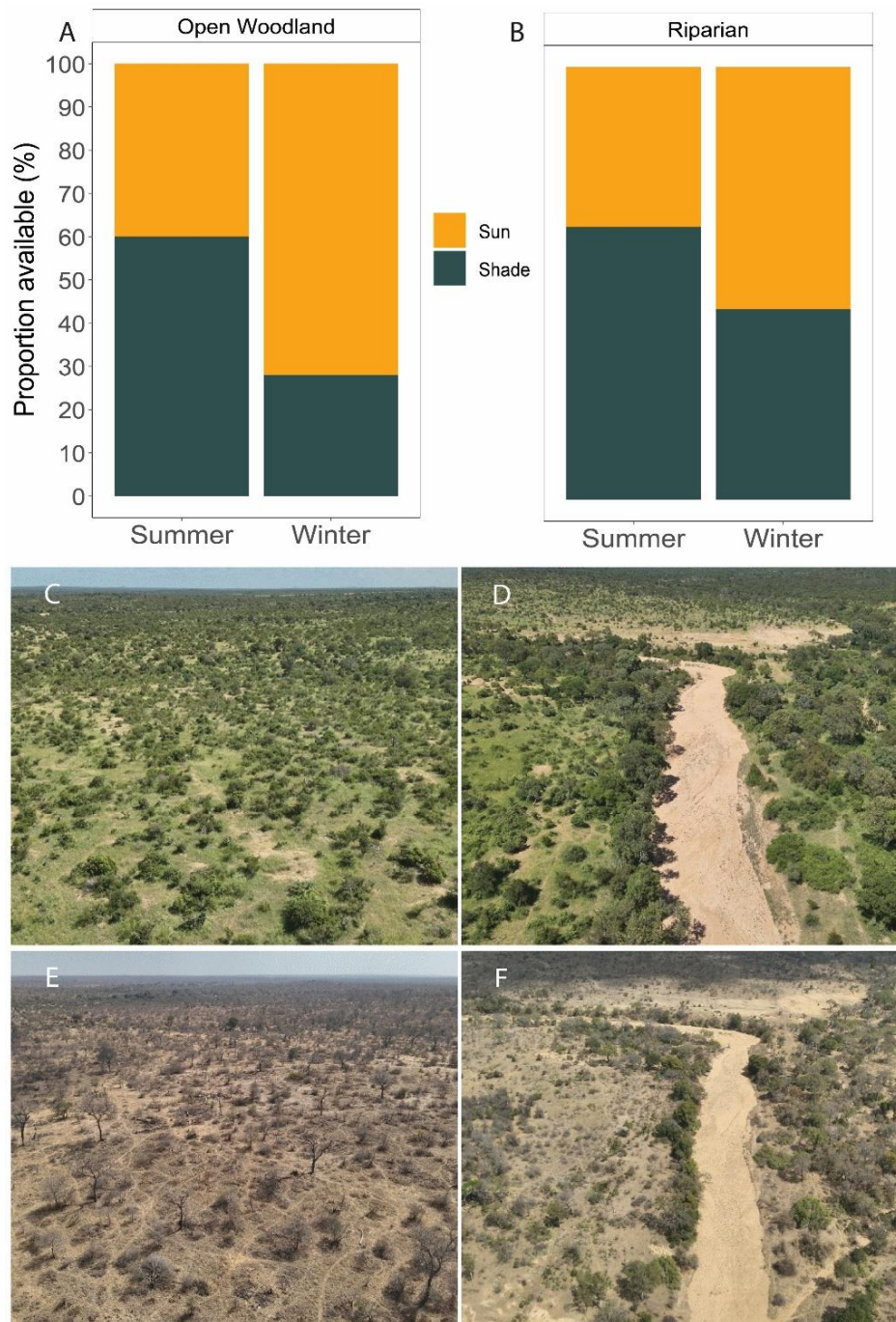


Figure 2.3. The proportion of shaded (grey) and sun-exposed (orange) microsites available to ground-hornbills during summer and winter across two surveyed habitats: open woodland (A) and riparian (B). Drone images of the surveyed woodland habitat in summer (C), and winter (E), and the riparian habitat in summer (D) and winter (F). In summer, both habitats appear lush with green grass and woody vegetation providing shade from leafy canopies. In contrast, winter sees deciduous trees shedding their leaves and grasses dying back, which reduces shade in the landscape and may increase re-radiation of heat from bare ground surfaces. However, the riparian habitat in winter retains some evergreen vegetation, supported by the presence of groundwater, which provides shade.

2.4.3. Landscape operative temperatures

Overall, during the time periods in which black bulb data were collected, midday average LandT_e was higher in summer than winter (open woodland summer: mean T_{air} = 31.7 °C, mean LandT_e = 37.0 °C; and winter: mean T_{air} = 23.2 °C, mean LandT_e = 31.6 °C. Riparian summer: mean T_{air} = 29.6 °C, mean LandT_e = 34.5 °C; and winter: mean T_{air} = 23.8 °C, mean LandT_e = 30.4 °C).

Despite this, at matched T_{air}, LandT_e was significantly higher in winter than summer in both habitats (Figure 2.4). In the open woodland habitat, LandT_e was on average 6.04 ± 0.41 °C higher in winter than summer (95% CI = [5.24 / 6.85]), and the slope of the correlation between T_{air} and LandT_e was significantly steeper in winter (interaction estimate = 1.90 ± 0.36 °C, 95% CI = [1.18 / 2.61]). Results remained similar when one especially cold day was removed from the open woodland dataset (see Table A2.3, Figure A2.8).

In the riparian habitat LandT_e was 3.52 ± 0.27 °C higher in winter than summer (95% CI = [3.00 / 4.06]); but there was no significant difference in the slope of the correlation between T_{air} and LandT_e between seasons (interaction estimate = -0.05 ± 0.31 °C, 95% CI = [-0.67 / 0.56], T_{air} main effect estimate = 6.97 ± 0.24 °C, 95% CI = [6.50 / 7.45]) (see Table A2.3, Figure 2.4).

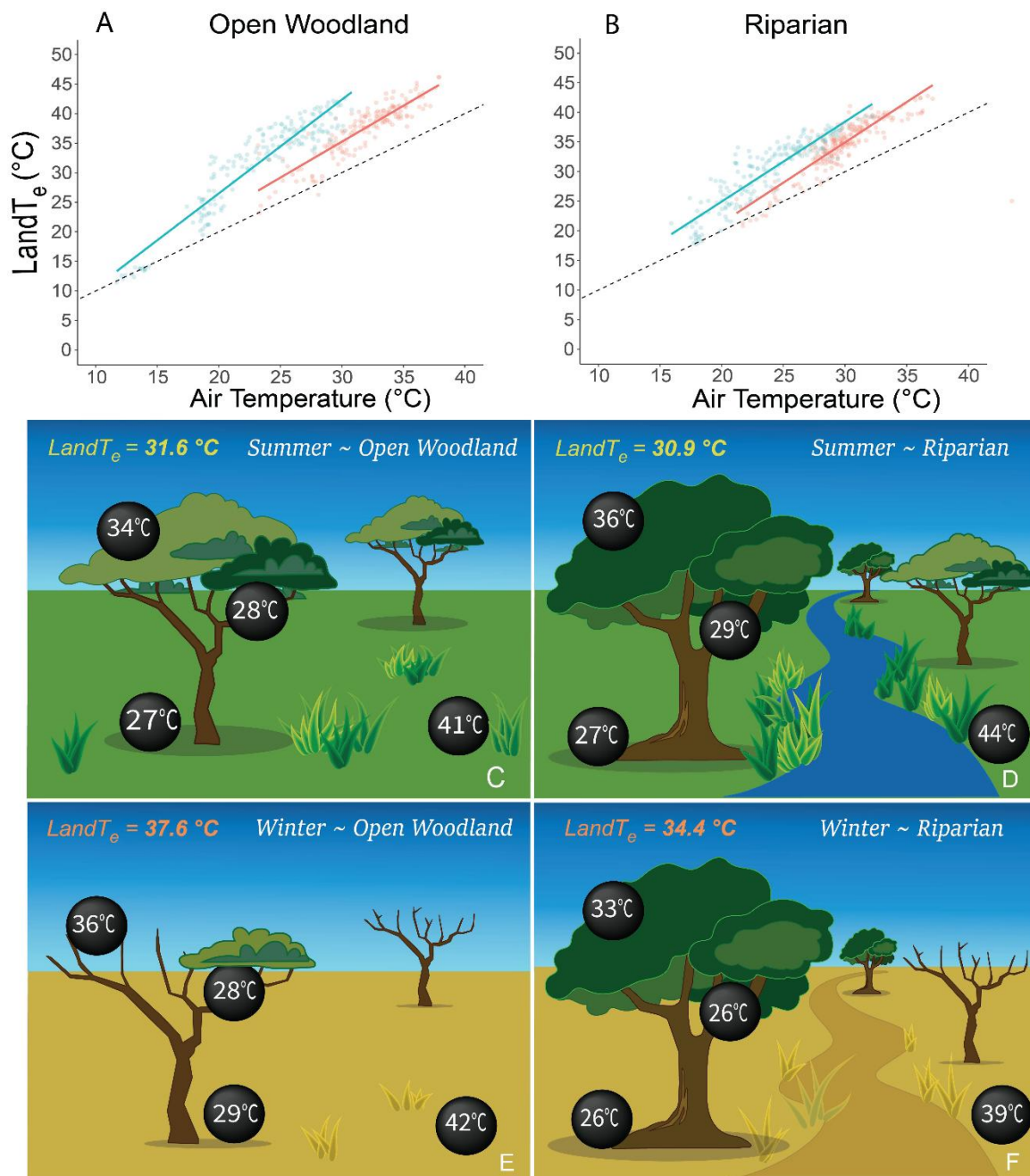


Figure 2.4. Operative temperatures in relation to air temperature across seasons and habitats. (A–B) Linear relationships between T_{air} and T_e at midday in (A) open woodland and (B) riparian habitats. Lines show regressions for summer (red) and winter (blue); the dashed 1:1 line indicates where T_e equals T_{air} . Points represent observed values. (C–F) Schematic representations of mean operative temperatures (black globes) across microsites (Sun ground, Sun tree, Shade ground, Shade tree) at a matched T_{air} of 27°C (the mean overlap between summer and winter observations at midday). (C) Summer, open woodland: mean Land $T_e = 31.6^{\circ}\text{C}$. (D) Summer, riparian: Land $T_e = 30.9^{\circ}\text{C}$. (E) Winter, open woodland: Land $T_e = 37.6^{\circ}\text{C}$. (F) Winter, riparian: Land $T_e = 34.4^{\circ}\text{C}$. At matched T_{air} , the overall landscape operative temperature is higher in winter than summer in both habitats, represented in orange. This is associated with reduced shade availability in the landscape in winter, meaning sun-exposed microsites contribute more heavily to landscape operative temperatures.

Estimated historic LandT_e in the open woodland habitat increased significantly between 1960 and 2023 in summer (estimate = 0.03 ± 0.01 °C per year, 95 % CI = [0.01 / 0.05], $r^2 = 0.19$) and in winter, where the slope was steeper (estimate = 0.05 ± 0.01 °C per year, 95 % CI = [0.03 / 0.07], $r^2 = 0.32$). In recent years, LandT_e has become higher on average in winter than summer (Figure 2.5). In the riparian habitat, estimated LandT_e also significantly increased in both summer (estimate = 0.04 ± 0.01 °C per year, 95 % CI = [0.02 / 0.06], $r^2 = 0.19$) and winter (estimate = 0.04 ± 0.01 °C per year, 95 % CI = [0.03 / 0.06], $r^2 = 0.33$), yet winter LandT_e remained lower than summer (Figure 2.5).

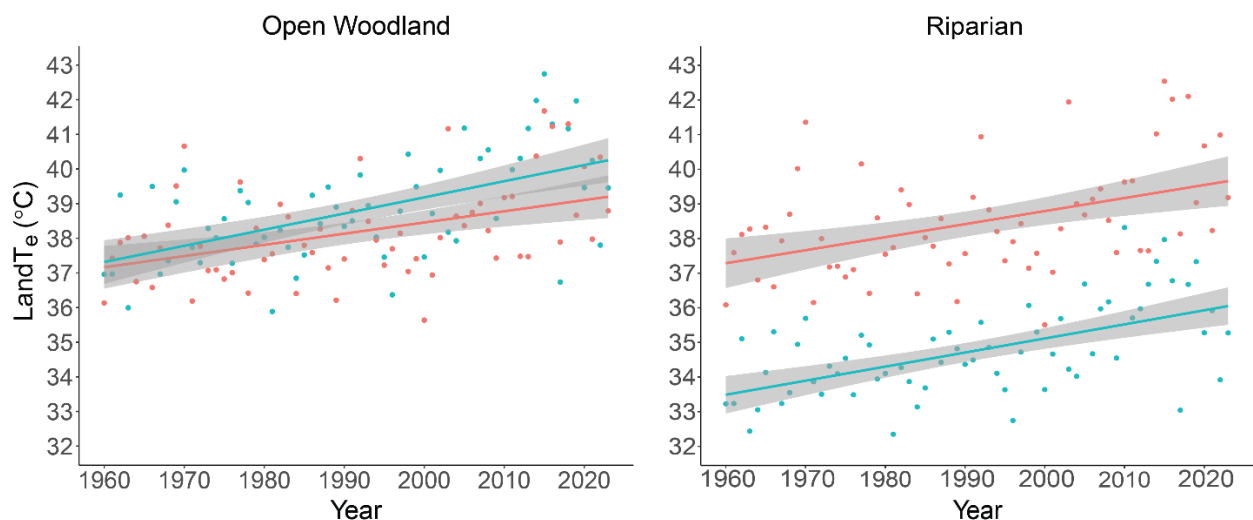


Figure 2.5. Predicted trend in landscape operative temperatures from historic mean maximum daily air temperatures (1960 -2023) in open woodland habitat on the left and riparian habitat on the right, assuming no change in vegetation structure over this time. Summer predicted values are shown in red and winter in blue with shaded 95% confidence intervals.

2.4.4. Thermoregulatory behaviour

A total of 469 behavioural observations of ground-hornbills was recorded in summer and 547 in winter from 2021 to 2023. T_{air} matched to these behavioural observations ranged from 16.2–40.0 °C (mean = 26.5 °C) in summer and 2.1–36.4 °C (mean = 22.2 °C) in winter. Humidity ranged from 8.29 – 24.4 g m⁻³ (mean = 17.0 g m⁻³) in summer and 5.2 – 17.0 g m⁻³ (mean = 11.1 g m⁻³) in winter (Figure A2.9).

Summer

In summer, there was a significant negative relationship between T_{air} and foraging (estimate = -0.31 ± 0.14 , 95% CI = $[-0.57 / -0.04]$, $Forage_{50} = 36.6$ °C; Table A2.5, Figure 2.6) and perching off ground behaviours (estimate = -0.64 ± 0.26 , 95% CI = $[-1.16 / -0.12]$, Table A2.5, Figure 2.6). Heat avoidance behaviour (shade-seeking), and dissipation behaviours (panting, wing drooping and ptiloerection) all increased significantly as T_{air} increased: (*shade-seeking*; estimate = 1.49 ± 0.26 , 95% CI = $[0.98 / 2.01]$, $Shade_{50} = 35.6$ °C), (*panting*; estimate = 1.75 ± 0.25 , 95% CI = $[1.25 / 2.25]$, $Pant_{50} = 36.1$ °C), (*wing drooping*; estimate = 2.10 ± 0.24 , 95% CI = $[1.63 / 2.58]$, $Wing_{50} = 31.8$ °C), (*ptiloerection*; estimate = 2.11 ± 0.24 , 95% CI = $[1.63 / 2.59]$, $Ptilo_{50} = 30.9$ °C) (Table A2.5, Figure 2.6).

Humidity appeared as a main effect and in interaction with T_{air} , in competing models for off ground, shade-seeking, panting, and ptiloerection behaviours (Table 2.1), however the interaction term was not significant in any of the models (Table A2.5). There was a weak significant main effect of humidity in the top model for panting behaviour, where it had a slight negative effect (estimate = -0.71 ± 0.29 , 95% CI: $[-1.27 / -0.14]$, Table A2.5, Figure 2.6, Figure A2.10), and in a competing model for perching off-ground, where it had a slight positive effect (estimate = 0.39 ± 0.19 , 95% CI: $[0.01 / 0.77]$, Table A2.5, Figure A2.10), but the main effect of humidity did not have a significant relationship with any other behaviours (Table A2.5).

Winter

In winter, the relationship between T_{air} and foraging was not significant (estimate = -0.26 ± 0.16 , 95% CI = $[-0.57 / 0.05]$, Table A2.5, Figure 2.6) and the null model appeared in the top model set (Table 2.1). Likewise, although T_{air} appeared in the top model set for shade-seeking and off ground behaviours (Table 2.1), it did not have a significant effect (*shade-seeking*; estimate = 0.19 ± 0.17 , 95% CI = $[-0.15 / 0.53]$; *off ground*; estimate = 0.63 ± 0.76 , 95% CI =

[-0.87 / 21.12]; Table A2.5, Figure 2.6). However, panting, wing drooping and ptiloerection all increased significantly as T_{air} increased in winter (*panting*; estimate = 1.61 ± 0.23 , 95 % CI = [1.16 – 20.06], $Pant_{50} = 31.8$ °C; *wing drooping*; estimate = 2.25 ± 0.31 , 95% CI = [1.61 / 2.83], $Wing_{50} = 32.9$ °C; *ptiloerection*; estimate = 1.55 ± 0.20 , 95% CI = [1.15 / 1.94], $Ptilo_{50} = 31.1$ °C; Table A2.5, Figure 2.6).

Humidity appeared as a main effect in the winter top model sets for shade-seeking, off ground and panting behaviour, and in interaction with T_{air} in the top model set for wing drooping (Table 2.1) but had no significant effects in any of these models (Table A2.5).

Table 2.1. Top (within 2 $\Delta AICc$) general linear mixed models (binomial distribution) for the probability of foraging, shade seeking, location (off ground), panting, wing drooping and ptiloerection in summer and winter. Separate models were fitted for summer and winter observations. The top model for each behaviour in each season is shown in bold.

Behaviour	Season	Model	AICc	$\Delta AICc$	Model Weight
Foraging	Summer	T_{air}	620.5	0.00	0.525
Foraging	Winter	T_{air}	448.9	0.00	0.400
		null	449.7	0.76	0.273
Shade Seeking	Summer	T_{air}	408.4	0.00	0.363
		T _{air} * humidity	408.7	0.26	0.320
		T _{air} + humidity	408.7	0.27	0.317
Shade Seeking	Winter	null	306.0	0.00	0.344
		T _{air}	306.7	0.80	0.230
		T _{air} + humidity	307.3	1.38	0.173
		humidity	307.4	1.43	0.168
Off Ground	Summer	T_{air} * humidity	499.3	0.00	0.353
		T _{air} + humidity	499.5	0.15	0.328
Off Ground	Winter	null	124.0	0.00	0.427
		humidity	125.4	1.34	0.219
		T _{air}	125.6	1.62	0.190
Panting	Summer	T_{air} + humidity	322.4	0.00	0.607
		T _{air} * humidity	323.6	1.20	0.334
Panting	Winter	T_{air}	370.4	0.00	0.603
		T _{air} + humidity	371.9	1.45	0.291
Wing Drooping	Summer	T_{air}	401.4	0.00	0.669
Wing Drooping	Winter	T_{air} + humidity	330.3	0.00	0.405
		T _{air}	330.7	0.40	0.332
		T _{air} * humidity	331.2	0.87	0.263
Ptiloerection	Summer	T_{air} + humidity	426.3	0.00	0.519
		T _{air}	427.6	1.28	0.274
		T _{air} * humidity	428.1	1.84	0.207
Ptiloerection	Winter	T_{air}	421.3	0.00	0.588

Summer: N = 469 observations from 84 groups. Winter: N = 547 observations from 73 groups.

Random terms: group ID and year (3)

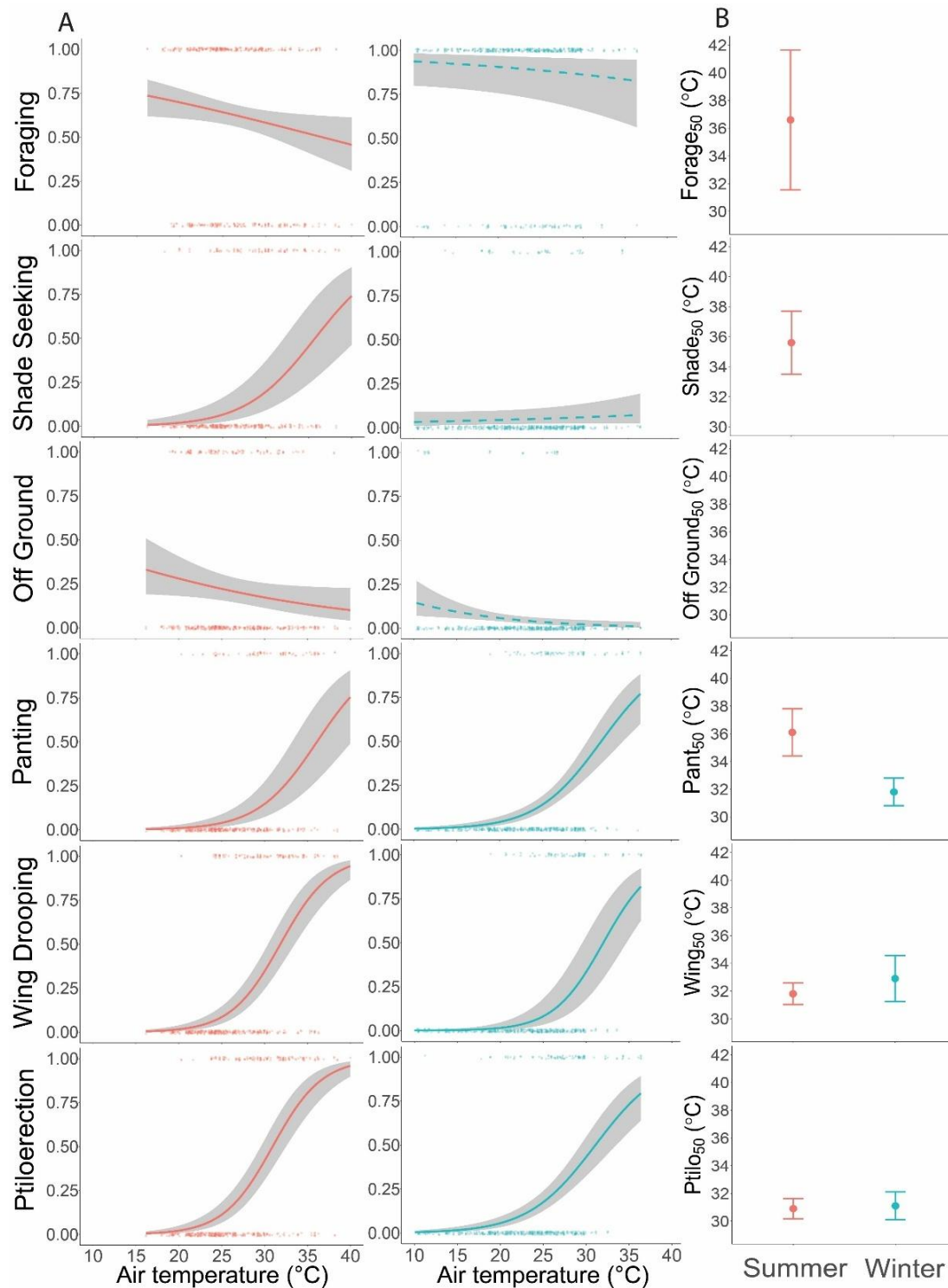


Figure 2.6. Probability of foraging, shade seeking, location (off ground = 1), panting, wing drooping and ptiloerection as a function of air temperature (T_{air}) in summer (red), and winter (blue). A) Presence of behaviour = 1, absence of behaviour = 0. Solid trend lines show predictions from the top logistic regression, where the relationship was significant, while dashed lines are non-significant. $N = 469$ observations from 84 groups in summer and $N = 547$ observations from 73 groups in winter. B) Threshold temperatures ($HD_{50} \pm SE$) estimated from top models, excluding values for Forage_{50} and Shade_{50} (winter) and OffGround_{50} (winter and summer) as values did not fall within T_{air} range of data collected.

2.5. Discussion

My data reveal that terrestrial animals in subtropical savannas face unexpectedly high thermal loads during winter, and that winter temperatures are rising, meaning these thermal loads could become increasingly challenging in future. In the savanna landscape in which this study was conducted, as predicted, reduced shade availability resulted in an overall hotter landscape in winter than summer, for the same T_{air} . In winter, riparian habitat provided more shade, cooler microsites and overall lower landscape operative temperature ($\text{Land}T_e$) than open woodland, highlighting the role of riparian habitats as a critical thermal refuge during this season. Animal behaviour is affected by high temperatures and, as I predicted, ground-hornbills significantly increased heat dissipation behaviours in response to high T_{air} year-round. However, there were seasonal differences observed in the onset of panting behaviour, which occurred at cooler T_{air} in winter than summer. Shade-seeking and reductions in foraging, were only evident in summer, consistent with the expectation that these responses could be constrained in the dry winter, potentially due to limited food forcing ground-hornbills to forage in exposed, hotter microsites, and limited shade availability. The combination of reduced food availability associated with low winter productivity in these systems, and increasingly hot winter $\text{Land}T_e$, are likely to make winters increasingly challenging for subtropical savanna animals as climate change progresses.

The thermal landscape and seasonality

In this system, the thermal landscape is hotter in winter than in summer by $\sim 5^\circ\text{C}$ on days of matched T_{air} , particularly in open woodland habitats, where this difference increases with increasing T_{air} . Such seasonal inversion of thermal conditions is rarely documented, and most existing research comparing seasonal thermal landscapes focuses on temperate regions

(Zellweger et al., 2019; Estevo et al., 2022; John et al., 2024) or urban environments (Liu et al., 2019; Ornelas, Cordeiro & Lameiras, 2023). When averaged over the whole season, winter T_e were cooler across microsites, due to lower average T_{air} , resulting in an overall cooler $LandT_e$. Yet, considerable overlap in daily maximum T_{air} between summer and winter (~52%) means wildlife may experience hotter $LandT_e$ in winter than in summer on more than half of days. Furthermore, over the last six decades, climate change has shifted seasonal temperature extremes, causing average winter mean maximum $LandT_e$ to now surpass summer temperatures in open woodlands, and approach historical summer temperatures in riparian habitats. Hot winter $LandT_e$ is associated with reduced shade quantity and quality in winter, causing sun-exposed microsites to have a greater input into total $LandT_e$ and shaded microsites to buffer heat loads less in winter than in summer (at least in open woodland habitat). Winter $LandT_e$ may be further intensified by reduced grass cover allowing increased reflected radiation from bare ground (Mitchell et al., 2024), and by clearer skies that allow more solar radiation compared to the cloudier summer rainy season. Similar conditions may occur in other subtropical regions with deciduous vegetation and dry winters, as well as in other habitat types, but there is currently a paucity of data from other areas to assess this.

My models of long-term trends in $LandT_e$ assume a constant vegetation structure through time, which may not be the case due to complex interacting factors, including historic bush encroachment (Peel, Kruger & MacFadyen, 2007), ongoing bush encroachment associated with rising CO_2 levels (Hovenden & Williams, 2010; O'Connor et al., 2022), and conservation strategies that promote high elephant densities, which reduce woody cover through browsing and uprooting (Haynes, 2012; APNR, 2023). These factors make it difficult to predict how ongoing changes in vegetation structure may collectively shape the thermal landscape and its buffering capacity under climate change. Future patterns may also be

influenced by intensifying elephant impacts and shifts in fire regimes linked to droughts or management practices (Smit & Prins, 2015).

Seasonal effects of temperature on behaviour

As landscapes heat up globally, wildlife increasingly face thermal challenges that influence how they experience seasonal changes. I found that ground-hornbills engage in heat dissipation behaviours in both summer and winter, and resort to water-costly evaporative cooling (panting) at lower T_{air} in winter than summer. This seasonal difference may reflect that panting is triggered at similar $\text{Land}T_e$ across seasons, which corresponds to lower T_{air} in winter, or that continued foraging at high T_{air} , which occurred in winter (see below), resulted in a need for birds to dissipate additional metabolic heat produced during activity.

Humidity further influences these responses: the probability of panting was slightly lower in summer when humidity was higher, and (in a competing model), ground-hornbills had an increased propensity to perch off ground during more humid periods in summer. However, humidity had no detectable effect on any other behaviours in summer, or on any behaviours in winter. Strong, threshold-driven effects of humidity on evaporative cooling have been reported in trumpeter hornbills *Bycanistes buccinator* (Coulson et al., 2025), where their ability to dissipate heat effectively declined sharply at high humidity (25 g m^{-3}) but not at lower levels ($6\text{--}13 \text{ g m}^{-3}$), suggesting a critical threshold somewhere between 13 and 25 g m^{-3} . Most observed humidity values fell below $\sim 18 \text{ g m}^{-3}$ in this study, suggesting that conditions rarely exceeded a critical threshold at which evaporative cooling or behaviour becomes severely constrained for this species. Thus, humidity does not yet appear to strongly limit thermoregulation in ground-hornbills. However, humidity did appear in top and competing models for many behaviours, despite a general lack of significant effects. Taken together with projected increases in temperature and humidity under climate change (IPCC, 2023), this

suggests such thresholds could be reached in the future, and that rising humidity may pose an incipient threat.

In summer, ground-hornbills tended to rest in shade instead of foraging during high T_{air} , but in winter this was not observed. This suggests that limited food resources during the dry winter might force ground-hornbills to forage even when T_e is high enough to require expenditure of water resources through panting. For species that rely entirely on food for water, like ground-hornbills, this trade-off significantly increases the risk of dehydration. Perhaps to mitigate this, ground-hornbills initiate less water costly non-evaporative cooling behaviours (wing drooping and ptiloerection), before panting, aligning with observations from other non-drinking species (e.g. Chestnut-rumped Thornbill *Acanthiza uropygialis*, Cactus wren *Campylorhynchus brunneicapillus*, Common Fiscal *Lanius collaris subcoronatus*, among others; Smit et al., 2016; Pattinson et al., 2020). Birds were also less often observed off ground in shaded tree canopies at high T_{air} in summer. This is contrary to what was expected, however might be due to detection biases: birds are harder to detect in trees during the day, but easily observed performing territorial calls in trees, which they do at dawn (Middleton, 2022), potentially masking temperature-dependence of off ground behaviour at warmer times of day.

Taken together, our behavioural data suggests that winter is particularly challenging for ground-hornbills, as food and shade are scarce, and they engage more in water-costly evaporative cooling behaviour, which together, likely impacts their body condition (du Plessis et al., 2012; Gardner et al., 2017; van de Ven, McKechnie & Cunningham, 2019). Conversely, in summer, when food is more plentiful, ground-hornbills can afford to rest when it is hot. Similar temperature-driven behavioural shifts have been observed in hoopoe-larks *Alaemon alaudipes*, where experimental food supplementation reduced foraging and increased resting

during high temperatures (Tieleman & Williams, 2002b), demonstrating the role of food limitation in shaping behavioural responses to heat.

Heat during winter can reshape annual life histories by introducing thermal challenges during a season often assumed to provide relief from summer heat. Minimum air temperatures at the study site can drop to $\sim 2^{\circ}\text{C}$ at night in winter, exposing animals to substantially colder conditions than during summer, while microsites can still reach very high daytime temperatures, resulting in greater within-day thermal variability and potentially increased energetic costs associated with thermoregulation. Some studies suggest that warmer winters alleviate cold-related pressures (Gardner et al., 2017; Chukwuka et al., 2021; Osland et al., 2021) and may even allow smaller individuals to survive (Gardner et al., 2011). However, these benefits may be offset by energetic costs, as warmer winters have also been linked to reduced survival in some Australian birds (Gardner et al., 2017). In fairy-wrens, increased mortality was observed under combined summer and winter heat exposure, possibly due to reduced opportunities for recovery between seasons (Lv et al., 2023), and warmer winters reduced dormancy and survival in small hibernating mammals, likely due to higher energy demands from shorter dormant periods (Turbill & Prior, 2015; Falvo, Koons & Aubry, 2019). Even if survival is not directly impacted, observed delays to the onset of breeding in ground-hornbills at this study site following hotter winters (Middleton et al., 2026) highlight that cumulative energetic costs could persist across seasons, and that warmer winters can have significant consequences for summer reproduction.

In the face of increasingly hot winters, animals' capacity to manage their exposure to heat may depend on landscape features in their environment (Sears et al., 2016; van de Ven, McKechnie & Cunningham, 2019; Mitchell et al., 2024). At small spatial scales, habitat heterogeneity can help buffer thermoregulatory costs, as found in lizards (Sears, Raskin & Angilletta, 2011) and birds (Londe et al., 2021; Whyte et al., 2026). Several studies have shown

that animals alter their habitat selection in response to high temperatures, selecting cooler microsites within habitats, and shifting between warmer and cooler habitat patches across the landscape (Bowyer, 2009; van Beest, Van Moorter & Milner, 2012; Carroll, Davis, Elmore & Fuhlendorf, 2015; Mason et al., 2017). Here I found that, at a landscape scale, riparian habitats, though still warmer in winter than in summer at the same T_{air} , were on average 3.2 °C cooler than open woodland habitats in winter, due to more shade and perhaps enhanced cooling from plant evapotranspiration (Tabacchi et al., 1998; Catterall, Lynch, & Jansen, 2012). This suggests that riparian habitats within savanna ecosystems could be important thermal refuges in winter and may become increasingly used by wildlife under future climate conditions especially during this season. This could potentially have consequences for habitat quality: in arid and semi-arid environments like this one, heavy use of water resources by animals can for example result in severe degradation of habitat around water points (Parker & Witkowski, 1999; Rispel & Lendelvo, 2016). Conservation managers need to be aware of the potential for similar effects in riparian areas during winter (even if riverbeds run dry) as animals increasingly seek shade in these areas. Tracking ground-hornbill movements and habitat use was beyond the scope of this study, but future studies should investigate how these, and other large animals, navigate savanna landscapes in response to high temperatures.

2.6. Conclusion

This study reveals that while rising summer temperatures continue to push species to their thermal limits, higher winter temperatures may also pose a previously overlooked threat. With reduced shade availability, associated with deciduous vegetation, winter conditions were hotter than summer at matched air temperatures at our study site. These hot conditions increased thermal challenges for ground-hornbills, which showed seasonal variation in their foraging and thermoregulatory behaviours. Taken together with prior data showing later breeding after hot

winters in this species (Middleton et al., 2026), this suggests that high winter temperatures, combined with reduced food availability in winter, may negatively impact body condition and fitness. These results have important implications for many other large terrestrial avian and mammalian species that inhabit subtropical savannas, and potentially other ecosystems with low vegetation density. Understanding how animals respond to increasingly constrained thermal landscapes through shifts in activity patterns and habitat use, and the impacts on fitness, is a key research priority.

Our results also show that riparian habitats may offer critical thermal refuge during winter in savanna landscapes and should therefore be a focus for conservation management, as they are likely to become increasingly important for wildlife thermoregulation. However, these habitats face growing degradation risks in winter from human use, herbivory, fire, and drought, (O'Connor & Page, 2014; Smit & Prins, 2015; Osborne et al., 2018), potentially intensifying resource competition and altering species interactions (Shepard et al., 2022). In regions where ecotourism funds conservation, such as APNR and KNP, riparian habitats are frequently developed for roads, lodging, and recreation. Managers should therefore develop these areas sensitively and prioritise the protection of woody vegetation to preserve their value as thermal refuges for wildlife in warming winters.

2.7. Appendix to Chapter 2

Study site, survey location and location of weather station for historic climate data

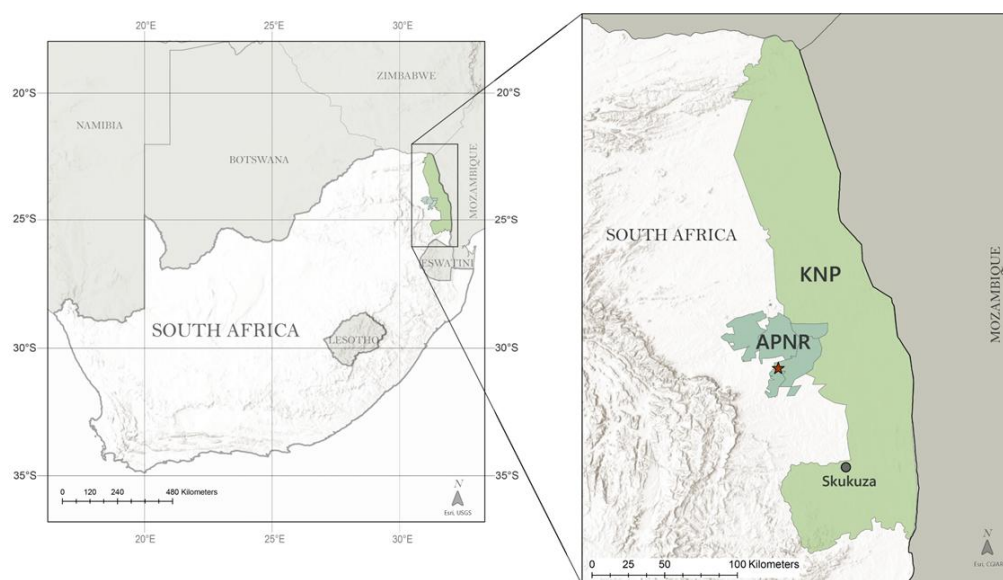


Figure A2.1. Map of the study site. The study site is located in the Northeast of South Africa in the Associated Private Nature Reserves (APNR) and Kruger National Park (KNP). The location where the black bulbs were deployed and where the microsite survey was conducted is marked by a red star in APNR. Location of Skukuza in KNP, from where the long-term climate data derives, is also shown on the map. Observation data on ground-hornbills were collected across the entire study region spanning both APNR and KNP, therefore long-term climate data from Skukuza are representative of conditions experienced by the study population. Maps were created using ArcGIS® software by Esri.

Confirming the representative nature of vegetation plots used to estimate shade availability in open woodland and riparian habitats

To assess whether the 1 km × 1 km plots used to quantify shade availability (hereafter “ground-truthed focal plots”) were representative of open woodland and riparian habitats across the study area, grayscale reflectance values from satellite imagery were compared with those from 110 randomly selected 1 km × 1 km plots distributed throughout the landscape in each habitat type. Representativeness was evaluated using dark-pixel grayscale metrics, which indicate areas of low reflectance associated with greater canopy cover and thus provide a proxy for

shade availability. Features such as open water from rivers or dams, dark soils, or burn scars appear can also appear as dark pixelated areas with low reflectance in the satellite imagery, but do not represent vegetated shade. NDVI (an index that provides a measure of vegetated versus non-vegetated surfaces based on spectral reflectance) was therefore used to automatically identify and remove these features from estimations of shade availability in each plot.

First, the grayscale imagery for the ground-truthed focal plots used in this study were identified using Google Earth Engine for both summer and winter days, as near as possible to the dates in February and July 2023 when ground surveys of the plots were carried out. Maximum cloud coverage was set to 20% (this was the lowest cloud-cover constraint that allowed for imagery to be obtained from all the plots while retaining sufficient coverage for analyses).

Second, 110 additional plots each for open woodland areas and riparian areas, were identified using ArcGIS Pro, by first delineating habitat types using a combination of available vegetation maps (most recent of which were made in 2005), updated with modern satellite imagery and our own on-the-ground knowledge of the study area, and then randomly selecting the plots (along a similar latitude) as follows:

For open woodland habitats: I started with a georeferenced vegetation map, then, using modern satellite imagery and our knowledge of the area, visually excluded areas dominated by dense mopane veld (a habitat type not commonly used by ground-hornbills; Wyness, 2011), as well as riparian areas and dams (many of which are not comprehensively mapped), then randomly selected plot locations from the remaining area (Figure A2.2).

For riparian habitats: substantial new infrastructure development has occurred since the maps available were made. I therefore started with the mapped riparian corridors, then excluded the new infrastructure along them, relying on visual assessment of satellite images and our on-

the-ground knowledge of the locations of riverside lodge developments etc. Plot locations were then selected at random points along each river in areas without infrastructure (Figure A2.2).

The coordinates of the plot locations for the open woodland and riparian habitats were then exported from ArcGIS Pro and imported into Google Earth Engine where the grayscale imagery for all additional plots for the summer and winter months were overlaid. Unfortunately, no imagery from February 2023 was available due to mostly cloudy weather, and imagery from March 2023 were therefore used in the analyses for summer. For winter, rainfall and cloud cover is uncommon, and imagery from July was used which matched exact dates over which the ground surveys were conducted.

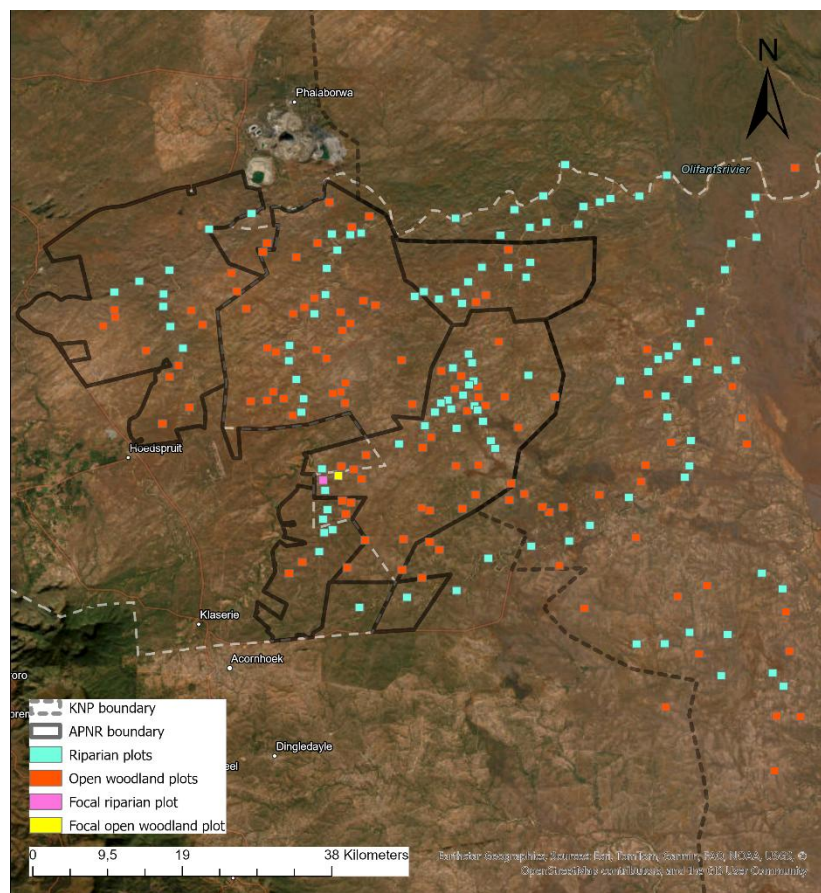


Figure A2.2. Map of riparian and open woodland plot locations within the APNR and Kruger National Park (along a similar latitude). The yellow square indicates the ground-truthed focal open woodland plot, while the purple square represents the riparian plot. Red squares represent the identified open woodland plots, and blue squares represent the identified riparian plots.

Third, the proportion of dark pixels within the grayscale imagery of each plot was calculated, once dark areas identified using NDVI as not due to vegetation were removed. Each grayscale image provides a range of darkness, quantified along a continuous gradient of black to white, that indicates different levels of reflectance, which can be used to provide a rough estimation of shade. However, to calculate the proportion of shade, a threshold needed to be set along this black-to-white gradient, in order to calculate the proportion based on the number of pixels above and below this threshold. In this study, the threshold values were determined by matching the proportions of shade from the satellite imagery of the ground-truthed focal plots, with the ground-truthed shade data collected in the field. For example, the proportion of shade surveyed in the field from the ground-truthed focal open woodland plot during winter was 0.287 (28.7%); therefore, the threshold for that plot was set to 0.795 on a unitless grayscale reflectance scale (0-1), as this produced the nearest proportion of pixels above the threshold (i.e. nearest to 0.287, indicating shade) to that of the ground-truthed shade data. Separate thresholds for each season and habitat were used due to the substantial seasonal variation in reflectance between summer and winter, and between open woodland and riparian areas. It is important to note, however, that there is some expected difference between the ground-truthed shade availability and the proxied shade cover identified through the imagery. This is due to the ground-truthed focal plot surveys being conducted on a three-dimensional scale, whereas the imagery only provides a two-dimensional scale.

Last, the thresholds determined from the ground-truthed focal plot imagery were then used to calculate the proportions of shade in the 110 additional open woodland and 110 riparian plots during summer and winter. These proportions were plotted against each season and habitat (Figure A2.3) to demonstrate that the focal plots used were valid representations of the overall landscape described in the main section of this chapter: in all cases the focal

plots' proportion of shade fell within 1 standard deviation of the mean of the 110 randomly selected plots for that habitat type.

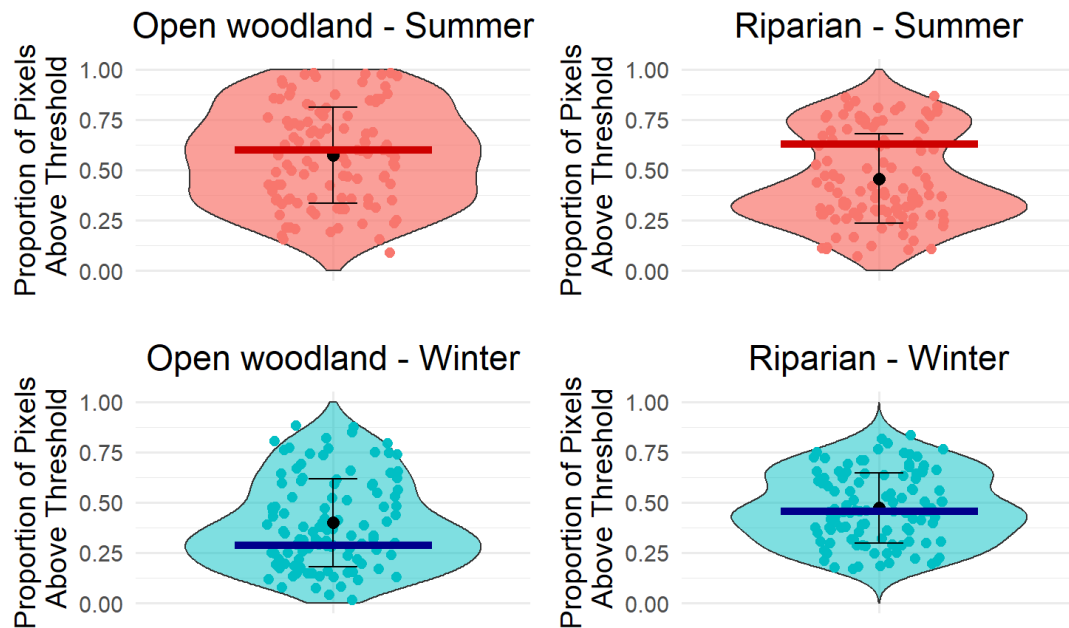


Figure A2.3. Violin plots indicating the grayscale proportions of pixels (shade) above the set thresholds for open woodland and riparian habitats in summer (in red) and winter (in blue). Each point represents the calculated proportion of shade within a plot. The dark red and blue lines indicate the proportions of shade calculated from imagery of the focal plots used in the survey. The black dots in each violin plot indicate the mean and the bars indicate the standard deviation from the mean.

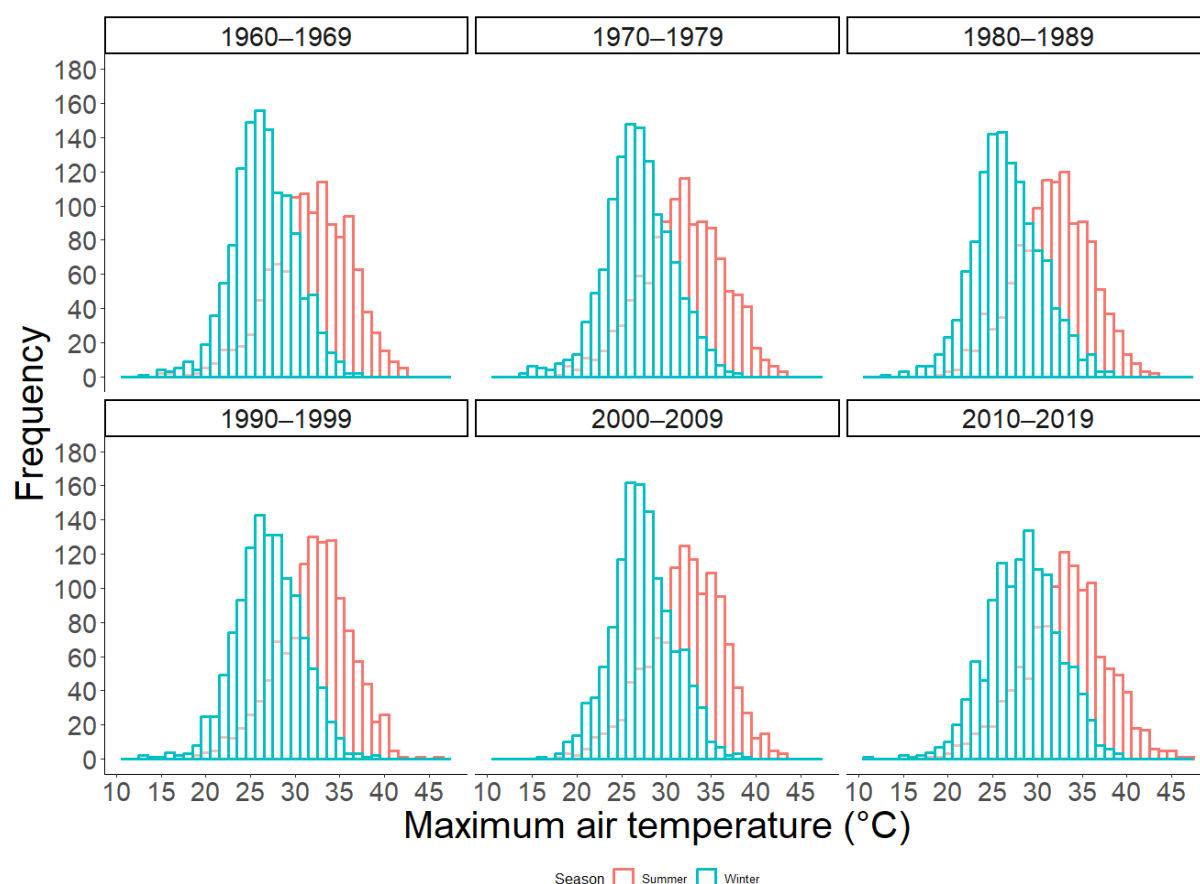
Historic climate data

Figure A2.4. Histogram showing the frequency distribution of maximum T_{air} (°C) recorded at the Skukuza Weather Station (SAWS) split into decades from 1960 - 2019. The blue bars represent the frequency of recorded air temperatures on winter days, while the red bars indicate the frequencies observed during summer. Histograms show that the high percentage overlap in T_{air} during summer and winter in the full dataset is reflected within each decade and is not simply a result of winters warming faster than summers.

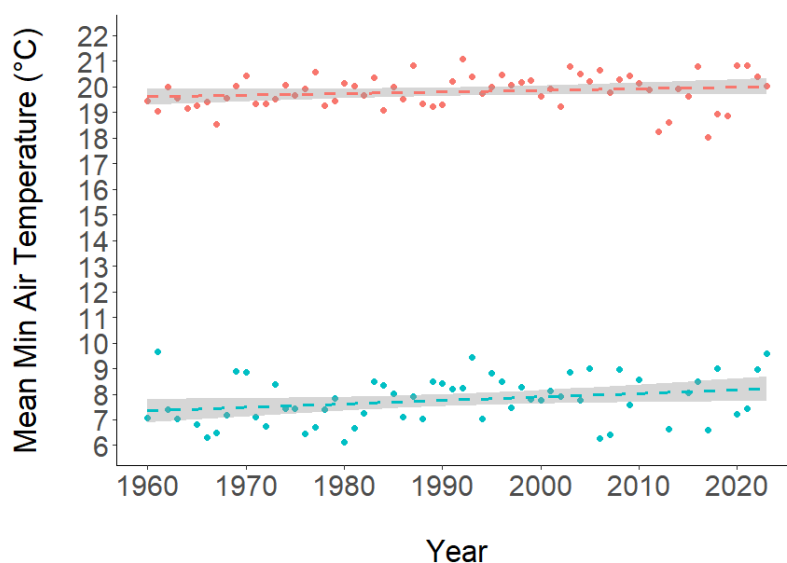


Figure A2.5. Trend in annual daily mean minimum air temperature (°C) over the summer and winter months each year from 1960 to 2023, from Skukuza Weather Station, with summer data shown in red and winter data in blue. Observed values are represented by dots, while lines are the predicted values with shaded 95% confidence intervals. There were no significant trends in yearly mean min T_{air} in summer (estimate = 0.006, SE = 0.004, 95 % CI = [- 0.003 / 0.015], r^2 = 0.03) or winter (estimate = 0.002, SE = 0.008, 95 % CI = [- 0.015 / 0.018], r^2 = 0.001).

Operative temperatures

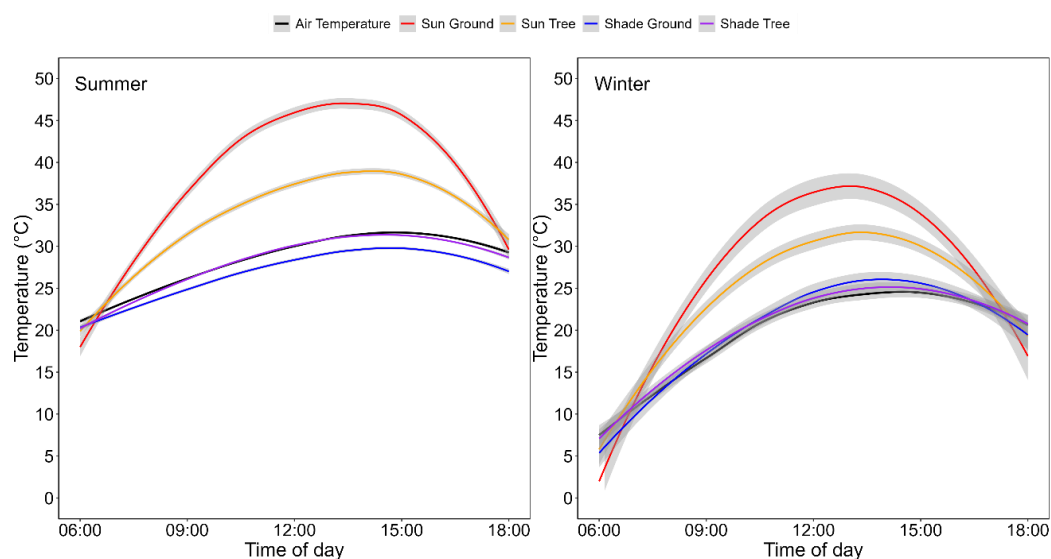


Figure A2.6. Mean operative temperature (T_e) in four microsites and air temperature (T_{air}) during summer (left) and winter (right) as a function of time of day. Data from open woodland and riparian sites were averaged together. Summer T_e and T_{air} are shown on the left and winter on the right. Sun ground (red); Sun tree (yellow); Shade ground (blue); Shade tree (purple); T_{air} (black). The hottest period of the day was between 11:00 – 14:00.

At midday (11:00-14:00), mean operative temperatures (T_e) were significantly higher in summer than winter across all microsites in both habitats: open woodland; *sun ground* (estimate = 11.7 °C, $t(339) = 13.4$), *sun tree* (estimate = 8.5 °C, $t(313) = 12.2$), *shade ground* (estimate = 5.4 °C, $t(300) = 11.2$), *shade tree* (estimate = 7.5 °C, $t(314) = 16.3$). Riparian; *sun ground* (estimate = 9.3 °C, $t(425) = 13.0$), *sun tree* (estimate = 6.8 °C, $t(425) = 12.1$), *shade ground* (estimate = 3.2 °C, $t(317) = 9.8$), *shade tree* (estimate = 5.7 °C, $t(391) = 16.4$) (all $p < 0.001$, Table A2.1, Figure A2.7).

However, at matched air temperatures (where overlap occurred at midday during summer and winter; *open woodland*: 23.2–30.8 °C, *riparian*: 21.2–32.2 °C), the pattern reversed in two microsites. In open woodland, mean T_e was significantly higher in winter than in summer in *sun tree* (estimate = 1.8 °C, $t(94) = -3.15$), and *shade ground* (estimate = 2.0 °C, $t(130) = -6.24$) microsites, while there was no significant seasonal difference in sun ground and shade tree microsites. In riparian habitat, mean T_e remained higher in summer than winter across all microsites (Table A2.2, Figure A2.7).

Table A2.1. Summary of Welch's two sample t-test results comparing seasonal mean operative temperatures (T_e) at midday (11:00–14:00) in each microsite in open woodland and riparian habitat. Statistically significant differences are shown in bold.

Habitat	Microsite	Season	Mean T_e (°C)	SD	Estimate (°C)	DF	T - value	P- value	95% CI
Open Woodland	Sun	Summer	47.2	7.0	11.71	339	13.4	<0.001	9.9 / 13.4
	Ground	Winter	35.49	9.4					
	Sun Tree	Summer	39.17	5.0	8.53	313	12.2	<0.001	7.16 / 9.90
		Winter	30.64	8.0					
	Shade	Summer	30.28	3.22	5.41	300	11.2	<0.001	4.46 / 6.36
	Ground	Winter	24.87	5.62					
	Shade Tree	Summer	31.17	3.28	7.53	314	16.3	<0.001	6.62 / 8.44
		Winter	23.64	5.26					
Riparian	Sun	Summer	45.15	7.6	9.33	425	13.0	<0.001	7.92 / 10.75
	Ground	Winter	35.82	7.3					
	Sun Tree	Summer	36.92	5.89	6.76	425	12.1	<0.001	5.67 / 7.86
		Winter	30.16	5.68					
	Shade	Summer	27.74	2.43	3.2	317	9.8	<0.001	2.74 / 24.54
	Ground	Winter	24.54	4.02					
	Shade Tree	Summer	30.06	3.22	5.6	391	16.4	<0.001	4.95 / 6.30
		Winter	24.41	3.83					

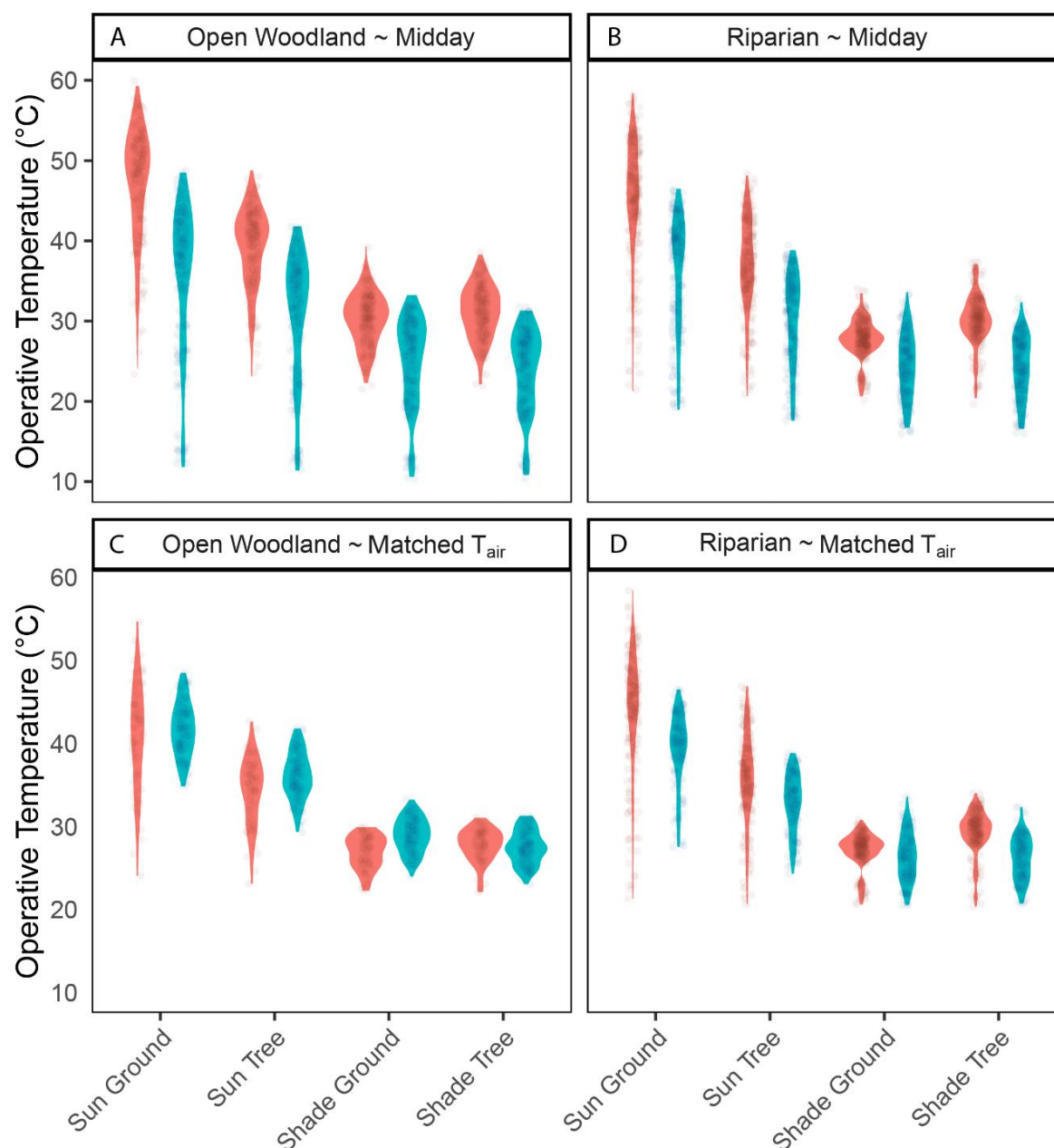


Figure A2.7. Violin plots showing the range of operative temperatures (T_e) recorded in (A) open woodland and (B) riparian habitats during midday (11:00 – 14:00), and at midday matched T_{air} (where overlap occurred at midday during summer and winter; *open woodland*: 23.2–30.8 °C, *riparian*: 21.2–32.2 °C) for (C) open woodland and (D) riparian habitats. Summer temperatures are in red, and winter temperatures in blue with jittered points overlaying the violin plots showing the recorded temperature data.

Table A2.2. Summary of Welch's two sample t-test results comparing seasonal mean operative temperatures (T_e) at matched T_{air} at midday in each microsite in open woodland and riparian habitat.

Statistically significant differences are shown in bold.

Habitat	Microsite	Season	Mean T_e (°C)	SD	Estimate (°C)	DF	T - value	P- value	95% CI
Open Woodland	Sun	Summer	40.8	6.6	0.9	78	- 1.04	0.301	- 2.72 / 0.851
	Ground	Winter	41.7	3.3					
	Sun Tree	Summer	34.3	4.1	1.8	94	- 3.15	0.002	- 3.06 / - 0.69
		Winter	36.1	2.9					
	Shade	Summer	26.9	2.0	2	130	- 6.24	<0.001	- 2.66 / -1.38
	Ground	Winter	28.9	2.1					
	Shade	Summer	27.7	2.0	0.2	127	0.81	0.422	- 0.38 / 0.89
	Tree	Winter	27.5	2.0					
Riparian	Sun	Summer	43.7	7.4	0.7	329	6.98	<0.001	3.26 / 5.82
	Ground	Winter	39.2	4.6					
	Sun Tree	Summer	35.7	5.6	2.8	332	5.79	<0.001	1.89 / 3.84
		Winter	32.9	3.6					
	Shade	Summer	27.1	2.1	0.7	247	2.58	0.001	0.17 / 1.30
	Ground	Winter	26.4	2.9					
	Shade	Summer	29.2	2.7	3	315	10.2	<0.001	2.40 / 3.55
	Tree	Winter	26.2	2.6					

Landscape operative temperatures

Table A2.3. Linear model estimates for the relationship between LandT_e and T_{air} at midday in the open woodland habitat, riparian and habitats combined, with interaction between season and T_{air} . Estimates, standard errors (SE), 95% confidence intervals (CI), and p-values are shown for each term in the model. Open woodland models are shown for the full dataset and with one cold day removed.

Habitat	Model	Variable	Estimate	SE	95 % CI	P Value
Open Woodland	T_{air}^* Season	T_{air}	6.23	0.30	5.64 / 6.83	<0.001
		Season (winter)	6.04	0.41	5.24 / 6.85	<0.001
		$T_{\text{air}}^* \text{ Season}$	1.90	0.36	1.18 / 2.61	<0.001
Open Woodland (cold day removed)	T_{air}^* Season	T_{air}	6.23	0.30	5.65 / 6.81	<0.001
		Season (winter)	5.75	0.40	4.95 / 6.55	<0.001
		$T_{\text{air}}^* \text{ Season}$	0.97	0.39	0.19 / 1.74	0.014
Riparian	T_{air}^* Season	T_{air}	6.97	0.24	6.50 / 7.45	<0.001
		Season (winter)	3.52	0.27	3.00 / 4.06	<0.001
		$T_{\text{air}}^* \text{ Season}$	- 0.05	0.31	- 0.67 / 0.56	0.861
Combined	T_{air}^* Season	T_{air}	6.67	0.19	6.28 / 7.05	<0.001
		Season (winter)	4.85	0.24	4.38 / 5.33	<0.001
		$T_{\text{air}}^* \text{ Season}$	0.88	0.25	0.39 / 1.36	<0.001

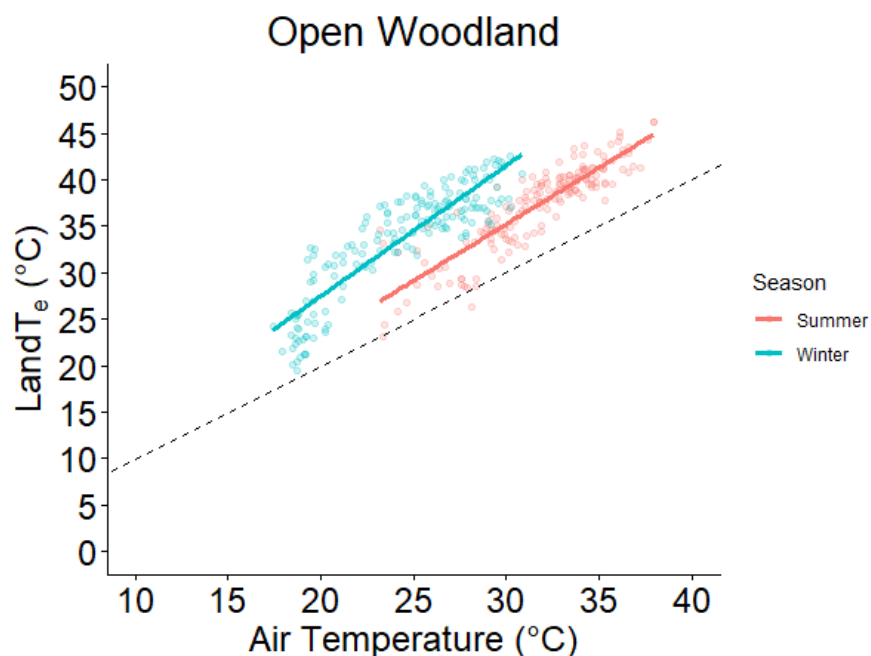


Figure A2.8. Linear relationships between T_{air} and T_e at midday in open woodland with one cold day removed. Lines show regressions for summer (red) and winter (blue); the dashed 1:1 line indicates where T_e equals T_{air} .

Thermoregulatory behaviour.

Table A2.4. Description of the explanatory variables used within different models for foraging, location, heat dissipation and heat avoidance behaviours.

Type	Variable (binary)	Explanation
Response	Sun / Shade (0 / 1)	Whether bird was in the sun or shade
	Not Foraging / Foraging (0 / 1)	Whether bird was foraging or not
	Ground / Off Ground (0 / 1)	Whether bird was on ground or off ground (perched)
	Not Panting / Panting (0 / 1)	Whether bird was panting or not
	Not Ptiloerection / Ptiloerection (0 / 1)	Whether ptiloerection of feathers was observed or not.
	Not Wing Drooping / Wing Drooping (0 / 1)	Whether bird was observed wing drooping or not.
Explanatory	T _{air}	Air temperature (°C) (continuous)
	Humidity	Absolute humidity (g m ⁻³) (continuous)
Random	Group identity	The name / identity of the group
	Year	The year in which behaviour was observed

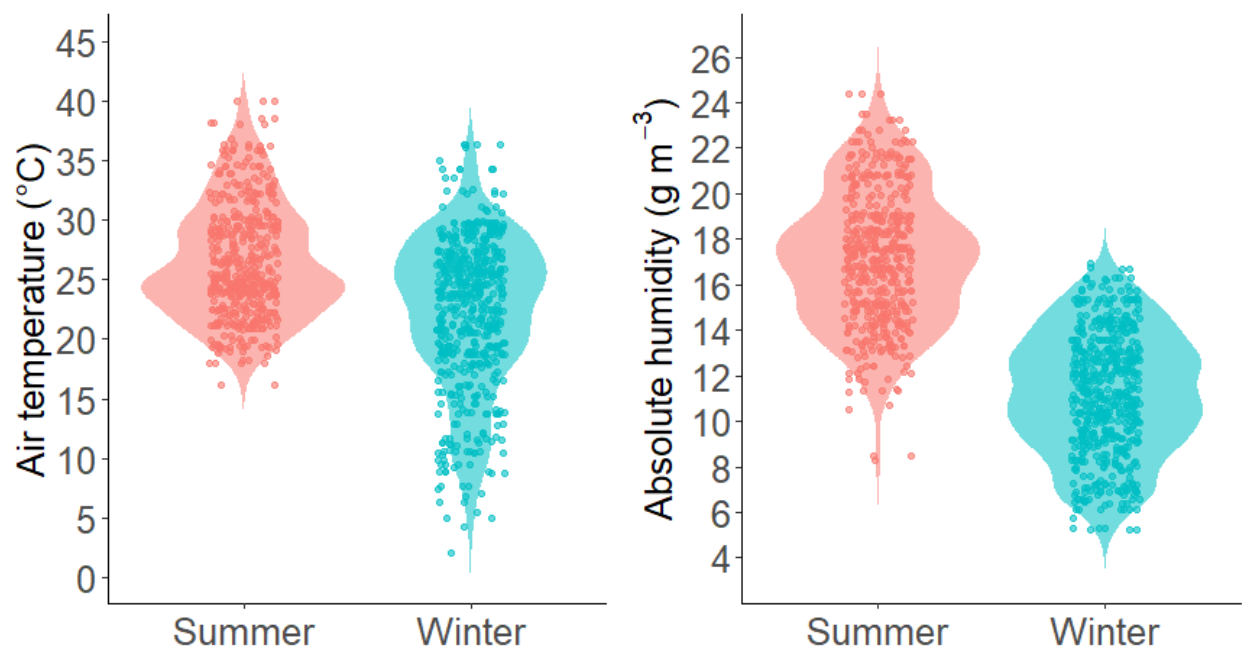


Figure A2.9. Air temperature (°C; left), and absolute humidity (g m⁻³; right), matched to the behavioural observations of ground-hornbills. Summer is shown in red, and winter is shown in blue, with jitter points overlaying violin plots showing the actual data point.

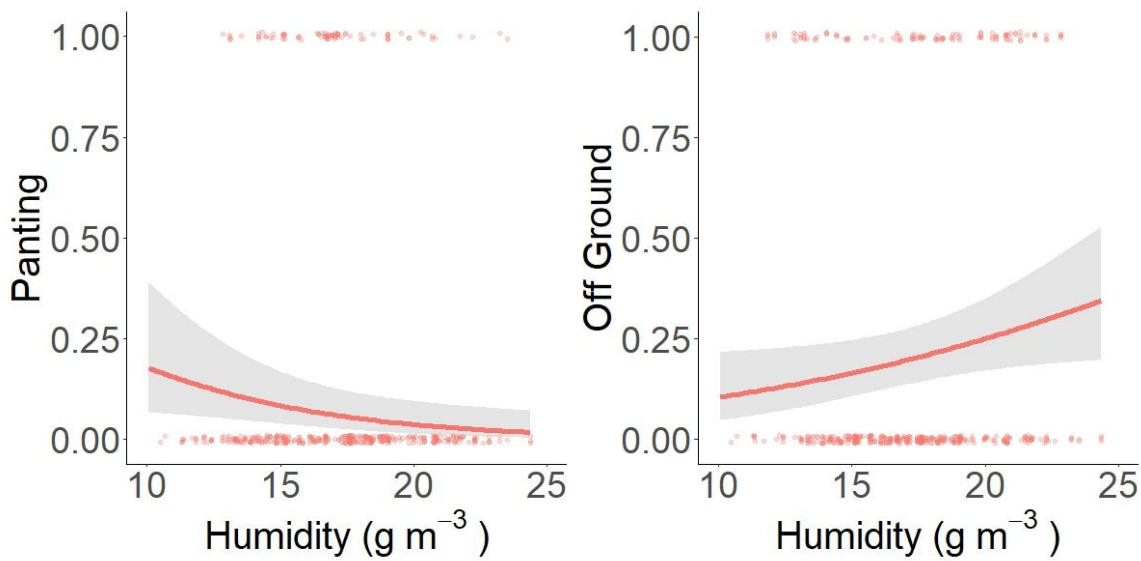


Figure A2.10. Probability of panting (A) and off ground (B) behaviour as a function of absolute humidity (g m^{-3}) in summer. Presence of behaviour = 1, absence = 0. The trend lines show predicted probabilities from logistic regression models. Panting predictions are based on the top-ranked model, in which humidity was a significant predictor, whereas off-ground behaviour predictions are derived from a competing model that also identified humidity as a significant predictor. Shaded areas represent 95% confidence intervals.

Table A2.5. All competing models ($< 2 \Delta AIC$), with factors predicting behaviours (foraging, shade seeking, off ground, panting, wing drooping and ptiloerection in summer and winter, estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Models in bold are the top models and the variables in bold are significant with 95 % CI that do not cross zero. HD_{50} values and standard error (SE) based on the top model for heat avoidance and heat dissipation behaviours where temperatures were biologically relevant are shown.

Behaviour	Season	Model	Variable	Estimate	SE	95 % CI	P Value	HD_{50}
Foraging	Summer	T_{air}	T_{air}	- 0.31	0.14	- 0.57 / - 0.04	0.024	36.6 °C ± 5.1
Foraging	Winter	T_{air}	T_{air}	- 0.26	0.16	- 0.57 / 0.05	0.101	
Shade-Seeking	Summer	T_{air}	T_{air}	1.49	0.26	0.98 / 2.01	<0.001	35.6 °C ± 2.1
		$T_{air} * \text{humidity}$	T_{air}	1.16	0.34	0.50 / 1.83	<0.001	
			humidity	0.02	0.33	- 0.62 / 0.66	0.952	
			$T_{air} * \text{humidity}$	0.54	0.38	- 0.20 / 1.28	0.150	
		$T_{air} + \text{humidity}$	T_{air}	1.49	0.27	0.97 / 2.02	<0.001	
Shade-Seeking	Winter		humidity	0.33	0.25	- 0.16 / 0.83	0.188	
		T_{air}	T_{air}	0.19	0.17	- 0.15 / 0.53	0.275	
		$T_{air} + \text{humidity}$	T_{air}	0.26	0.18	- 0.09 / 0.61	0.152	
			humidity	- 0.36	0.30	- 0.95 / 0.23	0.235	
Off Ground	Summer		humidity	- 0.22	0.28	- 0.77 / 0.34	0.446	
		$T_{air} * \text{humidity}$	T_{air}	- 0.64	0.26	-1.16 / -0.12	0.015	
			humidity	0.27	0.21	- 0.13 / 0.68	0.189	
			$T_{air} * \text{humidity}$	0.42	0.28	- 0.13 / 0.97	0.137	
Off Ground	Winter	$T_{air} + \text{humidity}$	T_{air}	- 0.38	0.19	- 0.75 / - 0.01	0.05	
			humidity	0.39	0.19	0.01 / 0.77	0.05	
		humidity	humidity	0.63	0.76	- 0.87 / 2.12	0.412	
		T_{air}	T_{air}	- 0.26	0.40	-1.04 / 0.53	0.521	

Behaviour	Season	Model	Variable	Estimate	SE	95 % CI	P Value	HD ₅₀
Panting	Summer	T_{air} + humidity	T_{air}	1.75	0.25	1.25 / 2.25	<0.001	36.1 °C ± 1.7
			humidity	-0.71	0.29	-1.27 / - 0.14	0.013	
		T _{air} * humidity	T_{air}	1.99	0.38	1.25 / 2.74	<0.001	
			humidity	- 0.47	0.39	- 1.23 / 0.28	0.222	
Panting	Winter	T_{air}	T_{air}	1.61	0.23	1.16 / 2.06	<0.001	31.8 °C ± 1.0
			T_{air}	1.60	0.22	1.15 / 2.05	<0.001	
		T _{air} + humidity	humidity	- 0.16	0.21	- 0.58 / 0.26	0.444	
			humidity	- 0.16	0.21	- 0.58 / 0.26	0.444	
Wing Drooping	Summer	T_{air}	T_{air}	2.10	0.24	1.63 / 2.58	<0.001	31.8 °C ± 0.77
Wing Drooping	Winter	T_{air} + humidity	T_{air}	2.25	0.31	1.61 / 2.83	<0.001	32.9 °C ± 1.66
			humidity	- 0.41	0.26	- 0.92 / 0.11	0.125	
		T _{air}	T_{air}	2.22	0.31	1.61 / 2.82	<0.001	
			T_{air}	1.86	0.44	1.00 / 2.72	<0.001	
Ptiloerection	Summer	T_{air} + humidity	T_{air}	2.11	0.24	1.63 / 2.59	<0.001	30.9 °C ± 0.73
			humidity	-0.39	0.22	- 0.82 / 0.03	0.070	
		T _{air}	T_{air}	2.08	0.25	1.61 / 2.57	<0.001	
			T_{air}	2.21	0.33	1.56 / 2.86	<0.001	
Ptiloerection	Summer	T _{air} * humidity	humidity	- 0.31	0.28	- 0.86 / 0.23	0.262	
			T _{air} * humidity	- 0.16	0.34	- 0.83 / 0.51	0.643	
		T _{air} * humidity	humidity	- 0.31	0.28	- 0.86 / 0.23	0.262	
			T _{air} * humidity	- 0.16	0.34	- 0.83 / 0.51	0.643	
Ptiloerection	Winter	T_{air}	T_{air}	1.55	0.20	1.15 / 1.94	<0.001	31.1 °C ± 1.0

Summer: N = 469 observations from 84 groups. Winter: N = 547 observations from 73 groups. Random terms: group ID and year (3)

CHAPTER 3

A long-lived cooperative breeder has dual investment strategies in same-clutch eggs with different survival probabilities



3.1. Abstract

Prenatal resource allocation can be influenced by environmental conditions affecting breeding females and the conditions under which offspring will develop (e.g. weather), and in cooperative breeders, social factors. In addition, theory predicts that investment in offspring should be influenced by their survival probability. For species that lay insurance eggs which are unlikely to be raised except if other eggs fail to hatch, females should invest differently in these eggs. However, whether environmental conditions influence this investment has not been examined empirically. Here, I investigate how lay date, weather and social factors (number of helpers) influence egg size in a long-lived cooperative breeder, the southern ground-hornbill *Bucorvus leadbeateri*, which lays two eggs but only raises a single chick, usually hatched from the first-laid egg. Using measurements of 125 first-laid eggs and 106 second-laid eggs collected over 13 years, I investigated whether the different survival probabilities of first and second-laid eggs were associated with different investment strategies by laying females. I also examined how these strategies related to the number of helpers in the group, lay date, or weather (rainfall and temperature) prior to laying. I found that variation in the size of first-laid eggs was best explained by female identity alone. Second-laid eggs were smaller but not more variable overall than first-laid eggs, though they decreased in size with later lay dates, higher temperatures and lower rainfall. Additionally, I found no evidence that helper presence influenced egg size. These results show that while females maintain stable investment in first eggs, second eggs are more flexibly adjusted. This suggests that investment in insurance eggs should be made only when the energetic costs to females are low, aligning with theoretical predictions for long-lived species and the different survival probabilities of the two eggs.

3.2. Introduction

Investment in offspring is crucial for reproductive success but energetically costly, and parents are expected to adjust breeding investment to maximise fitness based on the environmental conditions experienced (Stearns, 1992). For breeding females, this adjustment can begin with egg or embryo formation, with several studies documenting prenatal resource allocation in response to ecological and social factors that have predictable effects on reproductive success (e.g. Mousseau & Fox, 1998; Lindström, 1999; Fortuna et al., 2023). However, variation in breeders' reproductive investment is also expected to be influenced by their own survival prospects (Stearns, 1992). In long-lived species with low fecundity, breeders are expected to maximise their life-time reproduction by maximising the number of breeding events in life (Clutton-Brock 1988), potentially reducing flexibility in investment per attempt (Erikstad et al., 1998). This expectation should extend to prenatal maternal resource allocation, but it remains unclear how these adjustments are made in long-lived, low fecundity species.

Prenatal allocation is also expected to be influenced by the survival prospects of offspring (Stearns, 1992). A particularly interesting strategy found among some long-lived birds such as seabirds, raptors, and ground-hornbills, involves females laying more than one egg but rearing only a single chick (Kemp, 1988; Anderson, 1990; Simmons, 1997; Margalida et al., 2004; Davis et al., 2022). In these cases, the second or additional eggs are considered an insurance, if the first egg fails to hatch, but may also provide a potential food resource (Edwards & Collopy, 1983; Anderson, 1990; Simmons, 1997). This strategy involves a cost-benefit trade-off, where the energetic cost of producing additional eggs must be outweighed by the potential benefit of reproductive success if the first egg fails (Anderson, 1990; Forbes, 1990; Townsend & Anderson, 2007). Second-laid eggs are usually smaller than first eggs and have significantly lower chances of producing a fledgling (Gargett, 1977; Edwards & Collopy, 1983;

Evans, 1997; Carstens, 2014), but see Davis et al. (2022) and Dehnhard et al. (2015). Therefore, maternal investment strategies should differ between the egg that hatches first and the insurance egg(s), but maternal allocation strategies in species that lay insurance eggs also remain poorly understood.

Females can adjust their maternal investment by altering egg size, number, and composition in response to their body condition and the conditions under which offspring will develop (Christians, 2002; Lepage & Lloyd, 2004; Groothuis et al., 2005; Fortuna et al., 2021; Capilla-Lasheras, Wilson & Young, 2023; Montesana et al., 2025). When resources are favourable, females may be in better condition and able to invest more in reproduction by laying larger eggs (Hargitai et al., 2005), although the opposite could occur, allowing females to reduce their investment when conditions for offspring development are favourable (Sheldon, 2000). Larger eggs can be positively associated with hatching success (Wiebe & Bortolotti, 1995; Amundsen, Lorentsen & Tveraa, 1996) chick growth (Christians, 2002; Pinowska et al., 2004; Gladbach, Gladbach & Quillfeldt, 2010; Bosman, 2014), survival and immunity (Krist, 2011). However, adverse environmental conditions can limit the ability of females to invest in larger eggs or clutches. For example, in hot and dry climates, excessive heat or prolonged drought can be detrimental for adults' body condition, due to increased thermoregulatory demands, decreased foraging efficiency, and reduced food availability (du Plessis et al., 2012; van de Ven, McKechnie & Cunningham, 2019; Bourne et al., 2020a). As a result, temperature and rainfall are sometimes associated with variations in egg or clutch size (Lepage & Lloyd, 2004; Potti, 2008; Fortuna et al., 2021).

In addition, in species that breed cooperatively, helpers, which are non-breeding individuals, bring food to nestlings, improving rearing conditions (Cockburn, 1998; Valencia et al., 2006; Fortuna et al., 2021). In some species, the presence of additional helpers has been found to influence egg investment, leading females to lay smaller eggs (Russell et al., 2007;

Canestrari, Marcos & Baglione, 2011; Santos & Macedo, 2011). This is consistent with the load-lightening hypothesis, where females reduce their energetic investment, while helpers ensure the quality of the offspring is maintained (Crick, 1992; Dixit, English & Lukas, 2017; Van Boheemen et al., 2019; Van de Loock et al., 2023). Load lightening is generally considered typical in long-lived cooperatively breeding species, as conserving resources helps enhance future reproductive success of breeders (Hatchwell, 1999). However, other studies support the differential allocation hypothesis (Sheldon, 2000), where egg investment has been found to be higher when more helpers are present (Lejeune et al., 2016; Valencia et al., 2017; Fortuna et al., 2023; Van de Loock et al., 2023). This increased investment may reflect the enhanced survival prospects of offspring when helpers contribute to postnatal care (Russell & Lummaa, 2009; Langmore et al., 2016; Valencia et al., 2017).

Prenatal maternal allocation should therefore be determined by the interplay of parental and offspring survival prospects and further influenced by the weather and social conditions experienced at the time of breeding, but whether these factors have a clear influence on investment in eggs remains unclear. Fairy wrens *Malurus cyaneus* with more helpers laid smaller eggs under cooler conditions and larger eggs during hotter weather (Langmore et al., 2016). In other species, egg size correlated with temperature but showed no clear relationship with helper presence (Potti, 2008; Koenig, Walters & Haydock, 2009) and in sociable weavers *Philetairus socius* egg size was not influenced by rainfall, temperature or helpers (Fortuna et al., 2021).

In this study I investigate these hypotheses by taking advantage of a unique system, the southern ground-hornbill *Bucorvus leadbeateri*, where females typically lay two eggs but invariably only raise a single chick, usually originating from the first hatched egg (~90% of the clutches). In addition, the breeding females have been observed consuming the dead nestling (pers.obs.), therefore they may recover most of the investment made to produce the second egg.

Ground-hornbills are exceptionally long-lived (50-60 years), low fecundity, cooperative breeders that inhabit tropical and subtropical regions of southern Africa (Kemp, 1988; Wilson & Hockey, 2013; Carstens et al., 2019c). The two eggs are laid asynchronously about 3–5 days apart and second-laid eggs are usually smaller (Kemp, 1988; Carstens, 2014) (see Figure 3.1). Hatching is also asynchronous, and second-hatched chicks are consistently neglected by the adults, dying of starvation within a few days (Kemp, 1980). The function of the second egg has not been conclusively established, although it has been suggested to act as an insurance egg, as the chick will be fed and survive only if the first egg fails to hatch (Anderson, 1990; Wiebe, 1996; Clifford, 2001; Carstens, 2014). In this population, the second chick is raised ~10% of the time (in this dataset). Chick rearing, from laying to fledging, takes about 130 days, therefore, second clutches are rare unless attempts fail early in the season.

I used the ground-hornbill study system to test predictions of how varying social and environmental conditions affect maternal allocation in eggs with drastically different survival prospects. Specifically, I predicted the following: 1) First-laid eggs will be larger, and show less variation in size and lower response to environmental factors compared to second eggs; 2) in favourable weather conditions, such as cooler temperatures and more rainfall, females will lay larger first-laid eggs, as improved body condition and resource availability may allow greater egg investment; 3) under the load-lightening hypothesis, when more helpers are present, females will lay smaller first eggs, as helpers have been found to increase provisioning rates in this species (Middleton, 2022), and hence may compensate for smaller eggs through increased food being brought to the nest (i.e. load-lightening effect, see above); 4) investment in second-laid eggs is expected to be more variable and sensitive to weather conditions, as these eggs are less likely to produce fledged offspring, therefore, females should only invest more in them when the energetic cost to themselves is low (e.g. due to greater food availability and cooler temperatures), even though they may consume the dead chick and recover part of the

investment made; 5) helper presence is unlikely to affect second egg size, as helpers are expected to reduce provisioning costs rather than egg production costs, and these eggs have a lower chance of fledging and are usually smaller. Hence further reducing egg size based on helper numbers offers little benefit (Figure 3.2).

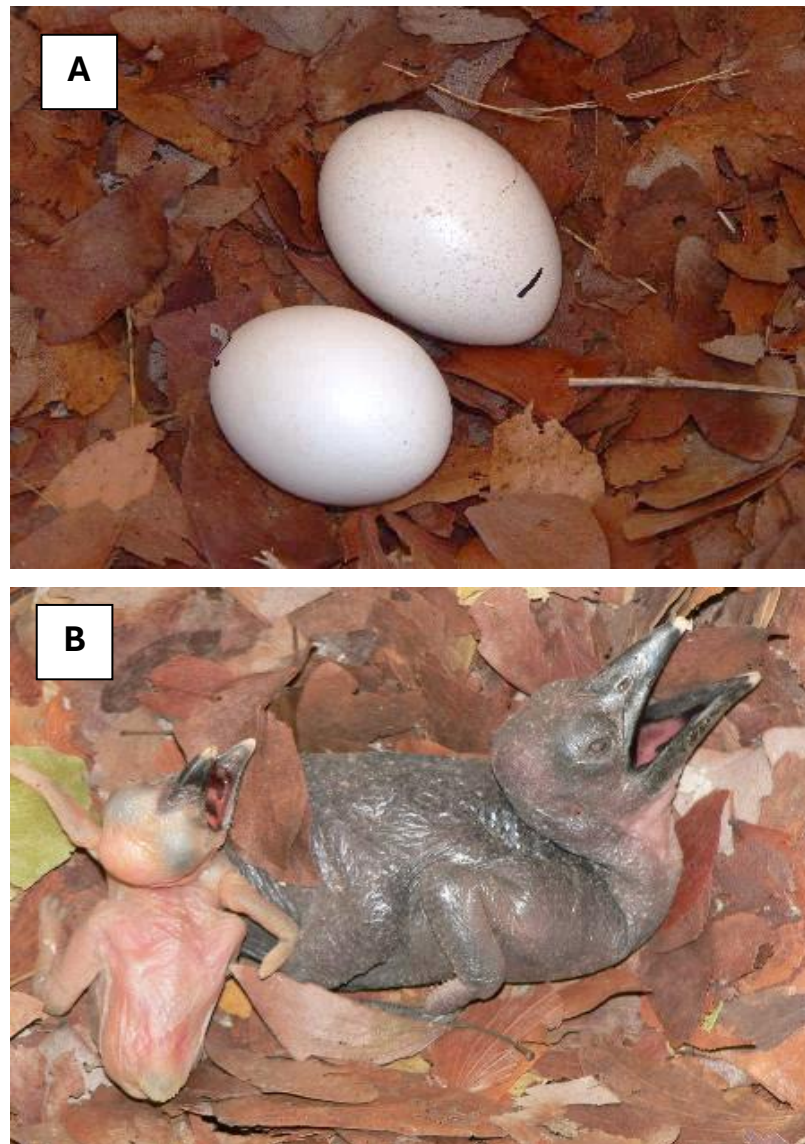


Figure 3.1. (A) Ground-hornbill eggs in a nest showing the size difference between the first-laid egg (top, marked '1') and the second-laid egg (bottom). (B) Size difference between first- and second-hatched chicks, which hatch asynchronously approximately 3–5 days apart. The second hatched chick is ignored by parents and succumbs to starvation within a few days

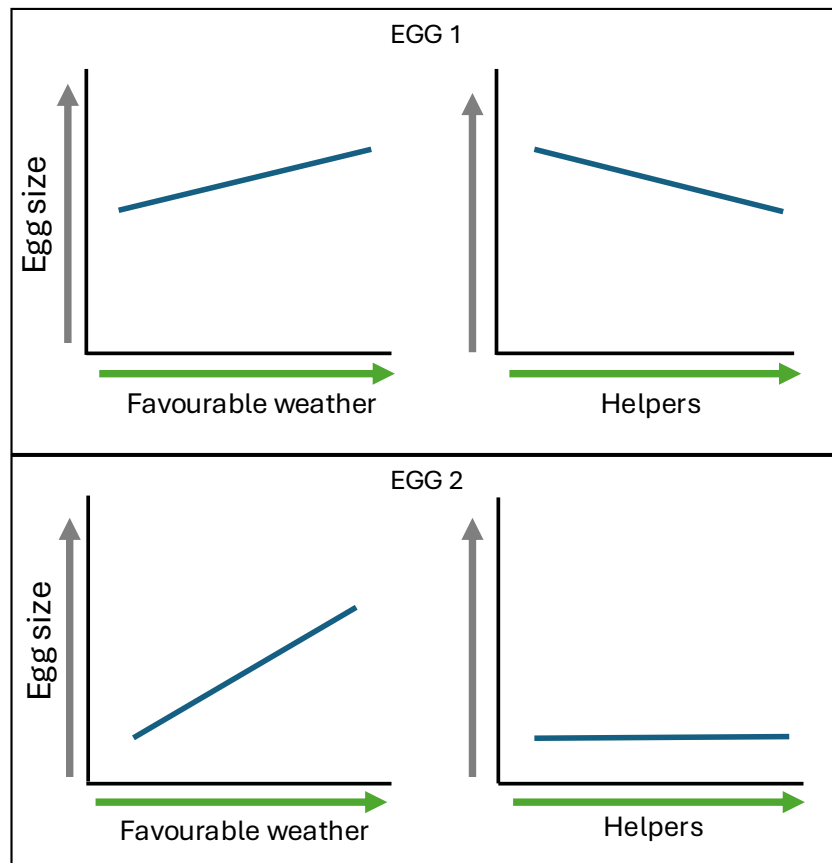


Figure 3.2. Schematic representation showing predictions for maternal investment (egg size) in southern ground-hornbills for first laid eggs (top panel) and second laid eggs (bottom panel), under favourable weather and with more helpers.

3.3. Methods

Ground-hornbills are obligate cavity nesting birds that typically occur in cooperatively-breeding groups of 2–7 birds (mean group size = 4.2 in this population), including one breeding female. Artificial nests have been used in the study site since 2000 to compensate for the lack of natural nests, aiding the monitoring of breeding and reproduction. Regular egg measurement data collection began in 2012.

3.3.1. Egg size

During breeding seasons from 2012 to 2024, nests were monitored every 7–10 days, starting in September, to assess breeding activity. The first-laid eggs found within nests were marked with a '1', in permanent marker. Five days after marking the first egg, the same nest was

checked, and, if present, the second-laid egg was marked '2'. If two eggs were found on the first visit, both eggs were candled, a process where a light is shone through the egg to check for embryo development (Resendiz et al., 2024), with the more developed egg assigned as '1', and less developed as '2'. Egg length (L) and maximum breadth (B) were measured (± 0.1 mm) using Vernier calipers and egg mass (0.1 g) was recorded (± 0.1 g) using a digital microscale. Measurements were obtained from 128 clutches, of which 16 were single-egg clutches (sample size: 128 first-laid and 109 second-laid eggs; three second-laid eggs were not measured). Since eggs lose mass once laid, but linear dimensions do not change, egg volume was used as a measure of egg size, as exact laying dates were sometimes unknown. I calculated the egg volume in cm^3 (Hoyt, 1979; Pinowska et al., 2004) using this formula:

$$V = 0.00051 \times L \times B^2$$

where (L) represents the length and (B) the maximum breadth of an egg.

3.3.2. Female identity and number of helpers

All ground-hornbills in our population are reliably identified by their distinctive facial features (red-throat pouch characteristics, sideburns, blue throat markings in females, which are individually unique; see Figure 3.3) and colour leg rings present on some individuals. Since 2016, adult birds have not been captured or handled (a decision prompted by logistical challenges and high stress associated with captures of adult birds), and only individuals born in the population are ringed as nestlings and not captured again. Although some individuals captured before 2016 still carry colour leg rings, identification is now based on facial features. From 2012 to 2016, female identity, group size and composition (i.e. number of adults, subadults and juveniles), were recorded by field observations and photographs taken by researchers of groups at nests and incubating females inside nests. From 2016 to 2024, individuals were identified using camera traps (Browning Trails Cameras, Alabama, USA;

models: Spec Ops Advantage, Spec Ops Edge, Spec Ops Elite, Patriot) set at nests to capture high-resolution 20-second videos when motion was detected (see Chapter 1: General methods) in addition to field observations. Age categories (adults, subadults, juveniles) were assigned based on facial skin and bill colour (Kemp, 1980; Middleton et al., 2026). 25 groups and 27 females were identified between 2012 and 2024 (two groups had two different breeding females). Breeding summaries for each female are provided in Table A3.3. Females contributed 1–12 breeding attempts each (mean = 4.7) to this dataset. However, female age and breeding experience could not be inferred reliably, as individuals can live > 50 years and monitoring began in 2000 (regular egg measurements from 2012).

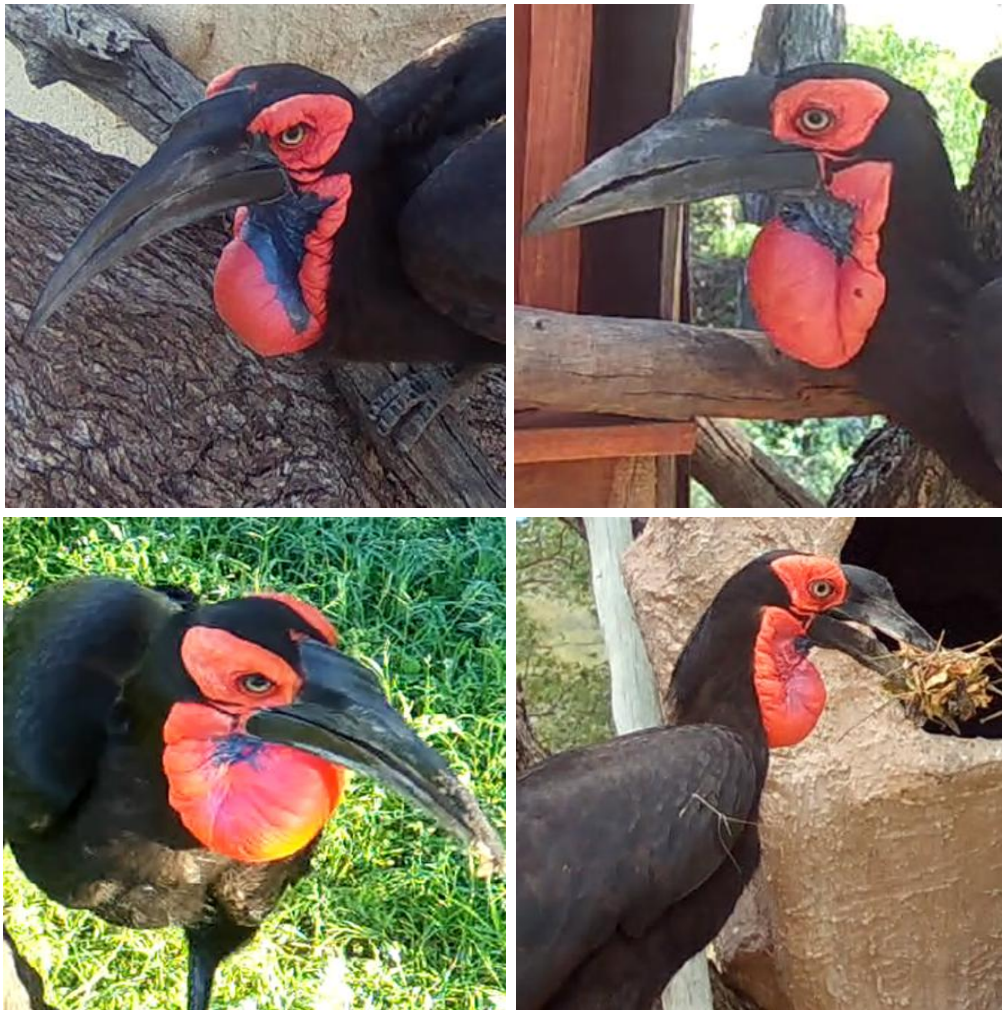


Figure 3.3. Photos showing four different females, identified by the unique blue coloration pattern on their throats.

3.3.3. Weather data

Daily air temperature and rainfall data were obtained from the South African Weather Services (SAWS) station at Hoedspruit Airforce Base (see Chapter 1: General methods). Recognising the potential variability of rainfall across the study area, I also obtained monthly rainfall data from 15 rain gauges distributed throughout the study site. For each ground hornbill territory, seasonal rainfall for the previous summer [October – March] and winter [April – September] prior to egg laying was determined using data from the nearest rain gauge, located within 5 ± 3 km of their nest. Data from the Hoedspruit Airforce Base station (SAWS) showed a strong correlation with the rainfall patterns observed across the study area (Figure A3.1). This correlation gives confidence in using the SAWS rainfall for the analysis of rainfall in the days before laying, which cannot be achieved with monthly rain data provided by the rain gauges distributed through the study site. I calculated weather variables for each breeding attempt, which were chosen *a priori* to represent both long and short-term effects of weather experienced by females before laying. The weather variables were grouped into categories: average maximum daily air temperatures (mean $T_{\max}$), the number of days above 35 °C (days > 35 °C, a threshold known to negatively affect breeding outcomes in other southern African savanna bird species (Bourne et al., 2020b; van de Ven et al., 2020)) and cumulative rainfall. These variables were calculated over time windows selected for their potential biological relevance: the previous summer; the winter prior to laying; and 15, 30, 60, and 90 days prior to laying (Table 3.1).

3.3.4. Statistical analyses

Statistical analyses were conducted in R v 4.4.1 (R core Team 2024). Linear mixed-effect models were fitted using the *lme4* package (Bates et al., 2015). Model selection with Akaike's information criterion corrected for small sample size (AICc) was used to explore models to determine which variables best explained egg size (Harrison et al., 2018). All predictors were

checked for pairwise correlations to avoid collinearity, and continuous variables were centred and scaled. Effects were considered significant when their confidence intervals did not overlap zero. Model assumptions were assessed using the package *performance* (Lüdtke et al., 2021).

Egg size and weather

I used a paired t-test to compare the size of first and second-laid eggs, and an F-test to assess differences in variance between the two. The sample size for these analyses were Egg 1: N = 128 and Egg 2: N = 109.

Due to limited knowledge of the weather conditions that influence maternal allocation in this system, I used an AICc-based candidate model approach (*MumIn* package; Bartoń, 2020) to identify predictors of egg size. Analyses for first (Egg 1) and second-laid eggs (Egg 2) were conducted separately since I expected different allocation strategies for each egg.

Step 1: Candidate models including different weather variables (mean $T_{\max}$, days > 35 °C, and rainfall) and time windows (Table 3.1) were compared against a null model using AICc. Step 2: For each weather variable category, only models with $\Delta AICc < 2$ were retained. When multiple time windows met this criterion, the best-supported time window (lowest AICc) was selected, resulting in one top-supported predictor per weather category. Step 3: These top-supported weather variables were then included in a final candidate set together with fixed effects lay date (number of days since 1 September; known to influence reproductive outcomes (Gladbach, Gladbach & Quillfeldt, 2010; Gienapp & Bregnballe, 2012; Reséndiz-Infante & Gauthier, 2020)), number of helpers, and number of juveniles to identify the best predictors of egg size. Female ID and year were included as random effects in all models. After excluding three groups with unknown group composition, the final sample sizes for these analyses were Egg 1: N = 125 and Egg 2: N = 106.

Weather models and the lay date model for first-laid eggs had ΔAIC values > 2 compared to the null model, indicating no improvement in model fit. For second-laid eggs, several weather variables improved the null model but in the final model set no weather variable models were within $\Delta\text{AICc} < 2$ of the lay date model, and therefore these were not considered competing models. However, as lay date (the top supported model) and the top weather variables were strongly correlated (all Pearson's $R > 0.73$, Figure A3.2), I could not rule out that the effect of lay date might be explained by the combined effects of weather. Therefore, I also explored the top-supported model from each weather category and time window to evaluate these potential effects. Additionally, I used a piecewise structural equation model to assess whether the lay date effect could be mediated by weather conditions in the lead-up to laying (see “piecewise SEM” below).

Group composition

The number of helpers was defined as the sum of adult and subadult group members, as these age classes contribute to cooperative behaviours such as nestling provisioning and territory defence. Juveniles from previous broods were considered separately, as they do not contribute significantly to these behaviours (Middleton, 2022). However, juveniles were retained as a predictor because their presence may still reflect variation in group, female, or territory quality and breeding history, and they represent an additional demand on provisioning resources, as they are still fed by group members.

Table 3.1. Summary of weather variables and time windows organised by weather category to assess long and short-term weather effects on egg size. In cases where multiple time windows within a weather category had competing models (within 2 $\Delta AICc$) only one time window (with the lowest $AICc$) was chosen for further analyses.

Weather category	Time windows tested
Mean maximum air temperature (Mean T_{max})	– Previous summer (October – March) – Winter prior to laying (April – September) – 15, 30, 60, and 90 days prior to laying
Number of days where air temperature exceeded 35 °C (days > 35 °C)	– Previous summer (October – March) – Winter prior to laying (April – September) – 15, 30, 60, and 90 days prior to laying
Cumulative rainfall	– Previous summer (October – March) – Winter prior to laying (April – September) – 15, 30, 60, and 90 days prior to laying

Piecewise SEM

To assess whether the effect of lay date on egg size in second-laid eggs was direct or mediated by weather variables, I fitted a Piecewise Structural Equation Model (SEM). Linear mixed effect models were fitted with Gaussian error distributions and bobyqa optimiser, including female ID as a random effect, using the packages *lme4* (Bates et al., 2015) and *piecewiseSEM* (Lefcheck, 2016). I used only the single best-supported temperature variable along with rainfall over the best supported time window of 90 days prior to laying (see results). In this analysis, standardised estimates were used, allowing for comparison of the relative strengths of the relationships between variables. Statistical significance was taken as $p < 0.05$.

3.4. Results

First laid eggs (Egg 1, $N=128$) were significantly larger than second laid eggs (Egg 2, $N=109$) ($t = 8.49$, $p < 0.001$, Figure 3.4). Egg 1 and Egg 2 volumes were positively correlated within clutches ($r = 0.73$, [95% CI = 0.63 / 0.81], $p < 0.001$; Figure A3.3). There was no significant difference in the variance of egg size between the first and second laid eggs across females ($F = 1.0054$, 95% CI = [0.70 / 1.44], $p = 0.98$).

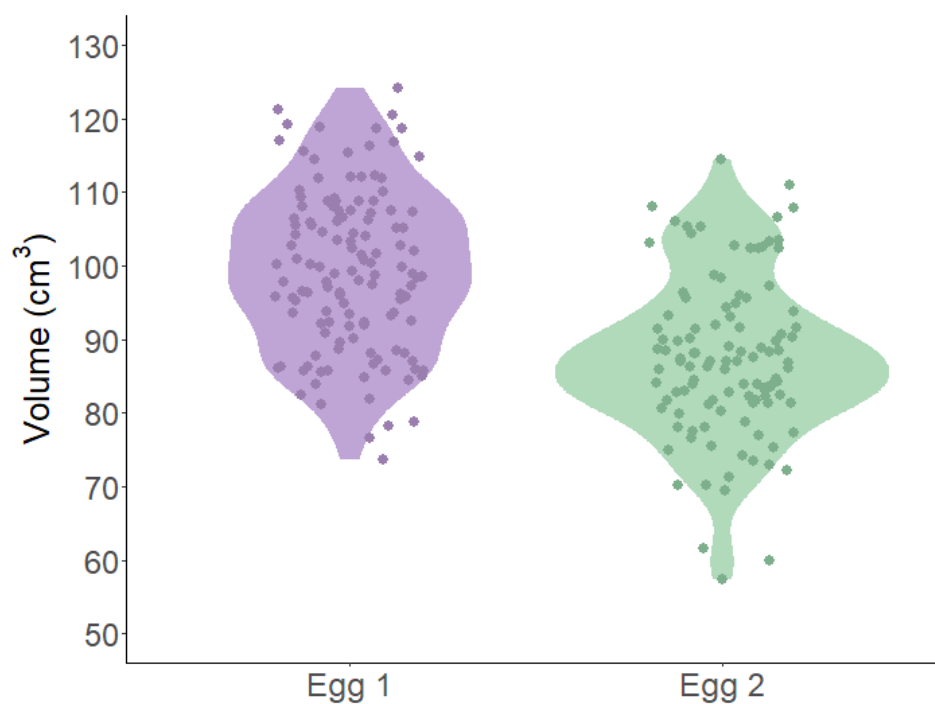


Figure 3.4. Violin plot showing the distribution of egg size (cm^3) for first-laid eggs (Egg 1), in purple and second-laid (Egg 2) in green, with overlaid jittered points representing observed values.

3.4.1. First laid eggs

The size (volume) of first-laid eggs ranged between 73.6 and 124.2 cm^3 (mean = 99.4 ± 10.9 cm^3). The null model, including only female ID and year as random effects, provided the best fit for first-laid egg size. Female identity explained most of the variation, with a variance of 0.846 (Table A3.1). Models including weather variables, lay date and helpers did not improve model fit (Table 3.2, Table 3.3).

Table 3.2. Model selection table to identify best weather variable explaining first-laid egg size (Egg 1), with top model highlighted in bold. All models include female ID and year as random effects. As no model outperformed the null model, no weather predictors were supported, and only the variance components from the null model are reported.

EGG 1				
Model no.	Model	AICc	Δ AICc	Weight
1	null	311.7	0.00	0.334
2	days > 35 °C _{winter}	314.3	2.26	0.089
3	mean T _{max} last 15 days	314.9	3.27	0.065
4	days > 35 °C last 15 days	315.3	3.65	0.054
5	rainfall last 15 days	315.6	3.91	0.047
6	rainfall last 60 days	315.6	3.98	0.046
7	days > 35 °C last 90 days	315.7	4.05	0.044
8	rainfall last 90 days	316.0	4.30	0.039
9	rainfall last 30 days	316.2	4.56	0.034
10	mean T _{max} last 90 days	316.2	4.57	0.034
11	days > 35 °C last 30 days	316.4	4.76	0.031
12	days > 35 °C last 60 days	316.5	4.86	0.029
13	mean T _{max} previous summer	316.8	5.09	0.026
14	mean T _{max} last 30 days	316.8	5.14	0.026
15	mean T _{max} last 60 days	316.9	5.21	0.025
16	mean T _{max} winter	317.2	5.52	0.021
17	days > 35 °C previous summer	317.3	5.52	0.021
18	winter rainfall	317.4	5.60	0.020
19	previous summer rainfall	317.5	5.86	0.019
<i>N = 125, Random terms: female ID = 27, year = 13</i>				

Table 3.3. Model selection table to investigate the effects of helpers and laydate on first-laid eggs size (Egg 1). All models female ID and year as random effects. No model improved the null model.

EGG 1				
Model no.	Model	AICc	Δ AICc	Weight
1	null	311.7	0.00	0.769
2	laydate	315.0	3.33	0.146
3	helpers + juv	316.4	4.69	0.074
4	laydate + helpers + juv	320.1	8.42	0.011
5	laydate * helpers + juv	325.5	13.80	0.001
<i>N = 125, Random terms: female ID = 27, year = 13.</i>				

3.4.2. Second laid eggs

Second-laid egg size ranged between 57.3 and 114.5 cm³ (mean = 87.4 ± 10.8 cm³). Multiple weather variables improved model fit compared to the null model. Consistent with the model-selection criteria outlined above, only the best-supported time window (lowest AICc) for each weather variable was considered. Consequently, the best weather predictors of second-laid egg size with Δ AICc within 2 were days > 35 °C last 90 days, mean $T_{\max}$ last 90 days, and rainfall last 90 days (Table 3.4). When these top weather variables were included alongside lay date and helpers in a subsequent model selection, lay date emerged as the strongest predictor of second-egg size, no other models within 2 Δ AICc (Table 3.5). There was a significant negative relationship between lay date and second-laid egg size (estimate = -0.31 ± 0.08 , 95% CI = [-0.48 / -0.16]; Table A3.2, Figure 3.5). Although none of the weather variables were competitive predictors in the final model selection, all correlated closely with lay date (Figure A3.2) and may have together explained why lay date emerged as the best predictor. I therefore examined their effects: days > 35 °C last 90 days (estimate = -0.26 ± 0.08 , 95% CI = [-0.42 / -0.09]), mean $T_{\max}$ last 90 days (-0.25 ± 0.08 , 95% CI = [-0.42 / -0.08]), and rainfall last 90 days (-0.24 ± 0.08 , 95% CI = [-0.41 / -0.07]) all showed a significant negative relationship with second-

laid egg size (Table A3.2, Figure 3.5). Models including the number of helpers or juveniles did not improve model fit and were not competitive predictors of second-laid egg size (Table 3.5).

Table 3.4. Model selection table to identify best weather variables explaining second-laid egg size (Egg 1). All models included female ID and year as random effects. Models with $\Delta\text{AICc} < 2$ (in bold) were selected for the final model set, choosing one top-supported model and time window from each weather category. Rainfall 60 days prior was not included because its fit was almost identical to the 90-day rainfall model ($\Delta\text{AICc} = 0.2$), so only the 90-day model was retained.

EGG 2				
Model no.	Model	AICc	ΔAICc	Weight
1	days > 35 °C last 90 days	298.2	0.00	0.260
2	mean T_{max} last 90 days	299.3	1.10	0.150
3	rainfall last 90 days	299.7	1.46	0.125
4	rainfall last 60 days	299.9	1.66	0.113
5	days > 35 °C last 60 days	301.1	2.76	0.065
6	rainfall last 30 days	302.0	3.78	0.039
7	null	302.0	3.82	0.038
8	days > 35 °C last 30 days	302.2	3.97	0.036
9	mean T_{max} last 60 days	302.4	4.25	0.031
10	days > 35 °C _{winter}	302.7	4.55	0.027
11	previous summer rainfall	302.8	4.64	0.026
12	days > 35 °C last 15 days	303.1	4.86	0.023
13	winter rainfall	303.4	5.22	0.019
14	mean T_{max} last 30 days	303.9	5.71	0.015
15	mean T_{max} last 15 days	304.6	6.39	0.011
16	rainfall last 15 days	304.7	6.52	0.010
17	mean T_{max} winter	306.0	7.76	0.005
18	mean T_{max} previous summer	306.7	8.56	0.004
19	days > 35 °C previous summer	306.9	8.74	0.003
<i>N = 106, Random terms: female ID = 27, year = 13</i>				

Table 3.5. Model selection table to investigate the effects of top-selected weather variables, lay date, and helpers on second-laid egg size (Egg 2). All models female ID and year as random effects. The top model is in bold with $\Delta\text{AICc} < 2$.

EGG 2				
Model no.	Model	AICc	ΔAICc	Weight
1	laydate	293.1	0.00	0.790
2	days > 35 °C last 90 days	298.2	5.09	0.062
3	laydate + helpers + juv	298.2	5.13	0.061
4	mean T_{max} last 90 days	299.3	6.19	0.036
5	rainfall last 90 days	299.7	6.55	0.030
6	null	302.0	8.91	0.009
7	days > 35 °C last 90 days + helpers + juv	302.8	9.72	0.006
8	mean T_{max} last 90 days + helpers + juv	304.0	10.85	0.003
9	rainfall last 90 days + helpers + juv	304.8	11.74	0.002
10	helpers + juv	306.8	13.67	0.001
<i>N = 106, Random terms: female ID = 27, year = 13</i>				

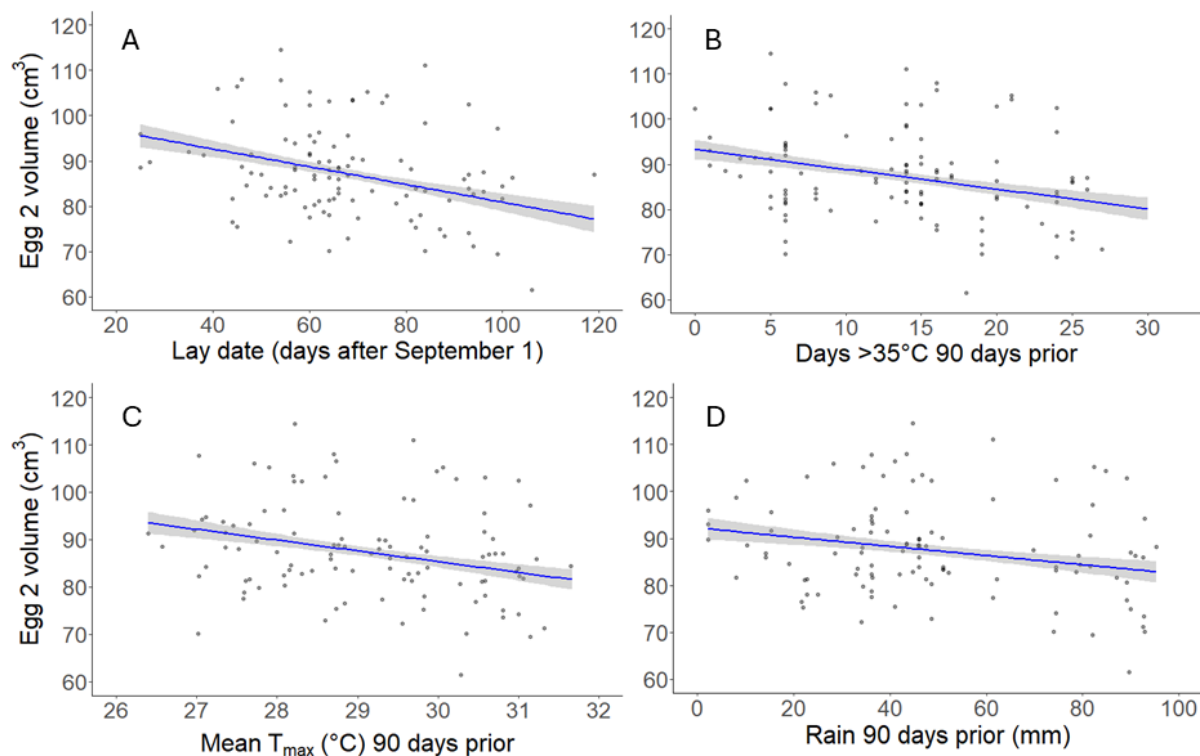


Figure 3.5. Relationships between predictor variables and second-laid egg size: (A) lay date (days after 1 September), (B) days > 35 °C 90 days prior, (C) mean maximum air temperature 90 days prior, and (D) rainfall 90 days prior. Points show observed values; blue lines and shaded bands show model predictions with 95% confidence intervals.

3.4.3. Piecewise SEM

An exploratory piecewise Structural Equation Model was used to investigate the direct and indirect effects of lay date on second-laid egg size, with weather variables included as potential mediators (Figure 3.6). Lay date was positively correlated with days > 35 °C (standardized effect size = 0.7508, $p < 0.001$) and rainfall (standardized estimate = 0.7484, $p < 0.001$). There was a negative indirect effect of lay date on egg size via days > 35 °C [standardized estimate = -0.0332 (calculated by multiplying the standardized estimates along the indirect path: $0.7508 * -0.0442$)] and a positive effect via rainfall [standardized effect size = 0.00449 ($0.7484 * 0.006$)]. The total indirect effect was -0.0287 and was primarily driven by the days > 35 °C pathway, which accounted for 88.1% of the total indirect effect, while rainfall contributed only 11.9%. The direct effect of lay date on egg size was negative and significant (standardized

estimate = -0.2780, $p = 0.05$), accounting for approximately 90% of the total effect, with the remaining 10% explained by the indirect pathways. This suggests that lay date captures additional factors not included in these weather variables. Overall, the model showed an adequate fit to the data (Fishers's $C = 5.538$, $p = 0.069$, $df = 2$).

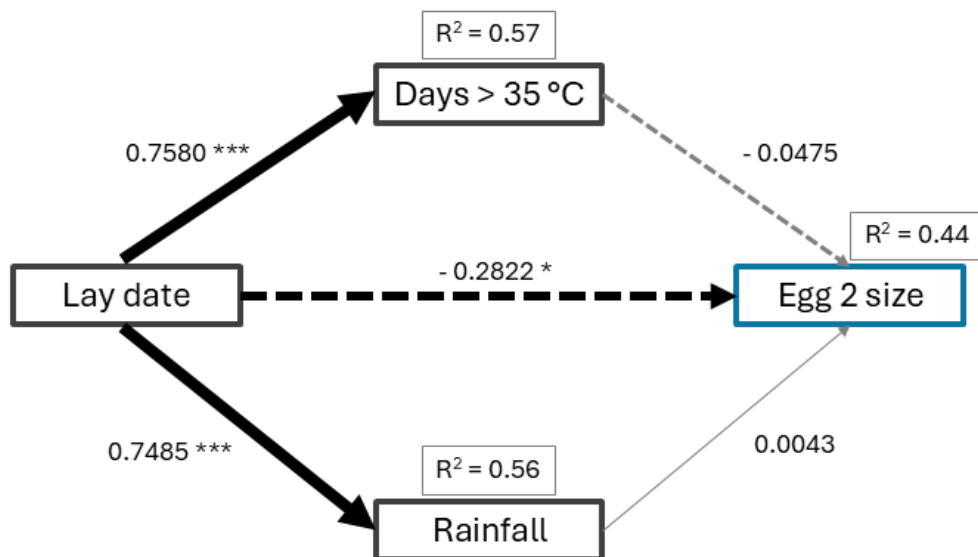


Figure 3.6. Piecewise SEM exploring the effects of lay date, rainfall and number of days above 35 °C on egg 2 size. Arrows show direction of relationship with standardized effect sizes. Arrow widths relate to the strength of the relationships based on standardized effect sizes. Asterisks indicate the level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. $N = 106$ eggs. Significant paths are in black and non-significant paths in grey with solid arrows showing positive effect and dashed arrows show negative effect. R^2 values for models are shown above response variables.

3.5. Discussion

This study used a bird that lays two eggs but but raises only the first-hatched chick to investigate the association between social and environmental factors, and maternal investment in size of eggs markedly differing in their survival probabilities. As expected, first-laid eggs were larger, and while overall they were not more variable in size than second eggs, their size was not influenced by weather conditions or the presence of helpers; instead, variation was best explained by female identity, suggesting consistent investment in the primary offspring within

individual females. Second-laid eggs were smaller than first-laid eggs, and contrary to expectations, at the population level, did not vary more in size. However, there was a tendency for these eggs to decrease in size after hotter temperatures and less rainfall, although we note that these effects were not among the top models and were largely accounted for by lay date, with females laying smaller eggs later in the season. I found no evidence that helper presence influenced egg size. Together, these results suggest that while females maintain stable investment in first eggs, which are commonly the ones that will produce a fledgling, second eggs are more flexibly adjusted. In addition, there is no indication that social factors influence maternal allocation in this species.

Investment in first-laid eggs

There was no evidence that weather or the number of helpers influenced the size of first-laid eggs. Females therefore appear to maintain a high investment in these first eggs. This is consistent with these being usually the offspring that survive, and underinvestment could incur a fitness cost to chicks that could reduce size, immunity, and survival (Krist, 2011). Therefore, for low fecundity species such as ground-hornbills, this strategy could increase the probability that the energetic cost of egg laying to the female is offset in each breeding attempt by the development of a high-quality chick. Furthermore, during adverse weather and when in poor body condition, females may choose to avoid breeding entirely instead of making a suboptimal egg investment. This is indirectly supported by the observation that, in our study area, groups only breed on average every 2–3 years (Table A3.3). Instead, female identity explained most of the variance in first egg size, indicating that traits such as female size, age, experience, or territory quality (Hipfner, Gaston & de Forest, 1997; Christians, 2002) may play a stronger role in their maternal investment than weather or social factors. This is in line with other studies that found consistent egg investment within females, and more variation between than within individuals (Christians, 2002; Krist, 2011; Fortuna et al., 2021). Because adult birds are not

captured in this study system, and ground-hornbills are very long-lived, I lack data on two key factors: female body mass and age. Longer-term data, and automatic scales placed at nest boxes (currently being developed for our study population) should allow us to address these questions in the future. Nonetheless, our results suggest that ground-hornbills adopt a stable investment strategy for the offspring most likely to survive.

Investment in second-laid eggs

Unlike first-laid eggs, second-laid ‘insurance’ eggs showed a clear relationship with lay date, which might indirectly capture seasonal variation in weather conditions. Females produced smaller second-laid eggs later in the season, after periods of higher mean maximum temperatures and more frequent heat extremes, indicating some flexibility in their maternal investment. This may be due to physiological constraints as many studies provide evidence for body mass declines in response to high temperatures (du Plessis et al., 2012; Gardner et al., 2016; van de Ven, McKechnie & Cunningham, 2019); therefore, females could be adjusting investment in insurance eggs, in response to their body condition. However, a piecewiseSEM showed that the influence of extreme heat was not significant and contributed to only 8% of the total model, suggesting that heat may exacerbate other factors captured by lay date, rather than having a direct effect on egg size. Rainfall appeared to negatively correlate with second egg size when modelled as a sole predictor, likely due to its association with lay date, with more rain accumulating when laying later. However, the piecewise SEM revealed that the effect of rainfall was not significant. Therefore, these weather effects were weak and should be interpreted with caution.

Instead, the strong direct negative effect of lay date on the size of second-laid eggs suggests this variable may capture additional factors beyond what this study measured. For example, it may be associated with progressive effects of the season advancing on the territory quality or female condition (Rowe, Ludwig & Schluter, 1994; Gladbach, Gladbach &

Quillfeldt, 2010), or may reflect that females in poorer body condition or with poorer-quality home ranges are constrained to lay later and have fewer resources to invest in second-laid eggs. Ground-hornbills likely benefit from laying eggs early in the breeding season because their long chick-rearing period aligns with resource abundance, while later hatching may result in smaller chicks due to declining food resources towards the end of summer (Dawson & Clark, 2000). Ground-hornbills typically delay the onset of breeding following hot winters (Middleton et al., 2026), possibly because low shade availability increases thermoregulatory demands in winter, during a season when food is also scarce (see Chapter 2). Earlier laying dates and larger eggs may therefore indicate that females are in better condition as they emerge from winter (Rowe, Ludwig & Schluter, 1994; Hargitai et al., 2005).

In long-lived species, life history theory predicts that during challenging conditions, parents prioritise their own survival over that of their offspring, reducing the immediate costs they incur (Clutton-Brock, 1991; Ghalambor & Martin, 2001). Even though ground-hornbill females appear to usually consume the dead chick (pers. obs.), they first have to produce the egg. Since only ~10% of second eggs result in fledged offspring, the reduced investment observed in the ground-hornbill second-laid eggs may reflect a strategic trade-off. Flexibility in reproductive investment in egg size has been observed in red-winged fairy wrens *Malurus elegans*, superb fairy wrens and collared flycatchers (Hargitai et al., 2005; Langmore et al., 2016; Lejeune et al., 2016). However, variation in egg size can also result from passive constraints linked to female body condition, as mentioned above. While here we cannot distinguish passive from active allocation, by varying the size of second eggs, females may be protecting their body condition, and their long-term reproductive potential and survival.

No helper effects

One prominent hypothesis to explain the benefits of helpers in cooperative breeders is the load-lightening effect, where helpers reduce the energetic costs to breeders of raising offspring

(Hatchwell, 1999). This is expected to be particularly important in long-lived species such as ground-hornbills, where breeder survival and lifetime reproductive success are particularly important to maximise fitness (Crick, 1992; Dixit, English & Lukas, 2017; Van Boheemen et al., 2019; Van de Loock et al., 2023). However, the results here provide no evidence that helpers influence females' investment in first or second eggs. This is in line with previous findings showing no helper-related adjustments in egg investment under adverse conditions in cooperatively-breeding species, such as sociable weavers (Fortuna et al., 2021), but contrasts with the load-lightening effect found in superb fairy wrens (Russell et al., 2007), and carrion crows *Corvus corone* (Canestrari, Marcos & Baglione, 2011). It is currently poorly understood why the presence of helpers is associated with load-lightening in some species and not in others. The ground-hornbills' extreme life-history, with very high longevity and low fecundity, provides some context to interpret these results. Although their life-time reproductive success should be maximised by the number of breeding events in life, their low fecundity, the strategy of raising a single offspring and forgoing breeding in some years, should favour a strategy where female allocation is set at a level that does not compromise offspring growth or survival (Stearns, 1992; Griesser et al., 2017). In addition, first eggs have a relatively high probability of producing a fledgling (~60% in our population with most failures resulting from predation). This, combined with the species longevity could favour a high maternal investment in offspring quality (here, in first-laid eggs). I suggest that taking into account parental and offspring survival prospects might allow us to improve our understanding of when evidence of load-lightening is expected to be found at the egg stage in cooperatively breeding species.

Overall, my results reveal no benefits of helpers at the egg stage in this species, concurring with previous research in this species which found no clear effects of helpers on reproductive output. The benefits of helpers to ground-hornbills may instead be associated with other group behaviours such as territory and nest defence or predator protection, rather than

directly improving the reproductive process (Gonzalez, Sheldon & Tobias, 2013; Middleton et al., 2026).

3.6. Conclusion

My results show that ground-hornbill females have two distinct investment strategies in the two eggs laid in the same clutch. These strategies agree with theoretical predictions based on the eggs' survival probability and the species' life-history. First-laid eggs, which have high survival, are usually buffered from environmental variability through consistent maternal investment, rather than the presence of helpers or modulation in relation to weather conditions. In contrast, low-survival second eggs appear more sensitive to environmental conditions and can decrease in size when laying occurs later in the season. Although chicks from second eggs are infrequently raised (~10% of fledglings), our results raise the question of whether reduced investment in insurance eggs could further limit reproductive output and recruitment under the sustained increases in temperature resulting from accelerating climate change, with warmer winters delaying lay dates (Middleton et al., 2026). More generally, our results suggest that a species' life-history strategy and, specifically, the survival probabilities of adults and offspring, are important for predicting when maternal load-lightening at the egg (or embryo) stage and modulation in relation to environmental factors might occur.

3.7. Appendix to Chapter 3

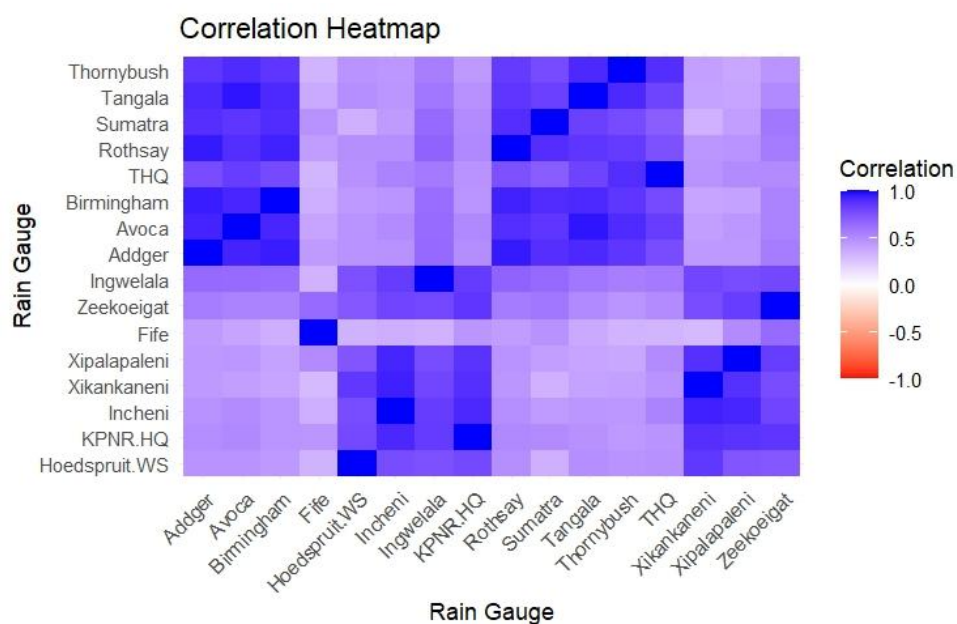


Figure A3.1. Correlation matrix between rainfall date from rain gauges distributed throughout the study site and rainfall data from weather station based at Hoedspruit Airforce Base. Positive correlations are shown in blue shades.

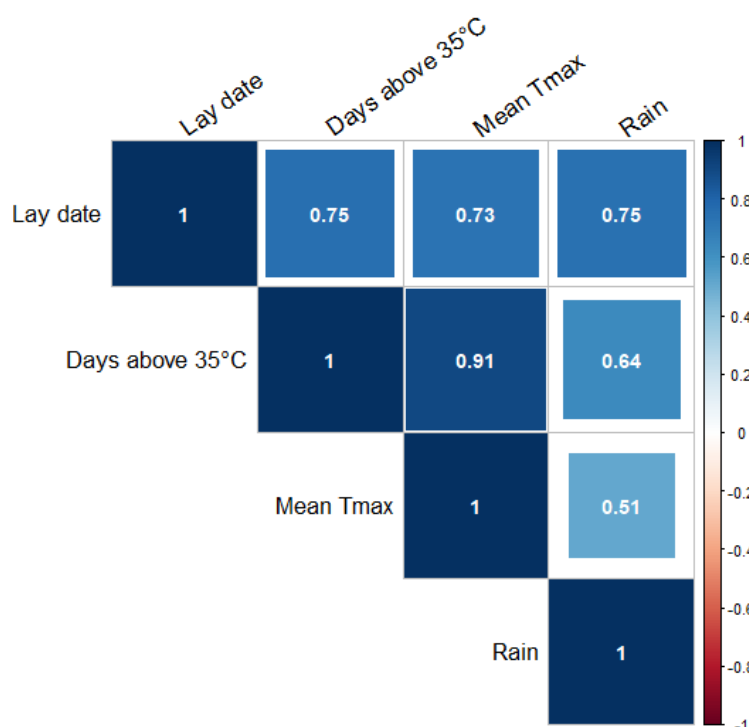


Figure A3.2. Pearson correlation coefficients between weather variables (days > 35 °C, mean T_{max} , Rainfall – 90 days prior to egg laying) and lay date. Blue squares indicate positive correlations, with darker shades and larger squares representing stronger relationships.

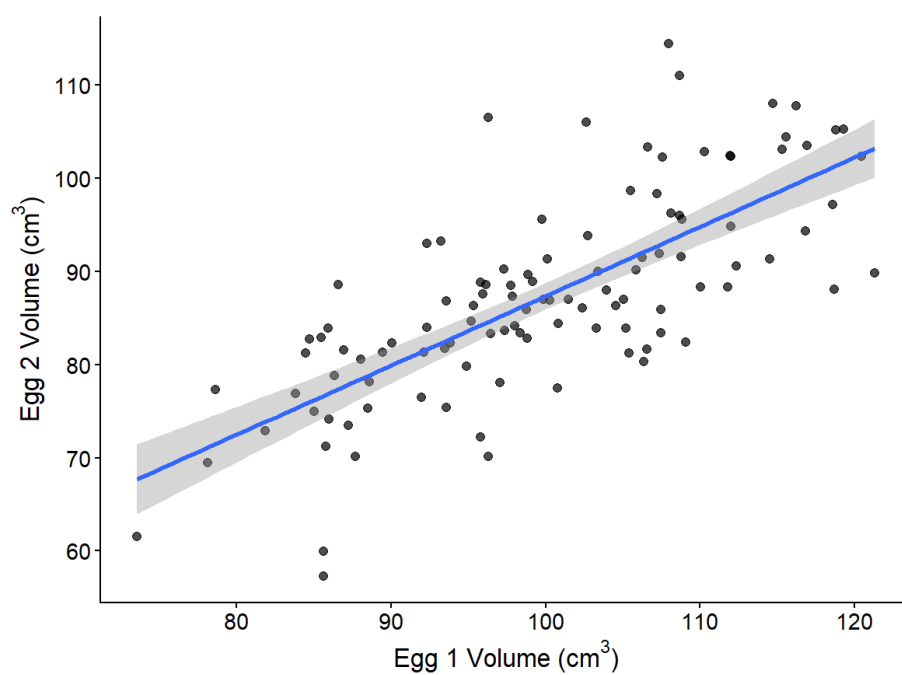


Figure A3.3. Within-clutch relationship between Egg 1 and Egg 2 volume (cm³), showing a significant positive association ($r = 0.73$).

First-laid eggs

Table A3.1. Variance components from the null model for first-laid egg size (Egg 1), showing contributions of female ID, year, and residual variation.

Model	Random effect	Variance	SD
null	Female ID	0.846	0.92
	Year	0.000	0.000
	Residual	0.390	0.624
<i>N</i> = 125, Random terms: female ID = 27, year = 13			

Second-laid eggs

Table A3.2. Factors predicting egg size for second-laid eggs (Egg 2) with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

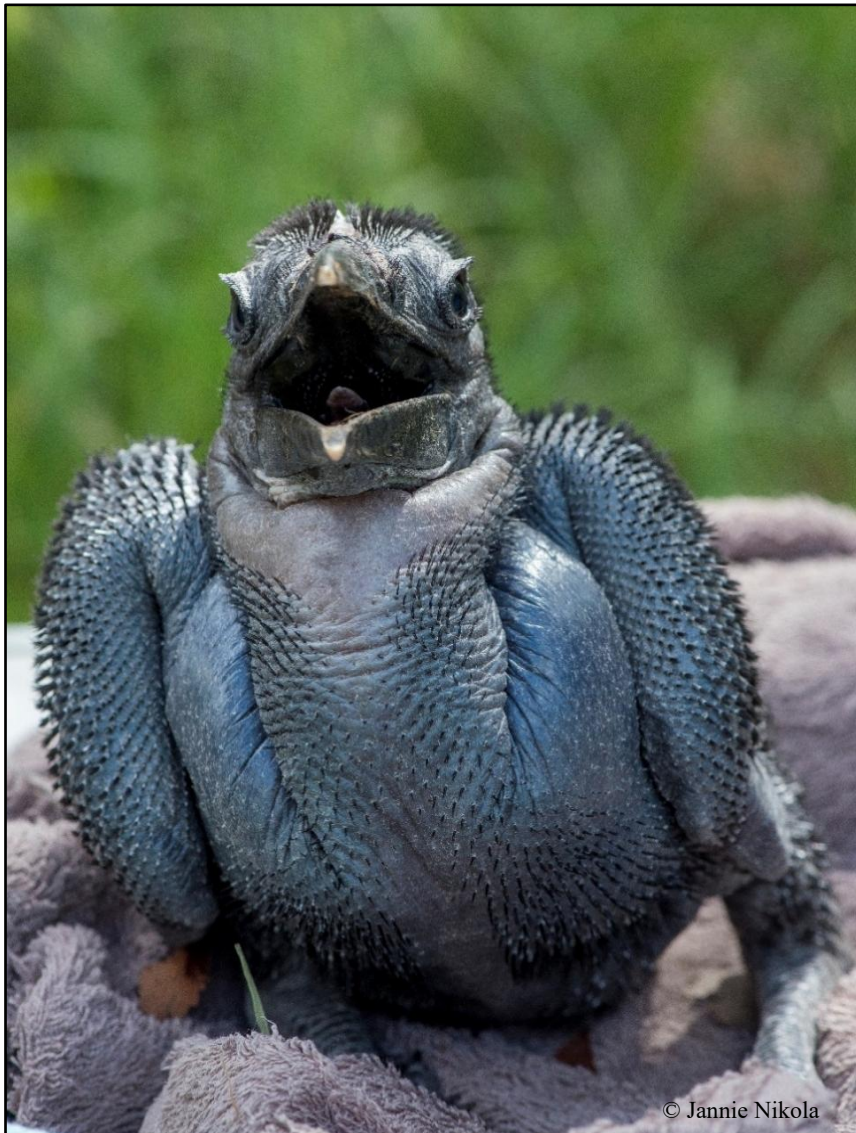
Model no.	Variable	Estimate	SE	95 % CI	P value
1	lay date	-0.31	0.08	- 0.48 / - 0.16	<0.001
2	days > 35 °C last 90 days	-0.26	0.08	- 0.42 / - 0.09	0.003
	lay date	-0.32	0.08	- 0.49 / - 0.16	<0.001
3	helpers	-0.05	0.10	- 0.25 / 0.15	0.607
	juveniles	0.00	0.09	- 0.18 / 0.18	0.987
4	mean T_{max} last 90 days	-0.25	0.08	- 0.42 / - 0.08	0.005
5	rainfall last 90 days	-0.24	0.08	- 0.41 / -0.07	0.006
<i>N</i> = 106, Random terms: female ID = 27, year = 13					

Table A3.3. The number of years each group and female has been monitored between 2012-2024 and summaries of breeding attempts, breeding success and egg size. While these data may give the impression that female age or breeding experience can be inferred, this is not possible with certainty. Monitoring at the study site only began in 2000, yet individuals can live for over 50 years, and some females may have bred previously in neighbouring Kruger National Park (KNP) before immigrating into the study population.

	Group name	Female ID	Number of years monitored	No. of breeding attempts	No. of successful attempts	Average Egg 1 size	Average Egg 2 size
1	Addger	ADD001	13	6	6	107.20	89.04
2	Argyle	ARG001	4	4	3	82.90	74.85
3	Caroline	CAR001	13	7	5	106.74	93.11
4	Charloscar	CHA001	13	1	1	112.32	90.6
5	Copenhagen	COP001	13	12	9	101.29	83.54
6	Dover	DOV001	5	3	2	86.69	69.36
7	Hermansburg	HER001	13	11	3	108.11	99.15
8	Ingwelala	ING001	2	2	1	85.64	57.3
9	Janovsky	JAN001	13	10	7	104.64	89.27
10	Java	JAV001	12	4	3	97.38	93.52
		JAV005	1	1	1	99.85	87
11	Jejane	JEJ001	8	4	0	79.44	71.17
12	Johnniesdale	JOH001	13	11	4	107.79	94.86
13	Karan Khaya	KAR001	13	12	11	96.76	93.9
14	Keer Keer	KEE001	13	1	1	111.8	88.28
15	Kempiana	KEM001	9	3	2	119.61	103.79
16	Lornay	LOR001	13	8	6	93.48	89.66
17	Masungulo	MAS001	3	1	0	90.7	82.3
18	Mohlabetsi	MOH001	5	3	3	120.14	104.39
19	Ntoma	NTO001	9	1	0	84.74	82.71
20	Ntsiri	NTS001	13	10	7	89.09	82.72
21	Pitlochry	PIT001	9	8	5	95.08	79.28
22	Rhino Road	RHI001	8	5	3	99.39	88.76
		RHI005	3	3	2	89.61	89.43
23	Senalala	SEN001	13	6	2	107.69	95.06
24	Strydom	STR001	13	7	2	101.42	83.28
25	Thornybush	THO001	9	7	5	89.71	82.94

CHAPTER 4

Early-life heat exposure affects growth and first-year survival in a large, slow-developing cooperative breeder



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4.1. Abstract

Global warming increasingly threatens wildlife populations, and developing offspring are particularly vulnerable to its impacts. In hot climates, temperatures exceeding species' thermal optima can limit growth and survival, yet how large, slow-developing birds respond to such conditions remains poorly understood. The cooperatively breeding southern ground-hornbill *Bucorvus leadbeateri* has a long nestling period (~3 months), increasing the chance of prolonged heat exposure during nestling development. In addition, as in many monitored bird populations, southern ground-hornbills can breed in artificial nest boxes, which may sometimes provide suboptimal thermal conditions compared to natural nests. Understanding how heat exposure affects ground-hornbill development is therefore essential for assessing climate-related vulnerability. In this study, I investigated nestling growth trajectories and first-year survival in southern ground-hornbills and assessed whether provisioning effort or helper presence offered any buffering against heat-related growth reductions. I collected body mass and size data from 68 nestlings (47 of which successfully fledged) across six breeding seasons (2019–2025), and quantified provisioning rates during early and late developmental stages. Higher nest temperatures were associated with reduced nestling mass, while high air temperatures were linked to reduced tarsus and wing growth, with no evidence that provisioning rates or helpers buffered these effects. Despite these early developmental constraints, high temperatures did not influence final fledging size or condition, suggesting that nestlings may employ compensatory growth when conditions improve. Post-fledging survival was not related to final fledging size or condition: instead, survival outcomes were negatively associated with high nest temperatures during development and high air temperatures during winter post-fledging. Together, these results provide novel evidence from a large, slow-developing bird that cumulative heat exposure reduces early-life survival, highlighting both the

species' vulnerability to climate change and the importance of temperature-sensitive conservation strategies for population persistence.

4.2. Introduction

Anthropogenic climate change is significantly impacting wildlife populations globally, altering behaviour, reproduction, and survival (Scheffers et al., 2016; Woodroffe, Groom & McNutt, 2017; Iknayan & Beissinger, 2018; Spooner, Pearson & Freeman, 2018). Developing young are particularly sensitive to environmental changes due to the high energy demands of rapid growth (Lindström, 1999; Nord & Giroud, 2020). Biological impacts of temperature are often quadratic, due to underlying non-linearity of physiological responses (Cunningham, Gardner & Martin, 2021), meaning exposure to warming can have opposite sign effects depending on background conditions relative to a thermal optimum (Levillain, Reichert & Massemin, 2025). Heat exposure above thermal optima has been found to reduce growth rates and survival across taxa (Selong et al., 2001; Cunningham et al., 2013; Andrew et al., 2017; Pérez-Barbería et al., 2020; van de Ven et al., 2020; Van de Ven, Fuller & Clutton-Brock, 2020; Oswald et al., 2021; Holmes et al., 2023; Khera et al., 2023; Zhang et al., 2023; Malik et al., 2025). While not always immediately lethal, the sub-lethal impacts of heat can have lasting consequences for individual fitness and population viability (Conradie et al., 2020; Pattinson et al., 2022). Therefore, understanding how warming affects offspring growth is important for assessing species vulnerability to climate change (van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021; Sauve, Friesen & Charmantier, 2021), and more research is needed globally to capture variation across species and life histories (Levillain, Reichert & Massemin, 2025).

Growth rates can be directly constrained by heat-induced physiological demands. For example, the increase in energy required for heat dissipation may reduce the energy available for growth (Dawson, Lawrie & O'Brien, 2005; Speakman & Król, 2010) and increase the risk

of dehydration (Catry et al., 2015; McKechnie & Wolf, 2019). If nestlings cannot dissipate enough heat, rising body temperatures can disrupt cellular metabolism, imposing performance costs (McKechnie & Wolf, 2019; Diehl et al., 2023). For altricial bird species, nestlings are confined to the nest and unable to endogenously regulate their body temperature during early developmental stages, relying instead on parental brooding and nest microclimate to maintain an optimum body temperature (Dunn, 1975; Weeks et al., 2022). Therefore, the nest microclimate can play a direct role in shaping nestling growth and development, especially during the early stages post-hatch (McCarty & Winkler, 1999; Catry et al., 2015; van de Ven et al., 2020; Corregidor-Castro & Jones, 2021). This might be exacerbated in populations of cavity nesting species where nest boxes have replaced natural cavities, either for monitoring convenience or as a result of habitat destruction and a lack of old trees which make natural cavities increasingly rarer (Camprodon, Salvanyà & Soler-Zurita, 2008; Larson et al., 2015; Carstens et al., 2019c; Scott-Baumann, Morgan & Cogan, 2022; Rzępała et al., 2023).

High temperatures can also limit growth indirectly by constraining parental food provisioning (van de Ven et al., 2020; Bourne et al., 2021) through declines in resources and prey activity (Garcia-Heras et al., 2017; Barras et al., 2021), and increased thermoregulatory demands that alter adult behaviour to favour shade-seeking and other thermoregulatory behaviours over foraging (du Plessis et al., 2012; Cunningham et al., 2013; van de Ven, McKechnie & Cunningham, 2019). Furthermore, as nestlings grow, their energetic and nutritional demands increase (Conrad & Robertson, 1993; Luck, 2001; te Marvelde et al., 2009; Browning et al., 2012; Wiebe & Slagsvold, 2014), which may require adults to increase food provisions. If heat-related foraging constraints for adults occur frequently, nestlings may not receive sufficient food or water for optimal growth and development (Oswald, Lee & Smit, 2018) potentially compromising developmental trajectories and limiting fledging size. These possible effects are concerning since smaller nestling and fledging size is commonly associated

with reduced lifetime fitness and lower survival rates in many small-to-medium sized bird species (Magrath, 1991; Lindström, 1999; Green & Cockburn, 2001; Greño, Belda & Barba, 2008; Salaberria et al., 2014; Rodríguez et al., 2016; Bourne et al., 2020a; van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021). Reduced survival is particularly concerning for long-lived species, which rely on survival more than fecundity to maximise their lifetime reproductive output (Clutton-Brock, 1988). However, there is limited information on whether large, slower-developing species exhibit similar growth and survival responses to high temperatures.

In cooperatively-breeding species, the number and behaviour of helpers can influence the amount of care offspring receive (Savage, Russell & Johnstone, 2015; MacLeod & Brouwer, 2018; Josi, Taborsky & Frommen, 2020), with the potential to mitigate negative effects of heat on nestling growth. Helpers may increase total provisioning (additive care) (Hatchwell, 1999; te Marvelde et al., 2009; Van Boheemen et al., 2019), or reduce the workload of breeders while maintaining overall provisioning (load-lightening) (Crick, 1992; Van Boheemen et al., 2019). These two strategies can occur simultaneously (Covas, du Plessis & Doutrelant, 2008; Van Boheemen et al., 2019; Middleton, 2022), and helpers have been associated with increased fledgling size and survival in some species (Legge, 2000; Ridley & Raihani, 2007; te Marvelde et al., 2009; D'Amelio et al., 2022) and have been suggested to buffer the impacts of adverse environmental conditions (Covas, du Plessis & Doutrelant, 2008; Rubenstein, 2011). However, recent studies found little evidence that helpers mitigate the negative effects of high temperatures on nestling size (Bourne, Ridley, Spottiswoode, et al., 2021; D'Amelio et al., 2022; Middleton et al., 2026) and may instead improve adult fitness more than offspring outcomes (Li et al., 2015; Wiley & Ridley, 2016; Middleton et al., 2026); but see Bourne, Ridley, McKechnie, et al., 2021; Bourne, Ridley & Cunningham, 2023, who found no detectable fitness benefits for adults), highlighting the need for further investigation.

In this study, I investigated the effect of high temperatures on growth and survival in the southern ground-hornbill *Bucorvus leadbeateri* (hereafter ‘ground-hornbill’), a large, slow-developing, cooperatively breeding bird endemic to sub-Saharan Africa. Ground-hornbill nestlings hatch altricial and remain in the nest for around three months (Kemp, 1980; Carstens et al., 2019a), during which time their growth could be strongly influenced by nest temperatures and parental care. They are obligate cavity nesters, vulnerable to the loss of large trees across their range, which has contributed to population declines, and in South Africa, they are classified as Endangered (Kemp & Rose, 2025). To mitigate this, artificial nest boxes are widely used as a conservation tool and are readily accepted by ground-hornbills (Wilson & Hockey, 2013; Carstens et al., 2019c). However, nest boxes may not buffer high air temperatures as effectively as some natural tree cavities (Combrink et al., 2017; Pattinson et al., 2022), although in some cases they can provide better protection from external conditions (such as reducing direct sunlight or exposure to rain) than suboptimal natural nests (Carstens et al., 2019a; pers.obs.). Given the adverse impacts of high temperatures on nestling development in other species (Cunningham et al., 2013; Mainwaring & Hartley, 2016; Andrew et al., 2017; van de Ven et al., 2020; Bourne et al., 2021; Sauve, Friesen & Charmantier, 2021), it is important to understand how heat affects developing ground-hornbills, particularly since artificial nests may expose them to different thermal conditions than natural nests. Previous research on ground-hornbills found that high temperatures were associated with reduced provisioning rates (Middleton, 2022), and lighter fledglings, with no evidence of helpers buffering the effects of high temperatures (Middleton et al., 2026). However, Middleton (2026) only analysed the size of nestlings at fledging age. For large-bodied, slow-reproducing birds, the potential for cumulative or age-specific effects of heat on growth and survival remains unknown, yet may have important consequences for population persistence.

In this chapter, I modelled the first growth curve for a wild population of ground-hornbills and investigated how high temperatures influence growth rate trajectories and survival outcomes. Although ground-hornbills are adapted to warm environments, they breed during the hottest months of the year and are increasingly exposed to temperatures that may exceed historical thermal conditions and physiological limits. I therefore hypothesised that high temperatures would negatively affect growth rates, constraining nestlings' fledging size and condition, thereby reducing survival probabilities, and that these effects could be mitigated by the presence of helpers. Specifically, I predicted that nestling growth would be negatively correlated with higher temperatures, due to direct physiological effects of heat and indirect effects of reduced parental provisioning. The presence of helpers may mitigate negative impacts of high temperatures by allowing groups to maintain provisioning rates to nests, but previous studies have found limited evidence for such buffering; therefore, helper effects may be weak or absent. Finally, I predicted that high temperatures would reduce post-fledging survival, while larger, heavier fledglings would have a higher probability of survival.

4.3. Methods

Data were collected over six breeding seasons between October 2019 and April 2025. Groups each have access to at least one nest within their home range: 30 artificial nest boxes, and 5 natural nests were monitored each season. To determine active nests and predict hatching dates, each nest was visited every 7–10 days from the beginning of October to the end of December, each breeding season. Ground-hornbills lay two eggs 3–5 days apart. When eggs were found, hatching dates were estimated based on the known incubation period (40–42 days) (Carstens et al., 2019a; Middleton, 2022) for newly laid eggs, and, when necessary, egg candling was used to estimate the stage of embryonic development (Resendiz et al., 2024) (Chapter 3). Nestlings fledged at an age of 85 days on average (range: 77–97 days).

4.3.1. Chick measurements

Chicks were measured (body mass, tarsus length, bill length, and wing length, details below) on days 1, 8, 20, 40, 60 and 75 post-hatching (Figure 4.1). In some cases, the first measurement occurred between days 2 and 4 ($N = 22$) due to small inaccuracies in predicting hatching dates. Measurements on other target days occasionally deviated by a maximum of two days due to logistical constraints (typically, adverse weather conditions). A total of 68 chicks were measured, of which 47 survived and fledged. All chicks that did not survive were depredated, either by leopards *Panthera pardus*, or genets *Genetta* spp. (see Chapter 1: Study species, Figure 1.7), which typically occurred within the first 30 days, as confirmed by camera trap footage or physical evidence at the nest site. On days 1, 8 and 20, body mass measurements (± 0.1 g) were taken by placing chicks on a top-pan scale. On days 40, 60 and 75 chicks were placed in a cloth bag and weighed with a hanging scale (± 10 g), due to their large size at these stages. Tarsus and bill length were measured (± 0.1 mm) using digital Vernier calipers, and wing length was measured using a long steel ruler (± 0.1 mm). Growth rates were calculated between successive measurements as: % mass change per day (ΔMass), % tarsus change per day (ΔTarsus) and % wing change per day (ΔWing) by the following:

$$\Delta\chi = \left(\frac{\chi^1 - \chi^2}{\chi^1} \right) / \Delta t \times 100$$

where $\Delta\chi$ is change in measurement (mass, tarsus, wing), χ^1 is initial measurement, χ^2 is final measurement and Δt is the number of days between measurements. This enabled the full dataset to be used, even when measurements did not fall exactly on target days. Chicks were sexed from blood samples collected on day 8 or day 75.



Figure 4.1. Ground-hornbill chicks at different ages during measurements. Chicks were measured on days 1, 8, 20, 40, 60, and 75 post-hatching.

4.3.2. Temperature data

Daily maximum temperature (°C) and rainfall (mm) data were obtained from an onsite weather station (see Chapter 1: General methods). From January 2025 – March 2025 the station failed to record data; therefore, data were obtained from a nearby weather station in Hoedspruit (18km from the onsite station) and calibrated via linear regression (Figure A4.1). Thermochron iButtons (see Chapter 1: General methods) were used to record internal nest temperatures in all active nests (N = 68), however, data were not obtained for three nests due to iButton recording failures. In this study only 4 out of the 68 chicks monitored were from a natural nest, all of which were from the same site sampled across multiple years.

4.3.3. Provisioning data

To determine provisioning rates, food size, and the number of helpers and juveniles in each group, camera traps (Browning trail cameras) were placed at nest sites (see Chapter 1: General methods) during two periods of nestling development: the early nesting period (days 1–8) and the late nesting period (days 40–60). Camera traps were placed approximately 1–3 metres from the nest entrance and were set to record 20 second videos with 5-second intervals between recordings when triggered by movement. They operated for the entire duration of the early and late nesting period (24 hours a day). As ground-hornbills are large birds and typically spend more than one minute at the nest entrance, provisioning events were reliably detected (Figure 4.2). The date, time, and individual identity (see Chapter 1: General methods) were recorded each time a bird came to the nest.

Females usually remain inside the nest with the chick for the first 20 days. After that, they spend more time away from the nest but sometimes enter the nest to feed the chick when returning with the group. If an individual delivered food to the female or chick inside the nest, this was considered a provisioning event (Figure 4.2). Ground-hornbills are known for their multi-prey provisioning behaviour, and ‘parcel’ provisioning, in which food and nesting materials are collected, with the food item wrapped amongst grass and large leaves (Kemp, 1980; Middleton, 2022). They are generalist feeders, capable of capturing a wide range of prey from small invertebrates to larger animals, including birds, mammals such as hares, and reptiles such as snakes and lizards. The size of the food item(s) held in the birds’ bills was classified using a scoring system based on the depth of the bill at its deepest point (including the casque) (Figure A4.3). The following categories were established: **1** = single small item, that is $\frac{1}{4}$ size of depth of the bill, **2** = item(s) $\frac{1}{2}$ size of depth of bill, **4** = item(s) equal to the depth of the bill, **6** = item(s) $1\frac{1}{2}$ times size of depth of bill, **8** = item(s) double the depth of bill, **12** = item(s) triple the depth of bill, **16** = item(s) four times the depth of bill. The food score

system was developed for this study using methods and classification criteria adapted from Middleton (2022), an unpublished PhD thesis investigating provisioning behaviour in ground-hornbills. As the size of food items increased, incremental size differences between categories became less pronounced. When birds deliver a parcel, small food items can go unnoticed, therefore, parcels with invisible food items received a score of 1, presuming an item was present, but this may be an underestimation of the actual size. Food items with a score of 4 or more were usually visible in the parcels.

To account for the large variation in prey size, provisioning rates were calculated as the sum of food scores over the period under consideration rather than as a count of provisioning events, providing a more accurate representation of the biomass delivered to chicks. The total food score for each chick was divided by the number of days between measurements to calculate a mean provisioning rate per day. This approach accounted for differing intervals between chick measurements (due to logistical constraints explained earlier); for example, some nests had 18 days between measurements, while others had up to 21, allowing for comparability across nests. Due to occasional camera trap failures (most caused by battery depletion or animal interference) I applied conservative criteria for data inclusion. For the early growth stage (d 1–8), only data with complete video coverage of the interval were used ($N = 47$). For the later stage (d 40–60), I included data if no more than two consecutive days of footage were missing ($N = 36$), as this was over a longer period. These criteria ensured adequate provisioning data while retaining sufficient sample sizes for analyses.



Figure 4.2. Camera trap footage showing a female ground-hornbill bringing food to the nestling.

4.3.4. Number of helpers and juveniles

Data were obtained for 19 groups, with group composition identified using the camera traps mentioned above (see Chapter 1: General methods). Helpers were defined as adult and subadult group members, as these age classes contribute significantly to key cooperative behaviours such as territory defence and chick provisioning (Middleton, 2022). Juveniles from previous broods, on the other hand, do not contribute significantly to these activities (Middleton, 2022) and have been observed stealing food from chicks in the nest (pers. obs.), so were included separately in analyses and not as helpers, as their presence may reflect either competition for resources with the chick or higher-quality groups or territories associated with improved breeding success, potentially leading to opposing effects.

4.3.5. Juvenile survival

To assess post-fledging overwinter survival, the presence of juveniles within groups was recorded at the start of the following breeding season. Camera traps were deployed each October at nest sites where a chick had successfully fledged the previous season. Groups

frequently revisit and defend nest sites, even in non-breeding years: this behaviour enabled reliable detection of group members, including juveniles. Survival was recorded as a binary response (0 = did not survive, 1 = survived) based on juvenile presence. Ground-hornbill juveniles remain with their natal group for extended periods post-fledging. Long-term observations at the study site found that, on average, females dispersed 12 months after fledging, while males dispersed after 48 months (Carstens et al., 2019b). More recent observations, however, have recorded males staying for over 16 years and females for up to six years (pers.obs.). These extended associations with the natal group support the use of presence at the nest site the following breeding season (typically 6 – 8 months post fledging) as a robust indicator of juvenile survival.

4.3.6. Statistical analyses

Statistical analyses were conducted in R v 4.4.1 (R core Team 2024). Linear mixed-effect models and generalised linear-mixed effect models were fitted using the *lme4* package (Bates et al., 2015) and the *MuMIn* package was used for model selection (Bartoń, 2020) unless otherwise stated. Akaike's information criterion corrected for small sample size (AICc) was used to select top models, with models having $\Delta\text{AICc} < 2$ considered competitive and retained for inference (Harrison et al., 2018). Variance inflation factors (VIF) in the *car* package (Fox, Weisberg & Price, 2025) were used to test for collinearity between explanatory variables. Continuous variables were centred and scaled. Model assumptions were assessed with the *performance* package (Lüdtke et al., 2021). Effect sizes, standard errors, and 95% confidence intervals were reported from top models ($\Delta\text{AICc} < 2$). Effects were reported as significant if confidence intervals did not overlap zero.

Growth curves for mass, tarsus and wing length

Growth curve analyses of body mass, tarsus and wing length were conducted on chicks that fledged (N = 47) using measurements from days 1, 8, 20, 40, 60, and 75. Growth curves were

initially fitted for each measurement (mass/tarsus/wing) comparing Gompertz, logistic, log-logistic, and Weibull functions, which are commonly applied nonlinear models in animal growth studies (Engelbrecht et al., 2007; Avalos-Castro et al., 2022; Ghavi Hossein-Zadeh, 2025). Model fit was evaluated using Akaike's Information Criterion (AIC), and the best-fitting functions (lowest AIC) were ranked and selected using the *drc* package (Ritz & Streibig, 2012). To test for sex differences, I fitted combined growth curve models including sex as a grouping factor, in the *drc* package (Ritz & Streibig, 2012), allowing for comparison of asymptotic size, growth rate, and age at 50% growth between males and females. Data used were collected from 47 chicks over 6 breeding seasons.

Growth rates

To assess the effects of temperature on chick growth trajectories, I fitted separate linear mixed-effects models (LMMs) for body mass, tarsus, and wing growth rates, to understand age-related changes in mass, skeletal size and feather development. Studying growth trajectories is important because they determine the size and condition chicks achieve at fledging, which can be key predictors of post-fledging survival (Magrath, 1991; Green & Cockburn, 2001; Bourne et al., 2020b). Growth was measured across five age intervals from hatching to fledging: (1) days 1–8, (2) 8–20, (3) 20–40, (4) 40–60, and (5) 60–75. The response variables used were % daily gain in mass (ΔMass), tarsus length (ΔTarsus) and wing length (ΔWing), calculated as described earlier.

Step 1: To determine which environmental variable was most strongly associated with chick growth, I used an AICc-based candidate model approach. Temperature variables compared included mean maximum nest temperature (mean T_{maxnest}), mean maximum air temperature (mean T_{maxair}), the number of days where nest temperature exceeded 35 °C (days $> 35\text{ }^{\circ}\text{C}_{\text{nest}}$), and air temperature exceeded 35 °C (days $> 35\text{ }^{\circ}\text{C}_{\text{air}}$). Rainfall was also tested

using cumulative rainfall over 30, 60, and 90 days prior to each measurement (rainfall₃₀, rainfall₆₀, rainfall₉₀), due to uncertainty in the relevant temporal window. These predictors were selected *a priori* based on known effects on breeding outcomes and survival in other bird species (Bourne et al., 2020b; van de Ven et al., 2020). The model selection set included age and sex as fixed effects, with chick ID, group ID, and season included as random effects to account for repeated measures and non-independence among observations. The best-supported temperature or rainfall variable (lowest AICc) was then retained for final model sets.

Step 2: Final growth models included the best supported weather variables (Mean T_{maxnest} for ΔMass , and mean T_{maxair} for ΔTarsus and ΔWing), age, sex, helpers, and juvenile number as fixed effects. Interactions between temperature and age interval and between temperature and helpers were also included to test for potential age-specific and helper buffering effects. Chick ID, group ID, and season were included as random effects. All chicks were incorporated regardless of whether they fledged ($N = 237$ measures of 57 chicks for tarsus and mass, $N = 212$ measures of 56 chicks for wing length). The lower sample size for wing length reflects missing measurements for some chicks at certain ages.

Step 3: Building on this, I focused on two developmental ages (days 1–8 [d1-8] and days 40–60 [d40-60]) where provisioning data were available (*mass and tarsus*: $N = 87$ measures of 53 chicks; *wing*: $N = 80$ measures of 52 chicks), to explore whether provisioning rates influenced growth and potentially buffered chicks from the effects of high temperatures. Provisioning rate was added to the final growth models (step 2), for these age intervals. Interactions between temperature and age and temperature and provisioning were included to assess age-specific effects, and whether provisioning buffered the effects of high temperatures on growth. The same best-supported temperature metrics from the main analysis were retained

(Mean T_{maxnest} for ΔMass , and mean T_{maxair} for ΔTarsus and ΔWing growth). Chick ID, group ID and season were again included as random effects.

Path analyses were initially explored to assess the direct and indirect effects of temperature on chick growth, via nest temperatures and provisioning rates, but sample sizes were insufficient to obtain reliable estimates. Therefore, linear mixed-effects models were used instead. Unlike in previous studies (e.g. Middleton, 2022) temperature did not directly affect provisioning rates in my dataset (see Appendix; Table A4.15, Table A4.16, Figure A4.5), allowing both temperature and provisioning to be included simultaneously as predictors in chick growth models.

Chick fledging size and condition

Linear mixed-effects models were used to assess how mean T_{maxair} , mean T_{maxnest} , and cumulative rainfall (measured from hatching to day 75 [d75]), number of helpers and juveniles, influenced fledging body size and condition. Fledging size was summarised using a principal component analysis (PCA) (Baur & Leuenberger, 2011) of mass, tarsus length, and wing length measured at d75. The first principal component (PC1) explained 65% of the variance and was interpreted as an index of overall fledging size and used as a response variable in linear mixed-effects models (see Appendix; Table A4.17). Body condition was calculated separately as a size-corrected body condition index (mass/tarsus length on d75) (Labocha & Hayes, 2012) and modelled separately. Because these indices represent a single measurement per chick at the end of the nestling period, sample size was limited ($N = 44$) therefore, weather and social variables were modelled in separate models. All models included sex as a covariate and group ID and season as random effects.

Chick size, temperature and post-fledging survival

To investigate whether post-fledging survival over winter (binary outcome: 0 = did not survive, 1 = survived) was influenced by temperature exposure, morphometric traits, rainfall, or social factors, I fitted generalized linear mixed-effects models (GLMMs) using a binomial distribution (logit link). Temperature predictors included: (1) the number of days above 35 °C during the nestling period for air temperature (days > 35 °C_{air}) and nest temperature (days > 35 °C_{nest}), (2) mean maximum nest and air temperatures during the nestling period (mean T_{maxnest}, mean T_{maxair}), and, (3) the number of days above 35 °C and mean maximum temperature during the post-fledging winter period (days > 35 °C_{winter}, mean T_{maxwinter}), due to previously observed impacts of winter heat in this species (Middleton, 2022; see Chapter 2). These temperature variables were tested both individually and in additive models as I expected they may have cumulative impacts, and nestling period temperatures were not correlated with subsequent winter temperatures. Additional predictors included chick fledging size (PC1) and body condition. I also tested the effects of egg size (see Chapter 3), fledgling sex, rainfall during the nestling and post-fledging winter periods, and the number of helpers and juveniles in the group. Due to the limited sample size (N = 35) as survival data were only obtained for the years 2020 - 2024, I used a simplified model-selection approach in which non-temperature predictors were tested individually, while temperature variables were tested either individually or in biologically justified pairs (e.g., nest + winter heat exposure). All models included group ID as a random effect and season was added as a random effect only when seasonal variation was not accounted for by fixed effects such as seasonal temperature or rainfall.

4.4. Results

4.4.1. Growth trajectories

Growth curves for both sexes were best described by the four-parameter Weibull model (W2.4) for mass; the logistic model (L.3) for tarsus length; and Gompertz (G.4) for wing length (Table A4.1, Table A4.3, Table A4.5). Males reached significantly higher asymptotic values for mass (3320.3 ± 44.4 g) and tarsus length (160.7 ± 1.1 mm) than females (2874.3 ± 35.0 g and 149.9 ± 0.9 mm, respectively), whereas wing length asymptotes did not differ significantly between sexes (*males*: 597.2 ± 26.6 mm; *females*: 580.5 ± 17.2 mm). Growth rate slopes were similar between sexes for mass (*males*: 2.07 ± 0.12 g/day, *females*: 2.00 ± 0.11 g/day), tarsus length (*males*: 0.09 ± 0.00 mm/day, *females*: 0.09 ± 0.00 mm/day), and wing length (*both sexes*: -0.04 ± 0.00 mm/day). Males reach 50% of their final tarsus length slightly later than females (*males* = 21.6 ± 0.4 , *females* = 20.4 ± 0.4 days), whereas no significant sex differences were observed in the age at 50% of final mass (*males* = 31.76 ± 0.81 , *females* = 30.73 ± 0.75 days) or wing length (*males* = 43.1 ± 1.3 , *females* = 43.0 ± 0.9 days) (Table A4.2, Table A4.4, Table A4.6, Figure 4.3).

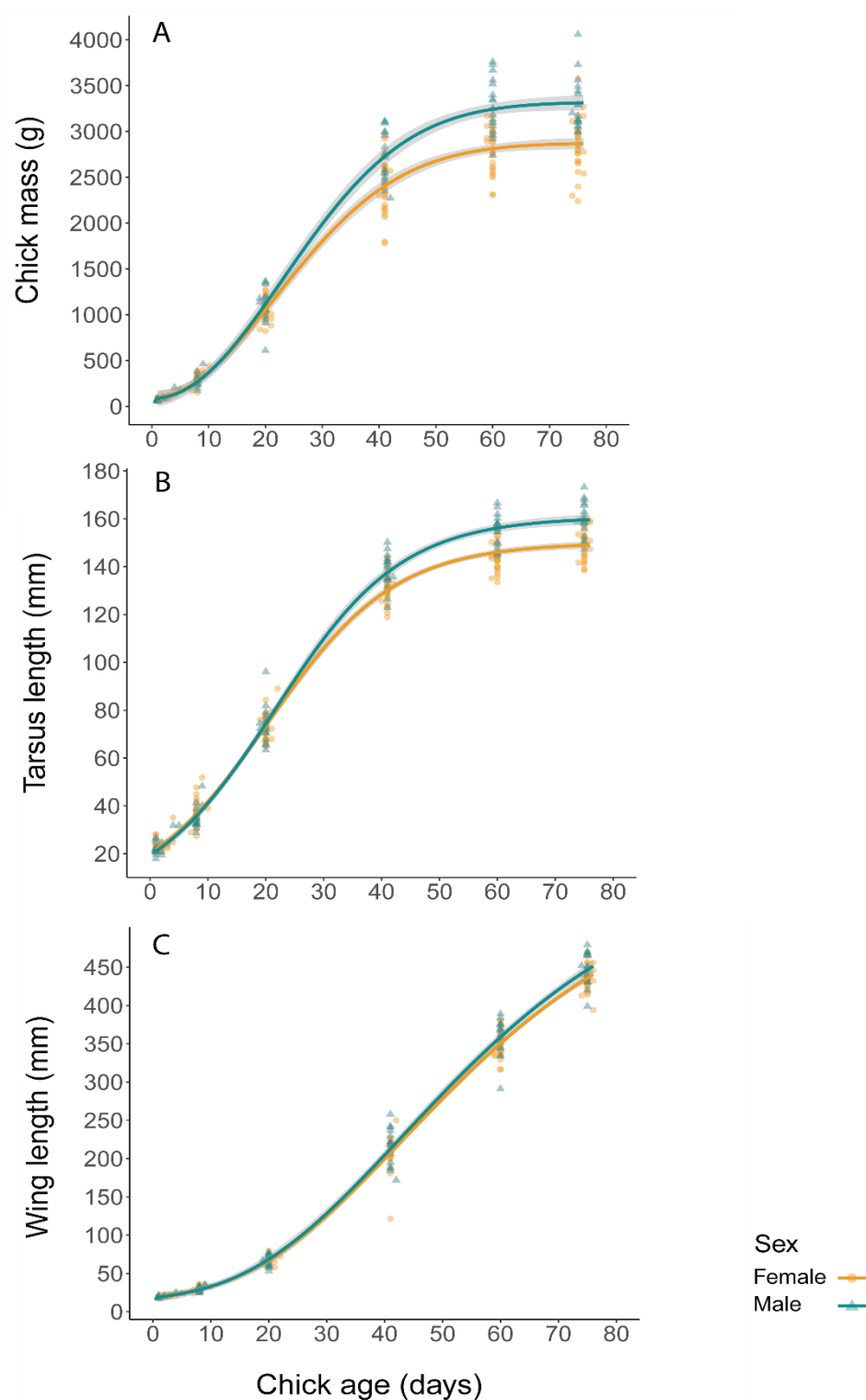


Figure 4.3. Growth curves of southern ground-hornbill morphological traits. Predicted growth trajectories are shown for males (green) and females (orange) with shaded areas indicating 95% confidence intervals around the fitted mean growth trajectories. Observed values are shown as green triangles (males) and orange circles (females). (A) Body mass (g), predicted from a four-parameter Weibull model. (B) Tarsus length (mm), predicted from a logistic model. (C) Wing length (mm), predicted from a Gompertz model.

4.4.2. Temperature effects on chick growth rates during development stages

Chick mass: Model comparison identified mean T_{maxnest} as the best weather predictor of body mass growth between measurement intervals (ΔMass) with the lowest AICc value (Table 4.1). The top model explaining ΔMass across the different stages included mean T_{maxnest} , sex and age (Table 4.2). Higher mean T_{maxnest} was significantly correlated with reduced ΔMass (estimate = -1.11 ± 0.35 , 95% CI = $[-1.79 / -0.43]$; Table A4.9, Figure 4.4). Males gained significantly more mass between measurements than females (estimate = 1.79 ± 0.70 , 95% CI = $[0.42 / 3.17]$). Mass gain was highest during ages d1–8 (estimate = 35.86 ± 0.79 , 95% CI = $[34.25 / 37.36]$) and was significantly lower during all later ages (*d8–20*: estimate = -13.27 ± 1.05 , 95% CI = $[-15.34 / -11.21]$, *d20–40*: estimate = -29.86 ± 1.06 , 95% CI = $[-32.00 / -27.80]$, *d40–60*: estimate = -35.71 ± 1.08 , 95% CI = $[-37.80 / -33.61]$, *d60–75*: estimate = -36.51 ± 1.07 , 95% CI = $[-38.63 / -34.39]$; Table A4.9, Figure 4.4).

Table 4.1. Model selection table to identify best weather variable explaining ΔMass in ground-hornbill chicks at different ages, with top model highlighted in bold (AICc < 2) and was used as weather variable in final model set (mean T_{maxnest}). Models included sex and age as fixed factors with group ID, chick ID and season as random factors.

Model	AICc	Δ AICc	Weight
mean T_{maxnest} + sex + age	1485.3	0.00	0.924
mean T_{maxair} + sex + age	1492.8	7.49	0.022
rainfall ₃₀ + sex + age	1493.6	8.32	0.014
days > 35 °C _{air} + sex + age	1494.1	8.77	0.012
days > 35 °C _{nest} + sex + age	1494.1	8.81	0.011
rainfall ₉₀ + sex + age	1494.3	9.02	0.010
rainfall ₆₀ + sex + age	1495.1	9.84	0.007
null	1985.0	499.76	0.000
<i>N</i> = 237, Random terms: group ID = 19, chick ID = 57, season = 6			

Table 4.2. Model selection table for factors explaining ΔMass in ground-hornbill chicks across different ages, with the top model highlighted in bold ($\text{AICc} < 2$). Models investigated the effects of mean T_{maxnest} and number of helpers on chick growth, including sex and age as fixed factors, and group ID, chick ID and season as random factors.

Model no.	Model	AICc	ΔAICc	Weight
1	mean T_{maxnest} + sex + age	1485.3	0.00	0.690
2	mean T_{maxnest} + helpers + juv + sex + age	1488.5	3.23	0.137
3	mean T_{maxnest} * helpers + sex + age	1489.5	4.19	0.085
4	mean T_{maxnest} * age + sex	1490.0	4.75	0.064
5	mean T_{maxnest} * age + helpers + juv + sex	1493.0	7.74	0.014
6	mean T_{maxnest} * helpers + juv + mean T_{maxnest} * age + sex	1493.8	8.51	0.010
5	mean T_{maxnest} * age * helpers + juv + sex	1509.9	24.65	0.000
6	null	1985.0	499.76	0.000
<i>N = 237, Random terms: group ID = 19, chick ID = 57, season = 6</i>				

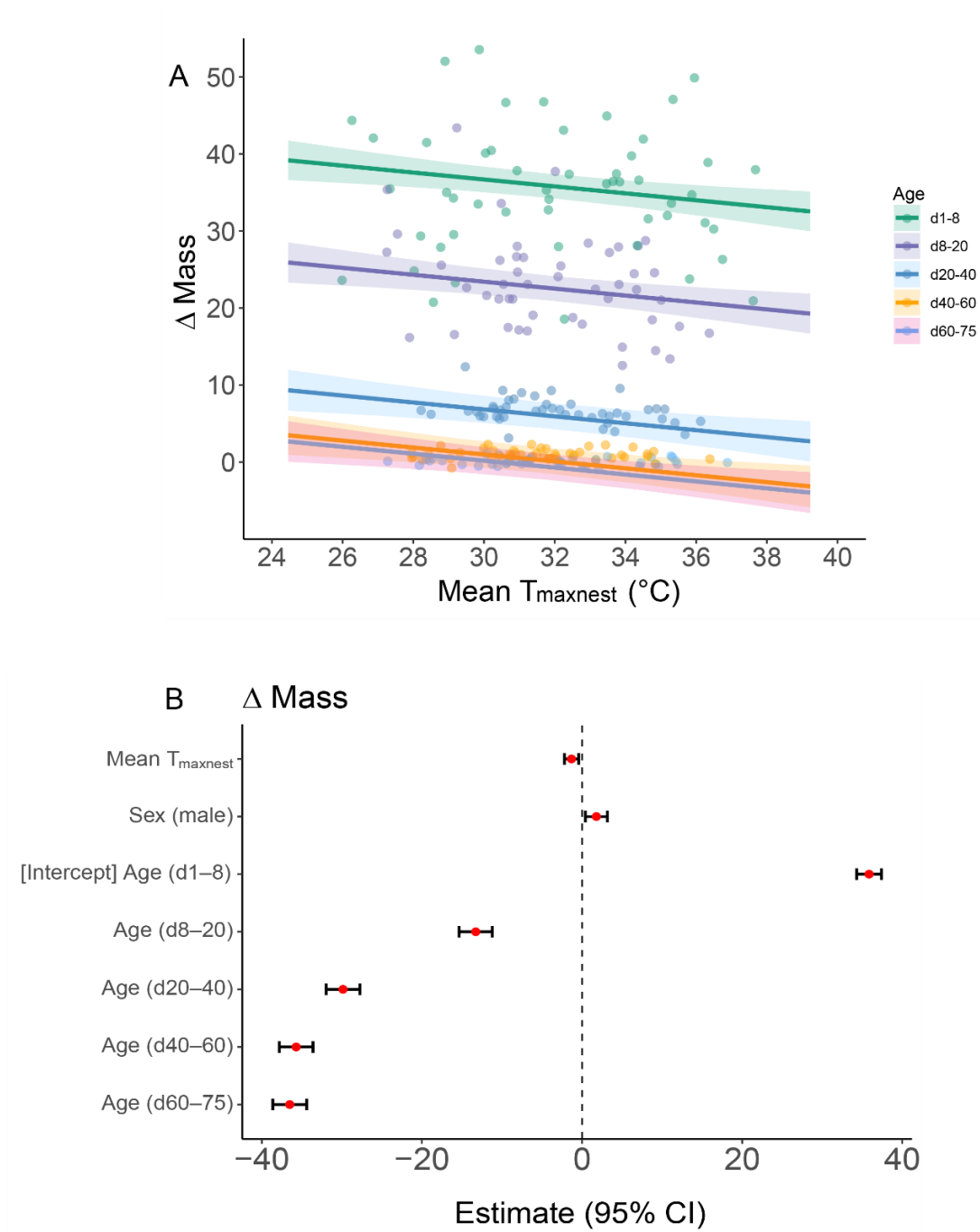


Figure 4.4. (A) Predicted linear relationship between mean T_{maxnest} and ΔMass across different chick ages. Lines represent predicted values for each age group from model 1, where the effect of T_{maxnest} is estimated as a main effect and averaged across ages. Shaded areas indicate 95% confidence intervals and points show observed data. Colours correspond to chick age in days. (B) Model means and 95% confidence intervals for variables included in model 1 predicting ΔMass . Filled red circles indicate statistically significant effects.

Tarsus length: Mean T_{maxair} was the best weather predictor of tarsus growth (ΔTarsus) with the lowest AICc value, though days $> 35^\circ\text{C}_{\text{air}}$ was included in a competing model (Table 4.3). The top model explaining ΔTarsus included mean T_{maxair} , age and sex (Table 4.4). Higher mean T_{maxair} was significantly correlated with reduced ΔTarsus (estimate = -0.26 ± 0.08 , 95% CI = $[-0.42 / -0.09]$, Table A4.10, Figure 4.5). Sex had no significant effect on ΔTarsus (Table A4.10). Tarsus growth was greatest during ages d1–8 (estimate = 8.01 ± 0.24 , 95% CI = $[7.51 / 8.49]$) and d8–20 (estimate = 0.81 ± 0.24 , 95% CI = $[0.33 / 1.29]$), and significantly lower during later ages: (d20–40: estimate = -4.11 ± 0.25 , 95% CI = $[-4.60 / -3.62]$, d40–60; estimate = -7.55 ± 0.25 , 95% CI = $[-8.04 / -7.07]$, d60–75: estimate = -7.92 ± 0.25 , 95% CI = $[-8.41 / -7.43]$; Table A4.10, Figure 4.5).

Table 4.3. Model selection table to identify best weather variable explaining ΔTarsus in ground-hornbill chicks at different ages, with top models with $\Delta\text{AICc} < 2$ highlighted in bold. Only one weather variable with lowest AIC was selected for final models (mean T_{maxair}). Models included sex and age as fixed factors with group ID, chick ID and season as random factors.

Model	AICc	ΔAICc	Weight
mean T_{maxair} + sex + age	801.0	0.00	0.616
days $> 35^\circ\text{C}_{\text{air}}$ + sex + age	802.3	1.36	0.312
days $> 35^\circ\text{C}_{\text{nest}}$ + sex + age	807.1	6.12	0.029
mean T_{maxnest} + sex + age	807.6	6.60	0.023
rainfall ₆₀ + sex + age	809.9	8.90	0.007
rainfall ₉₀ + sex + age	810.0	9.07	0.007
rainfall ₃₀ + sex + age	810.1	9.14	0.006
null	1327.2	526.20	0.000
<i>N</i> = 237, Random terms: group ID = 19, chick ID = 57, season = 6			

Table 4.4. Model selection table for factors explaining Δ Tarsus in ground-hornbill chicks across different ages with top model highlighted in bold (AICc < 2). Models investigated the effects of mean T_{maxair} and number of helpers on chick growth, including sex and age as fixed factors, and group ID, chick ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Weight
1	mean T_{maxair} + sex + age	801.0	0.00	0.720
2	mean T_{maxair} * helpers + juv + sex + age	804.1	3.12	0.151
3	mean T_{maxair} + helpers + juv + sex + age	803.0	3.68	0.114
3	mean T_{maxair} * age + sex	809.2	8.20	0.012
4	mean T_{maxair} * age + helpers + juv + sex	813.1	12.12	0.002
5	mean T_{maxair} * helpers + juv + mean T_{maxair} * age + sex	815.1	14.16	0.001
6	mean T_{maxair} * age * helpers + juv + sex	828.8	27.79	0.000
7	null	1327.2	526.20	0.000
<i>N = 237, Random terms: group ID = 19, chick ID = 57, season = 6</i>				

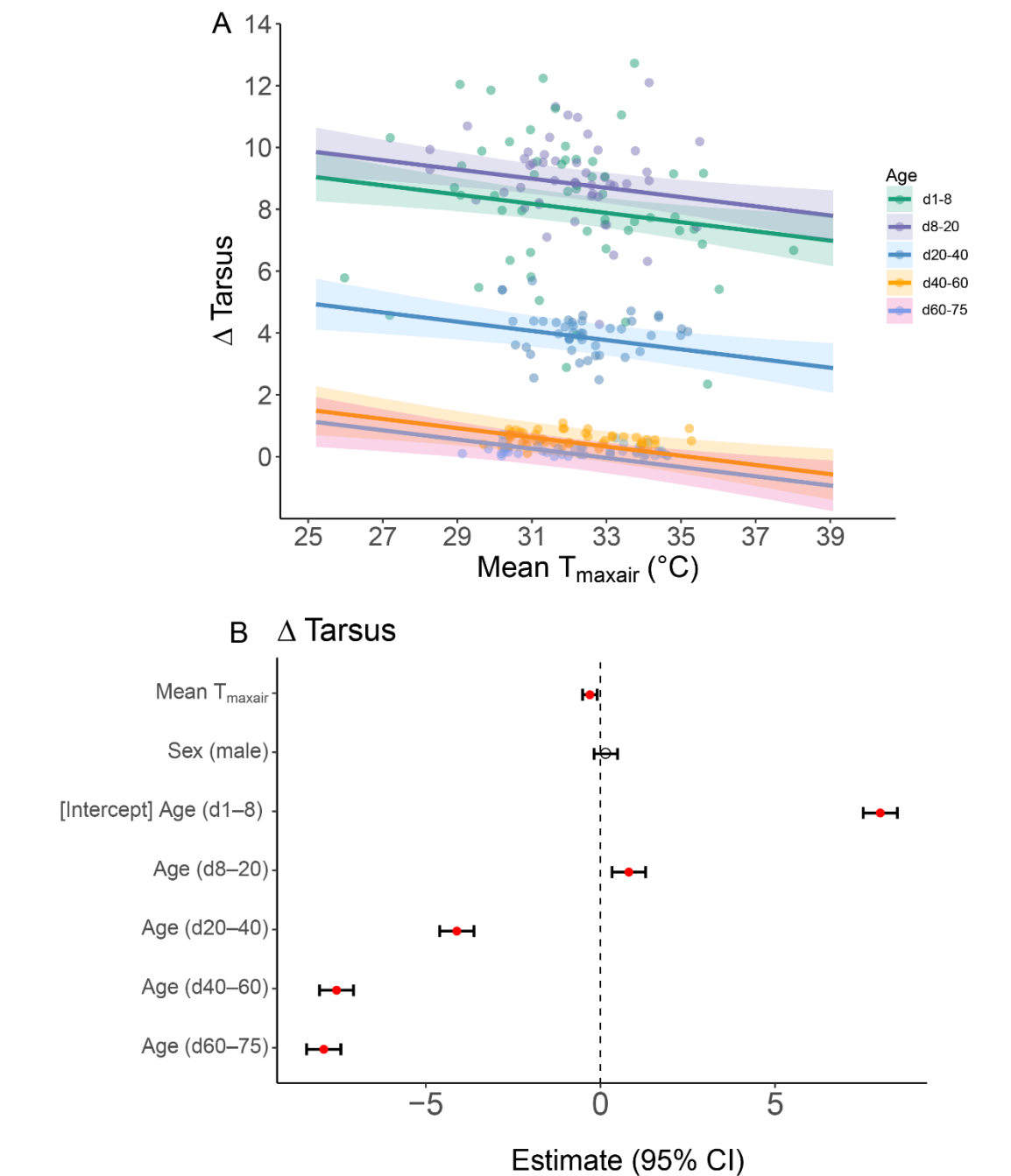


Figure 4.5. (A) Predicted linear relationship between mean T_{maxair} and ΔTarsus across different chick ages. Lines represent predicted values for each age group from model 1, where the effect of T_{maxair} is estimated as a main effect and averaged across ages. Shaded areas indicate 95% confidence intervals and points show observed data. Colours correspond to chick age in days. (B) Model means and 95% confidence intervals for variables included in model 1 predicting ΔTarsus . Filled red circles indicate statistically significant effects, while open circles indicate non-significant effects.

Wing length: Mean T_{maxair} was the best predictor of wing growth (ΔWing), with the lowest AICc value, though days > 35 $^{\circ}\text{C}_{\text{air}}$ was included in a competing model (Table 4.5). Two competing top models explained ΔWing ; one including mean T_{maxair} , while accounting for age and sex, and another including the interaction between mean T_{maxair} and age (Table 4.6). Higher mean T_{maxair} was significantly correlated with reduced ΔWing (estimate = -0.55 ± 0.16 , 95% CI = $[-0.87 / -0.22]$, Table A4.11, Figure 4.6). Sex had no significant effect on ΔWing (Table A4.11). Wing growth was greatest during ages d1–8 (estimate = 6.48 ± 0.36 , 95% CI = $[5.76 / 7.20]$), d8–20 (estimate = 3.66 ± 0.48 , 95% CI = $[2.71 / 4.60]$), and d20–40 (estimate = 3.74 ± 0.53 , 95% CI = $[2.69 / 4.77]$), but declined during later periods (d40–60: estimate = -3.27 ± 0.52 , 95% CI = $[-4.30 / -2.24]$; d60–75: estimate = -4.99 ± 0.50 , 95% CI = $[-5.98 / -4.01]$; Table A4.11, Figure 4.6). The interaction between mean T_{maxair} and age in the competing model was not significant (Table A4.11).

Table 4.5. Model selection table to identify best weather variable explaining ΔWing in ground-hornbill chicks at different ages, with top models with $\Delta\text{AICc} < 2$ highlighted in bold. Only one weather variable with lowest AIC was selected for final models (mean T_{maxair}). Models included sex and age as fixed factors with group ID, chick ID and season as random factors.

Model	AICc	ΔAICc	Weight
mean T_{maxair} + sex + age	998.3	0.00	0.597
days > 35 $^{\circ}\text{C}_{\text{air}}$ + sex + age	899.9	1.64	0.263
mean T_{maxnest} + sex + age	1002.4	4.13	0.076
rainfall ₆₀ + sex + age	1004.0	5.78	0.033
days > 35 $^{\circ}\text{C}_{\text{nest}}$ + sex + age	1004.2	5.94	0.031
rainfall ₉₀ + sex + age	1015.6	17.34	0.000
null	1226.7	228.48	0.000

N = 212, Random terms: group ID = 19, chick ID = 56, season = 6

Table 4.6. Model selection table for factors explaining Δ Wing in ground-hornbill chicks across different ages with top model highlighted in bold (AICc < 2). Models investigated the effects of mean T_{maxair} and number of helpers on chick growth, including sex and age as fixed factors, and group ID, chick ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Weight
1	mean T_{maxair} + sex + age	998.3	0.00	0.597
2	mean T_{maxair} * age + sex	999.9	1.64	0.263
3	mean T_{maxair} + helpers + juv + sex + age	1002.4	4.13	0.076
3	mean T_{maxair} * age + helpers + juv + sex	1004.0	5.78	0.033
4	mean T_{maxair} * helpers + juv + sex + age	1004.2	5.94	0.031
5	mean T_{maxair} * helpers + juv + mean T_{maxair} * age + sex	1015.6	17.34	0.000
6	mean T_{maxair} * age * helpers + juv + sex	1035.0	36.74	0.000
7	null	1226.7	228.48	0.000
<i>N = 212, Random terms: group ID = 19, chick ID = 56, season = 6</i>				

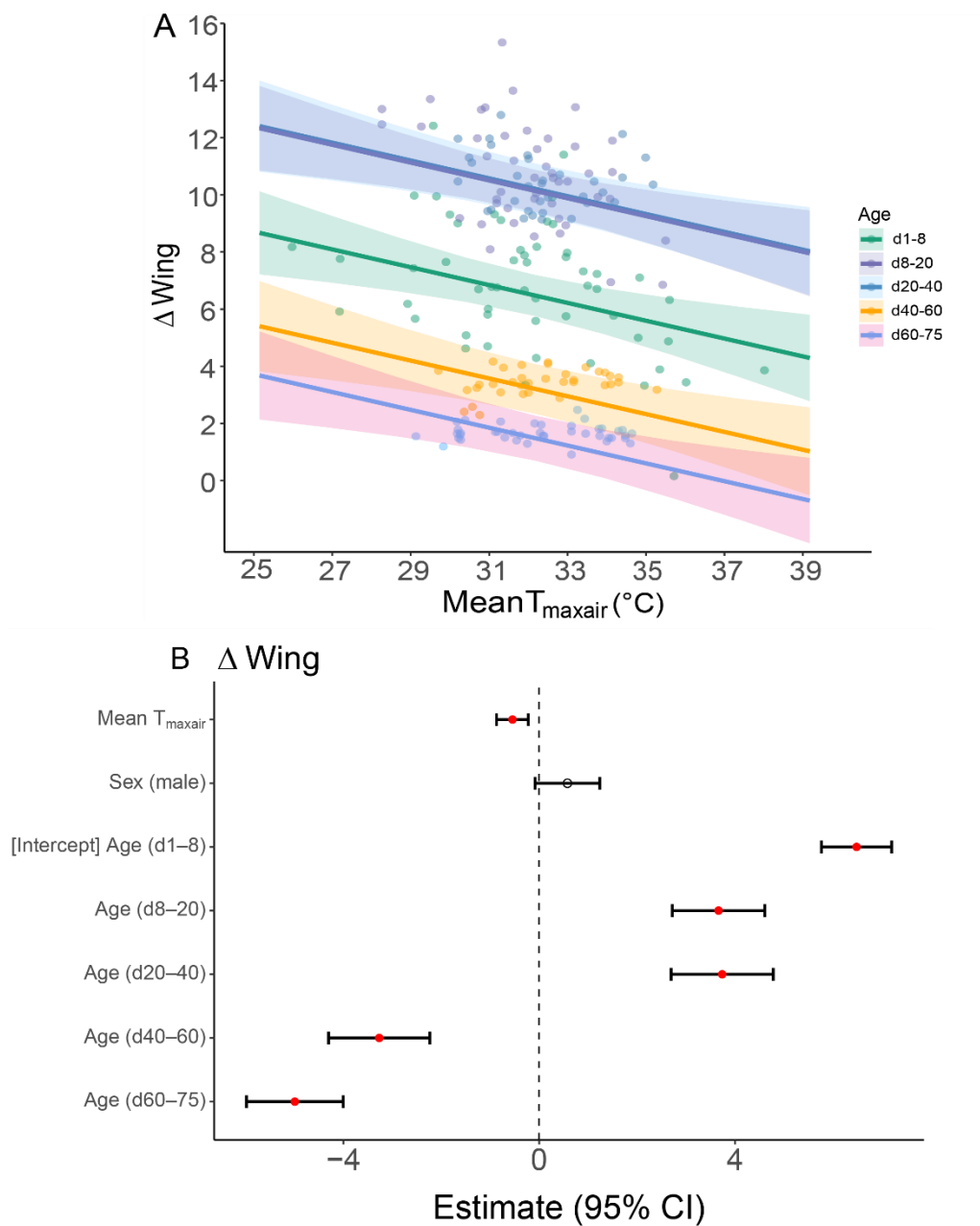


Figure 4.6. Predicted linear relationship between T_{maxair} and ΔWing across different chick ages. Lines represent predicted values for each age group from model 1, where the effect of T_{maxair} is estimated as a main effect and averaged across ages. Shaded areas indicate 95% confidence intervals and points show observed data. Colours correspond to chick age in days. (B) Model means and 95% confidence intervals for variables included in model 1 predicting ΔWing . Filled red circles indicate statistically significant effects, while open circles indicate non-significant effects.

4.4.3. Provisioning and temperature effects on growth rates during early and late development

Chick mass: The top model explaining ΔMass (during d1-8 and d40-60) included provisioning rate, mean T_{maxnest} , sex and age (Table 4.7). A competing model ($\Delta\text{AICc} < 2$) excluding mean T_{maxnest} , performed similarly (Table 4.7). However, neither provisioning rate, nor sex were significant predictors of ΔM in either model. Compared to models without provisioning rate, the age-related pattern of mass gain remained unchanged; (d1–8: estimate = 35.41 ± 12.6 , 95% CI = [32.95 / 37.86], d40–60: estimate = -35.34 ± 1.60 , 95 % CI = [-38.46 / -32.22]), but the effect of mean T_{maxnest} was no longer apparent (Table A4.12).

Table 4.7. Model selection table for factors explaining ΔMass during two development stages when including provisioning rates: early (d1-8) and late (d40-60), with top models highlighted in bold ($\text{AICc} < 2$). Models included chick ID, group ID and season as random factors.

Model no.	Model	AICc	ΔAICc	Weight
1	provisioning + mean T_{maxnest} + sex + age	613.0	0.00	0.342
2	provisioning + sex + age	613.2	0.17	0.314
3	provisioning * age + sex	615.0	2.39	0.104
4	provisioning * mean T_{maxnest} + sex + age	615.4	2.39	0.104
5	provisioning + mean T_{maxnest} + helpers + juv + sex + age	616.4	3.40	0.062
6	provisioning + helpers + juv + sex + age	616.8	3.85	0.050
7	null	770.4	157.47	0.000
<i>N = 87, Random terms: chick ID = 54, group ID = 19, season = 6</i>				

Tarsus: The top model explaining ΔTarsus during early (d1-8) and late (d40-60) development included provisioning rate, mean T_{maxair} , sex, and age (Table 4.8). As found in models without provisioning rates, Mean T_{maxair} remained negatively correlated with ΔTarsus (estimate = -0.41 ± 0.15 , 95 % CI = [-0.71 / -0.11], Table A4.13), while provisioning rate and sex were not significant (Table A4.13). Age related pattern of ΔTarsus gain remained unchanged compared

to models without provisioning rate; (*d1–8* estimate = 8.19 ± 0.15 , 95% CI = [7.28 / 9.05], *40–60*: estimate = -7.66 ± 0.35 , 95 % CI = [-8.35 / -6.97]) (Table A4.13).

Table 4.8. Model selection table for factors explaining Δ Tarsus during two development stages when including provisioning rates: early (*d1–8*) and late (*d40–60*), with top model highlighted in bold (AICc < 2). Models included chick ID, group ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Weight
1	provisioning + mean T_{maxair} + sex + age	354.0	0.00	0.522
2	provisioning + mean T_{maxair} + helpers + juv + sex + age	356.4	2.40	0.160
3	provisioning * mean T_{maxair} + sex + age	356.5	2.41	0.159
4	provisioning + sex + age	358.0	4.76	0.049
5	provisioning * age + sex	358.8	4.76	0.049
6	provisioning + helpers + juv + sex + age	360.3	6.22	0.024
7	null	505.0	150.97	0.000
<i>N</i> = 87, Random terms: chick ID = 53, group ID = 19, season = 6				

Wing length: The top model explaining Δ Wing (during *d1–8* and *d40–60*) included provisioning rate, mean T_{maxair} , sex and age (Table 4.9). A competing model (Δ AICc < 2), including an interaction with provisioning and T_{maxair} , performed similarly (Table 4.9). However, provisioning rate, and sex were not significant predictors of Δ Wing in either model nor was the interaction (Table A4.14). Mean T_{maxair} remained negatively correlated with Δ Wing (estimate = -0.48 ± 0.14 , 95 % CI = [-0.76 / -0.20]). Compared to models without provisioning rate, the age-related pattern of mass gain remained unchanged; (*d1–8*: estimate = 6.60 ± 0.31 , 95% CI = [5.96 / 7.22], *d40–60*: estimate = -3.01 ± 0.33 , 95 % CI = [-3.67 / -2.33]) (Table A4.14).

Table 4.9. Model selection table for factors explaining Δ Wing during two development stages when including provisioning rates: early (d1-8) and late (d40-60), with top models highlighted in bold (AICc < 2). Models included chick ID, group ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Weight
1	provisioning + mean T_{maxair} + sex + age	315.0	0.00	0.662
2	provisioning * mean T_{maxair} + sex + age	316.9	1.88	0.259
3	provisioning + mean T_{maxair} + helpers + juv + sex + age	319.7	4.72	0.062
4	provisioning + sex + age	323.2	8.22	0.011
5	provisioning * age + sex	325.0	9.96	0.005
6	provisioning + helpers + juv + sex + age	327.5	12.48	0.001
7	null	367.3	52.26	0.000
<i>N = 80, Random terms: chick ID = 53, group ID = 19, season = 6</i>				

4.4.4. Chick fledging size and condition

Fledging size: The top model explaining chick size at fledge (PC1; mass d75, tarsus d75, wing d75) included mean T_{maxair} , and sex as a covariate (Table 4.10), however, the effect of mean T_{maxair} was not significant (Table A4.18). Males had a greater fledging body size than females (estimate = 1.64 ± 0.36 , 95% CI = [0.95 / 2.36]; Table A4.18, Figure 4.7).

Table 4.10. Model selection table for factors explaining chick fledging size (from principal component analysis; PC1[mass d75, tarsusd75.wingd75]) with top model highlighted in bold (AICc < 2). Models included group ID and season as random factors.

Model No.	Model	AICc	Δ AICc	Weight
1	mean T_{maxair} + sex	150.1	0.00	0.520
2	mean T_{maxnest} + sex	152.2	2.09	0.183
3	helpers + juv + sex	152.5	2.31	0.164
4	rainfall _{nestling} + sex	152.9	2.72	0.133
5	null	162.7	12.59	0.001
<i>N = 44, Random terms: group ID = 17, season = 6</i>				

Fledging condition: The top model explaining chick body condition at fledge (mass d75 / tarsus d75) included the number of helpers and juveniles as main effects, and sex as a covariate (Table 4.11). Body condition was negatively associated with the number of juveniles (estimate = -0.86 ± 0.52 , 95% CI = $[-1.30 / -0.41]$, Table A4.19, Figure 4.7), while the number of helpers was not significant (Table A4.19). Males had a greater fledging body condition than females (estimate = 1.16 ± 0.47 , 95% CI = $[0.23 / 2.06]$; Table A4.19).

Table 4.11. Model selection table for factors explaining chick fledging body condition (mass on d75 / tarsus length d75) with top model highlighted in bold (AICc < 2). Models included group ID and season as random factors.

Model No.	Model	AICc	Δ AICc	Weight
1	helpers + juv + sex	175.1	0.00	0.856
2	rainfall _{nestling} + sex	180.0	4.95	0.072
3	mean T _{maxair} + sex	181.5	6.49	0.033
4	null	182.2	7.13	0.024
5	mean T _{maxnest} + sex	183.3	8.26	0.014
<i>N = 44, Random terms: group ID = 17, season = 6</i>				

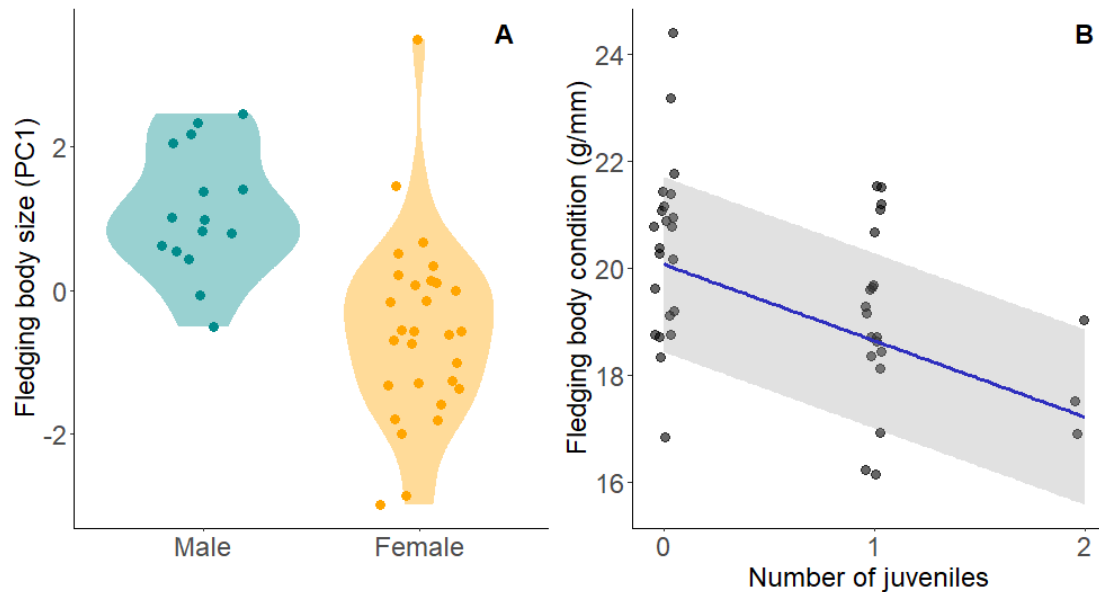


Figure 4.7. A) Fledging body size (PC1) by sex. PC1 was derived from a principal component analysis of mass, tarsus length, and wing length at day 75. Higher PC1 scores indicate larger body size. Violin plots show the distribution of scores for males (green) and females (orange), with overlaid points representing individual chicks. B) Predicted linear relationship between the number of juveniles and fledging body condition (mass/tarsus on d75), shaded areas indicate 95% confidence intervals and points show observed data.

4.4.5. Over winter survival

The top model explaining post-fledging overwinter survival included the number of days $> 35^{\circ}\text{C}$ in the nest and number of days $> 35^{\circ}\text{C}$ during the subsequent winter (Table 4.12). Both predictors had significant negative effects: days $> 35^{\circ}\text{C}_{\text{nest}}$ (estimate = -1.59 ± 0.79 , 95% CI = $[-4.20 / -0.39]$; Table A4.20) and days $> 35^{\circ}\text{C}_{\text{winter}}$ (estimate = -2.59 ± 1.28 , 95% CI = $[-7.28 / -1.07]$; Table A4.20) (Figure 4.8). A competing model ($\Delta\text{AICc} < 2$) that included mean T_{maxnest} and days $> 35^{\circ}\text{C}_{\text{winter}}$ also showed significant negative effects based on 95% CIs (but not P values): mean T_{maxnest} (estimate = -1.67 ± 0.93 , 95% CI = $[-5.76 / -0.34]$) and days $> 35^{\circ}\text{C}_{\text{winter}}$ (estimate = -2.82 ± 1.44 , 95% CI = $[-8.70 / -1.06]$; Table A4.20). However, the results for winter temperatures include a particularly hot winter in 2024 and therefore should be interpreted with caution. Chick body condition and chick size did not appear in the top

models, indicating they did not significantly influence post-fledging overwinter survival (Table 4.12).

Table 4.12. Model selection table for factors explaining post-fledging overwinter survival in ground-hornbills with top models highlighted in bold (AICc < 2). All models included group ID as a random effect, with season added as a random effect only when seasonal variation was not captured by fixed effects.

Model No.	Model	AICc	Δ AICc	Weight
1	days > 35 °C_{nest} + days > 35 °C_{winter}	32.9	0.00	0.525
2	mean T_{maxnest} + days > 35 °C_{winter}	33.2	0.35	0.441
3	days > 35 °C _{winter}	40.2	7.33	0.013
4	mean T _{maxnest} + mean T _{maxwinter}	40.9	8.06	0.009
5	days > 35 °C _{nest} + mean T _{maxwinter}	41.3	8.43	0.008
6	days > 35 °C _{nest}	44.4	11.52	0.002
7	mean T _{maxnest}	44.7	11.87	0.001
8	sex	46.5	13.65	0.001
9	mean T _{maxwinter}	47.6	14.78	0.000
10	egg size	48.5	15.62	0.000
11	rainfall _{winter}	50.0	17.18	0.000
12	chick size (PC1)	50.3	17.39	0.000
13	rainfall _{nestling}	52.9	20.08	0.000
14	days > 35 °C _{air}	54.4	21.49	0.000
15	null	62.4	29.50	0.000
16	helpers + juv	66.4	33.54	0.000
17	chick body condition	67.2	34.28	0.000
<i>N = 35, Random terms: group ID = 17, season = 5 (unless accounted for in main effect)</i>				

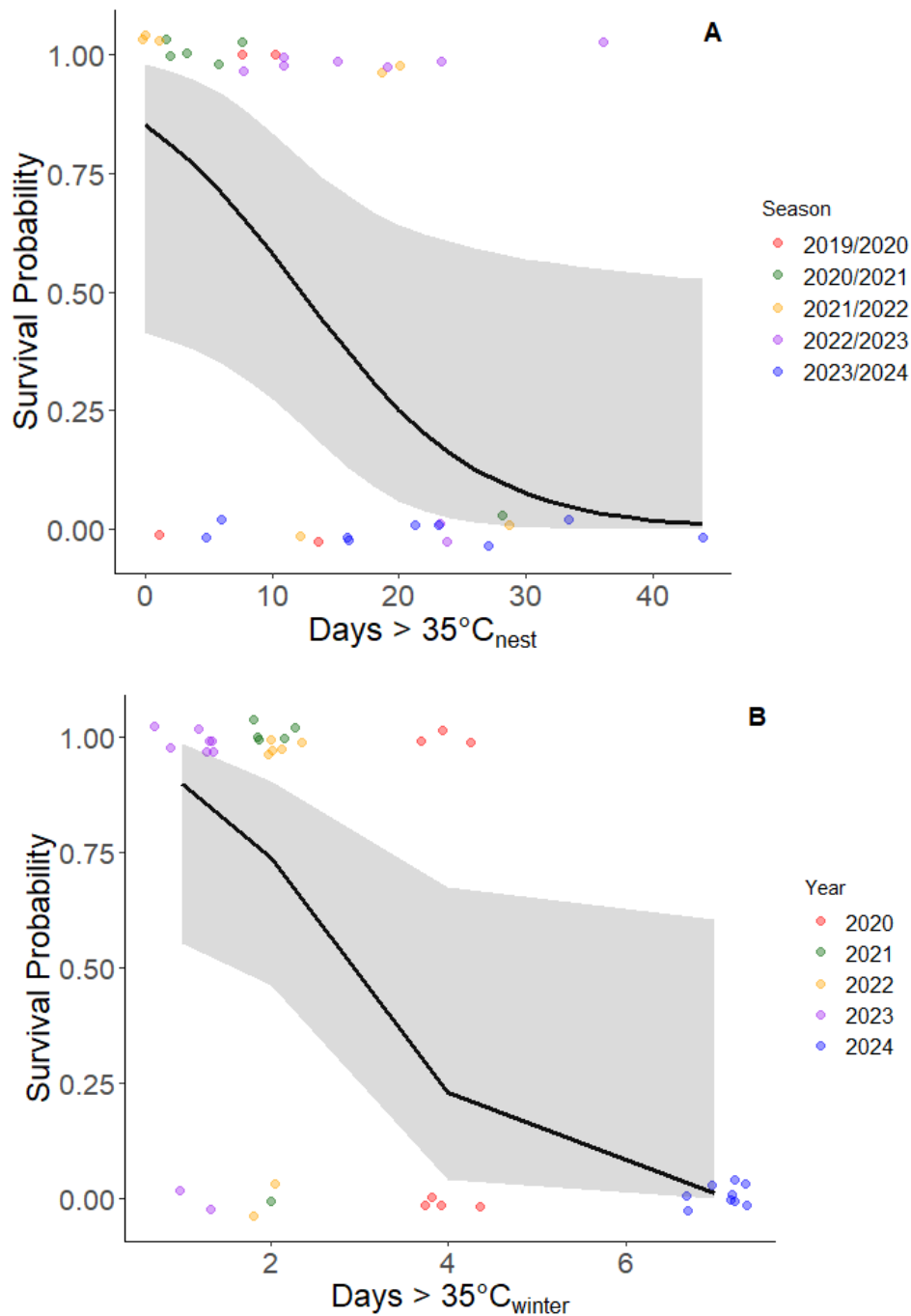


Figure 4.8. Probability of juvenile over winter survival in ground-hornbills as a function of (A) number of days where nest temperature exceeded 35 °C (days > 35 °C_{nest}) during nestling period and (B) number of days where air temperatures over the winter following fledging exceeded 35 °C (days > 35 °C_{winter}). The solid line shows model predictions with shaded 95% confidence intervals. Jittered points represent observed survival outcomes (0 = did not survive, 1 = survived), coloured by breeding season or winter year, highlighting no confound between season and nest temperatures (A), but that the trend in (B) is associated with a particularly hot winter in 2024. The model included group ID as a random effect.

4.5. Discussion

I investigated whether high temperatures influence growth rates and survival outcomes in a slow-developing, long-lived, cooperative breeder, the southern ground-hornbill, and whether social factors mitigated any negative effects. As predicted, high temperatures were negatively associated with growth rates for body mass, tarsus and wing length, while helpers did not appear to play a role in mediating any heat effects on growth. However, unexpectedly, growth trajectories were not related to fledging size or condition, and post-fledging survival was likewise unrelated to these fledging traits. Instead, survival outcomes were negatively associated with high nest temperatures during development and high air temperatures during winter post-fledging. These findings reveal the impact of high temperatures on growth and survival, highlighting the species' vulnerability to climate change, and contribute to the limited body of research on such impacts in large birds.

Impact of high temperatures on growth

High temperatures were associated with reduced mass, tarsus and wing growth in nestlings. Body mass was best explained by nest temperatures, perhaps because thermal conditions differ substantially between nests (see Chapter 5). The sensitivity of body mass to nest temperature likely reflects the increased energetic and water demands associated with thermoregulation under high temperatures. As nestlings expend energy to dissipate heat and avoid hyperthermia, less energy may be available for mass accumulation, and greater water loss may also contribute to lower body mass in hotter nests (Dawson, Lawrie & O'Brien, 2005; Speakman & Król, 2010; Catry et al., 2015; McKechnie & Wolf, 2019). Structural growth (tarsus and wing) was best predicted by air temperature, despite nestlings experiencing only the nest thermal environment. This suggests that structural growth may be more responsive to subtle thermal effects mediated indirectly through parent or helper behaviour, compared with

direct effects of nest temperature. Such effects could include aspects of parental care not captured by our provisioning rate metric (e.g. prey quality), which may influence structural growth more than body mass. While growth rates were similar for both sexes, males grew to a larger final mass with longer tarsi. Their larger size may make them more energetically costly to rear and more vulnerable to environmental stressors, raising intriguing questions about whether there could be differences in sex-allocation under more extreme or prolonged warming.

Despite the negative impact of high temperatures on growth rates, final fledging size and condition were unaffected, suggesting that nestlings may undergo compensatory growth (Metcalf & Monaghan, 2001). The species' extended nestling period (~3 months) may allow time for offspring to recover body condition and structural growth when conditions improve, particularly later in the breeding season when hot days become less frequent (Figure A4.6). During this time, chicks may allocate growth toward traits that are important for survival after fledging. Longer tarsi, for example, may reduce the energetic costs of walking (Heers & Dial, 2015), which constitutes most of ground-hornbills' daily activity (Kemp, 1980; Zoghby et al., 2015), and may also aid thermoregulation, as unfeathered legs are highly vascularised (Playà-Montmany et al., 2022). Similarly, longer wings may enhance post-fledging mobility and rapid escape from predators (Greño, Belda & Barba, 2008; Martin et al., 2018; Jones & Ward, 2020; Youngflesh et al., 2022), including ambush predators such as leopards (*Panthera pardus*). However, while compensatory growth might be effective in the short-term, it may entail physiological costs that are not immediately apparent (Metcalf & Monaghan, 2001).

Provisioning and helper effects

Provisioning did not influence nestling growth rates in this study, in contrast to other studies, for example on southern pied babblers *Turdoides bicolor* and southern yellow-billed hornbills *Tockus leucomelas*, in which provisioning influenced nestling growth and parental

care declined under high temperatures (Wiley & Ridley, 2016; van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021). During high temperatures, adults may reduce foraging to prioritise thermoregulation (van de Ven, McKechnie & Cunningham, 2019), thereby limiting food provisioning to nestlings (van de Ven et al., 2020; Bourne, Ridley, Spottiswoode, et al., 2021). A previous study on ground-hornbills found reduced provisioning rates during high temperatures (Middleton, 2022), but they measured nest visit rates only and did not take into account prey size. Ground-hornbills can capture large prey and carry multiple items per trip in their bill, meaning that visit rate alone may be a poor proxy for food delivery in this species. Provisioning in the present study was quantified using an index that incorporated both visit rate and prey size, and no temperature-related decline in provisioning was detected, indicating that biomass delivery to nestlings was maintained during hot periods – perhaps via individuals bringing larger prey less often. Only two growth periods were investigated for provisioning analyses, and small sample size prevented path analyses to disentangle the direct and indirect effects of heat on growth rates, but future studies should investigate this.

Additional helpers also did not appear to influence nestling growth rates, suggesting their presence does not necessarily mean that more food is delivered. However, more helpers perhaps reduce the number of contributions per carer, otherwise known as ‘load-lightening’ (Wiley & Ridley, 2016; Bourne et al., 2021; Middleton, 2022, but see te Marvelde et al., 2009). The presence of juveniles from previous years had an overall negative impact on fledging condition, which is likely to arise from continued feeding of these older juveniles by the adults, as juveniles can take several months to years to develop the skills required for foraging (Kemp, 1980). In addition, juveniles from previous broods have been observed stealing food from nestlings (pers.obs; see Figure A4.2).

Carry-over effects of heat on survival

Offspring survival was unrelated to fledging body condition or size but was instead influenced by heat experienced in the nest, and high air temperatures during the following winter post-fledging. These results reveal potential carry-over effects of early heat exposure, suggesting that such heat exposure may impose lasting physiological costs beyond any impacts on growth, potentially through oxidative stress (Monaghan, Metcalfe & Torres, 2009), impaired cognitive performance (Soravia et al., 2024) and compensatory growth costs (Metcalfe & Monaghan, 2001). They also indicate that hot weather in winter can include temperatures high enough to negatively affect survival (as opposed to simply relieving cold stress at this time of year (Gardner et al., 2017)). In semi-arid subtropical regions, winter days can still reach mid-30 °C, and reduced shade associated with deciduous vegetation (Singh & Kushwaha, 2016), can lead to hotter thermal landscapes in winter than in summer, increasing the need for heat dissipation (Chapter 2). Compounding this, food resources are more scarce during this season, potentially lowering body condition (du Plessis et al., 2012; Gardner et al., 2017; van de Ven, McKechnie & Cunningham, 2019). These combined thermal and nutritional impacts may compromise juveniles' resilience and survival. Similar winter heat impacts on survival have been found in some Australian birds (Gardner et al., 2017), with superb fairywrens *Malurus cyaneus* showing reduced survival when exposed to both hot summers and warm winters (Lv et al., 2023). Therefore, even if nestling growth can be maintained through compensatory mechanisms, the physiological costs of early heat exposure and subsequent winter heat may manifest later, reducing juvenile survival, and emphasising the value of thermally buffered nests and shaded microsites in the landscape. It is important to note that whilst these data span over 5 winters, the strongest impact of winter heat on survival occurred during a particularly hot winter, and the sample size is limited; therefore, further data across more years are needed to see if this trend holds.

4.6. Conclusion

High temperatures during early life have lasting impacts on ground-hornbills. While compensatory growth may allow chicks to fledge at a good size and in relatively good condition despite reduced growth rates earlier in the nestling period, these short-term adjustments may not fully offset the longer-term physiological costs of heat exposure. Furthermore, provisioning strategies and helper care do not seem to play a role in buffering offspring from the consequences of rising temperatures. Both hotter nests and high winter temperatures impacted juvenile survival, indicating that negative effects of early-life heat exposure carry over beyond the nestling period, and that warm winter weather may be associated with increased heat stress (rather than relaxed cold stress) in this environment (Chapter 2). Repeated exposure to high temperatures both during the nestling phase and during the first winter post-fledging could therefore reduce recruitment of individuals to the adult population, highlighting the species' vulnerability to climate change. This is further concerning given their low fecundity, with important implications for long-term population persistence. Conservation strategies should therefore prioritise providing thermally buffered artificial nests placed in shaded tree canopies and the preservation of woody vegetation and large trees, which provide shade to facilitate thermoregulation during both the breeding season and in winter.

4.7. Appendix to Chapter 4

Weather station calibration

Calibration of maximum daily air temperature ($T_{\max}$) data between the Klaserie and Hoedspruit weather stations was performed using linear regression on overlapping data from January 2022 to January 2025 ($N = 1076$), with $T_{\max}$ at Klaserie as the dependent variable and $T_{\max}$ at Hoedspruit as the predictor (intercept = 1.5505 ± 0.1901 , 95% CI [1.18, 1.92]; slope = 0.9463 ± 0.0062 , 95% CI [0.93, 0.96]; $R^2 = 0.9565$). Because the difference between the stations varied with temperature, Hoedspruit measurements were adjusted to match the Klaserie scale using the regression equation:

$$T_{\max \text{ calibrated}} = 1.5505 + 0.9463 * T_{\max \text{ Hoedspruit}}$$

where the intercept and slope correspond to the estimated offset and scaling relationship between the two stations. These calibrated values were used to fill missing $T_{\max}$ data for Klaserie ($N = 87$ days).

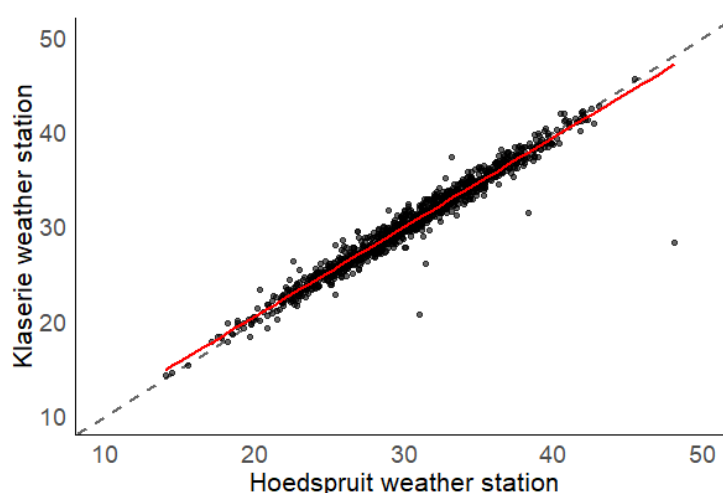


Figure A4.1. Calibration of maximum daily air temperatures between the Klaserie and Hoedspruit weather stations. Points show paired daily $T_{\max}$ measurements, the red line shows the linear regression used for calibration, and the dashed line represents the 1:1 reference line. The regression equation was used to adjust Hoedspruit values to the Klaserie scale.

Juvenile survival

Figure A4.2. Camera trap footage was used to assess survival of offspring from previous seasons to the following breeding season. *Top*: A one-year-old juvenile provisioning a centipede. *Bottom*: A one-year-old juvenile stealing a snake from a nestling and quickly swallowing it. The pale-yellow facial skin of the juvenile (compared to red skin in older birds) is a reliable indicator of age in this species.

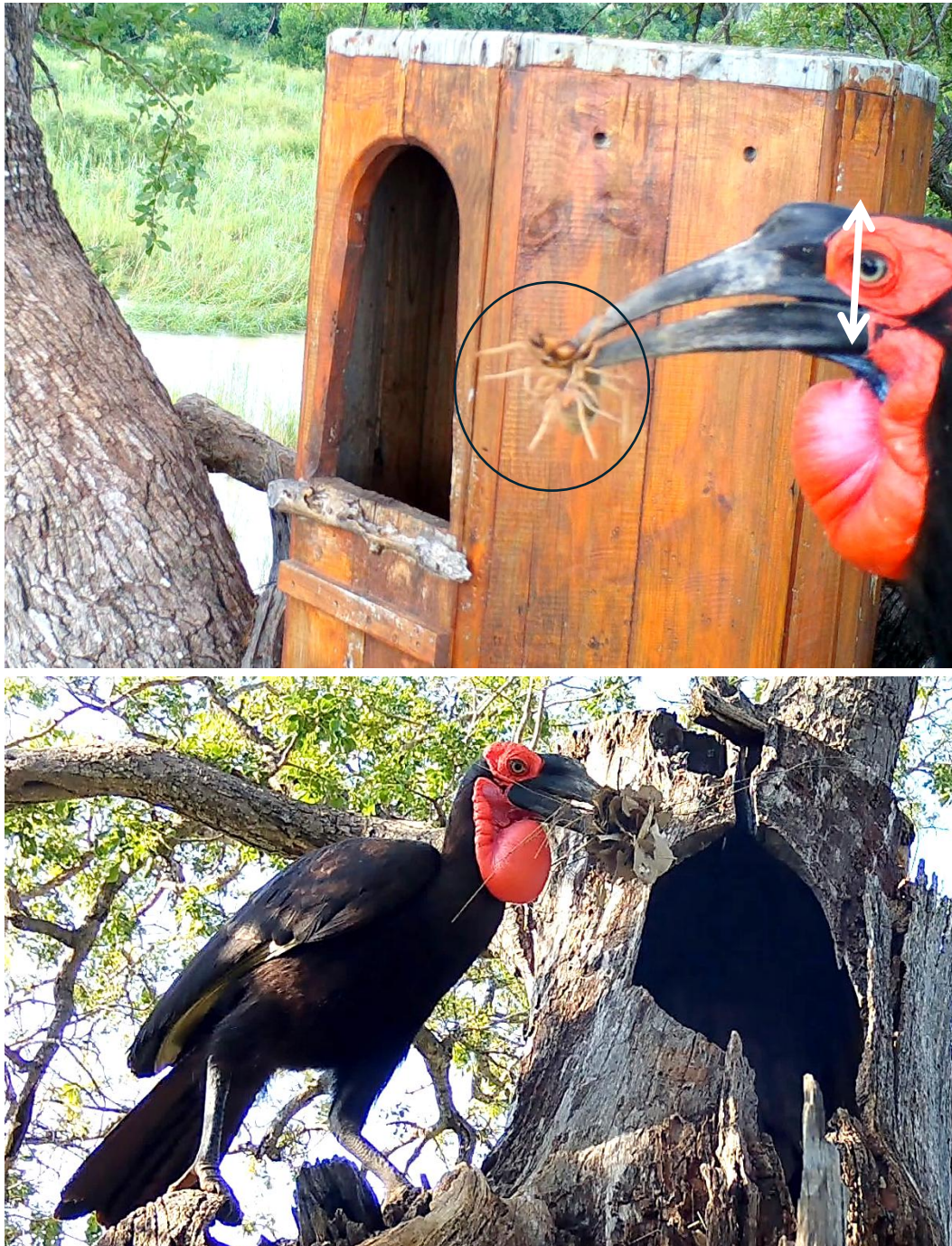
Provisioning food score

Figure A4.3. Camera trap footage showing provisioning events. *Top*: Arrow on the casque shows where food size was assessed relative to bill depth for scoring. This individual is provisioning a solifuge *Solifugae* to the nestling. *Bottom*: This individual is provisioning a parcel of leaves, likely containing invertebrates or other small prey.

Growth curve model selection

Chick mass

Table A4.1. Model selection table for growth curve models (functions: Gompertz [G], logistic [L], log-logistic [LL], and Weibull [W]) to body mass growth data of ground-hornbill chicks, categorised by sex. Models are ranked and ordered according to AIC, with the most suitable model in bold.

Sex	Model	Log likelihood	AIC	Δ AIC	Lack of fit	Residual variance
<i>Male</i>	W2.4	-731.2	1472.5	0.00	0.55	46229.5
	L.4	-731.4	1472.9	0.40	0.52	46406.1
	G.3	-732.8	1473.7	1.20	0.38	47166.6
	G.4	-732.1	1474.2	1.70	0.41	46952.4
	W2.3	-733.0	1474.2	1.70	0.39	47392.0
	LL.5	-731.4	1474.7	2.29	0.43	46789.3
	LL.4	-733.6	1477.2	4.70	0.21	48295.2
	L.3	-734.7	1477.4	4.90	0.17	48813.1
	LL.3	-737.7	1483.3	10.80	0.03	51559.3
	W1.4	-737.1	1484.3	11.80	0.03	51571.0
	W1.3	-747.1	1503.4	30.90	0.00	62167.5
	G.2	-987.1	1980.1	507.60	0.00	5178226.4
<i>Female</i>	W2.4	-1150.9	2311.8	0.00	0.86	42051.1
	L.4	-1150.8	2311.8	0.00	0.86	42034.44
	LL.5	-1150.8	2313.6	1.80	0.83	42248.4
	L.5	-1150.8	2313.7	1.90	0.82	42285.7
	G.3	-1152.9	2313.7	1.90	0.68	42771.4
	G.4	-1151.9	2313.8	2.00	0.75	42547.0
	W2.3	-1154.1	2316.2	4.40	0.52	43402.5
	L.3	-1155.0	2318.0	6.20	0.40	43864.2
	LL.4	-1154.2	2318.5	6.70	0.44	43721.0
	W1.4	-1159.8	2329.5	17.70	0.05	46638.1
	LL.3	-1161.3	2330.6	18.80	0.04	47212.0
	W1.3	-1176.2	2360.3	48.30	0.00	56163.3
	G.2	-1541.4	3088.8	777.00	0.00	56163.3

Table A4.2. Growth curve model (4-parameter Weibull type 2) results for body mass in male (N = 18) and female (N = 29) ground-hornbill chicks. Estimates include slope (growth rate), lower limit (initial mass), upper limit (asymptotic mass), and ED50 (age at 50% of asymptotic mass) with standard errors (SE) and 95% confidence intervals (CI). Sex differences were tested using a combined model and P values indicate whether parameters differ significantly between males and females, with significant differences highlighted in bold.

Parameter	Male estimate (SE)	Female estimate (SE)	Male 95 % CI	Female 95 % CI	P value (Male vs Female)
Slope	2.07 (0.12)	2.00 (0.11)	1.83 / 2.32	1.78 / 2.22	0.664
Lower limit	86.78 (43.5)	94.27 (36.89)	1.31 / 172.42	21.63 / 166.91	0.893
Upper limit	3320.3 (44.4)	2874.28 (35.04)	3329.8 / 3410.9	2805.3 / 2943.3	<0.001
ED50	31.76 (0.81)	30.73 (0.75)	30.16 / 33.36	29.26 / 32.20	0.359

Equation for W2.4 model used for chick mass:

$$(x) = c + (d - c)(1 - \exp(-\exp(b(\log(x) - \log(e))))))$$

Tarsus length

Table A4.3. Model selection table for fitting growth curve model (functions: Gompertz [G], logistic [L], log-logistic [LL], and Weibull [W]) to tarsus growth data of ground-hornbill chicks, categorised by sex. Models are ordered according to AIC, with the most suitable model in bold.

Sex	Model	Log likelihood	AIC	Δ AIC	Lack of fit	Residual variance
<i>Male</i>	L.3	-344.08	696.15	0.00	0.82	35.24
	L.4	-344.88	697.77	1.60	0.78	35.45
	W2.4	-344.58	699.16	3.00	0.66	35.91
	L.5	-343.76	699.53	3.40	0.73	35.71
	G.4	-344.92	699.84	3.70	0.59	36.13
	LL.4	-349.54	709.08	12.90	0.07	39.36
	G.3	-358.62	725.23	29.10	0.00	46.12
	W1.4	-362.72	735.45	39.30	0.00	50.25
	W2.3	-403.24	814.47	118.30	0.00	105.39
	LL.3	-409.40	826.79	130.60	0.00	118.12
	W1.3	-419.88	847.75	151.60	0.00	143.42
	G.2	-662.68	1331.36	635.20	0.00	12741.91
<i>Female</i>	L.3	-532.86	1073.7	0.00	0.23	30.32
	L.4	-532.51	1075.01	1.30	0.21	30.38
	LL.5	-531.85	1075.71	2.00	0.22	30.38
	L.5	-532.42	1076.8	3.10	0.17	30.54
	W2.4	-534.24	1078.47	4.80	0.10	31.01
	G.4	-534.44	1078.88	5.20	0.09	31.08
	LL.4	-541.97	1093.95	20.30	0.002	33.94
	G.3	-552.88	1113.75	40.10	0.00	38.33
	W1.4	-564.44	1138.88	65.20	0.00	44.14
	W2.3	-621.92	1251.85	178.20	0.00	85.95
	LL.3	-630.89	1269.78	196.10	0.00	95.45
	W1.3	-645.70	1299.41	225.70	0.00	113.51
	G.2	-1040.53	2087.07	1013.40	0.00	11428.40

Table A4.4. Growth curve model (logistic) results for tarsus length in male (N = 18) and female (N = 29) ground-hornbill chicks. Estimates include slope (growth rate), upper limit (asymptotic mass), and ED50 (age at 50% of asymptotic mass) with standard errors (SE) and 95% confidence intervals (CI). Sex differences were tested using a combined model and P values indicate whether parameters differ significantly between males and females, with significant differences highlighted in bold.

Parameter	Male estimate (SE)	Female estimate (SE)	Male 95 % CI	Female 95 % CI	P value (Male vs Female)
Slope	0.09 (0.10)	0.09 (0.00)	-0.10 / -0.09	-0.10 / -0.09	0.881
Upper limit	160.74 (1.14)	149.94 (0.89)	158.49 / 162.99	148.20 / 151.68	<0.001
ED50	21.63 (0.40)	20.43 (0.31)	20.88 / 22.37	19.82 / 21.05	0.018

Equation for L.3 model used for tarsus length:

$$f(x) = c + (1 + \exp(b(x - e)))^{-1} d - c$$

Wing length

Table A4.5. Model selection table for fitting growth curve model (functions: Gompertz [G], logistic [L], log - logistic [LL], and Weibull [W]) to wing growth data of ground-hornbill chicks, categorised by sex. Models are ordered according to AIC, with the most suitable model in bold.

Sex	Model	Log likelihood	AIC	Δ AIC	Lack of fit	Residual variance
<i>Male</i>	G.4	- 444.1	898.2	0.00	0.30	265.1
	LL.4	- 444.3	898.5	0.30	0.27	265.8
	W2.4	- 444.3	898.6	0.40	0.27	265.9
	LL.5	- 444.2	900.4	2.20	0.21	268.1
	L.5	- 444.2	900.5	2.30	0.20	268.4
	W1.4	- 446.1	902.1	3.90	0.11	275.0
	G.3	- 447.4	902.8	4.60	0.08	279.3
	L.4	- 446.5	903.1	4.90	0.09	277.4
	L.3	- 448.1	904.2	6.00	0.05	282.9
	W2.3	- 461.2	930.3	32.10	0.00	362.2
	LL.3	- 461.2	930.3	32.10	0.00	366.3
	W1.3	- 466.4	940.9	42.70	0.00	399.9
	G.2	- 735.8	1477.6	579.40	0.00	63829.4
<i>Female</i>	G.4	- 634.9	1279.8	0.00	0.71	176.5
	W2.4	- 635.4	1280.7	0.90	0.65	177.6
	L.5	- 634.8	1281.6	1.80	0.66	177.5
	LL.4	- 636.1	1282.1	2.30	0.54	179.2
	LL.5	- 635.2	1282.4	2.60	0.60	178.4
	L.4	- 637.4	1284.8	5.00	0.37	182.3
	L.3	- 639.4	1286.7	6.90	0.23	185.6
	W1.4	- 641.6	1293.1	13.30	0.07	192.0
	G.3	- 643.0	1294.0	14.20	0.04	194.3
	W2.3	- 672.9	1353.9	74.10	0.00	283.1
	LL.3	- 674.3	1356.5	76.70	0.00	287.9
	W1.3	-684.8	1377.5	97.70	0.00	328.5
	G.2	-1101.6	2209.2	929.40	0.00	61785.1

Table A4.6. Growth curve model (Gompertz) results for wing length in male (N = 18) and female (N = 29) ground-hornbill chicks. Estimates include slope (growth rate), lower limit, upper limit (asymptotic mass), and ED50 (age at 50% of asymptotic mass) with standard errors (SE) and 95% confidence intervals (CI). Sex differences were tested using a combined model and P values indicate whether parameters differ significantly between males and females.

Parameter	Male estimate (SE)	Female estimate (SE)	Male 95 % CI	Female 95 % CI	P value (Male vs Female)
Slope	- 0.04 (0.00)	- 0.04 (0.00)	- 0.04 / - 0.03	- 0.04 / - 0.03	0.919
Lower limit	15.07 (4.77)	16.33 (3.16)	5.61 / 24.53	10.09 / 22.57	0.814
Upper limit	597.16 (26.6)	580.50 (17.16)	544.49 / 649.84	546.6 / 614.4	0.587
ED50	43.05 (1.30)	43.04 (0.88)	40.47 / 45.62	41.30 / 44.78	0.995

Equation for G.4 model used for wing length:

$$f(x)=c+(d-c)(\exp(-\exp(b(x-$$

Bill length

Table A 4.7. Model selection table for fitting growth curve model (functions: Gompertz [G], logistic [L], log-logistic [LL], and Weibull [W]) to bill growth data of ground-hornbill chicks, categorised by sex. Models are ordered according to AIC, with the most suitable model in bold. LL.4 model chosen for both sexes to allow for comparison.

Sex	Model	Log likelihood	AIC	Δ AIC	Lack of fit	Residual variance
<i>Male</i>	W1.4	-322.74	655.48	0.00	0.78	23.96
	LL.4	-322.84	655.68	0.20	0.76	24.01
	W2.4	-323.12	656.05	0.57	0.73	24.09
	G.4	-323.28	656.57	1.09	0.68	24.21
	L.4	-323.31	656.62	1.14	0.67	24.22
	LL.5	-322.58	657.16	1.68	0.72	24.13
	L.5	-323.31	658.62	3.14	0.58	24.45
	G.3	-327.63	663.26	7.78	0.15	25.98
	L.3	-339.07	686.13	30.65	0.00	32.11
	W2.3	-352.67	713.34	57.86	0.00	41.32
	LL.3	-354.56	717.13	61.65	0.00	42.79
	W1.3	-377.38	762.76	107.28	0.00	65.29
	G.2	-632.37	1270.74	615.26	0.00	7268.94
	LL.4	-468.30	946.60	0.00	0.48	14.34
	W2.4	-468.44	946.88	0.28	0.47	14.36
<i>Female</i>	W1.4	-468.58	947.17	0.57	0.45	14.38
	G.4	-468.77	947.54	0.94	0.43	14.42
	L.4	-468.80	947.61	1.01	0.42	14.42
	LL.5	-468.21	948.42	1.82	0.43	14.41
	L.5	-468.82	949.63	3.03	0.35	14.51
	G.3	-477.09	962.20	15.60	0.16	15.80
	L.3	-499.32	1006.64	60.04	0.00	20.49
	W2.3	-523.07	1054.14	107.54	0.00	27.05
	LL.3	-527.37	1062.75	116.15	0.00	27.05
	W1.3	-567.71	1143.42	196.82	0.00	45.59
	G.2	-996.41	1998.81	1052.21	0.00	6821.13

Table A4.8. Growth curve model (Log logistic) results for bill length in male (N = 18) and female (N = 29) ground-hornbill chicks. Estimates include slope (growth rate), lower limit, upper limit (asymptotic mass), and ED50 (age at 50% of asymptotic mass) with standard errors (SE) and 95% confidence intervals (CI). Sex differences were tested using a combined model and P values indicate whether parameters differ significantly between males and females.

Parameter	Male estimate (SE)	Female estimate (SE)	Male 95 % CI	Female 95 % CI	P value (Male vs Female)
Slope	-1.16 (0.09)	- 1.16 (0.08)	- 1.34 / - 0.97	- 1.32 / - 1.00	0.959
Lower limit	18.66 (1.30)	19.20 (1.17)	16.09 / 21.24	16.89 / 21.52	0.756
Upper limit	267.45 (40.8)	237.40 (27.04)	187.2 / 347.7	184.2 / 290.6	0.555
ED50	88.53 (22.92)	78.81 (15.66)	43.4 / 109.7	47.97 / 109.7	0.737

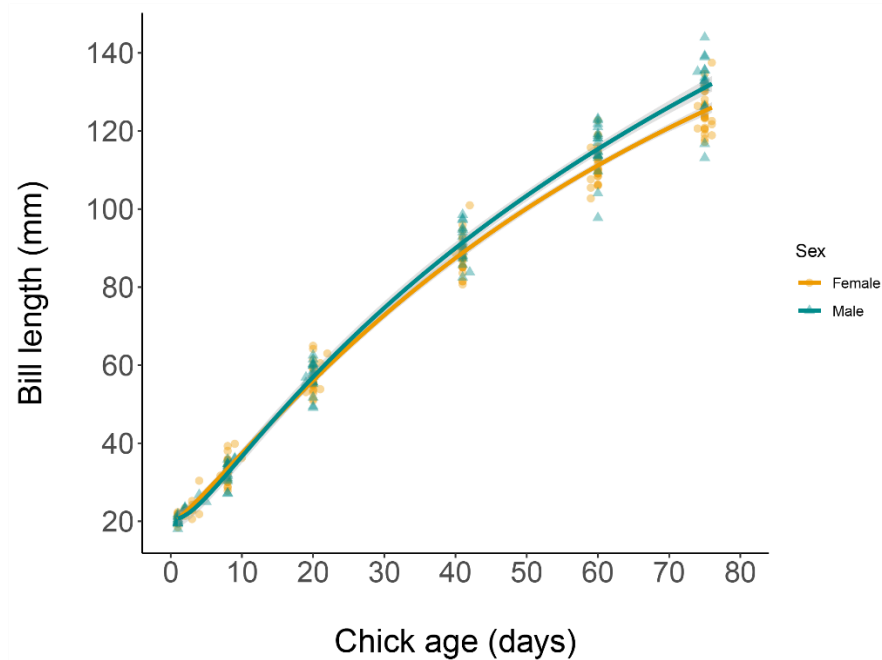


Figure A4.4. Growth curves of ground-hornbill bill length in mm. Predicted growth trajectories from a logistic model are shown as green lines for males, and orange for females and shaded areas indicate 95% confidence intervals. Observed values shown as green triangles (males) and orange circles (females).

Temperature effects on chick growth

Δ Mass

Table A4.9. Factors influencing Δ Mass in ground-hornbill chicks across different ages, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross.

Model no	Variable	Est	SE	95 % CI	P value
1	mean T_{maxnest}	- 1.11	0.35	- 1.79 / - 0.43	0.001
	sex (male)	1.79	0.70	0.42 / 3.17	0.011
	d1-8 (intercept)	35.86	0.79	34.25 / 37.36	<0.001
	d8-20	-13.27	1.05	-15.34 / -11.21	<0.001
	d20-40	-29.86	1.06	- 32.00 / - 27.80	<0.001
	d40-60	-35.71	1.08	- 37.80 / - 33.61	<0.001
	d60-75	-36.51	1.07	- 38.63 / - 34.39	<0.001
<i>N = 237, group ID = 19, chick ID = 57, season = 6</i>					

Δ Tarsus

Table A4.10. Factors influencing Δ Tarsus in ground-hornbill chicks across different ages, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model No	Variable	Est	SE	95 % CI	P value
1	Mean T_{maxair}	- 0.26	0.08	- 0.42 / - 0.09	0.002
	sex (male)	0.15	0.17	- 0.18 / 0.49	0.369
	d1-8 (intercept)	8.01	0.24	7.51 / 8.49	<0.001
	d8-20	0.81	0.24	0.33 / 1.29	0.001
	d20-40	- 4.11	0.25	- 4.60 / - 3.62	<0.001
	d40-60	-7.55	0.25	- 8.04 / -7.07	<0.001
	d60-75	-7.92	0.25	- 8.41 / - 7.43	<0.001
<i>N = 237, group ID = 19, chick ID = 57, season = 6</i>					

Δ Wing

Table A4.11. Factors influencing Δ Wing in ground-hornbill chicks across different ages, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no	Variable	Est	SE	95 % CI	P value
1	mean T_{maxair}	- 0.55	0.16	- 0.87 / - 0.22	0.001
	sex (male)	0.58	0.33	- 0.09 / 1.23	0.087
	d1-8 (intercept)	6.48	0.36	5.76 / 7.20	<0.001
	d8-20	3.66	0.48	2.71 / 4.60	<0.001
	d20-40	3.74	0.53	2.69 / 4.77	<0.001
	d40-60	- 3.27	0.52	- 4.30 / - 2.24	<0.001
	d60-75	- 4.99	0.50	- 5.98 / - 4.01	<0.001
2	mean T_{maxair}	- 0.72	0.24	- 1.19 / - 0.26	0.002
	sex (male)	0.61	0.33	- 0.04 / 1.26	0.067
	d1-8 (intercept)	6.45	0.36	5.74 / 7.16	<0.001
	d8-20	3.66	0.47	2.73 / 4.59	<0.001
	d20-40	3.70	0.52	2.66 / 4.74	<0.001
	d40-60	- 3.33	0.52	- 4.35 / - 2.31	<0.001
	d60-75	- 5.02	0.49	- 5.99 / - 4.05	<0.001
	mean T _{maxair} * d8-20	- 0.46	0.45	- 1.35 / 0.43	0.311
	mean T _{maxair} * d20-40	0.54	0.58	- 0.60 / 1.69	0.349
	mean T _{maxair} * d40-60	0.97	0.56	- 0.14 / 2.07	0.087
	mean T _{maxair} * d60-75	0.66	0.46	- 0.26 / 1.57	0.158
<i>N = 212, group ID = 19, chick ID = 56, season = 6</i>					

Provisioning and growth rates during early and late ages

Δ Mass (d1-8 and d40-60)

Table A4.12. Factors influencing ground-hornbill Δ Mass during early d1-8, and late d40-60 development when including provisioning rates, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	provisioning	- 1.00	0.81	-2.58 / 0.58	0.217
	mean T _{maxnest}	- 1.15	0.70	- 2.51 / 0.22	0.103
	sex (male)	2.54	1.61	- 0.61 / 5.69	0.118
	d1-8 (intercept)	35.41	1.26	32.95 / 37.86	<0.001
	d40-60	- 35.34	1.60	- 38.46 / - 32.22	<0.001
2	provisioning	- 1.22	0.82	- 2.81 / 0.37	0.137
	sex (male)	2.57	1.65	- 0.66 / 5.80	0.125
	d1-8 (intercept)	35.36	1.28	32.86 / 37.87	<0.001
	d40-60	-35.35	1.60	- 38.49 / -32.21	<0.001
<i>N = 87, chick ID = 54, group ID = 19, season = 6</i>					

Δ Tarsus (d1-8 and d40-60)

Table A4.13. Factors influencing ground-hornbill Δ Tarsus during early d1-8, and late d40-60 development when including provisioning rates, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	provisioning	0.17	0.18	- 0.18 / 0.53	0.337
	mean T_{maxair}	- 0.41	0.15	- 0.71 / -0.11	0.009
	sex (male)	-0.07	0.37	- 0.79 / 0.64	0.840
	d1-8 (intercept)	8.19	0.15	7.28 / 9.05	<0.001
	d40-60	-7.66	0.35	- 8.35 / - 6.97	<0.001
<i>N = 87, chick ID = 54, group ID = 19, season = 6</i>					

Δ Wing (d1-8 and d40-60)

Table A4.14. Factors influencing ground-hornbill ΔWing during early d1-8, and late d40-60 development when including provisioning rates, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	provisioning	- 0.02	0.18	- 0.44 / 0.42	0.896
	mean T_{maxair}	- 0.48	0.14	- 0.76 / - 0.20	0.001
	sex (male)	- 0.17	0.36	- 0.88 / 0.54	0.633
	d1-8 (intercept)	6.60	0.31	5.96 / 7.22	<0.001
	d40-60	- 3.01	0.33	- 3.67 / - 2.33	<0.001
2	provisioning	- 0.05	0.18	- 0.45 / 0.39	0.790
	mean T_{maxair}	- 0.48	0.14	- 0.76 / - 0.20	0.001
	sex (male)	- 0.21	0.36	- 0.92 / 0.50	0.557
	d1-8 (intercept)	6.58	0.32	5.93 / 7.22	<0.001
	d40-60	- 2.99	0.33	- 3.64 / - 2.32	<0.001
	provisioning * mean T _{maxair}	- 0.10	0.11	- 0.32 / 0.13	0.372
<i>N = 80, chick ID = 52, group ID = 19, season = 6</i>					

Temperature, helpers and provisioning rates

Table A4.15. Model selection table for factors explaining ground-hornbill chick provisioning rates during two development stages: early (d1-8) and late (d40-60), with top model highlighted in bold (AICc < 2). Models included chick ID, group ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Weight
1	mean T_{maxair} * age + helpers + juv + sex	571.0	0.00	0.757
2	mean T _{maxair} + age + helpers + juv + sex	574.3	3.32	0.144
3	mean T _{maxair} * helpers + juv + sex + age	575.8	4.82	0.068
4	mean T _{maxair} * age + sex	579.7	8.69	0.010
5	rainfall ₉₀ + sex + age	581.7	10.68	0.004
6	rainfall ₆₀ + sex + age	581.7	10.74	0.004
7	rainfall ₆₀ + sex + age	582.1	11.13	0.003
8	rainfall ₃₀ + sex + age	582.3	11.28	0.003
8	mean T _{maxair} + sex + age	582.6	11.63	0.003
9	null	582.8	11.82	0.002
10	rainfall ₉₀ + mean T _{maxair} + sex + age	582.3	11.28	0.002
11	rainfall ₆₀ + mean T _{maxair} + sex + age	583.0	12.00	0.002
12	rainfall ₃₀ + mean T _{maxair} + age + sex	583.4	12.41	0.000
<i>N = 86, Random terms: chick ID = 53, group ID = 19, season = 6</i>				

Table A4.16 . Factors influencing ground-hornbill chick provisioning rates during early d1-8, and late d40-60 development, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
	mean T _{maxair}	- 0.74	0.74	- 2.25 / 0.74	0.326
	d1-8 (intercept)	26.46	1.53	23.17 / 29.20	<0.001
	d40-60	-0.67	1.16	- 2.96 / 1.58	0.571
1	helpers	2.44	0.93	0.43 / 4.43	0.012
	juv	-2.03	0.92	- 2.31 / 4.50	0.034
	sex (male)	1.49	1.73	- 4.04 / - 0.07	0.395
	mean T _{maxair} * age	3.05	1.68	- 0.22 / 6.47	0.075
<i>N = 86, chick ID = 53, group ID = 19, season = 6</i>					

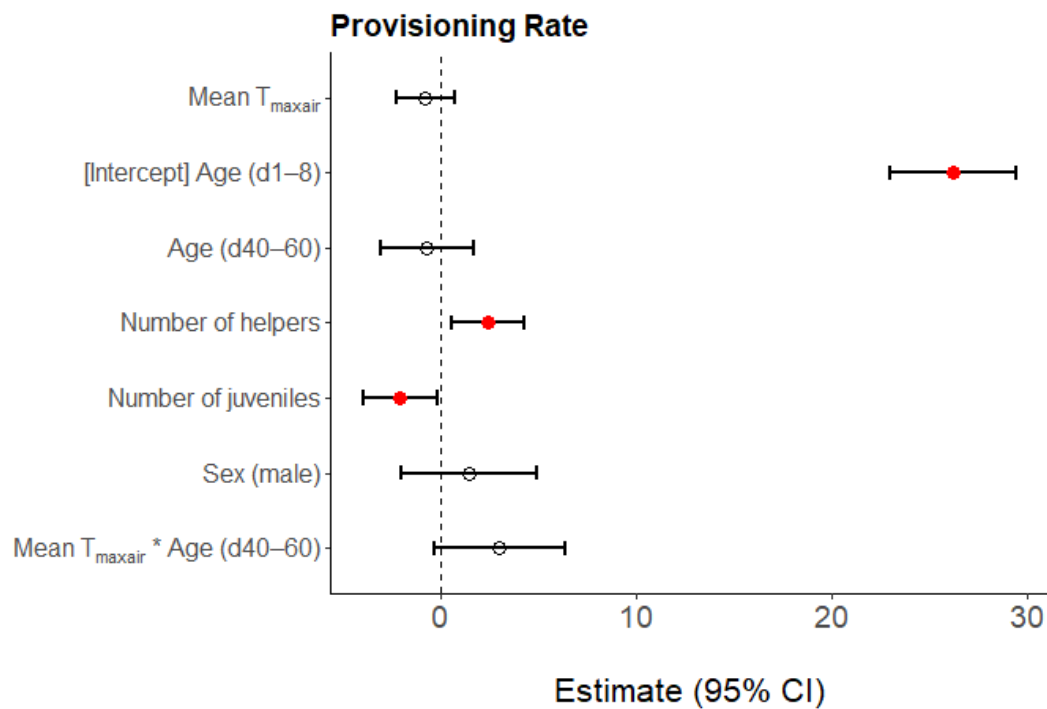


Figure A4.5. 95% confidence intervals for variables included in model 1 for predicting chick provisioning rates during d1-8 and d40-60. The model includes the main effect of mean T_{maxair} , helpers, juveniles, sex and the interaction between mean T_{maxair} and age. Filled red circles indicate statistically significant effects, while open black circles indicate non-significant effects.

Chick fledging size and condition

Fledging size

Table A4.17. Principal component analysis (PCA) loadings of chick morphology traits (mass, tarsus length, and wing length at d75, N=44). Traits were z-standardized prior to analysis. PC1 explained 65% of the variance and loaded negatively on all traits, representing overall body size. PC2 explained 28% of the variance and contrasted tarsus and wing length. Only PC1 was used in subsequent linear-mixed effects models as a size index.

Trait	PC1	PC2	PC3
Mass d75	- 0.669	0.096	- 0.738
Tarsus d75	- 0.594	0.528	0.607
Wing d75	- 0.448	0.843	0.296
<i>N = 44</i>			

Table A4.18. Factors explaining chick fledging body size (PC1), with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	mean T _{maxair}	0.41	0.31	- 0.20 / 1.06	0.191
	sex (male)	1.16	0.36	0.95 / 2.36	<0.001
<i>N = 44, Random terms: Group ID = 17, Season = 6</i>					

Fledging condition

Table A4.19. Factors explaining chick fledging body condition (mass on d75 / tarsus length d75), with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	helpers	0.21	0.34	- 0.52 / 0.89	0.546
	juv	-0.86	0.52	- 1.30 / - 0.41	<0.001
	sex (male)	1.16	0.47	0.23 / 2.06	0.018
<i>N = 44, Random terms: Group ID = 17, Season = 6</i>					

Over winter survival

Table A4.20. Factors explaining post-fledging overwinter survival in ground-hornbills, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables in bold are significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	days > 35 °C_{nest}	-1.59	0.79	- 4.20 / - 0.39	0.045
	days > 35 °C_{winter}	-2.59	1.28	- 7.28 / - 1.07	0.043
2	mean T_{maxnest}	- 1.67	0.93	- 5.76 / - 0.34	0.073
	days > 35 °C_{winter}	- 2.82	1.44	- 8.70 / - 1.06	0.050

N = 35, group ID = 17

Breeding season monthly average numbers of days above 35 °C (2019–2025)

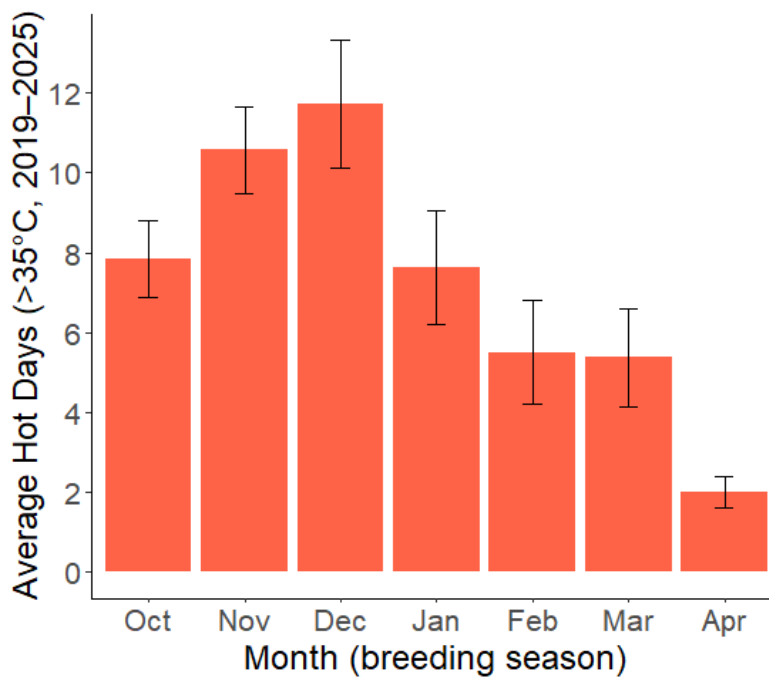
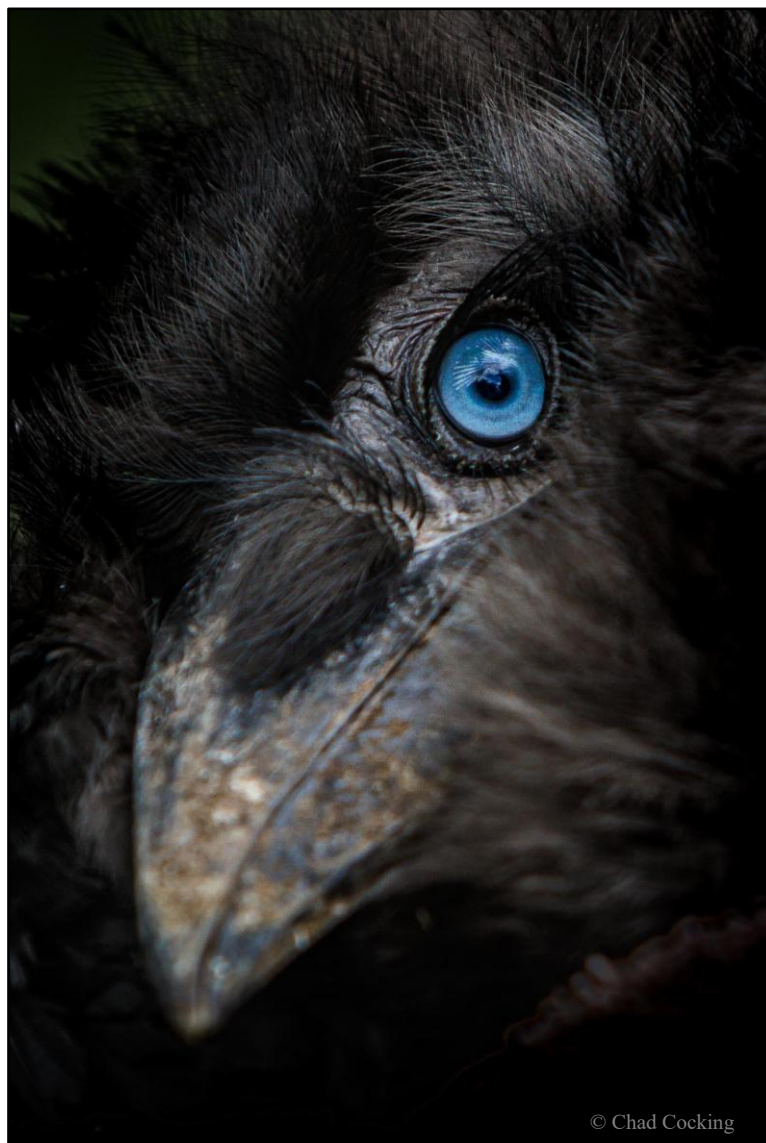


Figure A4.6. Average number of days where air temperatures exceed 35 °C per month during the breeding season (October–April), calculated as the mean for each calendar month across 6 breeding seasons from 2019 - 2025. Error bars show the standard error of the monthly averages. The number of hot days become less frequent later in ground-hornbills breeding season (February–April).

CHAPTER 5

Hotter nests during incubation are associated with early life telomere length and telomere dynamics in an endangered long-lived bird



5.1. Abstract

Environmental conditions experienced during early life can have long-lasting survival and fitness consequences. Rising temperatures and more frequent heat events, driven by climate change, are increasingly exposing wildlife to temperatures which have measurable negative impacts on development and physiology. Heat-induced oxidative stress can accelerate telomere erosion, potentially making telomere length a useful biomarker of the effects of heat exposure on fitness and survival. I investigated the impact of high nest and air temperatures on telomeres in wild southern ground-hornbill nestlings *Bucorvus leadbeateri*, a slow-developing, long-lived, cooperatively breeding species. I used blood samples collected from 34 nestlings over five years to assess whether temperatures during prenatal or postnatal stages influenced telomere length at fledging age (day 75) and telomere dynamics (change in telomere length over time) at the late nestling stage (between day 60 and 75). I also investigated whether having more helpers in the group could mitigate any negative heat impacts, thereby enabling nestlings to maintain telomere length. I found that the frequency of heat exposure (number of days above 35 °C) in the nest during incubation was the best predictor of both telomere length at fledging and telomere dynamics. Models revealed that hotter nests during incubation were associated with longer relative telomere length on day 75. However, nestlings from hotter nests also exhibited faster telomere shortening between day 60 and day 75. I found no helper effects on telomere length or telomere dynamics. To conclude, hotter nest conditions appear to provide an early life advantage for telomere length at fledging in ground-hornbills but may also carry physiological costs through accelerated telomere shortening late in nestling development.

5.2. Introduction

Early life is a brief but critical window during which environmental conditions influence growth, physiology, and behaviour, shaping individual phenotypes and fitness (Lindström,

1999; Metcalfe & Monaghan, 2001). Offspring are sensitive to environmental stressors because rapid growth and development demand high energy expenditure (Lindström, 1999; Monaghan, 2008; Nord & Giroud, 2020), and additional physiological stress can have long-lasting effects on survival, reproduction, and immunity (Metcalfe & Monaghan, 2001; Monaghan, Metcalfe & Torres, 2009). Rising temperatures, driven by climate change, are a critical factor influencing offspring fitness and survival across taxa, especially in hot climates where chronic sub-lethal heat exposure can reduce parental care, body condition, and survival rates (Cunningham et al., 2013; Andrew et al., 2017; Woodroffe, Groom & McNutt, 2017; Bourne et al., 2020b; Van de Ven, Fuller & Clutton-Brock, 2020; Khera et al., 2023). However, despite growing research on the physiological effects of heat in adult birds (McKechnie, Gerson & Wolf, 2021; Moagi et al., 2021; van Jaarsveld et al., 2021; Xu et al., 2024; Coulson et al., 2025), the impacts of heat on early life physiology remain poorly understood, particularly in wild, free-roaming long-lived species (but see Diehl et al., 2023).

To avoid lethal hyperthermia when exposed to high temperatures, birds must employ heat loss mechanisms that can be physiological (e.g. increased evaporative cooling) or behavioural (e.g. shade-seeking, wing-drooping, reduced activity; Carroll et al., 2015; Cunningham, Martin & Hockey, 2015; Smit et al., 2016; Cook et al., 2020; Pattinson et al., 2020). However, these mechanisms carry the risk of dehydration and reduced body condition (du Plessis et al., 2012; Albright et al., 2017; van de Ven, McKechnie & Cunningham, 2019; Diehl et al., 2023). Heat exposure resulting in elevated body temperature can trigger increases in heat shock proteins and glucocorticoid levels (Wingfield et al., 2017; McKechnie & Wolf, 2019; Moagi et al., 2021), leading to physiological disturbances such as oxidative stress (an imbalance between reactive oxygen species production and antioxidant defences) (Haussmann et al., 2012). Altricial nestlings are sensitive to heat because they are ectothermic during the egg and early hatching phases, relying on external temperatures and parental incubation to

regulate their body temperature (Price & Dzialowski, 2018). They are also vulnerable to heat due to high metabolic rates supporting rapid growth (Olson, 1992) and to being confined to the nest, unable to evade heat (Dunn, 1975; Weeks et al., 2022). In addition, nestlings rely on parental provisioning, which can decline during high temperatures, heightening their risk of dehydration and nutritional stress (du Plessis et al., 2012; Lamb, O'Reilly & Jodice, 2016; van de Ven et al., 2020; Barras et al., 2021; Bourne et al., 2021; Oswald et al., 2021). Therefore, heat-induced stress can disrupt growth rates (Catry et al., 2015; van de Ven et al., 2020; Corregidor-Castro & Jones, 2021) and physiological processes such as metabolic rates (Diehl et al., 2023), with lasting impacts on fitness and survival (Metcalf & Monaghan, 2001; Fuller et al., 2010; Kingsolver & Buckley, 2017; Conradie et al., 2019). Telomere length is a widely used molecular biomarker of how early life conditions influence individual quality (Heidinger et al., 2012; Dupont et al., 2018, 2023; Angelier et al., 2019; Eastwood et al., 2019, 2023; Fragueira, Verhulst & Beaulieu, 2019; Metcalfe & Olsson, 2022). Therefore, telomere measurements provide a promising method for assessing the effects of early life heat exposure on offspring phenotypes.

Telomeres are non-coding DNA sequences that cap the ends of chromosomes, protecting them from degradation (Horn, Robertson & Gemmell, 2010; Reichert & Stier, 2017; Belmaker et al., 2019). Telomere length is partly heritable (Asghar et al., 2015; Bauch et al., 2019) and varies between species, chromosomes, and sometimes sexes (Parolini et al., 2015; Criscuolo et al., 2020; Hansson et al., 2024). Over an individual's lifespan, telomeres shorten during cell division due to incomplete replication of chromosome ends (Blackburn, 2005). However, the enzyme telomerase is a maintenance mechanism that can counteract telomere shortening and also lengthen telomeres, meaning that telomere length is dynamic and shortening is not constant throughout life (Hausmann et al., 2007). Once critically eroded, telomeres lose their protective role, exposing coding DNA to degradation and triggering

cellular senescence, which contributes to ageing and eventual death (Hall et al., 2004; Horn, Robertson & Gemmell, 2010; Belmaker et al., 2019; Eastwood et al., 2019). This process is accelerated by oxidative stress, which damages telomeric DNA and inhibits telomerase (Angelier et al., 2018). Although telomere shortening occurs throughout life, it intensifies during early life due to rapid growth and cell division to reach adult size (Monaghan & Ozanne, 2018). Exposure to environmental stress on top of growth can accelerate shortening (Hall et al., 2004; Horn, Robertson & Gemmell, 2010; Watson, Bolton & Monaghan, 2015; Angelier et al., 2018; Fragueira, Verhulst & Beaulieu, 2019; van Lieshout et al., 2022; Eastwood et al., 2023), and heat-induced oxidative stress is one mechanism known to affect telomere dynamics (change in telomere length over time) (Ton et al., 2023). Other environmental stressors associated with telomere dynamics include weather catastrophes (e.g. tsunamis) (Mizutani et al., 2013), pollution (Blévin et al., 2016; Stauffer et al., 2017) and anthropogenic noise (Dorado-Correa et al., 2018; Grunst et al., 2020). In offspring, accelerated telomere shortening and short telomeres have been associated with reduced longevity, decreased fitness, and lower survival probabilities (Heidinger et al., 2012, 2021; Eastwood et al., 2019; Marasco, Smith & Angelier, 2022; van Lieshout et al., 2022; Dupont et al., 2023), and in several avian species, greater telomere shortening during the nestling stage reduced the likelihood of first year survival (Boonekamp et al., 2014; Wood & Young, 2019; Sheldon et al., 2022).

Cooperative breeding strategies have the potential to reduce the rate of telomere shortening by alleviating early life stress through enhanced parental care (Quque et al., 2021). In cooperatively breeding species, helpers (non-breeding individuals) assist in raising offspring that are not their own (Cockburn, 2006). Helpers are thought to improve breeding conditions by providing additional food to the nest and increasing predator protection and territory defence (Cockburn, 1998; te Marvelde et al., 2009; Kingma et al., 2010; Teunissen et al., 2021). They may also support greater maternal investment in offspring (Russell & Lummaa, 2009; Capilla-

Lasheras, Wilson & Young, 2023). However, in some cases, helpers are associated with reduced maternal investment under load-lightening, whereby they maintain offspring quality and allow females to invest less (Russell et al., 2007; Canestrari, Marcos & Baglione, 2011; Santos & Macedo, 2011). During adverse conditions, helpers may mitigate the negative impacts of environmental stress by increasing provisions to nestlings (Hatchwell, 1999; te Marvelde et al., 2009; Van Boheemen et al., 2019) which can improve fledging condition and survival prospects (Canestrari, Marcos & Baglione, 2011). These social benefits could mitigate heat-induced stress if helpers reduce other stressors (e.g. nutritional stress), although studies on telomere dynamics and the potential influence of helpers during early life are scarce.

This study investigates how temperature and social conditions influence physiology, by assessing telomere length and dynamics in southern ground-hornbill (*Bucorvus leadbeateri*, hereafter ‘ground-hornbill’) nestlings, and whether early life conditions have longer-lasting consequences for survival. I considered telomere length at fledging age (75 days old) and telomere dynamics during the late stage of development (60-75 days old). Ground-hornbills are large (3.3 – 4.4 kg) cooperatively breeding birds that are exceptionally long-lived (50–60 years) (Kemp, 1980). Because long-lived species often maintain telomeres more effectively than short-lived species, likely due to enhanced maintenance mechanisms (Hausmann et al., 2003; Dantzer & Fletcher, 2015; Wilbourn et al., 2018), understanding how heat exposure affects telomere dynamics in this species may be particularly relevant. Ground-hornbills inhabit semi-arid savanna habitats across sub-Saharan Africa (Kemp, 1980; Kemp & Rose, 2025) where their breeding season coincides with the hottest months of the year. Daily maximum air temperatures often exceed 30 °C and approach 40 °C, while average daily minimum temperatures remain around 20 °C. As a result, developing nestlings are regularly exposed to high temperatures above 35 °C. Nestlings are altricial and have a prolonged

development period (~85 days in the nest) (Kemp, 1980; Carstens et al., 2019a), making them especially vulnerable to sustained periods of high temperatures while confined to the nest.

Both prenatal (via maternal allocation and embryonic environment) (Stier, Metcalfe & Monaghan, 2020; Hope et al., 2022; Noguera, Da Silva & Velando, 2022) and postnatal conditions (Eastwood et al., 2022, 2023; Ton et al., 2023) have been associated with variation in offspring telomere length and dynamics in other species. Given that high temperatures can be physiologically stressful for organisms, I predict that heat exposure during either the prenatal stage (maternal/egg environment) or the post-hatching stage (nestling environment) will negatively affect telomere length near fledging age and accelerate telomere attrition between 60 and 75 days. However, with a long lifespan, this species may prioritise telomere maintenance, potentially weakening any observable effects. I further expect that groups with more helpers may mitigate any negative effects of heat on telomeres. I also predict that males could have shorter telomeres and faster telomere shortening than females due to faster growth and greater body mass accumulation (Chapter 4), likely requiring higher rates of cell division. Finally, I predict that shorter telomeres and/or faster telomere shortening will be negatively associated with the survival of chicks in their first year.

5.3. Methods

Fieldwork was conducted in the APNR reserves over five breeding seasons, from October 2019 to April 2024 (see Chapter 1: Study site). Ground-hornbill nests were monitored every 7–10 days at the beginning of each season from October – December to identify active nests and to predict hatching dates (see Chapter 1: General methods). Ground-hornbills depend on large tree cavities for nesting, and the loss of mature trees across their range has contributed to population declines (Kemp & Rose, 2025). At the study site, most nest sites are artificial nest boxes made from wood or M1 composite (see Chapter 1: Study site) which are readily

accepted by breeding ground-hornbills (Wilson & Hockey, 2013; Carstens et al., 2019c). Across the five breeding seasons, 22–28 groups were monitored annually. Some bred in multiple years, but only ~12–15 groups attempted to breed each year, with 7–10 of these groups successfully fledging nestlings per breeding season (Table A5.1). Ground-hornbills have very low fecundity, groups only raise one nestling per breeding attempt, and in this population, groups breed on average once every 2–3 years. Helpers contribute to nestling provisioning, but they also provision the incubating female, who is the sole incubator and remains in the nest for the ~42-day incubation period, and then for a further ~20 days while brooding the newly hatched nestling.

5.3.1. Nestling data collection

Telomere analyses focused on the late nestling period (day 60–75), when high-quality DNA was obtainable. At this age nestlings' body mass approaches its asymptote (Chapter 4), and the stress response system, the hypothalamic–pituitary–adrenal (HPA) axis, is likely mature (Blas et al., 2006). Energy balance at this stage shifts from rapid growth to maintenance and preparation for fledging, allowing us to assess how cumulative early life conditions (defined here as from the embryo to fledging stage) influence telomere dynamics prior to fledging. Blood samples (< 500 µL) were collected from the brachial vein of 37 nestlings at 60 and 75 days old (hereafter d60 and d75) (see Chapter 1: General methods). Although earlier sampling was initially intended (day 8), sufficient high-quality DNA could not be obtained from blood samples at this age. The final sample size was reduced to 34 because of missing data (see below). Samples from five additional nestlings were collected but were not included in the final analyses due to either nestling depredation before d75 (d60 collected) or incomplete data for other variables. However, all collected samples, including those excluded from analyses, were processed and included in the golden sample reference for calculating relative telomere length (see below), resulting in a total of $N = 79$ samples measured (74 from 37 nestlings at 60 and

75 days old, plus the 5 additional samples). Whole blood was immediately preserved in 95% ethanol and stored at room temperature until laboratory processing. The average storage duration between blood collection and laboratory processing was ~940 days (range: 269–1725 days). Morphometric measurements of nestling body mass, tarsus, and wing length were collected during nest visits to assess nestling size and condition (see Chapter 4). Nestlings fledge at an average age of 85 days (range: days 77–89); therefore, samples collected at d75 are considered to reflect their telomere state at the end of the nestling period.

5.3.2. DNA extraction and telomere measurements

To assess the effect of high temperatures on relative telomere length (rTL) and telomere dynamics (Δ rTL), rTL was calculated at both d60 and d75 post-hatching. All laboratory procedures were conducted at the Institut Pluridisciplinaire Hubert Curien (IPHC, Strasbourg, France). Genomic DNA was extracted from blood samples using an automated platform for magnetic bead-based DNA/RNA extraction (The MagentaPure 32, Dutscher SAS, Bernolsheim France) and the NucleoMag blood kit (Macherey Nagel, Düren, Germany). DNA quantity and quality were assessed based on spectrophotometer absorbance (Nano-Drop 1000, Thermo Fisher Scientific, Waltham, MA, USA, ratios A260/280 and A260/230) and gel migration. Individual DNA were all diluted to a concentration of 2.5 ng/ μ L and further used for rTL determination by qPCR.

Individual relative telomere length (rTL) was obtained following the qPCR methodology previously used in several bird species (e.g. Bize et al., 2009; Criscuolo et al., 2009, 2020; Quque et al., 2021). This technique is based on the amplification of two targeted DNA sequences (i.e. telomere and housekeeping genes) using specific primers and fluorescence. To control for variation in DNA concentrations among diluted samples (due to potential pipetting errors), which may induce a methodological bias in the final rTL values, a genomic DNA sequence with non-variable copy number was also amplified for each individual

(the housekeeping gene). The control gene used for ground-hornbills was EGR1 gene (early growth response 1 gene). Amplifications were conducted in a 384 wells-plate filled by a calibrated automated liquid handling workstation (Epmotion, Eppendorf, Montesson, France), using one distinct plate for telomere amplifications and one for the control gene, due to the different qPCR conditions for each gene because of primers sequences properties. Amplification conditions were 2 min at 95 °C followed by 40 cycles of 15 s at 95 °C, 30 s at 56 °C and 1 min 30s at 72 °C (control gene) and of 2 min at 95 °C followed by 30 cycles of 15 s at 95 °C, 30 s at 56 °C and 1 min 30 sec at 72 °C (telomere sequence).

Reactions were prepared in a master mix specific to each primer set, containing 5 µL GoTaq QPCR Mix (Promega, Madison, WI, USA) with telomere primers or control gene primers at 100 nM or 1 µM, respectively. Each reaction contained 5 ng of DNA. Each plate included: i) a negative control sample (ultra-pure water) to control for putative DNA contaminations, ii) a DNA golden sample (as a mix of 20 individual samples randomly selected) that was used as the reference value of 1 for rTL calculations, iii) a dilution curve obtained from the amplification of the golden sample that was serially diluted (from 20 to 0.3125 ng/µL). Dilution curves were used to assess the quality of the control gene and telomere sequences qPCR amplifications (i.e. efficiency values (control gene 100.2%; telomere sequences 99.7%) and r^2 (0.976 and 0.942, respectively)). All runs concluded with a fusion curve to verify the absence of non-specific amplifications. rTL values were calculated following Pfaffl (2001). The T/S ratio, which represents the relative signal of the telomere (T) versus the control gene (S), controlled for their respective amplification efficiencies, was expressed relative to the golden sample T/S value of 1, is calculated as:

$$T/S \text{ ratio (rTL)} = \frac{[(1 + E_{telomere})^{\Delta Cq_{telomere}}]}{[(1 + E_{EGR1})^{\Delta Cq_{EGR1}}]}$$

Where $\Delta Cq = Cq_{goldensample} - Cq_{individualsample}$, and E = the qPCR efficiency.

All samples were run in duplicates and intra-individual repeatability of rTL, evaluated using the Intra Class Coefficient (ICC), was 0.751.

5.3.3. Weather data

Daily maximum air temperature (°C) and rainfall (mm) data were obtained from an onsite weather station (See Chapter 1: general methods). For each nestling, exposure to high temperatures was quantified using two different measures during the periods of interest: (1) mean maximum daily air temperature (T_{maxair}) which reflects overall high temperature averages, and (2) the number of days exceeding 35 °C (days > 35 °C_{air}), which captures the frequency of heat events and represents a threshold associated with negative impacts on breeding in other southern African savanna birds (Bourne et al., 2020b; van de Ven et al., 2020), and is also a threshold above which ground-hornbills are less likely to forage (Chapter 2). In addition, cumulative rainfall was explored as a proxy for resource availability. Rainfall promotes plant growth and insect abundance, thereby influencing food availability, particularly in arid and semi-arid systems (Zhang et al., 2005; Hidalgo Aranzamendi et al., 2019) and often has a positive effect on nestling development and survival (Wiley & Ridley, 2016; D'Amelio et al., 2022). Temperature and rainfall variables were calculated for biologically relevant periods: prelay (90 days prior to egg laying), during which environmental conditions can influence maternal allocation to eggs (see Chapter 3); the incubation period (from egg laying to hatching), when embryos are exposed to thermal conditions; and the nestling period (hatching to d75), when nestlings are exposed to thermal conditions (Table 5.1). For rTL at d75, I focused on these stages because rTL is expected to reflect cumulative longer-term environmental conditions. Telomere dynamics measure changes in rTL between two time periods (d60-d75 in this study; see below); therefore, to capture more immediate environmental effects, short-term intervals immediately preceding and overlapping this period (days 40–60 and 60–75; Table 5.2) were included alongside the longer-term measures (prelay, incubation,

nestling). I explored the relationship between Mean T_{maxair} during the period between d60 and d75 to assess the immediate effects of conditions at the time of telomere shortening (even though this was not identified as the strongest predictor of Δ rTL (see results)). For these short windows, only air and nest temperature were considered, as rainfall is expected to have a lagged effect on food availability (Hidalgo Aranzamendi et al., 2019).

5.3.4. Nest temperature data

Thermochron iButtons (see Chapter 1: General methods) were used to record internal nest temperatures in all nests in which eggs were laid, throughout the period from egg laying to fledging. However, data were not obtained for three nests due to device recording failures, hence the final sample size was reduced from 37 to 34. Mean maximum daily nest temperature (mean T_{maxnest}) and the number of days nest temperature exceeded 35 °C (days > 35 °C_{nest}) were calculated for the same biologically relevant periods used for air temperature above, but only for the period from egg laying to fledging (Table 5.1, Table 5.2). Mean maximum nest temperature increased moderately with mean maximum air temperature (Figure A5.3). Nest temperatures varied substantially between nests due to differences in nest material and placement (e.g., shade, proximity to rivers). This variability was greater than that of the air temperature variability (Table A5.13).

5.3.5. Number of helpers and juveniles

Data were obtained for 16 unique groups, which correspond to all groups included in our analyses (some groups bred in multiple seasons). Group composition and individual identity were determined using cameras placed at the nests (see Chapter 1: General methods). Helpers were classified as adult and subadult group members, as these age classes contribute substantially to cooperative behaviours such as territory defence and nestling provisioning (Middleton, 2022). For analyses, adults and subadults were combined into a single continuous predictor representing the number of individuals actively contributing to care (range = 2–5,

mean = 3.3). Juveniles from previous years contribute little to these activities (Middleton, 2022) and have been observed stealing food from nestlings (pers.obs; Figure A4.2). In the studied groups, 0–2 juveniles were present per group (mean = 0.58) and were only classed as sub-adults when > 3 years old. Juvenile presence was included separately in all analyses as they may compromise nestling growth and parental care. To retain statistical power given the limited sample size, juvenile presence was treated as binomial (0 = absent, 1 = present).

5.3.6. Juvenile survival

Nestlings fledge between February and April. To assess post-fledging overwinter survival, the presence of the new juvenile was recorded within groups at the start of the following breeding season (October–December). Camera traps were deployed each October at nest sites where a chick had successfully fledged the previous season. Because groups frequently revisit and defend nest sites, even in non-breeding years, this behaviour enabled reliable detection of group members, including juveniles (resight probability was effectively 100%) (Figure 5.1). Survival was recorded as a binary response (0 = did not survive, 1 = survived) based on the presence of the juvenile that fledged the previous season (identified by pale colouration of throat and unique identity ring placed on leg prior to fledging). Their extended associations with the natal group (see Chapter 1: Study species) support the use of presence at the nest site the following breeding season (typically 6 – 8 months post-fledging) as a robust indicator of juvenile survival.



Figure 5.1. Juveniles from previous years can be identified in subsequent breeding seasons using camera traps placed at nests, allowing their survival to be recorded. Pictured is a two-year-old juvenile with three adults and a nestling. Groups return to the nest as a cohesive unit when provisioning, and even if they do not breed, they continue to visit their nest sites frequently during the breeding season.

5.3.7. Statistical analysis

Statistical analyses were conducted in R v 4.4.1 (R core Team 2024). Linear mixed-effects models (LMMs) were fitted using the *lme4* package (Bates et al., 2015), and model selection was performed using the *MuMIn* package (Bartoń, 2020). Akaike's information criterion corrected for small sample size (AICc) was used to identify top models, with $\Delta\text{AICc} < 2$ (Harrison et al., 2018). Variance inflation factors (VIF) in the *car* package (Fox, Weisberg & Price, 2025) was used to test for collinearity between explanatory variables. All VIF values were below 2, indicating that collinearity was not a concern in this study. Relative telomere length (rTL) was modelled in its unstandardised form, to preserve biological interpretability and capture the full variance explained by environmental and group-level factors, while all continuous predictors were centered and scaled. Model assumptions were assessed using the *performance* package (Lüdtke et al., 2021). Effect sizes, standard errors, and 95% confidence intervals were reported from top models in final model sets ($\Delta\text{AICc} < 2$), and effects reported

as significant if confidence intervals did not overlap zero. A small number of samples were flagged by the laboratory as potentially unreliable: one at d60 and one at d75. Therefore, all models were run both including and excluding these samples, and results excluding them are reported in Appendix (Tables A5.4–S5.6 and A5.9–S5.11) but did not alter the main conclusions.

Relative telomere length

Males are slightly larger than females in this species (Chapter 4); therefore, I first evaluated whether body size or growth measures should be included as covariates, since larger individuals undergo more cell divisions and may therefore exhibit greater telomere loss. rTL was plotted against body mass, tarsus length, and their growth rates, but no significant associations were detected (see Appendix, Figure A5.5–S5.8). Similarly, no difference in mean rTL was observed between sexes, but females showed greater variability than males (Figure A5.1). The blood storage method (mentioned above) can affect DNA integrity over time (Reichert et al., 2017), therefore the storage duration (number of days stored) was included as a predictor in preliminary models of the response variables, but it did not change the results and was therefore excluded from the final analyses. To avoid overfitting with the limited sample size, body size and growth measures were excluded from candidate models, and sex was retained as a separate predictor due to its potential effects on telomere dynamics and individual responses to early life stress (Parolini et al., 2015; Hansson et al., 2024).

I first fitted a series of LMMs to identify the most informative environmental predictor of rTL at fledging (d75), using a final sample of 34 nestlings. All combinations of candidate environmental variables and time windows described above were modelled separately and compared (Table 5.1). Only one top-performing combination with lowest AICc (e.g. one environmental variable in one time window) was retained for the final model set, which then included social factors (number of helpers and juvenile presence) and sex. Group ID and season

were included as independent random effects in all models to account for repeated measures of the same social group and environmental variation between breeding seasons. Including season as a random effect also partially accounted for DNA degradation over time (described above).

Table 5.1. Summary of environmental variables and time windows used to assess pre- and post-hatching conditions of relative telomere length at fledging. All combinations were compared but only one environmental variable–time window combination with the lowest AICc was retained for further analyses.

Environmental variable	Time windows tested
Mean maximum air temperature (Mean T_{maxair})	– 90 days prior to egg laying ($_{\text{prelay}}$)
	– Incubation period ($_{\text{incubation}}$) from egg laying to hatching
	– Nestling period ($_{\text{nestling}}$) from chick hatching to day 75
Number of days where air temperature exceeded 35 °C (days > 35 °C $_{\text{air}}$)	– 90 days prior to egg laying ($_{\text{prelay}}$)
	– Incubation period ($_{\text{incubation}}$) from egg laying to hatching
	– Nestling period ($_{\text{nestling}}$) from chick hatching to day 75
Mean maximum nest temperature (Mean T_{maxnest})	– Incubation period ($_{\text{incubation}}$) from egg laying to hatching
	– Nestling period ($_{\text{nestling}}$) from chick hatching to day 75
Number of days where nest temperature exceeded 35 °C (days > 35 °C $_{\text{nest}}$)	– Incubation period ($_{\text{incubation}}$) from egg laying to hatching
	– Nestling period ($_{\text{nestling}}$) from chick hatching to day 75
Cumulative rainfall	– 90 days prior to egg laying ($_{\text{prelay}}$)
	– Incubation period ($_{\text{incubation}}$) from egg laying to hatching
	– Nestling period ($_{\text{nestling}}$) from chick hatching to day 75

Change in relative telomere length

To assess changes in rTL between d60 and d75, I calculated within-individual differences in rTL and corrected for regression to the mean using Verhulst’s D, using unstandardised rTL values (a standard approach for repeated telomere measurements, Verhulst et al., 2013; Wood et al., 2022; see Appendix for formula). D was multiplied by –1 so that negative values indicate telomere shortening. This correction accounts for the fact that individuals with longer initial telomeres tend to show more apparent telomere shortening.

These D values were then used as the response variable (ΔrTL) in LMMs testing the impact of environmental conditions. The same environmental variables described above (mean $T_{maxnest}$, mean T_{maxair} , days $> 35^{\circ}C_{nest}$, days $> 35^{\circ}C_{air}$, and cumulative rainfall) were tested separately across the five biologically relevant time windows described earlier for ΔrTL (Table 5.2). Each combination was modelled separately and compared and only one top-performing combination with lowest AICc (e.g. one environmental variable in one time window) was retained for the final model set, which then included social factors (number of helpers and juvenile presence) and sex. Although ΔrTL was corrected for regression to the mean, I included d60 rTL as a covariate in all models to account for any residual influence of baseline telomere length consistent with Wood et al. (2022). Group ID and season were included as random effects in all models.

Table 5.2. Summary of environmental variables and time windows used to assess pre- and post-hatching conditions of ΔrTL between d60 and d75. All combinations were compared but only one environmental variable–time window combination with the lowest AICc was retained for further analyses.

Environmental variable	Time windows tested
Mean maximum air temperature (Mean T_{maxair})	– 90 days prior to egg laying ($_{prelay}$) – Incubation period ($_{incubation}$) from egg laying to hatching – 20 days prior to the 60-day sampling point ($_{d40-60}$) – Period from day 60 -75 ($_{d60-75}$) – Nestling period ($_{nestling}$) from chick hatching to day 75
Number of days where air temperature exceeded 35 °C ($days > 35\text{ }^{\circ}C_{air}$)	– 90 days prior to egg laying ($_{prelay}$) – Incubation period ($_{incubation}$) from egg laying to hatching – 20 days prior to the 60-day sampling point ($_{d40-60}$) – Period from day 60 -75 ($_{d60-75}$) – Nestling period ($_{nestling}$) from chick hatching to day 75
Mean maximum nest temperature (Mean $T_{maxnest}$)	– Incubation period ($_{incubation}$) from egg laying to hatching – 20 days prior to the 60-day sampling point ($_{d40-60}$) – Period from day 60 -75 ($_{d60-75}$) – Nestling period ($_{nestling}$) from chick hatching to day 75
Number of days where nest temperature exceeded 35 °C ($days > 35\text{ }^{\circ}C_{nest}$)	– Incubation period ($_{incubation}$) from egg laying to hatching – 20 days prior to the 60-day sampling point ($_{d40-60}$) – Period from day 60 -75 ($_{d60-75}$) – Nestling period ($_{nestling}$) from chick hatching to day 75
Cumulative rainfall	– 90 days prior to egg laying ($_{prelay}$) – Incubation period ($_{incubation}$) from egg laying to hatching – Nestling period ($_{nestling}$) from chick hatching to day 75

Telomeres and post-fledging survival

I tested whether telomere length or dynamics predict post-fledging overwinter survival (binary outcome: 0 = did not survive, 1 = survived), I fitted two separate generalised linear mixed-effects models (GLMMs) with a binomial distribution (logit link). The first model included rTL at d75 as a fixed effect, while the second model included ΔrTL between d60 and d75 and

rTL at d60 to control for starting rTL. Group ID and season were included as independent random variables, as described above.

5.4. Results

5.4.1. Relative telomere length before fledging

Model comparison identified days $> 35^{\circ}\text{C}_{\text{nest_incubation}}$ (number of days above 35°C in the nest during egg incubation) as the best weather predictor and time window for rTL on day 75, with the lowest AICc value and no competing models within 2 AICc (Table 5.3). None of the social factors (helpers, juvenile presence) or sex improved model fit, so they were not retained in the top model (Table 5.4). More days $> 35^{\circ}\text{C}_{\text{nest_incubation}}$ was significantly associated with longer relative telomere length (estimate = 0.12 ± 0.03 , 95% CI = [0.04 / 0.19]; Table A5.3, Figure 5.2).

Table 5.3. Model selection table to identify best weather variable and weather time window explaining rTL on d75 in ground-hornbill nestlings, with top model highlighted in bold (AICc < 2). All models included group ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Model weight
1	days > 35 °C nest_incubation	-10.7	0.00	0.612
2	mean T _{max} nest_incubation	- 8.5	2.17	0.207
3	null	- 4.5	6.13	0.029
4	mean T _{max} air_incubation	- 4.3	6.38	0.025
5	days > 35 °C air_incubation	- 4.1	6.55	0.023
6	mean T _{max} nest_nestling	- 3.8	6.84	0.020
7	days > 35 °C nest_nestling	- 3.4	7.26	0.016
8	rainfall _{incubation}	- 2.8	7.82	0.012
9	days > 35 °C air_nestling	- 2.8	7.83	0.012
10	days > 35 °C air_prelay	- 2.6	8.04	0.011
11	mean T _{max} air_nestling	- 2.2	8.45	0.009
12	rainfall _{nestling}	- 2.1	8.57	0.008
13	rainfall _{prelay}	- 2.1	8.60	0.008
14	mean T _{max} air_prelay	- 1.9	8.81	0.007
<i>N = 34, Random terms: group ID = 16, season = 5</i>				

Table 5.4. Model selection table to investigate the effects of temperature, social factors, and chick sex on rTL on d75 in ground-hornbill nestlings, with top model highlighted in bold (AICc < 2). All models included group ID and season as random factors.

Model no.	Model	AICc	Δ AICc	Model weight
1	days > 35 °C nest_incubation	- 10.7	0.00	0.675
2	days > 35 °C nest_incubation + sex	- 7.7	2.93	0.156
3	days > 35 °C nest_incubation + helpers + juv	- 6.9	3.81	0.100
4	null	- 4.5	6.13	0.031
5	days > 35 °C nest_incubation * helpers + juv	- 3.5	7.14	0.019
6	days > 35 °C nest_incubation + helpers + juv + sex	- 3.4	7.23	0.018
<i>N = 34, Random terms: group ID = 16, season = 5</i>				

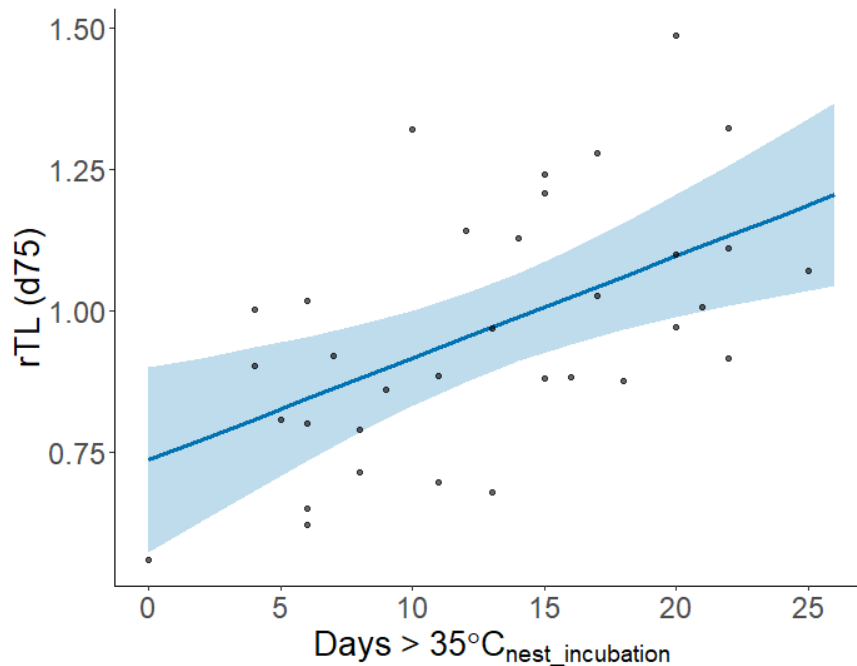


Figure 5.2. Predicted linear relationship between days > 35 °C nest during incubation and relative telomere length (rTL) on d75. Lines represent predicted values from the top model (model 1). Shaded areas indicate 95% confidence intervals and points show observed data.

5.4.2. Change in relative telomere length between day 60 and 75

Model comparison identified days > 35 °C_{nest_incubation} (days above 35 °C in the nest during egg incubation) as the best weather predictor and time window for Δ rTL with lowest AICc value and no competing models within 2 AICc (Table 5.5). None of the social factors (helpers, juvenile presence) or sex improved model fit, so the top model included only days > 35 °C_{nest_incubation} and rTL on d60 as a covariate (Table 5.6). Nestlings that experienced more days > 35 °C in the nest during incubation had significantly greater Δ rTL (i.e. telomere shortening) between d60 and d75 (estimate = -0.12 ± 0.04 , 95% CI = $[-0.19 / -0.04]$; Table A5.7, Figure 5.3). rTL on d60 showed a marginal positive effect on Δ rTL between d60 and d75, but the effect was not significant (estimate = 0.06 ± 0.03 , 95% CI $[-0.01 / 0.13]$; Table A5.7).

Table 5.5. Model selection table to identify best weather variable and weather time window explaining ΔrTL between d60 and d75 in ground-hornbill nestlings, with top model highlighted in bold (AICc < 2). All models included group ID and season as random factors and RTL on day 60 as covariate.

Model no.	Model	AICc	$\Delta AICc$	Model weight
1	days > 35 °C nest_incubation + rTL_d60	- 7.7	0.00	0.480
2	mean T _{max} nest_incubation + rTL_d60	- 5.5	2.18	0.162
3	mean T _{max} nest_d60-75 + rTL_d60	- 4.3	3.40	0.088
4	null	- 3.2	4.54	0.050
5	days > 35 °C nest_d60-75 + rTL_d60	- 3.1	4.59	0.048
6	mean T _{max} air_incubation + rTL_d60	- 1.3	6.38	0.020
7	days > 35 °C air_incubation + rTL_d60	- 1.2	6.56	0.018
8	mean T _{max} nest_nestling + rTL_d60	- 1.0	6.68	0.017
9	days > 35 °C nest_nestling + rTL_d60	- 0.5	7.19	0.013
10	mean T _{max} air_d60-75 + rTL_d60	0.1	7.77	0.010
11	days > 35 °C air_nestling + rTL_d60	0.1	7.80	0.010
12	rainfall _{incubation} + rTL_d60	0.1	7.83	0.010
13	days > 35 °C air_d60-75 + rTL_d60	0.2	7.95	0.009
14	mean T _{max} nest_prev20days + rTL_d60	0.3	8.01	0.009
15	days > 35 °C air_prelay + rTL_d60	0.3	8.05	0.009
16	mean T _{max} air_nestling + rTL_d60	0.6	8.29	0.008
17	rainfall _{nestling} + rTL_d60	0.6	8.34	0.007
18	rainfall _{prelay} + rTL_d60	0.7	8.40	0.007
19	days > 35 °C nest_prev20days + rTL_d60	0.8	8.49	0.007
20	mean T _{max} air_prev20days + rTL_d60	0.9	8.59	0.007
21	days > 35 °C air_prev20days + rTL_d60	1.0	8.67	0.006
22	mean T _{max} air_prelay + rTL_d60	1.0	8.67	0.006
<i>N = 34, Random terms: group ID = 16, season = 5</i>				

Table 5.6. Model selection table to investigate the effects of temperature, social factors, and chick sex on ΔrTL between d60 and d75 in ground-hornbill nestlings, with top model highlighted in bold (AICc < 2). All models included group ID and season as random factors and rTL on day 60 as covariate.

Model no.	Model	AICc	$\Delta AICc$	Model weight
1	days > 35 °C_{nest_incubation} + rTL_{d60}	- 7.7	0.00	0.734
2	days > 35 °C _{nest_incubation} + sex + rTL _{d60}	- 4.6	3.16	0.151
3	null	- 3.2	4.54	0.076
4	days > 35 °C _{nest_incubation} + helpers + juv + rTL _{d60}	- 0.9	6.84	0.024
5	days > 35 °C _{nest_incubation} * helpers + juv + rTL _{d60}	0.1	7.83	0.015
<i>N = 34, Random terms: group ID = 16, season = 5</i>				

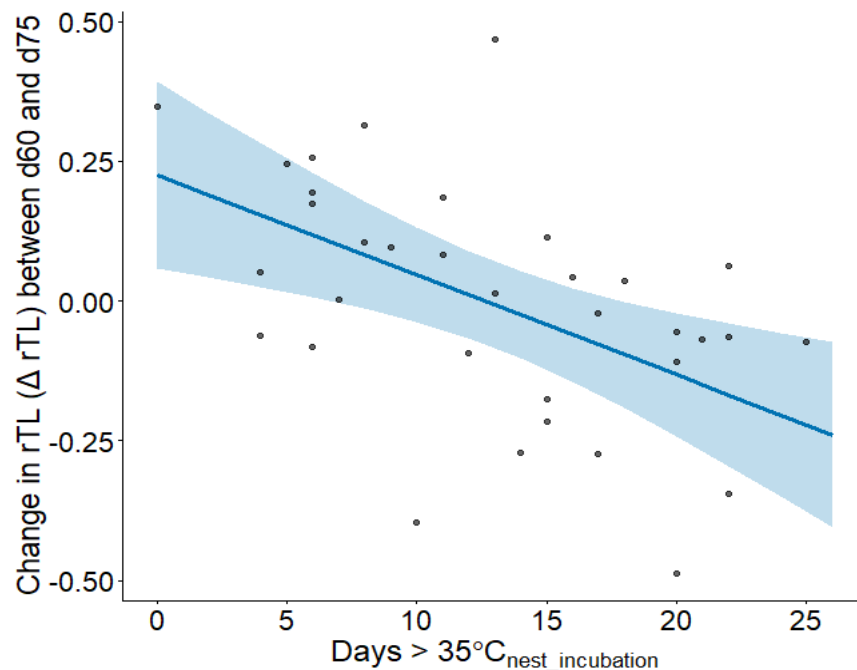


Figure 5.3. Predicted linear relationship between days > 35 °C nest during incubation and change in relative telomere length (ΔrTL) between d 60 and d75 in ground-hornbill nestlings. Negative ΔrTL values (y-axis) indicate telomere shortening, while positive values indicate telomere lengthening. Lines represent predicted values from the top model (model 1). Shaded areas indicate 95% confidence intervals and points show observed data.

5.4.3. Telomeres and post-fledging survival

Neither rTL (d75) nor ΔrTL (d60-d75) had a statistically significant effect on post-fledging overwinter survival in ground-hornbills (rTL : estimate = -0.57 ± 0.49 , [95% CI = $-1.54 / 0.40$]; ΔrTL : estimate = 3.25 ± 0.85 , [95% CI = $-1.63 / 8.13$]; Table 5.7).

Table 5.7. Effect of relative telomere length (RTL) and change in RTL (d60-75) on post-fledging overwinter survival in ground-hornbills, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values.

Model	Variable	Est	SE	95 % CI	P value
ΔrTL (d60-75) + rTL (d60)	ΔrTL (d60-75)	3.54	2.59	-1.54 / 8.61	0.172
	rTL (d60)	0.54	0.64	- 0.71 / 1.80	0.398
rTL (d75)	rTL (d75)	-0.57	0.49	- 1.54 / 0.40	0.250

N = 34, Random terms: group ID = 16, season = 5

5.5. Discussion

I investigated the effects of high temperatures on telomere length and dynamics in ground-hornbill nestlings, and whether the presence of helpers in the group mitigated any negative effects. Contrary to predictions, relative telomere length (rTL) at fledging age (d75) was positively associated with heat during incubation, specifically, the number of days on which nest temperature exceeded 35 °C. However, consistent with the prediction that higher temperatures accelerate telomere shortening, nestlings from hotter nests during incubation showed faster telomere shortening between day 60 and 75. Sex had no detectable effect on telomere length or shortening. Likewise, there was no evidence that helper presence mitigated the effects of high nest temperatures on telomere length or dynamics, and there was no evidence that telomere length or attrition was related to short-term survival (to one year). Together, these results suggest that early thermal conditions experienced during embryo formation influence telomere length and telomere dynamics later in development, while associations with social factors were not apparent.

Prenatal conditions and telomere length on day 75

By fledging age (d75), nestlings that experienced heat more frequently in the nest during incubation had longer telomeres, suggesting a potential early life (prenatal) advantage of heat on telomere length. One possible explanation is that hotter nests may maintain embryos closer to their optimal developmental temperature (~38–39 °C, for many birds; Carey, 1980), reducing energetic costs and oxidative stress during embryonic development (Stier, Metcalfe & Monaghan, 2020), therefore supporting the protection of telomeres (Reichert & Stier, 2017). In ground-hornbills, females are the sole incubators and typically leave the nest during the coolest period at dawn, spending ~20–30 minutes participating in group territorial vocalisations (Middleton, 2022). Some may take additional off-bouts during the day if disturbed or to forage (pers. obs.). Temperatures in nests that recorded more days above 35 °C, were generally higher than outside air temperatures (see Table A5.12), therefore, may buffer embryos from cooling during female absences, whereas cooler nests may expose eggs to lower suboptimal temperatures, or more temperature variation, which may increase embryos' energetic costs and lead to greater telomere loss (Stier, Metcalfe & Monaghan, 2020).

However, my results contrast with experimental studies in common terns *Sterna hirundo*, wood ducks *Aix sponsa*, and Japanese quails *Coturnix japonica*, which all report shorter telomeres at hatching under higher incubation temperatures, associated with faster embryonic growth, which may increase cell division and oxidative stress (Stier, Metcalfe & Monaghan, 2020; Hope et al., 2022; Vedder et al., 2018). These studies all used artificial incubation, and only the quail study included incubation temperature fluctuations mimicking female off-bouts, which correlated with shorter telomeres. In our study, nest temperatures were a measurement of the nest environment rather than directly in or under the eggs, so they do not exactly reflect incubation temperature experienced by the embryos. Additionally, while those studies measured telomere length at hatching, I assessed telomere length at fledging age. These

species also differ in their thermal ecology; terns, ducks, and quails inhabit temperate or subarctic regions, whereas ground-hornbills occur in the subtropics and are likely more heat-adapted. Laboratory incubation ranges were narrower and more controlled (34–38 °C) than the natural variability observed in our study; minimum and maximum temperatures recorded within nests over the incubation period ranged from 11.9–17.7 °C (mean minimum = 15.3 °C) and 37.1–48.7 °C (mean maximum = 41.3 °C), respectively (Table A5.12, Figure A5.2). Therefore, direct comparisons are challenging and highlight the need for studies in wild, natural settings.

Prenatal temperatures influence telomere dynamics during later development

Telomere length at d75 is the outcome of initial telomere length, which can be heritable (Horn et al., 2011) and subsequent shortening or lengthening, whereas telomere dynamics isolate the rate of change over a period of time and can provide information about DNA damage that is not apparent from telomere length alone (Boonekamp et al., 2014). Consequently, although exposure to higher incubation temperatures was associated with longer telomeres at d75, nestlings that experienced hotter nests during incubation also showed faster telomere shortening between days 60 and 75 post-hatch, indicating that early heat exposure during the incubation stage may influence longer-term physiological trajectories. Patterns of similar delayed effects of heat on telomere dynamics have been observed in zebra finches *Taeniopygia castanotis* (Ton et al., 2023) and purple-crowned fairy-wrens *Malurus coronatus*, where early heat exposure did not immediately affect telomere length but telomere shortening became evident at later stages (Eastwood et al., 2023). The effects of early life heat could therefore be stage dependent, potentially beneficial during the embryonic (ectothermic) stage (reducing energetic costs; Stier, Metcalfe & Monaghan, 2020;) but perhaps costly during the later nestling (endothermic) stage when nestlings must actively thermoregulate (Nord & Giroud, 2020; Ton

et al., 2023) and the HPA axis (stress response system) is more mature (Blas et al., 2006). However, because I did not measure telomere length at hatching, it remains unclear whether the patterns observed between day 60 and 75 primarily reflect prenatal effects, postnatal effects, or a combination of both. Future work incorporating measurements at hatching and fledging would help separate prenatal and postnatal effects on telomere dynamics.

Nests that were hot during incubation tended to remain hot post-hatching (Figure A5.4), and post-hoc analyses confirmed that higher mean maximum temperatures during days 60–75 were also associated with faster telomere shortening (Table A5.8). However, because these temperature measurements are correlated ($r = 0.59$), their effects cannot be fully disentangled. Several mechanisms could explain why nestlings exposed to higher temperatures show accelerated telomere shortening later in development. One possibility is the energetic costs of heat dissipation. Nestlings in hotter nests likely engage in evaporative cooling (panting) more frequently than nestlings in cooler nests, and this behaviour is associated with increases in metabolic rate and can therefore impose physiological costs (Oswald, Lee & Smit, 2018; McKechnie & Wolf, 2019; Smith et al., 2017). A second potential mechanism is compensatory growth. In Chapter 4, I found that higher temperatures were associated with reduced growth rates, but final fledging size and condition were unaffected, suggesting that heat-exposed nestlings may undergo compensatory growth when conditions improve (e.g. during cooler periods). However, compensatory growth can be energetically costly and may later manifest as increased telomere shortening (Metcalf & Monaghan, 2001). Although the precise mechanism remains unresolved, oxidative stress is likely a mediator between early heat exposure and later telomere shortening (Monaghan, Metcalf & Torres, 2009). Future work should measure oxidative stress at different developmental stages to assess whether periods of compensatory growth or heat exposure are associated with increased oxidative stress and thereby shed light on the underlying telomere dynamics.

No helper effects

There was no evidence that the presence of helpers influenced telomere length or dynamics, nor did they mediate the effects of heat on either of these measures, suggesting that additional helpers do not necessarily buffer offspring from the physiological costs of high temperatures. Helpers themselves may be forced to reduce foraging at high temperatures to meet their own thermoregulatory needs (Bourne, Ridley & Cunningham, 2023; also see Chapter 2), which may limit the potential for increased provisioning to offset heat-induced stress in nestlings. There is mixed evidence for social buffering as a mechanism to mitigate adverse environmental conditions in this (Middleton et al., 2026) and other cooperative breeders (Covas, du Plessis & Doutrelant, 2008; Bourne, 2020; Borger et al., 2023). Although helper effects on telomere length have been observed in the cooperatively breeding sociable weaver *Philetairus socius* (Quque et al., 2021), these effects were not examined in relation to environmental conditions. My results suggest that ecological and life-history traits may be stronger determinants of telomere dynamics than sociality in ground-hornbills.

Conservation and climate warming implications

Long-lived birds, such as ground-hornbills, may be inherently more resistant to damage by oxidative stress than short-lived birds, which could help them maintain telomere length over time (Haussmann, Vleck & Nisbet, 2003). In this study, telomere length and attrition rates were not related to short-term survival, but accelerated telomere shortening during later development suggests that early life heat exposure could carry costs that manifest later in life, potentially affecting reproductive success and longevity (Eastwood et al., 2019). From a conservation perspective, this is particularly important because ground-hornbills in the study site rely on artificial nest boxes, to mitigate the shortage of natural cavities. That hotter nests are associated with faster telomere shortening late in the nestling stage reveals that some nest boxes may inadvertently expose nestlings to greater heat-induced stress than others during development.

Artificial nest boxes can be poor at buffering external temperatures (Rowland, Briscoe & Handasyde, 2017; Niffenegger et al., 2024), and improved insulation or placement can substantially reduce internal heat loads (Honey et al., 2021; Corregidor-Castro et al., 2023). As climate warming intensifies and temperatures continue to rise, ensuring that artificial nests provide safe thermal conditions for nestlings will be crucial to support long-term survival, and the effectiveness of nest boxes as a conservation intervention for ground-hornbills.

5.6. Conclusion

My findings suggest that while higher temperatures during incubation may initially benefit telomere length, they are also associated with accelerated telomere shortening during later development, highlighting that the effects of early life heat exposure can depend on the developmental stage. Although telomere dynamics did not predict survival in the short-term, telomere shortening is closely linked to survival in other long-lived birds (Heidinger et al., 2012; Boonekamp et al., 2014; Whittemore et al., 2019). Therefore, heat exposure during early life may have delayed consequences, potentially accelerating telomere loss later in development which may affect longer-term survival, fitness, and population resilience of this species.

5.7. Appendix to Chapter 5

Table A5.1. Summary of ground-hornbill nest monitoring across five breeding seasons. Number of groups monitored, number of artificial and natural nests monitored, breeding attempts, and successful breeding attempts (where a nestling fledged) are shown for each season.

Breeding Season	Number of groups monitored	Number of artificial nests monitored	Number of natural nests monitored	Number of breeding attempts	Number of successful breeding attempts
2019-2020	22	25	2	12	8
2020-2021	24	26	4	13	7
2021-2022	24	27	2	13	7
2022-2023	26	27	3	15	9
2023-2024	28	29	4	15	10

Relative telomere length

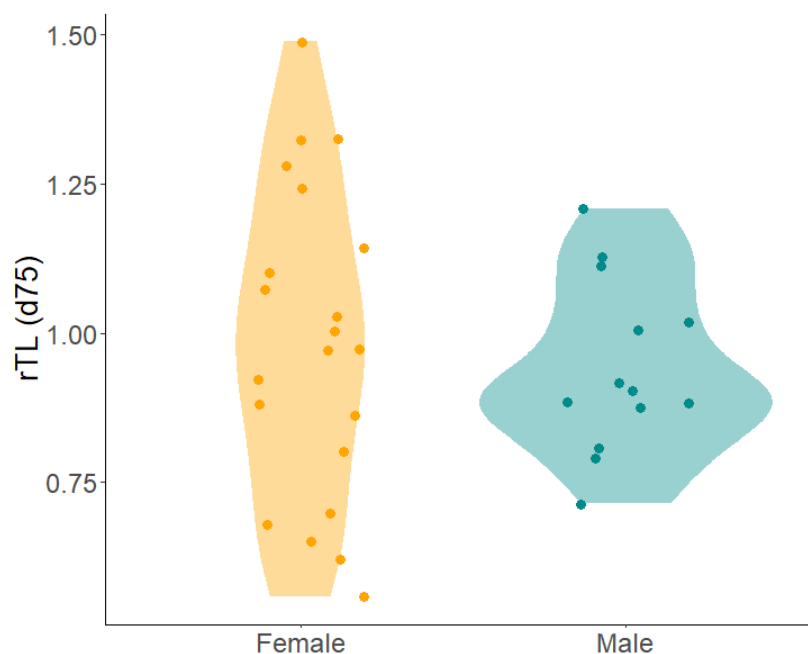


Figure A5.1. Distribution of relative telomere length (rTL) by sex in ground hornbill nestlings. Violin plots show the range of telomere length values for females (orange) and males (blue) and, with individual data points overlaid. There is no significant difference in mean telomere length between sexes ($t = 0.78$, $df = 30.55$, $p = 0.4412$), but variation is significantly different ($F = 3.15$, $df = 19$, $p = 0.046$).

Table A 5.2. Model comparison including and excluding sex with main predictor variables (days > 35 °C_{nest_incubation}, helpers and juveniles) to evaluate their effects on rTL on d75. Models include group ID and season as random variables.

Model	AICc	ΔAICc	Model weight
days > 35 °C _{nest_incubation} + helpers + juv	-13.2	0.00	0.563
days > 35 °C _{nest_incubation}	- 11.0	2.16	0.157
days > 35 °C _{nest_incubation} + helpers + juv + sex	-10.3	2.98	0.104
days > 35 °C _{nest_incubation} + sex	- 8.3	4.84	0.041
<i>N = 34, Random terms: group ID = 16, season = 5</i>			

Relative telomere length before fledging

Table A5.3. Factor influencing rTL on d75 in ground-hornbill nestlings, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variable shown in bold is significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	days > 35 °C_{nest_incubation}	0.12	0.03	0.04 / 0.19	0.003
<i>N = 34, Random terms: group ID = 16, season = 5</i>					

Model selection and results with a single potential problematic sample removed from analyses:

Table A5.4. Model selection table to identify best weather variable and weather time window explaining rTL on d75 in ground-hornbill nestlings (with 1 potential problematic sample removed). The top model is highlighted in bold (AICc < 2) and all models included group ID and season as random factors.

Model no.	Model	AICc	ΔAICc	Model weight
1	days > 35 °C nest_incubation	-11.0	0.00	0.575
2	mean T _{max} nest_incubation	- 9.1	1.84	0.229
3	null	-5.1	5.94	0.030
4	days > 35 °C air_nestling	- 4.6	6.43	0.023
5	days > 35 °C air_incubation	- 4.5	6.53	0.023
6	mean T _{max} nest_nestling	- 4.4	6.62	0.021
7	mean T _{max} air_incubation	- 4.4	6.62	0.021
8	days > 35 °C nest_nestling	- 4.2	6.83	0.019
9	rainfall _{incubation}	- 3.8	7.23	0.015
10	days > 35 °C air_prelay	- 3.2	7.78	0.012
11	mean T _{max} air_nestling	- 2.8	8.23	0.009
12	rainfall _{nestling}	- 2.5	8.47	0.008
13	mean T _{max} air_prelay	- 2.3	8.65	0.008
14	rainfall _{prelay}	- 2.3	8.69	0.007
<i>N = 33, Random terms: group ID = 16, season = 5</i>				

Table A5.5. Model selection table for factors explaining relative telomere length (RTL) on day 75 in ground-hornbill nestlings (with 1 potential problematic sample removed), with top models highlighted in bold (AICc < 2). All models included group ID and season as random factors.

Model no.	Model	AICc	ΔAICc	Model weight
1	days > 35 °C nest_incubation	- 11.0	0.00	0.552
2	days > 35 °C nest_incubation + helpers + juv	- 9.2	1.80	0.224
3	days > 35 °C nest_incubation + sex	- 8.3	2.68	0.145
4	days > 35 °C nest_incubation * helpers + juv	- 5.7	5.31	0.039
5	null	- 5.1	5.94	0.028
6	days > 35 °C nest_incubation + helpers + juv + sex	- 3.4	7.55	0.013
<i>Random terms: group ID = 16, season = 5</i>				

Table A5.6. Factors influencing relative telomere length (RTL) on day 75 in ground-hornbill nestlings (with 1 potential problematic sample removed), with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variables shown in bold is significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	days > 35 °C nest_incubation	0.12	0.03	0.05 / 0.18	0.002
2	days > 35 °C nest_incubation	0.13	0.03	0.06 / 0.20	<0.001
	helpers	- 0.4	0.03	- 0.11 / 0.03	0.202
	juv	0.11	0.06	- 0.00 / 0.22	0.062
<i>N = 33, Random terms: group ID = 16, season = 5</i>					

Change in relative telomere length between day 60 and 75

To account for regression to the mean, Δ RTL from the baseline (d60) measurement (X_1) to the follow-up (d75) (X_2) were corrected using Verhulst's D (Verhulst et al., 2013). The corrected value, D, was calculated as:

$$D = \rho(X_1 - \bar{X}_1) - (X_2 - \bar{X}_2)$$

where

$$\rho = \frac{2rS_1S_2}{S_1^2 + S_2^2}$$

In which r is the correlation between X_1 and X_2 .

Table A5.7. Factors influencing ΔrTL between day 60 and 75 in ground-hornbill nestlings, with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variable shown in bold is significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	days > 35 °C nest_incubation	- 0.12	0.04	- 0.19 / - 0.04	0.003
	RTL_d60	0.06	0.03	- 0.01 / 0.13	0.053
<i>N = 34, Random terms: group ID = 16, season = 5</i>					

Table A5.8. Estimates of effect sizes, standard errors (SE), 95% confidence intervals (95% CI), and P values from a non-competing model including mean maximum air temperature during days 60–75 on ΔrTL between day 60 and 75 in ground-hornbill nestlings. This model was not among the top competing models but is presented to illustrate the significant effect of mean maximum air temperature during this developmental window and is discussed in the main text.

Model no.	Variable	Est	SE	95 % CI	P value
3	mean T_{max} nest_d60-75	- 0.10	0.04	- 0.19 / - 0.01	0.011
	RTL_d60	0.07	0.03	- 0.01 / 0.14	0.038
<i>N = 34, Random terms: group ID = 16, season = 5</i>					

Model selection and results with potential problematic samples (N=2) removed from analyses for change in relative telomere length between d60 and d75:

Table A5.9. Model selection table to identify best weather variable and weather time window explaining Δ rTL between day 60 and day 75 in ground-hornbill nestlings (with 2 potential problematic samples removed). The top model is highlighted in bold (AICc < 2). All models include group ID and season as random factors and RTL on day 60 as a covariate.

Model no.	Model	AICc	Δ AICc	Model weight
1	days > 35 °C nest_incubation + rTL_d60	- 9.3	0.00	0.500
2	mean T _{max} nest_incubation + rTL_d60	- 7.0	2.29	0.159
3	null	- 5.6	3.65	0.081
4	mean T _{max} nest_d60-75 + rTL_d60	- 5.1	4.16	0.063
5	mean T _{max} nest_nestling + rTL_d60	- 3.3	5.98	0.025
6	days > 35 °C nest_d60-75 + rTL_d60	- 3.1	6.20	0.022
7	days > 35 °C nest_nestling + rTL_d60	- 2.9	6.35	0.021
8	days > 35 °C air_nestling + rTL_d60	- 2.6	6.73	0.017
9	mean T _{max} nest_prev20days + rTL_d60	-1.9	7.35	0.013
10	mean T _{max} air_incubation + rTL_d60	- 1.6	7.65	0.011
11	rainfall_incubation + rTL_d60	- 1.6	7.70	0.011
12	mean T _{max} air_nestling + rTL_d60	- 1.3	8.02	0.009
13	days > 35 °C nest_prev20days + rTL_d60	- 1.2	8.11	0.009
14	days > 35 °C air_incubation + rTL_d60	- 1.1	8.15	0.008
15	days > 35 °C air_prev20days + rTL_d60	- 1.0	8.31	0.008
16	mean T _{max} air_d60-75 + rTL_d60	- 0.7	8.55	0.007
17	days > 35 °C air_d60-75 + rTL_d60	- 0.6	8.72	0.006
18	rainfall_prelay + rTL_d60	- 0.6	8.73	0.006
19	days > 35 °C air_prelay + rTL_d60	- 0.5	8.78	0.006
20	mean T _{max} air_d60-75 + rTL_d60	- 0.5	8.79	0.006
21	mean T _{max} air_prev20days + rTL_d60	- 0.5	8.80	0.006
22	rainfall_nestling + rTL_d60	-0.5	8.80	0.006
<i>N = 32, Random terms: group ID = 16, season = 5</i>				

Table A5.10. Model selection table to identify factors explaining ΔrTL between d60 and d75 in ground-hornbill nestlings (with 2 potential problematic samples removed), with top model highlighted in bold (AICc < 2). All models included group ID and season as random factors RTL on day 60 as a covariate.

Model no.	Model	AICc	$\Delta AICc$	Model weight
1	days > 35 °C nest_incubation + rTL __d60	- 9.3	0.00	0.644
2	days > 35 °C nest_incubation + sex + rTL __d60	- 6.3	3.01	0.143
3	null	- 5.6	3.65	0.104
4	days > 35 °C nest_incubation + helpers + juv + rTL __d60	- 5.4	3.86	0.093
5	days > 35 °C nest_incubation * helpers + juv + rTL __d60	- 1.9	7.38	0.016
<i>N = 32, Random terms: group ID = 16, season = 5</i>				

Table A5.11. Factors influencing ΔrTL between d60 and d75 in ground-hornbill nestlings (with 2 potential problematic samples removed), with estimates of effect sizes, standard errors (SE), 95 % confidence intervals (95 % CI), and P values. Variable shown in bold is significant with 95 % CI that do not cross zero.

Model no.	Variable	Est	SE	95 % CI	P value
1	days > 35 °C nest_incubation	- 0.11	0.03	- 0.18 / - 0.04	0.004
	rTL __d60	0.06	0.04	- 0.02 / 0.15	0.086
<i>N = 32, Random terms: group ID = 16, season = 5</i>					

Nest temperature information

Table A5.12. Summary of nest temperatures during incubation for 16 groups across years. nests each year. For some groups, different nests were used in different years. Includes the mean, standard deviation, maximum, minimum, and range of nest temperatures, the number of days > 35 °C, and the mean and standard deviation of the difference between nest and air temperatures.

Season	Group ID	Nest ID	Type	Mean nest temperature (°C)	Nest temperature SD (°C)	Max nest temperature (°C)	Min nest temperature (°C)	Nest temperature range (°C)	Days > 35 °C	Mean difference (Nest – Air) (°C)	SD Temperature difference (Nest – Air) (°C)
2019/2020	KAR	Karan Khaya	Artificial	26.655	5.082	39.005	16.642	22.363	8	0.212	2.291
2019/2020	JOH	McBride	Artificial	27.155	5.243	43.085	17.096	25.989	20	0.094	1.657
2019/2020	SEN	Senalala	Artificial	28.450	4.018	42.395	17.313	25.082	8	1.850	3.557
2019/2020	THO	Thornybush	Natural	26.708	4.097	37.129	17.261	19.868	4	0.149	2.842
2020/2021	COP	Charloscar	Artificial	26.622	5.370	42.86	14.813	28.047	18	1.051	2.436
2020/2021	KAR	Karan Khaya	Artificial	27.126	4.233	38.783	17.485	21.298	9	1.347	3.200
2020/2021	JOH	McBride	Artificial	27.305	5.701	42.748	16.141	26.607	22	1.675	2.434
2020/2021	DOV	Pitlochry	Artificial	26.811	4.504	39.741	17.062	22.679	11	0.806	2.917
2020/2021	HER	Von Tonder	Artificial	26.088	4.232	37.871	16.318	21.553	6	0.308	2.987
2020/2021	MOH	York	Artificial	27.119	4.994	38.604	17.313	21.291	15	1.357	2.074
2021/2022	COP	Copenhagen	Artificial	25.314	5.320	41.382	14.655	26.727	18	-0.079	1.189
2021/2022	KAR	Karan Khaya	Artificial	24.649	4.704	38.507	16.639	21.868	6	0.255	1.923
2021/2022	LOR	Lornay	Artificial	25.570	6.361	41.628	13.457	28.171	17	0.299	2.024
2021/2022	NTS	Yankee Dam	Artificial	27.389	4.343	40.418	18.135	22.283	15	2.355	2.598
2021/2022	DOV	Pitlochry	Artificial	28.148	2.833	35.155	21.412	13.743	6	1.000	3.349
2021/2022	STR	Senalala	Artificial	26.276	5.520	40.511	15.219	25.292	16	1.149	0.988
2021/2022	THO	Thornybush	Natural	25.358	3.096	34.235	16.485	17.750	0	-0.129	2.042
2022/2023	COP	Copenhagen	Artificial	26.948	4.760	39.194	15.951	23.243	13	0.067	1.137
2022/2023	KAR	Karan Khaya	Artificial	25.473	4.112	37.824	17.465	20.359	4	0.471	1.607
2022/2023	LOR	Lornay	Artificial	26.551	5.778	43.765	13.100	30.665	20	0.256	2.033
2022/2023	ARG	Ntsiri	Artificial	27.290	3.806	36.778	18.729	18.049	5	0.857	1.682

2022/2023	PIT	Oppenheimer	Artificial	28.649	4.654	40.542	17.509	23.033	20	2.252	0.917
2022/2023	STR	Senalala	Artificial	26.973	4.704	39.221	16.929	22.292	13	0.924	1.293
2022/2023	JAV	Tawane	Artificial	26.215	4.458	38.125	17.700	20.425	7	0.376	1.424
2022/2023	NTS	Yankee Dam	Artificial	28.805	4.654	40.539	17.308	23.231	21	2.448	1.087
2022/2023	MOH	York	Artificial	27.159	4.592	38.454	17.907	20.547	10	0.732	1.329
2023/2024	RHI	Addger	Artificial	26.205	7.315	41.114	12.249	28.865	15	1.623	1.776
2023/2024	KAR	Karan Khaya (New)	Artificial	25.460	6.522	41.553	13.072	28.481	11	1.116	1.426
2023/2024	ARG	Ntsiri	Artificial	27.381	5.217	39.153	16.603	22.550	12	0.624	1.961
2023/2024	PIT	Oppenheimer	Artificial	28.402	5.974	42.407	15.628	26.779	22	2.141	0.935
2023/2024	CAR	Thandiwe	Artificial	25.761	7.864	48.731	11.945	36.786	25	1.210	1.852
2023/2024	HER	Von Tonder	Artificial	27.367	2.757	38.008	18.138	19.870	6	1.448	3.774
2023/2024	NTS	Yankee Dam	Artificial	29.325	5.942	42.437	16.466	25.971	22	2.043	0.955
2023/2024	MOH	York	Artificial	27.208	5.226	40.081	16.218	23.863	17	0.567	1.466

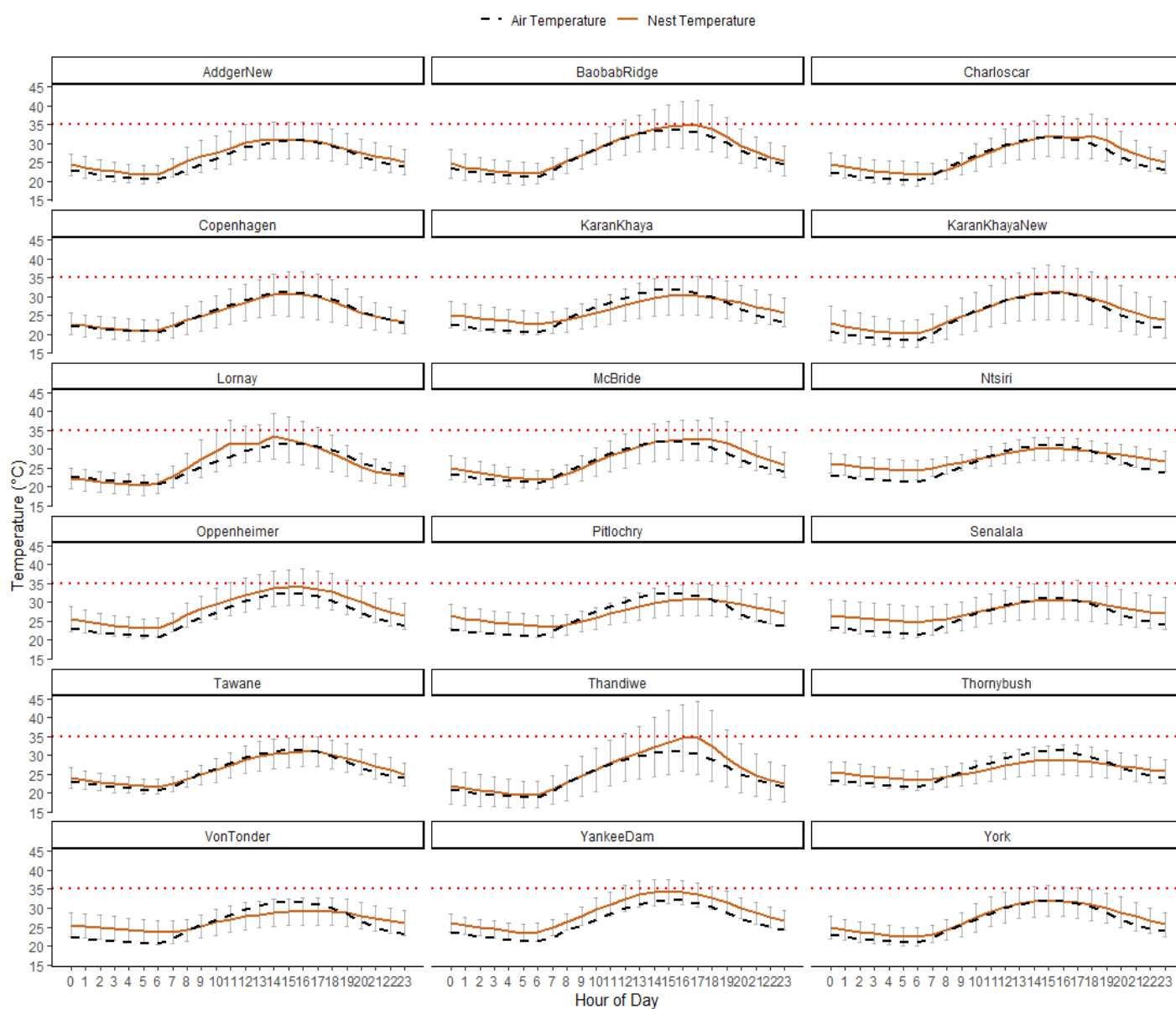


Figure A5.2. Average hourly nest and air temperatures during the incubation period for each nest, averaged across all years monitored. Solid orange lines show mean nest temperatures with standard deviation shown as shaded as error bars, dashed black lines show mean air temperature, and the red dotted line indicates the 35 °C threshold.

Variance in environmental variables

Table A5.13. Summary of variability in environmental variables used in the analyses. Variance and standard deviation (SD) are shown for each.

Variable	Variance	SD
rainfall _{nestling}	14228.43608	119.2830083
rainfall _{incubation}	1935.703708	43.99663291
rainfall _{prelay}	628.913975	25.07815733
days > 35 °C _{nest_nestling}	125.2736185	11.19256979
days > 35 °C _{nest_incubation}	42.04634581	6.484315369
days > 35 °C _{air_prelay}	21.01604278	4.584325772
days > 35 °C _{air_nestling}	18.93761141	4.351736597
days > 35 °C _{air_incubation}	12.61319073	3.551505418
days > 35 °C _{nest_prev20days}	11.56149733	3.400220188
days > 35 °C _{nest_d60-75}	9.967914439	3.157200412
days > 35 °C _{air_prev20days}	9.590909091	3.09691929
days > 35 °C _{air_d60-75}	6.046345811	2.458931844
mean T _{max} nest_d60-75	5.86442333	2.421657145
mean T _{max} nest_prev20days	4.659159184	2.158508555
mean T _{max} nest_nestling	3.106036072	1.762394982
mean T _{max} air_d60-75	2.947354784	1.716786179
mean T _{max} nest_incubation	2.596158378	1.611259873
mean T _{max} air_prev20days	2.295305269	1.515026491
mean T _{max} air_prelay	1.561497326	1.249598866
mean T _{max} air_incubation	0.736622906	0.858267386
mean T _{max} air_nestling	0.385666781	0.621020757

Exploratory plots and correlations

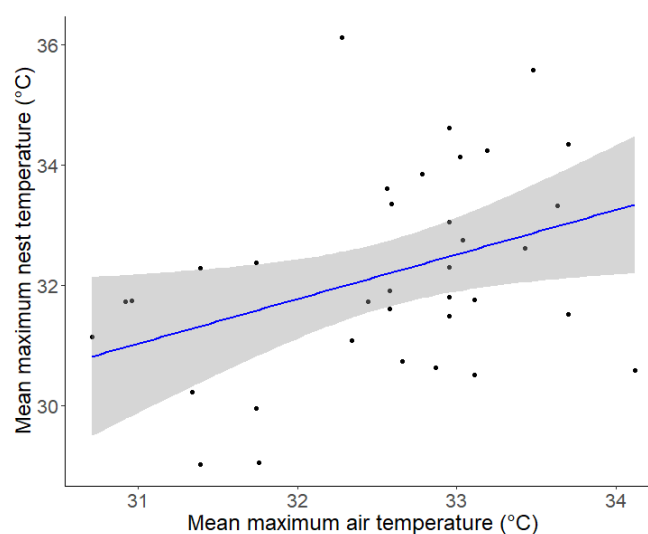


Figure A5.3. Relationship between mean maximum air temperature and mean maximum nest temperatures. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick. Pearson's correlation showed a moderate positive association between mean maximum air temperature and mean maximum nest temperatures ($r(33) = 0.38$, 95% CI [0.05, 0.63], $p = 0.02$).

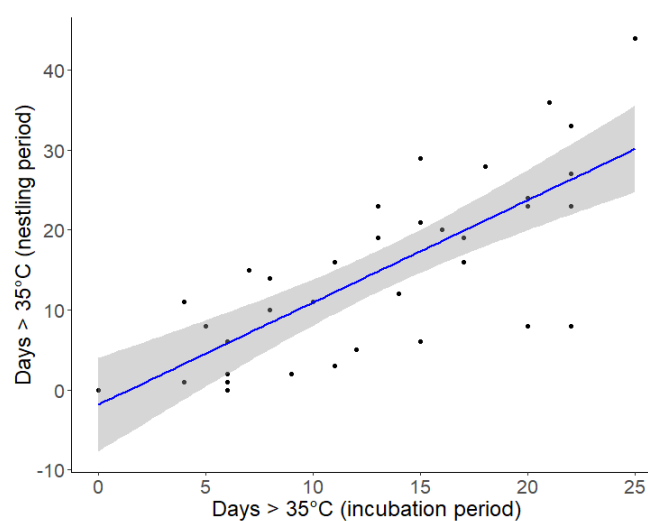


Figure A5.4. Relationship between days above 35 °C in the nest during incubation and during the nestling period. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick. Pearson's correlation showed a strong positive association between hot days during incubation and nestling periods ($r(33) = 0.75$, 95% CI [0.56, 0.87], $p < 0.001$).

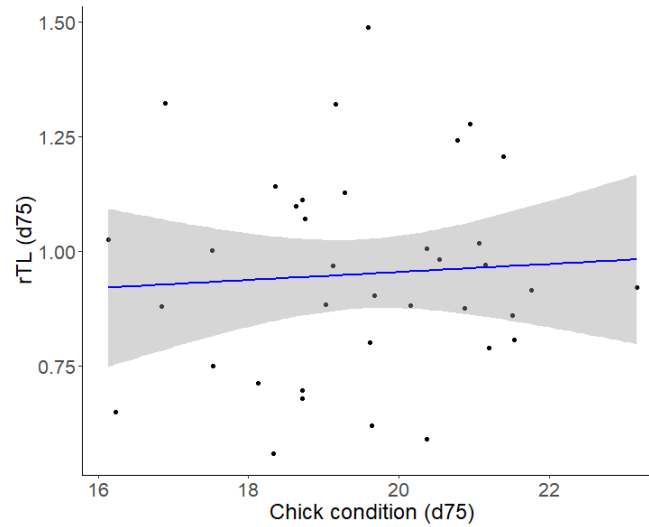


Figure A5.5. Relationship between chick condition on day 75 and relative telomere length on day 75 in ground hornbill nestlings. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick.

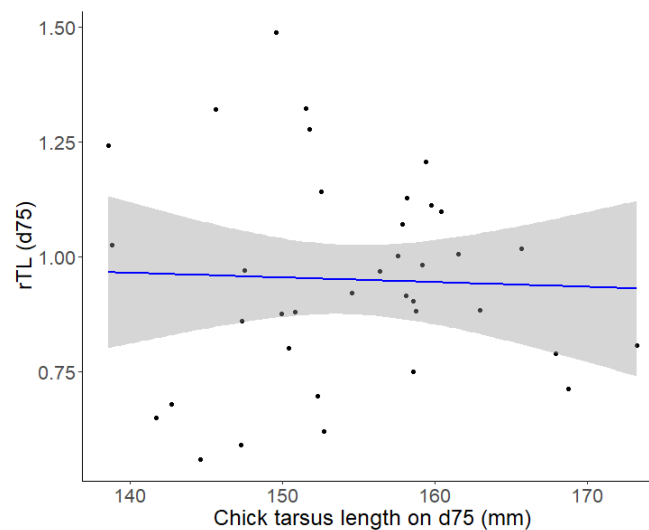


Figure A5.6. Relationship between chick tarsus length on day 75 and relative telomere length on day 75 in ground hornbill nestlings. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick

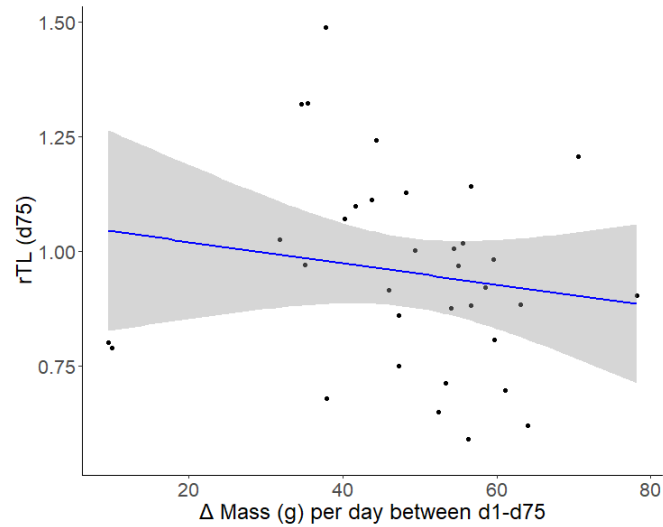


Figure A5.7. Relationship between Δ Mass (mean mass gain *per* day between d1-75) and relative telomere length on day 75 in ground hornbill nestlings. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick.

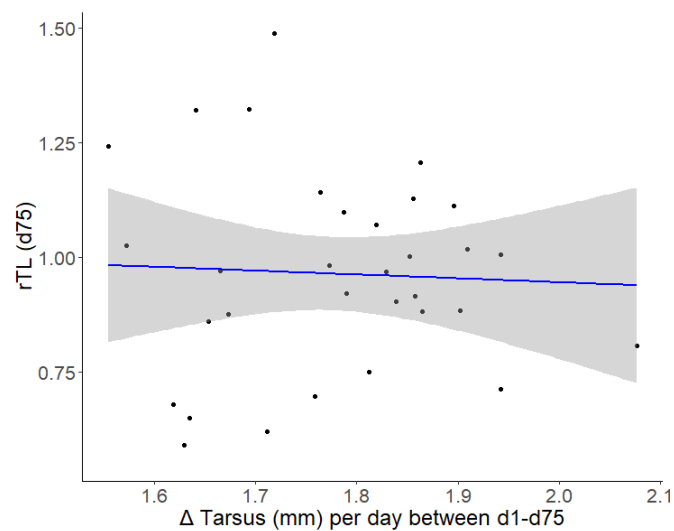


Figure A5.8. Relationship between Δ Tarsus (mean tarsus length growth *per* day between d1-75) and relative telomere length on day 75 in ground hornbill nestlings. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick.

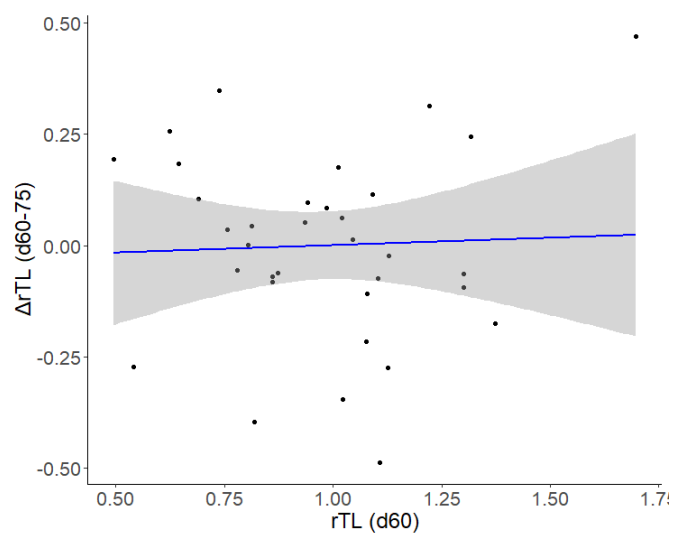


Figure A5.9. Relationship between relative telomere length on day 60 and change in relative telomere length between day 60 and day 75. The blue line represents the fitted linear regression with 95% confidence interval, and dots are observed values for each chick.

CHAPTER 6

Synthesis and Conclusions



6.1. General Discussion

Overview

This study extends our current understanding of how animals in hot environments respond to increasing temperatures, their vulnerability to rapid climate warming, and the potential for cooperative breeding to buffer the effects of climate change. I examined long-term seasonal temperature trends in my study area and investigated how heat shapes behaviour, maternal investment, and chick development and physiology in southern ground-hornbills. Additionally, since cooperative breeding strategies have been suggested to buffer the negative impacts of adverse environmental conditions (Covas, du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Bourne, 2020), I also explored whether the presence of helpers mitigated the effects of heat and improved breeding outcomes. In the fields of climate change impacts and cooperative breeding, especially in the avian literature, most studies have focused on small, relatively short-lived species, but see Schou et al. (2021), meaning that there is a lack of empirical research on large, long-lived species with slow life histories, which are likely to face very different ecological and climatic challenges. Here, I address this gap using the southern ground-hornbill as a model species, where the results from this study may be relevant for other terrestrial foraging species (e.g. bustards *Otididae*, guinea fowl *Numididae*, secretary birds *Sagittarius serpentarius*), cavity-nesting birds (e.g. owls *Strigiformes* and other hornbills *Bucerotidae*), and medium-sized mammals in similar habitats (e.g. jackals *Lupulella* spp., common duikers *Sylvicapra grimmia*, steenbok *Raphicerus campestris*; Chapter 2).

Summary of key results

The first data chapter investigated seasonal variations in thermal landscapes across two savanna habitats (open woodland and riparian), and examined long-term temperature trends, and seasonal thermoregulatory behaviours of ground-hornbills. Landscape operative temperatures

in both habitats were almost 5 °C hotter in winter than in summer at matched air temperatures, associated with lower shade availability. Long-term climate data revealed that open woodland habitats have become hotter on average in winter than in summer, whereas riparian habitats have remained cooler in winter but are reaching historical summer temperatures. Ground-hornbills show seasonal differences in foraging and shade-seeking behaviours and began panting at lower air temperatures in winter than in summer (Chapter 2). Chapters 3–5 focused on the impact of heat on reproductive processes. The second data chapter used long-term data (2012–2024) to investigate how the size of first- and second-laid eggs varied in relation to lay date, prior weather conditions, and the number of helpers. Females maintained stable investment in first-laid eggs, whereas second-laid “insurance” eggs were smaller and decreased in size when laid later in the season. The number of helpers in a group did not influence female investment in either egg (Chapter 3). The third and fourth data chapters used data collected over six breeding seasons and focused on whether high temperatures influenced the growth rates, survival, and physiology (measured as telomere length and dynamics) of ground-hornbill nestlings, and whether helpers could mitigate any negative effects. These studies showed that exposure to heat affects ground-hornbills at multiple early life stages during the nestling and post-fledging periods. Nestling growth rates were negatively affected by high temperatures, but final fledging size and body condition were not. Despite this, exposure to hotter nests and subsequent hot winters reduced post-fledging survival to the following season (Chapter 4). Heat exposure also had a measurable physiological effect, as chicks from hotter nests during incubation had longer telomeres at fledging age (day 75) but also faster telomere shortening between day 60-75 (Chapter 5). Across chapters, I found no evidence that helpers mitigated the effects of high temperatures on nestling growth or physiology.

In this discussion, I synthesise the results and consider the wider implications of my data chapters under three main themes: 1) impacts of a warming savanna on behaviour,

reproduction, and development; 2) cooperative breeding and the role of helpers; and 3) conservation in a warming world. I also highlight directions for future research.

Impacts of a warming savanna on behaviour, reproduction, and development

The African continent is warming faster than the global average, and heatwaves are becoming more frequent and intense (Engelbrecht et al., 2015; IPCC, 2023; World Meteorological Organization, 2023). Ecological studies on climate impacts are underrepresented in the global south, particularly within tropical regions, as most of the existing research is still concentrated in temperate ecosystems, especially of the northern hemisphere (Chambers et al., 2013; Cohen, Lajeunesse & Rohr, 2018; Butt, 2019; Taheri et al., 2021; Parker et al., 2024; Hickinbotham et al., 2025). In temperate regions, warming winters can be associated with potential benefits for animals, alleviating cold stress (McCaffery & Maxell, 2010; Pakanen et al., 2018; Chukwuka et al., 2021; Loe et al., 2021). However, in hot subtropical systems, higher winter temperatures can extend the period during which animals are exposed to heat and reduce thermal respite. My results reveal that rising maximum daily air temperatures combined with lower shade and food availability in winter mean that ground-hornbills must forage in hotter microsites and engage in evaporative cooling more frequently in winter than in summer (Chapter 2), which may make it more difficult for them to maintain an optimum water balance and body condition going into the summer breeding season. Therefore, ground-hornbills and likely other ground-foraging avian and mammalian species in subtropical ecosystems face increasing trade-offs between thermoregulation and foraging year-round.

Adverse conditions experienced outside breeding seasons have been found to influence subsequent reproductive timing and investment in birds and mammals through carry-over effects on adult condition (Salton et al., 2015; Millán et al., 2022; Steenweg et al., 2022). Higher pre-breeding temperatures have been associated with delayed breeding in ground-

hornbills (Carstens et al., 2019a; Middleton et al., 2026), and, in my study, later breeding was associated with smaller second-laid “insurance” eggs (Chapter 3). Although second-laid eggs are seldom the offspring that is raised to fledging, they account for about ~10% of all fledglings in this study population (CH, unpublished data) and declines in their investment could still negatively impact population recruitment, as reduced egg size may lower offspring immunity or survival prospects (Krist, 2011). Similar population-level effects may occur in other species that lay insurance eggs such as raptors and seabirds (Anderson, 1990; Simmons, 1997; Margalida et al., 2004; Davis et al., 2022). Monitoring the body mass of adults may help to understand the mechanisms behind delayed breeding, but capturing ground-hornbills is extremely challenging and stressful for the birds. To address this issue, non-invasive automatic perch scales placed at the entrance of nests are currently under development, with the aim of recording body weights throughout the breeding season, including the critical post-winter period when birds first return to their nests. Such approaches could provide a way to link adult condition following heat exposure during non-breeding seasons to subsequent reproductive timing and investment, in ground-hornbills and in other free-roaming species that are difficult to capture.

Early life is an energetically demanding period (Lindström, 1999), and heat exposure during this period has been shown to reduce growth rates and survival in birds and mammals (Catry et al., 2015; Bourne et al., 2020a; van de Ven et al., 2020; Corregidor-Castro & Jones, 2021). Consistent with this, my results revealed that higher temperatures were associated with reduced nestling growth rates in ground-hornbills. However, the final fledging size and condition of nestlings were not influenced by high temperatures, suggesting that they may have undergone compensatory growth when conditions improved, perhaps prioritising fledging size to improve short-term survival (Metcalf & Monaghan, 2003) (Chapter 4). For many species, being larger at fledging is likely an advantage for mobility and survival, and for ground-

dwelling species, this may include prioritising longer tarsi that facilitate efficient walking and longer wings to escape from predators (Heers & Dial, 2015; Martin et al., 2018). Compensatory growth has been documented in response to short-term food restriction in other birds (e.g. zebra finches *Taeniopygia guttata* (Fisher, Nager & Monaghan, 2006), alpine swifts *Tachymarptis melba* (Bize, Metcalfe & Roulin, 2006)) and in mammals (e.g. yellow-bellied marmots *Marmota flaviventris* (Heissenberger et al., 2020)), and therefore may also occur following heat-exposure, though evidence for this in wild animals is currently lacking. In slow developing species, compensatory growth after heat exposure may be plausible because extended nest periods mean that it is unlikely nestlings experience extreme heat continuously. Instead, heatwaves may be followed by cooler days, allowing periods in which they can allocate energy to growth rather than thermoregulation. However compensatory growth is known to be physiologically costly, and may elevate metabolic activity and oxidative damage which may reduce longevity (Metcalfe & Monaghan, 2001, 2003).

The costs of early-life sublethal heat exposure may therefore manifest later in life. (Metcalfe & Monaghan, 2001; Eastwood et al., 2019). In line with this, although telomere dynamics or fledging size and condition in this study did not directly predict survival in the short term (overwinter), higher temperatures during nestling growth and hotter winters post-fledging were both associated with reduced survival in the first year (Chapter 4 and 5). Similar associations were found in juvenile pied babblers, where individuals exposed to high nestling temperatures and hot and dry conditions after fledging were less likely to survive (Bourne et al., 2020a), and in great tit nestlings, where higher temperatures during the nesting period were associated with lower survival rates (Greño, Belda & Barba, 2008). Therefore, the results of my study contribute evidence from a larger-bodied species that early-life heat exposure can have implications for offspring survival and suggest that these effects may involve physiological impacts not fully reflected by body size, condition, or telomere measures.

Across my measures of chick growth and physiology (telomere length and dynamics), temperature emerged as the strongest environmental predictor, whereas rainfall did not appear to influence developmental trajectories. This likely reflects the generally average rainfall that occurred during my study period (see Chapter 1: Study site, Figure 1.3), which coincided mostly with La Niña periods (the cool phase of the El Niño–Southern Oscillation (ENSO), typically associated with higher rainfall in southern Africa (Mpheshea, Blamey & Reason, 2025)). Therefore, the population did not experience any low rainfall years between 2019–2025, when nestling development was monitored. In other more arid regions with higher rainfall variability that experienced droughts during study periods, rainfall was an important constraint on growth and survival (e.g. in pied babblers *Turdoides bicolor* (Bourne, Ridley, Spottiswoode, et al., 2021) and yellow-billed hornbills *Tockus leucomelas* (Pattinson, 2023)). However, even during better rainfall seasons, heat exposure still significantly reduced growth and survival rates in those species (Bourne, Ridley, Spottiswoode, et al., 2021; Pattinson, 2023). Had my study encompassed drought years, the negative effects of high temperatures on nestling growth and physiology may have been exacerbated by reduced food availability, leading to poorer developmental outcomes than those observed here. Humidity may also influence development by constraining effective thermoregulation, although it did not appear to strongly limit adult thermoregulation in this study, suggesting conditions at the study site may not yet regularly exceed dangerous humidity thresholds (Chapter 2). However, because I did not measure humidity inside nests, it remains unclear whether nestlings experienced levels that could exceed physiological thresholds. Under future climate scenarios that predict more frequent and prolonged heatwaves and droughts, or higher humidity, nestling development and survival could be more severely compromised than indicated by the results of this study. Long-term datasets are therefore vital for modelling and predicting the effects of extreme weather

and interannual variation across multiple years and generations (Clutton-Brock & Sheldon, 2010; Blanc & Thrall, 2024).

Cooperative breeding and the role of helpers

In cooperatively breeding species, non-breeding individuals assist the breeders in raising offspring (Cockburn, 1998; Riehl, 2013). One proposed benefit of this system is load-lightening, where helpers reduce the energetic costs of reproduction for the breeding individuals, allowing them to conserve resources for future reproductive attempts (Hatchwell, 1999). Contrary to evidence in support of the ‘load-lightening’ hypothesis found at the egg stage in some species (such as superb fairy-wrens *Malurus cyaneus* (Russell et al., 2007) and carrion crows *Corvus corone* (Canestrari, Marcos & Baglione, 2011)), I did not identify any association between helpers at the nest, and egg size in ground-hornbills. My results are consistent with findings in other species (e.g. sociable weavers *Philetairus socius* (Fortuna et al., 2021)), and while it remains unclear why helpers are associated with load-lightening in some cooperatively breeding species and not others, ground-hornbills offer important context for interpreting these results. Specifically, their low fecundity and exceptionally long lifespan, combined with raising a single offspring at a time, may favour a strategy in which females maintain egg investment at a level that ensures offspring growth and survival are not compromised (Stearns, 1992; Griesser et al., 2017).

Cooperative breeders occur mainly in regions with lower rainfall and high environmental variability (Rubenstein & Lovette, 2007; Jetz & Rubenstein, 2011). This distribution led to the suggestion that the additional care to offspring provided by helpers may buffer the negative effects of adverse conditions and allow for sustained reproduction (Rubenstein & Lovette, 2007; Covas, du Plessis & Doutrelant, 2008; Jetz & Rubenstein, 2011; Rubenstein, 2011). Evidence of this buffering strategy during harsh conditions were initially shown in sociable weavers (Covas, du Plessis & Doutrelant, 2008), and has also been shown

in meerkats (Groenewoud & Clutton-Brock, 2021) and superb starlings (Rubenstein, 2011). However, these cases now appear to be more the exception than the rule. Increasing evidence from cooperatively breeding species has found no buffering effects on reproduction during adverse environmental conditions (e.g. in pied babblers (Bourne, 2020; Bourne et al., 2021), sociable weavers (D'Amelio et al., 2022), Seychelles warblers *Acrocephalus sechellensis* (Borger et al., 2023), and ground-hornbills (Middleton, 2022; Middleton et al., 2026)). Consistent with these findings, my study found no evidence that helpers buffered the effects of high temperatures on nestling growth (Chapter 4) or on telomeres (Chapter 5). The benefits of breeding cooperatively for some species might emerge over longer timescales or via other types of group behaviours. For example, in pied babblers, larger groups with more helpers produced more surviving young and engaged in compensatory breeding following drought years (Bourne et al., 2020c). While comparative work on the hornbill family by Gonzalez et al. (2013) suggested that the species' life-history strategies may play a role in when buffering effects of helpers should be expected on reproduction. They proposed that large, long-lived, low fecundity species, such as ground-hornbills, which might skip breeding if conditions are not suitable, may benefit from a cooperative strategy through other group functions such as enhanced territory defence or predator deterrence. For example, larger groups may be better able to defend high-quality territories, potentially improving access to breeding sites and food resources to all group members (Cockburn, 1998; Cant, Otali & Mwanguhya, 2002; Golabek, Ridley & Radford, 2012; Humphries et al., 2021; Middleton, 2022). Overall, evidence suggests that cooperative breeding does not universally buffer reproductive outcomes under harsh environmental conditions, at least at within-season or within-breeding attempt scales. Therefore, the capacity of helpers in cooperatively breeding species to offset climate-driven challenges could vary with life-history strategies and environmental conditions. More research

is needed to establish these possible benefits and to assess whether they arise over longer-time periods or through the survival of group members, making them harder to detect.

Conservation in a warming world

Ground-hornbills are listed as globally Vulnerable by IUCN (IUCN, 2021) and regionally Endangered in South Africa (Kemp & Rose, 2025). This status is primarily due to human expansion, habitat alteration such as bush encroachment in savannas, the loss of large trees for nesting sites, secondary poisoning, and persecution, often due to pecking at reflections and shattering windows (Kemp & Rose, 2025). These existing pressures already constrain population growth in some regions, meaning that additional climate-driven impacts on reproduction and recruitment may have disproportionate consequences for population persistence. Given their non-drinking ecology, ground-hornbills are unlikely to be constrained by surface water availability (e.g. during droughts). Instead, climate sensitivity is more likely driven by physiological limits to heat dissipation, especially under hot and humid conditions that reduce evaporative cooling efficiency (Coulson et al., 2025). My results show that high temperatures reduce nestling growth rates and post-fledging survival, demonstrating that early-life heat exposure imposes developmental and survival costs. When combined with ground-hornbills' slow life history (low fecundity, delayed maturation, and a tendency to skip or delay breeding under suboptimal conditions) these effects could increase population vulnerability to ongoing climate warming. Although phenotypic plasticity, may allow individuals to modify their physiology, behaviour, or morphology in response to environmental fluctuations (Bonamour et al., 2019), climate warming is accelerating too quickly for most species to adapt genetically (Parmesan, 2006). Therefore, conservation strategies that protect key habitats, maintain nesting trees, and reduce exposure to extreme heat will be critical for supporting ground-hornbill population persistence. The output of this thesis provides guidance for

management strategies and policy decisions that could benefit not only ground-hornbills but also other savanna species under changing climatic conditions.

I found that high nest temperatures play a key role in influencing nestling development. The microclimate within nest boxes varies between nests, and some nests are better at buffering both cold and hot air temperatures than others. Natural materials, such as hollowed tree stumps that mimic the thick-walled structure of natural cavities, or nest boxes constructed with a double layer of wood separated by an insulating air gap, have proven to be the most effective at buffering temperature extremes in this study site (unpublished data; Carstens, 2017) and in other regions for other species (Griffiths et al., 2018). The orientation and placement of nests may be equally important; for example, positioning to avoid direct sunlight and beneath well-shaded tree canopies, such as those found in riparian habitats, may help reduce nest temperatures. However, this may also increase the risk of predation from predators that use denser vegetation for cover in which to ambush prey (Janecke & Bolton, 2020), or increase encounters with other species using densely shaded areas for thermoregulation, potentially leading to higher levels of competition or disturbance. Nonetheless, well-insulated nests and careful site selection may lessen the negative impacts of climate warming on birds and other species (Catry et al., 2015; Griffiths et al., 2018; Martin Bideguren et al., 2019; Honey et al., 2021; Corregidor-Castro et al., 2023).

Savanna ecosystems face degradation from human use, herbivory, fire, drought, and rising temperatures (O'Connor & Page, 2014; Smit & Prins, 2015; Osborne et al., 2018; Case et al., 2019; Scholes, 2020; Vermeulen et al., 2025) and, in this study site, from conservation strategies that promote high elephant densities (APNR, 2023), which reduce woody cover through browsing and uprooting (Haynes, 2012). Furthermore, ecotourism adds to these pressures, as roads, infrastructure, and recreation are frequently concentrated in riparian habitats. In parallel, increasing temperatures may alter animal habitat use, as large mammals

and other ground-dwelling birds in other ecosystems have been observed to seek cooler locations to escape rising temperatures (Beest, Van Moorter & Milner, 2012; Carroll et al., 2015; Mason et al., 2017). My findings in Chapter 2 indicate that riparian habitats provide meaningful thermal refuge in this savanna habitat, particularly in winter, however, increased utilisation of these areas by wildlife under future warming could increase ecological pressures. For instance, in arid and semi-arid environments, heavy use of water resources by animals can lead to habitat degradation around water points (Rispel & Lendelvo, 2016). Therefore, conservation strategies should protect and restore woody vegetation, and riparian habitats should be developed sensitively to preserve their value as thermal refuges for wildlife, particularly under future climate scenarios.

6.1.1.Future research

Several additional questions have emerged throughout this study. The following section highlights several promising avenues for future research.

Impacts of warming on behaviour, foraging, and physiology:

1. **Investigate how temperature and rainfall influence prey availability and prey preference.** Climate change can alter species interactions by affecting prey abundance, distribution, and nutritional quality (Morin, Chamaillé-Jammes & Valeix, 2021; Hardison & Eliason, 2024). Ground-hornbills consume a wide range of prey (Combrink, 2016; Middleton, 2022), and they may shift prey preferences and favour more water rich foods during high temperatures. I found no temperature-related decline in provisioning, indicating that biomass delivery to nestlings was maintained during hot periods, perhaps via individuals bringing larger prey less often. Investigating these dietary and provisioning responses may help explain why changes in provisioning behaviour seem important in mediating climate impacts on reproduction in some species but not others and whether flexible feeding behaviour buffers offspring against

environmental stress or whether prey limitation constrains reproduction. This work also addresses the question of how climate-driven changes in prey availability may influence species interactions (e.g. competition and predation) with potential effects on vegetation structure (e.g. through grazing or browsing) and ecosystem functioning (Gaynor et al., 2019).

2. Assess the body mass of group members to investigate how trade-offs between foraging and thermoregulation during high temperatures affect body condition.

Trade-offs between heat dissipation/avoidance behaviours (e.g., panting, shade-seeking) and foraging behaviours can impose sub-lethal costs on body condition (van de Ven, McKechnie & Cunningham, 2019), which in turn may influence reproductive decisions and offspring survival. Understanding how animals balance the demands of thermoregulation and foraging is important for predicting species vulnerability to climate warming. My results show that winter landscapes have higher operative temperatures than summer at matched air temperatures, exposing ground-hornbills to elevated heat loads while foraging in winter. Investigating seasonal trends in adult body condition (e.g. at the end of winter when food is scarce and during summer when it is more plentiful), could reveal the impacts of increased heat exposure and reduced food availability. Because capturing adult ground-hornbills is challenging and stressful for the birds, the project decided to stop doing so in 2016 to maintain natural behaviour and promote habituation for behavioural observations. Perch scales are currently being developed under postdoctoral research at the APNR Ground-Hornbill Project, which will be placed at nest entrances and record the weight when a bird lands on it. This offers a promising and non-invasive approach for collecting weight data that will help understand temperature-related trade-offs in foraging behavioural and seasonal changes in body condition.

3. **Investigate group movements using tracking devices.** Understanding how animals move across their landscape can help identify critical areas for shade and food, reveal how they respond to heat by shifting between habitats, and show how resources are used across landscapes and seasons. This method is currently being pioneered by the APNR Ground-Hornbill Project, which places tracking rings on ground-hornbill juveniles prior to fledging to record data at fine spatial and temporal scales. This allows monitoring of the entire group's movements (since juveniles remain with the group after fledging and they forage together), providing valuable insights into territory use and seasonal movements. These data are important for conservation planning, as they may help identify key habitats and resources that should be prioritised for protection to support survival, reproductive success, and population resilience under climate change.
4. **Collect physiological data on metabolic and evaporative water loss rates to use predictive modelling, such as biophysical models.** Biophysical models integrate an animal's physiology, behaviour, and environmental conditions to help predict how species respond to different future climate scenarios (Conradie et al., 2023). Incorporating respirometry data, such as metabolic rate, evaporative water loss, and heat tolerance limits, alongside behavioural data from Chapter 2, would allow realistic estimates of energy and water costs under high heat loads (McKechnie, Gerson & Wolf, 2021). However, collecting respirometry data in large animals is challenging due to the need for large specialised metabolic chambers, but the insights would help assess heat tolerance limits and vulnerability to climate warming in ground-hornbills and other large-bodied species.
5. **Investigate early-life physiological effects of heat to better understand how development under thermal stress shapes survival and fitness.** It remains unclear whether the patterns I observed in telomere dynamics between day 60 and 75 reflect

prenatal effects, postnatal effects, or a combination of both. Future research incorporating measurements at hatching and fledging would help separate prenatal and postnatal effects on telomere dynamics. Additionally, my results revealed neither body size, condition, nor telomere length or dynamics measured at the late nestling stage predicted juvenile overwinter survival, yet chicks from hotter nests and hotter subsequent winters had lower survival rates. This suggests that key physiological consequences of heat during the nestling stage were not fully captured by measures of growth, size or late-stage telomere length or dynamics in my study. Furthermore, I found that nestlings may be undergoing physiologically costly compensatory growth. Tracking telomere dynamics from hatching through fledging, combined with additional indicators of acute stress responses such as oxidative stress (Monaghan, Metcalfe & Torres, 2009) or glucocorticoids (Moagi et al., 2021), could provide a more complete picture of how early-life heat exposure, and potential periods of compensatory growth, affects physiology and fitness. Such an approach would require blood sampling at earlier ages. My initial intention for Chapter 5 was to analyse telomere length of chicks at a younger age. I collected blood samples from one-week-old chicks using a fine needle puncture on the toe pad and blotted blood onto FTA paper. However, DNA from FTA-stored samples was insufficient for reliable telomere analysis. Drawing blood from very young ground-hornbills is challenging due to their low blood pressure and the presence of substantial subcutaneous air. Non-invasive sampling (e.g. faecal samples) for glucocorticoid measurements could be explored as an alternative, or in addition to oxidative stress and telomere measures (when blood sampling is possible). Integrating these physiological markers could help clarify how early-life thermal stress and compensatory growth influence stress physiology, and survival and longevity.

Cooperative breeding and the role of helpers:

6. **Investigate behavioural trade-offs between foraging, vigilance and thermoregulation, and how these are influenced by temperature, habitat type, and group size.** Spending more time in shaded areas, which are often more densely vegetated, can increase predation risk, forcing birds to invest additional time in vigilance which may create further trade-offs with foraging, and affect body condition. In cooperatively breeding species, helpers may provide group-level benefits by improving predator detection for all members, and by allowing individuals to rest or reduce activity during hot periods, supporting thermoregulation. This could be investigated by conducting focal observations on group behaviours and would provide insight into the potential benefits of helpers in cooperatively breeding species. I attempted to collect such behavioural data for this study, but it was challenging due to their vast territories which made it difficult to locate groups, and their nervous nature (associated with history of adult captures in past phases of the long-term project) which makes sustained focal observations challenging. The recent deployment of tracking rings could make locating groups easier by gaining knowledge of their preferred locations and locating birds more regularly, which might allow birds to become more habituated to the presence of researchers.
7. **Investigate whether helpers help secure better-quality resources.** Given the limited effect of helpers on reproduction, future studies should investigate whether helpers provide other benefits such as defending better quality territories with better access to resources (e.g., optimal foraging or nesting sites, or access to more shaded habitats). This could involve identifying the features and measures of a “good” territory, using remote sensing to quantify canopy cover and thermal refuges. Or assessing and surveying prey abundance (e.g. pitfall traps for invertebrates), and landscape operative

temperatures across multiple habitat types and group territories, expanding on what was achieved in Chapter 2. This work could also draw on data collected from tracking devices, investigating locations where the birds spend more time foraging. Linking habitat characteristics and resource availability to group size and reproductive success could help test whether cooperative breeding provides advantages in acquiring and defending higher-quality territories.

8. Investigate the genetic relatedness of individuals within ground-hornbill groups.

Understanding genetic relatedness is important for interpreting the evolutionary basis of cooperative behaviour. While groups appear to be primarily made up of relatives, genetic research is necessary to verify the relatedness among individuals in groups. This is challenging in ground-hornbills as it is difficult to obtain samples from individuals (other than juveniles). Non-invasive methods, such as faecal or feather sampling (from dropped feathers obtained around nests), may address this issue. Relatedness data would reveal whether helpers gain indirect fitness benefits by assisting kin, or whether some groups consist of non-relatives, which may help for their own direct benefits such as territory inheritance, predator protection, or social advantages (Cockburn, 1998; Riehl, 2013).

6.2. Conclusions

This thesis provides novel information on the mechanisms by which birds respond to increasing temperatures, using a savanna-dwelling bird, the southern ground-hornbill, as a model species. I showed that both rising summer and winter temperatures, the latter of which are often overlooked, are thermally challenging for ground-hornbills, with implications that are likely relevant for other species in these, and potentially other, ecosystems. Winter heat can reduce breeding investment, while high temperatures during nestling development can impair growth

rates and influence telomere dynamics. However, nestlings' ability to fledge in good condition despite these setbacks indicates compensatory growth, which may have hidden physiological costs. In keeping with this, heat exposure during the nestling period, coupled with hot conditions during winter, both contributed to reduced juvenile survival to the next breeding season. I found no evidence that having more helpers in a group moderated the effects of temperature, thereby contributing to a growing body of evidence from this and other species, that helpers might not be able to buffer against reproductive failure during hot weather (Bourne, Ridley, Spottiswoode, et al., 2021; D'Amelio et al., 2022; Middleton et al., 2026), and that cooperatively breeding species therefore might not be more resilient to climate change. Overall, these results show that warming throughout the year has the potential to affect ground-hornbill populations as well as other species inhabiting savanna ecosystems.

REFERENCES

- Akinwande, M.O., Dikko, H.G. & Samson, A. 2015. Variance inflation factor: as a condition for the inclusion of suppressor variable(s) in regression analysis. *Open Journal of Statistics*. 05(07):754–767. DOI: 10.4236/ojs.2015.57075.
- Albright, T.P., Mutiibwa, D., Gerson, Alexander.R., Smith, E.K., Talbot, W.A., O'Neill, J.J., McKechnie, A.E. & Wolf, B.O. 2017. Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*. 114(9):2283–2288. DOI: 10.1073/pnas.1613625114.
- Alston, J.M., Joyce, M.J., Merkle, J.A. & Moen, R.A. 2020. Temperature shapes movement and habitat selection by a heat-sensitive ungulate. *Landscape Ecology*. 35(9):1961–1973. DOI: 10.1007/s10980-020-01072-y.
- Amundsen, T., Lorentsen, S.-H. & Tveraa, T. 1996. Effects of egg size and parental quality on early nestling growth: an experiment with the Antarctic Petrel. *The Journal of Animal Ecology*. 65(5):545. DOI: 10.2307/5735.
- Anderson, D.J. 1990. Evolution of Obligate Siblicide in Boobies. 1. A Test of the Insurance-Egg Hypothesis. *The American Naturalist*. 135(3):334–350. DOI: 10.1086/285049.
- Andrew, S.C., Hurley, L.L., Mariette, M.M. & Griffith, S.C. 2017. Higher temperatures during development reduce body size in the zebra finch in the laboratory and in the wild. *Journal of Evolutionary Biology*. 30(12):2156–2164. DOI: 10.1111/jeb.13181.
- Angelier, F., Costantini, D., Blévin, P. & Chastel, O. 2018. Do glucocorticoids mediate the link between environmental conditions and telomere dynamics in wild vertebrates? A review. *General and Comparative Endocrinology*. 256:99–111. DOI: 10.1016/j.ygcen.2017.07.007.
- Angelier, F., Weimerskirch, H., Barbraud, C. & Chastel, O. 2019. Is telomere length a molecular marker of individual quality? Insights from a long-lived bird. *Functional Ecology*. 33(6):1076–1087. DOI: 10.1111/1365-2435.13307.
- Angilletta, M.J., Cooper, B.S., Schuler, M.S. & Boyles, J.G. 2010. The evolution of thermal physiology in endotherms. *Frontiers in Bioscience*. E2(3):861–881. DOI: 10.2741/e148.
- APNR, 2023. Association Private Nature Reserves annual wildlife census data (2003 – 2023). Unpublished report.
- Asghar, M., Bensch, S., Tarka, M., Hansson, B. & Hasselquist, D. 2015. Maternal and genetic factors determine early life telomere length. *Proceedings of the Royal Society B: Biological Sciences*. 282(1799). DOI: 10.1098/rspb.2014.2263.
- Avalos-Castro, R., Segura-Correa, J.C., Palacios-Espinosa, A. & Romero-Santillan, F. 2022. Growth curves through non-linear models in Creole lambs from the Mixteca region of

- Oaxaca, Mexico. *Tropical and Subtropical Agroecosystems*. 25(2). DOI: 10.56369/tsaes.4218.
- Bailey, L.D. & van de Pol, M. 2016. climwin: An R Toolbox for Climate Window Analysis. *PLOS ONE*. 11(12). DOI: 10.1371/journal.pone.0167980.
- Bakken, G.S., Santee, W.R. & Erskine, D.J. 1985. Operative and standard operative temperature: tools for thermal energetics studies. *American Zoologist*. 25(4):933–943. DOI: 10.1093/icb/25.4.933.
- Barras, Arnaud.G., Niffenegger, Carole.A., Candolfi, I., Hunziker, Yannick.A. & Arlettaz, R.S. 2021. Nestling diet and parental food provisioning in a declining mountain passerine reveal high sensitivity to climate change. *Journal of Avian Biology*. 52(2). DOI: 10.1111/jav.02649.
- Bartholomew, G.A. & Dawson, W.R. 1979. Thermoregulatory behavior during incubation in heermann's gulls. *Physiological Zoology*. 52(4):422–437. DOI: 10.1086/physzool.52.4.30155934.
- Bartoń, K. 2020. *MuMIn: Multi-Model Inference R package*. Available: <https://CRAN.R-project.org/package=MumIn> [2024, February 01].
- Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67(1):1–48. DOI: 10.18637/jss.v067.i01.
- Bauch, C., Boonekamp, J.J., Korsten, P., Mulder, E. & Verhulst, S. 2019. Epigenetic inheritance of telomere length in wild birds. *PLOS Genetics*. 15(2):e1007827. DOI: 10.1371/journal.pgen.1007827.
- Baur, H. & Leuenberger, C. 2011. Analysis of ratios in multivariate morphometry. *Systematic Biology*. 60(6):813–825. DOI: 10.1093/sysbio/syr061.
- van Beest, F.M. & Milner, J.M. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS ONE*. 8(6). DOI: 10.1371/journal.pone.0065972.
- van Beest, F.M., Van Moorter, B. & Milner, J.M. 2012a. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour*. 84(3):723–735. DOI: 10.1016/j.anbehav.2012.06.032.
- Belmaker, A., Hallinger, K.K., Glynn, R.A., Winkler, D.W. & Haussmann, M.F. 2019. The environmental and genetic determinants of chick telomere length in Tree Swallows (*Tachycineta bicolor*). *Ecology and Evolution*. 9(14):8175–8186. DOI: 10.1002/ece3.5386.
- Bennett, P.M. & Owens, I.P.F. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 264(1380):401–408. DOI: 10.1098/rspb.1997.0057.
- Berry, P., Dammhahn, M., Hauptfleisch, M., Hering, R., Jansen, J., Kraus, A. & Blaum, N. 2024. African dryland antelope trade-off behaviours in response to heat extremes. *Ecology and Evolution*. 14(6):e11455. DOI: 10.1002/ece3.11455.

- Bize, P., Metcalfe, N.B. & Roulin, A. 2006. Catch-up growth strategies differ between body structures: interactions between age and structure-specific growth in wild nestling Alpine Swifts. *Functional Ecology*. 20(5):857–864. DOI: 10.1111/j.1365-2435.2006.01157.x.
- Bize, P., Criscuolo, F., Metcalfe, N.B., Nasir, L. & Monaghan, P. 2009. Telomere dynamics rather than age predict life expectancy in the wild. *Proceedings of the Royal Society B: Biological Sciences*. 276(1662):1679–1683. DOI: 10.1098/rspb.2008.1817.
- Blackburn, E.H. 2005. Telomeres and telomerase: their mechanisms of action and the effects of altering their functions. *FEBS Letters*. 579:859–862. DOI: 10.1016/j.febslet.2004.11.036.
- Bladon, A.J., Donald, P.F., Jones, S.E.I., Collar, N.J., Deng, J., Dadacha, G., Abebe, Y.D. & Green, R.E. 2019. Behavioural thermoregulation and climatic range restriction in the globally threatened Ethiopian bush-crow *Zavattariornis stresemanni*. *Ibis*. 161(3):546–558. DOI: 10.1111/ibi.12660.
- Bladon, A.J., Donald, P.F., Collar, N.J., Denge, J., Dadacha, G., Wondafrash, M. & Green, R.E. 2021. Climatic change and extinction risk of two globally threatened Ethiopian endemic bird species. *PLOS ONE*. 16(5):e0249633. DOI: 10.1371/journal.pone.0249633.
- Blanc, S. & Thrall, Peter.H. 2024. Editorial: the critical role of very long-term studies in ecology and evolution. *Ecology Letters*. 27(12):e70049. DOI: 10.1111/ele.70049.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology*. 75(4):385–407. Available: <http://www.jstor.org/stable/2664968>.
- Blas, J., Baos, R., Bortolotti, G.R., Marchant, T.A. & Hiraldo, F. 2006. Age-related variation in the adrenocortical response to stress in nestling white storks (*Ciconia ciconia*) supports the developmental hypothesis. *General and Comparative Endocrinology*. 148(2):172–180. DOI: 10.1016/j.ygcen.2006.02.011.
- Blévin, P., Angelier, F., Tartu, S., Ruault, S., Bustamante, P., Herzke, D., Moe, B., Bech, C., et al. 2016. Exposure to oxychlordan is associated with shorter telomeres in arctic breeding kittiwakes. *Science of The Total Environment*. 563–564:125–130. DOI: 10.1016/j.scitotenv.2016.04.096
- Bonamour, S., Chevin, L.-M., Charmantier, A. & Teplitsky, C. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 374(1768):20180178. DOI: 10.1098/rstb.2018.0178.
- Boonekamp, J.J., Mulder, G.A., Salomons, H.M., Dijkstra, C. & Verhulst, S. 2014. Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. *Proceedings of the Royal Society B: Biological Sciences*. 281(1785):20133287. DOI: 10.1098/rspb.2013.3287.

- Borger, M.J., Richardson, D.S., Dugdale, H., Burke, T. & Komdeur, J. 2023. Testing the environmental buffering hypothesis of cooperative breeding in the Seychelles warbler. *acta ethologica*. 26:211–224. DOI: 10.1007/s10211-022-00408-y.
- Bosman, D.S. 2014. Effects of intraclutch variation in egg size and hatching asynchrony on nestling development and survival in semi-precocial Herring Gulls. *Journal of Field Ornithology*. 85(4):379–390. DOI: 10.1111/jof.12077.
- Bourne, A.R. 2020. Can sociality buffer the impacts of climate change on a cooperatively-breeding bird, the southern pied babbler *Turdoides bicolor*? Unpublished doctoral thesis. University of Cape Town.
- Bourne, A.R., Cunningham, S.J., Spottiswoode, C.N. & Ridley, A.R. 2020a. Hot droughts compromise interannual survival across all group sizes in a cooperatively breeding bird. *Ecology Letters*. 23(12):1776–1788. DOI: 10.1111/ele.13604.
- Bourne, A.R., Cunningham, S.J., Spottiswoode, C.N. & Ridley, A.R. 2020b. High temperatures drive offspring mortality in a cooperatively breeding bird. *Proc R Soc B*. 287(1931). DOI: 10.1098/rspb.2020.1140.
- Bourne, A.R., Cunningham, S.J., Spottiswoode, C.N. & Ridley, A.R. 2020c. Compensatory breeding in years following drought in a desert-dwelling cooperative breeder. *Frontiers in Ecology and Evolution*. 8. DOI: 10.3389/fevo.2020.00190.
- Bourne, A.R., Ridley, A.R., Spottiswoode, C.N. & Cunningham, S.J. 2021. Direct and indirect effects of high temperatures on fledging in a cooperatively breeding bird. *Behavioral Ecology*. 32(6):1212–1223. DOI: 10.1093/beheco/arab087.
- Bourne, A.R., Ridley, A.R., McKechnie, A.E., Spottiswoode, C.N. & Cunningham, S.J. 2021. Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the southern pied babbler *Turdoides bicolor*. *Conservation Physiology*. 9(1):coab043. DOI: 10.1093/conphys/coab043.
- Bourne, A.R., Ridley, A.R. & Cunningham, S.J. 2023. Helpers don't help when it's hot in a cooperatively breeding bird, the Southern Pied Babbler. *Behavioral Ecology*. 34(4):562–570. DOI: 10.1093/beheco/arad023.
- Bowyer, R.T. 2009. Thermal landscapes and resource selection by black-tailed deer: implications for large herbivores. *California Fish and Game*. 95(3):128–139. Available: <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=47335>.
- Briscoe, N.J., Handasyde, K.A., Griffiths, S.R., Porter, W.P., Krockenberger, A. & Kearney, M.R. 2014. Tree-hugging koalas demonstrate a novel thermoregulatory mechanism for arboreal mammals. *Biology Letters*. 10(6):20140235. DOI: 10.1098/rsbl.2014.0235.
- Brivio, F., Apollonio, M., Anderwald, P., Filli, F., Bassano, B., Bertolucci, C. & Grignolio, S. 2024. Seeking temporal refugia to heat stress: increasing nocturnal activity despite predation risk. *Proceedings of the Royal Society B: Biological Sciences*. 291(2015):20231587. DOI: 10.1098/rspb.2023.1587.

- Brockmann, H.J. 1997. Cooperative breeding in wasps and vertebrates: the role of ecological constraints. In *The Evolution of Social Behaviour in Insects and Arachnids*. B.J. Crespi & J.C. Choe, Eds. Cambridge: Cambridge University Press. 347–371. DOI: 10.1017/CBO9780511721953.018.
- Brooks, M., Bolker, B., Kristensen, K., Mächler, M., Magnusson, A., Skaug, H., Nielsen, A., Berg, C., et al. 2017. *glmmTMB: Generalized linear mixed models using Template Model Builder*. DOI: 10.32614/CRAN.package.glmmTMB.
- Brouwer, L., Richardson, D.S. & Komdeur, J. 2012. Helpers at the nest improve late-life offspring performance: evidence from a long-term study and a cross-foster experiment. *PLOS One*. 74. DOI: 10.1371/journal.pone.0033167.
- Brouwer, L., Pol, M. van de & Cockburn, A. 2014. The role of social environment on parental care: offspring benefit more from the presence of female than male helpers. *Journal of Animal Ecology*. 83(2):491–503. DOI: 10.1111/1365-2656.12143.
- Browning, L.E., Young, C.M., Savage, J.L., Russell, D.J.F., Barclay, H., Griffith, S.C. & Russell, A.F. 2012. Carer provisioning rules in an obligate cooperative breeder: prey type, size and delivery rate. *Behavioral Ecology and Sociobiology*. 66(12):1639–1649. DOI: 10.1007/s00265-012-1419-z.
- Butt, N. 2019. Geographical bias constrains global knowledge of phenological change. *Pacific Conservation Biology*. 25(4):345–347. DOI: 10.1071/PC18073.
- Camprodon, J., Salvanyà, J. & Soler-Zurita, J. 2008. The abundance and suitability of tree cavities and their impact on hole-nesting bird populations in beech forests of NE iberian peninsula. *Acta Ornithologica*. 43(1):17–31. DOI: 10.3161/000164508X345293.
- Canestrari, D., Marcos, J.M. & Baglione, V. 2011. Helpers at the nest compensate for reduced maternal investment in egg size in carrion crows. *Journal of Evolutionary Biology*. 24(9):1870–1878. DOI: 10.1111/j.1420-9101.2011.02313.x.
- Cant, M.A., Oтали, E. & Mwanguhya, F. 2002. Fighting and mating between groups in a cooperatively breeding mammal, the banded mongoose. *Ethology*. 108(6):541–555. DOI: 10.1046/j.1439-0310.2002.00795.x.
- Capilla-Lasheras, P., Wilson, A.J. & Young, A.J. 2023. Mothers in a cooperatively breeding bird increase investment per offspring at the pre-natal stage when they will have more help with post-natal care. *PLOS Biology*. 21(11):e3002356. DOI: 10.1371/journal.pbio.3002356.
- Carey, C. 1980. The ecology of avian incubation. *BioScience*. 30(12):819–824. DOI: 10.2307/1308374.
- Carroll, J.M., Davis, C.A., Elmore, R.D., Fuhlendorf, S.D. & Thacker, E.T. 2015. Thermal patterns constrain diurnal behavior of a ground-dwelling bird. *Ecosphere*. 6(11):art222. DOI: 10.1890/ES15-00163.1.

- Carroll, J.M., Davis, C.A., Elmore, R.D. & Fuhlendorf, S.D. 2015. A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. *PLOS ONE*. 10(11):e0143676. DOI: 10.1371/journal.pone.0143676.
- Carroll, J.M., Davis, C.A., Fuhlendorf, S.D. & Elmore, R.D. 2016. Landscape pattern is critical for the moderation of thermal extremes. *Ecosphere*. 7(7):2–16. DOI: 10.1002/ecs2.1403.
- Carstens, K. 2017. Nest boxes as a conservation tool for the southern ground hornbill *Bucorvus leadbeateri*. Unpublished doctoral thesis. University of Cape Town.
- Carstens, K.F. 2014. Egg-capping in the southern ground-hornbill *Bucorvus leadbeateri*. *Ostrich*. 85(1):89–91. DOI: 10.2989/00306525.2014.895438.
- Carstens, K.F., Kassanje, R., Little, R.M., Ryan, P.G. & Hockey, P.A.R. 2019a. The effects of weather, group size and type of nest on the timing of egg-laying in the southern ground-hornbill *Bucorvus leadbeateri*. *Journal of Ornithology*. 160: 633–640. DOI: 10.1007/s10336-019-01654-x.
- Carstens, K.F., Kassanje, R., Little, R.M., Ryan, P.G. & Hockey, P.A. 2019b. Natal dispersal in the Southern Ground Hornbill *Bucorvus leadbeateri*. *Ostrich*. 90(2):119–127. DOI: 10.2989/00306525.2019.1590474.
- Carstens, K.F., Kassanje, R., Little, R.M., Ryan, P.G. & Hockey, P.A.R. 2019c. Breeding success and population growth of southern ground hornbills *Bucorvus leadbeateri* in an area supplemented with nest-boxes. *Bird Conservation International*. 29(4):627–643. DOI: 10.1017/S0959270919000108.
- Case, M.F., Wigley-Coetsee, C., Nzima, N., Scogings, P.F. & Staver, A.C. 2019. Severe drought limits trees in a semi-arid savanna. *Ecology*. 100(11):e02842. DOI: 10.1002/ecy.2842.
- Catry, I., Catry, T., Patto, P., Franco, A.M.A. & Moreira, F. 2015. Differential heat tolerance in nestlings suggests sympatric species may face different climate change risks. *Climate Research*. 66(1):13–24. DOI: 10.3354/cr01329.
- Catterall, C.P., Lynch, & Jansen, A. 2012. Riparian wildlife and habitats. In *Principles for riparian lands management*. 141–158.
- Chambers, L.E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L.J., Crawford, R.J.M., Durant, J.M., Hughes, L., et al. 2013. Phenological changes in the southern hemisphere. *PLoS ONE*. 8(10):e75514. DOI: 10.1371/journal.pone.0075514.
- Christians, J.K. 2002. Avian egg size: variation within species and inflexibility within individuals. *Biological Reviews*. 77(1):1–26. DOI: 10.1017/S1464793101005784.
- Chukwuka, C.O., Mello, R.S.R., Cree, A. & Monks, J.M. 2021. Thermal heterogeneity of selected retreats in cool-temperate viviparous lizards suggests a potential benefit of future climate warming. *Journal of Thermal Biology*. 97:102869. DOI: 10.1016/j.jtherbio.2021.102869.

- Cilliers, D., Evans, S., Coetzee, H. & van Rensburg, L. 2013. Developing a site selection tool to assist reintroduction efforts for the southern ground-hornbill *Bucorvus leadbeateri*. *Ostrich*. 84(2). DOI: 10.2989/00306525.2013.823129.
- Clifford, L.D. 2001. Experimental demonstration of the insurance value of extra eggs in an obligately siblicidal seabird. *Behavioral Ecology*. 12(3):340–347. DOI: 10.1093/beheco/12.3.340.
- Clutton-Brock, T. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*. 296(5565):69–72. DOI: 10.1126/science.296.5565.69.
- Clutton-Brock, T.H. 1988. *Reproductive success: studies of individual variation in contrasting breeding systems*. University of Chicago Press.
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton University Press.
- Clutton-Brock, T. & Sheldon, B.C. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*. 25(10):562–573. DOI: 10.1016/j.tree.2010.08.002.
- Cockburn, A. 1998. Evolution of helping behaviour in cooperatively breeding birds. *Annual Review of Ecology and Systematics*. 29(1):141–177. DOI: 10.1146/annurev.ecolsys.29.1.141.
- Cockburn, A. 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences*. 273(1592):1375–1383. DOI: 10.1098/rspb.2005.3458.
- Cockburn, A., Sims, R.A., Osmond, H.L., Green, D.J., Double, M.C. & Mulder, R.A. 2008. Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*. 77(3):430–438. DOI: 10.1111/j.1365-2656.2007.01351.x.
- Combrink, L. 2016. The habitat, nesting and foraging requirements of southern ground hornbills in the Kruger National Park, South Africa. Unpublished doctoral thesis. University of Kwazulu-Natal.
- Combrink, L., Combrink, H.J., Botha, A.J. & Downs, C.T. 2017. Nest temperature fluctuations in a cavity nester, the southern ground-hornbill. *Journal of Thermal Biology*. 66:21–26. DOI: 10.1016/j.jtherbio.2017.03.003.
- Combrink, L., Combrink, H.J., Botha, A.J. & Downs, C.T. 2020. Habitat preferences of Southern Ground-hornbills in the Kruger National Park: implications for future conservation measures. *Scientific Reports*. 10(1):16195. DOI: 10.1038/s41598-020-73236-4.
- Conrad, K.F. & Robertson, R.J. 1993. Patterns of parental provisioning by eastern phoebes. *The Condor*. 95(1):57–62. DOI: 10.2307/1369386.
- Conradie, S.R., Woodborne, S.M., Cunningham, S.J. & McKechnie, A.E. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African

- arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences*. 116(28):14065–14070. DOI: 10.1073/pnas.1821312116.
- Conradie, S.R., Woodborne, S.M., Wolf, B.O., Pessato, A., Mariette, M.M. & McKechnie, A.E. 2020. Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology*. 8(1):coaa048. DOI: 10.1093/conphys/coaa048.
- Conradie, S.R., Kearney, M.R., Wolf, B.O., Cunningham, S.J., Freeman, M.T., Kemp, R. & McKechnie, A.E. 2023. An evaluation of a biophysical model for predicting avian thermoregulation in the heat. *Journal of Experimental Biology*. 226(15):jeb245066. DOI: 10.1242/jeb.245066.
- Cook, T.R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., Meyer, C., Sparks, E., Underhill, L.G., et al. 2020. Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conservation Physiology*. 8(1):coz109. DOI: 10.1093/conphys/coz109.
- Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A. & Griffin, A.S. 2017. Cooperation facilitates the colonization of harsh environments. *Nature Ecology & Evolution*. 1(3):0057. DOI: 10.1038/s41559-016-0057.
- Corregidor-Castro, A. & Jones, O. 2021. The effect of nest temperature on growth and survival in juvenile Great Tits *Parus major*. *Ecology and Evolution*. (May, 1):1–8. DOI: 10.1002/ece3.7565.
- Corregidor-Castro, A., Morinay, J., McKinlay, S.E., Ramellini, S., Assandri, G., Bazzi, G., Glavaschi, A., De Capua, E.L., et al. 2023. Experimental nest cooling reveals dramatic effects of heatwaves on reproduction in a Mediterranean bird of prey. *Global Change Biology*. 29(19):5552–5567. DOI: 10.1111/gcb.16888.
- Coulson, B. 2023. Physiological avenues of heat dissipation in Afrotropical forest hornbills. Unpublished masters thesis. University of Pretoria.
- Coulson, B., Freeman, M.T., Conradie, S.R. & McKechnie, A.E. 2025. Increases in humidity will intensify lethal hyperthermia risk for birds occupying humid lowlands. *Conservation Physiology*. 13(1). DOI: 10.1093/conphys/coaf036.
- Coumou, D. & Rahmstorf, S. 2012. A decade of weather extremes. *Nature Climate Change*. 2(7):491–496. DOI: 10.1038/nclimate1452.
- Covas, R., du Plessis, M.A. & Doutrelant, C. 2008. Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behavioral Ecology and Sociobiology*. 63(1):103–112. DOI: 10.1007/s00265-008-0640-2.
- Crick, H.Q.P. 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis*. 134(1):56–61. DOI: 10.1111/j.1474-919X.1992.tb07230.x.
- Criscuolo, F., Bize, P., Nasir, L., Metcalfe, N.B., Foote, C.G., Griffiths, K., Gault, E.A. & Monaghan, P. 2009. Real-time quantitative PCR assay for measurement of avian

- telomeres. *Journal of Avian Biology*. 40(3):342–347. DOI: 10.1111/j.1600-048X.2008.04623.x.
- Criscuolo, F., Torres, R., Zahn, S. & Williams, T.D. 2020. Telomere dynamics from hatching to sexual maturity and maternal effects in the ‘multivariate egg’. *Journal of Experimental Biology*. 223(23):jeb232496. DOI: 10.1242/jeb.232496.
- Cunningham, S.J., Martin, R.O., Hojem, C.L. & Hockey, P.A.R. 2013. Temperatures in excess of critical thresholds threaten nestling growth and survival in a rapidly-warming arid savanna: a study of common fiscals. *PLoS ONE*. 8(9):e74613. DOI: 10.1371/journal.pone.0074613.
- Cunningham, S.J., Martin, R.O. & Hockey, P.A. 2015. Can behaviour buffer the impacts of climate change on an arid-zone bird? *Ostrich*. 86(1–2): 119–126. DOI: 10.2989/00306525.2015.1016469.
- Cunningham, S.J., Gardner, J.L. & Martin, R.O. 2021. Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*. 19(5):300–307. DOI: 10.1002/fee.2324.
- Czenze, Z.J., Kemp, R., van Jaarsveld, B., Freeman, M.T., Smit, B., Wolf, B.O. & McKechnie, A.E. 2020. Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. *Functional Ecology*. 34(8):1589–1600. DOI: 10.1111/1365-2435.13573.
- D’Amelio, P.B., Ferreira, A.C., Fortuna, R., Paquet, M., Silva, L.R., Theron, F., Doutrelant, C. & Covas, R. 2022. Disentangling climatic and nest predator impact on reproductive output reveals adverse high-temperature effects regardless of helper number in an arid-region cooperative bird. *Ecology Letters*. 25(1):151–162. DOI: 10.1111/ele.13913.
- Dantzer, B. & Fletcher, Q.E. 2015. Telomeres shorten more slowly in slow-aging wild animals than in fast-aging ones. *Experimental Gerontology*. 71:38–47. DOI: 10.1016/j.exger.2015.08.012.
- Davis, L.S., Renner, M., Houston, D., Zhu, L., Finkler, W. & Mattern, T. 2022. The breeding biology of erect-crested penguins, *Eudyptes sclateri*: hormones, behavior, obligate brood reduction and conservation. *PLOS ONE*. 17(10):e0275106. DOI: 10.1371/journal.pone.0275106.
- Dawson, R.D. & Clark, R.G. 2000. Effects of hatching date and egg size on growth, recruitment, and adult size of lesser scaup. *The Condor*. 102(4):930–935. DOI: 10.1093/condor/102.4.930.
- Dawson, R.D., Lawrie, C.C. & O’Brien, E.L. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia*. 144(3):499–507. DOI: 10.1007/s00442-005-0075-7.

- Dean, W.R.J. & Milton, S.J. 2001. Responses of birds to rainfall and seed abundance in the southern Karoo, South Africa. *Journal of Arid Environments*. 47(1):101–121. DOI: 10.1006/jare.2000.0693.
- Dehnhard, N., Eens, M., Demongin, L., Quillfeldt, P., Suri, D. & Poisbleau, M. 2015. Limited individual phenotypic plasticity in the timing of and investment into egg laying in southern rockhopper penguins under climate change. *Marine Ecology Progress Series*. 524:269–281. DOI: 10.3354/meps11154.
- Diehl, J.N., Alton, L.A., White, C.R. & Peters, A. 2023. Thermoregulatory strategies of songbird nestlings reveal limited capacity for cooling and high risk of dehydration. *Journal of Thermal Biology*. 103707. DOI: 10.1016/j.jtherbio.2023.103707.
- Dixit, T., English, S. & Lukas, D. 2017. The relationship between egg size and helper number in cooperative breeders: a meta-analysis across species. *PeerJ*. 5:e4028. DOI: 10.7717/peerj.4028.
- Dorado-Correa, A.M., Zollinger, S., Heidinger, B. & Brumm, H. 2018. Timing matters: traffic noise accelerates telomere loss rate differently across developmental stages. *Frontiers in Zoology*. 15(29). DOI: <https://doi.org/10.1186/s12983-018-0275-8>.
- Dunn, E.H. 1975. The Timing of Endothermy in the Development of Altricial Birds. *The Condor*. 77(3):288–293.
- Dupont, S.M., Barbraud, C., Chastel, O., Delord, K., Ruault, S., Weimerskirch, H. & Angelier, F. 2018. Young parents produce offspring with short telomeres: a study in a long-lived bird, the black-browed albatross (*Thalassarche melanophrys*). *PLOS ONE*. 13(3):e0193526. DOI: 10.1371/journal.pone.0193526.
- Dupont, S.M., Barbraud, C., Chastel, O., Delord, K., Pallud, M., Parenteau, C., Weimerskirch, H. & Angelier, F. 2023. How does maternal age influence reproductive performance and offspring phenotype in the snow petrel (*Pagodroma nivea*)? *Oecologia*. 203(1–2):63–78. DOI: 10.1007/s00442-023-05451-5.
- van Dyk, M., Noakes, M.J. & McKechnie, A.E. 2019. Interactions between humidity and evaporative heat dissipation in a passerine bird. *Journal of Comparative Physiology B*. 189(2):299–308. DOI: 10.1007/s00360-019-01210-2.
- Eastwood, J.R., Hall, M.L., Teunissen, N., Kingma, S.A., Hidalgo Aranzamendi, N., Fan, M., Roast, M., Verhulst, S., et al. 2019. Early-life telomere length predicts lifespan and lifetime reproductive success in a wild bird. *Molecular Ecology*. 28(5):1127–1137. DOI: 10.1111/mec.15002.
- Eastwood, J.R., Connallon, T., Delhey, K., Hall, M.L., Teunissen, N., Kingma, S.A., La Porte, A.M., Verhulst, S., et al. 2022. Hot and dry conditions predict shorter nestling telomeres in an endangered songbird: Implications for population persistence. *PNAS*. 119(25). DOI: 10.1073/pnas.2122944119.

- Eastwood, J.R., Dupoué, A., Verhulst, S., Cockburn, A. & Peters, A. 2023. Cool, dry nights and short heatwaves during growth result in longer telomeres in temperate songbird nestlings. *Molecular Ecology*. 32(19):5382–5393. DOI: 10.1111/mec.17107.
- Edwards, T.C. & Collopy, M.W. 1983. Obligate and facultative brood reduction in eagles: An examination of factors that influence fratricide. *The Auk*. 100(3):630–635. DOI: 10.1093/auk/100.3.630.
- Engelbrecht, D., De Waal, D., Du Ploy, D., Theron, N., Turner, A. & Wilkinson, S. 2007. Growth curve analysis of hand-reared southern and northern ground hornbill nestlings. *Proceedings of the 4th International Hornbill Conference, Mabula Game Lodge, Bela-Bela, South Africa. Naturalists & Nomads, Pretoria*. 397–401.
- Engelbrecht, F., Adegoke, J., Bopape, M.-J., Naidoo, M., Garland, R., Thatcher, M., McGregor, J., Katzfey, J., et al. 2015. Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters*. 10(8):085004. DOI: 10.1088/1748-9326/10/8/085004.
- Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*. 79(5):1781–1788. DOI: 10.1890/0012-9658(1998)079%5B1781:OTCORI%5D2.0.CO;2.
- Estevo, C.A., Stralberg, D., Nielsen, S.E. & Bayne, E. 2022. Topographic and vegetation drivers of thermal heterogeneity along the boreal–grassland transition zone in western Canada: Implications for climate change refugia. *Ecology and Evolution*. 12(6):e9008. DOI: 10.1002/ece3.9008.
- Evans, R.M. 1997. Parental investment and quality of insurance offspring in an obligate brood-reducing species, the American white pelican. *Behavioral Ecology*. 8(4):378–383. DOI: 10.1093/beheco/8.4.378.
- Falvo, C.A., Koons, D.N. & Aubry, L.M. 2019. Seasonal climate effects on the survival of a hibernating mammal. *Ecology and Evolution*. 9(7):3756–3769. DOI: 10.1002/ece3.5000.
- Fisher, M.O., Nager, R.G. & Monaghan, P. 2006. Compensatory growth impairs adult cognitive performance. *PLOS Biology*. 4(8):e251. DOI: 10.1371/journal.pbio.0040251.
- Forbes, L.S. 1990. Insurance offspring and the evolution of avian clutch size. *Journal of Theoretical Biology*. 147(3):345–359. DOI: 10.1016/S0022-5193(05)80492-8.
- Fortuna, R., Paquet, M., Ferreira, A.C., Silva, L.R., Theron, F., Doutrelant, C. & Covas, R. 2021. Maternal allocation in relation to weather, predation and social factors in a colonial cooperative bird. *Journal of Animal Ecology*. 90(5):1122–1133. DOI: 10.1111/1365-2656.13438.
- Fortuna, R., Paquet, M., Biard, C., Élard, L., Ferreira, A.C., Leroux-Coyaux, M., Parenteau, C., Silva, L.R., et al. 2023. Egg components and offspring survival vary with group size and laying order in a cooperative breeder. *Oecologia*. 202(1):129–142. DOI: 10.1007/s00442-023-05379-w.

- Fox, J., Weisberg, S. & Price, B. 2025. *car: Companion to Applied Regression. R Package version No. 3.1-3*. Available: <https://CRAN.R-project.org/package=car> [2025, August 05].
- Fragueira, R., Verhulst, S. & Beaulieu, M. 2019. Morph- and sex-specific effects of challenging conditions on maintenance parameters in the Gouldian finch. *Journal of Experimental Biology*. 222(7):jeb196030. DOI: 10.1242/jeb.196030.
- Francis, A.M., Hailman, J.P. & Woolfenden, G.E. 1989. Mobbing by Florida scrub jays: behaviour, sexual asymmetry, role of helpers and ontogeny. *Animal Behaviour*. 38(5):795–816. DOI: 10.1016/S0003-3472(89)80112-5.
- Freeman, M., Czenze, Z., Schoeman, K. & McKechnie, A. 2022. Adaptive variation in the upper limits of avian body temperature. *Proceedings of the National Academy of Sciences*. 119(26). DOI: 10.1073/pnas.2116645119.
- Fuller, A., Dawson, T., Helmuth, B., Hetem, R.S., Mitchell, D. & Maloney, S.K. 2010. Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*. 83(5):713–720. DOI: 10.1086/652242.
- Fuller, A., Mitchell, D., Maloney, S.K., Hetem, R.S., Fonsêca, V.F.C., Meyer, L.C.R., Van De Ven, T.M.F.N. & Snelling, E.P. 2021. How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water. *Journal of Experimental Biology*. 224(Suppl_1). DOI: 10.1242/jeb.238113.
- Garcia-Heras, M.-S., Mougeot, F., Simmons, R.E. & Arroyo, B. 2017. Regional and temporal variation in diet and provisioning rates suggest weather limits prey availability for an endangered raptor. *Ibis*. 159(3):567–579. DOI: 10.1111/ibi.12478.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. 2011. Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*. 26(6):285–291. DOI: 10.1016/j.tree.2011.03.005.
- Gardner, J.L., Amano, T., Sutherland, W.J., Clayton, M. & Peters, A. 2016. Individual and demographic consequences of reduced body condition following repeated exposure to high temperatures. *Ecology*. 97(3):786–795. DOI: 10.1890/15-0642.1.
- Gardner, J.L., Rowley, E., De Rebeira, P., De Rebeira, A. & Brouwer, L. 2017. Effects of extreme weather on two sympatric Australian passerine bird species. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 372(1723). DOI: 10.1098/rstb.2016.0148.
- Gardner, J.L., Clayton, M., Allen, R., Stein, J. & Bonnet, T. 2022. The effects of temperature extremes on survival in two semi-arid Australian bird communities over three decades, with predictions to 2104. *Global Ecology and Biogeography*. 31(12):2498–2509. DOI: 10.1111/geb.13591.
- Gargett, V. 1977. A 13-year population study of the black eagles in the Matopos, Rhodesia, 1964–1976. *Ostrich*. 48(1–2):17–27. DOI: 10.1080/00306525.1977.9634075.

- Gaynor, K.M., Brown, J.S., Middleton, A.D., Power, M.E. & Brashares, J.S. 2019. Landscapes of fear: spatial patterns of risk perception and response. *Trends in Ecology & Evolution*. 34(4):355–368. DOI: 10.1016/j.tree.2019.01.004.
- Gertenbach, W.P.D. 1983. Landscapes of the Kruger National Park. *Koedoe*. 26(1):9–121. DOI: 10.4102/koedoe.v26i1.591.
- Ghalambor, C.K. & Martin, T.E. 2001. Fecundity-survival trade-offs and parental risk-taking in birds. *Science*. 292(5516):494–497. DOI: 10.1126/science.1059379.
- Ghavi Hossein-Zadeh, N. 2025. Comparison of nonlinear models for describing the growth curve of pekin ducks. *Veterinary Medicine and Science*. 11(2):e70268. DOI: 10.1002/vms3.70268.
- Gienapp, P. & Bregnballe, T. 2012. Fitness consequences of timing of migration and breeding in cormorants. *PLoS ONE*. 7(9):e46165. DOI: 10.1371/journal.pone.0046165.
- Gladbach, A., Gladbach, D.J. & Quillfeldt, P. 2010. Seasonal clutch size decline and individual variation in the timing of breeding are related to female body condition in a non-migratory species, the upland goose *Chloephaga picta leucoptera*. *Journal of Ornithology*. 151(4):817–825. DOI: 10.1007/s10336-010-0518-8.
- Golabek, K.A., Ridley, A.R. & Radford, A.N. 2012. Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird. *Animal Behaviour*. 83(3):613–619. DOI: 10.1016/j.anbehav.2011.11.034.
- Gonzalez, J.C.T., Sheldon, B.C. & Tobias, J.A. 2013. Environmental stability and the evolution of cooperative breeding in hornbills. *Proceedings of the Royal Society B: Biological Sciences*. 280(1768). DOI: 10.1098/rspb.2013.1297.
- Green, D.J. & Cockburn, A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. *Journal of Animal Ecology*. 70(3):505–514. DOI: 10.1046/j.1365-2656.2001.00503.x.
- Greño, J.L., Belda, E.J. & Barba, E. 2008a. Influence of temperatures during the nestling period on post-fledging survival of great tit *Parus major* in a Mediterranean habitat. *Journal of Avian Biology*. 39(1):41–49. DOI: 10.1111/j.0908-8857.2008.04120.x.
- Griesser, M., Wagner, G.F., Drobniak, S.M. & Ekman, J. 2017a. Reproductive trade-offs in a long-lived bird species: condition-dependent reproductive allocation maintains female survival and offspring quality. *Journal of Evolutionary Biology*. 30(4):782–795. DOI: 10.1111/jeb.13046.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Molecular Ecology*. 7(8):1071–1075. DOI: 10.1046/j.1365-294x.1998.00389.x.
- Griffiths, S., Lentini, P., Semmens, K., Watson, S., Lumsden, L. & Robert, K. 2018. Chainsaw-carved cavities better mimic the thermal properties of natural tree hollows than nest boxes and log hollows. *Forests*. 9(5):235. DOI: 10.3390/f9050235.

- Groenewoud, F. & Clutton-Brock, T. 2021. Meerkat helpers buffer the detrimental effects of adverse environmental conditions on fecundity, growth and survival. *Journal of Animal Ecology*. 90(3):641–652. DOI: 10.1111/1365-2656.13396.
- Groothuis, T.G.G., Müller, W., von Engelhardt, N., Carere, C. & Eising, C. 2005. Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience & Biobehavioral Reviews*. 29(2):329–352. DOI: 10.1016/j.neubiorev.2004.12.002.
- Grunst, M.L., Grunst, A.S., Pinxten, R. & Eens, M. 2020. Anthropogenic noise is associated with telomere length and carotenoid-based coloration in free-living nestling songbirds. *Environmental Pollution*. 260:114032. DOI: 10.1016/j.envpol.2020.114032.
- Hall, M.E., Nasir, L., Daunt, F., Gault, E.A., Croxall, J.P., Wanless, S. & Monaghan, P. 2004. Telomere loss in relation to age and early environment in long-lived birds. *Proc R Soc B*. 271(1548). DOI: 10.1098/rspb.2004.2768.
- Halupka, L., Arlt, D., Tolvanen, J., Millon, A., Bize, P., Adamík, P., Albert, P., Arendt, W.J., et al. 2023. The effect of climate change on avian offspring production: A global meta-analysis. *Proceedings of the National Academy of Sciences*. 120(19):e2208389120. DOI: 10.1073/pnas.2208389120.
- Hansson, A., Wapstra, E., While, G.M. & Olsson, M. 2024. Sex and early-life conditions shape telomere dynamics in an ectotherm. *Journal of Experimental Biology*. 227(3):jeb246512. DOI: 10.1242/jeb.246512.
- Hardison, E.A. & Eliason, E.J. 2024. Diet effects on ectotherm thermal performance. *Biological Reviews*. 99(4):1537–1555. DOI: 10.1111/brv.13081.
- Hargitai, R., Török, J., Tóth, L., Hegyi, G., Rosivall, B., Szigeti, B. & Szöllösi, E. 2005. Effects of environmental conditions and parental quality on inter- and intracatch egg-size variation in the collared flycatcher (*Ficedula albicollis*). *The Auk*. 122(2):509–522.
- Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*. 80(1):4–18. DOI: 10.1111/j.1365-2656.2010.01740.x.
- Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E.D., Robinson, B.S., Hodgson, D.J., et al. 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*. 6:e4794. DOI: 10.7717/peerj.4794.
- Hatchwell, B.J. 1999. Investment strategies of breeders in avian cooperative breeding systems. *The American Naturalist*. 154(2):205–219. DOI: 10.1086/303227.
- Hatchwell, B.J. & Russell, A.F. 1996. Provisioning rules in cooperatively breeding long-tailed tits *Aegithalos caudatus*: an experimental study. *Proceedings of the Royal Society B: Biological Sciences*. 263(1366):83–88. DOI: 10.1098/rspb.1996.0014.
- Hausmann, M.F., Winkler, D.W., O'Reilly, K.M., Huntington, C.E., Nisbet, I.C.T. & Vleck, C.M. 2003. Telomeres shorten more slowly in long-lived birds and mammals than in

- short-lived ones. *Proceedings of the Royal Society of London. Series B: Biological Sciences*. 270(1522):1387–1392. DOI: 10.1098/rspb.2003.2385.
- Haussmann, M.F., Vleck, C.M. & Nisbet, I.C.T. 2003. Calibrating the telomere clock in common terns, *Sterna hirundo*. *Experimental Gerontology*. 38(7):787–789. DOI: 10.1016/S0531-5565(03)00109-8.
- Haussmann, M.F., Winkler, D.W., Huntington, C.E., Nisbet, I.C.T. & Vleck, C.M. 2007. Telomerase activity is maintained throughout the lifespan of long-lived birds. *Experimental Gerontology*. 42(7):610–618. DOI: 10.1016/j.exger.2007.03.004.
- Haussmann, M.F., Longenecker, A.S., Marchetto, N.M., Juliano, S.A. & Bowden, R.M. 2012. Embryonic exposure to corticosterone modifies the juvenile stress response, oxidative stress and telomere length. *Proceedings of the Royal Society B: Biological Sciences*. 279(1732):1447–1456. DOI: 10.1098/rspb.2011.1913.
- Haynes, G. 2012. Elephants (and extinct relatives) as earth-movers and ecosystem engineers. *Geomorphology*. 157–158:99–107. DOI: 10.1016/j.geomorph.2011.04.045.
- Heers, A.M. & Dial, K.P. 2015. Wings versus legs in the avian bauplan: Development and evolution of alternative locomotor strategies. *Evolution*. 69(2):305–320. DOI: 10.1111/evo.12576.
- Heidinger, B.J., Blount, J.D., Boner, W., Griffiths, K., Metcalfe, N.B. & Monaghan, P. 2012. Telomere length in early life predicts lifespan. *Proceedings of the National Academy of Sciences*. 109(5):1743–1748. DOI: 10.1073/pnas.1113306109.
- Heidinger, B.J., Kucera, A.C., Kittilson, J.D. & Westneat, D.F. 2021. Longer telomeres during early life predict higher lifetime reproductive success in females but not males. *Proceedings of the Royal Society B: Biological Sciences*. 288(1951):20210560. DOI: 10.1098/rspb.2021.0560.
- Heissenberger, S., De Pinho, G.M., Martin, J.G.A. & Blumstein, D.T. 2020. Age and location influence the costs of compensatory and accelerated growth in a hibernating mammal. *Behavioral Ecology*. 31(3):826–833. DOI: 10.1093/beheco/araa013.
- Hickinbotham, E.J., Ridley, F.A., Rushton, S.P. & Pattison, Z. 2025. 30 years of climate related phenological research: themes and trends. *International Journal of Biometeorology*. 69(6):1459–1473. DOI: 10.1007/s00484-025-02903-w.
- Hidalgo Aranzamendi, N., Hall, M.L., Kingma, S.A., van de Pol, M. & Peters, A. 2019. Rapid plastic breeding response to rain matches peak prey abundance in a tropical savanna bird. *Journal of Animal Ecology*. 88(11):1799–1811. DOI: 10.1111/1365-2656.13068.
- Hipfner, J.M., Gaston, A.J. & de Forest, L.N. 1997. The role of female age in determining egg size and laying date of thick-billed murres. *Journal of Avian Biology*. 28(4):271–278. DOI: 10.2307/3676939.
- Holmes, S.M., Dressel, S., Morel, J., Spitzer, R., Ball, J.P., Ericsson, G., Singh, N.J., Widemo, F., et al. 2023. Increased summer temperature is associated with reduced calf mass of a

- circumpolar large mammal through direct thermoregulatory and indirect, food quality, pathways. *Oecologia*. 201(4):1123–1136. DOI: 10.1007/s00442-023-05367-0.
- Holt, K.A. & Boersma, P.D. 2022. Unprecedented heat mortality of Magellanic penguins. *Ornithological Applications*. 124(1):duab052. DOI: 10.1093/ornithapp/duab052.
- Honey, R., McLean, C., Murray, B.R. & Webb, J.K. 2021. Insulated nest boxes provide thermal refuges for wildlife in urban bushland during summer heatwaves. *Journal of Urban Ecology*. 7(1):juab032. DOI: 10.1093/jue/juab032.
- Hope, S.F., Angelier, F., Ribout, C., Groffen, J., Kennamer, R.A. & Hopkins, W.A. 2022. Warmer incubation temperatures and later lay-orders lead to shorter telomere lengths in wood duck (*Aix sponsa*) ducklings. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology*. 339(1):101–111. DOI: 10.1002/jez.2659.
- Horn, T., Robertson, B.C. & Gemmell, N.J. 2010. The use of telomere length in ecology and evolutionary biology. *Heredity*. 105(6):497–506. DOI: 10.1038/hdy.2010.113.
- Horn, T., Robertson, B.C., Will, M., Eason, D.K., Elliott, G.P. & Gemmell, N.J. 2011. Inheritance of telomere length in a bird. *PLOS ONE*. 6(2):e17199. DOI: 10.1371/journal.pone.0017199.
- Hovenden, M.J. & Williams, A.L. 2010. The impacts of rising CO₂ concentrations on Australian terrestrial species and ecosystems. *Austral Ecology*. 35(6):665–684. DOI: 10.1111/j.1442-9993.2009.02074.x.
- Hoyt, D.F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. *The Auk*. 97:73–77.
- Humphries, D.J., Nelson-Flower, M.J., Bell, M.B.V., Finch, F.M. & Ridley, A.R. 2021. Kinship, dear enemies, and costly combat: The effects of relatedness on territorial overlap and aggression in a cooperative breeder. *Ecology and Evolution*. 11(23):16365–17567. DOI: 10.1002/ece3.8342.
- Iknayan, K.J. & Beissinger, S.R. 2018. Collapse of a desert bird community over the past century driven by climate change. *Proceedings of the National Academy of Sciences*. 115(34):8597–8602. DOI: 10.1073/pnas.1805123115.
- IPCC. 2023. *Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, H. Lee and J. Romero (eds.)]*. IPCC, Geneva, Switzerland. Intergovernmental Panel on Climate Change (IPCC). DOI: 10.59327/IPCC/AR6-9789291691647.
- IUCN. 2024. *IUCN*. Available: <https://www.iucnredlist.org/en> [2022, July 22].
- van Jaarsveld, B., Bennett, N.C., Czenze, Z.J., Kemp, R., van de Ven, T.M.F.N., Cunningham, S.J. & McKechnie, A.E. 2021. How hornbills handle heat: sex-specific thermoregulation in the southern yellow-billed hornbill. *Journal of Experimental Biology*. 224(4):jeb232777. DOI: 10.1242/jeb.232777.

- Janecke, B.B. & Bolton, J.G. 2020. Variation in mammal diversity and habitat affect heterogeneity and processes of a granite catena. *KOEDOE - African Protected Area Conservation and Science*. 62(2). DOI: 10.4102/koedoe.v62i2.1592.
- Jetz, W. & Rubenstein, D.R. 2011. Environmental Uncertainty and the Global Biogeography of Cooperative Breeding in Birds. *Current Biology*. 21(1):72–78. DOI: 10.1016/j.cub.2010.11.075.
- Jezkova, T. & Wiens, J.J. 2016. Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. *Proceedings of the Royal Society B: Biological Sciences*. 283(1843):20162104. DOI: 10.1098/rspb.2016.2104.
- John, A., Olden, J.D., Oldfather, M.F., Kling, M.M. & Ackerly, D.D. 2024. Topography influences diurnal and seasonal microclimate fluctuations in hilly terrain environments of coastal California. *PLoS ONE*. 19(3):e0300378. DOI: 10.1371/journal.pone.0300378.
- Jones, T.M. & Ward, M.P. 2020. Pre- to post-fledging carryover effects and the adaptive significance of variation in wing development for juvenile songbirds. *Journal of Animal Ecology*. 89(10):2235–2245. DOI: 10.1111/1365-2656.13285.
- Josi, D., Taborsky, M. & Frommen, J.G. 2020. Investment of group members is contingent on helper number and the presence of young in a cooperative breeder. *Animal Behaviour*. 160:35–42. DOI: 10.1016/j.anbehav.2019.11.013.
- Kemp, A.C. 1974. Factors affecting the onset of breeding in African hornbills. *Proceedings of the 16th International Ornithological Congress*. 10.
- Kemp, A.C. 1980. The biology of the southern ground hornbill *Bucorvus leadbeateri* (Vigors) (aves: *Bucerotidae*). *Annals of the Transvaal Museum*. (32(4):65–100.).
- Kemp, A.C. 1988. The behavioural ecology of the southern ground hornbill: are competitive offspring at a premium? *Proceedings of the 16th International Ornithological Congress*. 10:3.
- Kemp, A.C. & Begg, K.S. 1996. Nest sites of the southern ground hornbill *Bucorvus leadbeateri* in the Kruger National Park, South Africa, and conservation implications. *Ostrich*. 67(1). DOI: 10.1080/00306525.1996.9633773.
- Kemp, L. & Rose, S. 2025. *The 2025 Red Data Book of Birds of South Africa, Lesotho and Eswatini*. Johannesburg, South Africa: BirdLife South Africa. Available: <https://www.birdlife.org.za/red-list/southern-ground-hornbill/> [2025, July 01].
- Kemp, L.V., Kotze, A., Jansen, R., Dalton, D.L., Grobler, P. & Little, R.M. 2020. Review of trial reintroductions of the long-lived, cooperative breeding southern ground-hornbill. *Bird Conservation International*. 30(4):533–558. DOI: 10.1017/S0959270920000131.
- Khera, M., Arbuckle, K., Mwanguhya, F., Kyabulima, S., Mwesige, K., Businge, R., Blount, J.D., Cant, M.A., et al. 2023. Small increases in ambient temperature reduce offspring body mass in an equatorial mammal. *Biology Letters*. 19(11):20230328. DOI: 10.1098/rsbl.2023.0328.

- Kingma, S.A. 2017. Direct benefits explain interspecific variation in helping behaviour among cooperatively breeding birds. *Nature Communications*. 8(1):1094. DOI: 10.1038/s41467-017-01299-5.
- Kingma, S.A., Hall, M.L., Arriero, E. & Peters, A. 2010. Multiple benefits of cooperative breeding in purple-crowned fairy-wrens: a consequence of fidelity? *Journal of Animal Ecology*. 79(4):757–768. DOI: 10.1111/j.1365-2656.2010.01697.x.
- Kingsolver, J.G. & Buckley, L.B. 2017. Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Philosophical Transactions of the Royal Society B: Biological Sciences*. DOI: 10.1098/rstb.2016.0147.
- Koenig, W.D., Walters, E.L. & Haydock, J. 2009. Helpers and egg investment in the cooperatively breeding acorn woodpecker: testing the concealed helper effects hypothesis. *Behavioral Ecology and Sociobiology*. 63(11):1659–1665. DOI: 10.1007/s00265-009-0773-y.
- Krist, M. 2011. Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews*. 86(3):692–716. DOI: 10.1111/j.1469-185X.2010.00166.x.
- Labocha, M.K. & Hayes, J.P. 2012. Morphometric indices of body condition in birds: a review. *Journal of Ornithology*. 153(1):1–22. DOI: 10.1007/s10336-011-0706-1.
- Lamb, J.S., O'Reilly, K.M. & Jodice, P.G.R. 2016. Physical condition and stress levels during early development reflect feeding rates and predict pre- and post-fledging survival in a nearshore seabird. *Conservation Physiology*. 4(1):cow060. DOI: 10.1093/conphys/cow060.
- Langmore, N.E., Bailey, L.D., Heinsohn, R.G., Russell, A.F. & Kilner, R.M. 2016. Egg size investment in superb fairy-wrens: helper effects are modulated by climate. *Proceedings of the Royal Society B: Biological Sciences*. 283(1843):20161875. DOI: 10.1098/rspb.2016.1875.
- Larson, E.R., Eastwood, J.R., Buchanan, K.L., Bennett, A.T.D. & Berg, M.L. 2015. How does nest-box temperature affect nestling growth rate and breeding success in a parrot? *Emu - Austral Ornithology*. 115(3):247–255. DOI: 10.1071/MU14081.
- Latest Sightings. 2025. Available: <https://www.latestsightings.com/> [2025, July 21].
- Lefcheck, J.S. 2016. PIECEWISESEM : Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*. 7(5):573–579. DOI: 10.1111/2041-210X.12512.
- Legge, S. 2000. Helper contributions in the cooperatively breeding laughing kookaburra: feeding young is no laughing matter. *Animal Behaviour*. 59(5):1009–1018. DOI: 10.1006/anbe.2000.1382.
- Lejeune, L., Van De Pol, M., Cockburn, A., Louter, M. & Brouwer, L. 2016. Male and female helper effects on maternal investment and adult survival in red-winged fairy-wrens. *Behavioral Ecology*. 27(6):1841–1850. DOI: 10.1093/beheco/arw121.

- Lepage, D. & Lloyd, P. 2004. Avian clutch size in relation to rainfall seasonality and stochasticity along an aridity gradient across South Africa. *Ostrich*. 75(4):259–268. DOI: 10.2989/00306520409485453.
- Levillain, A., Reichert, S. & Massemin, S. 2025. The complex relationship between high temperatures and avian breeding success: insights from a global review. *Ecology and Evolution*. 15(8):e71771. DOI: 10.1002/ece3.71771.
- Li, Y., Li, S., Guo, C., Zhang, G., Zhou, Y. & Lu, X. 2015. Nest helpers improve parental survival but not offspring production in a high-elevation passerine, the ground tit *Pseudopodoces humilis*. *Ibis*. 157(3):567–574. DOI: 10.1111/ibi.12266.
- Liddle, N., Freeman, M.T., Cunningham, S.J., Conradie, S.R. & McKechnie, A.E. 2025. A heat-sensitive songbird's risk of lethal hyperthermia increases with humidity. *Biology Letters*. 21(10):20250284. DOI: 10.1098/rsbl.2025.0284.
- van Lieshout, S.H.J., Badás, E.P., Bright Ross, J.G., Bretman, A., Newman, C., Buesching, C.D., Burke, T., Macdonald, D.W., et al. 2022. Early-life seasonal, weather and social effects on telomere length in a wild mammal. *Molecular Ecology*. 31(23):5993–6007. DOI: 10.1111/mec.16014.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*. 14(9):343–348. DOI: 10.1016/S0169-5347(99)01639-0.
- Liu, H., Zhan, Q., Gao, S. & Yang, C. 2019. Seasonal variation of the spatially non-stationary association between land surface temperature and urban landscape. *Remote Sensing*. 11(9):1016. DOI: 10.3390/rs11091016.
- Loe, L.E., Liston, G.E., Pigeon, G., Barker, K., Horvitz, N., Stien, A., Forchhammer, M., Getz, W.M., et al. 2021. The neglected season: warmer autumns counteract harsher winters and promote population growth in Arctic reindeer. *Global Change Biology*. 27(5):993–1002. DOI: 10.1111/gcb.15458.
- Loftie-Eaton, M. 2018. Woody Cover and Birds. Unpublished doctoral thesis. University of Cape Town.
- Loidi, J. & Marcenò, C. 2022. The temperate deciduous forests of the northern hemisphere. A review. *Mediterranean Botany*. 43:e75527. DOI: 10.5209/mbot.75527.
- Londe, D.W., Elmore, R.D., Davis, C.A., Fuhlendorf, S.D., Hovick, T.J., Luttbeg, B. & Rutledge, J. 2021. Fine-scale habitat selection limits trade-offs between foraging and temperature in a grassland bird. *Behavioral Ecology*. 32(4). DOI: 10.1093/beheco/arab012.
- Lone, K., Loe, L.E., Gobakken, T., Linnell, J.D.C., Odden, J., Remmen, J. & Mysterud, A. 2014. Living and dying in a multi-predator landscape of fear: roe deer are squeezed by contrasting pattern of predation risk imposed by lynx and humans. *Oikos*. 123(6):641–651. DOI: 10.1111/j.1600-0706.2013.00938.x.

- Louw, A.S., MacFadyen, S., Ferreira, S. & Hui, C. 2021. Erratum: Elephant population responses to increased density in Kruger National Park. *KOEDOE - African Protected Area Conservation and Science*. 63(1). DOI: 10.4102/koedoe.v63i1.1691.
- Luck, G.W. 2001. Variability in provisioning rates to nestlings in the cooperatively breeding Rufous Treecreeper, *Climacteris rufa*. *Emu-Austral Ornithology*. 101:221–224. DOI: 10.1071/MU00028.
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P. & Makowski, D. 2021. performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*. 6(60):3139. DOI: 10.21105/joss.03139.
- Lv, L., van de Pol, M., Osmond, H.L., Liu, Y., Cockburn, A. & Kruuk, L.E.B. 2023. Winter mortality of a passerine bird increases following hotter summers and during winters with higher maximum temperatures. *Science Advances*. 9(1). DOI: 10.1126/sciadv.abm0197.
- MacLeod, K.J. & Brouwer, L. 2018. Social context-dependent provisioning rules in red-winged fairy-wrens do not vary with signals of increased chick need. *Animal Behaviour*. 143:105–111. DOI: 10.1016/j.anbehav.2018.07.010.
- Magrath, R.D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *The Journal of Animal Ecology*. 60(1):335. DOI: 10.2307/5464.
- Mainwaring, M.C. & Hartley, I.R. 2016. Local weather conditions have complex effects on the growth of blue tit nestlings. *Journal of Thermal Biology*. 60:12–19. DOI: 10.1016/j.jtherbio.2016.05.005.
- Malik, T.G., Tsai, M.-T., Jarrett, B.J.M. & Sun, S.-J. 2025. Heat stress effects on offspring compound across parental care. *Proceedings of the Royal Society B: Biological Sciences*. 292(2042):20250026. DOI: 10.1098/rspb.2025.0026.
- Marasco, V., Smith, S. & Angelier, F. 2022. How does early-life adversity shape telomere dynamics during adulthood? Problems and paradigms. *BioEssays*. 44(2). DOI: 10.1002/bies.202100184.
- Mares, R., Doutrelant, C., Paquet, M., Spottiswoode, C.N. & Covas, R. 2017. Breeding decisions and output are correlated with both temperature and rainfall in an arid-region passerine, the sociable weaver. *Royal Society Open Science*. 4(9):170835. DOI: 10.1098/rsos.170835.
- Margalida, A., Bertran, J., Boudet, J. & Heredia, R. 2004. Hatching asynchrony, sibling aggression and cannibalism in the Bearded Vulture *Gypaetus barbatus*. *Ibis*. 146(3):386–393. DOI: 10.1111/j.1474-919X.2004.00261.x.
- Martin, R.O., Cunningham, S.J. & Hockey, P.A. 2015. Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich*. 86(1–2):127–135. DOI: 10.2989/00306525.2015.1029031.

- Martin, T.E., Tobalske, B., Riordan, M.M., Case, S.B. & Dial, K.P. 2018. Age and performance at fledging are a cause and consequence of juvenile mortality between life stages. *Science Advances*. 4(6):eaar1988. DOI: 10.1126/sciadv.aar1988.
- Martin Bideguren, G., López-Baucells, A., Puig-Montserrat, X., Mas, M., Porres, X. & Flaquer, C. 2019. Bat boxes and climate change: testing the risk of over-heating in the Mediterranean region. *Biodiversity and Conservation*. 28(1):21–35. DOI: 10.1007/s10531-018-1634-7.
- te Marvelde, L., McDonald, P.G., Kazem, A.J.N. & Wright, J. 2009. Do helpers really help? Provisioning biomass and prey type effects on nestling growth in the cooperative bell miner. *Animal Behaviour*. 77(3):727–735. DOI: 10.1016/j.anbehav.2008.12.008.
- Mason, T.H.E., Brivio, F., Stephens, P.A., Apollonio, M. & Grignolio, S. 2017. The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. *Behavioral Ecology*. 28(3):908–918. DOI: 10.1093/beheco/arx057.
- Massetti, L., Petralli, M., Napoli, M., Brandani, G., Orlandini, S. & Pearlmutter, D. 2019. Effects of deciduous shade trees on surface temperature and pedestrian thermal stress during summer and autumn. *International Journal of Biometeorology*. 63(4):467–479. DOI: 10.1007/s00484-019-01678-1.
- Mbokodo, I., Bopape, M.J., Chikoore, H., Engelbrecht, F. & Nethengwe, N. 2020. Heatwaves in the future warmer climate of South Africa. *Atmosphere*. 11(7):1–18. DOI: 10.3390/atmos11070712.
- McCaffery, R.M. & Maxell, B.A. 2010. Decreased winter severity increases viability of a montane frog population. *Proceedings of the National Academy of Sciences*. 107(19):8644–8649. DOI: 10.1073/pnas.0912945107.
- Mccarty, J.P. & Winkler, D.W. 1999. Relative importance off environmental variables in determining the growth off nestling tree swallows *Tachycineta bicolor*. *Ibis*. 141(2):286–296. DOI: 10.1111/j.1474-919X.1999.tb07551.x.
- McKechnie, A.E. & Wolf, B.O. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*. 6(2):253–256. DOI: 10.1098/rsbl.2009.0702.
- McKechnie, A.E. & Wolf, B.O. 2019. The physiology of heat tolerance in small endotherms. *Physiology*. 34(5):302–313. DOI: 10.1152/physiol.00011.2019.
- McKechnie, A.E., Rushworth, I.A., Myburgh, F. & Cunningham, S.J. 2021. Mortality among birds and bats during an extreme heat event in eastern South Africa. *Austral Ecology*. 46(4):687–691. DOI: 10.1111/aec.13025.
- McKechnie, A.E., Gerson, A.R. & Wolf, B.O. 2021. Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *Journal of Experimental Biology*. 224(Suppl_1):jeb229211. DOI: 10.1242/jeb.229211.

- Meade, J., Nam, K.-B., Beckerman, A.P. & Hatchwell, B.J. 2010. Consequences of ‘load-lightening’ for future indirect fitness gains by helpers in a cooperatively breeding bird. *Journal of Animal Ecology*. 79(3):529–537. DOI: 10.1111/j.1365-2656.2009.01656.x.
- Mentesana, L., Hau, M., D’Amelio, P.B., Adreani, N.M. & Sánchez-Tójar, A. 2025. Do egg hormones have fitness consequences in wild birds? A systematic review and meta-analysis. *Ecology Letters*. 28(3):e70100. DOI: 10.1111/ele.70100.
- Metcalfe, N.B. & Monaghan, P. 2001. Compensation for a bad start: Grow now, pay later? *Trends in Ecology and Evolution*. 16(5):254–260. DOI: 10.1016/S0169-5347(01)02124-3.
- Metcalfe, N.B. & Monaghan, P. 2003. Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology*. 38(9):935–940. DOI: 10.1016/S0531-5565(03)00159-1.
- Metcalfe, N.B. & Olsson, M. 2022. How telomere dynamics are influenced by the balance between mitochondrial efficiency, reactive oxygen species production and DNA damage. *Molecular Ecology*. 31(23):6040–6052. DOI: 10.1111/mec.16150.
- Middleton, K.-M. 2022. Individual contributions to group behaviour in the southern ground-hornbill (*Bucorvus leadbeateri*). Unpublished doctoral thesis. University of Cape Town.
- Middleton, K.-M., Hickman, C., Spottiswoode, C.N., Rybak, F. & Covas, R. 2026. Hot-dry weather is associated with worse reproductive outcomes regardless of group composition in a long-lived cooperatively breeding bird. *The American Naturalist*. 207(4):000–000. DOI: 10.1086/739305.
- Millán, M.F., Carranza, J., Seoane, J.M. & Pérez-González, J. 2022. Forage quality of consecutive years interact to affect body condition, reproductive rate and rut phenology in Iberian red deer. *PLOS ONE*. 17(12):e0278367. DOI: 10.1371/journal.pone.0278367.
- Mitchell, D., Maloney, S.K., Snelling, E.P., Carvalho Fonsêca, V.D.F. & Fuller, A. 2024. Measurement of microclimates in a warming world: problems and solutions. *Journal of Experimental Biology*. 227(13). DOI: 10.1242/jeb.246481.
- Moagi, L.L., Bourne, A.R., Cunningham, S.J., Jansen, R., Ngcamphalala, C.A., Ganswindt, A., Ridley, A.R. & McKechnie, A.E. 2021. Hot days are associated with short-term adrenocortical responses in a southern African arid-zone passerine bird. *Journal of Experimental Biology*. 224(10):jeb242535. DOI: 10.1242/jeb.242535.
- Mole, M.A., Rodrigues D’Áraujo, S., van Aarde, R.J., Mitchell, D. & Fuller, A. 2016. Coping with heat: behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology*. 4(1):cow044. DOI: 10.1093/conphys/cow044.
- Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 363(1497):1635–1645. DOI: 10.1098/rstb.2007.0011.

- Monaghan, P. & Ozanne, S.E. 2018. Somatic growth and telomere dynamics in vertebrates: relationships, mechanisms and consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 373(1741):20160446. DOI: 10.1098/rstb.2016.0446.
- Monaghan, P., Metcalfe, N.B. & Torres, R. 2009. Oxidative stress as a mediator of life history trade-offs: mechanisms, measurements and interpretation. *Ecology Letters*. 12(1):75–92. DOI: 10.1111/j.1461-0248.2008.01258.x.
- Moreno, J. & Møller, A.P. 2011. Extreme climatic events in relation to global change and their impact on life histories. *Current Zoology*. 57(3):375–389. DOI: 10.1093/czoolo/57.3.375.
- Morin, A., Chamaillé-Jammes, S. & Valeix, M. 2021. Climate effects on prey vulnerability modify expectations of predator responses to short- and long-term climate fluctuations. *Frontiers in Ecology and Evolution*. 8. DOI: 10.3389/fevo.2020.601202.
- Mousseau, T. & Fox, C.W. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution*. 13(10):403–407. DOI: 10.1016/S0169-5347(98)01472-4.
- Mpheshea, L.E., Blamey, R.C. & Reason, C.J.C. 2025. The influence of ENSO-type on rainfall characteristics over southern Africa during the austral summer. *Climate Dynamics*. 63(3):161. DOI: 10.1007/s00382-024-07489-4.
- Nelson-Flower, M.J., Wiley, E.M., Flower, T.P. & Ridley, A.R. 2018. Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance. *Journal of Animal Ecology*. 87(5):1227–1238. DOI: 10.1111/1365-2656.12814.
- Niffenegger, C.A., Dirren, S., Schano, C. & Korner-Nievergelt, F. 2024. Natural nest cavities in a high elevation habitat provide a more constant thermal environment than human-made nest cavities. *Journal of Ornithology*. 165(2):545–549. DOI: 10.1007/s10336-023-02130-3.
- Noguera, J.C., Da Silva, A. & Velando, A. 2022. Egg corticosterone can stimulate telomerase activity and promote longer telomeres during embryo development. *Molecular Ecology*. 31(23):6252–6260. DOI: 10.1111/mec.15694.
- Nord, A. & Giroud, S. 2020. Lifelong effects of thermal challenges during development in birds and mammals. *Frontiers in Physiology*. 11:419. DOI: 10.3389/fphys.2020.00419.
- Nunez, S., Arets, E., Alkemade, R., Verwer, C. & Leemans, R. 2019. Assessing the impacts of climate change on biodiversity: is below 2 °C enough? *Climatic Change*. 154(3):351–365. DOI: 10.1007/s10584-019-02420-x.
- O'Connor, T.G. & Page, B.R. 2014. Simplification of the composition, diversity and structure of woody vegetation in a semi-arid African savanna reserve following the re-introduction of elephants. *Biological Conservation*. 180:122–133. DOI: 10.1016/j.biocon.2014.09.036.

- O'Connor, R.C., Blumenthal, D.M., Ocheltree, T.W. & Nippert, J.B. 2022. Elevated CO₂ counteracts effects of water stress on woody rangeland-encroaching species. *Tree Physiology*. 44(13):46–57. DOI: 10.1093/treephys/tpac150.
- O'Connor, R.S., Wolf, B.O., Brigham, R.M. & McKechnie, A.E. 2017. Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *Journal of Comparative Physiology B*. 187(3):477–491. DOI: 10.1007/s00360-016-1047-4.
- Olson, J.M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. *Physiological Zoology*. 65(1). DOI: 10.1086/physzool.65.1.30158243.
- Ornelas, A., Cordeiro, A. & Lameiras, J.M. 2023. Thermal comfort assessment in urban green spaces: contribution of thermography to the study of thermal variation between tree canopies and air temperature. *Land*. 12(8):1568. DOI: 10.3390/land12081568.
- Osborne, C.P., Charles-Dominique, T., Stevens, N., Bond, W.J., Midgley, G. & Lehmann, C.E.R. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*. 220(1):10–24. DOI: 10.1111/nph.15236.
- Osland, M.J., Stevens, P.W., Lamont, M.M., Brusca, R.C., Hart, K.M., Waddle, J.H., Langtimm, C.A., Williams, C.M., et al. 2021. Tropicalization of temperate ecosystems in North America: The northward range expansion of tropical organisms in response to warming winter temperatures. *Global Change Biology*. 27(13):3009–3034. DOI: 10.1111/gcb.15563.
- Oswald, K.N., Lee, A.T. & Smit, B. 2018. Comparison of physiological responses to high temperatures in juvenile and adult cape rockjumpers *Chaetops frenatus*. *Ostrich*. 89(4):377–382. DOI: 10.2989/00306525.2018.1509905.
- Oswald, K.N., Smit, B., Lee, A.T.K., Peng, C.L., Brock, C. & Cunningham, S.J. 2021. Higher temperatures are associated with reduced nestling body condition in a range-restricted mountain bird. *Journal of Avian Biology*. 52(8). DOI: 10.1111/jav.02756.
- Ozgul, A., Childs, D.Z., Oli, M.K., Armitage, K.B., Blumstein, D.T., Olson, L.E., Tuljapurkar, S. & Coulson, T. 2010. Coupled dynamics of body mass and population growth in response to environmental change. *Nature*. 466(7305):482–485. DOI: 10.1038/nature09210.
- Pakanen, V.-M., Ahonen, E., Hohtola, E. & Rytönen, S. 2018. Northward expanding resident species benefit from warming winters through increased foraging rates and predator vigilance. *Oecologia*. 188(4):991–999. DOI: 10.1007/s00442-018-4271-7.
- Paquet, M., Doutrelant, C., Hatchwell, B.J., Spottiswoode, C.N. & Covas, R. 2015. Antagonistic effect of helpers on breeding male and female survival in a cooperatively breeding bird. *Journal of Animal Ecology*. 84(5):1354–1362. DOI: 10.1111/1365-2656.12377.

- Parker, A.H. & Witkowski, E.T.F. 1999. Long-term impacts of abundant perennial water provision for game on herbaceous vegetation in a semi-arid African savanna woodland. *Journal of Arid Environments*. 41(3):309–321. DOI: 10.1006/jare.1998.0484.
- Parker, E.J., Weiskopf, S.R., Oliver, R.Y., Rubenstein, M.A. & Jetz, W. 2024. Insufficient and biased representation of species geographic responses to climate change. *Global Change Biology*. 30(7):e17408. DOI: 10.1111/gcb.17408.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. 37:637–669. DOI: 10.1146/annurev.ecolsys.37.091305.110100.
- Parolini, M., Romano, A., Khorauli, L., Nergadze, S.G., Caprioli, M., Rubolini, D., Santagostino, M., Saino, N., et al. 2015. Early-life telomere dynamics differ between the sexes and predict growth in the barn swallow (*Hirundo rustica*). *PLOS ONE*. 10(11):e0142530. DOI: 10.1371/journal.pone.0142530.
- Pattinson, N. 2023. Effects of temperature and food availability on the reproductive ecology of an arid-zone bird. Unpublished doctoral thesis. University of Cape Town.
- Pattinson, N.B., van de Ven, T.M.F.N., Finnie, M.J., Nupen, L.J., McKechnie, A.E. & Cunningham, S.J. 2022. Collapse of breeding success in desert-dwelling hornbills evident within a single decade. *Frontiers in Ecology and Evolution*. 10. DOI: 10.3389/fevo.2022.842264.
- Pattinson, N.B., Thompson, M.L., Griego, M., Russell, G., Mitchell, N.J., Martin, R.O., Wolf, B.O., Smit, B., et al. 2020. Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns? *Journal of Avian Biology*. 51(2):jav.02350. DOI: 10.1111/jav.02350.
- Peel, M. j. s., Kruger, J. m. & MacFadyen, S. 2007. Woody vegetation of a mosaic of protected areas adjacent to the Kruger National Park, South Africa. *Journal of Vegetation Science*. 18(6):807–814. DOI: 10.1111/j.1654-1103.2007.tb02597.x.
- Peel, M.C., Finlayson, B.L. & McMahon, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*. DOI: 10.5194/hess-11-1633-2007.
- Pérez-Barbería, F.J., García, A.J., Cappelli, J., Landete-Castillejos, T., Serrano, M.P. & Gallego, L. 2020. Heat stress reduces growth rate of red deer calf: Climate warming implications. *PLOS ONE*. 15(6):e0233809. DOI: 10.1371/journal.pone.0233809.
- Perkins-Kirkpatrick, S.E. & Lewis, S.C. 2020. Increasing trends in regional heatwaves. *Nature Communications*. 11(1):3357. DOI: 10.1038/s41467-020-16970-7.
- Pfaffl, M.W. 2001. A new mathematical model for relative quantification in real-time RT–PCR. *Nucleic Acids Research*. 29(9):e45. DOI: 10.1093/nar/29.9.e45.
- Pike, K.N., Ashton, B.J., Morgan, K.V. & Ridley, A.R. 2019. Social and individual factors influence variation in offspring care in the cooperatively breeding Western Australian magpie. *Frontiers in Ecology and Evolution*. 7:92. DOI: 10.3389/fevo.2019.00092.

- Pinowska, B., Barkowska, M., Pinowski, J., Bartha, A., Hahm, K.-H. & Lebedeva, N. 2004. The effect of egg size on growth and survival of the tree sparrow *Passer montanus* nestlings. *Acta Ornithologica*. 39(2):121–135. DOI: 10.3161/068.039.0209.
- Playà-Montmany, N., González-Medina, E., Cabello-Vergel, J., Parejo, M., Abad-Gómez, J.M., Sánchez-Guzmán, J.M., Villegas, A. & Masero, J.A. 2022. Behavioural and physiological responses to experimental temperature changes in a long-billed and long-legged bird: a role for relative appendage size? *Behavioral Ecology and Sociobiology*. 77(1):7. DOI: 10.1007/s00265-022-03280-9.
- du Plessis, K.L., Martin, R.O., Hockey, P.A.R., Cunningham, S.J. & Ridley, A.R. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*. 18(10):3063–3070. DOI: 10.1111/j.1365-2486.2012.02778.x.
- Potti, J. 2008. Temperature during egg formation and the effect of climate warming on egg size in a small songbird. *Acta Oecologica*. 33(3):387–393. DOI: 10.1016/j.actao.2008.02.003.
- Price, E.R. & Dzialowski, E.M. 2018. Development of endothermy in birds: patterns and mechanisms. *Journal of Comparative Physiology B*. 188(3):373–391. DOI: 10.1007/s00360-017-1135-0.
- Pruvot, M., Cappelle, J., Furey, N., Hul, V., Heng, H.S., Duong, V., Dussart, P. & Horwood, P. 2019. Extreme temperature event and mass mortality of insectivorous bats. *European Journal of Wildlife Research*. 65(3):41. DOI: 10.1007/s10344-019-1280-8.
- Quque, M., Paquet, M., Zahn, S., Théron, F., Faivre, B., Sueur, C., Criscuolo, F., Doutrelant, C., et al. 2021. Contrasting associations between nestling telomere length and pre and postnatal helpers' presence in a cooperatively breeding bird. *Oecologia*. 196(1):37–51. DOI: 10.1007/s00442-021-04917-8.
- Reichert, S. & Stier, A. 2017a. Does oxidative stress shorten telomeres in vivo? A review. *Biology Letters*. 13(12):20170463. DOI: 10.1098/rsbl.2017.0463.
- Reichert, S., Froy, H., Boner, W., Burg, T.M., Daunt, F., Gillespie, R., Griffiths, K., Lewis, S., et al. 2017. Telomere length measurement by qPCR in birds is affected by storage method of blood samples. *Oecologia*. 184(2):341–350. DOI: 10.1007/s00442-017-3887-3.
- Reiner, R., Zedrosser, A., Zeiler, H., Hackländer, K. & Corlatti, L. 2021. Forests buffer the climate-induced decline of body mass in a mountain herbivore. *Global Change Biology*. 27(16):3741–3752. DOI: 10.1111/gcb.15711.
- Resendiz, E., Ditzel, P., Kessler, P.W., Buckley, E.R., Huff, C.E., Poje, C., Lamb, J.B., Kennerley, J.A., et al. 2024. A photographic guide for determining egg incubation stage in the superb fairy-wren *Malurus cyaneus*. *Australian Field Ornithology*. 41:150–154. DOI: 10.20938/af041150154.

- Reséndiz-Infante, C. & Gauthier, G. 2020. Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird. *Scientific Reports*. 10(1):22067. DOI: 10.1038/s41598-020-78565-y.
- Ridley, A.R. & Heuvel, I.M. van den. 2012. Is there a difference in reproductive performance between cooperative and non-cooperative species? A southern African comparison. *Behaviour*. 149(8):821–848. DOI: 10.1163/1568539X-00003005.
- Ridley, A.R. & Raihani, N.J. 2007. Variable postfledging care in a cooperative bird: causes and consequences. *Behavioral Ecology*. 18(6):994–1000. DOI: 10.1093/beheco/arm074.
- Riehl, C. 2013. Evolutionary routes to non-kin cooperative breeding in birds. *Proceedings of the Royal Society B: Biological Sciences*. 280(1772):20132245. DOI: 10.1098/rspb.2013.2245.
- Rispel, M. & Lendelvo, S. 2016. The utilization of water points by wildlife species in Nyae Nyae Conservancy, Namibia. *Environment and Natural Resources Research*. 6(4):91. DOI: 10.5539/enrr.v6n4p91.
- Ritz, C. & Streibig, J.C. 2012. *Dose response curves and other nonlinear curves in Weed Science and Ecotoxicology with the add-on package drc in R*. Available: <https://cran.r-project.org/web/packages/drc/>.
- Roberts, J.A., Coulson, G., Munn, A.J. & Kearney, M.R. 2016. A continent-wide analysis of the shade requirements of red and western grey kangaroos. *Temperature*. 3(2):340–353. DOI: 10.1080/23328940.2016.1163452.
- Rodríguez, S., Noordwijk, A.J. van, Álvarez, E. & Barba, E. 2016. A recipe for postfledging survival in great tits *Parus major*: be large and be early (but not too much). *Ecology and Evolution*. 6(13):4458. DOI: 10.1002/ece3.2192.
- Rowe, L., Ludwig, D. & Schluter, D. 1994. Time, Condition, and the Seasonal Decline of Avian Clutch Size. *The American Naturalist*. 143(4):698–722. Available: <http://www.jstor.org/stable/2462907>.
- Rowland, J.A., Briscoe, N.J. & Handasyde, K.A. 2017. Comparing the thermal suitability of nest-boxes and tree-hollows for the conservation-management of arboreal marsupials. *Biological Conservation*. 209:341–348. DOI: 10.1016/j.biocon.2017.02.006.
- Rubenstein, D.R. 2011. Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. *Proceedings of the National Academy of Sciences*. 108(Supplement 2):10816–10822. DOI: 10.1073/pnas.1100303108.
- Rubenstein, D.R. & Lovette, I.J. 2007. Temporal Environmental Variability Drives the Evolution of Cooperative Breeding in Birds. *Current Biology*. 17(16):1414–1419. DOI: 10.1016/j.cub.2007.07.032.

- Russell, A.F. & Lummaa, V. 2009. Maternal effects in cooperative breeders: from hymenopterans to humans. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 364(1520):1143–1167. DOI: 10.1098/rstb.2008.0298.
- Russell, A.F., Langmore, N.E., Cockburn, A., Astheimer, L.B. & Kilner, R.M. 2007. Reduced egg investment can conceal helper effects in cooperatively breeding birds. *Science*. 317(5840):941–944. DOI: 10.1126/science.1146037.
- Rzępała, M., Kasprzykowski, Z., Obłóza, P., Mitrus, C. & Golawski, A. 2023. The influence of habitat and the location of nest-boxes on the occupation of boxes and breeding success of the kestrel *Falco tinnunculus*. *The European Zoological Journal*. 90(1):1–9. DOI: 10.1080/24750263.2022.2152504.
- Salaberria, C., Celis, P., López-Rull, I. & Gil, D. 2014. Effects of temperature and nest heat exposure on nestling growth, dehydration and survival in a Mediterranean hole-nesting passerine. *Ibis*. 156(2):265–275. DOI: 10.1111/ibi.12121.
- Salton, M., Saraux, C., Dann, P. & Chiaradia, A. 2015. Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *Royal Society Open Science*. 2(1):140390. DOI: 10.1098/rsos.140390.
- Santangeli, A. & Lehikoinen, A. 2017. Are winter and breeding bird communities able to track rapid climate change? Lessons from the high north. *Diversity and Distributions*. 23(3):308–316. DOI: 10.1111/ddi.12529.
- Santos, E.S.A. & Macedo, R.H. 2011. Load lightening in southern lapwings: group-living mothers lay smaller eggs than pair-living mothers. *Ethology*. 117(6):547–555. DOI: 10.1111/j.1439-0310.2011.01905.x.
- Sauve, D., Friesen, V.L. & Charmantier, A. 2021. The effects of weather on avian growth and implications for adaptation to climate change. *Frontiers in Ecology and Evolution*. 9:569741. DOI: 10.3389/fevo.2021.569741.
- Savage, J.L., Russell, A.F. & Johnstone, R.A. 2015. Maternal allocation in cooperative breeders: should mothers match or compensate for expected helper contributions? *Animal Behaviour*. 102:189–197. DOI: 10.1016/j.anbehav.2015.01.015.
- Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H.M., Pearce-Kelly, P., et al. 2016. The broad footprint of climate change from genes to biomes to people. *Science*. 354(6313):aaf7671. DOI: 10.1126/science.aaf7671.
- Scholes, R.J. 2020. The future of semi-arid regions: A weak fabric unravels. *Climate*. 8(3):43. DOI: 10.3390/cli8030043.
- Schou, M.F., Bonato, M., Engelbrecht, A., Brand, Z., Svensson, E.I., Melgar, J., Muvhali, P.T., Cloete, S.W.P., et al. 2021. Extreme temperatures compromise male and female fertility in a large desert bird. *Nature Communications*. 12(666). DOI: 10.1038/s41467-021-20937-7.

- Scott-Baumann, J.F., Morgan, E.R. & Cogan, T.A. 2022. Effects of nest-box environment on fledgling success rate and pathogen load. *Parasitology*. 149(9):1186–1192. DOI: 10.1017/S0031182022000695.
- Sears, M.W., Raskin, E. & Angilletta, M.J., Jr. 2011. The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integrative and Comparative Biology*. 51(5):666–675. DOI: 10.1093/icb/icr111.
- Sears, M.W., Angilletta, M.J., Schuler, M.S., Borchert, J., Dilliplane, K.F., Stegman, M., Rusch, T.W. & Mitchell, W.A. 2016. Configuration of the thermal landscape determines thermoregulatory performance of ectotherms. *Proceedings of the National Academy of Sciences*. 113(38):10595–10600. DOI: 10.1073/pnas.1604824113.
- Selong, J.H., McMahon, T.E., Zale, A.V. & Barrows, F.T. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance in fishes. *Transactions of the American Fisheries Society*. 130(6):1026–1037. DOI: 10.1577/1548-8659(2001)130<1026:EOTOGA>2.0.CO;2.
- Sharpe, L.L., Bayter, C. & Gardner, J.L. 2021. Too hot to handle? Behavioural plasticity during incubation in a small, Australian passerine. *Journal of Thermal Biology*. 98:102921. DOI: 10.1016/j.jtherbio.2021.102921.
- Sharpe, L.L., Prober, S.M. & Gardner, J.L. 2022. In the hot seat: behavioral change and old-growth trees underpin an Australian songbird's response to extreme heat. *Frontiers in Ecology and Evolution*. 10. DOI: 10.3389/fevo.2022.813567.
- Sheldon, B.C. 2000. Differential allocation: tests, mechanisms and implications. *Trends in Ecology & Evolution*. 15(10):397–402. DOI: 10.1016/S0169-5347(00)01953-4.
- Sheldon, E.L., Eastwood, J.R., Teunissen, N., Roast, M.J., Aranzamendi, N.H., Fan, M., Louise Hall, M., Kingma, S.A., et al. 2022. Telomere dynamics in the first year of life, but not later in life, predict lifespan in a wild bird. *Molecular Ecology*. 31(23):6008–6017. DOI: 10.1111/mec.16296.
- Shepard, I.D., Wissinger, S.A., Wood, Z.T. & Greig, H.S. 2022. Predators balance consequences of climate-change-induced habitat shifts for range-shifting and resident species. *Journal of Animal Ecology*. 91(2):334–344. DOI: 10.1111/1365-2656.13631.
- Silva, L.R., Lardy, S., Ferreira, A.C., Rey, B., Doutrelant, C. & Covas, R. 2018. Females pay the oxidative cost of dominance in a highly social bird. *Animal Behaviour*. 144:135–146. DOI: 10.1016/j.anbehav.2018.08.006.
- Simmons, R.E. 1997. Why don't all siblicidal eagles lay insurance eggs? The egg quality hypothesis. *Behavioral Ecology*. 8(5):544–550. DOI: 10.1093/beheco/8.5.544.
- Singh, K.P. & Kushwaha, C.P. 2016. Deciduousness in tropical trees and its potential as indicator of climate change: A review. *Ecological Indicators*. 69:699–706. DOI: 10.1016/j.ecolind.2016.04.011.

- Smit, B. 2013. Taking the heat: integrating behavioural and physiological variables to predict avian responses to climate change in the Kalahari desert. Unpublished doctoral thesis. University of Pretoria.
- Smit, I.P.J. & Prins, H.H.T. 2015. Predicting the effects of woody encroachment on mammal communities, grazing biomass and fire frequency in African savannas. *PLoS ONE*. 10(9):e0137857. DOI: 10.1371/journal.pone.0137857.
- Smit, B., Harding, C.T., Hockey, P. a. R. & McKechnie, A.E. 2013. Adaptive thermoregulation during summer in two populations of an arid-zone passerine. *Ecology*. 94(5):1142–1154. DOI: 10.1890/12-1511.1.
- Smit, B., Zietsman, G., Martin, R.O., Cunningham, S.J., McKechnie, A.E. & Hockey, P.A.R. 2016. Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Climate Change Responses*. 3(1):9. DOI: 10.1186/s40665-016-0023-2.
- Smith, E.K., O'Neill, J.J., Gerson, A.R., McKechnie, A.E. & Wolf, B.O. 2017. Avian thermoregulation in the heat: resting metabolism, evaporative cooling, and heat tolerance in Sonoran Desert songbirds. *Journal of Experimental Biology*. (January, 1):jeb.161141. DOI: 10.1242/jeb.161141.
- Soravia, C., Ashton, B.J., Thornton, A., Bourne, A.R. & Ridley, A.R. 2024. High temperatures during early development reduce adult cognitive performance and reproductive success in a wild animal population. *Science of The Total Environment*. 912:169111. DOI: 10.1016/j.scitotenv.2023.169111.
- Speakman, J.R. & Król, E. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*. 79(4):726–746. DOI: 10.1111/j.1365-2656.2010.01689.x.
- Spooner, F.E.B., Pearson, R.G. & Freeman, R. 2018. Rapid warming is associated with population decline among terrestrial birds and mammals globally. *Global Change Biology*. 24(10):4521–4531. DOI: 10.1111/gcb.14361.
- Stauffer, J., Panda, B., Eeva, T., Rainio, M. & Ilmonen, P. 2017. Telomere damage and redox status alterations in free-living passerines exposed to metals. *Science of The Total Environment*. 575:841–848. DOI: 10.1016/j.scitotenv.2016.09.131.
- Stearns, S.C. 1992. *The evolution of life histories*. Oxford University Press.
- Steenweg, R.J., Crossin, G.T., Hennin, H.L., Gilchrist, H.G. & Love, O.P. 2022. Favorable spring conditions can buffer the impact of winter carryover effects on a key breeding decision in an Arctic-breeding seabird. *Ecology and Evolution*. 12(2):e8588. DOI: 10.1002/ece3.8588.
- Stier, A., Metcalfe, N.B. & Monaghan, P. 2020. Pace and stability of embryonic development affect telomere dynamics: an experimental study in a precocial bird model. *Proceedings of the Royal Society B: Biological Sciences*. 287(1933):20201378. DOI: 10.1098/rspb.2020.1378.

- Strydom, L.H., Conradie, S.R., Smit, I.P.J., Greve, M., Boucher, P.B., Davies, A.B. & McKechnie, A.E. 2025. Mapping tree canopy thermal refugia for birds using biophysical models and LiDAR. *International Journal of Biometeorology*. 69(10):2461–2474. DOI: 10.1007/s00484-024-02833-z.
- Svensson, E.I., Schou, M.F., Melgar, J., Waller, J., Engelbrecht, A., Brand, Z., Cloete, S. & Cornwallis, C.K. 2024. Heritable variation in thermal profiles is associated with reproductive success in the world's largest bird. *Evolution Letters*. 8(2):200–211. DOI: 10.1093/evlett/grad049.
- Tabacchi, E., Correll, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A. & Wissmar, R.C. 1998. Development, maintenance and role of riparian vegetation in the river landscape. *Freshwater Biology*. 40(3):497–516. DOI: 10.1046/j.1365-2427.1998.00381.x.
- Tabh, J.K.R., Persson, E., Correia, M., Cuív, C.Ó., Thorat, E. & Nord, A. 2025. Limited evidence that body size shrinking and shape-shifting alleviate thermoregulatory pressures in a warmer world. *Communications Biology*. 8(1):707. DOI: 10.1038/s42003-025-08131-7.
- Taheri, S., Naimi, B., Rahbek, C. & Araújo, M.B. 2021. Improvements in reports of species redistribution under climate change are required. *Science Advances*. 7(15):eabe1110. DOI: 10.1126/sciadv.abe1110.
- Teplitsky, C., Mills, J.A., Alho, J.S., Yarrall, J.W. & Merilä, J. 2008. Bergmann's rule and climate change revisited: Disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences*. 105(36):13492–13496. DOI: 10.1073/pnas.0800999105.
- Teunissen, N., Kingma, S.A., Fan, M., Roast, M.J. & Peters, A. 2021. Context-dependent social benefits drive cooperative predator defense in a bird. *Current Biology*. 31(18):4120–4126.e4. DOI: 10.1016/j.cub.2021.06.070.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*. 31(1):79–92. DOI: 10.1046/j.0305-0270.2003.00994.x.
- Theron, N., Jansen, R., Grobler, P. & Kotze, A. 2013. The home range of a recently established group of southern ground-hornbill (*Bucorvus leadbeateri*) in the Limpopo Valley, South Africa. *Koedoe*. 55(1):8 pages. DOI: 10.4102/koedoe.v55i1.1135.
- Tieleman, B.I. & Williams, J.B. 2002a. Cutaneous and respiratory water loss in larks from arid and mesic environments. *Physiological and Biochemical Zoology*. 75(6):590–599. DOI: 10.1086/344491.
- Tieleman, B.I. & Williams, J.B. 2002b. Effects of food supplementation on behavioural decisions of hoopoe-larks in the Arabian desert: balancing water, energy and thermoregulation. *Animal Behaviour*. 63(3):519–529. DOI: 10.1006/anbe.2001.1927.

- Ton, R., Boner, W., Raveh, S., Monaghan, P. & Griffith, S.C. 2023. Effects of heat waves on telomere dynamics and parental brooding effort in nestlings of the zebra finch (*Taeniopygia castanotis*) transitioning from ectothermy to endothermy. *Molecular Ecology*. 32(17):4911–4920. DOI: 10.1111/mec.17064.
- Townsend, H.M. & Anderson, D.J. 2007. Production of insurance eggs in Nazca boobies: costs, benefits, and variable parental quality. *Behavioral Ecology*. 18(5):841–848. DOI: 10.1093/beheco/arm056.
- Turbill, C. & Prior, S. 2016. Thermal climate-linked variation in annual survival rate of hibernating rodents: shorter winter dormancy and lower survival in warmer climates. *Functional Ecology*. 30(8):1366–1372. DOI: 10.1111/1365-2435.12620.
- Turner, M.G. & Gardner, R.H. 2015. *Landscape Ecology in Theory and Practice: Pattern and Process*. New York, NY: Springer. DOI: 10.1007/978-1-4939-2794-4.
- Valencia, J., De La Cruz, C., Carranza, J. & Mateos, C. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. *Animal Behaviour*. 71(5):1021–1028. DOI: 10.1016/j.anbehav.2005.06.021.
- Valencia, J., Mateos, C., De La Cruz, C. & Carranza, J. 2017. Maternal allocation in eggs when counting on helpers in a cooperatively breeding bird. *Journal of Avian Biology*. 48(4):536–543. DOI: 10.1111/jav.01020.
- Van Boheemen, L.A., Hammers, M., Kingma, S.A., Richardson, D.S., Burke, T., Komdeur, J. & Dugdale, H.L. 2019. Compensatory and additive helper effects in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). *Ecology and Evolution*. 9(5):2986–2995. DOI: 10.1002/ece3.4982.
- Van de Loock, D., Cousseau, L., Apfelbeck, B., Githiru, M., Lens, L. & Matthysen, E. 2023. Contrasting effects of cooperative group size and number of helpers on maternal investment in eggs and nestlings. *Animal Behaviour*. 198:107–116. DOI: 10.1016/j.anbehav.2023.01.013.
- van de Ven, T.M.F.N., Fuller, A. & Clutton-Brock, T.H. 2020. Effects of climate change on pup growth and survival in a cooperative mammal, the meerkat. *Functional Ecology*. 34(1):194–202. DOI: 10.1111/1365-2435.13468.
- Van Der Waal, C. 2010. Nutrients in an African savanna: the consequences of supply heterogeneity for plants and animals. Unpublished doctoral thesis. Wageningen University. DOI: 10.18174/146149.
- Vedder, O., Verhulst, S., Zuidersma, E. & Bouwhuis, S. 2018. Embryonic growth rate affects telomere attrition: an experiment in a wild bird. *Journal of Experimental Biology*. jeb.181586. DOI: 10.1242/jeb.181586.
- van de Ven, T.M.F.N., McKechnie, A.E. & Cunningham, S.J. 2019. The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*. 191:205–215. DOI: 10.1007/s00442-019-04486-x.

- van de Ven, T.M.F.N., McKechnie, A.E., Er, S. & Cunningham, S.J. 2020. High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia*. 193(1):225–235. DOI: 10.1007/s00442-020-04644-6.
- Verhulst, S., Aviv, A., Benetos, A., Berenson, G.S. & Kark, J.D. 2013. Do leukocyte telomere length dynamics depend on baseline telomere length? An analysis that corrects for ‘regression to the mean’. *European Journal of Epidemiology*. 28(11):859–866. DOI: 10.1007/s10654-013-9845-4.
- Vermeulen, L.M., Van Meerbeek, K., Bernardino, P.N., Slingsby, J., Verbist, B. & Somers, B. 2025. Woody cover and geology as regional-scale determinants of semi-arid savanna stability. *Remote Sensing in Ecology and Conservation*. 11(5):539–554. DOI: 10.1002/rse2.70005.
- Wang, C., Li, Z., Chen, Y., Li, Y., Ouyang, L., Zhu, J., Sun, F., Song, S., et al. 2024. Changes in global heatwave risk and its drivers over one century. *Earth's Future*. 12(10):e2024EF004430. DOI: 10.1029/2024EF004430.
- Watson, M.J. & Kerr, J.T. 2025. Climate-driven body size changes in birds and mammals reveal environmental tolerance limits. *Global Change Biology*. 31(5):e70241. DOI: 10.1111/gcb.70241.
- Watson, H., Bolton, M. & Monaghan, P. 2015. Variation in early-life telomere dynamics in a long-lived bird: links to environmental conditions and survival. *Journal of Experimental Biology*. 218(5):668–674. DOI: 10.1242/jeb.104265.
- Weeks, B.C., Klemz, M., Wada, H., Darling, R., Dias, T., O'Brien, B.K., Probst, C.M., Zhang, M., et al. 2022. Temperature, size and developmental plasticity in birds. *Biology Letters*. 18(12):20220357. DOI: 10.1098/rsbl.2022.0357.
- Welbergen, J.A., Klose, S.M., Markus, N. & Eby, P. 2007. Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B: Biological Sciences*. 275(1633):419–425. DOI: 10.1098/rspb.2007.1385.
- Whitehead, P.J., Russell-Smith, J. & Woinarski, J.C.Z. 2005. Fire, landscape heterogeneity and wildlife management in Australia's tropical savannas: introduction and overview. *Wildlife Research*. 32(5):369–375. DOI: 10.1071/WR05069.
- Whitfield, M.C., Smit, B., McKechnie, A.E. & Wolf, B.O. 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *Journal of Experimental Biology*. 218(11):1705–1714. DOI: 10.1242/jeb.121749.
- Whittemore, K., Vera, E., Martínez-Nevado, E., Sanpera, C. & Blasco, M.A. 2019. Telomere shortening rate predicts species life span. *Proceedings of the National Academy of Sciences*. 116(30):15122–15127. DOI: 10.1073/pnas.1902452116.
- Whyte, J.R.D., McKechnie, A.E., Crossley, J.K. & Cunningham, S.J. 2026. Behavioural responses to heat in an arid-zone bird vary with thermal, hygric and social factors. *Oecologia*. 208(4):53. DOI: 10.1007/s00442-026-05888-4.

- Wickham, H. 2016. *ggplot2: Elegant Graphics for Data Analysis (3e)*. Available: <https://ggplot2-book.org/> [2024, July 08].
- Wiebe, K.L. 1996. The insurance-egg hypothesis and extra reproductive value of last-laid eggs in clutches of American kestrels. *The Auk*. 113(1):258–261. DOI: 10.2307/4088961.
- Wiebe, K.L. & Bortolotti, G.R. 1995. Egg size and clutch size in the reproductive investment of American Kestrels. *Journal of Zoology*. 237(2):285–301. DOI: 10.1111/j.1469-7998.1995.tb02763.x.
- Wiebe, K.L. & Slagsvold, T. 2014. Prey size increases with nestling age: are provisioning parents programmed or responding to cues from offspring? *Behavioral Ecology and Sociobiology*. 68(5):711–719. DOI: 10.1007/s00265-014-1684-0.
- Wiens, J.J. 2016. Climate-related local extinctions are already widespread among plant and animal species. *PLOS Biology*. 14(12):e2001104. DOI: 10.1371/journal.pbio.2001104.
- Wigley, B.J., Coetsee, C., February, E.C., Dobelmann, S. & Higgins, S.I. 2024. Will trees or grasses profit from changing rainfall regimes in savannas? *New Phytologist*. 241(6):2379–2394. DOI: 10.1111/nph.19538.
- Wilbourn, R.V., Moatt, J.P., Froy, H., Walling, C.A., Nussey, D.H. & Boonekamp, J.J. 2018. The relationship between telomere length and mortality risk in non-model vertebrate systems: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 373(1741):20160447. DOI: 10.1098/rstb.2016.0447.
- Wilcox, R.C., Benson, T.J., Brawn, J.D. & Tarwater, C.E. 2024. Observed declines in body size have differential effects on survival and recruitment, but no effect on population growth in tropical birds. *Global Change Biology*. 30(8):e17455. DOI: 10.1111/gcb.17455.
- Wiley, E.M. & Ridley, A.R. 2016. The effects of temperature on offspring provisioning in a cooperative breeder. *Animal Behaviour*. 117:187–195. DOI: 10.1016/j.anbehav.2016.05.009.
- Wilkin, T.A., Perrins, C.M. & Sheldon, B.C. 2007. The use of GIS in estimating spatial variation in habitat quality: a case study of lay-date in the great tit *Parus major*. *Ibis*. 149(s2):110–118. DOI: 10.1111/j.1474-919X.2007.00757.x.
- Williams, C.M., Henry, H.A.L. & Sinclair, B.J. 2015. Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*. 90(1):214–235. DOI: 10.1111/brv.12105.
- Wilson, G. & Hockey, P.A.R. 2013. Causes of variable reproductive performance by Southern Ground-hornbill *Bucorvus leadbeateri* and implications for management. *Ibis*. 155(3):476–484. DOI: 10.1111/ibi.12042.
- Wingfield, J.C., Pérez, J.H., Krause, J.S., Word, K.R., González-Gómez, P.L., Lisovski, S. & Chmura, H.E. 2017. How birds cope physiologically and behaviourally with extreme climatic events. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 372(1723). DOI: 10.1098/rstb.2016.0140.

- Wolf, B. 2000. Global warming and avian occupancy of hot deserts: a physiological and behavioral perspective. *Revista chilena de historia natural*. 73(3). DOI: 10.4067/S0716-078X2000000300003.
- Wood, E.M. & Young, A.J. 2019. Telomere attrition predicts reduced survival in a wild social bird, but short telomeres do not. *Molecular Ecology*. 28(16):3669–3680. DOI: 10.1111/mec.15181.
- Wood, E.M., Capilla-Lasheras, P., Cram, D.L., Walker, L.A., York, J.E., Lange, A., Hamilton, P.B., Tyler, C.R., et al. 2022. Social dominance and rainfall predict telomere dynamics in a cooperative arid-zone bird. *Molecular Ecology*. 31(23):6141–6154. DOI: 10.1111/mec.15868.
- Woodroffe, R., Groom, R. & McNutt, J.W. 2017. Hot dogs: High ambient temperatures impact reproductive success in a tropical carnivore. *Journal of Animal Ecology*. 86(6):1329–1338. DOI: 10.1111/1365-2656.12719.
- World Meteorological Organization. 2023. *State of the Climate in Africa*. Geneva, Switzerland. Available: <https://public.wmo.int/publication-series/state-of-climate-africa-2022>.
- Wu, N.C., Anderson, R.O., Borzée, A., Buttner, S., Dezetter, M., Dubiner, S., Li, Q.-H., Navas, C.A., et al. 2025. A user's guide for understanding reptile and amphibian hydoregulation and climate change impacts. *Conservation Physiology*. 13(1):coaf038. DOI: 10.1093/conphys/coaf038.
- Wyness, W. 2011. Home range use by southern ground-hornbills (*Bucorvus leadbeateri*) - quantifying seasonal habitat selection and vegetation characteristics. Unpublished honours thesis. University of Cape Town.
- Xu, X., Wang, J., Lv, K., Jin, H., Li, M. & Liu, J. 2024. Thermoregulation and antioxidant defense mechanisms in Eurasian tree sparrows (*Passer montanus*) under acute heat stress. *The European Zoological Journal*. 91(1):406–419. DOI: 10.1080/24750263.2024.2344627.
- Youngflesh, C., Saracco, J.F., Siegel, R.B. & Tingley, M.W. 2022. Abiotic conditions shape spatial and temporal morphological variation in North American birds. *Nature Ecology & Evolution*. 6(12):1860–1870. DOI: 10.1038/s41559-022-01893-x.
- Zellweger, F., Coomes, D., Lenoir, J., Depauw, L., Maes, S.L., Wulf, M., Kirby, K.J., Brunet, J., et al. 2019. Seasonal drivers of understory temperature buffering in temperate deciduous forests across Europe. *Global Ecology and Biogeography*. 28(12):1774–1786. DOI: 10.1111/geb.12991.
- Zeng, H., Jia, G. & Epstein, H. 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. *Environmental Research Letters*. 6(4):045508. DOI: 10.1088/1748-9326/6/4/045508.
- Zhang, X., Friedl, M.A., Schaaf, C.B., Strahler, A.H. & Liu, Z. 2005. Monitoring the response of vegetation phenology to precipitation in Africa by coupling MODIS and TRMM

instruments. *Journal of Geophysical Research: Atmospheres*. 110(D12). DOI: 10.1029/2004JD005263.

Zoghby, B.A., Ryan, P.G., Little, R.M., Reid, T. & Hockey, P.A. 2015. Seasonal changes in movement and habitat use by southern ground-hornbills in the South African lowveld. *Ostrich*. 86(1–2):87–95. DOI: 10.2989/00306525.2015.1030794.

