Effects of temperature and food availability on the reproductive ecology of an arid-zone bird

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Doctor of Philosophy

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Co-supervised by Prof. Andrew E. McKechnie (University of Pretoria)

1. Abstract

For arid-zone birds that breed in spring and summer, the heightened energy, water, and time demands of reproduction and development coincide with the hottest period of the year. For these species, rapid anthropogenic climate warming is exacerbating trade-offs between thermoregulation and self-maintenance or reproduction, posing a severe threat to breeding and population dynamics. There has been a surge in research into the effects of high and increasing environmental temperature on avian ecology. However, the potential for resource availability to moderate environmental temperature effects on birds' behaviour, physiology, morphology, and success during breeding remains understudied. I investigated these lesser-known concepts through monitoring breeding, conducting a supplementary feeding experiment (providing breeding pairs with access to either a high supplementation (high supp.) treatment of ~25g of *Zophobas morio* or a low supplementation (low supp.) treatment of ~5g of *Z. morio* every day of the breeding attempt), and analysing long-term data from a population of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hornbills) in the Kalahari Desert. These hornbills are long-lived and have an unusual breeding strategy whereby the female seals herself inside the nest cavity for the majority of the breeding attempt, leaving the free-ranging male as the sole provisioner to the nest. Hornbills do not drink, with their water inputs comprised entirely of dietary and metabolic water. Therefore, 'food' equates to 'resources' (i.e., food and water combined) in this species. I found that supplementary feeding affected the thermoregulation of free-ranging male parents, incarcerated female parents in the nest, and chicks: hornbills in the high supp. treatment showed more gradual increases in body temperature (T_b) and increased hyperthermia avoidance in response to rising nest temperature (T_{nest}), although high air temperature (T_{air}) and T_{nest} still resulted in facultative hyperthermic responses. Some negative effects of high environmental temperatures persisted regardless of resource availability: breeding male hornbills showed T_{air}-dependent nest provisioning patterns and chicks showed impaired development (i.e., reduced structural growth) and increased stress responses (indicated by increased feather corticosterone [CORT]) at high T_{nest} irrespective of resource availability. Collectively, these patterns suggested there were some mediating effects of resource availability on hornbill breeding ecology, but that high environmental temperatures nonetheless had negative effects. This

study took place during a period of unprecedented climate extremes, from 2018 – 2021. Therefore, it includes detailed data from two very different summer breeding seasons: a hot and dry breeding season (2019/20) and a cool and very wet breeding season which included a 1-in-100-year flooding event (2020/21). During an earlier year of the study (2018/19), drought conditions were so extreme that no hornbills attempted to breed at the study site, therefore no data for this breeding season are included in the thesis. In the cool and wet breeding season, I recorded a) higher provisioning effort by male parents, b) improved hyperthermia avoidance and more gradual increases in T_b in male and female parents and chicks, c) higher post-hatch body mass (M_b), faster tail feather growth, and lower tail feather barb density in breeding females, d) less time in the nest (i.e., fledging sooner), faster M_b gain, and longer tarsi at fledge and faster tail feather growth in chicks, and e) higher breeding success, compared to the hot and dry breeding season. These differences were mostly unexplained by environmental temperature effects, suggesting they were driven by higher resource availability or quality in the cool and wet breeding season. The lack of any effects of the supplementary feeding experiment on variables other than thermoregulation indicated that it could be resource quality, rather than availability, that was the most important resource-related factor affecting the hornbill ecology during this study. However, I did not have resource quality data to test that possibility. An alternative explanation is that the supplementary feeding experiment did not provide enough extra food and water to influence factors other than thermoregulation, or the signal was simply swamped by the unprecedented influx of natural resources associated with incredibly high primary productivity in the flood year. In systems or periods where resources are not limiting one might not expect a significant effect of resource supplementation. Either of these could have undermined my ability to detect potential resource availability effects. Crucially, I found no significant T_{nest} effects on female parent morphology or on breeding success, in strong contrast to previous findings in this study population, and in the long-term breeding data analysed in this thesis. This was likely a result of significantly reduced T_{nest} caused by new nest boxes with an insulation layer, compared to previous studies on this population using uninsulated nest boxes. These findings highlight the need for multi-season studies, and the possibility that improved design of nest boxes can positively affect nest microclimate, thereby mitigating severe high T_{nest} effects. Overall, this thesis attempted to investigate

whether high environmental temperatures are currently limiting because of a concurrent lack of energy and water aggravating costly trade-offs. If so, then provisioning of supplementary food and water may present viable conservation options for severely affected and conservation dependant species. Moreover, successful breeding in high rainfall years (corresponding to high resource availability) despite high environmental temperatures may facilitate population persistence. Broadly, based on the predominant lack of supplementary feeding effects, results suggested resource availability was not a strong driver of variation in hornbill reproductive ecology. Rather, the results indicated that high environmental temperatures were limiting regardless of resource availability (i.e., for provisioning rate and developing chicks), despite improved hyperthermia avoidance and more gradual increases in T_b at high T_{nest}. The results also indicated potential effects of resource quality, or that the supplementary feeding experiment was not completely effective, in that the amount of supplementary food may still not have been enough, or may not have met the nutrient or water requirements (i.e., food quality requirements) of the female parents or chicks. The amount of food in the high supp. treatment was designed to be ~100% of the daily requirements of the nest based on previous studies of this population, but the males in the cool and wet season showed that they could considerably increase the amount of food provisioned to the nest compared to what had been recorded before, suggesting that the amount of supplementary food was well-below what could possibly be provisioned. I lacked the data to investigate these possibilities. Results, therefore, leave avenues for future research to investigate, for example, quality *versus* quantity effects or the effects of *ad libitum* food and water supplementation. This PhD contributes to disentangling the independent effects of high environmental temperatures and resource availability on arid-zone avian ecology. Several key potential effects of resource availability or quality on behaviour, physiology, morphology, and breeding success were identified, which ultimately will hopefully aid in understanding avian ecology and designing future research and conservation interventions in the face of rapid climate warming.

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3. Funding, ethical statement, and permits

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4. Declaration by student

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

Signed: Date: December 2023

5. Scientific articles from this thesis

Pattinson NB, van de Ven TMFN, Finnie MJ, Nupen LJ, McKechnie AE and Cunningham SJ (2022) Collapse of Breeding Success in Desert-Dwelling Hornbills Evident Within a Single Decade. Frontiers in Ecology and Evolution 10:842264. doi: 10.3389/fevo.2022.84226.

Chapter 5 represents an edited version (inclusive of results which appear in the supplementary materials of the published paper and additional discussion text on the thesis context of the Chapter) of the accepted manuscript (prior to typesetting and publication) submitted to Frontiers in Ecology and Evolution. Andrew E. McKechnie, Susan J. Cunningham, Tanja M.F.N. van de Ven and myself developed the conceptual framework. Lisa J. Nupen, Mike J. Finnie, Tanja M.F.N. van de Ven and myself collected data. I analysed the data and wrote the manuscript. All the authors contributed to editing and revising the manuscript, and all read and approved the version submitted for publication. As the version presented in the thesis is not a *verbatim* reproduction of the paper, it falls under Rule GP7 of UCT Handbook 3: 'A candidate may, subject to the prior written approval of his or her supervisor and subject to the provisions of rule GP9, publish a part or the whole of the work done by him or her under supervision for the degree before presenting his or her thesis for examination.' As per rule GP7, my supervisor, Dr Susan Cunningham, provided prior written approval for the inclusion of this work (letter reproduced below).

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Mr Nicholas Pattinson
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02/10/2022

Dear Nicholas:

Re: Permission to include published material in your PhD thesis

As your PhD supervisor, I hereby give my prior written permission for you to include material already published in your first-author paper “Pattinson NB, van de Ven TMFN, Finnie MJ, Nupen LJ, McKechnie AE and Cunningham SJ (2022) Collapse of Breeding Success in Desert-Dwelling Hornbills Evident Within a Single Decade. Frontiers in Ecology and Evolution 10:842264” in your PhD thesis entitled “Effects of temperature and food availability on the reproductive ecology of an arid-zone bird”.

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1. General Introduction

1.1 Rapid climate change and arid zones

Global biodiversity currently faces unprecedented challenges due to anthropogenic climate change (Walther et al. 2002, Parmesan and Yohe 2003, Pacifici et al. 2015, Li et al. 2018, IPCC 2022). Arid and semi-arid zones are among those regions experiencing the highest rates of warming (Zhou 2016), making arid-zone species among the most vulnerable to climate change, especially since they are already living close to their physiological limits (Lima et al. 2008, Boyles et al. 2011, Maestre et al. 2012, Moses et al. 2012, Vale and Brito 2015, Ma et al. 2023).

Arid zones typically experience low humidity, scarce water sources, and high summer environmental temperatures (Wolf 2000, Nagy 2004). The general food availability across the system is low and the energy available to the entire trophic cascade depends on annual rainfall, which often falls during a concentrated period of a few months of the year, driving primary productivity (Bolger et al. 2005, Lima et al. 2008, Mares et al. 2017). As a result, increases in frequency and severity of droughts and high environmental temperatures induced by climate change in arid zones (Sharma and Mujumdar 2017, Spinoni et al. 2018, Ye et al. 2019) exacerbate the challenge of balancing energy and water intake and expenditure for animals, thereby having strong effects on survival and lifetime reproductive success (Greenville et al. 2012, Maron et al. 2015, Williams et al. 2016, Lambert et al. 2018). The most conspicuous effects of droughts and high environmental temperatures (even outside arid regions) are when they cause direct mortality, such as recent mass die-offs in endotherms during heat waves (Welbergen et al. 2008, McKechnie and Wolf 2010, Jones et al. 2018, Ratnayake et al. 2019, McKechnie et al. 2021b, Holt and Boersma 2022, Quintana et al. 2022), or disastrous reproductive failures (Bolger et al. 2005, Yackel Adams et al. 2006, Albright et al. 2010a, Piatt et al. 2020, Riddell et al. 2021). However, they may also have insidious non-lethal effects (Conradie et al. 2019, Cunningham et al. 2021, Fuller et al.

2021, Schou et al. 2021), such as reduced egg and clutch size in birds and reptiles (Pendlebury et al. 2004, Albright et al. 2010a), offspring suffering diminished fitness potential (Lee et al. 2016, van de Ven et al. 2020a), or in the case of many long-lived species, adults foregoing breeding altogether (Illera and Díaz 2006, Moreno and Møller 2011).

1.2 Arid-zone avifauna and increasing temperatures

In arid zones, birds, in comparison to other desert-dwelling taxa, are considered to be especially vulnerable to climate change (Wolf 2000). Birds are mostly diurnal, small (causing a low capacity for storage of energy and water), live above ground, and exhibit high mass-specific metabolic and evaporative water loss rates (Wolf 2000, Albright et al. 2017). Moreover, optimal performance in birds occurs at a relatively narrow range of body temperature (T_b; active phase, when an organism is awake and active, approximately 38 – 42 °C) which is especially challenging to defend when environmental temperatures can far exceed T_b and resource availability is low (Prinzinger et al. 1991, Angilletta et al. 2010, Nilsson and Nord 2021). Essentially, arid-zone birds face a considerable challenge to maintain energy and water balance, especially at the hottest times of the year (McKechnie et al. 2016b, Noakes et al. 2016, Sharpe et al. 2019). With increasing environmental temperatures due to climate change set to likely increase global average by at least 2 °C by the end of the century, and far more in some regions such as the Arctic (IPCC 2022), this challenge is set to increase markedly (McKechnie and Wolf 2010, Smit and McKechnie 2015, Ma et al. 2023).

Behaviourally, when exposed to high environmental temperatures, birds can reduce their activity levels, display shade-seeking behaviour, and increase evaporative water loss through heat dissipation behaviours (e.g., panting) (Walsberg 1993, Pattinson et al. 2020). These behaviours help to conserve resources or mediate the avoidance of lethal hyperthermia, thereby reducing the risk of heat stress related mortality (Davies 1982, Cunningham et al. 2015, Martin et al. 2015). However, these behavioural adjustments are often associated with significant costs (Cunningham et al. 2021). Panting behaviour considerably increases evaporative water loss, thereby incurring risk of dehydration stress, and can potentially interfere directly with foraging (du Plessis et al. 2012). Reductions in foraging effort may reduce energy and water acquisition, while shade-seeking behaviour and panting can considerably reduce foraging success and efficiency (Cunningham et al. 2015, Pattinson and Smit 2017, Cunningham et al. 2021). For birds which acquire all their water from their diet (i.e., those that do not drink), the reduction in foraging efficiency, thus reducing water intake, coupled with increased evaporative water loss demands can be particularly threatening (Smit et al. 2016, Abdu et al. 2018a, Czenze et al. 2020).

Physiologically, at high environmental temperatures, birds must attempt to defend a narrow range of T_b (Angilletta et al. 2010, Glanville and Seebacher 2010). This is a difficult task, especially in arid-zones which are generally typified by large seasonal shifts in air temperature (T_{air} > 45 °C between the minimum in winter and the maximum in summer), and extremely high T_{air} in summer (Tieleman and Williams 1999, 2000, Smit et al. 2013, Pattinson and Smit 2017). High summer T_{air} are particularly pertinent to birds, as they do not, for the most part, show the heat stress avoidance behaviours typical of small arid-zone mammals, such as retreating to underground burrows in the heat of the day, or becoming more nocturnal (Williams et al. 1999, McKechnie et al. 2016b, Alagaili et al. 2017). Birds generally, therefore, perform vital functions, including physiological and behavioural processes associated with reproduction, during the day when environmental temperatures can far exceed T_b (Smith et al. 2015). In physiological response, birds may allow their T_b to increase above the optimal active phase range, displaying facultative hyperthermia. This facilitates passive heat loss to the environment (if it increases T_b above T_{air}), delaying and reducing the need for panting, and thereby conserving energy and water (Tieleman and Williams 1999, Smith et al. 2015, Freeman et al. 2022). However, by expressing facultative hyperthermia, a bird can put its T_b dangerously close to lethal limits (45 – 48 °C; Boyles et al. 2011, McKechnie et al. 2017, Freeman et al. 2020). To avoid lethal hyperthermia, the only avenue available to birds to dissipate heat once environmental temperature exceeds T_b is evaporative water loss, which incurs a dehydration risk via heightened water demands (the loss of up to 7% body mass (M_b) per hour; Wolf and Walsberg 1996, McKechnie et al. 2016b, Albright et al. 2017). Notably, although birds can show drastic elevations of evaporative water loss at $T_{air} > T_b$, there are limits to the rate at which heat can be dissipated (Speakman and Król 2010, Boyles et al. 2011, Whitfield et al. 2015, Wingfield et al. 2017). Indeed, while it has been shown that birds can maintain their T_b up to 20 °C below the T_{air} (McKechnie et al. 2016b), they will eventually reach a thermal endpoint – the T_{air} where heat dissipation is insufficient to maintain T_b control – at which point their T_b will uncontrollably, and lethally, rise (Rezende and Bacigalupe 2015, Whitfield et al. 2015, McKechnie et al. 2016a, Albright et al. 2017, McKechnie et al. 2017). Therefore, at high T_{air}, anything that upregulates endogenous heat production (e.g., mobility, reproduction), or increases heat gain from the environment (e.g., moving into a hot microsite), could increase T_b faster than the bird's ability to dissipate heat to regulate it, causing mortality (Rezende and Bacigalupe 2015).

High environmental temperatures can affect morphological traits of arid-zone species. The effects can change individuals within their lifetime, such as alterations to the structural size, structural quality, and M_b of chicks at fledge (Gardner et al. 2016, Andrew et al. 2017), or manifest as the accumulative effects of selection on individuals over generations to affect population level phenotypes (Gardner et al. 2011, Gardner et al. 2014b). Morphological responses to high environmental temperatures could be adaptive if they are heritable and increase fitness (Ryding et al. 2021). Morphology and fitness are often linked. In some instances, morphology is directly related to fitness (Olson et al. 2009). In other cases, the link is partially because of relationships morphological traits share with behaviour and physiology. For instance, relatively high M_b may indicate increased reserves to allocate towards metabolic heat generation or evaporative water loss (Gardner et al. 2011), thereby influencing behavioural thermoregulation and foraging decisions (du Plessis et al. 2012, van de Ven et al. 2019).

1.3 Breeding in the arid zone: the concurrence of heat and rain, and the case for potential underappreciated effects of resource availability

The challenges imposed by high environmental temperatures in arid zones are most severe in the spring and summer months, which for some arid zones (e.g., the Kalahari Desert) can be when most annual rain falls (Bhattachan et al. 2012, Yu et al. 2017). High rainfall leads to a significant increase in primary productivity and hence food availability, which various higher trophic level species rely on to breed successfully, or in some cases to breed at all (Dean and Milton 2001, Keynan and Yosef 2010, Saunders et al. 2013). Consequently, the heightened energy, water, and time demands of reproduction and development often coincide with the most thermally challenging period of the year (Conway and Martin 2000a, Álvarez and Barba 2014).

In light of rapid climate warming, and the concurrence of breeding and high environmental temperatures, it is unsurprising but important that research into environmental temperature effects on ecology, breeding and population dynamics has surged worldwide over the last two decades (see for e.g., Iknayan and Beissinger 2018, Nord and Nilsson 2019, Riddell et al. 2019, Stillman 2019, Andreasson et al. 2020, Ma et al. 2023). However, less attention has been paid to the influence of resource availability on the ability of birds to survive and breed under high heat loads. Life history theory predicts that if resources are limited then investment in costly traits, such as thermoregulation, must come at the expense of investment in other costly traits, such as provisioning or growth (Stearns 1992, Dawson et al. 2005). This implies that when resource limitations are relaxed, animals may be able to decrease the need for and cost of trade-offs between thermoregulation and other traits. Essentially, it is possible that the currently established negative effects of high environmental temperatures on birds and other animals and their breeding may only manifest or may be more severe in the presence of resource limitation (Tieleman and Williams 2002, Tschirren et al. 2009, Rodríguez et al. 2016, Cooper et al. 2019, Bourne et al. 2020c).

There is some evidence for resource availability mediating environmental temperature effects in arid-zone species, although studies explicitly testing for it are rare. Measurements of T_b in free-ranging White-browed Sparrow-weavers (*Plocepasser mahali*) in the Kalahari Desert showed that thermoregulation was significantly more precise in a wet summer compared to a dry summer, suggesting a significant effect of rainfall and perhaps consequent increased resource availability on thermoregulatory ability (Smit et al. 2013). In terms of breeding, at the scale of individual breeding attempts, reductions in nestling growth rates and body condition at fledging under high environmental temperatures are partly driven by reduced provisioning rates (i.e., the number of provisions per time unit) or efficiency (i.e., the biomass provisioned per time unit), suggesting a potential influence of resource availability (Cunningham et al. 2013a, Wiley and Ridley 2016, Oswald et al. 2021). Some studies have shown a negative effect of high environmental temperatures on breeding only in the absence of drought, but not in normal or high rainfall years. For example, the body condition of White-plumed Honeyeaters (*Ptilotula penicillatus*) declined significantly with an increase in the number of days in the summer exceeding 35 °C, which led to a significantly reduced annual survival rate, but only in drought conditions (Gardner et al. 2016). In Southern Pied Babblers (*Turdoides bicolor*) juvenile growth, mass maintenance in adults and survival of both juveniles and adults were severely reduced in hot, drought years, compared to hot years without drought (Bourne et al. 2020c). These cases suggest that resource availability or quality plays an important role in mediating the relationships between high environmental temperatures and breeding performance.

1.4 Southern Yellow-billed Hornbills and the Kalahari Desert

To contribute toward knowledge concerning the effects of resource availability and how it influences the established negative effects of high environmental temperatures on breeding performance, I studied a desert population of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hereafter hornbills). In the arid, seasonally hot, south-western Kalahari Desert, hornbills initiate breeding in response to rainfall which coincides with the hottest period of the year (Kemp 1995, van de Ven et al. 2020b). They are cavity nesters, although their breeding strategy is unusual; the female seals herself inside the nest cavity for the majority of the breeding attempt. The seal is created from sand, faeces, and arthropods such as millipedes, leaving only a small slit for the sole-provisioning male to feed her and their offspring (Kemp 1995, Chan et al. 2007). The female seals in at the start of the breeding attempt and remains incarcerated until her flight feathers have regrown and the chicks are old enough to seal the entrance again once she breaks out (57 ± 7 SD days (n = 27, range 49 – 76) in nests that successfully produce at least one fledgling; van de Ven (2017)). During her incarceration, the female lays eggs asynchronously, laying one approximately every two days, for a typical total of 2 – 6 eggs (Finnie 2018). These then hatch asynchronously. During incarceration, around the time that the first egg is laid, the female also undergoes a catastrophic moult of all of her flight feathers, creating an overlap between moult and breeding (van de Ven et al. 2020b).

Laboratory measurements have indicated that the upper limit of the thermoneutral zone (the range of environmental temperatures where an organism does not require regulatory changes in its metabolic heat production or evaporative heat loss to maintain T_b) for these hornbills is ~39 °C (van Jaarsveld et al. 2021). The heat tolerance limit (the maximum sub-lethal environmental temperature an organism can tolerate during acute heat exposure having reached its maximum evaporative cooling capacity (Whitfield et al. 2015)), inside respirometry chambers is ~50 °C, at which point the hornbills reach thermal endpoint T_b of ~45 °C (van Jaarsveld et al. 2021). Interestingly, thermoregulation between the sexes differs, with females expending significantly less energy and water to maintain the same T_b as males at the same chamber temperature during laboratory experiments (van Jaarsveld et al. 2021). Ambient temperature in respirometry chambers more closely approximates environmental temperature than T_{air}, so caution must be applied comparing these values directly to T_{air} or T_{nest} in the wild (Cunningham et al. 2021).

In my study population of hornbills at Kuruman River Reserve, South Africa (26°58′ S, 21°49′ E), which has been monitored since 2008, the mechanistic links between high environmental temperatures and reduced breeding success are well-documented (van de Ven et al. 2019, van de Ven et al. 2020b, van Jaarsveld et al. 2021). Variation in breeding performance appears largely driven by direct effects of high nest temperatures (T_{nest}) on incarcerated females and chicks (van de Ven et al. 2020b). However, several lines of evidence suggest possible significant influences of resource availability – where 'resource' refers to both energy and water: hornbills do not drink open water, they acquire both energy and water from their food (Witman and LaGreco 2020). Firstly, similar to other arid-zone species (e.g., Catry et al. 2011, Cunningham et al. 2013b, Wiley and Ridley 2016, Bourne et al. 2020b), breeding success in hornbills is also affected via indirect effects of T_{air} on provisioning rates (van de Ven et al. 2019, van de Ven et al. 2020b). The effect of T_{air} on breeding for various birds suggests that high T_{air} creates a trade-off between self-maintenance (including critical thermoregulatory processes) and provisioning (Ydenberg 1994, Cunningham et al. 2013a, Wiley and Ridley 2016, van de Ven et al. 2019), but raises the possibility that higher resource availability could reduce the severity of that trade-off for the provisioning parent and therefore the impact of high T_{air} on breeding success. Secondly, failure to hatch or fledge in hornbills is usually because of cannibalism; the female consumes her own eggs or nestlings (Engelbrecht 2013, Finnie 2018). This may suggest that at high T_{nest} dehydration, malnutrition, or some other source such as injury or disease, exacerbated by the high temperature conditions, kills eggs or nestlings (Catry et al. 2015, Bourne et al. 2020b, Bourne et al. 2021, McCowan and Griffith 2021), in which case the female consumes the already dead eggs or nestlings to recoup resources and / or prevent issues associated with the carcass remaining in the nest cavity (the sealed entrance makes it impossible for the deceased offspring to be removed from the nest). Alternatively, limited resources for thermoregulation and self-maintenance may reduce the female parent's ability to raise a large brood or maintain condition, in which case she cannibalises live offspring for brood reduction or to avoid starvation (Chan et al. 2007, Ng et al. 2011). High resource availability, contingent on increased provisioning of more abundant or higher quality food (and indirectly, water) by the free-ranging male parent, may lessen potential trade-offs between thermoregulation and reproduction in the female parent. Consequently, the likelihood that high T_{nest} will result in cannibalism to recoup resources for thermoregulation would be reduced. Thirdly, the period during which chicks develop thermoregulation overlaps with other important stages of growth and development (Marrot et al. 2017), meaning resource limitation has huge potential to aggravate trade-offs between thermoregulation and somatic investment (Conway and Martin 2000b, Salaberria et al. 2014). Furthermore, although hornbill females exit nests with similar M_b regardless of variation in M_b at the beginning of the nest attempt, breeding success or failure, or time spent in the nest (van de Ven 2017), there may be long-term breeding effort costs other than nest exit M_b to females (i.e., quality of feathers grown post catastrophic moult, corticosterone [CORT] levels) (Hemborg and Lundberg 1998). Overall, these traits combine to make hornbills an excellent taxon on which to test the possibility that resource availability mediates high environmental temperature effects.

Notably, up until the start of data collection for this study, the nest boxes that the hornbills bred in at my study site were uninsulated, orientated in various directions at various heights off the ground, and often exposed to direct sunlight during the hottest periods of the day (Finnie 2018, van de Ven et al. 2020b). Prior to the start of the 2019/2020 breeding season in this study, all the nest boxes were refurbished, insulated, painted a similar colour to the grey-brown bark of the camelthorn trees (*Vachellia erioloba*) on which they were placed, and orientated south-east (placing them in the shade at the hottest periods of the day) approximately 1.5m off the ground. This served two purposes: first, based on the trajectory of breeding in the previous nest boxes (see Chapter 5), leaving the nest boxes as they were (i.e., some in very exposed microsites, reaching high T_{nest} during the hottest parts of the day) risked there being little successful breeding at all for this study; second, it standardised the nest box placement and design to reduce ‘noise’ introduced by large variability between nests, allowing investigation of the effects of temperature and resources without large confounding effects of nest box design and placement. The change then allowed for a comparison in nest box thermal conditions between the present study, previous studies on this population, as well as data previously collected for natural cavities at the field site. That comparison then allowed for determination of whether the new nest box design was effective at creating more natural, cooler thermal nest environments for the hornbills (Griffiths et al. 2017, Maziarz et al. 2017, Larson et al. 2018, Briggs and Mainwaring 2021), which would help improve the ecological relevance of the data collected.

1.5 Natural variation and a supplementary feeding experiment at Kuruman River Reserve

I monitored environmental variables (T_{air}, T_{nest}, rainfall, wind speed) at the study site, which allowed me to correlate variation in the reproductive ecology of the hornbills to environmental variation. However, to experimentally investigate the role of resource availability, I conducted a supplementary feeding programme. Lack (1968) proposed that various facets of reproduction have evolved primarily in response to resource availability during the nestling period. Providing supplementary food affects both energy and hydration, since hornbills do not drink open water and acquire all their water from their diet (Witman and LaGreco 2020). Therefore, throughout the thesis supplementary food will be referred to as manipulation of ‘resource’ availability, rather than just food availability, where ‘resource’ refers to the combination of energy and water provided by the supplementary food. Supplementary feeding provides a mechanism for understanding both the role of resource availability, and its interaction with temperature, on reproductive performance (Pendlebury et al. 2004). Therefore, supplementary feeding experiments present a means of teasing apart the potential effects of both increasing temperatures and changes in resource (i.e., energy and water) availability associated with climate change (Tieleman and Williams 2002, Ruffino et al. 2014). This understanding is vital for predicting avian vulnerability to climate change (Wellicome et al. 2013), and for developing conservation management strategies (Gonzalez et al. 2006, Schoech et al. 2008, Herring et al. 2011).

Food supplementation and limitation experiments have indicated that resource availability at least partly drives patterns in reproductive performance (i.e., laying date, clutch size, hatching success, nestling development, and fledging success and survival), stress hormone responses, and the behaviour of parents in many avian taxa

(Martin 1987, Robb et al. 2008, Ruffino et al. 2014). Increased resources bring laying dates forward (Arcese and Smith 1988, Schoech et al. 2008), increase clutch size (Clifford and Anderson 2001, Illera and Díaz 2006), increase egg quality and size (Wiebe and Bortolotti 1995, Reynolds et al. 2003), and improve hatching success, nestling growth and condition (Korpimäki 1989, Simons and Martin 1990, Arnold 2011, Haley and Rosenberg 2013, Wellicome et al. 2013), as well as fledging success and post-fledge survival (Soler and Soler 1996, Robb et al. 2008). Food supplementation can also reduce circulating plasma and feather corticosterone (Kitaysky et al. 2001, Schoech et al. 2008, Sears and Hatch 2008, Herring et al. 2011, Will et al. 2014, Patterson et al. 2015, Fitzsimmons et al. 2017). Chronic elevated corticosterone levels can be highly detrimental to an individual, so reduced levels may confer significant fitness benefits (Fitzsimmons et al. 2017, Salleh Hudin et al. 2017). Provision of supplementary resources can allow adult birds to invest more in self-maintenance, and reduce energy and time expended on reproduction or other costly activities (Martin 1987, Cook and Hamer 1997, Harding et al. 2002, Tieleman and Williams 2002, Robb et al. 2008, Olinger 2017). Therefore, adults with access to supplementary food (or parents of nestlings which receive supplementary food) may benefit from a reduced distance to foraging patches, and the ability to display higher prey selectivity (Grieco 2002, Tremblay et al. 2005). Ultimately, adults with access to supplementary food often benefit from better body condition (e.g., Tieleman and Williams 2002), and enhanced reproductive performance as a result of increased investment in reproduction afforded by increased availability of energy and time (Robb et al. 2008).

T_b regulation should also vary with resource availability, especially in hot environments where resource availability partly dictates the hydration state of individuals, and therefore their ability to evaporatively cool (Angilletta et al. 2010). Therefore, supplementary feeding should also affect T_b regulation. Interestingly, despite the importance of understanding patterns in T_b regulation in the context of evolutionary ecology (Boyles et al. 2011), little is known about T_b during heat exposure in wild birds (Ardia et al. 2010, Smit et al. 2013). In wild birds, T_b regulation has been monitored primarily in temperate species (Haftorn and Reinertsen 1990, Bize et al. 2007, Ardia et al. 2010, Møller 2010, Nilsson and Nord 2018). One of the only studies available for wild birds in a hot, arid-zone is on non-breeding white-browed sparrow-weavers (*Plocepasser mahali*) (Smit et al. 2013). These birds did not receive supplementary feeding. However, a seasonal comparison of fluctuations in T_b (heterothermy index, see Boyles et al. 2010) within a population revealed that thermoregulation was significantly more precise in a wet summer compared to a dry summer (Smit et al. 2013). This suggests that higher resource availability (i.e., higher food and water availability associated with higher rainfall) allowed more precise thermoregulation (Smit et al. 2013). The effects of the interaction between temperature and resource availability on thermoregulation in wild birds, especially from arid zones in summer and while breeding, requires further attention.

The effects of supplementary feeding depend on the general range, abundance, and quality of resources available in the environment (Schoech et al. 2008, Haley and Rosenberg 2013). In systems or seasons where resources are not limiting, supplementation would not be predicted to have a significant effect (Tremblay et al. 2005, De Neve et al. 2007, Ruffino et al. 2014). However, considering the low resource availability and high thermoregulatory demands typical of arid zones, resource supplementation could be expected to have a significant effect (Tieleman and Williams 2002, Illera and Díaz 2006). For example, brood loss in burrowing owls (*Athene cunicularia*) varies substantially between years, but is minimised by both supplementary feeding, and in years where their primary prey (small mammals) is plentiful (Wellicome et al. 2013). Supplementary feeding would be expected to have a significant influence on the reproductive physiology and behaviour of summer breeding, arid-zone birds, given the high demand on energy and water (Tieleman and Williams 2002, Illera and Díaz 2006).

The supplementary feeding in this study began the day of or day after females laid their first egg. Feeding stations (a small wooden box ~1.5m off the ground with one transparent side facing the nest for the hornbills to see the contents and a lid with a small slit made from duct tape for the hornbills to push their beaks through) were set up

~2.5m from nests. After several iterations this feeder design was chosen because it ensured other birds were prevented from accessing the food or the supplementary prey escaping; other species did not have the strength to push through the duct tape, or long enough bills to reach the larvae. However, the hornbills could easily learn to use the feeders and access all the supplementary food provided. As breeding attempts began, they were alternately assigned to either high supplementation (high supp.) or low supplementation (low supp.) treatments as they started. Essentially, the first breeding attempt of the breeding season was assigned to high supp., the second attempt to start was assigned to low supp., the third to start to high supp., and so on. This meant that treatments were assigned equally to each supplementation treatment over a range of nest initiation dates. In the morning every day, nests on the high supp. treatment were provided ~25g of live darkling beetle *Zophobias morio* larvae (30 individual larvae, = ~10% average hornbill male body mass and 100% of mean daily biomass provisioned by male hornbills in previous studies on this population (van de Ven 2017)), while nests on the low supp. treatment were provided ~5g (7 individual larvae) via the feeding stations. The low supp. treatment provided several benefits of the feeding process, including standardising the daily visitation and feeding procedure to all nests, standardising a habituation process associated with visitation and feeding, and providing a location and setup useful for capturing the male hornbills, which were easy to capture using spring traps next to the feeders. However, the amount of food given was designed to be as low (~2% of adult M_b) as possible while garnering those benefits. Therefore, while the low supp. birds did receive food, the treatment was designed to be close to an experimental ‘control’ in that the amount of food (and water) was designed to be too small to significantly affect the reproductive ecology. However, due to sample size constraints, this experimental design did not have a ‘true’ control group of birds visited in the same way as though receiving food, but not fed any food, and the findings should be considered in that context. Future work should be designed to overcome this constraint. Observations of male hornbills showed that they learned to use the feeding stations within two days of them being installed. Males were usually observed for at least 5-15 min in the morning immediately after the supplementary food was provided, to observe the supplementary food provisioning behaviour. These observations showed that males usually immediately provisioned all the supplementary food to the nest, although occasionally the high supp. males consumed < 5 larvae themselves once they had provisioned the majority to the nest. Once the females broke out of the nest they assisted males in provisioning the nest. However, observations showed that females did not ever access the supplementary feeders, and the males remained the ones which accessed the supplementary food and provisioned it to the chicks.

The study site was a private reserve in the Northern Cape of South Africa (Kuruman River Reserve; 26°58′ S, 21°49′ E; hereafter KRR). The KRR is within the Kalahari Desert and is dominated by arid grassland interspersed with large trees, mostly camelthorn (*Vachellia erioloba*). Rainfall occurs primarily in the Austral spring and summer between October and April; rainfall amount varies significantly between years (Bourne et al. 2020a). The October to April period is hot, with mean daily maximum T_{air} typically > 34 °C (van de Ven et al. 2019). Research on hornbills at KRR has been ongoing since 2008.

This study was originally designed to investigate the effects of experimental, supplementation manipulation over the course three of similar breeding seasons, to build up sufficient sample sizes in each treatment for sound statistical comparisons. However, the stochastic nature of the environment, likely exacerbated by recent climate change trends to a higher frequency of extreme weather events, led to complete breeding failure in the 2018/2019 breeding season, in which a heavy drought led to no hornbill nesting attempts being made. The subsequent 2019/2020 and 2020/2021 breeding seasons were vastly different from each other in terms of weather conditions. The 2019/2020 breeding season saw rainfall and T_{air} similar to long term averages for the study area, while the 2020/2021 breeding season experienced extraordinary rainfall causing a one-in-100 year flood through the field site and abnormally low T_{air}[1]. Flooding in 2020/2021 resulted in the Kuruman River flowing for the first time since 1974. At the height of the flood, lasting ~4 weeks, the river was 3 m deep and only crossable by boat. This unprecedented natural variation altered the original study design and

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[1] https://www.sabcnews.com/sabcnews/excitement-as-kuruman-river-flows-after-more-than-4-decades/

demanded a retrospective comparison between a ‘hot and dry’ 2019/2020 and a ’cool and wet’ 2020/2021 breeding season.

The hornbills at the KRR are partially habituated (i.e., generally accustomed to humans, but not trained or completely unwary around humans), and typically breed between October and the end of March (van de Ven et al. 2020b). Wooden nest boxes were available at KRR throughout the study period for the hornbills to breed in (43 boxes 2008 – 2011, 44 boxes 2012 – 2015, 38 boxes 2015 – 2017, 33 boxes 2017 – 2018, 36 boxes 2018 – 2019, 50 boxes 2019 – 2021).

1.6 Objectives, aims, and study design

With ongoing climate warming, numerous studies have focussed on identifying the negative effects of high environmental temperatures on the ecology of arid-zone birds (e.g., Pattinson et al. 2020, Cunningham et al. 2021, Riddell et al. 2021, Sharpe et al. 2021). However, the potential for resource availability to mediate environmental temperature effects has remained less well-studied, despite the possibility that for some arid-zone species high environmental temperatures are currently only limiting because of concurrent low resource availability (Tieleman and Williams 2002, Gardner et al. 2016, Mares et al. 2017, Bourne et al. 2020c, Czenze et al. 2020). Essentially, the knowledge gap that motivated this PhD was that the established effects of high environmental temperatures on birds to date have predominantly been studied without explicitly testing for the potential influence of resource availability. However, life history theory suggests that resources should have a significant role in trade-offs between costly traits such as between thermoregulation and activity or development (Kiat and Sapir 2018, de Zwaan et al. 2019).

Therefore, my overall main objective was to determine the role of resource availability (both naturally varying and experimentally manipulated) in the established relationships between high environmental temperatures and the behaviour, physiology, morphology, and breeding outcomes of a spring and summer breeding arid-zone bird. Determining this would disentangle the independent effects of high environmental temperatures and resource availability on arid-zone avian ecology and shed light on the vulnerability of arid-zone birds to rising environmental temperatures. Finally, while studies on short-term effects have proliferated (e.g., within a single breeding season), fewer studies investigate these impacts on population-level breeding outputs over longer timescales in relation to ongoing climate change trends. Therefore, a secondary objective was to determine patterns in the breeding success of an arid-zone bird over a decade-long period of rapid climate warming. This would contribute to a broader understanding of the potential longer-term, population level effects of climate warming on arid-zone birds.

I attempted to achieve these overarching objectives in four data chapters. The individual aims of each chapter are summarised below:

Chapter 2: Effects of air temperature and resource availability on the breeding behaviour and thermoregulation of male desert-dwelling hornbills

Focusing on breeding male hornbills, I aimed to assess the role of resource availability in mediating the relationships between T_{air} and provisioning behaviour and T_b regulation, and to quantify the effect of T_{air} on free-ranging heart rates (as a proxy for metabolic demands).

Chapter 3: Interannual climate variation and resource availability affect breeding success and thermoregulation, but not morphology, in nesting female hornbills

Monitoring breeding attempts and focusing on the influence of breeding female hornbills, I aimed to assess the role of resource availability on the relationship between T_{nest} and hatch and fledge probability, and female parent T_b regulation, morphometrics, and body condition (i.e., M_b, feather quality, and feather CORT).

Chapter 4: Improved thermoregulation with increased resource availability does not buffer against negative effects of high nest temperatures on chicks of an arid-zone bird

Looking specifically at hornbill chicks which successfully fledged, I aimed to determine potential effects of resource availability and T_{nest} on growth, thermoregulation, and fledging condition (i.e., M_b, structural size, feather quality, feather CORT).

Chapter 5: Collapse of breeding success in desert-dwelling hornbills evident within a single decade

The overall aim was to describe the response of an arid-zone bird, the Southern Yellow-billed Hornbill, to a decade-long period of rapid climate warming, identify potential drivers of variability in breeding performance, and empirically demonstrate likely mechanistic links between climate change and collapse of breeding output.

The data for Chapters 2, 3, and 4 were collected simultaneously over the course of each breeding season. All breeding data for Chapters 2, 3, and 4 were necessarily collected from hornbills breeding in nest boxes (no data were collected from natural cavities, accessing these nests is impossible because of the hornbill's unique behaviour of sealing up the nest entrance during breeding). The study design and data collection setup for each breeding season was as follows (Figures 1.1 and 1.2):

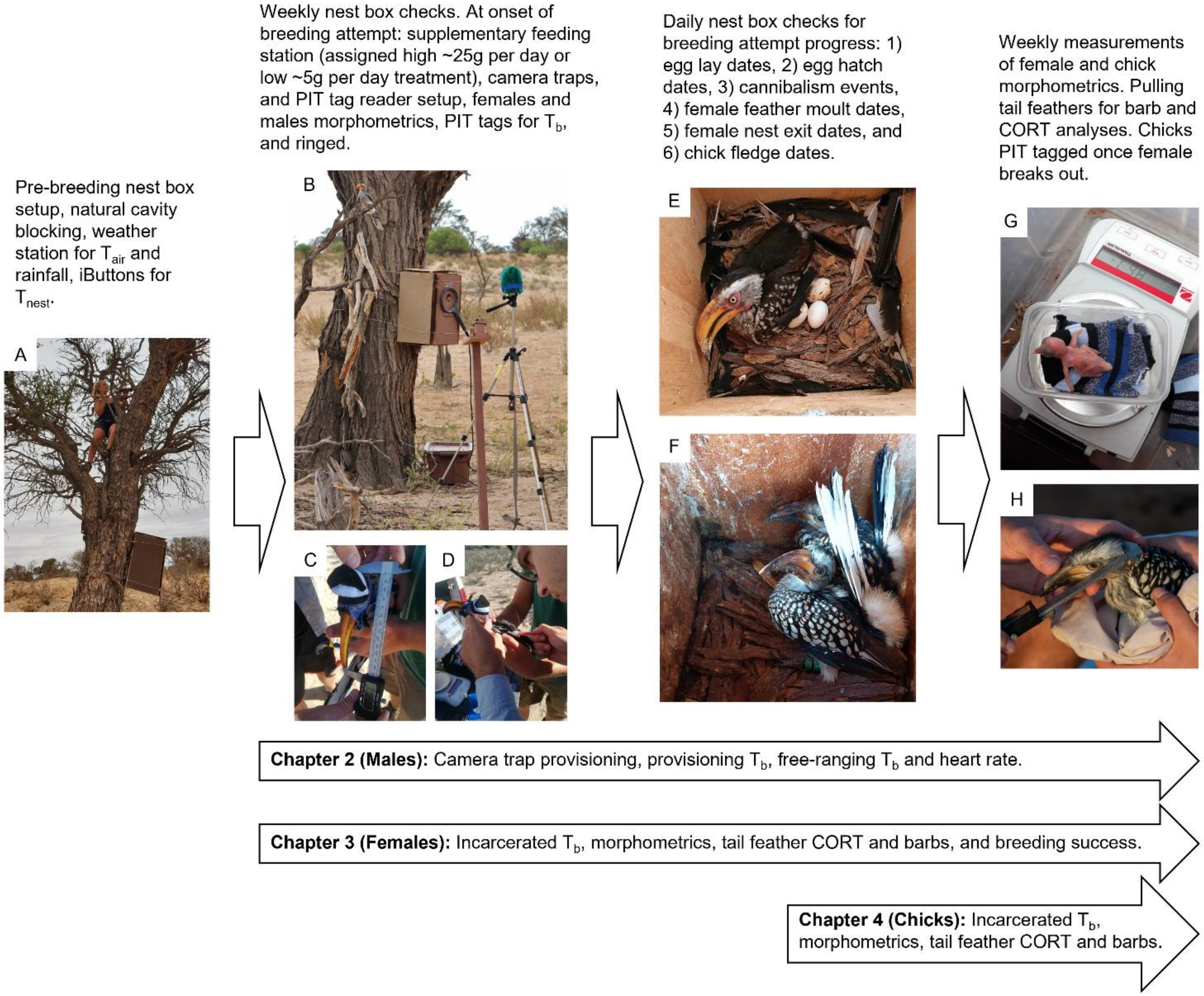
- A weather station at the site, the Hot Birds Research Project (HBRP) weather station, was active continually through the year. The station collected T_{air}, rainfall, and wind speed data every ten minutes to inform analyses for Chapter 2 (and Chapter 5).
- Prior to the hot and dry (2019/2020) breeding season I constructed or repaired and insulated 50 nest boxes and put them up across the field site. These were constantly maintained. This nest box redesign was done, firstly, to combat the increasing T_{nest} associated with breeding failure that may have led to no breeding data being collected (see Chapter 5), secondly, to standardise the nest box design for all breeding pairs and reduce variation in T_{nest}, and thirdly, to make the nest boxes more similar to natural cavities for a more meaningful biological

comparison (see Chapter 3). The effects of the change are analysed and discussed in Chapter 3. When a hornbill pair was found to be prospecting a natural cavity, the cavity was blocked, and a nest box moved to the same tree to encourage the pair to use the nest box instead.

- From the beginning of October each breeding season, I would begin monitoring nest boxes once per week to track when breeding attempts were about to begin. The hornbills would prospect a nest box by beginning to build a seal in the entrance. Once interest in a box was confirmed, I would install a Thermochron Hi-Res iButton (DS1922-L, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, accuracy ± 0.5°C) inside the box to measure T_{nest} (for Chapters 3 and 4). I would also begin monitoring the nest more closely to get the exact date a female sealed herself inside the box. This signalled the beginning of the breeding attempt. In many cases hornbill pairs would add bark nest material to boxes and begin a seal at the start of the breeding season, sometimes at more than one box simultaneously, without ever committing to the nest. These behaviours were therefore classified as ‘prospecting’ rather than ‘nest building’. The completion of the seal and incarceration of the female was the best indicator that a breeding attempt had indeed been properly initiated.
- Once a breeding attempt began, I visited nests once per day and took a photo of the contents via a removable lid on the nest boxes to see when the female laid the first egg. Photos were taken by sliding a smartphone under the lid (keeping the lid mostly closed with just a small gap for the phone) and taking a picture with no flash. I did not look inside to minimise disturbance and the risk of the female or chicks escaping the nest box during checks. Immediately after the female laid the first egg, I: 1) set up a supplementary feeding stations and assigned a supplementary resource treatment – resource supplementation happened every morning for the rest of the breeding attempt; 2) captured the females so that they could be colour-ringed, injected them with a passive integrated transponder (PIT) tag to measure T_b, and took morphometric measurements; 3) captured the males to be colour-ringed, inject with a PIT tag, and take morphometric measurements; 4) set up a camera trap (where available, only 5 camera traps were available and

rotated between nests) at the nest to monitor male provisioning visitations; and 5) set up a PIT tag reader (where possible, only 3 were available and rotated between nests) at the nest to monitor the T_b of the female inside the box and of the male upon visiting the nest (provisioning T_b). After these actions had been completed, daily supplementary feeding (Chapters 2-4), and data collection for provisioning rate and T_b of the males (Chapter 2), and T_b for the females (Chapter 3), were under way. Females were returned to nests, and males released at the nest, immediately after capture.

- Thereafter, the nests were visited once per day to take a photo of the contents of the nest to keep track of the progress of the attempt. Checks allowed recording of the dates of 1) egg lay, 2) egg hatch, 3) cannibalism events, 4) female feather moult, 5) female nest exit, and 6) chick fledge. These data were used to inform nest stage, used for male provisioning rate analyses (Chapter 2) and breeding success analyses (Chapter 3).
- When the female laid the first egg, and once a week thereafter, morphometric measurements were taken from the female. This provided the data for the morphometric analyses for the females (Chapter 3). After approximately 4 weeks since nest initiation (i.e., when the female sealed in the nest box), a tail feather was pulled from the females for the feather corticosterone (CORT) and feather barb density analyses (Chapter 3).
- Once a chick hatched, morphometric measurements were taken on chicks once per week (Chapter 4). After approximately 6 weeks since hatching, a tail feather was pulled from the chicks for feather CORT and feather barb density analyses (Chapter 4).
- Once a female exited the nest, the oldest chick was injected with a PIT tag to measure chick T_b in the nest (Chapter 4).
- In the second breeding season (cool and wet 2020/2021), six males were captured to have data storage tag heart rate and temperature loggers (DST micro-HRT logger; Star-Oddi, Gardabaer, Iceland) implanted to measure T_b and heart rates throughout the 24hr cycle – i.e., not just when they visited the nest (Chapter 2).



Pre-breeding nest box setup, natural cavity blocking, weather station for T_{air} and rainfall, iButtons for T_{nest}.

Weekly nest box checks. At onset of breeding attempt: supplementary feeding station (assigned high ~25g per day or low ~5g per day treatment), camera traps, and PIT tag reader setup, females and males morphometrics, PIT tags for T_b, and ringed.

Daily nest box checks for breeding attempt progress: 1) egg lay dates, 2) egg hatch dates, 3) cannibalism events, 4) female feather moult dates, 5) female nest exit dates, and 6) chick fledge dates.

Weekly measurements of female and chick morphometrics. Pulling tail feathers for barb and CORT analyses. Chicks PIT tagged once female breaks out.

Chapter 2 (Males): Camera trap provisioning, provisioning T_b, free-ranging T_b and heart rate.

Chapter 3 (Females): Incarcerated T_b, morphometrics, tail feather CORT and barbs, and breeding success.

Chapter 4 (Chicks): Incarcerated T_b, morphometrics, tail feather CORT and barbs.

Figure 1.1. Schematic showing the study design and points of data collection over the course of a breeding season. Data for Chapters 2, 3, and 4 were collected simultaneously as breeding attempts progressed. Images show A) nest box setup (with iButtons for measuring nest temperature (T_{nest})) and natural cavity blocking, B) nest box, passive integrated transponder (PIT) tag reader for measurement of body temperature (T_b), camera trap, and supplementary feeding station setup (high and low supp. treatments), C) Southern Yellow-billed Hornbill (*Tockus leucomelas*) morphometric measurement, D) inserting PIT tag, E) female post-moult with eggs in nest box, F) ringed chicks close to fledging, G) measurement of chick body mass (M_b), and H) morphometric measurements of chicks, and pulling of a tail feather for corticosterone (CORT) analysis.

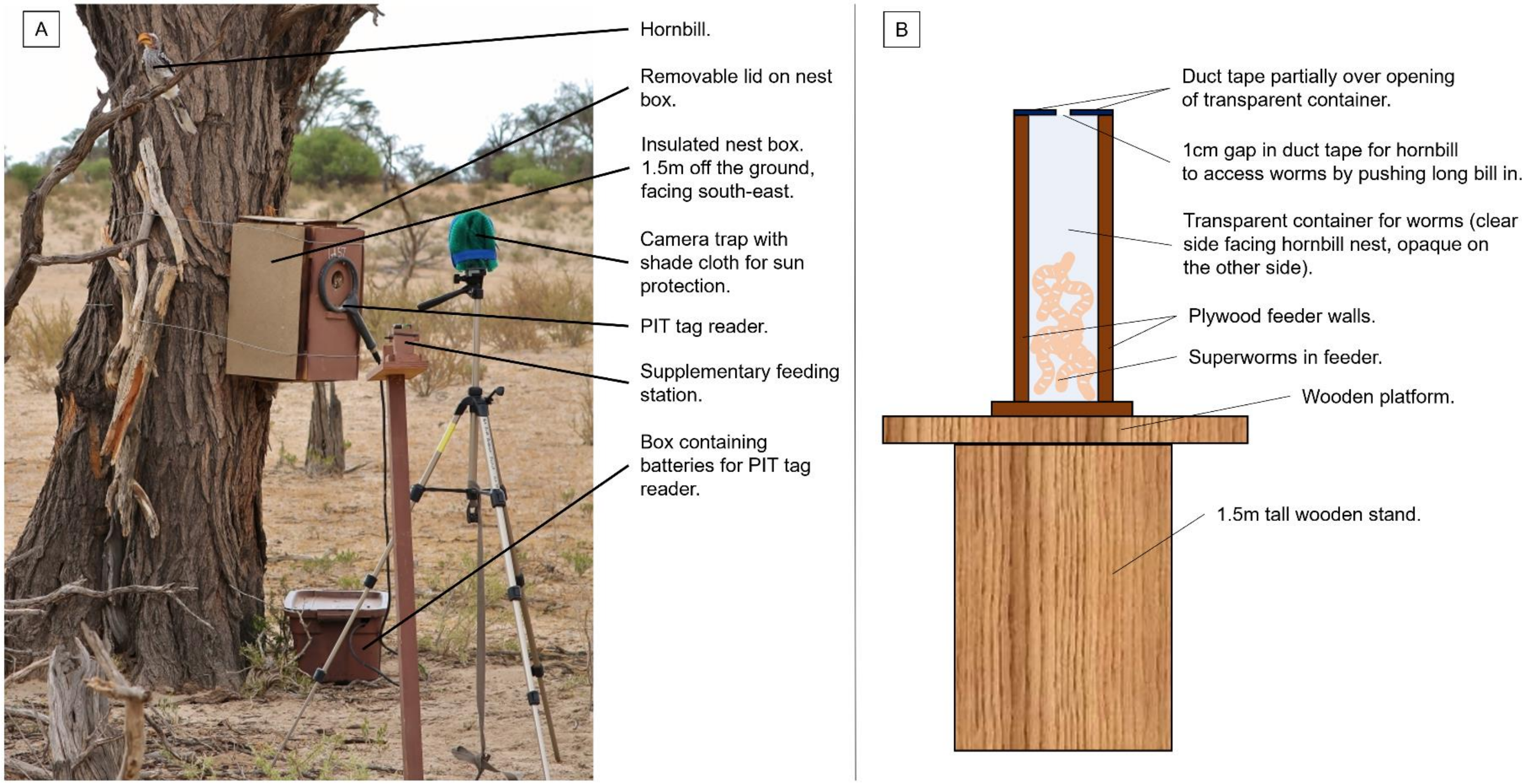


Figure 1.2. Annotated A) picture showing the typical setup to monitor breeding and collect data on the provisioning behaviour, body temperature (T_b), morphology, and breeding success of Southern Yellow-billed Hornbills (*Tokus leucomelas*) in insulated nest boxes placed on trees ~1.5m off the ground and facing south-east, and B) diagram showing the design of the supplementary feeding stations, which allowed hornbills to access the food while excluding access to non-target species.

1.7 Mixed modelling approach

Throughout this thesis statistical analyses were conducted in the R statistical environment, version 3.5.1 (R Core Team 2023), using the R Studio platform (R Studio Team 2023). Each chapter includes mixed modelling using the package lme4 (Bates et al. 2015). Mixed modelling followed one of three approaches depending on sample size and detectable effect size (i.e., the effect size detectable with a given sample size calculated by the package pwr (Champely 2020) based on the concept that f^2 ~ 0.02, ~0.15, and ~0.35 represent small, medium, and large effect sizes respectively (Cohen 2013)) and model stability:

1) **Sufficient sample size and stable models**: Where the sample sizes were sufficient to include interaction terms (Cohen's $f^2 \leq 0.35$ for interactions based on calculating the determinable effect size in the package pwr; Champely 2020) and inclusion of a random effect did not destabilise models, a candidate set of five models was built for each response variable. Each candidate model included independent variables predicted *a priori* to be biologically informative and bird identity as a random effect: i) a full model with all variables of interest and interaction terms between temperature (T_{air}, T_{max}, or T_{nest}) and breeding season, and between temperature and resource supplementation, ii) a model with all variables of interest and an interaction between temperature and breeding season, iii) a model with all variables of interest and an interaction between temperature and resource supplementation, iv) a model with all variables of interest but with no interaction terms, and v) the null model. I used variance inflation factors (VIF) in package car (Fox and Weisberg 2019) to test for collinearity between explanatory variables. However, because I was interested in whether resource availability could moderate environmental temperature effects, I fit interaction terms between temperature and breeding season, and between temperature and resource supplementation regardless of VIF (see Disatnik and Sivan 2016).

2) **Insufficient sample size for interactions and unstable models**: Where the sample size was large enough to fit multiple fixed effects ($f^2 \leq 0.35$) but the power to detect interaction terms was lower than recommended to detect large effects ($f^2 \geq 0.35$; Champely 2020), a single model including all fixed effects determined *a priori* to be biologically informative was fit. No model selection was performed; results from this model were reported. Inclusion of random effects in these models made them unstable due to convergence or singular fit issues (overfit due to small sample sizes). Therefore, after careful examination of potential pseudoreplication issues, the random effects were excluded to simplify and stabilise the models (e.g., Wilson et al. 2019, Wang et al. 2020, Burrow and Maerz 2021, Larue et al. 2021, Liebherr et al. 2021, Höfer et al. 2022) following recommendations to simplify the mixed modelling approach by removing random effects in the event of singular fit issues (Heise et al. 2022, Murphy et al. 2022). I carefully assessed the datasets, and in all cases pseudoreplication was minimal. For Chapter 3, only three females (of a total sample of 17 females) bred in both breeding seasons, such that there was a single data point for the majority of females. For Chapter 4, three nests had a single fledgling, five nests had two, five had three, and a one nest had four fledglings. These low numbers of repeat measures per female and per nestbox / brood likely explain the singular fit errors caused when attempting to fit random effects for these models. To further assess the potential impact of omitting female and brood identity as random effects, I also performed some exploratory analyses (not shown) testing these variables as fixed effects instead (where possible without destabilising models). These exploratory analyses suggested no significant variation in responses was predicted by female identity or nestbox/brood identity e.g., female identity had no significant effect on egg hatch probability ($p = 0.142$) or chick fledge probability ($p = 0.190$), and nestbox/brood identity had no significant effect on the days spent in the nest by chicks ($p = 0.284$) or chick tail feather growth rate ($p = 0.680$). Nonetheless, the results of models where no random effect could be specified should be interpreted in that context (for more details see the Statistical Analyses

sections of Chapters 3 and 4). These simpler models still provide insights into relevant patterns (McNabb and Murayama 2021).

3) **Small sample sizes**: Where the sample size was small and the power to fit multiple fixed effects or interaction terms was lower than recommended to detect large effects ($f^2 \geq 0.35$; Champely 2020), models were further simplified by modelling each main effect individually with no random effect. This approach had similar drawbacks to approach (2) above and was the most simplified, but still provided basic insights.

For approaches (1) and (3), model selection was performed by comparing the candidate model set using the model.sel function in package MuMIn (Barton 2020). For approach (1) results for the top model were reported. However, where more than one model was within ΔAICc <2, they were averaged in package MuMIn (Barton 2020) and the model average reported. For approach (3), the results from all models with Δ AICc <2 were reported. In each case, I report the statistical power of each model set to detect main fixed effects and interaction effects, as calculated using the package pwr (Champely 2020).

For all analyses, continuous variables were scaled for model stability, as is common practice in ecology and evolution research (Schielzeth 2010). As such, reported model estimates are standardised and do not have units on the original scale of the response variable. Residual deviance and residual degrees of freedom were estimated to check dispersion (packages DHARMa & RVAideMemoire, Hartig 2021, Hervé 2021). Where there was overdispersion in generalised linear mixed model (GLMer) models with a poisson model family, I switched to GLMer with a negative binomial model family using package MASS (Venables and Ripley 2002). Plotting was performed using packages jtools (Long 2020) and ggplot2 (Wickham 2016).

1.8 Abbreviations, acronyms and initialisms

In this thesis I use numerous abbreviations, acronyms and initialisms. For reference, they are listed here:

AIC – Akaike's Information Criterion, **AICc** – Akaike's Information Criterion adjusted for small sizes, **CI** – confidence interval, **CORT** – corticosterone, **DST micro-HRT** – data storage tag micro-heart rate & temperature, **ECG** – electrocardiogram, **GAM** – general additive model, **GLM** – generalised linear model, **GLMer** – generalised linear mixed model, **HBRP** – Hot Birds Research Project, **KRR** – Kuruman River Reserve, **LMer** – linear mixed model, $\mathbf{M_b}$ – body mass, $\mathbf{n_{lowsupp}}$ – sample size of individuals in the low resource supplementation treatment, $\mathbf{n_{highsupp}}$ - sample size of individuals in the high resource supplementation treatment, **PIT** – passive integrated transponder, **QI** – quality index, **SD** – standard deviation, **SE** – standard error, $\mathbf{T_{air}}$ – air temperature, $\mathbf{T_b}$ – body temperature, $\mathbf{T_{max}}$ – mean maximum daily T_{air}, $\mathbf{T_{nest}}$ – nest temperature, **TR** – Twee-Rivieren, **VIF** – variance inflation factors, **VZ** – Van Zylsrus.

1.9 Glossary

Corticosterone (CORT): Avian glucocorticoid hormone involved in maintaining homeostasis; also termed the avian 'stress hormone' (Wingfield and Romero 2001, Bonier et al. 2009, Wingfield 2013, Hau et al. 2016).

Environmental temperature: The temperature a passive object will equilibrate to, integrating influences of abiotic factors such as T_{air}, solar and reflected radiation, and wind, as well as biotic factors such as animal morphology, into a single-number variable. Can be thought of as the integrated thermal environment experienced by an animal (Bakken et al. 1985, Cunningham et al. 2015, Cunningham et al. 2021).

Incubation status: For the purposes of Chapter 3 of this thesis, the incubation status of the females was split into three stages: 1) when no chicks had hatched and the female was in the nest with only eggs (termed ‘incubating’), 2) post-hatch of the first chick when the female was with eggs and chicks (the female T_b during this period were not included in female T_b analyses), and 3) post-hatch of the last egg, when the female was with only chicks (termed ‘with chicks’).

Lay and hatch sequence: Hornbills lay the eggs asynchronously, which then hatch asynchronously. Lay and hatch sequence refers to the sequence in which the eggs are laid, and the sequence in which the chicks hatch.

Nest initiation: When the female sealed herself inside the nest box to begin the breeding attempt.

Nest stage: For the purposes of analysing male provisioning rates in Chapter 2 of this thesis, the breeding attempt was split into three nest stages: 1) female and eggs; when the female was incarcerated in the nest with eggs and no chicks had hatched, 2) female with chicks; when the female was incarcerated in the nest and at least one chick had hatched, and 3) chicks only; when the female had exited the nest and was assisting with provisioning to the chicks incarcerated in the nest.

Provisioning efficiency: The biomass of food brought to the nest in a given time period.

Provisioning rate: The number of times a parent brings items to the nest in a given time period.

Resource availability / quality / supplementation: Throughout the thesis I refer to the availability, quality, and supplementation of ‘resources’. Southern Yellow-billed Hornbills do not drink from open water sources – all the water they get is from their diet. Therefore, in reference to the hornbills and this thesis, I use ‘resources’ to refer to food and water. Other ‘resources’ such as shade, potential breeding mates, or nest sites are not included. Throughout the thesis, ‘resources’ refers explicitly to food and water for the hornbills, unless specifically stated to be otherwise.

T_{air}: Atmospheric air temperature (T_{air}) as measured at the weather station by a probe sheltered within a Stevenson screen. T_{air} is the temperature of the air with influences from solar radiation etc excluded. It is not a synonym for environmental temperature (Cunningham et al. 2021).

T_b: Body temperature (T_b) as measured by either passive integrated transponder (PIT) tags injected beneath the skin between the scapulae, or by data storage tag micro-heart rate & temperature (DST micro-HRT) loggers surgically implanted in the body cavity.

T_{air} or T_{nest} break-point: The T_{air} or T_{nest} at which T_b showed a significant change in slope in its relationship with T_{air} or T_{nest}.

T_{max}: Daily maximum air temperature (T_{air}).

T_{nest}: T_{air} within the nest (T_{nest}) measured using Thermochron Hi-Res iButtons (DS1922-L, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, accuracy ± 0.5°C) mounted within the nests on the underside of the nest box lids in plastic iButton wall holders.

2. Effects of air temperature and resource availability on the breeding behaviour and thermoregulation of male desert-dwelling hornbills

N.B. Pattinson

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2.1 Abstract

Southern Yellow-billed Hornbills (*Tockus leucomelas*; hornbills) breed during the hottest period of the year in the Kalahari Desert. Because of rapid climate warming, they are facing increasingly difficult breeding conditions associated with the progressively severe negative effects of high environmental temperatures. This study used breeding male hornbills as a model to investigate (partially experimentally through supplementary feeding) the potential influence of resource (i.e., food and water) availability on the established relationships between air temperature (T_{air}) and the breeding behaviour and thermoregulation of an arid-zone bird. The study took place over two breeding seasons, retrospectively defined as a hot and dry (mean daily maximum T_{air}, T_{max} = 34.2 °C ± 3.8 SD, rainfall = 130.6mm; 2019/2020) and a cool and wet (T_{max} = 33.1 °C ± 3.1 SD, rainfall = 328.9mm; 2020/2021) breeding season. The daily number of nest provisioning attempts (hereafter 'provisioning rate') by breeding male hornbills were significantly higher in the cool and wet breeding season (estimate 0.31 ± 0.14 SE, $p = 0.031$; estimates do not have units, since continuous predictor variables were scaled) and when the female was sealed in the nest with chicks (estimate 0.47 ± 0.06, $p < 0.001$), and declined significantly with increasing T_{air} in both breeding seasons (estimate -0.12 ± 0.03, $p < 0.001$). The models indicated no significant effect of supplementary feeding (high, 25g of *Zophobas morio* larvae daily, *versus* low, 5g larvae daily, supp.) on provisioning rates, but considering the underrepresentation of supplementary food items in provisioning rate data from camera traps (despite observations that they fed almost all supplemented food to the nest), it appeared that high supp. males in the hot and dry breeding season reduced the amount of natural food they provisioned but maintained a similar total provisioning rate to low supp. males, and attained considerably higher overall provisioning rates compared to low supp. males in the cool and wet season. All males showed hyperthermic responses to increasing T_{air} but the patterns varied; males in the high resource supplementation treatment (high supp.) showed hyperthermic responses in their provisioning body temperature (T_b; measured by temperature-sensitive passive integrated transponder [PIT] tags when hornbills provisioned at the nest) at lower T_{air} than low resource supplementation males, and high supp. males and males in the cool and wet breeding season showed more gradual increases in T_b at high T_{air} than low resource supplementation males in the hot and dry breeding season. Free-ranging heart rates (a proxy for work rate) declined with increasing T_{air}. The declines in provisioning rates and free-ranging heart rates with increasing T_{air} in both breeding seasons suggested a limiting, negative effect of high T_{air} on male activity regardless of resource availability. Thermoregulatory patterns suggested that increased resource availability improved hyperthermia avoidance and allowed for slower rates of T_b increase with T_{air}. Overall, these results suggested that high T_{air} were limiting for activity regardless of resource availability. These findings highlight that even without an increase in the frequency or intensity of drought (and the associated reductions in resource availability), ongoing climate warming poses a major threat to reproductive performance of this arid-zone species via the resource-independent limiting effects of high T_{air} on hornbills' ability to provision nests. However, they also indicate that resource availability or quality may play an important role in reproductive behavioural ecology.

2.2 Introduction

For endothermic animals, maintaining energy and water balance during hot or cold weather depends on costly physiological and behavioural adjustments (Miller 1963, Wolf 2000), costs exacerbated during breeding (Stevenson and Bryant 2000, Salvante et al. 2010, Londoño et al. 2017, Andreasson et al. 2020, Sauve et al.

2021). For example, reductions in activity in response to high environmental temperatures during breeding may reduce energy and water intake of the parent and compromise crucial behaviours such as territory and predator defence, courtship display, provisioning, or incubating (Wiley and Ridley 2016, Funghi et al. 2019, Gudka et al. 2019, Sharpe et al. 2021). Increased costs of thermoregulatory adjustments during breeding are elevated in seasonally hot, arid environments because arid-zone species typically breed following rainfall events, which often coincide with the hottest time of the year (Zann et al. 1995, Lloyd 1999, McCreedy and van Riper III 2015).

With rapid anthropogenic climate warming, research on the negative effects of high environmental temperatures on animal ecology has increased markedly (Andreasson et al. 2020, Cunningham et al. 2021). However, life history theory predicts that resource limitation leads to trade-offs between costly traits (Stearns 1992). For example, resource limitation might force an individual to invest in thermoregulation, rather than provisioning or development (van de Ven et al. 2019). With relaxed resource limitations, animals may be able to decrease the need for and cost of trade-offs between thermoregulation and other traits (Tieleman and Williams 2002, Tschirren et al. 2009, Rodríguez et al. 2016, Bourne et al. 2020c). Consequently, impacts of high environmental temperatures on survival and reproductive success could be partially mediated by resource availability, especially in arid ecosystems where resource availability is generally low.

The range of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hereafter hornbills) includes the arid western parts of southern Africa, where they breed in response to rainfall during the hot spring and summer (Kemp 1995, van de Ven et al. 2020b). Like most hornbills, they employ an unusual breeding strategy whereby the female seals herself into the nest cavity at the start of the breeding attempt and remains incarcerated for the majority of the attempt, undergoing a flightless moult during this time. The seal at the nest entrance created by the female (and repaired and resealed by the nestlings when the female leaves the nest after her flight feathers have regrown) largely keeps nestlings safe from predators, meaning that breeding success is primarily dependent on other factors such as dehydration, starvation, or disease (Moreau and Moreau 1941, Kemp 1995). In my study population, breeding success is reduced during hot periods due to a combination of direct negative effects of high nest temperatures (T_{nest}) on females and nestlings, and high air temperatures (T_{air}) correlating to reduced provisioning rates (i.e., the number of provisioning attempts per day) by males (van de Ven et al. 2019, van de Ven et al. 2020b). Considering 1) the relationships between high T_{air} and the behaviour, physiology, and breeding performance of hornbills are relatively well studied, and 2) resource availability is predicted to have a significant effect on breeding performance, especially in a challenging, low productivity system such as the Kalahari Desert, I argue that this population of hornbills provides an ideal study system for investigating how resource availability factors into the relationship between environmental temperature and reproductive behaviour and physiology.

I ran a supplementary feeding experiment while monitoring breeding hornbills over two breeding seasons. The study also took advantage of significant breeding season scale differences in T_{air} and rainfall, allowing a natural comparison between a hot and dry breeding season (2019/2020) and a cool and wet breeding season (2020/2021). I aimed to investigate how T_{air} and resource availability affected provisioning behaviour, body temperature (T_b) regulation and free-range heart rates of breeding male hornbills. Hornbills do not drink from open water sources – all the water they get is from their diet. Therefore, I use ‘resource availability’ to refer to food and water. This use of ‘resources’ excludes other resources such as shade, potential breeding mates, or nest sites; it specifically refers to food and water for the hornbills. I measured heart rates using data storage tag heart rate and temperature loggers (DST micro-HRT logger; Star-Oddi, Gardabaer, Iceland) surgically implanted into the body cavity. Free-ranging heart rate is correlated with energy expenditure, though a conversion to a quantitative measure of energy expenditure requires calibration at the individual or population level (Green 2011). To that end, a short pilot study was carried out on a single wild-caught hornbill held in captivity and implanted with a DST micro-HRT logger to test if there was a relationship between heart rate and metabolic rate. The pilot data (not shown) were limited, but suggested a strong linear relationship between heart rate and VCO_2, as demonstrated in other species, suggesting that heart rate could be used as a proxy for metabolic rate in the hornbills (Green et al. 2001, Green et al. 2009, Steiger et al. 2009, Guillemette et al. 2012, Green et al. 2013, Portugal et al. 2016, Brown et al. 2022). I hypothesised that provisioning rate, T_b regulation, and heart rates would be partially dependent on T_{air}, but that the relationships would be moderated by resource availability. Specifically, I predicted that provisioning rate would decrease, that males would show facultative hyperthermia, and that males would show reduced heart rates with increasing T_{air}, but that provisioning rates would increase, and hyperthermia would be less pronounced in response to increased resource availability. Teasing apart whether high T_{air} alone, or high T_{air} in conjunction with low resource availability, is limiting for reproductive performance is critical for understanding the vulnerability of arid-zone birds to climate change.

2.3 Methods

2.3.1 Study species

Southern Yellow-billed Hornbills are listed as Least Concern by the IUCN, but are thought to be declining (BirdLife International 2022). Their distribution includes most of southern Africa, with a large portion falling within the Kalahari Desert. They are socially monogamous and live up to 23 years in captivity (Strehlow 2001), although the oldest known marked bird at my study site was 8 years old. Like most Bucerotidae hornbills, female Southern Yellow-billed Hornbills (hereafter, hornbills) seal themselves inside the nest cavity for most of the breeding attempt. Females create the seal at the nest entrance using mud and faeces and leaving a small slit through which the male can pass food (and indirectly, water, since the hornbills do not drink). The female seals in to begin the breeding attempt and breaks out when the breeding attempt is ~70% complete in successful attempts. Once incarcerated in the nest, females moult all their flight feathers simultaneously, leaving the male as the sole-provisioner. This strategy protects against nest predation, meaning other factors, such as dehydration, starvation, or disease, are primarily responsible for variation in breeding success (Moreau and Moreau 1941). After the female breaks out of the sealed cavity, she aids in provisioning of nestlings. Breaking out usually occurs once the female has regrown flight feathers and the chicks are old enough to reseal the nest entrance. At my study site, pairs attempt a single brood per breeding season (though this species may be multi-brooded in more mesic areas, Stanback et al. 2021), and the mean duration from date of first egg lay until the female completes sufficient feather regrowth and breaks out is 57 ± 7 SD days (n = 27, range 49 – 76) in nests that successfully produce at least one fledgling. Once females break out, the chicks reseal the nest entrance, and females assist with provisioning until the chicks fledge. Research on hornbills at my study site (Kuruman River Reserve in the southern Kalahari Desert, Northern Cape province, South Africa; 26°58′ S, 21°49′ E; hereafter, KRR) has been ongoing since 2008 and data for two breeding seasons (2019/2020 & 2020/2021) were used for this study. The hornbills at KRR typically breed between October and the end of March in wooden nest boxes (50 available boxes 2019 – 2021). Breeding adults were captured using baited spring-traps and fitted with a metal SAFRing and a colour ring combination for unique identification. Data were collected for Chapters 2 (this chapter), 3, and 4, simultaneously over the course of the breeding season. All breeding data were collected from hornbills breeding in nest boxes, because the sealing behaviour means natural cavities are completely inaccessible for research.

2.3.2 Study site and weather data collection

The KRR consists of arid savanna dominated by grasses interspersed with large trees (mainly camelthorn, *Vachellia erioloba*; grey camelthorn, *Vachellia haematoxylon*; shepherds’ tree, *Boscia albitrunca*; and buffalo thorn, *Ziziphus mucronata*). In 2011 the study site was equipped with a weather station (Hot Birds Research Project [HBRP] Weather Station; Vantage Pro2, Davis Instruments, Hayward, U.S.A.) set to record T_{air} (°C), wind speed ($m.s^{-1}$), relative humidity (%), and solar radiation ($W.m^{-2}$) at 5-min intervals. Rainfall occurs primarily in the Austral summer (between October and April), mean rainfall recorded over the hornbill breading season is 155 mm ± 86 SD (1993 – 2020, Van Zylsrus weather station approximately 30km east of the field site, South African Weather Service [SAWS]). Mean breeding season T_{max} = 34.9 ± SD 1.19 °C (1991 – 2020, at Van Zylsrus), which is above the threshold air temperature (T_{air}) at which male hornbills showed a 50% likelihood of engaging in heat dissipation behaviour i.e., panting [$T_{air} \geq 34.5$ °C] (van de Ven et al. 2019).

Breeding season (19 October – 24 March) T_{max} and rainfall for the hot and dry (2019/2020) and cool and wet (2020/2021) breeding season were calculated from weather data collected on site by the HBRP weather station.

2.3.3 Supplementary feeding

Females begin a breeding attempt by sealing themselves inside a nest box. The day following a female laying the first egg of the breeding attempt, feeding stations were set up approximately 2.5m away from nests. Feeders were ~1.5m off the ground. Feeders comprised a small wooden box with one transparent side facing the nest for the hornbills to see the contents. The top of the box was sealed with duct tape which had a narrow slit opening in the middle for the hornbills to push their beaks through. This feeder design prevented other birds from accessing the food and prey escaping. As breeding attempts began, they were alternately assigned to either high supplementation (high supp.) or low supplementation (low supp.) treatments as they started. Essentially, the first breeding attempt of the breeding season was assigned to high supp., the second attempt to start was assigned to low supp., the third to start to high supp., and so on. This meant that treatments were assigned equally to each supplementation treatment over a range of nest initiation dates. In the morning every day, nests on the high supp. treatment were provided ~25g of live darkling beetle *Zophobias morio* larvae (30 individual larvae, = ~10% average hornbill male body mass and 100% of mean daily biomass provisioned by male hornbills in previous studies on this population (van de Ven 2017)), while nest on the low supp. treatment were provided ~5g (7 individual larvae) via the feeding stations. Males learned to use the feeders within 2 days of feeders being put up. Males were often observed for at minimum 5-15 min each morning after the supplementary food had been provided specifically to observe the supplementary food provisioning behaviour. During these observations, the males were usually observed to immediately provision all the supplementary food to the nest, although in some instances high supp. males consumed < 5 larvae themselves once they had provisioned the majority to the nest.

2.3.4 Camera trap data collection

Five camera traps (Bushnell Trophy Camera HD, Bushnell Outdoor Products, Kansas, USA) were set up ~2m from nest boxes ~1.6m off the ground and set to record 10s of HD video footage upon registering movement. Camera traps recorded for 5 days at a single nest before being moved to a nest without a camera trap and rotated in this way continually throughout the breeding season. All footage was analysed manually. Only days on which the camera traps reliably functioned for the entire day were included in analyses. Colour ring combinations provided bird identity and where possible the item provisioned was identified although the majority (70.5%) of items provisioned were unidentifiable. The camera traps were unreliable at capturing provisioning of supplemented items. This was likely due to the rapidity of provisioning supplemented items (often several within a single minute) causing the cameras to miss visits due to sensor delay; the camera sensors might not have been fast enough to capture very quick visits and were also set to allow a 5 s gap in between triggering to save battery and SD card space via constant triggering for wind-related movement. The likelihood of missing naturally provisioned prey is considered lower since the sensor delay would not be as affected by provisioning attempts in slower succession, as opposed to the male flying to and from the nest several times per minute when provisioning food from the nearby feeder – flights which might be too fast or within the 5 s delay period.

2.3.5 Body temperature and heart rate data collection

Temperature-sensitive passive integrated transponder tags (PIT tags; model HPT8, 8.4mm ISO FDXB, Biomark, Boise, Idaho, USA) were injected subcutaneously between the scapulae of breeding male hornbills (hot and dry breeding season $n_{lowsupp} = 4$, $n_{highsupp} = 5$; cool and wet breeding season $n_{lowsupp} = 5$, $n_{highsupp} = 4$) following Oswald et al. (2018a). Cord antenna readers (Biomark, Boise, Idaho, USA) and HPR Plus readers (Biomark, Boise, Idaho, USA) were installed on the nest boxes to record the unique identity and provisioning T_b of the males, as measured by the PIT tags which send that information each time they come into proximity with a reader, each time they visited the nest to provision. In a subset of six males in the population, data storage tag heart rate and temperature loggers (DST micro-HRT logger; Star-Oddi, Gardabaer, Iceland) were surgically implanted through a midline incision by a veterinarian at the beginning of the 2020/2021 breeding season. These were set to record heart rate and free-ranging T_b were recorded at 30-min intervals for six months. This represents ‘free-ranging’ $T_{b,}$ since T_b recorded by the DST micro-HRT loggers were recorded every 30 min wherever the hornbill was in the landscape. All six males survived the surgery, though one died in an unrelated accident a month post-surgery when its leg was tragically caught in wire at the study site. Of the five remaining, I was able to recapture four (all low supp.) for retrieval of the loggers. Capturing males was always done using spring traps, except for the recapture of males with the DST micro-HRT loggers. These males avoided spring traps (presumably having learnt to avoid them) and so had to be recaptured using bal-chatri traps that caught the males by their feet. One could not be recaptured. Of the four recaptured, two had bred in nest boxes, while two did not breed. After explantation, all four were observed regularly until the investigators left the study site. Heart rates were calculated from electrocardiograms (ECGs) recorded in addition to a unitless measurement known as the quality index (QI) by the logger. The QI represents the quality of the ECG signal recorded: QI_0 = very good quality, QI_1 = good quality, QI_2 = poor quality, and QI3 = no heart rate could be calculated (Zrini and Gamperl 2021). Only records with QI_0 or QI_1 were retained.

2.3.6 Statistical analyses

Statistical analyses were conducted in the R statistical environment, version 3.5.1 (R Core Team 2023), using the R Studio platform (R Studio Team 2023). Details on the general mixed modelling approach are given in the general introduction (see Chapter 1). Based on analyses of statistical power (Cohen’s f^2, the measure of determinable effect size), calculated using the package pwr (Champely 2020), for provisioning rate analyses there was statistical power to detect small main effects (f^2 = 0.038) and moderate interaction effects (f^2 = 0.152; Table S2.1) based on needing a four times larger sample size for detecting interaction effects (Leon and Heo 2009). There was statistical power to detect small main and interaction effects for models of provisioning T_b both below and above break points (all $f^2 < 0.009$; Table S2.1). For analyses of provisioning rates and T_b, mixed models with interaction terms were fitted, and a set of five candidate models were compared, as per the Chapter 1 General Introduction (detailed below).

Provisioning rates

Camera trap footage of nest provisioning cumulatively represented 383 camera-days of data collection (hot and dry breeding season camera-days n = 203, nest $n_{lowsupp}$ = 4, nest $n_{highsupp}$ = 5; cool and wet breeding season camera-days n = 180, nests $n_{lowsupp}$ = 5, nests $n_{highsupp}$ = 4). I used generalised linear mixed models (GLMer) with a negative binomial model family in package MASS (Venables and Ripley 2002) to model the total provisioning rate as a function of the variables 1) breeding season, 2) T_{max}, 3) resource supplementation, and 4) nest stage (i.e., female and eggs, female with chicks, and chicks only). I specified a candidate set of 5 models predicted *a priori* to be biologically informative: i) the full model with all variables of interest and interaction terms between T_{max} and breeding season, and between T_{max} and resource supplementation, ii) a model with all variables of interest with the interaction between T_{max} and resource supplementation removed, iii) a model with all variables of interest with the interaction between T_{max} and breeding season removed, iv) a model with all variables of interest with both interaction terms removed, and v) the null model. Male identity was included in all models as a random term. I performed model selection based on Akaike's Information Criterion adjusted for small sizes (AICc) (model.sel function in package MuMIn, Barton 2020) on this candidate set, and reported results for the average (Barton 2020) of the three top performing models within Δ AICc < 2.

Body temperature and heart rate

Provisioning T_b from PIT tags were collected for males across two breeding seasons (hot and dry breeding season $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season $n_{lowsupp}$ = 5, $n_{highsupp}$ = 4) totalling 16038 records. Exploratory analyses suggested different, non-linear, segmented relationships between T_b and T_{air} for males in each breeding season and resource supplementation treatment. Therefore, to identify the break-points in the data (i.e., the T_{air} at which T_b showed a significant change in slope and began increasing more rapidly with increasing T_{air}), male T_b was split by breeding season and resource supplementation and modelled with Gaussian family as a function of T_{air} specifying one, two, or three break-points (package segmented, Muggeo 2017). Additionally, generalised additive model (GAM) family gaussian (package mgcv, Wood 2011) were fitted to provide a visual estimate of the break-points for confirmation of the segmented analyses. Linear model outcomes were compared using Akaike Information Criterion (AIC), and the break-points in the model with the lowest AIC, and which most closely matched the visual estimate of the breakpoint from the GAM, were selected. Subsets of data below and above break-points were then modelled using linear mixed models (LMer) family Gaussian as functions of 1) breeding season, 2) T_{air}, 3) resource supplementation, 4) an interaction between T_{air} and breeding season, and 5) an interaction between T_{air} and resource supplementation. Male identity was included in analyses as a random factor. Model selection, power analysis, and reporting followed the protocol detailed above. The interactions between T_{nest} and breeding season above break-points, and the interaction between T_{air} and resource supplementation both below and above break-points were significant, so data were post-hoc split by breeding season and resource supplementation and modelled using LMers with family Gaussian, as functions of T_{air}.

I used LMer with family Gaussian to model a) free-ranging T_b and b) free-ranging daytime (06:00 – 18:00) heart rates as functions of T_{air} (cool and wet breeding season $n = 4$, n breeding males = 2, all low supp.). Male identity was included as a random factor. The same process as above for identifying break-points was followed for the relationship between free-ranging T_b and T_{air}, and free-ranging heart rates and T_{air}.

2.4 Results

2.4.1 Weather

The two breeding seasons were distinguished by their T_{max} and rainfall differences. Breeding season T_{max} was 34.2 °C ± 3.8 SD (T_{max} range 20.4 °C to 41.0 °C) in the hot and dry breeding season (2019/2020) and 33.1 °C ± 3.1 SD (T_{max} range 24.1 °C to 39.6 °C) in the cool and wet breeding season (2020/2021), with near-drought conditions (130.6mm, 6mm above drought threshold, see Chapter 5) in hot and dry breeding season and over double the average rainfall (328.9mm) in the cool and wet breeding season. Moreover, the cool and wet breeding season also had the lowest breeding season T_{max} since monitoring on the hornbills began in 2008 (see Chapter 5, section 5.3.2).

2.4.2 Provisioning

There were 3 top models for provisioning rates within Δ AICc < 2 (Table S2.2). Model averaged estimates showed the provisioning rates were significantly higher in the cool and wet breeding season compared to the hot and dry breeding season (estimate 0.31 ± 0.14 SE, $p = 0.031$; Figures 2.1 & S2.2) and during the female & chicks nest stage (estimate 0.47 ± 0.06, $p < 0.001$; Figure 2.1; Table 2.1). Provisioning rates declined significantly with increasing T_{max} (estimate -0.12 ± 0.03, $p < 0.001$; Figures 2.1 & S2.1; Table 2.1). Provisioning rates were not significantly affected by resource supplementation, the interaction between T_{max} and breeding season, or the interaction between T_{max} and resource supplementation (Tables 2.1 & S2.2). However, provisioning rates were on average lower in high supp. males in the hot and dry breeding season (48.86 ± 21.59 SD provisions.day^{-1} in low supp. and 31.82 ± 14.67 in high supp.). Provisioning rate was similar between resource supplementation treatments in the cool and wet breeding season (62.74 ± 30.39 SD provisions.day^{-1} in low supp. and 65.66 ± 33.15 in high supp.; Figure S2.2). These values greatly underestimated the contribution of supplementary food to provisioning, since the camera traps were poor at capturing rapid-succession provisioning of supplementary items; 6.5 ± 5.8 SD supplemented items per day captured out of 30 supplied to high supp. nests, 2.2 ± 1.5 SD out of 7 supplied to low supp. nests. Therefore, an addition of ~20 (conservatively) provisioning attempts per day for high supp. and ~5 to low supp. indicated that total provisioning rates would have been similar between low and high supp. males in the hot and dry breeding season (although the number of natural prey provisioned by high supp. would have been reduced), and considerably higher in high supp. males in the cool and wet breeding season.

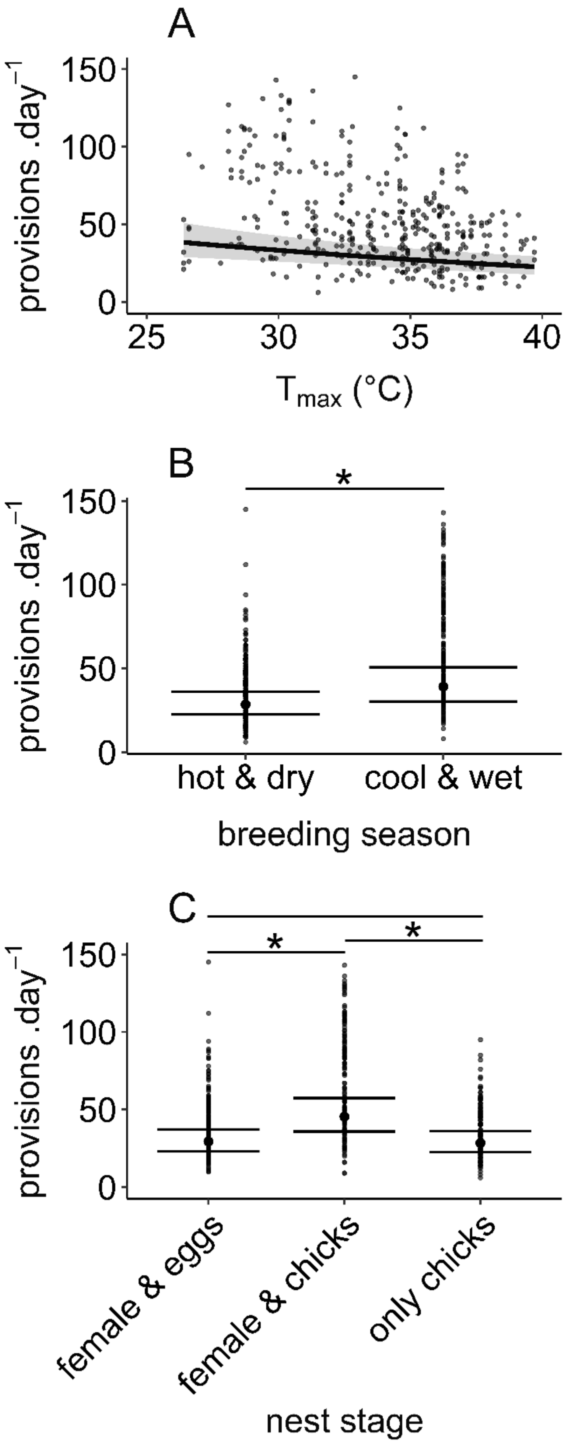


Figure 2.1. The number of daily provisioning attempts (plotted from negative binomial generalised linear mixed effects model) by Southern Yellow-billed Hornbill (*Tockus leucomelas*) males as a function of A) T_{max} (mean maximum daily air temperature; T_{air}), B) breeding season (hot and dry [2019/2020, n males = 9] and cool and wet [2020/2021, n males = 9] breeding seasons), and C) nest stage. For A, 95% confidence interval (CI) shown and the relationship between provisioning rate and T_{max} is significant ($p < 0.05$). For B & C means with standard errors are shown and * indicate significant ($p < 0.05$) differences.

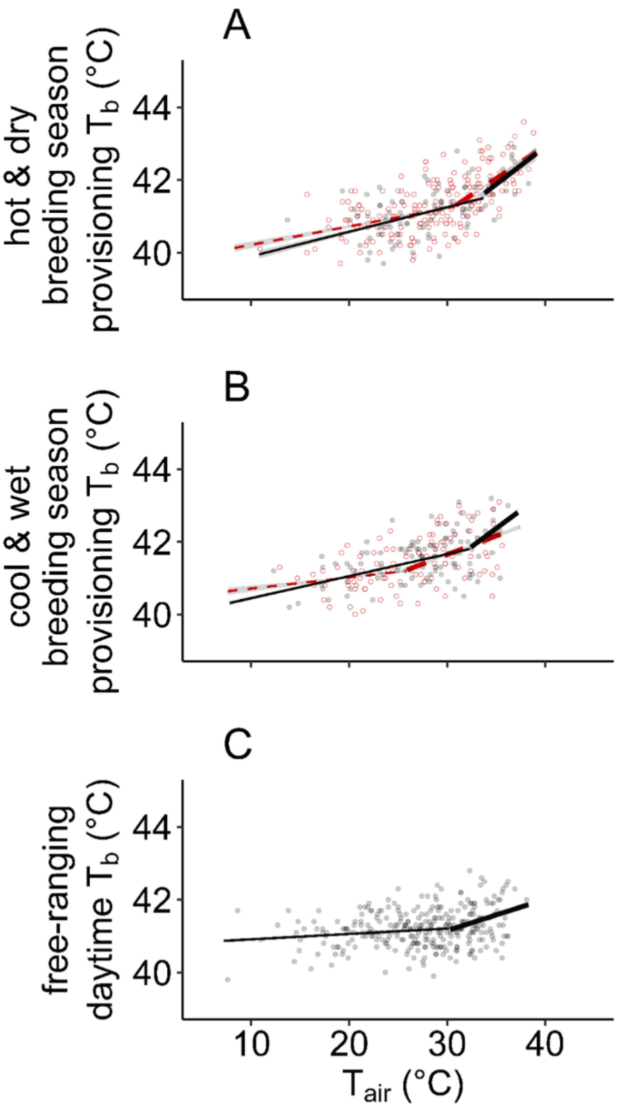
Table 2.1. Model averaged estimates (from 3 models within Δ AICc < 2) for the daily number of provisioning attempts (provisioning rate) recorded by camera traps modelled using generalised linear mixed models (GLMer) with a negative binomial family as a function of breeding season (hot and dry [2019/2020, $n_{highsupp} = 5$, $n_{lowsupp} = 4$] and cool and wet [2020/2021, $n_{highsupp} = 4$, $n_{lowsupp} = 5$]), T_{max} (maximum daily air temperature [T_{air}]), nest stage (female & eggs, female and chicks, and chicks only), resource supplementation treatment (low resource supplementation [low supp.] and high resource supplementation [high supp.]), the interaction between T_{max} and breeding season, and the interaction between T_{max} and resource supplementation for male Southern Yellow-billed Hornbills (*Tockus leucomelas*). Independent variables not shown were those absent in the model averaged estimates following model selection. Significant ($p \leq 0.05$) effects are highlighted in bold. * indicates an interaction between terms.

breeding season	**number of top models**	**independent variable**	**estimate ± SE**	**z**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
combined	**3**	**T_{max}**	**-0.12 ± 0.03**	**4.81**	**383**	**0.001**	**-0.17**	**-0.07**
		breeding season (cool and wet)	**0.31 ± 0.14**	**2.16**	**383**	**0.031**	**0.03**	**0.59**
		nest stage (female & chicks)	**0.47 ± 0.06**	**8.45**	**383**	**0.001**	**0.36**	**0.58**
		supp. (low)	0.14 ± 0.14	0.95	383	0.345	-0.15	0.42
		T_{max} * breeding season	-0.01 ± 0.02	0.22	383	0.825	-0.11	0.06
		supp * breeding season	0.01 ± 0.02	0.25	383	0.802	-0.06	0.11

2.4.3 Body temperatures and heart rates

In both breeding seasons and both resource supplementation treatments, at T_{air} both below and above break-points, provisioning T_b (collected from PIT tags) increased significantly with increasing T_{air} (T_{air} break-points summarised in Table 2.2, slopes summarised in Table 2.3; Figures 2.2 & 2.3). In both the hot and dry ($n_{lowsupp} = 4$, $n_{highsupp} = 5$) and cool and wet ($n_{lowsupp} = 5$; $n_{highsupp} = 4$) breeding seasons, high supp. males began showing a hyperthermic response at lower T_{air} than low supp. males (30.87 °C vs 33.74 °C in the hot and dry breeding season; 25.89 °C vs 32.33 °C in the cool and wet breeding season; Figures 2.2 & 2.3; Table 2.2). There was one top model each for provisioning T_b below and above break-points, respectively, with Δ AICc < 2 (Table S2.3). Model estimates showed provisioning T_b below break-points were on average significantly higher in the cool and wet breeding season (estimate 0.29 ± 0.02 SE, $p < 0.001$) compared to the hot and dry breeding season, significantly higher in low supp males (estimate 0.10 ± 0.02 SE, $p < 0.001$) compared to high supp, and that the slopes of increase in T_b with increasing T_{air} were significantly higher in low supp males (estimate 0.10 ± 0.01 SE, $p < 0.001$) and lower in the cool and wet season (estimate -0.08 ± 0.01 SE, $p < 0.001$; Figures 2.2 & 2.3; Table 2.3). Model estimates showed provisioning T_b above break-points were on average significantly higher in the cool and wet breeding season (estimate 0.45 ± 0.04 SE, $p < 0.001$) compared to the hot and dry breeding season, significantly lower in low supp. males (estimate -0.15 ± 0.05 SE, $p < 0.003$) compared to high supp., and that the slopes of increase in T_b with increasing T_{air} were significantly higher in low supp. males compared to high supp. males (estimate 0.18 ± 0.04 SE, $p < 0.001$) and lower in the cool and wet breeding season compared to the hot and dry breeding season (estimate -0.14 ± 0.03 SE, $p < 0.001$; Figure 2.2; Table 2.3).

The provisioning and free-ranging (collected from surgically implanted DST micro-HRT loggers) T_b maxima for all males were similar (between 43.3 and 44.1°C; Table 2.2). Free-ranging ($n = 4$, all low supp. in the cool and wet breeding season) male T_b increased with increasing T_{air} below (estimate 0.01 ± 0.00 SE, $p < 0.001$) and above (estimate 0.09 ± 0.01 SE, $p < 0.001$) break-point T_{air} similarly to that of provisioning T_b of high supp. males in the cool and wet breeding season (Figure 2.2 & 2.3; Table 2.3). The daytime (06:00 – 18:00) heart rates of free-ranging males declined significantly more steeply with increasing T_{air} below the break-point point of T_{air} = 25.48 °C ± 0.81 SE (slope = -3.78 ± 0.47 SE bpm.°C^{-1}, $p < 0.001$), compared to above the break-point (slope = -2.99 ± 0.31 SE bpm.°C^{-1}, $p < 0.001$; Figure 2.4; Table 2.3).



gure 2.2. Male Southern Yellow-lled Hornbills (*Tockus leucomelas*) ovisioning body temperatures (T_b; otted from linear mixed models Mer] family Gaussian) in A) hot and y breeding season (2019/2020, $_{owsupp}$ = 4, $n_{highsupp}$ = 5), and B) cool nd wet breeding season 020/2021, $n_{lowsupp}$ = 5, $n_{highsupp}$ = 4).) Cool and wet breeding season ee-ranging, daytime (06:00 – 18:00) (n$_{lowsupp}$ = 4). All T_b as functions of r temperature (T_{air}). Provisioning T_b as recorded from subcutaneously-planted passive integrated ansponder (PIT) tags using readers nests, free-ranging T_b was corded at 30-min intervals by DST icro-HRT loggers surgically planted in the body cavity. Only % of all data points are shown for sual clarity, and trendlines do not xtend beyond the data to which models were fitted; 95% confidence intervals (CI) are shown. Provisioning T_b split by supplementation (dark grey-black circles, solid black line low supp.; open, red circles, dashed line high supp.). Each relationship between T_b and T_{air} for both supplementations in both breeding seasons is significant ($p < 0.05$).

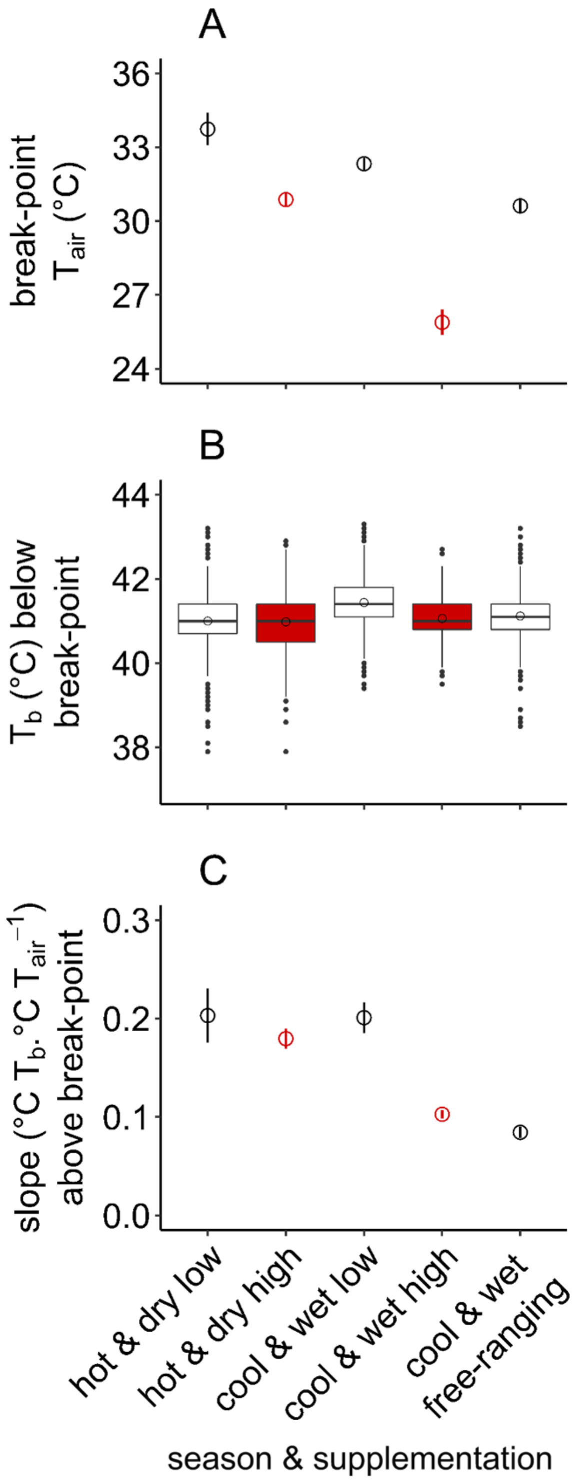


Figure 2.3. Southern Yellow-billed Hornbill (*Tockus leucomelas*) provisioning (recorded from subcutaneously-implanted passive integrated transponder (PIT) tags using readers at nests) and free-ranging (recorded at 30-min intervals by DST micro-HRT loggers surgically implanted in the body cavity) body temperatures (T_b) shown as functions of A) The break-point ± SE air temperature (T_{air}) at which T_b began to increase significantly more rapidly with increasing T_{air}, B) T_b below the break-point T_{air}; boxes indicate median with upper and lower quartiles; means indicated as clear circles , and C) the slope ± SE of the increase in T_b above the break-point T_{air} in the hot and dry (2019/2020, provisioning males $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5), and the cool and wet (2020/2021, provisioning males $n_{lowsupp}$ = 5, $n_{highsupp}$ = 4; free-ranging males n = 4, all low supp.) breeding seasons. Low supp. black, high supp. red.

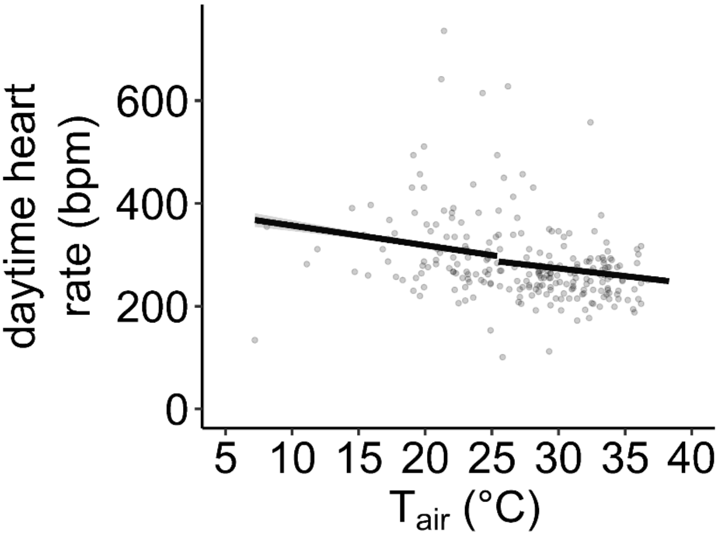


Figure 2.4. Breeding male Southern Yellow-billed Hornbill (*Tockus leucomelas*; n = 2, low supp., cool and wet breeding season) daytime (06:00 – 18:00) heart rates (beats per minute [bpm]; plotted from a Gaussian linear mixed model [LMer]) as a function of air temperature (T_{air}) below and above the break-point T_{air}. Only 5% of data points are shown for visual clarity, and trendlines do not extend beyond the data to which models were fitted. Heart rates were recorded at 30-min intervals by DST micro-HRT loggers surgically implanted in the body cavity. 95% confidence intervals (CI) are shown, and each relationship between heart rate and T_{air} is significant ($p < 0.05$).

Table 2.2. Southern Yellow-billed Hornbill (*Tockus leucomelas*) male provisioning body temperatures (T_b) were modelled using a using linear mixed models (LMer) with Gaussian family as a function of 1) breeding season, 2) air temperature (T_{air}), 3) resource supplementation (hot and dry breeding season [2019/2020] males $n_{lowsupp} = 4$, $n_{highsupp} = 5$; cool and wet breeding season [2020/2021] males $n_{lowsupp} = 5$, $n_{highsupp} = 4$), 4) an interaction between T_{air} and breeding season, and 5) an interaction between T_{air} and resource supplementation. In the model averaged estimates below (from 2 top models with Δ AICc < 2) and top model above (1 top models with Δ AICc < 2) both interactions were significant, so analyses were post-hoc split by breeding season and resource supplementation. Free-ranging T_b (n males = 4; all low supp., cool and wet breeding season) were modelled using a LMer family Gaussian as a function of T_{air}. All relationships had significant break-point T_{air} above which T_b began increasing more rapidly. Estimated break-points T_{air} for each relationship, the mean and mode T_b below each break-point, and maximum T_b with the maximum T_{air} experienced in brackets shown.

breeding season		**treatment**	**break-point T_{air} °C ± SE**	**mean T_b °C ± SD below break-point**	**mode T_b °C below break-point**	**Maximum T_b °C (max. T_{air} °C experienced)**
hot and dry	provisioning T_b	low supp.	33.74 ± 0.66	41.00 ± 0.65	41.0	44.1 (39.1)
		high supp.	30.87 ± 0.29	40.98 ± 0.60	41.0	44.2 (39.1)
cool and wet	provisioning T_b	low supp.	32.33 ± 0.24	41.44 ± 0.58	41.6	44.0 (37.4)
		high supp.	25.89 ± 0.52	41.06 ± 0.51	40.9	43.9 (37.2)
cool and wet	free-ranging T_b	low supp.	30.29 ± 0.32	41.12 ± 0.47	41.2	43.3 (38.4)

Table 2.3. Model averaged estimates for Southern Yellow-billed Hornbill (*Tockus leucomelas*) male provisioning body temperatures (T_b) below (model 1; a single top model with Δ AICc < 2) and the top model above (model 2; a single top model with Δ AICc < 2) break-points modelled using a using linear mixed model (LMer) with Gaussian family as a function of 1) breeding season, 2) air temperature (T_{air}), 3) resource supplementation (hot and dry breeding season [2019/2020] males $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season [2020/2021] males $n_{lowsupp}$ = 5, $n_{highsupp}$ = 4), 4) an interaction between T_{air} and breeding season, and 5) an interaction between T_{air} and resource supplementation. Both interactions were significant, so post-hoc data below and above break-points were split by breeding season and resource supplementation and modelled (models 3 – 10) as functions of T_{air}. Free-ranging (n males = 4; all low supp., cool and wet breeding season) T_b (model 11 & 12) and heart rates (models 13 & 14) below and above break-points were modelled using LMer family Gaussian as functions of T_{air}. Provisioning T_b recorded at the nest using passive integrated transponder (PIT) tags when males provisioned. Heart rates and T_b of free-ranging birds recorded at 30-min intervals by data storage tag heart rate and temperature loggers (DST micro-HRT logger; Star-Oddi, Gardabaer, Iceland) surgically implanted in the body cavity of males. Significant ($p \leq 0.05$) effects are highlighted in bold. * indicate interactions between terms.

model	breeding season	no. top models	response	treatment	independent variable	estimate ± SE	t	df	p ≤	lower 95% CI	upper 95% CI
1	combined	1	provisioning T_b below break-point		**T_{air}**	**0.24 ± 0.01**	**21.61**	**10020**	**0.001**	**0.22**	**0.26**
					breeding season (cool and wet)	**0.29 ± 0.02**	**14.31**	**4751**	**0.001**	**0.25**	**0.33**
					supp. (low)	**0.10 ± 0.02**	**4.91**	**4993**	**0.001**	**0.06**	**0.14**
					T_{air} * supp.	**0.10 ± 0.01**	**7.19**	**9985**	**0.001**	**0.07**	**0.12**
					T_{air} * breeding season	**-0.08 ± 0.01**	**-6.3**	**9950**	**0.001**	**-0.11**	**-0.06**
2	combined	1	provisioning T_b above		**T_{air}**	**0.42 ± 0.03**	**16.43**	**6120**	**0.001**	**0.37**	**0.47**
					breeding season	**0.45 ± 0.04**	**10.36**	**2775**	**0.001**	**0.36**	**0.53**

		break-point		**(cool and wet)**						
				supp. (low)	**-0.15 ± 0.05**	**-2.95**	**3280**	**0.003**	**-0.24**	**-0.05**
				T_{air} * supp.	**0.18 ± 0.04**	**4.57**	**6058**	**0.001**	**0.1**	**0.26**
				T_{air} * breeding season	**-0.14 ± 0.03**	**-4.97**	**6110**	**0.001**	**-0.19**	**-0.08**
3	hot and dry	provisioning T_b	low supp.	**T_{air} (below break-point)**	**0.07 ± 0.00**	**19.00**	**1427**	**0.001**	**0.06**	**0.08**
4				**T_{air} (above break-point)**	**0.20 ± 0.03**	**7.39**	**380**	**0.001**	**0.15**	**0.26**
5			high supp.	**T_{air} (below break-point)**	**0.05 ± 0.00**	**16.71**	**2303**	**0.001**	**0.05**	**0.06**
6				**T_{air} (above break-point)**	**0.18 ± 0.01**	**17.26**	**1421**	**0.001**	**0.16**	**0.20**
7	cool and wet	provisioning T_b	low supp.	**T_{air} (below break-point)**	**0.06 ± 0.00**	**35.71**	**4259**	**0.001**	**0.06**	**0.07**
8				**T_{air} (above break-point)**	**0.20 ± 0.02**	**12.87**	**1126**	**0.001**	**0.17**	**0.23**
9			high supp.	**T_{air} (below break-point)**	**0.03 ± 0.00**	**8.616**	**1929**	**0.001**	**0.02**	**0.04**
10				**T_{air} (above break-point)**	**0.10 ± 0.00**	**24.06**	**3176**	**0.001**	**0.09**	**0.11**
11	cool and wet	free-ranging T_b	low supp.	**T_{air} (below break-point)**	**0.01 ± 0.00**	**11.54**	**6356**	**0.001**	**0.01**	**0.02**
12				**T_{air} (above break-point)**	**0.09 ± 0.01**	**17.47**	**3667**	**0.001**	**0.08**	**0.10**

13	cool and wet	heart rate	low supp.	**T_{air} (below break-point)**	**-3.78 ± 0.47**	**-7.97**	**2796**	**0.001**	**-4.71**	**-2.85**
14				**T_{air} (above break-point)**	**-2.99 ± 0.31**	**-9.80**	**5705**	**0.001**	**-3.58**	**-2.39**

2.5 Discussion

My data reveal that T_{air} partially drives patterns in the reproductive ecology of male hornbills in an arid environment. Provisioning rate and free-ranging heart rates (a proxy for work rate; Green 2011) declined with increasing T_{air} in both breeding seasons suggesting a limiting, negative effect of high T_{air} on male behaviour. Resource availability also affected behaviour and thermoregulation; high supp. males in the hot and dry breeding season reduced the amount of natural food they provisioned but maintained a similar total provisioning rate to low supp. males, high supp. males in the cool and wet breeding season showed improved hyperthermia avoidance and more gradual increases in T_b above break-point T_{air} and increased provisioning rates compared to low supp. males. The comparison between the vastly different breeding seasons showed that increased natural resources associated with rainfall in the cool and wet breeding season (Zann et al. 1995, Lloyd 1999, McCreedy and van Riper III 2015) were associated with increased provisioning rates in low and high supp. males. These findings suggest that high T_{air} are limiting for provisioning rate regardless of resource availability, highlighting that even without an increase in the frequency or intensity of drought, ongoing climate warming poses a threat to reproductive performance of this arid-zone species. However, they also show that resources influence thermoregulation and behaviour, potentially impacting survival or breeding outcomes.

2.5.1 Provisioning rate

Provisioning data showed first that provisioning rates were higher in the cool and wet breeding season at all T_{max}, and second that provisioning rates declined with increasing T_{max} at a similar rate in both breeding seasons. Resource supplementation did not have a significant effect in the model. However, camera traps and the resultant data underestimated the contribution of supplemented items to the number of provisioning attempts per day; 6.5 ± 5.8 SD supplemented items per day captured out of 30 supplied to high supp. nests, 2.2 ± 1.5 SD out of 7 supplied to low supp. nests. Therefore, the total provisioning rates inclusive of supplementary items would have been similar for low and high supp. males in the hot and dry breeding season, and considerably higher for high supp. males compared to low supp. males in the cool and wet breeding season.

Provisioning rates of males in the hot and dry breeding season were likely limited by food availability (Hollander et al. 2013, Garcia-Heras et al. 2017) and heat dissipation limits (Nord and Nilsson 2019). High supp. males in the hot and dry breeding season provisioned fewer naturally found items, as seen in other systems (Grieco 2002, Tremblay et al. 2005, Cauchard et al. 2021). High supp. males may have done this because it potentially reduced overall effort, since attaining the same provisioning rate as low supp. males was achieved through rapid provisioning of supplementary food provided adjacent to nests in the morning (thereby potentially avoiding needing to provision at hotter times of the day). This strategy may benefit high supp. males by enabling them to meet minimum breeding requirements while reducing the costs of low-payoff provisioning. Moreover, breeding males face trade-offs between allocating energy and water to self-maintenance (including critical thermoregulatory processes) or to provisioning to offspring (Ydenberg 1994, Cunningham et al. 2021). Therefore, increased resource availability may provide the opportunity to consume more naturally-caught prey themselves rather than provision, or simply reduce natural foraging and provisioning effort altogether, both potentially reducing the severity of trade-offs between self-maintenance and breeding investment (Ydenberg 1994, Tieleman and Williams 2002, van de Ven et al. 2019). Ultimately, considering the energetic and water costs of provisioning, especially at the hottest times of the day, and the potential to prioritise self-feeding, males with access to high supp. food possibly benefit from better body condition and improved survival (e.g. Bryant 1988, Tieleman and Williams 2002, van de Ven et al. 2019). High supp. males in the hot and dry breeding season did not show a difference in T_b regulation compared to low supp. males. However, given the resource poor environment they perhaps still did not have access to enough food, and therefore, water, to allocate toward both thermoregulation and provisioning. Moreover, they may have shown active phase (i.e., when awake and active) T_b benefits elsewhere throughout the day (e.g., during foraging) if they consumed more food themselves, rather than during provisioning. I did not have data on self-feeding or free-ranging T_b in high supp. males to assess these possibilities.

Higher resource availability in the cool and wet season appeared to allow higher provisioning rates by all males at all T_{max}. This may also have been related to reduced severity of trade-offs between thermoregulation and activity; higher resource availability afforded improved hyperthermia avoidance and more gradual increases in T_b, reducing the limiting effect of hyperthermia on provisioning rate (Nilsson and Nord 2018, Nord and Nilsson 2019). However, low supp. males in the cool and wet breeding season showed a similar T_b profile to all males in the hot and dry breeding season, but provisioned considerably more. This may again indicate that free-ranging T_b is a limiting factor, as opposed to provisioning T_b. Without data on food quality, male self-feeding rates, or free-ranging T_b for males in both breeding seasons and resource supplementation treatments, much of this is speculative and requires further research.

High T_{max} did limit provisioning rate regardless of resource availability. This was supported by the decline in heart rates with increasing T_{air}, which likely reflected declines in activity at high T_{air} (Pattinson et al. 2020). This pattern also potentially represented active metabolic suppression (i.e., reducing metabolic rate in response to environmental stress to improve survival) in response to high T_{air} as a method of thermoregulation (Green et al. 2009, Lovegrove et al. 2014, van Jaarsveld et al. 2021). Regardless, the partial effect of high T_{air} remains significant. Limitation of provisioning rate at high T_{air} negatively affects reproductive outcomes (van de Ven et al. 2019, Bourne et al. 2021), which over time may lead to breeding failure and ultimately negatively affect population persistence (Riddell et al. 2019). Significantly higher provisioning rates during the ‘female & chicks’ nest stage suggested that hornbills do increase provisioning effort to compensate for increased demands from the nest occupants, similar to other species (Wright et al. 1998, Cauchard et al. 2021).

2.5.2 Body temperatures

Defending a narrow range of T_b is challenging, especially in summer in seasonally hot, arid zones (Tieleman and Williams 1999, Angilletta et al. 2010). Despite the metabolic heat load associated with provisioning activity, male hornbills maintained mean provisioning T_b within the known normothermic range 41 – 42 °C at relatively low (< 31 °C) T_{air} (Prinzinger et al. 1991). However, at high T_{air} (>31 °C) male hornbills showed facultative hyperthermia, suggesting they make use of the benefits of hyperthermia (i.e., water conservation, maintenance of activity without regulating a set-point T_b) to continue provisioning (Tieleman and Williams 1999). The pattern of hyperthermia varied between resource supplementation treatments: low supp. males delayed engaging in hyperthermia to higher T_{air} and showed steeper increases in T_b above break-points than high supp. males within each breeding season. This was possibly because low supp. males had fewer resources (e.g., lower body water reserves for evaporative water loss) available to control T_b once it began to rise (Smit et al. 2013, Tapper et al. 2020, Wojciechowski et al. 2021). Hornbills do not drink from surface water sources and water intake is from their diet (Witman and LaGreco 2020). Therefore, the difference between low and high supp. males may have been because low supp. males lacked access to high water content prey, while high supp. males could provision ~25g of supplemented water-rich darkling beetle larvae and thus consume more water rich prey themselves (Smit et al. 2016, Abdu et al. 2018a, Czenze et al. 2020). However, this study did not have the requisite data on the diet or foraging behaviour of the male hornbills away from nests to test this possibility. Moreover, one might predict that if this were the case, the pattern would be more pronounced in the naturally resource limited hot and dry breeding season, which was not clear. Therefore, this difference in thermoregulatory pattern between low and high supp. males remains difficult to interpret.

Provisioning T_b > 44.2 °C were not recorded in either breeding season, an upper T_b limit close to the heat tolerance limit of T_b = 44.8 °C for male hornbills in respirometry chambers (van Jaarsveld et al. 2021). This indicates a possible physiological T_b limit to provisioning rate (Speakman and Król 2010, Nilsson and Nord 2018, Tapper et al.

2021). Considering low supp. males had steeper slopes of T_b increase above the break-point T_{air}, they may reach this T_b limit faster (i.e., at lower T_{air}) than high supp. males. This may thereby physiologically limit provisioning rate at lower T_{air} than is the case for males experiencing high resource availability. This supports the concept of sublethal, missed opportunity costs associated with changes in behaviour playing a critical role in reduced fitness (Conradie et al. 2019, Cunningham et al. 2021). For both low and high supp. males, increasing T_b above the normal optimal range will likely reduce aspects of physiological and behavioural performance (Nilsson and Nord 2018, Cunningham et al. 2021, Nilsson and Nord 2021). This suggests that, regardless of resource availability, high T_{air} still incurred the need for a hyperthermic response in the hornbills and likely imposed a trade-off between optimal T_b regulation and activity.

Free-ranging T_b showed a break-point T_{air} = 30.6 °C, above which T_b began increasing more rapidly indicating use of facultative hyperthermia. This T_{air} break-point was considerably lower than the T_{air} at which hornbills males show a 50% likelihood of engaging in panting behaviour (T_{air} = 34.5 °C) (van de Ven et al. 2019), suggesting that wild birds employ facultative hyperthermia significantly earlier than they begin panting, perhaps as a mechanism to delay panting and conserve water (Gerson et al. 2019). The free-ranging males also showed the shallowest slope of increase in T_b above the break-point T_{air} compared to the low and high supp. provisioning birds. This likely reflected the cool and wet breeding season providing ample resources, especially water rich food for evaporative cooling, to thermoregulate at high T_{air} (Boyles et al. 2011) and that the metabolic heat loads associated with provisioning flights were not uniformly part of these data.

2.5.3 The importance of multi-season comparisons and study limitations

In this two-season study, large breeding season differences in background resource availability and / or quality and T_{air} appeared to have significant effects on breeding behaviour and thermoregulation. Evidence for differences in thermal physiology and behaviour between populations within the same species (Noakes et al. 2016), for example, may therefore be partly due to phenotypic flexibility in response to background breeding season variation. Consequently, these findings highlight the need for multi-season or long-term studies before making inferences about patterns in physiology and behaviour, especially for birds in highly variable environments (Cockburn 2014).

The amount of supplementary food assigned to high supp. breeding attempts equalled approximately 100% of mean daily biomass previously found to be provisioned by male hornbills in this population (van de Ven 2017). However, it was only provided in the morning each day which may not have affected the reproductive ecology of the hornbills throughout the day. Moreover, it may still not have been enough food, and, hence, water, to offset resource or environmental temperature constraints and alter behavioural patterns, despite having detectable effects on thermoregulation. Providing *ad libitum* food for the hornbills was not possible in this study but doing so or providing access to supplementary food (and water) throughout the day may provide valuable insight into these possibilities. It is also possible that there were resource quality effects acting at the scale of breeding seasons, which could explain breeding season variation. However, I did not have data on self-feeding or food quality to test this possibility. Generally, these findings are based on small sample sizes within breeding season and resource supplementation treatments. Consequently, the findings reported here must be interpreted with caution.

2.5.4 Conclusions

Arid-zone birds, including hornbills, are severely negatively affected by high T_{air}, which is correlated with reduced foraging and provisioning efficiency, reduced nest attendance, body mass loss, poor nestling growth, and ultimately to reduced fitness (Conradie et al. 2019, Riddell et al. 2019, Sharpe et al. 2019, Bourne et al. 2020b). However, the role of resource availability in mediating the effects of high T_{air} on arid-zone species remains less well studied. In this study on male hornbills, increased resource availability or quality affected thermoregulation by allowing hyperthermia avoidance., However, increased resource availability or quality did not completely offset the negative effects of high T_{air} on behaviour; high T_{air} still reduced provisioning rates. Resources (either in quantity or quality) did affect provisioning rate, highlighting the potential for future research to disentangle resource availability *versus* quality effects on reproductive ecology. These results are important for informing vulnerability assessments regarding climate warming for ectotherms and endotherms that show behavioural trade-offs in response to heat stress (Kearney et al. 2009, Abram et al. 2017, Beale et al. 2018, Brivio et al. 2019, Cunningham et al. 2021, Verzuh et al. 2021). If high T_{air} only become limiting in the absence of the energy and water required to thermoregulate then several conservation strategies such as providing artificial water points (Smit et al. 2019, Czenze et al. 2020) or food may be viable options. In addition, high rainfall years may provide arid-zone species opportunities to breed successfully despite increasing T_{air}, thus allowing for population persistence beyond what might be expected based on increases in average T_{air} (Bourne et al. 2020c). However, where high T_{air} is limiting regardless of resource availability, climate warming poses a severe threat to population persistence across the hottest parts of species' ranges (Sinervo et al. 2010, Conradie et al. 2019).

2.6 Supplementary materials

Provisioning rate

Provisioning rates were significantly higher in the cool and wet breeding season compared to the hot and dry breeding season (estimate 0.31 ± 0.14 SE, $p = 0.031$; Figures 2.1 & S2.1) and declined significantly with increasing T_{max} in both breeding seasons (estimate -0.12 ± 0.03, $p < 0.001$; Figures 2.1 & S2.1; Table 2.1). The lack of a significant interaction between T_{max} and breeding season showed that provisioning rate declined with increasing T_{max} at similar rates in both breeding seasons (Figure S2.1).

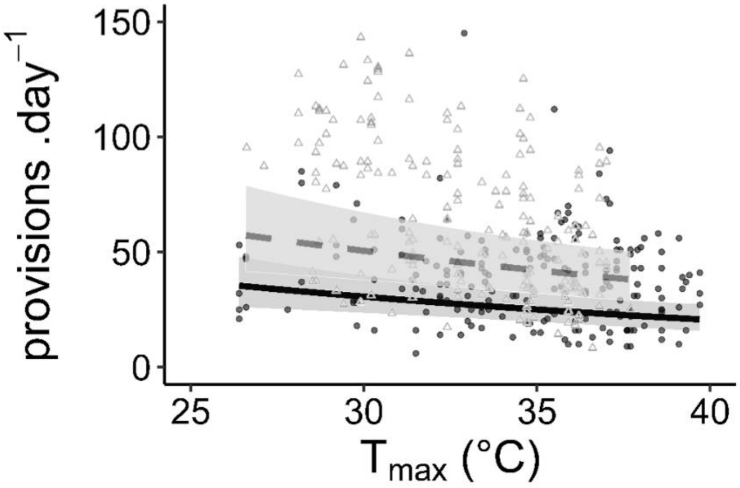


Figure S2.1. The number of daily provisioning attempts (plotted from negative binomial generalised linear mixed effects model) by Southern Yellow-billed Hornbill (*Tockus leucomelas*) males during the hot and dry (2019/2020, n males = 9; solid black line, black circles) and cool and wet (2020/2021, n males = 9; dashed grey line, grey triangles) breeding seasons modelled as a function of T_{max} (mean maximum daily air temperature [T_{air}]). 95% confidence intervals (CI) shown. Both relationships between provisioning rate and T_{max} are significant ($p < 0.05$).

Table S2.1. Statistical power analyses used to determine the determinable effect size of main effects and interaction effects within generalised linear mixed modelling (GLMer); u = model degrees of freedom; v = sample size, α = the significance level, and power = probability of finding an effect that is there; Cohen's f^2 = measure of determinable effect size (values of ~ 0.02, ~0.15, and ~0.35 represent small, moderate, and large determinable effect sizes respectively).

response	**effect**	***u***	***v***	***α (p value)***	***power***	***f^2***
provisioning rate	main	7	375	0.05	0.8	0.038
	interaction	7	94	0.05	0.8	0.152
provisioning T_b below break-point	main	5	10024	0.05	0.8	0.001
	interaction	5	2506	0.05	0.8	0.005
provisioning T_b above break-point	main	5	6120	0.05	0.8	0.002
	interaction	5	1530	0.05	0.8	0.008

Table S2.2. Model selection table for an *a priori* determined biologically relevant candidate set of five generalised linear mixed models (GLMer) model with a negative binomial model family was used to model the total provisioning rate (number of daily provisioning attempts) as a function of breeding season (hot and dry [2019/2020, $n_{highsupp}$ = 5, $n_{lowsupp}$ = 4] and cool and wet [2020/2021, $n_{highsupp}$ = 4, $n_{lowsupp}$ = 5]), T_{max} (maximum daily air temperature [T_{air}]), nest stage (female & eggs, female and chicks, and chicks only), resource supplementation treatment (low resource supplementation [low supp.] and high resource supplementation [high supp.]), the interaction between T_{max} and breeding season, and the interaction between T_{max} and resource supplementation for male Southern Yellow-billed Hornbills (*Tockus leucomelas*). Models ranked by Akaike's Information Criterion adjusted for small sizes (AICc) with top models (Δ AICc < 2) highlighted in bold. Models were averaged where more than one top model was identified. * indicate interactions between terms.

			independent variables									
response	**model no.**	**int.**	**nest stage (chicks)**	**T_{max}**	**season (cool and wet)**	**supp. (low)**	**T_{max} * season**	**T_{max} * supp.**	**df**	**AICc**	**Δ AICc**	**weight**
provisioning rate	**4**	**3.35**	**+**	**-0.12**	**+**	**+**			**8**	**3270.5**	**0**	**0.5**
	3	**3.35**	**+**	**-0.13**	**+**	**+**		**+**	**9**	**3272.2**	**1.75**	**0.21**
	2	**3.35**	**+**	**-0.11**	**+**	**+**	**+**		**9**	**3272.3**	**1.83**	**0.2**
	1	3.35	+	-0.12	+	+	+	+	10	3274	3.59	0.08
	5	3.78							3	3400.3	129.85	0

Table S2.3. Model selection table for an *a priori* determined biologically relevant candidate set of five linear mixed models (LMer) family Gaussian of Southern Yellow-billed Hornbill (*Tockus leucomelas*) male body temperature (T_b) below and above break-point air temperatures (T_{air}) as a function of 1) T_{air}, 2) breeding season, 3) resource supplementation (hot and dry breeding season [2019/2020] males $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season [2020/2021] males $n_{lowsupp}$ = 5, $n_{highsupp}$ = 4), 4) an interaction between T_{air} and breeding season, and 5) an interaction between T_{air} and resource supplementation. Models ranked by Akaike's Information Criterion adjusted for small sizes (AICc) with top models (Δ AICc < 2) highlighted in bold. Models were averaged where more than one top model was identified. * indicate interactions between terms.

			Independent variables								
response	**model no.**	**int.**	**T_{max}**	**season (cool and wet)**	**supp. (low)**	**T_{max} * season**	**T_{max} * supp.**	**df**	**AICc**	**Δ AICc**	**weight**
provisioning T_b below break-point	**1**	**40.94**	**0.28**	**+**	**+**	**+**	**+**	**8**	**14986.4**	**0**	**1**
	2	40.95	0.21	+	+		+	7	15017	30.61	0
	3	40.96	0.28	+	+	+		7	15029	42.65	0
	4	40.96	0.25	+	+			6	15034	47.63	0
	5	41.19						3	16978.3	1991.88	0
provisioning T_b above break-point	**1**	**41.52**	**0.42**	**+**	**+**	**+**	**+**	**8**	**11782.4**	**0**	**1**
	2	41.52	0.45	+	+	+		7	11796.5	14.17	0
	3	41.59	0.31	+	+		+	7	11799.7	17.35	0

	4	41.61	0.32	+	+		6	11818.6	36.28	0
	5	41.91					3	12755.8	973.41	0

3. Interannual climate variation and resource availability affect breeding success and thermoregulation, but not morphology, in nesting female hornbills

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3.1 Abstract

For birds, trade-offs between thermoregulation and self-maintenance or reproductive investment are pronounced in seasonally hot, arid zones. According to life history theory, the severity of those trade-offs may depend on resource availability. This study monitored the breeding success, morphology and physiology of a Kalahari Desert resident, the Southern Yellow-billed Hornbill (*Tockus leucomelas*; hornbill), over two breeding seasons (a hot and dry breeding season 2019/2020, T_{max} [mean daily maximum air temperature (T_{air})] = 34.2 °C ± 3.8 SD and rainfall = 130.6mm; and a cool and wet breeding season 2020/2021, T_{max} = 33.1 °C ± 3.1 SD and rainfall = 328.9mm) to investigate whether variation in resource (i.e., food and water) availability, due both to a supplementary-feeding experiment and the differences between the breeding seasons, had the potential to alter the impact of environmental temperature on reproductive, physiological, and morphological variables. Hatch probability (estimate = 4.52 ± 1.68 SE, p = 0.008; estimates do not have units, since continuous predictor variables were scaled), fledge probability (estimate = 3.20 ± 1.14 SE, p = 0.006) and the number of fledglings per female (estimate = 1.05 ± 0.40 SE, p = 0.009; hot and dry breeding season mean 0.9 ± 0.7 SD, n fledglings = 8; cool and wet breeding season mean 2.6 ± 0.8 SD, n fledglings = 28) were significantly higher in the cool and wet breeding season compared to the hot and dry breeding season, but not significantly affected by nest temperature (T_{nest}) or supplementary feeding (high *versus* low supp. treatments). Hatch and fledge probability were significantly negatively correlated with later lay (estimate = -3.11 ±

0.86, $p < 0.001$) and hatch (estimate = -2.16 ± 0.61, $p < 0.001$) sequence respectively. While incubating, females on both high and low resource supplementation treatments showed similar, shallow hyperthermic relationships with T_{nest}. However, comparatively steeper increases in body temperature (T_b) with increasing T_{nest} in the hot and dry breeding season caused incubating female T_b to exceed potentially deleterious egg temperatures at lower T_{nest} and more frequently than in the cool and wet breeding season. In females with chicks, low supp. individuals had steeper increases in T_b with increasing T_{nest} than high supp. females in both breeding seasons. Taken together, these results suggested that regardless of resource availability, females alter their thermoregulatory strategy when incubating versus when not, potentially to keep eggs cooled despite high T_{nest}. Weekly female body mass (M_b) was stable during incubation (estimate = -3.33 ± 1.69 SE, $p = 0.053$) but decreased significantly post-hatch (estimate = -21.02 ± 1.40 SE, $p < 0.001$) with increasing days since nest initiation. Weekly female tail feather lengths increased linearly with increasing days since nest initiation more rapidly in the cool and wet breeding season (estimate = 50.13 ± 0.65 SE, $p < 0.001$) than in the hot and dry breeding season (estimate = 44.16 ± 1.13 SE, $p < 0.001$), a significant difference (estimate = 0.63 ± 0.21 SE, $p = 0.007$). Feather barb density was significantly lower (estimate = -0.05 ± 0.02 SE, $p < 0.046$) in the cool and wet breeding season. Female M_b loss rate during incubation and post-hatch, female nest exit M_b, and tail feather corticosterone (CORT) concentration were not affected by breeding season, mean maximum T_{nest} during incarceration or growth, or resource supplementation. The lack of evidence for any T_{nest} or supp. effects on female breeding success, morphology suggested that neither T_{nest} nor resource availability were responsible for the observed breeding season differences in these parameters. However, differing nutritional quality of natural prey available between breeding seasons may have influenced females' M_b and feather growth rate and quality, although I did not have data to test this possibility. A new nest box design resulted in an average T_{nest} decrease of 3.99 °C compared to previous studies on this population, potentially accounting for the removal of previously demonstrated T_{nest} effects. Together, these findings highlight the possibility of improved (relatively cool, more thermally buffered) nest boxes being used as a conservation mechanism to reduce the impact of rapid climate warming for cavity nesting species, and the need for future research into potential resource quality effects on reproductive ecology in seasonally hot, arid environments.

3.2 Introduction

Ongoing climate change is increasing mean annual environmental temperatures and the frequency and intensity of heat waves (Mbokodo et al. 2020, IPCC 2022). For birds, the reproductive period may be particularly vulnerable to these increases, since the heightened energy, water, and time demands of reproduction often coincide with the hottest period of the year (Andreasson et al. 2020). High environmental temperatures elicit trade-offs between thermoregulation and self-maintenance or reproductive investment, which may cause chronic elevated corticosterone (CORT) levels, and reduced immune function, body condition, and breeding success (Ganendran et al. 2016, Conradie et al. 2020, Cook et al. 2020, Cunningham et al. 2021, Moagi et al. 2021). These high-temperature trade-offs are perhaps most pronounced and best-described in seasonally hot, arid zones, which are typically water-scarce with low primary productivity (Wolf 2000, Nagy 2004, Riddell et al. 2019).

Life history theory predicts that resource-limited organisms face trade-offs between costly traits (Stearns 1992). Therefore, costly trade-offs associated with high or low environmental temperatures might be caused by or aggravated by limited resources for thermoregulation (Sharpe et al. 2021). Increased resources can improve reproductive outcomes such as hatching success, offspring growth and condition (Korpimäki 1989, Simons and Martin 1990, Arnold 2011, Haley and Rosenberg 2013, Wellicome et al. 2013), increase fledging success and post-fledge survival (Soler and Soler 1996, Robb et al. 2008), reduce CORT (Kitaysky et al. 2001, Kitaysky et al. 2007, Schoech et al. 2008, Herring et al. 2011, Patterson et al. 2015), and improve thermoregulatory ability (Angilletta et al. 2010, Smit et al. 2013, Czenze et al. 2020). Generally, increased resources (naturally or via resource supplementation) can allow adult animals to invest more in self-maintenance, and reduce energy and time expended on reproduction or other costly activities (Martin 1987, Cook and Hamer 1997, Harding et al. 2002, Tieleman and Williams 2002, Robb et al. 2008, Olinger 2017). Some evidence suggests that high environmental temperatures in arid habitats are only limiting if they co-occur with drought and the associated low resource availability, indicating that resource availability may partially mediate environmental temperature effects (Cruz-McDonnell and Wolf 2016, Mares et al. 2017, Iknayan and Beissinger 2018, Bourne et al. 2020c, D'Amelio et al. 2022).

To investigate the effects of resource availability on the relationship between environmental temperature and breeding performance I monitored breeding and ran a supplementary feeding experiment over two breeding seasons of a population of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hereafter hornbills) in the Kalahari Desert in South Africa. Hornbills do not drink from open water sources, they get all their water from their diet. Consequently, I use 'resource availability' to refer to food and water. This use of 'resources' excludes other resources such as shade, potential breeding mates, or nest sites. The study took advantage of extreme and unpredictable natural climate variation which meant the two breeding seasons were very different: comprising a hot and dry breeding season, 2019/2020, and a cool and wet breeding season, 2020/2021. Hornbills are cavity nesters, breeding during the Austral spring and summer – the hottest period of the year. In the Kalahari, this period sees air temperatures (T_{air}) regularly exceed 40 °C. The study population of hornbills have bred in nest boxes at the site since 2008. Up until the start of data collection for this study, the nest boxes were uninsulated and orientated in various directions, often in direct sunlight during the hottest periods of the day (Finnie 2018, van de Ven et al. 2020b). At the start of the study, nest boxes were refurbished, insulated, painted, and orientated south-east approximately 1.5m off the ground. This standardised the nest placement and design and served to make nest box temperature (T_{nest}) profiles more similar between boxes, cooler than in previous studies on this population, and more similar to natural cavities (Griffiths et al. 2017, Maziarz et al. 2017, Larson et al. 2018, Briggs and Mainwaring 2021).

Previous work on this study population demonstrated that poor breeding performance was largely attributed to direct negative effects of high T_{nest} (van de Ven et al. 2020), directly associated with high T_{air}. However, high T_{air} also reduced provisioning rates, and lower provisioning rates also influenced nest outcomes. This indicated a potential resource availability effect (van de Ven et al. 2019, van de Ven et al. 2020b). Failure to hatch or fledge in hornbills is usually because of cannibalism; the female consumes her own eggs or nestlings (Engelbrecht 2013, Finnie 2018). Therefore, the negative effects of high T_{nest} may be because the female does not have sufficient resources to raise a large brood, thermoregulate, or maintain condition, in which case she cannibalises for brood reduction, to recoup resources for thermoregulation, or to avoid starvation (Chan et al. 2007, Ng et al. 2011). The unusual breeding strategy of hornbills means the female is unable to forage for herself while incarcerated in the nest and undergoes highly costly catastrophic moult and breeding simultaneously (van de Ven et al. 2020b). In light of these costs, although all hornbill females exit nests with similar M_b (van de Ven et al. 2020b), there may be long-term breeding effort costs other than to M_b for females, such as compromised feather quality or chronically elevated CORT levels (Hemborg et al. 1998, Fitzsimmons et al. 2017, Salleh Hudin et al. 2017, Martin et al. 2019).

I assessed whether resource availability could buffer the relationship between T_{nest} and hatch and fledge probability of eggs; and how it modifies the impact of T_{nest} on female parent T_b regulation, morphometrics, and body condition (including, body mass (M_b), feather quality, and feather CORT concentration). Ultimately, I aimed to improve our understanding of the vulnerability of arid-zone birds to climate change.

3.3 Methods

3.3.1 Study species, site, & weather data collection

Details on the study species, Southern Yellow-billed Hornbills (hereafter, hornbills), study site, and weather data collection are described in Chapter 2 (sections 2.2.1 & 2.2.2). Hornbills are cavity nesters and females seal themselves inside the nest cavity for most of the breeding attempt, leaving only a small slit through which the male passes food (and hence, indirectly, water, since the hornbills do not drink). The female seals in at the start of the breeding attempt and in successful attempts breaks out with about 70% of the breeding attempt completed – once she has regrown flight feathers and the chicks are old enough to reseal the nest entrance. Once incarcerated, females lay eggs asynchronously, laying one approximately every two days, culminating in approximately 2 – 6 eggs (Finnie 2018, van de Ven et al. 2020b). These hatch asynchronously in the order they were laid. While incarcerated, and at a similar time as the first egg is laid, the females moult all their flight feathers simultaneously. This means that the new feathers are grown in the nest over a known period. After breaking out, the female aids in provisioning to the chicks for several more weeks until the chicks fledge. The hornbills at the study site, Kuruman River Reserve (KRR), typically breed in wooden nest boxes (50 available boxes 2019 – 2021). Weather data in this study came from a weather station installed at the study site in 2011 (Hot Birds Research Project [HBRP] Weather Station; Vantage Pro2, Davis Instruments, Hayward, U.S.A.) set to record T_{air} (°C), wind speed ($m.s^{-1}$), relative humidity (%), and solar radiation ($W.m^{-2}$) at 5-min intervals. Data for Chapters 2, 3 (this chapter), and 4, were collected simultaneously over the course of the breeding season.

3.3.2 Supplementary feeding

Details on supplementary feeding are described in Chapter 2 (section 2.2.3). Briefly, nesting attempts were assigned a daily ration of darkling beetle larvae (*Zophobas morio*); low (low supp.; ~5g of darkling beetle larvae (7 individuals)) or high resource supplementation (high supp.; ~25g of darkling beetle larvae (30 individuals)). The sole-provisioning males consistently accessed and provisioned the supplementary food, and thus indirectly, water, to the nests, immediately after food was provided in the morning (see Chapter 2).

3.3.3 Nest temperatures

All breeding data were necessarily collected from birds breeding in nest boxes because the entrance sealing behaviour of females means nests in natural cavities are completely inaccessible for research. Nest box nest temperatures (T_{nest}) were recorded using Thermochron Hi-Res iButtons (DS1922-L, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, accuracy ± 0.5°C) mounted within the nests boxes on the underside of the nest box lids in plastic iButton wall holders. Monitoring of this population has been ongoing since 2008, but in 2019 all nest boxes were insulated by adding an outer layer of plywood, leaving a 2-cm gap between the plywood and the inner wood of the box. The outer insulation was then painted a brown-grey colour similar to the bark of the *Vachellia erioloba* trees on which the boxes were fixed, and boxes were places on the south-east side of tree trunks. I compared T_{nest} between previous measurements of occupied natural cavities (data collected between 2012 – 2015), occupied nest boxes between 2012 – 2015, and occupied nest boxes between 2019 – 2021. No natural cavity data were collected between 2019 – 2021. This gave a comparison between natural conditions in cavities between 2012 – 2015, nest box temperatures between 2012 – 2015 experienced by nest occupants when strong effects of T_{nest} on reproduction were demonstrated by (van de Ven et al. 2020b), and nest box temperatures in this study. For natural cavity measurements, iButtons were placed in an iButton reader holster secured with threading wire at the top of the cavity via the nest opening (van de Ven et al. 2020b).

3.3.4 Morphometrics, and hatching and fledging success / failure

Once a female sealed the nest entrance, nests were visited each day to record egg lay, female moult, chick hatch, egg or chick cannibalism by the female, female exit, and fledge dates. These were monitored by taking photos of the nest contents using a smartphone, after partially removing the lid on the nest boxes. Cannibalism was recorded when an egg or chick disappeared from the nest, which is known to be caused by cannibalism in hornbills (Engelbrecht 2013, Finnie 2018), and which, due to the small size of the slit the female leaves in the nest seal for the male to pass her food, cannot occur in any other way (i.e., the sealed nest prevents partial predation events by any animal other than the female hornbill herself, and prevents the parent birds removing eggs or chicks from the nest). Upon an incarcerated female laying her first egg, the female M_b and egg mass were measured (OHAUS TA502 electronic scale, Port Melbourne, VIC, Australia; resolution = 0.01g) and un-ringed females were ringed with a unique metal SAFRing and colour-ring combination (some females in the population were already ringed from previous research). Once a week following the initial measurements, the female M_b and egg mass was recorded. The day of or day after the first chick hatched the M_b of the chick and female were recorded, and once a week thereafter. Concurrently, I used a metal ruler (resolution 1mm) to measure the regrowth of the first tail feather to the dorsal-left of the central pair of the female, and the growth of the same feather in the chicks when they began growing feathers.

3.3.5 Body temperature

After laying the first egg (i.e., simultaneous with ringing and initial M_b measurements), each female was fitted with a passive integrated transponder tag (PIT tag; model HPT8, 8.4mm ISO FDXB, Biomark, Boise, Idaho, USA) implanted subcutaneously in between the scapulae to measure female T_b (PIT tags weighed 0.06g, approximately 0.024% of the mean initial breeding M_b of females). Cord antenna readers (Biomark, Boise, Idaho, USA; Figure) and HPR Plus readers (Biomark, Boise, Idaho, USA; Figure) were installed on the nest boxes to record unique identity and T_b of females at one-min intervals. Female T_b data were split according to incubation status (incubating only eggs, and with only chicks [after the last egg hatched; hereafter 'with chicks']; the period where females had both eggs and chicks were not included in T_b analyses) to compare thermoregulation during and post-incubation. This was because at high T_{nest} above incubating female T_b, the eggs could only be as cool as the female T_b – egg evaporation and brood patch effects notwithstanding. Egg temperatures above 41 °C can be lethal in some species of birds (Webb 1987, DuRant et al. 2013). Therefore, for eggs to stay below potentially lethal temperatures at $T_{nest} > 41$ °C, the female would have to incubate them to keep them cooled (O'Connor et al. 2016, O'Connor et al. 2018, McCowan and Griffith 2021). This contrasts the general model for incubation, where the incubating parents attempt to keep eggs warm.

3.3.6 Feather barb density and corticosterone

The first tail feather to the dorsal-left of the central pair was pulled after 26.7 ± 1.8SD days of growth (range 23 – 32 days; hot and dry breeding season [2019/2020] tail feather $n_{lowsupp} = 4$, $n_{highsupp} = 5$; cool and wet breeding season [2020/2021] tail feather $n_{lowsupp} = 6$, $n_{highsupp} = 3$ [two high supp. female tail feathers not pulled because one did not moult all of its tail feathers, and another could not be reached to pull the feather due to 4-week long flooding]). The tail feathers were stored in brown paper envelopes sealed inside a container with silica gel to remove moisture. At the end of the study, all the pulled tail feathers were transported to a laboratory and photographed (Canon 700D, Ōta, Tokyo, Japan) and weighed (Labotec Precision Analytical Balance, Midrand, South Africa; resolution = 0.1mg). The number of barbs in the middle third of the left dorsal side of each feather vane were counted in ImageJ software and divided by the length of the section to calculate the barb density of each feather (Pap et al. 2015). Feathers were then clipped at the base of the vane, and the calamus discarded. The remaining vane was then chopped into pieces (<1 mm). A keratinase solution was prepared with a standardised mass (0.0150 – 0.0155 g) of feather pieces by adding RONOZYME® ProAct (DSM, Kaiseraugst, Aargau, Switzerland) powder and alkaline phosphate buffered saline (PBS, pH9.0) at a ratio of 1 g of enzyme per 30 mL of PBS and feather mass of 88 mg (Alba et al. 2019). The keratinase solutions were incubated in a water bath incubator shaker (LABEX PTY LTD, JP Selecta ®, UNITRONIC-OR, Johannesburg, South Africa) at a speed of 30 rpm and a water temperature of 45°C. After completion of the liquifying process (i.e., 5 days) the solutions were centrifuged for 10 min at 1500 x g (Heraeus Megafuge 1.0R, Thermo Electron Corporation, Osterode, Germany). Thereafter, 1 mL of supernatant was stored at -20°C before corticosterone (CORT) enzyme immunoassays (EIA) were used to measure the CORT concentration in the feathers. Sensitivity of the assay was 28 ng.g^{-1} feather mass. The coefficients of variation for intra-assay variance determined by repeated measurements of high- and low-quality controls were 4.57% and 5.74%. The inter-assay coefficients of variation, also determined by repeated measurements of high- and low-quality controls, were 10.92% and 11.76%, similar to previous values for faecal CORT for hornbills (Bouwer et al. 2021). Samples collected during both breeding seasons were all analysed in mid-2021 to minimise any possible batch effects.

3.3.7 Statistical analyses

Statistical analyses were conducted in the R statistical environment, version 3.5.1 (R Core Team 2023), using the R Studio platform (R Studio Team 2023). Further details on the general statistical and general mixed modelling approach are given in the General Introduction (see Chapter 1). Based on analyses of statistical power (Cohen's f^2, the measure of determinable effect size), as calculated using the package pwr (Champely 2020), there was statistical power to detect moderate main ($f^2 \leq 0.221$) effects for models of hatch and fledge probability; very large main effects ($f^2 = 0.465$) for models of the number of fledglings produced per female; small main and interaction effects for models of T_b (all $f^2 \leq 0.006$); and very large main effects for models of female morphometrics (all f^2 between 0.465 – 0.568; Table S3.1).

Weather

Breeding season (19 October – 24 March) T_{max} and rainfall for 2019/2020 and 2020/2021 were calculated from weather data collected on site by the HBRP weather station (see Chapter 5).

Nest temperatures

Linear mixed models (LMer) family Gaussian were used to model maximum daily T_{nest} as a function of T_{max} for occupied natural cavities (n = 9), nest boxes in 2012 – 2015 (n = 27, prior to insulation and painting), and nest boxes in 2019 – 2021 (n = 20, insulated, painted grey-brown, and placed 1.5m off the ground on the south-east side of *Vachellia erioloba* trees). Box identity was included as a random effect. Tukey HSD post-hoc tests were used to test for differences in mean maximum daily T_{nest} between the nest types (i.e., natural cavities, nest boxes prior to insulation and painting, and nest boxes post insulation and painting), and between nest boxes in 2019/2020 and 2020/2021.

Breeding success

Welch Two Sample t-tests were used to test differences in the number of eggs laid per female as a function of breeding season.

Generalised linear models (GLMs) family binomial were used to model a) probability of an egg hatching (hereafter 'hatch probability') and b) probability of progressing from hatch to fledge (hereafter 'fledge probability') as functions of predictor variables determined *a priori* as likely to be biologically relevant, including 1) breeding season, 2) egg lay / hatch sequence, 3) mean maximum T_{nest} from lay until hatch / fail or hatch to fledge / fail, and 4) resource supplementation. No interaction terms were included given that the power to detect interactions was prohibitively low ($f^2 = 0.72$ and $f^2 = 0.95$ for interaction terms in hatch and fledge probability models, respectively). No model selection was performed for the hatch or fledge probability models; the results of each model with all four variables were reported.

Generalised linear models (family Poisson) were used to model the number of fledglings produced per female as a function of 1) breeding season, 2) mean maximum T_{nest} during female incarceration, 3) resource supplementation, and 4) the null model. Small sample sizes for the number of fledglings produced per female precluded fitting multiple fixed effect or interaction terms. Therefore, each model included only one fixed effect. Model selection was performed by comparing the AICc of each model. Results for all models with Δ AICc < 2 were reported.

Three females (of a total sample of 17 females) bred in both breeding seasons, however, small sample sizes (hot and dry breeding season females $n_{lowsupp} = 4$, $n_{highsupp} = 5$; cool and wet breeding season $n_{lowsupp} = 6$, $n_{highsupp} = 5$) meant that inclusion of nest box or female identity as a random effect in mixed models for hatch and fledge probability created issues of singular fit (overfit due to small sample sizes), so no random effects were specified (see Chapter 1). Inclusion of female identity as a fixed effect also destabilised models, but exploratory analyses suggested that neither hatch nor fledge probability had significant variance explained by female identity fit as a single fixed effect.

Body temperature

Female daytime T_b was measured at 1-min intervals for all females across both breeding seasons (hot and dry breeding season $n_{lowsupp} = 3$, $n_{highsupp} = 5$; cool and wet breeding season $n_{lowsupp} = 6$, $n_{highsupp} = 5$) totalling 233 610 T_b records while females were incarcerated. Exploratory analyses and previous literature (e.g., Smit et al. 2018) suggested different, segmented relationships between T_b and T_{nest} for females with different incubation statuses (incubating, versus with chicks), females in different breeding seasons and in different resource supplementation treatments. Therefore, T_b data were subset by breeding season, incubation status, and resource supplementation and modelled with Gaussian family as a function of T_{nest} so that the break-points for relationships between female T_b and T_{nest} within each subset (e.g., hot and dry breeding season, incubating, low supp. female T_b as a function of T_{nest}) could be identified. Break-points were estimated using segmented analyses (package segmented, Muggeo 2017), with visual inspection of generalised additive models (GAM) (package mgcv, Wood 2011) used to confirm the break-points identified by the segmented models. Subsets of data below break-points were then split by incubation status prior to further analyses, since T_b regulation was *a priori* expected to be different given the different thermal requirements of eggs and chicks; generally egg temperatures above 41 °C for sustained periods are thought to be potentially lethal, although the value of the critical temperature probably differs among species (Webb 1987, DuRant et al. 2013, McCowan and Griffith 2021). This 41 °C threshold was also included in trend visualisation and for contextualising T_b patterns concerning the ability of females to incubate eggs to keep them cool at T_{nest} > 41 °C and ensure embryo survival.

Therefore, subsets of data below break points, split by incubating status, were then modelled using LMer family Gaussian as functions of 1) breeding season, 2) T_{nest}, 3) resource supplementation, 4) an interaction between T_{nest} and breeding season, and 5) an interaction between T_{nest} and resource supplementation. This was repeated for subsets of data above break-points. The interactions between T_{nest} and breeding season were significant in all full models, so data were post-hoc split by breeding season to explore the different relationships between T_b and T_{nest} within each breeding season further.

Data below break-points within each breeding season were modelled using LMer family Gaussian as a function of 1) T_{nest}, 2) resource supplementation, and 3) an interaction between T_{nest} and resource supplementation. This was repeated for data above break-points. The interactions between T_{nest} and resource supplementation were significant in all global models, so data were further post-hoc split by resource supplementation treatment to explore the individual relationships between T_b and T_{nest} within each breeding season and resource supplementation treatment further.

Female identity was included in all T_b analyses as a random effect. Model selection and reporting for all T_b analyses followed the protocol detailed above for hatch and fledge probability.

Female morphometrics and CORT

To generate curves of female M_b change over time, I subset weekly measurements of female M_b by incubation status (incubating, and post-hatch of the first chick) since female mass maintenance is known to differ between these periods (van de Ven et al. 2020b). I then modelled LMer family Gaussian weekly measurements of female M_b within each subset as a function of days since nest initiation, including female identity as a random effect. To generate a post-moult tail feather growth curve over time, I modelled LMer family Gaussian weekly measurements of female tail feather length (the first tail feather to the dorsal-left of the central pair, which was eventually pulled and used for CORT and feather quality measurements) as a function of days since nest initiation, including female identity as a random effect.

GLM family Gaussian were used to model female a) M_b loss rate over the course of incarceration ([nest initiation M_b - nest exit M_b] / days incarcerated), b) exit M_b, d) tail feather growth rate, c) tail feather barb density, and d) tail feather CORT concentration as functions of 1) breeding season, 2) mean maximum T_{nest} over the course of incarceration / feather growth, 3) resource supplementation, and 4) the null. Small sample sizes for these morphometric parameters precluded fitting multiple fixed effects, interaction terms, or random effects. Therefore, each model included only one fixed effect. Model selection was performed by comparing the AICc of each model. Results for all models with Δ AICc < 2 were reported.

3.4 Results

3.4.1 Weather and nest temperatures

Breeding season T_{max} = 34.2 °C ± 3.8 SD and rainfall = 130.6mm (6mm above the drought threshold) in the hot and dry breeding season (2019/2020); and T_{max} = 33.1 °C ± 3.1 SD and rainfall = 328.9mm (> double the long-term breeding season average) in the cool and wet breeding season (2020/2021). Mean daily maximum

T_{nest} increased linearly with T_{max} in all nest types, with the nest boxes showing a near 1:1 relationship with T_{max} in 2012 – 2015 (estimate = 1.05 ± 0.02, $p < 0.001$) and 2019 – 2021 (estimate = 1.03 ± 0.02, $p < 0.001$), while natural cavity mean maximum T_{nest} increased more slowly (estimate = 0.80 ± 0.03, $p < 0.001$; Figure 3.1, Table 3.1). Mean maximum T_{nest} in boxes in 2012 – 2015 (40.23 °C ± 5.79 SD) were on average 5.51 °C higher than natural cavities (34.72 °C ± 4.60 SD), whereas mean maximum T_{nest} in boxes in 2019 – 2021 (36.24 °C ± 4.34 SD) were only 1.52 °C higher than natural cavities (Figure 3.1, Table 3.2). Mean maximum T_{nest} were on average 1.34 °C higher in hot and dry breeding season (37.00 °C ± 4.31 SD) compared to the cool and wet breeding season (35.66 °C ± 4.24 SD; Table 3.2). The mean maximum T_{nest} of all the nest types and periods were significantly different from each other (Table 3.2).

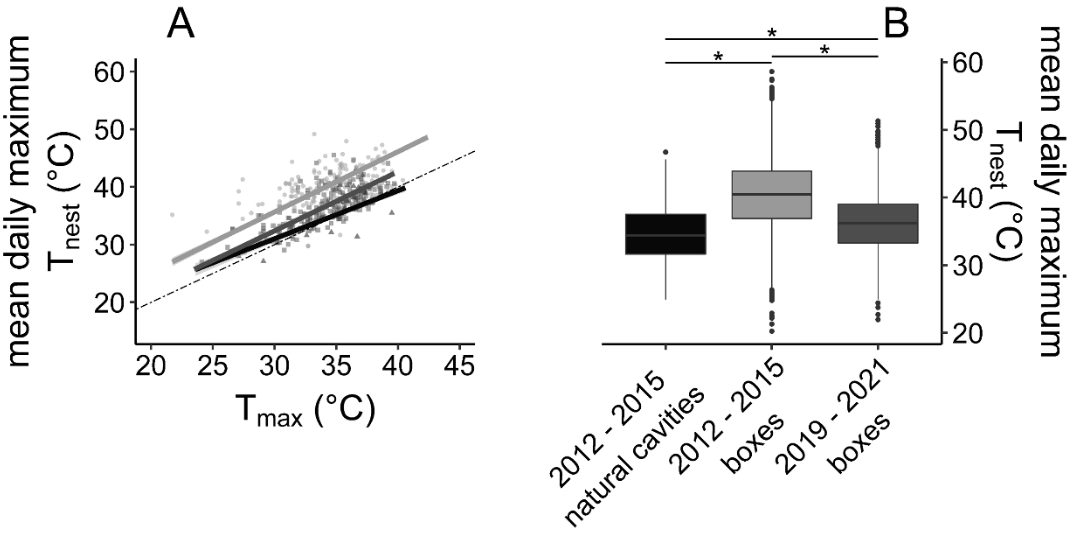

Figure 3.1. Mean maximum daily nest temperature (T_{nest}) for natural cavities in 2012 – 2015 (black line and box; n = 9), nest boxes in 2012 – 2015 (light-grey line and box, n = 27) and nest boxes in 2019 – 2021 (dark-grey line and box, n = 20) occupied by Southern Yellow-billed Hornbills (*Tockus leucomelas*) A) as functions of T_{max} (mean maximum daily air temperature [T_{air}]; plotted from a Gaussian linear mixed model [LMer]), and B) plotted as boxplots showing medians and upper and lower quartiles where * indicate significant differences.

Table 3.1. Linear mixed models (LMer) family Gaussian of the relationship between mean maximum daily nest temperature (T_{nest}) and mean maximum daily air temperature (T_{max}) for Southern Yellow-billed Hornbill (*Tockus leucomelas*) occupied natural cavities in 2012 – 2015 (n = 9), nest boxes in 2012 – 2015 (n = 27), and nest boxes in 2019 – 2021 (n = 20).

breeding seasons and nest	**response variable**	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
2012 – 2015 natural cavities	mean max. T_{nest} (°C)	T_{max}	**0.80 ± 0.03**	**28.45**	**409**	**0.001**	**0.75**	**0.86**
2012 – 2015 nest boxes	mean max. T_{nest} (°C)	T_{max}	**1.05 ± 0.02**	**46.08**	**2443**	**0.001**	**1.00**	**1.09**
2019 – 2021 nest boxes	mean max. T_{nest} (°C)	T_{max}	**1.03 ± 0.02**	**58.80**	**1809**	**0.001**	**1.00**	**1.07**

Table 3.2. Mean maximum daily nest temperatures (T_{nest}) and Tukey HSD post-hoc test for differences in mean maximum daily T_{nest} in Southern Yellow-billed Hornbill (*Tockus leucomelas*) occupied natural cavities (n = 9), nest boxes in 2012 – 2015 (n = 27), and nest boxes in 2019 – 2021 (n = 20), and between occupied nest boxes in 2019/2020 (n = 9) and 2020/2021 (n = 11).

T_{nest} comparison	**mean maximum T_{nest} °C ± SD**	**diff. (°C)**	**lower 95% CI**	**upper 95% CI**	**p adj. ≤**
2012 – 2015 natural cavities	34.72 ± 4.60				
2012 – 2015 nest boxes	40.23 ± 5.79				
2019 – 2021 nest boxes	36.24 ± 4.34				
2019/2020 nest boxes	37.00 ± 4.31				
2020/2021 nest boxes	35.66 ± 4.24				
2012 – 2015 natural cavities - 2012 – 2015 nest boxes		**-5.51**	**-6.16**	**-4.86**	**0.001**
2019 – 2021 nest boxes - 2012 – 2015 nest boxes		**-3.99**	**-4.36**	**-3.61**	**0.001**
2019 – 2021 nest boxes - 2012 – 2015 natural cavities		**1.52**	**0.86**	**2.19**	**0.001**
2020/2021 nest boxes - 2019/2020 nest boxes		**-1.34**	**-1.74**	**-0.94**	**0.001**

3.4.2 Breeding success

The number of eggs laid per female did not differ significantly between breeding seasons (Tables 3.3 & S3.2). Model estimates showed that hatch probability (estimate = 4.52 ± 1.64 SE, $p = 0.006$) and fledge probability (estimate = 3.14 ± 1.11 SE, $p = 0.005$) were significantly higher in the cool and wet breeding season compared to the hot and dry breeding season (Figure 3.2; Table 3.3). Hatch and fledge probability were significantly negatively correlated with later lay (estimate = -3.01 ± 0.79, $p < 0.001$) and hatch (estimate = -2.14 ± 0.60, $p < 0.001$) sequence respectively (Figure 3.3, Table 3.3). Neither hatch probability nor fledge probability were significantly correlated with T_{nest} from lay / hatch until hatch / fledge / fail or resource supplementation (Table 3.3). The number of fledglings per female was significantly higher in the cool and wet season (estimate = 1.05 ± 0.40 SE, $p = 0.009$; hot and dry breeding season mean 0.9 ± 0.7 SD, n fledglings = 8; cool and wet breeding season mean 2.6 ± 0.8 SD, n fledglings = 28), but not significantly correlated with T_{nest} during female incarceration, or with resource supplementation (Figure 3.2; Tables 3.3 & S3.3).

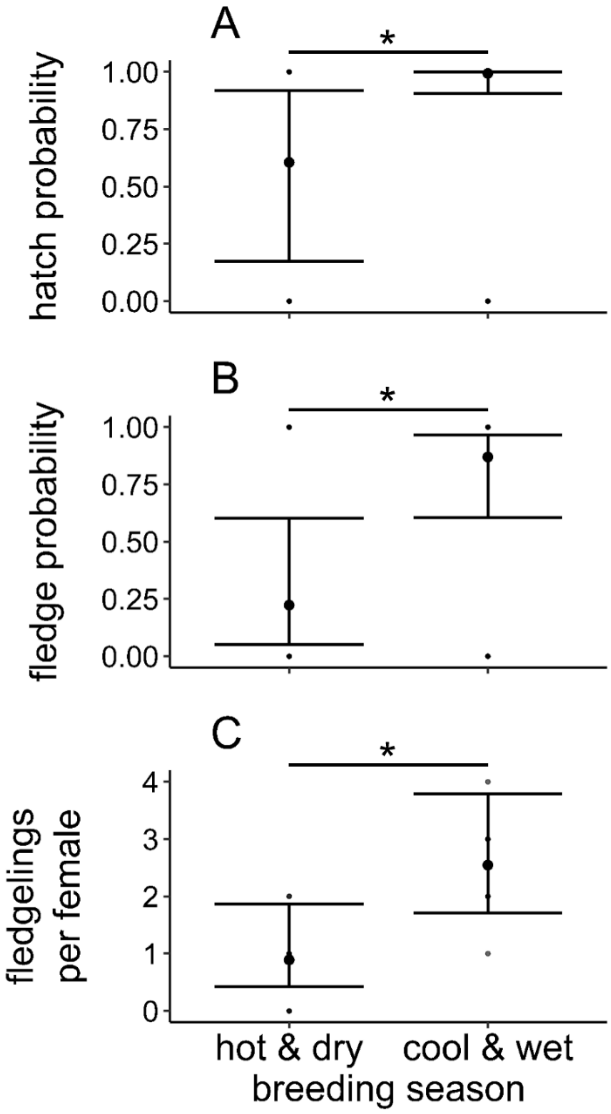

Figure 3.2. Breeding season difference in A) the probability of an egg hatching (hatch probability; plotted from binomial generalised linear model [GLM]; 1 = hatch, 0 = fail; hot and dry [2019/2020] breeding season n eggs = 33, cool and wet [2020/2021] breeding season n eggs = 47), B) the probability of a chick progressing from hatch to fledge (fledge probability; plotted from binomial GLM; 1 = fledge, 0 = fail; hot and dry breeding season chicks = 21, cool and wet breeding season n chicks = 39), and C) the number of fledglings produced per female (plotted from Poisson GLM; hot and dry breeding season n fledglings = 8, cool and wet breeding season n fledglings = 28) for breeding Southern Yellow-billed Hornbills (*Tockus leucomelas*). Means with standard errors are shown. * indicates a significant difference.

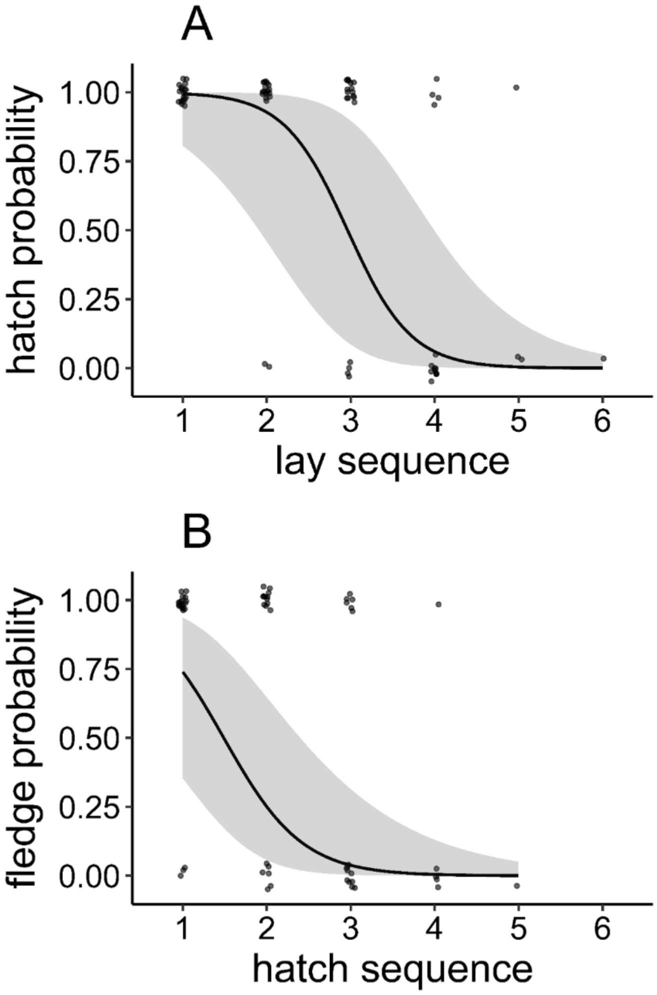

Figure 3.3. A) The probability of an egg hatching (hatch probability; plotted from a binomial generalised linear model [GLM]; 1 = hatch, 0 = fail; hot and dry [2019/2020] breeding season n chicks = 21, cool and wet [2020/2021] breeding season n chicks = 39), and B) the probability of a chick progressing from hatch to fledge (fledge probability; plotted from a binomial GLM; 1 = fledge, 0 = fail; hot and dry breeding season n fledglings = 8, cool and wet breeding season n fledglings = 26), for breeding Southern Yellow-billed Hornbills (*Tockus leucomelas*). Both the relationship between hatch probability and lay sequence and between fledge probability and hatch sequence are significant ($p < 0.05$).

Table 3.3. Welch two-sample T-test results for the number of eggs laid by breeding Southern Yellow-billed Hornbills (*Tockus leucomelas*) as a function of breeding season. Model estimates for the probability of an egg hatching (hatch probability; hot and dry [2019/2020] breeding season n eggs = 33, cool and wet [2020/2021] breeding season n eggs = 47) and the probability of a chick progressing from hatch to fledge (fledge probability; hot and dry breeding season chicks = 21, cool and wet breeding season n chicks = 39), modelled using generalised linear models (GLM) families binomial as functions of 1) breeding season, 2) resource supplementation (hot and dry breeding season breeding attempts $n_{lowsupp} = 4$, $n_{highsupp} = 5$; cool and wet breeding season breeding attempts $n_{lowsupp} = 6$, $n_{highsupp} = 5$), 3) egg lay / chick hatch sequence, and 4) mean max. T_{nest} from lay / hatch to hatch / fledge / fail. Top model results for the number of fledglings produced per female (hot and dry breeding season n fledglings = 8, cool and wet breeding season n fledglings = 26) modelled using GLM family Poisson as a function of 1) breeding season, 2) resource supplementation, 3) mean max. T_{nest} during female incarceration, and 4) the null; each fixed effect was fit on its own. Independent variables not shown for the number of fledglings produced per female were those not present in the top model following model selection. Significant ($p \leq 0.05$) effects are highlighted in bold.

response variable	independent variables	estimate ± se	z	df	p ≤	lower 95% CI	upper 95% CI
number of eggs	season (cool and wet)		-1.9	18	0.076	-1.28	0.07
hatch probability	**season (cool and wet)**	**4.52 ± 1.64**	**2.76**	**74**	**0.006**	**1.77**	**8.31**
	egg lay sequence	**-3.01 ± 0.79**	**-3.79**	**74**	**0.001**	**-4.93**	**-1.73**
	mean max. T_{nest} lay to hatch / fail	0.81 ± 0.71	1.14	74	0.254	-0.47	2.35
	supp (low)	-0.45 ± 1.00	-0.45	74	0.655	-2.49	1.53
fledge probability	**season (cool and wet)**	**3.14 ± 1.11**	**2.82**	**59**	**0.005**	**1.21**	**5.70**
	egg lay sequence	**-2.14 ± 0.60**	**-3.57**	**59**	**0.001**	**-3.54**	**-1.13**

	mean max. T_{nest} hatch to fledge / fail	-0.82 ± 0.47	-1.75	59	0.080	-1.84	0.03
	supp (low)	0.08 ± 0.77	0.1	59	0.918	-1.61	1.46
number of fledglings	**season (cool and wet)**	**1.05 ± 0.40**	**2.624**	**19**	**0.009**	**0.31**	**1.91**

3.4.3 Female body temperature

There were single top models within Δ AICc < 2 for female T_b while incubating and with chicks both below and above break-points (with the exception of incubating females in the cool and wet season where 2 top models were averaged; Table S3.4). The top models (Table S3.4) included significant interactions between T_{nest} and breeding season. Post-hoc top models showed that within each breeding season female T_b was significantly affected the interaction between T_{nest} and resource supplementation, except T_b below and above break-points for incubating females in the hot and dry season and below and above break-points for incubating females in the cool and wet breeding season (Table S3.5). Further post-hoc analyses showed that for incubating females and females with chicks, in both breeding seasons and both resource supplementation treatments, below and above break-points, all relationships between T_b and T_{nest} were significant (T_{nest} break-points summarised in Table 3.4, slopes summarised in Table 3.5). Mean and modal T_b below break-points were between T_b = 39.5 – 40.5 °C (Figures 3.4 & 3.5; Table 3.4). Female T_b maxima were lowest while incubating in both breeding seasons, and highest in high supp. females with chicks in the hot and dry breeding season (T_b maxima summarised in Table 3.4). Slopes of change in T_b with increasing T_{nest} below break-points were shallow for females in the both the hot and dry breeding season ($n_{lowsupp}$ = 3, $n_{highsupp}$ = 5) and the cool and wet breeding season ($n_{lowsupp}$ = 6, $n_{highsupp}$ = 5; Figures 3.4 & 3.5; Table 3.5). Incubating female T_b showed similar relationships with T_{nest} for both resource supplementation treatments below and above break-points within each breeding season; comparing breeding seasons, incubating females in the hot and dry breeding season had steeper slopes in T_b above break-points than in the cool and wet breeding season, causing T_b to exceed 41 °C at lower T_{nest} and more frequently in the hot and dry breeding season (Figures 3.4 & 3.5; Table 3.5). Low supp. females with chicks in both breeding seasons had steeper increases in T_b above the break-points than high supp. females (Figures 3.4 & 3.5; Table 3.5).

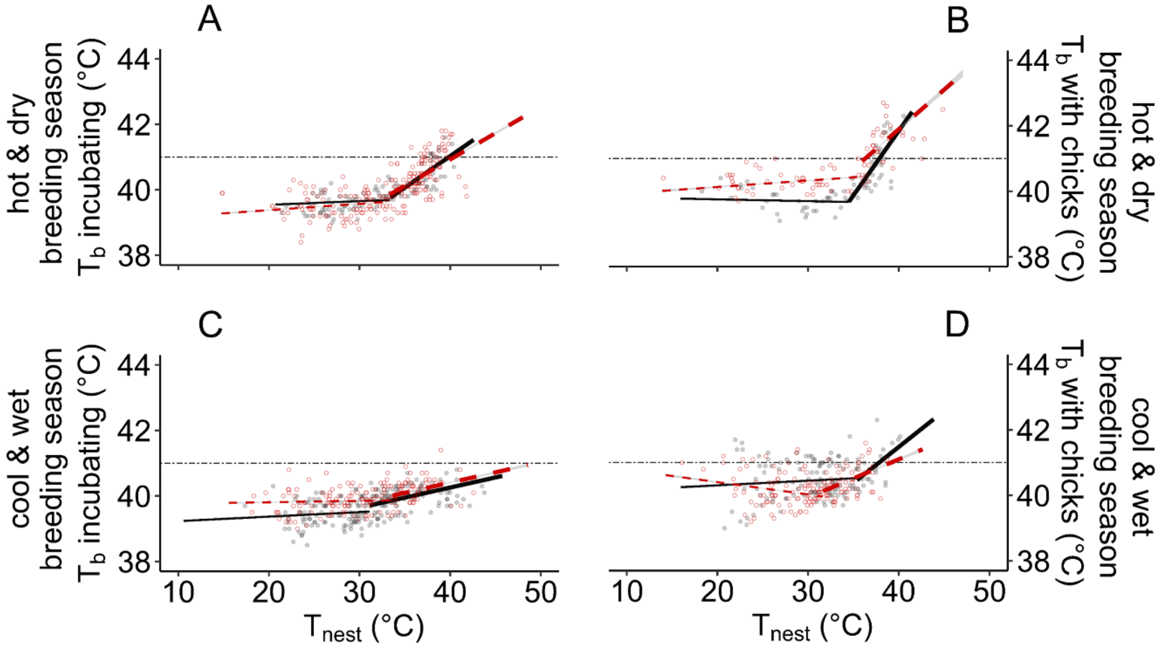

Figure 3.4. Southern Yellow-billed Hornbill (*Tockus leucomelas*) daytime body temperature (T_b; plotted from Gaussian linear mixed models [LMer]) in females A) incubating in the hot and dry breeding season ($n_{lowsupp}$ = 3, $n_{highsupp}$ = 5) and B) with chicks in the hot and dry breeding season, C) incubating in cool and wet breeding season ($n_{lowsupp}$ = 6, $n_{highsupp}$ = 5), and D) with chicks in the cool and wet breeding season. Female T_b split by resource supplementation, (low supp. black solid lines, dark grey-black filled circles; high supp. red dashed lines, open red circles). Two-dash horizontal line at T_b = 41 °C; egg temperatures > 41 °C for several hours can be lethal (Webb 1987). 95% confidence intervals (CI) are shown. Trend lines do not in reality extend beyond the data points to which models were fitted: only1% of data are plotted for visual clarity. Each relationship between T_b and T_{nest} for both resource supplementations in both breeding seasons is significant ($p < 0.05$).

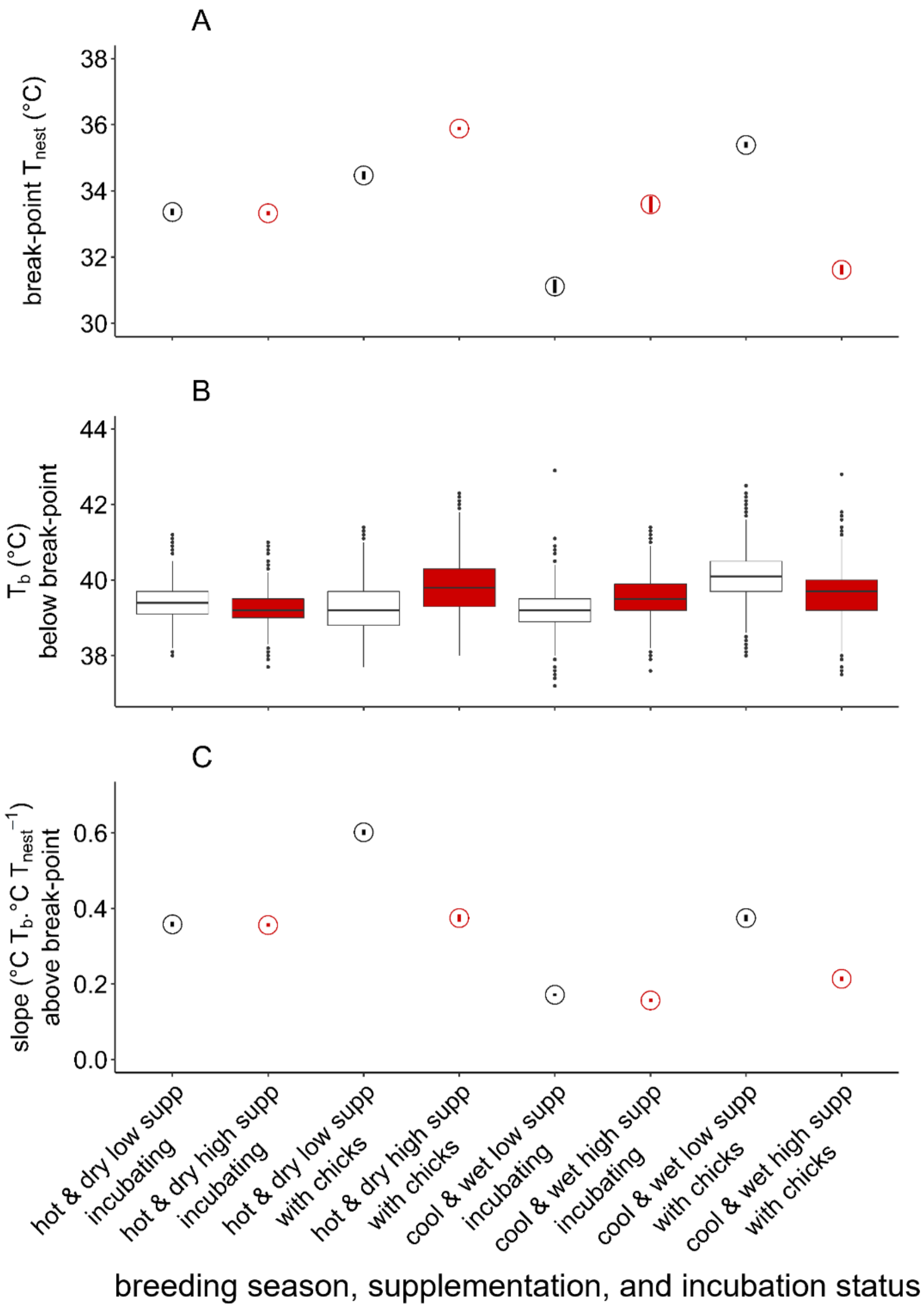

Figure 3.5. A) The break-point nest temperature (T_{nest}) at which breeding female Southern Yellow-billed Hornbills (*Tockus leucomelas*) daytime body temperature (T_b) began to increase or increase significantly more rapidly with increasing T_{nest}, B) median T_b with upper and lower quartiles below the break-point T_{nest}, and C) the slope of the increase in T_b above the break-point T_{nest}, over the hot and dry (2019/2020, $n_{lowsupp}$ = 3, $n_{highsupp}$ = 5) and cool and wet (2020/2021, $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5) breeding seasons. Data split according to resource supplementation (low supp. black, high supp. red), and incubation status.

Table 3.4. Female Southern Yellow-billed Hornbill (*Tockus leucomelas*) body temperature (T_b) was modelled using a linear mixed model (LMer) family Gaussian as a function of nest temperature (T_{nest}) split by incubation status (incubating, and with chicks), breeding season, and resource supplementation (hot and dry breeding season [2019/2020] females $n_{lowsupp} = 3$, $n_{highsupp} = 5$; cool and wet breeding season [2020/2021] females $n_{lowsupp} = 6$, $n_{highsupp} = 5$). All relationships had significant break-point T_{nest} above which T_b began increasing or increased more rapidly. Estimated break-point T_{nest} for each relationship, the mean and mode T_b below each break-point, and maximum T_b with the maximum T_{nest} experienced in brackets shown.

response	**breeding season**	**incubation status**	**supp.**	**break-point T_{nest} °C ± SE**	**mean T_b °C ± SD below break-point**	**mode T_b °C below break-point**	**maximum T_b °C (max. T_{nest} °C experienced)**
female T_b	hot and dry	incubating	low supp.	33.36 ± 0.10	39.63 ± 0.35	39.7	42.9 (42.6)
			high supp.	33.33 ± 0.07	39.53 ± 0.42	39.5	42.1 (48.0)
		with chicks	low supp.	34.47 ± 0.13	39.71 ± 0.33	39.8	42.3 (41.5)
			high supp.	35.88 ± 0.05	40.30 ± 0.41	40.2	43.7 (47.1)
female T_b	cool and wet	incubating	low supp.	31.11 ± 0.20	39.46 ± 0.40	39.7	42.9 (45.8)
			high supp.	33.59 ± 0.25	39.84 ± 0.38	39.8	41.6 (48.6)
		with chicks	low supp.	35.39 ± 0.09	40.45 ± 0.59	40.1	42.5 (43.8)
			high supp.	31.62 ± 0.15	40.16 ± 0.52	39.9	42.8 (42.6)

Table 3.5. Results for top models of female Southern Yellow-billed Hornbill (*Tockus leucomelas*) body temperature (T_b) below and above break-point nest temperatures (T_{nest}) split by breeding season and incubation status (incubating, and with chicks) modelled using a linear mixed model (LMer) family Gaussian as a function of 1) nest temperature (T_{nest}), 2) resource supplementation (hot and dry breeding season [2019/2020] females $n_{lowsupp}$ = 3, $n_{highsupp}$ = 5; cool and wet breeding season [2020/2021] females $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5), and 3) an interaction between T_{nest} and resource supplementation. A single top model for each analysis was identified following model selection. Significant estimates are highlighted in bold.

breeding season	**response**	**status / treatment**	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
hot and dry	female T_b (below break-point)	incubating	**T_{nest}**	**0.06 ± 0.00**	**21.79**	**15980**	**0.001**	**0.05**	**0.06**
			supp. (low)	0.01 ± 0.19	0.07	15980	0.947	-0.35	0.37
		low supp. incubating	**T_{nest}**	**0.04 ± 0.00**	**9.49**	**6441**	**0.001**	**0.03**	**0.05**
		high supp. incubating	**T_{nest}**	**0.07 ± 0.00**	**20.00**	**9535**	**0.001**	**0.06**	**0.07**
	female T_b (below break-point)	with chicks	**T_{nest}**	**0.08 ± 0.01**	**14.17**	**7922**	**0.001**	**0.07**	**0.09**
			supp. (low)	**-0.56 ± 0.06**	**-9.31**	**7922**	**0.001**	**-0.67**	**-0.44**
			T_{nest} * supp. (low)	**-0.1 ± 0.01**	**-11.32**	**7987**	**0.001**	**-0.12**	**-0.08**

	low supp. with chicks	**T_{nest}**	**-0.02 ± 0.01**	**-3.65**	**3354**	**0.001**	**-0.03**	**-0.01**
	high supp. with chicks	**T_{nest}**	**0.08 ± 0.01**	**13.25**	**4617**	**0.001**	**0.07**	**0.09**
female T_b (above break-point)	incubating	**T_{nest}**	**0.33 ± 0.00**	**92.48**	**15910**	**0.001**	**0.32**	**0.33**
		supp. (low)	-0.04 ± 0.21	-0.17	15910	0.872	-0.45	0.37
	low supp. incubating	**T_{nest}**	**0.28 ± 0.01**	**41.66**	**3748**	**0.001**	**0.26**	**0.29**
	high supp. incubating	**T_{nest}**	**0.34 ± 0.00**	**82.16**	**12170**	**0.001**	**0.33**	**0.35**
female T_b (above break-point)	with chicks	**T_{nest}**	**0.41 ± 0.01**	**40.93**	**6992**	**0.001**	**0.39**	**0.43**
		supp. (low)	-0.33 ± 0.18	-1.79	6992	0.123	-0.68	0.03
		T_{nest} * supp. (low)	**0.17 ± 0.01**	**12.91**	**7145**	**0.001**	**0.15**	**0.20**
	low supp. with chicks	**T_{nest}**	**0.56 ± 0.01**	**72.77**	**3683**	**0.001**	**0.54**	**0.57**
	high supp. with chicks	**T_{nest}**	**0.4 ± 0.01**	**37.08**	**3463**	**0.001**	**0.38**	**0.42**

cool and wet	female T_b (below break-point)	incubating	**T_{nest}**	**0.05 ± 0.00**	**20.32**	**21060**	**0.001**	**0.04**	**0.05**
			supp. (low)	-0.27 ± 0.16	-1.66	21060	0.131	-0.59	0.05
		low supp. incubating	**T_{nest}**	**0.03 ± 0.00**	**10.83**	**10080**	**0.001**	**0.03**	**0.04**
		high supp. incubating	**T_{nest}**	**0.05 ± 0.00**	**17.02**	**10970**	**0.001**	**0.05**	**0.06**
	female T_b (below break-point)	with chicks	**T_{nest}**	**-0.02 ± 0.0**	**-3.84**	**19640**	**0.001**	**-0.03**	**-0.01**
			supp. (low)	0.25 ± 0.26	0.93	19640	0.377	-0.27	0.76
			T_{nest} * supp. (low)	**0.13 ± 0.01**	**23.29**	**19640**	**0.001**	**0.12**	**0.14**
		low supp. with chicks	**T_{nest}**	**0.11 ± 0.00**	**31.35**	**10860**	**0.001**	**0.10**	**0.11**
		high supp. with chicks	**T_{nest}**	**-0.02 ± 0.00**	**-3.90**	**8783**	**0.001**	**-0.02**	**-0.01**
	female T_b (above break-point)	incubating	**T_{nest}**	**0.16 ± 0.00**	**59.88**	**17010**	**0.001**	**0.16**	**0.17**
			supp. (low)	-0.13 ± 0.09	-1.45	17010	0.180	-0.31	0.05
		low supp. incubating	**T_{nest}**	**0.16 ± 0.00**	**52.82**	**11270**	**0.001**	**0.16**	**0.17**

female T_b (above break-point)	high supp. incubating	**T_{nest}**	**0.14 ± 0.01**	**29.29**	**5740**	**0.001**	**0.13**	**0.15**
	with chicks	**T_{nest}**	**0.24 ± 0.01**	**45.83**	**8236**	**0.001**	**0.23**	**0.25**
		supp. (low)	0.09 ± 0.23	0.38	8236	0.714	-0.36	0.54
		T_{nest} * supp. (low)	**0.09 ± 0.01**	**8.81**	**8240**	**0.001**	**0.07**	**0.11**
	low supp. with chicks	**T_{nest}**	**0.24 ± 0.01**	**31.22**	**2577**	**0.001**	**0.23**	**0.26**
	high supp. with chicks	**T_{nest}**	**0.19 ± 0.00**	**50.31**	**5661**	**0.001**	**0.18**	**0.20**

3.4.4 Female morphometrics

Weekly female M_b (M_b change curve) was stable during incubation (estimate = -3.33 ± 1.69 SE, $p = 0.053$) but decreased significantly post-hatch (estimate = -21.02 ± 1.40 SE, $p < 0.001$) with increasing days since nest initiation (Figure 3.6). Weekly female tail feather lengths increased linearly with increasing days since nest initiation more rapidly in the cool and wet season (estimate = 50.13 ± 0.65 SE, $p < 0.001$) than in the hot and dry season (estimate = 44.16 ± 1.13 SE, $p < 0.001$; Figure 3.6; Table 3.6).

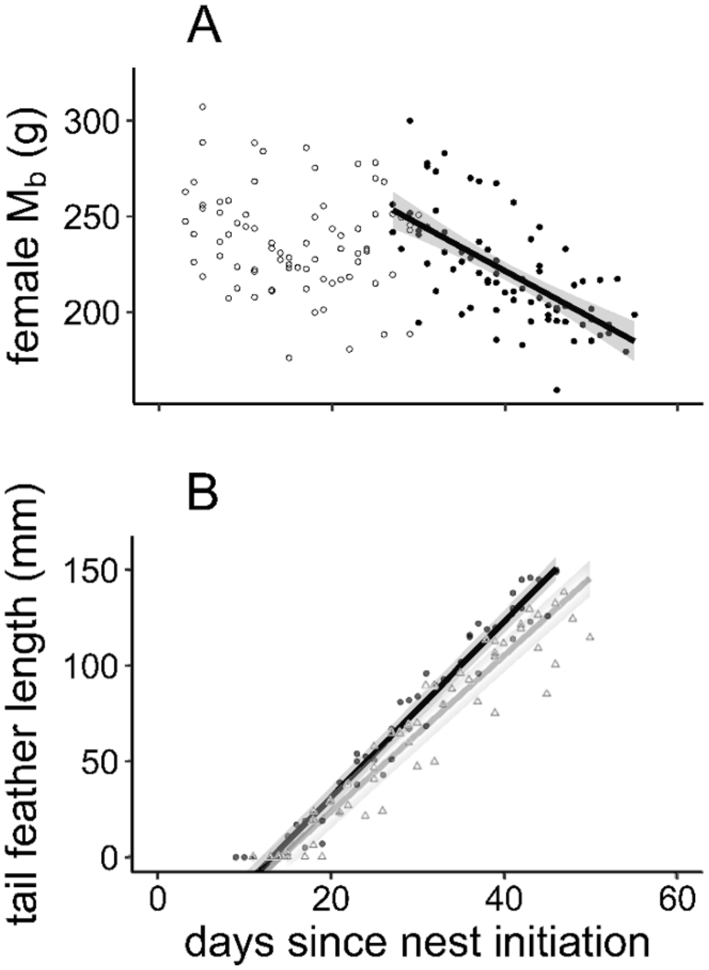

Figure 3.6. Female Southern Yellow-billed Hornbill (*Tockus leucomelas*) A) body mass (M_b) change as a function of days since nest initiation(hot and dry breeding season ($n_{lowsupp}$ = 4, $n_{highsupp}$ = 5), and the cool and wet breeding season ($n_{lowsupp}$ = 6, $n_{highsupp}$ = 5); plotted from Gaussian linear mixed models [LMer]); female M_b did not change significantly with increasing days since nest initiation while incubating (open circles), but declined significantly ($p < 0.05$) post hatch of the first chick; and B) post-moult length of female tail feathers (plotted from Gaussian generalised linear model [GLM]) as a function of the number of days since nest initiation in the hot and dry ($n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; grey line and open triangles) and the cool and wet ($n_{lowsupp}$ = 6, $n_{highsupp}$ = 3; solid black line and closed circles) breeding seasons.

Table 3.6. Model results for Southern Yellow-billed Hornbill (*Tockus leucomelas*) female (hot and dry breeding season, n females = 9; cool and wet breeding season, n females = 11) a) weekly body mass (M_b; M_b change curve) while incubating and post-hatch and b) weekly tail feather length (tail feather growth curve) modelled using linear mixed models (LMer) family Gaussian as functions of the number of days since nest initiation ('days since entry'). Female identity was included as a random effect. Significant ($p \leq 0.05$) effects are highlighted in bold.

response	**status / treatment**	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
weekly female M_b	incubating	days since entry	-3.33 ± 1.69	-1.97	61.54	0.053	-6.69	-0.01
	post-hatch	**days since entry**	**-21.02 ± 1.40**	**-14.98**	**60.14**	**0.001**	**-23.76**	**-18.17**
weekly female tail feather length	**hot and dry breeding season**	**days since entry**	**44.16 ± 1.13**	**39.22**	**40.69**	**0.001**	**41.89**	**46.37**
	cool and wet breeding season	**days since entry**	**50.13 ± 0.65**	**76.83**	**49.17**	**0.001**	**48.83**	**51.41**

Top model (Table S3.6) estimates showed that female M_b loss rate during incubation and post-hatch and female nest exit M_b, and tail feather CORT concentration were not affected by breeding season, mean maximum T_{nest} during incarceration (for M_b loss rate and exit M_b) or growth (for tail feather CORT), or resource supplementation (Table 3.7). Female tail feather growth rate was significantly higher in the cool and wet breeding season (estimate = 0.63 ± 0.21 SE, $p = 0.007$; Figure 3.6), but not significantly affected by mean maximum T_{nest} during incarceration or growth or resource supplementation (Table 3.7). Female tail feather barb density was significantly lower (estimate = -0.05 ± 0.02 SE, $p = 0.046$) in the cool and wet breeding season compared to the hot and dry breeding season (Figure 3.7; Table 3.7), but not significantly affected by mean maximum T_{nest} during incarceration / growth or resource supplementation (Table S3.6).

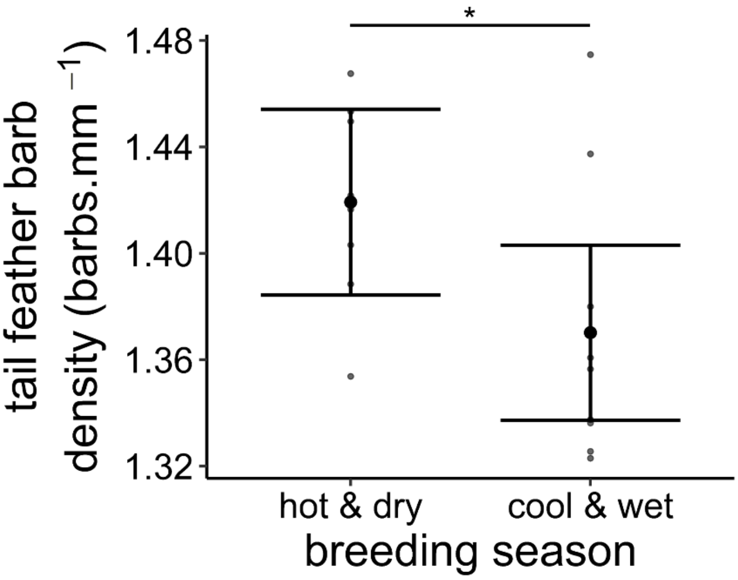

Figure 3.7. Female Southern Yellow-billed Hornbills (*Tockus leucomelas*) tail feather barb density as a function of breeding season (plotted from a Gaussian generalised linear model; hot and dry breeding season n tail feathers = 9; cool and wet breeding season n tail feathers = 9). Means with standard errors are shown.* indicates significant difference.

Table 3.7. Top model(models within Δ AICc <2 shown) estimates for Southern Yellow-billed Hornbill (*Tockus leucomelas*) female a) body mass (M_b) loss rate while incubating, b) M_b loss rate post-hatch, c) exit M_b, d) tail feather growth rate, , e) tail feather barb density, and f) tail feather corticosterone (CORT) concentration, modelled using a generalised linear models (GLM) family Gaussian as functions of 1) breeding season (hot and dry breeding season, n females = 9; cool and wet breeding season, n females = 11), 2) mean maximum nest temperature (T_{nest}) during incarceration / growth, 3) resource supplementation (hot and dry breeding season females $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season females $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5 [tail feathers $n_{highsupp}$ = 3]), and 4) the null. Independent variables not shown were those not present in the top model set following model selection. Significant ($p \leq 0.05$) effects are highlighted in bold.

response	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
female M_b loss rate incubating	null						
	mean max. T_{nest} during incubation	0.25 ± 0.24	1.07	19	0.299	-0.21	0.71
	supp. (low)	-0.42 ± 0.46	-0.92	19	0.372	-1.33	0.48
female M_b loss rate post-hatch	null						
	supp. (low)	-0.72 ± 0.55	-1.31	19	0.207	-1.79	0.36
female exit M_b	null						
	mean max. T_{nest} during growth	4.06 ± 2.95	1.38	19	0.186	-1.72	9.83
female feather growth rate	**season (cool and wet)**	**0.63 ± 0.21**	**3.08**	**17**	**0.007**	**0.23**	**1.03**

female tail feather barb density	**season (cool and wet)**	**-0.05 ± 0.02**	**-2.18**	**17**	**0.046**	**-0.09**	**-0.01**
	null						
female CORT conc.	null						

3.5 Discussion

This study demonstrated significant breeding season differences in hornbill breeding ecology; the cool and wet (2020/2021) breeding season correlated with improved female parent self-maintenance (i.e., faster, and higher quality post-moult tail feather regrowth), improved female T_b regulation during incubation (i.e., hyperthermia avoidance and more gradual increases in T_b above break-points), increased hatching and fledging probability, and ultimately more fledglings per female compared to the hot and dry (2019/2020) breeding season. However, little evidence for any resource supplementation or T_{nest} effects on female breeding success, morphology, or physiology, other than thermoregulation, suggested that neither T_{nest} nor resource availability were responsible for the observed breeding season differences. Consequently, the most likely alternative explanations were either that differences in natural resource quality between breeding seasons drove breeding season differences, or that the supplementary feeding experiment was ineffectual to elicit resource availability responses. Any effects of resource supplementation in the cool and wet breeding season could also have been overcome by the likely exceptional natural resource availability and quality caused by the extraordinary rainfall and flooding. I did not have the data to test these possibilities, so they remain speculative. Larger sample sizes over more breeding seasons could investigate these options and increase statistical power to provide insight about whether supplementation effects were too small to be detected with small sample sizes in my analyses. Overall, the lack of T_{nest} or resource supplementation effects rendered it difficult to draw any firm conclusions regarding the aim of the study to investigate potential buffering effects of resource availability against the previously established (van de Ven et al. 2019, van de Ven et al. 2020b) negative effects of high environmental temperatures.

A priori, one might expect breeding season differences in both T_{nest} and resource availability could have driven breeding season variation in breeding outcomes considering the mean maximum T_{nest} were on average 1.34 °C cooler and breeding season rainfall was over double the average in the cool and wet breeding season leading to greatly increased food availability and quality in the system. However, I found little evidence to support any significant effects of supplementary feeding or direct T_{nest} effects on breeding success or female physiology and morphometrics. The only evidence for resource supplementation effects were that high supp. females showed less pronounced hyperthermia at high T_{nest} when with chicks. Increased resource availability, especially water rich food, would be expected to improve thermoregulation since thermoregulatory capacity is linked to hydration status in hot and arid environments (Boyles et al. 2011). In that regard, this study demonstrated that female T_b regulation was dependent on incubation status; females showed increased hyperthermia avoidance and more gradual increases in T_b during incubation. Egg development is strongly dependent on egg temperature; optimal embryo development in wild birds is thought to be at egg temperatures between 35 – 40 °C (Tieleman et al. 2008, Álvarez and Barba 2014, Griffith et al. 2016). The effect of egg temperature on development is nonlinear and precipitously more severe at egg temperatures above the thermal optimum than those below (Conway and Martin 2000a, Griffith et al. 2016). Essentially, development rate declines below ~35 °C until it ceases at ~25 °C (Conway and Martin 2000a, Tieleman et al. 2008). In contrast, egg temperatures only 1 °C above the upper end of the optimum development range (i.e., 41 °C) are expected to be lethal if maintained for a few hours, while egg temperatures of > 43 °C are thought to be lethal after only a few minutes (Webb 1987, Williams 1996, Tieleman et al. 2008, DuRant et al. 2013, but see Griffith et al. 2016). Therefore, the hyperthermia avoidance during incubation suggested that females increased investment in thermoregulation when T_{nest} >41 °C during incubation to stop egg temperature tracking T_{nest} and exceeding 41 °C for long periods (Webb 1987, Carroll et al. 2018, Englert Duursma et al. 2019).

Alternatively, the ability of females to thermoregulate may have declined coincidentally with their declining body condition post-hatch if that caused a diminished ability to avoid hyperthermia. Body condition begins to decline post-hatch as females begin assigning food to chicks rather than themselves, correlating with when eggs no longer need to be incubated. Exploratory analyses (not shown) indicate that there is an abrupt step increase in expression of facultative hyperthermia upon the hatch of the last egg. The pattern suggests a change in thermoregulatory strategy in response to females no longer needing to incubate eggs below 41 °C, rather than thermoregulation changing more gradually to track body condition. However, the two explanations are not mutually exclusive and may be acting together. This presents an interesting avenue for future work. Regardless, energy and water expenditure on thermoregulation while incubating and brooding, in addition to the fact that female parents lost significant M_b raising chicks, reiterated the significant costs of breeding to females (Nord and Williams 2015, Mueller et al. 2019, Sharpe et al. 2021).

Hatch and fledge probability decreased with later lay and hatch sequence, suggesting later laid or hatched young were produced in case they could be raised but were consumed by the breeding female if not. That said, hatch and fledge probability, the number of fledglings, female M_b loss rate during incarceration, nest exit M_b, tail feather mass and barb density, and tail feather CORT concentration were not significantly affected by resource supplementation or T_{nest}. Therefore, the breeding season differences may not have been due to resource availability or T_{nest} effects. Hatch and fledge success in hornbills are driven primarily by variation in the prevalence of cannibalism by the female (Engelbrecht 2013, Finnie 2018). Consequently, the most likely alternative explanation for breeding season differences was that breeding season differences in resource *quality* affected the likelihood for cannibalism. Essentially, nutrient or water poor natural food in the hot and dry breeding season may have forced female parents to cannibalise their own nutrient or water rich eggs or chicks. Although cannibalism in birds is relatively rare (Stanback and Koenig 1992, Bose 2022), it is common in hornbills, and would present an example of the classic life history trade-off between survival (and future reproductive potential) and current reproduction (Williams et al. 2010, Flatt and Heyland 2011, Fabian and Flatt 2012). Moreover, resource quality, rather than quantity, has been shown to drive breeding performance differences in a range of species (e.g., Kadin et al. 2012, Pollock et al. 2017, Coogan et al. 2018, Catto et al. 2021).

That said, I did not have the data to determine if cannibalism caused mortality of eggs and chicks, supporting the above contention, or if cannibalism was opportunistic in response to eggs and chicks dying from other causes, such as dehydration, malnutrition, or injury. This could be explored further, since cannibalism in hornbills is a fascinating phenomenon. It should also be noted that food in the system reaches the nest via the male while the female is incarcerated, making the male act as a filter for the external resources available to the female. Resource supplementation did not affect the overall amount of food provisioned to the females by the free-ranging males in the hot and dry breeding season, even though they provisioned nearly all the supplementary food (see Chapter 2). However, in the cool and wet breeding season high resource supplementation led to significantly higher overall provisioning rates in high supp. compared to low supp. males and did correlate to significantly increased provisioning rates at all T_{air} in both resource supplementation treatments (see Chapter 2). Therefore, another alternative was that the supplementary feeding experiment may have been ineffectual at eliciting resource availability related responses if the amount of food (and thus water) provided to the female via the male for high supp. treatment breeding attempts was not enough, at least in the hot and dry breeding season. The high supp. treatment was designed to provide the full amount of food recorded being provisioned to nests in previous studies on this population (van de Ven et al. 2019, van de Ven et al. 2020b), rendering this explanation unlikely, as those data were collected during “normal” climate years (i.e., not during specifically resource poor years). However, this explanation cannot be completely ruled out (for further discussion see Chapter 6). I did not have data to test these possibilities, but they warrant further attention through future experiments which manipulate resource quality or provide *ad libitum* food. It should also be noted that these findings are based on small sample sizes of females within seasons and between supplementary treatments, so any conclusions should be drawn with caution.

The lack of clear, direct effects of T_{nest} on female morphometrics or breeding success contrasted strongly with previous findings in the same population of hornbills (van de Ven et al. 2020b), including Chapter 5 of this thesis. These also contrasted with studies on a range of other ectotherms and endotherms, showing significant negative effects of high environmental temperatures on survival and breeding success (Hansen 2009, Takahashi 2012, Kingsolver et al. 2013, Bourne et al. 2020b, Cook et al. 2020, Olin et al. 2023). van de Ven et al. (2020b) showed that 70% of T_{max}-driven variation in breeding success in this population of hornbills was due to T_{nest} effects and 30% to temperature-related changes in provisioning rates by the males (also seen in Chapter 2). However, during the van de Ven et al. (2020b) study, nest boxes were not painted or insulated, and were not all placed on the south-east part of trees to be shaded during the hottest parts of the day, whereas the nest boxes for the present study were. This meant that mean and maximum T_{nest} in the present study were significantly lower at the same T_{max} compared to nest boxes in van de Ven et al. (2020b): maximum T_{nest} = 59 °C in van de Ven et al. (2020b), while in the present study maximum T_{nest} = 48.6 °C. This may have strongly influenced the effect of T_{nest} on hornbill breeding ecology (Corregidor-Castro and Jones 2021), and highlights the potential for artificial nest design to drastically affect breeding success through moderating T_{nest} effects for birds and other species (Catry et al. 2011, Larson et al. 2015, Combrink et al. 2017, Griffiths et al. 2017, Maziarz et al. 2017, Bobek et al. 2018, Larson et al. 2018, Martin Bideguren et al. 2019, Briggs and Mainwaring 2021, Corregidor-Castro and Jones 2021, Crawford and O'Keefe 2021, Goldingay and Thomas 2021, Czenze et al. 2022). Notably, the T_{nest} profiles in the new, insulated, and specifically placed and oriented nest boxes were more similar to, though still significantly higher than, natural cavities than the previous boxes. Therefore, while this study was based on a biased sample of only birds breeding in nest boxes, it was likely more closely representative of the experience of wild birds breeding in natural cavities, than previous studies in this nestbox-breeding population.

In the hot and dry breeding season, females grew their tail feathers slower and exited the nest with tail feathers that had higher barb density, indicative of poorer feather quality (de la Hera et al. 2009, Sándor et al. 2022). Consequently, these patterns in feather growth supported the notion that feather development costs are traded off against reproductive investment, and that potentially lower natural resource quality in the hot and dry breeding season compromised female investment in self-maintenance (Vágási et al. 2012).

Overall, these findings demonstrated a large breeding season difference in female hornbills' physiology, morphology, and breeding success. Carry-over effects on the morphology of females in the hot and dry breeding season have potential to continue to affect females after the end of the breeding attempt: post-moult female feather regrowth resulting in poorer quality feathers in the hot and dry breeding season may compromise flight performance and feather longevity, and hinder thermoregulation, thereby potentially negatively impacting post-breeding survival (Carbonell and Tellería 1999, de la Hera et al. 2009, Kiat and Sapir 2018, Nord and Nilsson 2019, Sándor et al. 2022). However, limited evidence for direct T_{nest} or resource supplementation effects in this study meant that I could neither corroborate previous findings of negative effects of high environmental temperatures (van de Ven et al. 2019, van de Ven et al. 2020b), nor make robust conclusions about potential effects of resource availability. These findings suggested that the breeding season differences in breeding success potentially arose due to breeding season scale differences in resource quality which altered the likelihood of cannibalism and therefore hatching and fledging success. However, I did not have the data to test that possibility. The breeding season differences may also have impacted lifetime fitness: fledging success and number directly affect reproductive success, while feather quality may influence post-breeding survival and future reproductive output (Hemborg and Lundberg 1998, Carbonell and Tellería 1999, Blums et al. 2005, de la Hera et al. 2009, Nord and Nilsson 2019, Sándor et al. 2022). Considering these potential fitness consequences, it remains important to investigate the mechanisms underlying breeding season differences to aid in understanding the vulnerability of arid-zone birds to ongoing climate change.

3.6 Supplementary Tables

Table S3.1. Statistical power analyses used to determine the determinable effect size of main effects and interaction effects within generalised linear mixed modelling; u = model degrees of freedom; v = sample size, α = the significance level, and power = probability of finding an effect that is there; Cohen's f^2 = measure of determinable effect size (values of ~ 0.02, ~0.15, and ~0.35 represent small, moderate, and large determinable effect sizes respectively).

response	**effect**	***u***	***v***	***α (p value)***	***power***	***f^2***
hatch probability	main	6	67	0.05	0.8	0.173
fledge probability	main	6	52	0.05	0.8	0.221
number of fledglings	main	1	17	0.05	0.8	0.465
all female T_b models	main	3-5	≥7211	0.05	0.8	≤0.002
	interaction	3-5	≥1803	0.05	0.8	≤0.006
female M_b loss rate incubating	main	1	17	0.05	0.8	0.465
female M_b loss rate post-hatch	main	1	17	0.05	0.8	0.465
female exit M_b	main	1	17	0.05	0.8	0.465
feather growth rate	main	1	15	0.05	0.8	0.529
tail feather barb density	main	1	14	0.05	0.8	0.568
CORT conc.	main	1	14	0.05	0.8	0.568

Table S3.2. Total number of Southern Yellow-billed Hornbill (*Tockus leucomelas*) eggs and chicks in the hot and dry breeding season (2019/2020; n breeding attempts = 9) and the cool and wet breeding season (2020/2021; n breeding attempts = 11) split by lay / hatch sequence and resource supplementation (low and high supp.). Number laid / hatched followed by the number which hatched / fledged in brackets.

breeding season	egg lay sequence	chick hatch sequence	n low supp. (hatch / fledge)	n high supp. (hatch / fledge)
hot and dry breeding season	1		4 (4)	5 (5)
	2		4 (2)	5 (5)
	3		4 (2)	5 (3)
	4		4 (0)	2 (0)
cool and wet breeding season	1		5 (5)	5 (5)
	2		5 (5)	5 (5)
	3		5 (5)	5 (5)
	4		4 (2)	4 (2)
	5			3 (1)
	6			1 (0)
hot and dry breeding season		1	4 (2)	5 (4)
		2	2 (1)	5 (1)
		3	2 (0)	3 (0)
cool and wet breeding season		1	6 (6)	5 (5)
		2	6 (6)	5 (3)
		3	6 (3)	5 (4)
		4	2 (1)	2 (0)

5	1 (0)

Table S3.3. Model selection table for candidate sets of five binomial family generalised linear models (GLM) determined *a priori* to be biologically relevant for breeding Southern Yellow-billed Hornbills (*Tockus leucomelas*) for a) the probability of an egg hatching (hatch probability; hot and dry [2019/2020] season n eggs = 33, cool and wet [2020/2021] season n eggs = 47), and b) the probability of a chick progressing from hatch to fledge (fledge probability; hot and dry breeding season chicks = 21, cool and wet breeding season n chicks = 39) as functions of 1) breeding season, 2) resource supplementation (hot and dry breeding season breeding attempts $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season breeding attempts $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5), 3) egg lay / chick hatch sequence, 4) mean max. T_{nest} from lay / hatch to hatch / fledge / fail, 5) an interaction between T_{nest} and season, and 6) an interaction between T_{nest} and resource supplementation. Model selection also shown for the number of fledglings produced per female (hot and dry breeding season n fledglings = 8, cool and wet breeding season n fledglings = 26) modelled using GLM family Poisson as a function of 1) breeding season, 2) resource supplementation, 3) mean max. T_{nest} during female incarceration, and 4) the null Models were ranked using Akaike's Information Criterion adjusted for small sizes (AICc). For hatch and fledge probability results were reported for the model average of the top models (ΔAICc <2; highlighted in bold). For the number of fledglings produced per female results from all models with ΔAICc <2 (highlighted in bold) were reported.

			independent variables									
response variable	**model no.**	**Int.**	**egg lay / hatch sequence**	**T_{nest}**	**season**	**supp.**	**T_{nest} * season**	**T_{nest} * supp.**	**df**	**AICc**	**ΔAICc**	**weight**
hatch probability	**4**	**0.43**	**-3.01**	**0.81**	**+**	**+**			**5**	**49.4**	**0**	**0.33**
	2	**0.45**	**-3.08**	**1.26**	**+**	**+**		**+**	**6**	**49.5**	**0.04**	**0.32**
	1	**1.1**	**-3.3**	**0.6**	**+**	**+**	**+**	**+**	**7**	**50.1**	**0.7**	**0.23**

	3	0.58	-3.05	0.59	+	+	+		6	51.6	2.13	0.11
	5	1.08							1	86.9	37.53	0
fledge probability	**4**	**-1.25**	**-2.14**	**-0.82**	**+**	**+**			**5**	**55.1**	**0**	**0.56**
	3	**-1.42**	**-2.22**	**-1.21**	**+**	**+**		**+**	**6**	**57.1**	**1.99**	**0.21**
	2	-1.24	-2.13	-0.86	+	+	+		6	57.6	2.47	0.16
	1	-1.49	-2.23	-2.11	+	+	+	+	7	59.1	3.99	0.08
	5	0.41							1	82.8	27.68	0
number of fledglings	**1**	**-0.12**			**+**				**2**	**58.9**	**0**	**0.73**
	2	0.51		-0.41					2	61.4	2.52	0.21
	4	0.59							1	64.5	5.63	0.04
	3	0.53				+			2	66.9	8	0.01

Table S3.4. Model selection table for candidate sets of five Gaussian family linear mixed models (LMer) determined *a priori* to be biologically relevant for breeding female Southern Yellow-billed Hornbill (*Tockus leucomelas*) body temperature (T_b) above and below break-point nest temperature (T_{nest}), split by incubation status (incubating, and with chicks) as a function of 1) breeding season, 2) nest temperature (T_{nest}), 3) resource supplementation (hot and dry breeding season [2019/2020] females $n_{lowsupp} = 3$, $n_{highsupp} = 5$; cool and wet breeding season [2020/2021] females $n_{lowsupp} = 6$, $n_{highsupp} = 5$), 4) an interaction between T_{nest} and season, and 5) and an interaction between T_{nest} and resource supplementation. The interactions between T_{nest} and season were significant, so analyses were post-hoc split by breeding season. Within each season the interactions between T_{nest} and resource supplementation were significant, so analyses were further post-hoc split by resource supplementation. All relationships had significant break-point T_{nest} above which T_b began increasing or increased more rapidly. Models were ranked using Akaike's Information Criterion adjusted for small sizes (AICc), with the top models (ΔAICc <2) highlighted in bold. Where more than one top model was identified, an averaged top model was calculated.

				independent variables								
response variable	**breeding season**	**model no.**	**int.**	**T_{nest}**	**season**	**supp.**	**T_{nest} * season**	**T_{nest} * Supp.**	**df**	**AICc**	**ΔAICc**	**weight**
T_b below break-point incubating	combined	**1**	**39.70**	**0.06**	**+**	**+**	**+**	**+**	**8**	**20770.6**	**0**	**0.47**
		3	**39.70**	**0.06**	**+**	**+**	**+**		**7**	**20770.7**	**0.11**	**0.45**
		2	39.70	0.06	+	+		+	7	20774.7	4.18	0.06
		4	39.70	0.05	+	+			6	20777.1	6.53	0.02
		5	39.64						3	21709.2	938.61	0
T_b below break-point	combined	**3**	**40.27**	**0.03**	**+**	**+**		**+**	**7**	**20190.5**	**0**	**0.78**
		1	40.27	0.02	+	+	+	+	8	20193	2.50	0.22

with chicks		2	40.27	0.04	+	+	+		7	20306.7	116.17	0
		4	40.27	0.05	+	+			6	20322.5	132.00	0
		5	40.26						3	20993.8	803.24	0
T_b above break-point incubating	combined	**2**	**40.17**	**0.40**	**+**	**+**	**+**		**7**	**27723.6**	**0**	**0.99**
		1	40.17	0.40	+	+	+	+	8	27733.8	10.25	0.01
		3	40.16	0.31	+	+		+	7	29600.2	1876.56	0
		4	40.14	0.24	+	+			6	30278.8	2555.23	0
		5	40.21						3	40995.9	13272.34	0
T_b above break-point with chicks	combined	**1**	**40.59**	**0.64**	**+**	**+**	**+**	**+**	**8**	**15182.2**	**0**	**1**
		2	40.57	0.72	+	+	+		7	15380.7	198.53	0
		3	40.75	0.32	+	+		+	7	16684.6	1502.44	0
		4	40.74	0.42	+	+			6	17397.8	2215.56	0
		5	40.94						3	23254.5	8072.32	0
T_b below break-point incubating	hot and dry	**2**	**39.58**	**0.06**		**+**			**5**	**10359.5**	**0**	**0.91**
		1	39.58	0.06		+		+	6	10364.1	4.59	0.09
		3	39.59						3	10811.8	452.28	0
T_b below break-point with chicks	hot and dry	**1**	**40.27**	**0.08**		**+**		**+**	**6**	**6440.5**	**0**	**1**
		2	40.27	0.04		+			5	6558	117.48	0
		3	40.06						3	6639.7	199.17	0
T_b above break-point	hot and dry	**2**	**40.44**	**0.33**		**+**			**5**	**17356.3**	**0**	**0.98**
		1	40.44	0.33		+		+	6	17364.2	7.86	0.02

incubating		3	40.42				3	24187.9	6831.61	0
T_b above break-point with chicks	hot and dry	**1**	**41.19**	**0.41**	**+**	**+**	**6**	**9796.4**	**0**	**1**
		2	41.15	0.50	+		5	9952.4	155.96	0
		3	41.11				3	14069.8	4273.36	0
T_b below break-point incubating	cool and wet	**2**	**39.80**	**0.05**	**+**		**5**	**10288.3**	**0**	**0.93**
		1	39.80	0.05	+	+	6	10293.6	5.29	0.07
		3	39.65				3	10684.2	395.86	0
T_b below break-point with chicks	cool and wet	**1**	**40.15**	**-0.02**	**+**	**+**	**6**	**13043.2**	**0**	**1**
		2	40.18	0.06	+		5	13567.5	524.34	0
		3	40.31				3	14015.6	972.42	0
T_b above break-point incubating	cool and wet	**2**	**40.14**	**0.16**	**+**		**5**	**8777.7**	**0**	**0.99**
		1	40.14	0.16	+	+	6	8787.6	9.84	0.01
		3	40.04				3	12019.9	3242.16	0
T_b above break-point with chicks	cool and wet	**1**	**40.54**	**0.24**	**+**	**+**	**6**	**3733.4**	**0**	**1**
		2	40.55	0.26	+		5	3801.3	67.91	0
		3	40.67				3	6588.3	2854.97	0

Table S3.5. Model estimates for top models of female Southern Yellow-billed Hornbill (*Tockus leucomelas*) body temperature (T_b) below and above break-point nest temperatures (T_{nest}) split by incubation status (incubating, and with chicks) modelled using a linear mixed model (LMer) family Gaussian as a function of 1) breeding season, 2) nest temperature (T_{nest}), 3) resource supplementation (hot and dry breeding season [2019/2020] females $n_{lowsupp} = 3$, $n_{highsupp} = 5$; cool and wet breeding season [2020/2021] females $n_{lowsupp} = 6$, $n_{highsupp} = 5$), 4) an interaction between T_{nest} and season, and 5) and an interaction between T_{nest} and resource supplementation. Where more than one top model was identified, results for an averaged top model are reported. Independent variables not shown were those absent in the model averaged estimates following model selection. Significant estimates are highlighted in bold.

no. top models	**response**	**status**	**independent variable**	**estimate ± SE**	**z**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
2	female T_b (below break-point)	incubating	**season (cool and wet)**	**-0.02 ± 0.01**	**2.04**	**37045**	**0.041**	**-0.05**	**0.00**
			T_{nest}	**0.06 ± 0.00**	**18.66**	**37045**	**0.001**	**0.05**	**0.07**
			supp. (low)	**-0.1 ± 0.01**	**8.28**	**37045**	**0.001**	**-0.12**	**-0.08**
			T_{nest} * season (cool and wet)	**-0.01 ± 0.00**	**4.06**	**37045**	**0.001**	**-0.02**	**-0.01**
			T_{nest} * supp. (low)	-0.01 ± 0.01	0.95	37045	0.344	-0.02	-0.01
1	female T_b (below break-point)	with chicks	**season (cool and wet)**	**0.04 ± 0.01**	**3.57**	**27646**	**0.001**	**0.02**	**0.05**
			T_{nest}	**0.03 ± 0.00**	**7.40**	**27646**	**0.001**	**0.02**	**0.03**
			supp. (low)	**-0.1 ± 0.01**	**-9.92**	**27646**	**0.001**	**-0.12**	**-0.08**

			T_{nest} * supp. (low)	**0.06 ± 0.01**	**11.97**	**27646**	**0.001**	**0.05**	**0.07**
1	female T_b (above break-point)	incubating	**season (cool and wet)**	**-0.19 ± 0.02**	**-9.89**	**32932**	**0.001**	**-0.22**	**-0.15**
			T_{nest}	**0.4 ± 0.00**	**105.66**	**32932**	**0.001**	**0.39**	**0.40**
			supp. (low)	**0.27 ± 0.02**	**14.55**	**32932**	**0.001**	**0.23**	**0.31**
			T_{nest} * season (cool and wet)	**-0.25 ± 0.01**	**-51.66**	**32932**	**0.001**	**-0.26**	**-0.24**
1	female T_b (above break-point)	with chicks	**season (cool and wet)**	**0.22 ± 0.02**	**12.89**	**15456**	**0.001**	**0.18**	**0.25**
			T_{nest}	**0.64 ± 0.01**	**64.96**	**15456**	**0.001**	**0.62**	**0.66**
			supp. (low)	**0.04 ± 0.02**	**2.31**	**15456**	**0.021**	**0.01**	**0.07**
			T_{nest} * season (cool and wet)	**-0.41 ± 0.01**	**-39.85**	**15456**	**0.001**	**-0.43**	**-0.39**
			T_{nest} * supp. (low)	**0.15 ± 0.01**	**14.47**	**15456**	**0.001**	**0.13**	**0.17**

Table S3.6. Model selection table for Southern Yellow-billed Hornbill (*Tockus leucomelas*) female a) body mass (M_b) loss rate during incubation, b) M_b loss rate post-hatch, c) exit M_b, d) tail feather growth rate, e) tail feather barb density, and f) tail feather corticosterone (CORT) concentration modelled using a generalised linear models (GLM) family Gaussian as functions of 1) breeding season (hot and dry breeding season, n females = 9; cool and wet breeding season, n females = 11), 2) mean maximum nest temperature (T_{nest}) during incarceration / growth, 3) resource supplementation (hot and dry breeding season females $n_{lowsupp}$ = 4, $n_{highsupp}$ = 5; cool and wet breeding season females $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5 [tail feathers $n_{highsupp}$ = 3]), and 4) the null. Each model included only one fixed effect. Models were ranked using Akaike's Information Criterion adjusted for small sizes (AICc), with the top models (ΔAICc <2) highlighted in bold. Results for all models with Δ AICc < 2 were reported.

response variable	model no.	int.	season	mean max T_{nest} during incarceration	supp.	df	AICc	ΔAICc	weight
female M_b loss rate incubating	**4**	**-0.48**				**2**	**61.5**	**0**	**0.47**
	2	-0.48		0.25		3	63.0	1.56	0.22
	3	-0.27			+	3	63.3	1.88	0.18
	1	-0.61	+			3	64.0	2.54	0.13
female M_b loss rate post-hatch	**4**	**-2.57**				**2**	**69.3**	**0**	**0.47**
	3	**-2.22**			**+**	**3**	**70.3**	**0.98**	**0.29**
	2	-2.57		-0.07		3	72.1	2.73	0.12
	1	-2.53	+			3	72.1	2.77	0.12
female nest exit M_b	4	194.90				2	163.5	0	0.41
	2	194.90		4.06		3	164.3	0.79	0.28
	3	198.30			+	3	164.8	1.31	0.21

	1	194.30	+			3	166.2	2.75	0.1
female tail feather growth rate	**1**	**3.82**	**+**			**3**	**26.7**	**0**	**0.84**
	3	3.92			+	3	31.8	5.09	0.07
	4	4.13				2	32.2	5.47	0.05
	2	4.13		-0.19		3	32.6	5.89	0.04
female tail feather barb density	**1**	**1.42**	**+**			**3**	**-50.5**	**0**	**0.62**
	4	**1.39**				**2**	**-48.8**	**1.69**	**0.26**
	3	1.39			+	3	-45.8	4.68	0.06
	2	1.39		0		3	-45.8	4.68	0.06
female tail feather CORT conc.	**4**	**4.30**				**2**	**15.3**	**0**	**0.58**
	2	4.30		0.05		3	18.0	2.69	0.15
	3	4.33			+	3	18.1	2.83	0.14
	1	4.30	+			3	18.3	2.99	0.13

4. Improved thermoregulation with increased resource availability does not buffer negative effects of high nest temperatures on chicks of an arid-zone bird

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4.1 Abstract

The negative effects of high environmental temperatures on breeding in arid-zone endotherms are often mediated by costly trade-offs between thermoregulation and self-maintenance or development. As a result, variation in resource availability has the potential to mediate effects of high environmental temperature by mitigating or lessening the severity of those trade-offs. This study on Southern Yellow-billed Hornbill (*Tockus leucomelas*; hornbill) chicks over two breeding seasons (a hot and dry breeding season, 2019/2020, with T_{max} (average daily maximum T_{air}) = 34.2 ± 3.8 SD °C and rainfall = 130.6 mm; and a cool and wet breeding season, 2020/2021, T_{max} = 33.1± 3.1 SD °C and rainfall = 328.9 mm) investigated whether resource availability (i.e., food and water, partly experimentally manipulated through supplementary feeding – high *versus* low resource supplementation [supp.], and partly through a comparison between naturally different resource availabilities between breeding seasons) could potentially affect chick thermoregulation and the established relationships between chick development and nest temperature (T_{nest}) in arid-zone birds. All chicks showed hyperthermic responses to high T_{nest}, but chicks in the cool and wet season showed shallower rates of increase in body temperature (T_b) compared to chicks in the hot and dry breeding season. In the hot and dry breeding season low supp. chicks engaged in hyperthermia at a higher T_{nest} and had a significantly steeper increase in T_b at high T_{nest} (estimate = 0.55 ± 0.01 SD, $p < 0.001$; n = 2; estimates do not have units, since continuous predictor variables were scaled) than high supp. chicks (estimate = 0.23 ± 0.00 SD, $p < 0.001$; n = 4). Chicks spent significantly less time in the nest (i.e., fledged sooner; estimate = -3.29 ± 1.58, p = 0.046; days in the nest = 48.65 ± 7.53 and 53.29 ± 3.95 in the cool and wet and hot and dry breeding seasons, respectively), gained M_b (estimate = 0.67 ± 0.32, p = 0.047) and grew tail feathers (estimate = 0.46 ± 0.21, p = 0.036) significantly faster, and had significantly longer tarsi at fledge (estimate = 2.32 ± 0.86, p = 0.011) in the cool and wet breeding season compared to the hot and dry breeding season. Tarsus length at fledge decreased (estimate = -1.00 ± 0.38, p = 0.012) and tail feather corticosterone (CORT) concentration increased (estimate = 0.20 ± 0.06, p = 0.002) significantly with increasing mean daily maximum T_{nest} from hatch until fledge, and during feather growth, respectively. Fledge M_b, fledge head plus culmen length, and tail feather barb density of chicks which fledged were not significantly affected by any of the modelled predictor variables. Overall, this study demonstrated that high resource availability may have partially buffered thermoregulatory costs at high T_{nest} but did not completely buffer T_{nest} effects on stress or morphometrics; chicks still showed negative responses (i.e., reduced tarsi length at fledge and increased feather CORT) to high T_{nest}. The lack of significant effects of resource supplementation, other than on thermoregulation, suggested that resource availability was not the primary driver of between breeding season differences in chick morphology and development times. Therefore, natural resource quality differences between the breeding seasons presented the most likely alternative explanation for the physiological and morphometric breeding season differences, though I did not have data to test the possibility. These findings highlight that high T_{nest} appears limiting for chick development regardless of resources, but that further research into the potential influences of resource availability and quality on the relationships between T_{nest} and chick development is required.

4.2 Introduction

Seasonally hot, arid zones are characterised by low primary productivity and high spring and summer environmental temperatures. Resource availability is driven by rainfall, which often occurs during the hottest times of the year (McCreedy and van Riper III 2015, Mares et al. 2017). Consequently, animals which breed in response to rainfall in seasonally hot, arid regions, concurrently face increased thermoregulatory costs because of high air temperatures (T_{air}) and nest temperatures (T_{nest}) associated with the hottest periods of the year, as well as the high costs of breeding (Andreasson et al. 2020, Bourne et al. 2020a, McCowan and Griffith 2021). In birds, the period from hatch to fledge involves development of various crucial, interlinked traits, including thermoregulation, hormone profiles, body mass (M_b), and growth of bones and feathers for nestlings, and is, therefore, sensitive to environmental effects and critical to long-term fitness (Dawson et al. 2005, Tieleman et al. 2008, Hau et al. 2016, Bleu et al. 2017, Ton et al. 2021). High environmental temperatures during this period are associated with reductions in the condition of fledglings, and in the probability of fledging at all, either because of direct effects on chicks, or indirect effects on parental behaviour (Catry et al. 2011, Cunningham et al. 2013a, Larson et al. 2015, Wiley and Ridley 2016, Bourne et al. 2020b, Bourne et al. 2021, Sharpe et al. 2021, D’Amelio et al. 2022). The negative effects of high T_{nest} on condition can manifest in a variety of ways, such as reduced M_b or bone development, or compromised feather structure (Hemborg et al. 1998, Oswald et al. 2021, Sauve et al. 2021). In some cases the effects are less externally obvious, resulting in reduced immune function or internal organ development, or chronically elevated corticosterone (CORT) stress hormone levels, all potentially correlating to reduced performance or fitness (Mashaly et al. 2004, Ardia 2005, Breuner et al. 2008, Love et al. 2013, Pigeon et al. 2013, Hau et al. 2016).

Life history theory suggests that resource-limited organisms face trade-offs between costly life history components (Stearns 1992, Jodice et al. 2008, Flatt and Heyland 2011, Nilsson and Nord 2017). In response to low resource availability, parents may trade-off investment in current reproduction against survival and potential future reproduction (Sharpe et al. 2021), while offspring may trade-off growth against thermoregulation (Salaberria et al. 2014, Rodríguez et al. 2016, Nilsson and Nord 2017, van de Ven et al. 2020b). For example, when nutritionally limited, the investment chicks make in stress hormone production and thermoregulation might come at the expense of investment in bone or feather growth, leading to lower quality structural development and costs to lifetime fitness (Landys et al. 2006, Breuner et al. 2008, Angelier and Wingfield 2013, Salaberria et al. 2014, Nilsson and Nord 2017, Salleh Hudin et al. 2017). Therefore, the established negative effects of high environmental temperatures on avian breeding outcomes might manifest partially because of limited resources creating or exacerbating trade-offs costly to offspring survival or condition (Álvarez and Barba 2014, Nilsson and Nord 2017).

Some evidence suggests that high environmental temperatures may be limiting for offspring in arid zones only in conjunction with limited resources (Cruz-McDonnell and Wolf 2016, Mares et al. 2017, Bourne et al. 2020c, D'Amelio et al. 2022). For example, juvenile growth and survival are severely reduced in hot, drought years, compared to hot years without drought in Southern Pied Babblers (*Turdoides bicolor*) (Bourne et al. 2020c). If increased resource availability can buffer the negative effects of high environmental temperatures, chick survival, development and fledging condition may improve despite high environmental temperatures. Increased survival to fledge has a clear direct effect on offspring fitness (Schwagmeyer and Mock 2008). However, sub-lethal effects on fledge condition or timing can also strongly influence fitness (Dawson et al. 2005, Catry et al. 2015, Gardner et al. 2017), primarily through post-fledging effects on predator avoidance abilities, or capacity to deal with disease, handle food shortages post-fledging, and compete with conspecifics (Moreno et al. 2005, Greno et al. 2008, Schwagmeyer and Mock 2008, Sakaluk et al. 2014).

To examine the potential for high resource availability to buffer impacts of T_{nest} on nestling development and fledging condition, I experimentally manipulated food, and, therefore, water (since the hornbills gain all their water from their diet), availability in the environment over two breeding seasons in a population of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hereafter, hornbills). Hornbills get all their water from their diet since they do not drink from open water sources. Therefore, I use 'resource availability' to refer specifically to food and water, and not to other resources such as shade, potential breeding mates, or nest sites. Hornbill females seal themselves inside the nest cavity for the majority of the breeding attempt, typically breaking out when chicks are large enough to reseal the cavity themselves. The study population is in the arid south-western edge of their range and breeding occurs during the hottest period of the year, coinciding with the rainy season. The timing of the rainy season is fairly consistent between years, although the amount of rainfall is unpredictable and highly variable (Mares et al. 2017). This study capitalised on a large difference in the T_{air} and rainfall between the two breeding seasons to compare the hornbill's reproductive ecology across them as a 'hot and dry', 2019/2020, compared to a 'cool and wet', 2020/2021, breeding season. In this hornbill population T_{nest} is a key determinant of breeding success (van de Ven et al. 2019, van de Ven et al. 2020b). However, indirect limiting effects of high T_{air} on provisioning rates suggests a potential resource availability effect (van de Ven et al. 2019, van de Ven et al. 2020b). Therefore, it is unclear whether high T_{nest} is directly detrimental to breeding success or whether high T_{nest} is only limiting because of a concomitant reduction in the resources needed to regulate T_b and grow under heat stress.

I aimed to determine potential effects of resource availability in the system and T_{nest} on the growth, thermoregulation, and fledging timing and condition (M_b, structural bone and beak size, feather quality, feather CORT) of hornbill chicks. Supplementary food was accessed by the male parents at feeding stations alongside the nest boxes. For the majority of the breeding attempt the males then provisioned the food to the incarcerated female. After she broke out of the nest, he provisioned the food directly to the chicks. Therefore, resource availability to the chicks is strongly mediated by parental decisions on how to allocate food. No data were gathered on how food was allocated in the nests, but it was assumed that 1) the females would consume some themselves and provision the rest to the chicks, and 2) increased food provisioned to the nest would correlate to increased food to chicks, as per the natural situation for these birds (van de Ven et al. 2019, van de Ven et al. 2020b). I hypothesised that increased resource availability in the system, correlating to more food for chicks, would increase the capacity of chicks to thermoregulate and decrease the severity of developmental trade-offs (e.g., between growth and thermoregulation). I therefore predicted that, among chicks thermally challenged by high T_{nest}, those with access to high resource availability (high supp. and cool and wet breeding season) would show improved thermoregulation (i.e., less pronounced hyperthermia and more gradual increases in body temperature (T_b) at high T_{nest}), decreased stress (i.e., lower tail feather CORT), and improved fledging condition (i.e., higher M_b, longer tarsi, higher quality feathers). The potential for resource availability to mediate the effects of high T_{nest} on fledging development, condition and timing may change our current understanding of the fitness consequences of high environmental temperatures, as well as the potential conservation mechanisms available.

4.3 Methods

4.3.1 Study species, site, and weather data collection

Details of the study species, study site, and weather data collection are provided in Chapter 2 (sections 2.2.1 & 2.2.2). As with most Bucerotidae hornbills, the sealing of the nest entrance, by the adult female and later by large chicks, for the majority of the nestling period limits predation, making other factors primarily responsible for variation in breeding success (Moreau and Moreau 1941). During the study, 50 nest boxes were available for the hornbills to breed in. These were insulated and painted compared to boxes used in previous studies on the population (see section 3.2.3 for more detail; van de Ven et al. 2019, van de Ven et al. 2020b). All breeding data were necessarily collected from hornbills breeding in nest boxes because data cannot be collected from sealed natural cavities which preclude any access to the nest. Generally, 2 – 6 eggs are laid and hatch asynchronously, approximately two days apart (Finnie 2018, van de Ven et al. 2020b). The weather data used in this study were collected by an on-site weather station (Hot Birds Research Project [HBRP] Weather Station; Vantage Pro2, Davis Instruments, Hayward, U.S.A.) set to record T_{air} (°C), wind speed ($m.s^{-1}$), relative humidity (%), and solar radiation ($W.m^{-2}$) at 5-min intervals. Data for Chapters 2, 3, and 4 (this chapter), were collected simultaneously over the course of two breeding seasons.

4.3.2 Supplementary feeding

Details on supplementary feeding are described in Chapter 2 (section 2.2.3). Once a female laid the first egg, a feeding station was set up and supplied with a daily ration of darkling beetle larvae (*Zophobas morio*); low (low supp.; ~5g of darkling beetle larvae (7 individuals)) or high resource supplementation (high supp.; ~25g of darkling beetle larvae (30 individuals)). The sole-provisioning males accessed and provisioned the supplementary food (and, hence, water) to the nest. Once the female parent broke out, she aided in provisioning to offspring but only the male parents were observed to continue accessing the supplementary food and provisioning it to the nest (see Chapter 2).

4.3.3 Nest temperature

Nest temperature (T_{nest}) data collection is detailed in Chapter 3 (section 3.2.3.). Nest box and natural cavity temperatures were recorded using Thermochron iButtons (DS1922-L, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, accuracy ± 0.5°C). I compared nest box temperatures in this study with conditions in natural nest cavities (in camelthorn *Vachellia erioloba* trees) between 2012 – 2015, and with nest box temperatures in this study population between 2012 – 2015 (the time period during which effects of T_{nest} on reproduction were documented by van de Ven et al. (2020)).

4.3.4 Body temperature

Once the female exited the nest, the oldest chick was tagged with a temperature sensitive passive integrated transponder (PIT tag; model HPT8, 8.4mm ISO FDXB, Biomark, Boise, Idaho, USA) to record body temperature (T_b). The chicks could not be PIT-tagged any earlier due to reader interference that would be caused by the female's PIT tag, in addition to the risk that the female would cannibalise the chick along with the tag (see Chapter 3). Only the oldest chicks were tagged to avoid tag interference that would occur if multiple chicks were tagged, to allow comparability between nests, and since some nests only had a single chick. The PIT tags used to measure chick T_b weighed 0.06g, approximately 0.03% of the average chick fledging M_b. Pre-loaded tags (calibrated and sterilized) in individual single-use implanting syringes (N165, 18-gauge) were injected subcutaneously in between the scapulae, following Oswald et al. (2018). Cord antenna readers (Biomark, Boise, Idaho, USA) and HPR Plus readers (Biomark, Boise, Idaho, USA) were installed on the nest boxes to record unique identity and T_b of chicks at 1-min intervals.

4.3.5 Morphometrics

Nests were visited each day from the first appearance of a completed nest seal, to record egg lay, chick hatch, egg or chick cannibalism, female exit, and fledge / failure dates. Cannibalism was recorded when an egg or chick disappeared from the nest while the female was still present, which is known to be caused exclusively by cannibalism by the breeding female in hornbills (Engelbrecht 2013, Finnie 2018). The day or day after the first chick hatched, chick M_b were recorded (OHAUS TA502 electronic scale, Port Melbourne, VIC, Australia; resolution = 0.01g), and once a week thereafter. Concurrently, I used digital callipers to measure tarsi and head plus culmen (i.e., the ridge along the top of the beak) lengths, and a metal ruler (resolution 1 mm) to measure the length of one of each chick's tail feathers – I measured the tail feather to the dorsal-left of the central pair which I would later pull for CORT (see section 4.2.6. below) and barb density analyses. The tail feather was pulled once the chicks were 38.2 ± 7.7 SD days old (range 29 – 63 days).

4.3.6 Feather barb density and corticosterone

Feather processing and analyses were as per those detailed in Chapter 3 (section 3.2.6.). Pulled tail feathers were photographed to calculate barb density in ImageJ software. Feathers were then weighed at a resolution of 0.1mg before being finely cut up into pieces for CORT analysis. Tail feather CORT was extracted with a keratinase solution before CORT enzyme immunoassays (EIAs) were used to measure the CORT concentration in the feathers.

4.3.7 Statistical analyses

Statistical analyses were conducted in the R statistical environment, version 3.5.1 (R Core Team 2023), using the R Studio platform (R Studio Team 2023). Based on analyses of statistical power (Cohen's f^2, the measure of determinable effect size), as calculated using the package pwr (Champely 2020), there was statistical power to detect small main ($f^2 \leq 0.001$) and interaction effects ($f^2 \leq 0.002$) for models of T_b, and moderate main effects (all f^2 between 0.238 – 0.271) for models of the chick morphometrics (Table S4.1). For further details on the modelling approach see Chapter 1.

Weather

Breeding season (19 October – 24 March) mean daily maximum air temperature (T_{max}) and rainfall for 2019/2020 and 2020/2021 were calculated from weather data collected on site by the HBRP weather station (see Chapters 3 and 5).

Nest temperatures

The same nest temperature data as those recorded and analysed in Chapter 3 are used here. The analyses and results are summarised here as they pertain to this Chapter. As covered in Chapter 3, linear mixed models (LMer) family Gaussian were used to model maximum daily T_{nest} as a function of T_{max} for occupied natural cavities (n = 9), nest boxes in 2012 – 2015 (n = 27, prior to insulation and painting), and nest boxes in 2019 – 2021 (n = 20, insulated and painted; see Chapter 3). A Tukey HSD post-hoc test was used to test for differences in mean maximum daily T_{nest} between the nest types, and between nest boxes in 2019/2020 and 2020/2021. For more details and results see Chapter 3.

Body temperature

Chick daytime (06:00 – 18:00) T_b was collected at one-min intervals for oldest chicks across both seasons (2019/2020 $n_{lowsupp} = 2$, $n_{highsupp} = 4$; 2020/2021 $n_{lowsupp} = 6$, $n_{highsupp} = 5$) totalling 88 044 T_b records. Exploratory analyses suggested different, segmented (i.e., has break-points in the slope) relationships between chick T_b and T_{nest} within each season and resource supplementation treatment. Therefore, to identify each break-point, chick T_b was modelled with Gaussian family as a function of T_{nest} split by breeding season and resource supplementation. Break-points were estimated using a combination of visual inspection of generalised additive models (GAM) (package mgcv, Wood 2011) and segmented analyses (package segmented, Muggeo 2017). Subsets of data below and above break-points were then modelled using LMer family Gaussian as functions of 1) breeding season, 2) T_{nest}, 3) resource supplementation, 4) an interaction between T_{nest} and season, and 5) an interaction between T_{nest} and resource supplementation. Chick identity was included as a random effect. I performed model selection by comparing Akaike's Information Criterion adjusted for small sizes (AICc) within the package MuMIn (Barton 2020) for a candidate set of 5 models predicted *a priori* to be biologically informative (see Chapters 1 and 3 for more detail). I reported results for the top performing model, or the average of the top performing models where more than one within Δ AICc < 2 was identified. Both the interactions between T_{nest} and season and between T_{nest} and resource supplementation were significant, so chick T_b below and above break-points were additionally modelled with Gaussian family as a function of T_{nest} for subsets of data split by breeding season and resource supplementation.

Morphometrics and corticosterone

All analyses were completed on chicks which fledged, since the majority of chicks which failed were cannibalised within a week after hatching (only three of the 44 chicks that failed to fledge survived to three weeks old before being cannibalised). A chick body mass (M_b) growth curve was developed by fitting Gompertz, logistic, log-logistic and Weibull functions to weekly measurements of chick M_b and comparing goodness of fit based on Akaike's Information Criterion (AIC) (package drc, Ritz et al. 2015). Growth curves of chick tail feather growth were developed by modelling GLM family Gaussian weekly measurements of chick tail feather length as a function of chick age.

Generalised linear models (GLM) family Gaussian were used to model a) the number of days spent in the nest by chicks, b) M_b gain rate, c) fledge M_b, d) fledge tarsus length, e) fledge head plus culmen length (i.e., distance from the back of the head to the front of the bill), f) tail feather growth rate, g) tail feather barb density, and h) tail feather CORT concentration as functions of 1) breeding season, 2) chick hatch sequence, 3) mean daily maximum T_{nest} from hatch until fledge, 4) resource supplementation, and 5) the null. Fitting multiple fixed effects in a single model reduced the statistical power lower than recommended to detect large effects (all $f^2 \geq 0.40$) so a single fixed effect was fit at a time. Inclusion of nest box identity as a random effect created issues of singular fit due to small sample sizes per box (i.e., many nests only produced one chick), so no random effects were specified. Three nests had a one fledgling, five nests had two, five had three, and a single nest had four fledglings. Consequently, the effects of the nest box (i.e., clutch or brood identity) were likely small, and had sample sizes too small to test for statistically. Moreover, limited exploratory analyses fitting nest box identity as a fixed effect (where possible without destabilising the model) showed that it did not explain significant variation in any of the dependent variables. However, any effects of nest box identity remained untested and the results should be considered in that context. I then performed model selection by comparing models using Akaike's Information Criterion adjusted for small sizes (AICc) (package MuMIn, Barton 2020) and reported results for all models within Δ AICc < 2. Left and right tarsi were similar at fledge (right - left = 0.03 mm ± 0.26 SD, n = 36), so only left tarsi lengths were used in analyses.

4.4 Results

4.4.1 Weather and nest temperatures

Weather and T_{nest} results are reported in detail in Chapter 3 (section 3.3.1) above. Breeding season T_{max} = 34.2± 3.8 SD °C and rainfall = 130.6 mm in the hot and dry breeding season (2019/2020) and T_{max} = 33.1± 3.1 SD °C and rainfall = 328.9 mm in the cool and wet breeding season (2020/2021). Mean maximum T_{nest} were on average 5.51 °C and 1.52 °C higher than natural cavities in boxes in 2012 – 2015 and in 2019 – 2021 respectively (Chapter 3, Figure 3.1; Tables 3.1 & 3.2). Mean maximum T_{nest} were on average 1.34 °C higher in 2019/2020 compared to 2020/2021 (Chapter 3, Table 3.2).

4.4.2 Chick body temperatures

One top model each were identified for chick T_b below and above break-points, respectively (Table S4.2). The top models indicated significant effects of the interactions between T_{nest} and season (below break-point estimate = 0.16 ± 0.01 SD, $p \leq 0.001$; above break-point estimate = -0.33 ± 0.01 SD, $p \leq 0.001$) and T_{nest} and resource supplementation (below break-point estimate = 0.03 ± 0.01 SD, $p \leq 0.001$; above break-point estimate = 0.07 ± 0.01 SD, $p \leq 0.001$; Table 4.1). Analyses were therefore split post hoc by breeding season and resource supplementation. In both seasons and both resource supplementation treatments, below and above break-points, all relationships between T_b and T_{nest} were significant (T_{nest} break-points summarised in Table 4.2, steepness and direction of slopes summarised in Table 4.1). The slopes of change in T_b with increasing T_{nest} below break-points were shallow and similar in both seasons for both resource supplementation treatments (Table 4.1). In the hot and dry breeding season low supp. chicks (n = 2) engaged in hyperthermia at a higher T_{nest} (i.e., higher break-point T_{nest}) and had a significantly steeper increase in T_b above the break-point (estimate = 0.55 ± 0.01 SD, $p < 0.001$) than high supp. chicks (n = 4, estimate = 0.23 ± 0.00 SD, $p < 0.001$; Figure 4.1 & 4.2; Table 4.1). The slopes of T_b above similar break-points were shallower in low supp. (estimate = 0.12 ± 0.00 SD, $p < 0.001$) and high supp. (estimate = 0.21 ± 0.01 SD, $p < 0.001$) chicks in the cool and wet breeding season ($n_{lowsupp} = 6$, $n_{highsupp} = 5$) compared to the hot and dry breeding season (Figure 4.1 & 4.2; Table 4.1). Mean and modal T_b below break-points were between T_b = 39.5 – 40.5 °C for all the groups, with T_b maxima only 1 – 2 °C above modal T_b even at T_{nest} > 45 °C (Table 4.2).

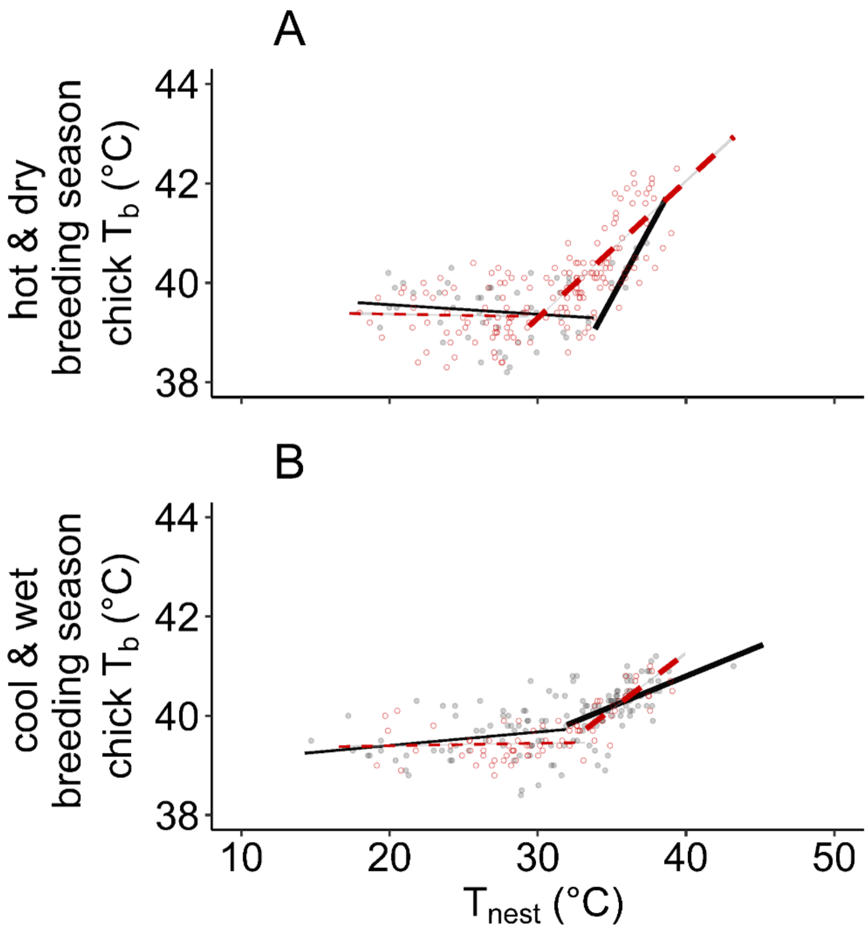

Figure 4.1. Body temperature (T_b; plotted from Gaussian linear mixed models [LMer]) for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks which fledged split by resource supplementation treatment (low supp. dark grey-black circles, solid black lines, high supp. open red circles, red dashed lines) in A) the hot and dry breeding

season (2019/2020, $n_{lowsupp} = 2$, $n_{highsupp} = 4$), and B) the cool and wet breeding season (2020/2021, $n_{lowsupp} = 6$, $n_{highsupp} = 5$) as functions of nest temperature (T_{nest}). Each relationship between T_b and T_{nest} for both resource supplementations in both breeding seasons is significant ($p < 0.05$). Trend lines do not extend beyond the data collected: only 1% of data are shown for visual clarity.

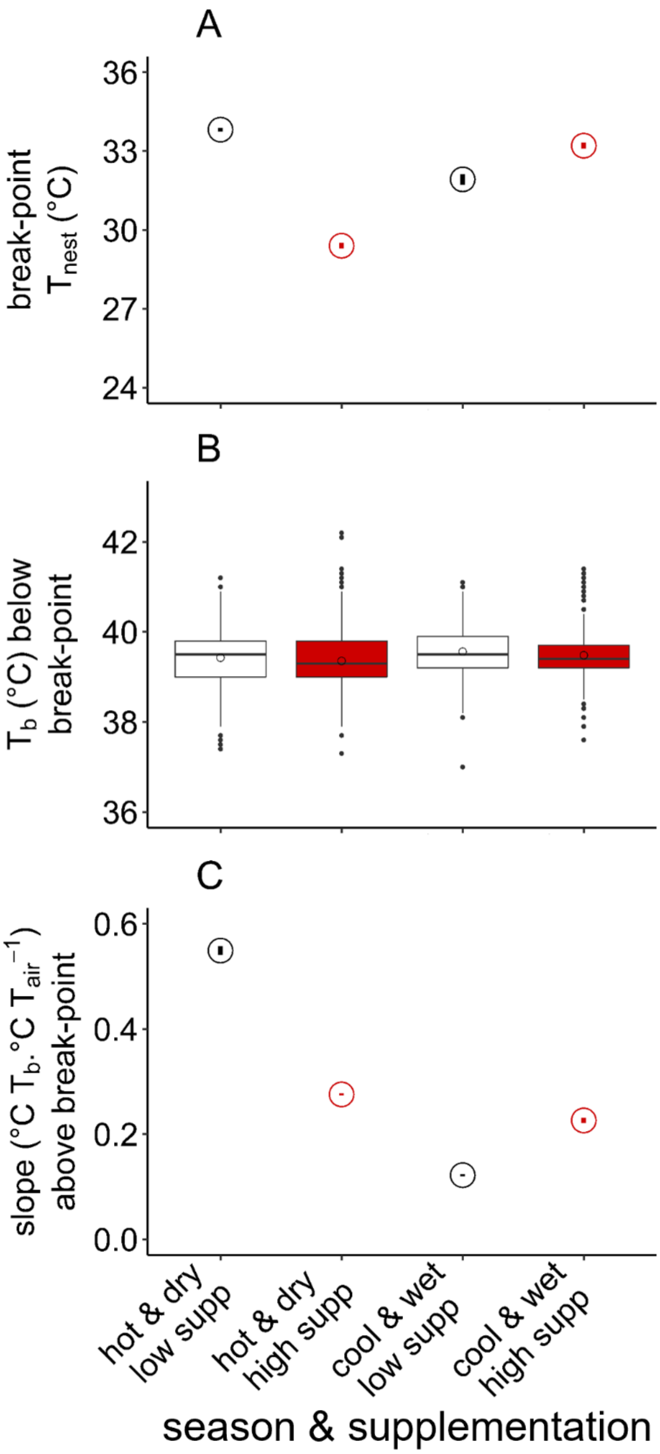

Figure 4.2. A) the break-point temperature (T_{nest}, ± 1 SE) at which T_b began to increase significantly more rapidly with increasing T_{nest}, B) T_b below the break-point T_{nest}, boxplots indicate median, upper and lower quartiles with means indicated as clear circles, and C) the slope (± 1 SE) of the increase in T_b above the break-point T_{nest} for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks in the hot and dry (2019/2020, $n_{lowsupp} = 2$, $n_{highsupp} = 4$), and the cool and wet (2020/2021, $n_{lowsupp} = 6$, $n_{highsupp} = 5$) breeding seasons. Low supp. black, high supp. red.

Table 4.1. Top model results for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chick body temperature (T_b) below and above break-points modelled using a linear models (LMer) family Gaussian as a function of 1) nest temperature (T_{nest}), 2) breeding season, 3) resource supplementation (hot and dry breeding season [2019/2020] chicks $n_{lowsupp}$ = 2, $n_{highsupp}$ = 5; cool and wet breeding season [2020/2021] chicks $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5), 4) an interaction between T_{nest} and season, and 5) an interaction between T_{nest} and resource supplementation. A single top model within Δ AICc < 2 was identified following model selection for each analysis. Both interactions were significant, so analyses were post-hoc split by breeding season and resource supplementation. All relationships had significant break-point T_{nest} above which T_b began increasing or increased more rapidly. Significant ($p \le 0.05$) estimates are highlighted in bold.

season	**response**	**treatment**	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**
	chick T_b (below break-point)		**T_{nest}**	**-0.11 ± 0.01**	**-18.84**	**23600**	**0.001**	**-0.12**	**-0.10**
			supp. (low)	0.00 ± 0.22	0.01	23600	0.992	-0.41	0.42
			season (cool and wet)	-0.16 ± 0.23	-0.70	23600	0.499	-0.58	0.26
			T_{nest} * supp.	**0.03 ± 0.01**	**5.37**	**23600**	**0.001**	**0.02**	**0.05**
			T_{nest} * season	**0.16 ± 0.01**	**26.82**	**23600**	**0.001**	**0.15**	**0.18**
	chick T_b (above break-point)		**T_{nest}**	**0.58 ± 0.00**	**142.59**	**21490**	**0.001**	**0.57**	**0.59**
			supp. (low)	-0.19 ± 0.23	-0.85	21490	0.414	-0.62	0.23

			season (cool and wet)	-0.26 ± 0.23	-1.10	21490	0.292	-0.69	0.18
			T_{nest} * supp.	**0.07 ± 0.01**	**5.28**	**21500**	**0.001**	**0.04**	**0.09**
			T_{nest} * season	**-0.33 ± 0.01**	**-26.47**	**21500**	**0.001**	**-0.35**	**-0.30**
hot and dry breeding season	chick T_b	low supp.	**T_{nest} (below break-point)**	**-0.02 ± 0.00**	**-11.29**	**5053**	**0.001**	**-0.03**	**-0.02**
			T_{nest} (above break-point)	**0.55 ± 0.01**	**64.20**	**1040**	**0.001**	**0.53**	**0.57**
		high supp.	**T_{nest} (below break-point)**	**-0.02 ± 0.00**	**-11.67**	**6749**	**0.001**	**-0.03**	**-0.02**
			T_{nest} (above break-point)	**0.23 ± 0.00**	**124.30**	**9904**	**0.001**	**0.22**	**0.23**
cool and wet breeding season	chick T_b	low supp.	**T_{nest} (below break-point)**	**0.03 ± 0.00**	**22.95**	**6609**	**0.001**	**0.03**	**0.03**
			T_{nest} (above break-point)	**0.12 ± 0.00**	**62.95**	**7992**	**0.001**	**0.11**	**0.12**
		high supp.	**T_{nest} (below break-point)**	**0.01 ± 0.00**	**9.91**	**5186**	**0.001**	**0.01**	**0.01**
			T_{nest} (above break-point)	**0.21 ± 0.00**	**52.34**	**2448**	**0.001**	**0.20**	**0.22**

Table 4.2. Southern Yellow-billed Hornbill (*Tockus leucomelas*) chick body temperature (T_b) modelled using a linear mixed model (LMer) family Gaussian as a function of nest temperature (T_{nest}), split by breeding season and resource supplementation (hot and dry breeding season [2019/2020] chicks $n_{lowsupp}$ = 2, $n_{highsupp}$ = 4; cool and wet breeding season [2020/2021] chicks $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5). All relationships had significant break-point T_{nest} above which T_b began increasing or increased more rapidly. Estimated break-points T_{nest} for each relationship, the mean and mode T_b below each break-point, and maximum T_b with the maximum T_{nest} experienced in brackets shown.

breeding season	**response**	**treatment**	**break-point T_{nest} °C ± SE**	**mean T_b °C ± SD below break-point**	**mode T_b °C below break-point**	**maximum T_b °C (max. T_{nest} °C experienced)**
hot and dry breeding season	chick T_b	low supp.	33.82 ± 0.07	39.43 ± 0.57	39.7	42.1 (38.67)
		high supp.	29.40 ± 0.14	39.35 ± 0.57	39.1	42.5 (43.24)
cool and wet breeding season	chick T_b	low supp.	31.92 ± 0.20	39.58 ± 0.52	39.4	42.1 (45.2)
		high supp.	33.21 ± 0.11	39.44 ± 0.33	39.3	41.7 (39.94)

4.4.3 Chick morphometrics and CORT

The M_b gain of chicks which fledged was best described by a four-parameter Weibull function in both the hot and dry and cool and wet breeding season (Figure 4.3; Tables 4.3 & S4.3). Chick tail feather lengths increased linearly with age (estimate = 30.09 ± 1.64 SD, $p \leq 0.001$).

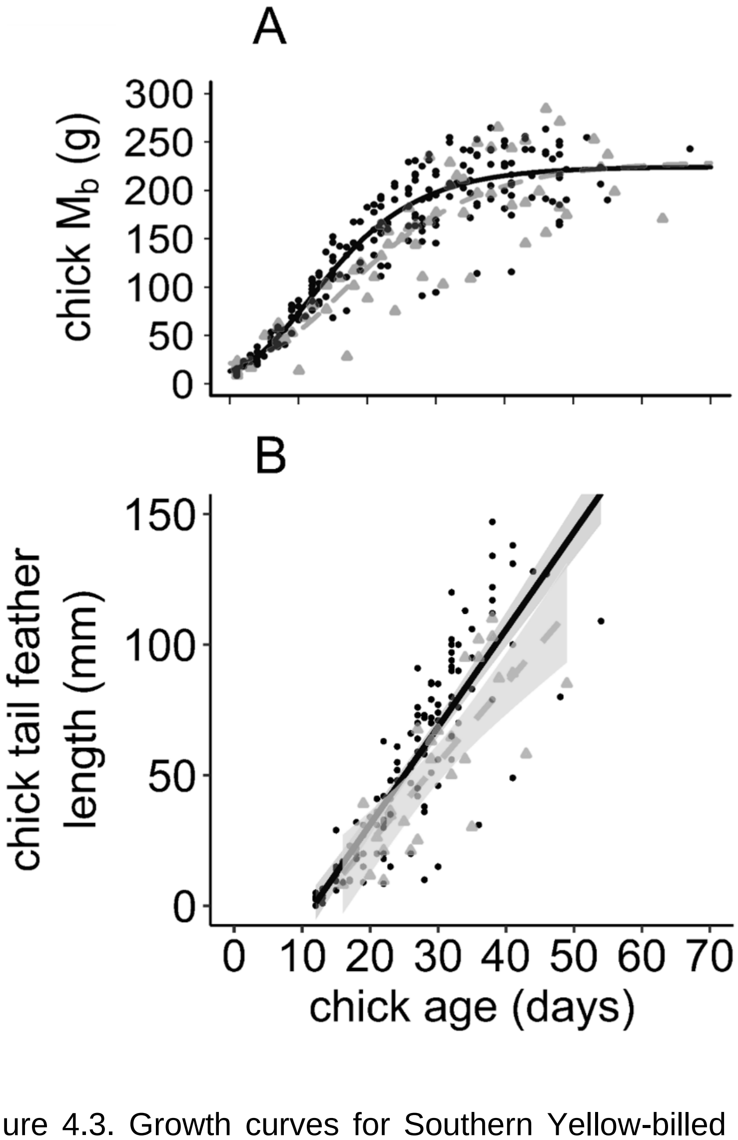

Figure 4.3. Growth curves for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chick A) body mass (M_b; four-parameter Weibull function) and B) tail feather length (measured weekly, plotted from Gaussian generalised linear models [GLM]) as a function of chick age for chicks which fledged over the hot and dry (n fledglings = 8; grey dashed line and triangles) and the cool and wet (n fledglings = 28; black solid line and circles) breeding seasons.

Table 4.3. Model results for the log logistic growth curve of body mass (M_b) of Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks which fledged in the hot and dry (n = 8) and cool and wet (n = 28) breeding seasons. Significant ($p < 0.05$) effects highlighted in bold.

breeding season		**estimate ± se**	**t-value**	**p-value**	**lower 95% CI**	**upper 95% CI**
hot and dry	**slope**	**-0.04 ± 0.01**	**-7.12**	**0.001**	**-0.05**	**-0.03**
	lower limit	**18.24 ± 6.50**	**2.81**	**0.007**	**5.27**	**31.20**
	upper limit	**230.16 ± 7.74**	**29.72**	**0.001**	**214.70**	**245.61**
	ED50	**19.49 ± 4.17**	**4.68**	**0.001**	**11.17**	**27.80**
cool and wet	**slope**	**-0.05 ± 0.00**	**-13.10**	**0.001**	**-0.06**	**-0.04**
	lower limit	7.20 ± 4.09	1.76	0.080	-0.85	15.25
	upper limit	**224.35 ± 4.33**	**51.85**	**0.001**	**215.82**	**232.88**
	ED50	**13.62 ± 0.93**	**14.60**	**0.000**	**11.78**	**15.46**

Top model estimates (models within Δ AICc < 2; Table S4.4) showed that chicks spent significantly less time in the nest (i.e., fledged sooner) (estimate = -3.29 ± 1.58, p = 0.046; days in the nest = 48.65 ± 7.53 and 53.29 ± 3.95 in the cool and wet and hot and dry breeding seasons, respectively; Figure 4.4), gained M_b (estimate = 0.67 ± 0.32, p = 0.047; Figure 4.3) and grew tail feathers (estimate = 0.46 ± 0.21, p = 0.036; Figure 4.3) significantly faster, and had significantly longer tarsi at fledge (estimate = 2.32 ± 0.86, p = 0.011; Figure 4.4) in the cool and wet breeding season compared to the hot and dry breeding season. Tarsus length at fledge decreased (estimate = -1.00 ± 0.38, p = 0.012; Figure 4.5) and tail feather CORT concentration increased (estimate = -0.20 ± 0.06, p = 0.002; Figure 4.5) significantly with increasing mean daily maximum T_{nest} from hatch until fledge, and during growth, respectively. Though chicks in the cool and wet season gained M_b faster, fledge M_b was not significantly different between seasons; mean fledge M_b = 218.75 g ± 27.48 SD (Figure 4.3). Despite some other predictor variables being identified in the top model sets, none of the dependent variables were significantly affected by any other modelled predictor variables (Table 4.4).

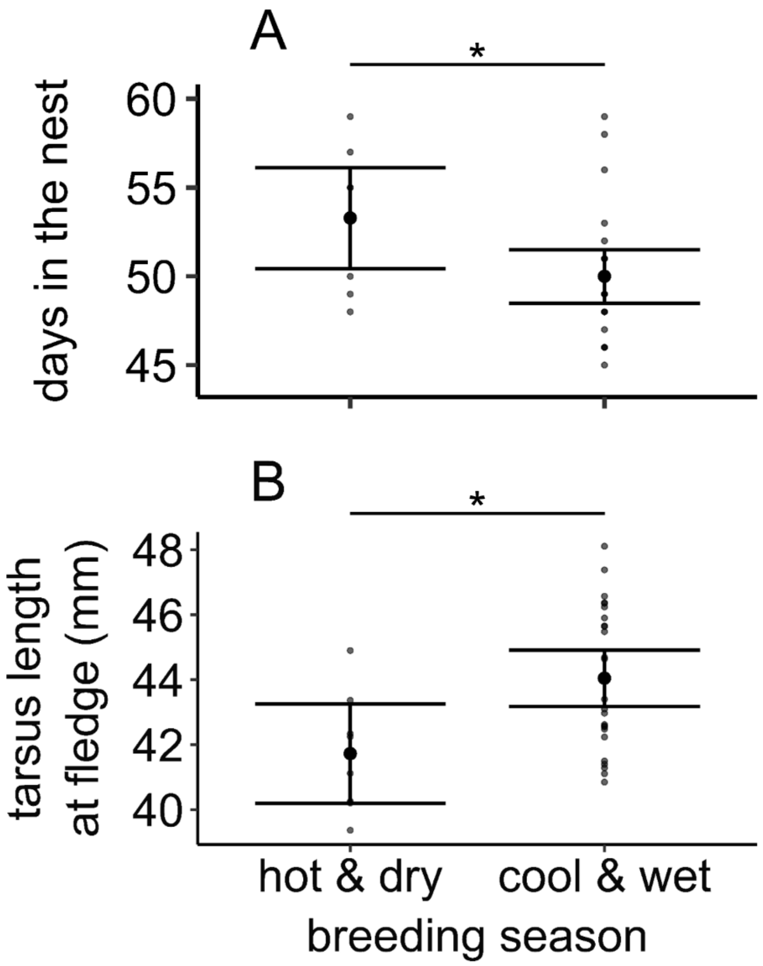

Figure 4.4. The A) number of days spent in the nest before fledging, and B) tarsus length at fledge (both plotted from a Gaussian generalised linear models [GLM]) of Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks in a hot and dry breeding season (2019/2020 n fledglings = 8) and a cool and wet breeding season (2020/2021 n fledglings = 28). Means with standard errors are shown. * indicates significance.

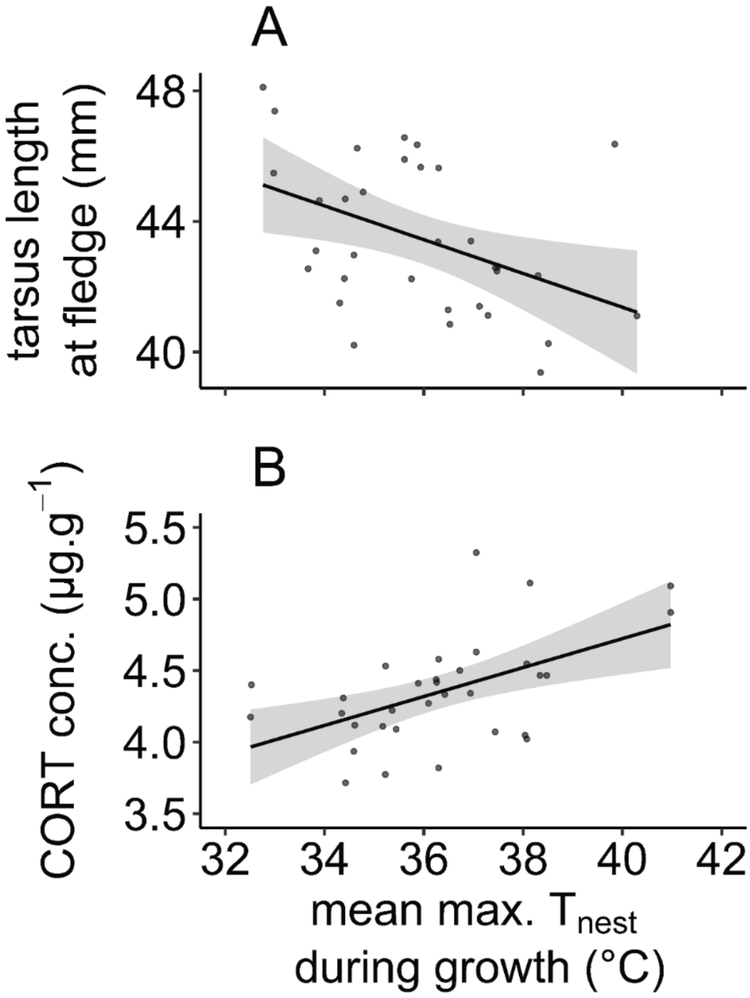

Figure 4.5. The A) tarsus length at fledge, and B) tail feather corticosterone (CORT) concentration of Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks as functions of mean maximum nest temperature (T_{nest}; plotted from Gaussian generalised linear models [GLM]) during growth from hatch to fledge, or during tail feather growth, respectively. Both the relationships between tarsus length at fledge and mean maximum T_{nest} during growth and between CORT concentration and mean maximum T_{nest} during growth are significant ($p < 0.05$). 95% confidence intervals (CI) are shown.

Table 4.4. Top model estimates (top models identified as those within Δ AICc < 2) from individual generalised linear models (GLM) family Gaussian used to model a) the number of days spent in the nest by chicks, b) M_b gain rate, c) fledge M_b, d) fledge tarsus length, e) fledge head plus culmen length, f) tail feather growth rate, g) tail feather barb density, and h) tail feather CORT concentration of Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks as functions of 1) breeding season, 2) chick hatch sequence, 3) mean daily maximum T_{nest} from hatch until fledge, 4) resource supplementation (hot and dry breeding season [2019/2020] chicks $n_{lowsupp} = 2$, $n_{highsupp} = 4$; cool and wet breeding season [2020/2021] chicks $n_{lowsupp} = 6$, $n_{highsupp} = 5$), and 5) the null. Significant ($p \leq 0.05$) effects are highlighted in bold.

response	**independent variable**	**estimate ± SE**	**t**	**df**	**p ≤**	**lower 95% CI**	**upper 95% CI**	**Δ AICc**	**weight**
days spent in nest	**season (cool and wet)**	**-3.29 ± 1.58**	**-2.09**	**31**	**0.046**	**-6.37**	**-0.2**	**0.00**	**0.55**
	null							1.89	0.22
M_b gain rate	**season (cool and wet)**	**0.67 ± 0.32**	**2.06**	**35**	**0.047**	**0.03**	**1.3**	**0.00**	**0.55**
	null							1.85	0.22
fledge M_b	hatch order	8.02 ± 4.8	1.67	32	0.105	-1.39	17.43	0.00	0.34
	null							0.42	0.28
	mean max. T_{nest} hatch until fledge / fail	-6.31 ± 4.88	-1.29	32	0.205	-15.88	3.25	1.11	0.20
fledge tarsus length	**season (cool and wet)**	**2.32 ± 0.86**	**2.69**	**32**	**0.011**	**0.63**	**4.01**	**0.00**	**0.47**
	mean max. T_{nest} hatch until fledge / fail	**-1.00 ± 0.38**	**-2.67**	**32**	**0.012**	**-1.74**	**-0.27**	**0.10**	**0.45**
fledge head	mean max. T_{nest} hatch	-1.55 ± 0.92	-1.69	32	0.102	-3.35	0.25	0.00	0.38

plus culmen	until fledge / fail								
	null							0.46	0.30
tail feather growth rate	**season (cool and wet)**	**0.46 ± 0.21**	**2.19**	**35**	**0.036**	**0.05**	**0.86**	**0.00**	**0.44**
	hatch order	-0.17 ± 0.09	-1.91	35	0.065	-0.35	0.01	1.07	0.26
tail feather barb density	season (cool and wet)	-0.06 ± 0.03	-1.99	32	0.056	-0.13	0	0.00	0.44
	supp (low)	-0.05 ± 0.03	-1.59	32	0.122	-0.1	0.01	1.37	0.22
	null							1.54	0.20
tail feather CORT conc.	**mean max. T_{nest} during growth**	**0.20 ± 0.06**	**3.4**	**31**	**0.002**	**0.08**	**0.31**	**0.00**	**0.94**

4.5 Discussion

This study provided evidence that high T_{nest} was perceived as a stressor by hornbill chicks and compromised structural growth: high T_{nest} correlated with higher tail feather CORT and shorter tarsi. These findings suggested chicks were more vulnerable than adult females to T_{nest} effects, given that I found no T_{nest} effects on female morphology or breeding success (which is intricately linked to T_{nest} effects on females via cannibalism, see Chapter 3). However, these T_{nest} effects on chicks were less marked than those found by van de Ven et al. (2020b). For example, this study found no T_{nest} effects on any other morphological measurement or time-to-fledge. The much-ameliorated T_{nest} effects were most likely due to comparatively lower T_{nest} in the present study than in van de Ven et al. (2020b) (see Chapter 3). There was some evidence of a buffering effect of environmental resource availability against thermoregulatory costs in the T_b data; the rate of increase in T_b above breakpoints was ~2 – 4x higher in the low supp., hot and dry breeding season chicks than in any other group (i.e., high supp. hot and dry, low supp. cool and wet, high supp. cool and wet) – all of which could be assumed to have higher resource availability than low supp. hot and dry chicks. However, this did not seem to translate through to an impact on CORT concentration or any morphological quality measures, perhaps due to low sample sizes to detect these effects. Intuitively, resources appeared to buffer T_{nest} effects on chick morphology given that tarsi lengths at fledge were longer, chicks gained M_b and grew tail feathers faster (resulting in longer feathers at fledge), and spent less days in the nest (i.e., fledged sooner) in the cool and wet breeding season. The lack of any significant effects of supplementary feeding on these parameters suggested these patterns were not the result of a buffering of resource availability on T_{nest}. The most likely alternative explanation was that the patterns were driven by differences in natural resource quality at the breeding season scale since food quality, rather than quantity, has been shown to have important impacts on nestling growth in other studies (Twining et al. 2018, Catto et al. 2021, Freeman et al. 2021), although I did not have the data to test this possibility. The reduced T_{nest} in the cool and wet breeding season may also have lessened the costs of thermoregulation on the chicks and parents, allowing improved growth in the chicks

(Cunningham et al. 2015, Bourne et al. 2020a). Overall, I found some T_{nest} effects, but also showed that resources, likely via quality rather than availability, did seem potentially important in (a) stimulating breeding in the first place illustrated by many more chicks being produced in the cool and wet breeding season (also see Chapter 3) and (b) improving some aspects of chick condition over and above any impacts of T_{nest} effects, as demonstrated by the faster growth in M_b and tail feather length, shorter period to fledge, and longer tarsi and tail feathers at fledge in the cool and wet breeding season.

During the hot, dry season, high supp. hornbill chicks increased T_b above normothermic levels at lower T_{nest} and showed improved T_b regulation, indicated by improved hyperthermia avoidance and more gradual increases in T_b, than low supp. chicks. Low supp. chicks in the hot and dry breeding season showed the most pronounced increase in T_b above break-points of all the chicks in both seasons. In combination, these patterns suggested that higher resource availability allowed more improved thermoregulation (Tieleman and Williams 1999, Smit et al. 2013). Despite the rapid rate of increase in T_b above the break-point, low supp. chicks in the hot and dry breeding season only attained relatively low T_b maximum (42.1 °C) compared to the maximum tolerable T_b limits previously demonstrated in this species of T_b = 44.8 °C (van Jaarsveld et al. 2021). This T_b maximum was comparable with the other chicks (highest T_b maximum in high supp. chicks in the hot and dry season T_b = 42.5 °C), which all showed T_b maxima well below maximum tolerable T_b limits. The degree of hyperthermia was potentially partially dependent on T_{nest}; in the hot and dry breeding season the maximum T_{nest} = 38.67 °C experienced by low supp. chicks was far below the maximum T_{nest} = 43.24 °C experienced by high supp. chicks. The much lower T_{nest} may have reduced the need for equally pronounced hyperthermia in low supp. chicks, potentially explaining their lower T_b maximum. Increased resource availability or quality allowing increased investment in thermoregulation would explain the improved hyperthermia avoidance and more gradual increases in T_b shown by chicks in the cool and wet breeding season, when the high rainfall would have had significantly enhanced resource availability and likely quality compared to the hot and dry breeding season (McCreedy and van Riper III 2015, Mares et al. 2017, Sauve et al. 2021).

Chicks with limited resources face developmental trade-offs, such as investing in thermoregulation at the cost of reduced investment in organ, bone or feather growth (Dawson et al. 2005, Monaghan 2008, Andreasson et al. 2020, Sauve et al. 2021). High T_{nest} correlated to higher tail feather CORT concentrations and reduced tarsi lengths at fledge, illustrating high T_{nest} was perceived as a stressor, potentially causing trade-offs between thermoregulation and investment in growth (Dawson et al. 2005, Jenni-Eiermann et al. 2015, Lamb et al. 2016, Henderson et al. 2017). There is also the non-mutually exclusive possibility that chicks with high T_b associated with high T_{nest} may be less capable of digesting and assimilating food (May et al. 1998, Abu-Dieyeh 2006, Rodríguez and Barba 2016). High T_{air} outside the nest may also have reduced provisioning efficiency of parents (provisioning rate of male parents was decreased at high T_{air}, see Chapter 2), negatively impacting chick development (Oswald et al. 2021). The lack of resource supplementation effects on variables other than those related to thermoregulation suggested that resource availability was not the key indirect mechanism through which high T_{nest} affected chicks. However, natural resource quality, rather than overall resource availability, effects may have been responsible for the observed patterns (e.g., Boag 1987, Johnston 1993, Newhouse et al. 2008, Pollock et al. 2017, Catto et al. 2021). I did not have the requisite data to test this possibility, highlighting that breeding season differences in provisioning efficiency (rather than rate) and resource quality warrant further attention. Notably, it is unlikely that tarsus length was the only trait which received reduced investment; several other traits not measured here, such as immune function and organ development, are commonly reduced in chicks developing in sub-optimal conditions (Lindström 1999, Dawson et al. 2005, Monaghan 2008). Future attention could also be dedicated to investigating more potential avenues for resource availability or quality effects on the physiology or morphology of chicks experiencing heat stress.

Although the slowed growth in the hot and dry breeding season did not change M_b at fledge, it meant that chicks spent up to two weeks longer in the nest (on average approximately 4 days longer) to achieve fledge M_b. Reaching a certain fledge M_b might be prioritised over fledging quickly since M_b at fledge has a strong influence on post-fledge survival and recruitment (Linden et al. 1992, Both et al. 1999, Naef-Daenzer et al. 2001), and nest predation rates in this species are almost nil, due to the seal at the nest entrance which excludes predators. However, spending longer in the nest increases the cost of breeding to the provisioning parents (see Chapters 2 and 3; and van de Ven et al. 2019, van de Ven et al. 2020b). That may reduce their end of breeding season condition, reducing their survival and future reproductive prospects (Barba et al. 1995, Barba et al. 2009, Jones et al. 2020). Moreover, while spending longer in the nest does not increase predation risk in the nest in the hornbills, as it does in other species (e.g., Cunningham et al. 2013b), chicks that take longer to fledge may suffer reduced survival and recruitment potential if post-fledge predation pressure increases later in the season, resources are less abundant, or competition with more developed, earlier fledged chicks is challenging (Both et al. 1999, Lindström 1999, Naef-Daenzer et al. 2001, Mumme et al. 2015, Rodríguez et al. 2016).

When developmental trade-offs result in reduced condition (such as being structurally smaller) at fledge, this can have severe negative impacts on survival, recruitment probability, and lifetime fitness (Both et al. 1999, Monaghan 2008, Mumme et al. 2015, Rodríguez et al. 2016, Nord and Giroud 2020). Chick M_b and head plus culmen length were not different between breeding seasons, and were unaffected by resource supplementation or T_{nest}, suggesting that chicks may favour some traits (such as M_b and head plus culmen length), at the cost of investment in others (i.e., tarsus growth) (Kunz and Ekman 2000). Fledge M_b is a well-known determinant of post-fledging survival (Linden et al. 1992, Both et al. 1999, Naef-Daenzer et al. 2001, Moreno et al. 2005, Greno et al. 2008, Sakaluk et al. 2014), while head and culmen size at fledge may have long-term consequences for reproduction, foraging ability, or even thermoregulation (Maan and Seehausen 2011, Hughes 2014, van de Ven et al. 2016). The faster growth rates of tail feathers in the cool and wet breeding season may also have benefited chicks; faster feather growth might allow improved flight performance at fledge, which may positively affect post-fledge survival (de la Hera et al. 2009, Sándor et al. 2022).

In contrast to previous findings in this study population, I study found no evidence of an effect of T_{nest} on chick M_b gain or fledge M_b. In van de Ven et al.'s (2020) study, T_{nest} was considerably higher than in the present study because of different nest box design and construction; mean maximum T_{nest} were on average 5.51 °C higher than natural cavities in boxes in 2012 – 2015 during the van de Ven et al. (2020b) study, compared to 1.52 °C (on average 3.99 °C cooler) in the present study. Consequently, while one might predict that higher T_{nest} aggravates the trade-offs between thermoregulation and development (Andrew et al. 2017, Gardner et al. 2017), the T_{nest} in this study may not have been high enough to cross biologically meaningful thresholds for negative impacts on M_b gain, despite the impacts on thermoregulation, increased stress, and reduced tarsal growth (Cunningham et al. 2013a, Conradie et al. 2019). For example, van de Ven et al. (2020b) showed that nestling hornbills in their study experienced 24hr M_b loss at T_{max} = 40.6 °C, corresponding to T_{nest} ~ 47 °C. Due to the more thermally-buffered nest box design, this T_{nest} would have only been achieved at T_{max} = 44.6 °C in my study period, which was never reached. The fact that high T_{nest} still had negative effects on the chicks, but that those effects were reduced compared to the previous studies on this population likely as a result of thermally buffered nest boxes, illustrates the potential for nest box design and construction to have significant consequences for T_{nest} effects on birds and other species (Griffiths et al. 2017, Larson et al. 2018, Goldingay and Thomas 2021, Czenze et al. 2022). Boxes designed to thermally buffer the occupants may, therefore, present powerful conservation mechanisms for species that use cavities (Larson et al. 2015, Griffiths et al. 2017, Maziarz et al. 2017, Martin Bideguren et al. 2019, Crawford and O'Keefe 2021, Goldingay and Thomas 2021).

This study also predominantly contrasted my expectations regarding the effects of supplementary food and water, based on significant effects of supplementary food in previous studies (e.g., Tieleman and Williams 2002, Gonzalez et al. 2006, Hudgens et al. 2009, Ruffino et al. 2014, Fitzsimmons et al. 2017, Cooper et al. 2019, Cooper et al.

2020). The amount of food provided to high supp. nests equalled approximately 100% of mean daily biomass previously demonstrated to be provisioned by male hornbills in this population (van de Ven 2017). However, it may still not have been enough food or water, or may not have met the nutrient or water requirements (i.e., food quality requirements) of the female parents or chicks (Seress et al. 2020, Catto et al. 2021). For example, wild zebra finches (*Taeniopygia guttata*) facing high T_{air} showed the ability to maintain M_b with access to *ad libitum* food and water (Cooper et al. 2019), but appear naturally limited by high T_{air} (Conradie et al. 2020, 2022), suggesting that the amount of food (and water) provided or the timing of supplementary resource provisioning (i.e., once per day in the morning) may have been inadequate to illicit significant effects in this study. Moreover, the males in the cool and wet season showed that they could considerably increase the amount of food provisioned to the nest compared to what was provided via supplementation (see Chapter 2), and had been recorded in previous studies (van de Ven et al. 2019), also suggesting that the amount of supplementary food was below what could be provisioned. Providing *ad libitum* access to nutrient and water rich food would provide valuable insight into this possibility and demonstrate whether the resource supplementation in this study was inadequate to significantly affect chick mass gain. It should also be noted that supplementary food was provided to the parents, rather than directly to the chicks. Therefore, the fate of supplementary food was determined by the provisioning parents. While males did provision almost all the supplementary food to nests when it was available, I did not collect data on how the female in the nest allocated the food. Therefore, the resource effects discussed here are based on the assumption that increased food provisioned to the nest correlated to more food for chicks. Impacts on thermoregulation of the chicks, in addition to previous work on this population (van de Ven et al. 2020) would suggest that this was the case. However, investigating the effects of variation in resource availability on the parental behavioural decision making regarding provisioning, especially in terms of the incarcerated females, presents an interesting avenue for future work.

In conclusion, this study showed some evidence that both resource availability and T_{nest} affect hornbill chick thermoregulation and development. The lack of significant effects of resource supplementation other than on thermoregulation suggested that resource availability was not a strong driver of variation in development between breeding seasons. Rather, it appeared that either the supplementary feeding experiment was not fully effective, or that natural resource quality effects acting at the breeding season scale were primarily responsible for breeding season differences in development. Alternatively, chicks may prioritise allocating resources to growth, rather than thermoregulation, during resource-poor periods, but split resources across these functions during resource-rich periods, making impacts of supplementation easier to detect in the thermoregulatory data than in morphology. There was also a significant difference in T_{nest} between the breeding seasons. It is likely that a combination of cooler T_{nest} and increased resources acted to affect chick growth and thermoregulation in the cool and wet season. These possibilities require further attention since this study did not have the data to test them. Ultimately, the negative effects of high T_{nest} and reduced resource availability or quality, on chick development may have long-term effects on recruitment and lifetime fitness, considering early life development and fledge condition critically affect those traits (Dawson et al. 2005, Salaberria et al. 2014, Hau et al. 2016). With ongoing climate change, understanding the effects of environmental temperature and resource availability and quality, especially during the sensitive chick development stage, will be critical for accurate vulnerability assessments and developing mitigation strategies (Lindström 1999, Rodríguez and Barba 2016, Oswald et al. 2021, Sauve et al. 2021).

4.6 Supplementary Tables

Table S4.1. Statistical power analyses used to determine the determinable effect size of main effects and interaction effects within generalised linear mixed modelling; u = model degrees of freedom; v = sample size, α = the significance level, and power = probability of finding an effect that is there; Cohen's f^2 = measure of determinable effect size (values of ~ 0.02, ~0.15, and ~0.35 represent small, moderate, and large determinable effect sizes respectively).

Response	**effect**	***u***	***v***	***α (p value)***	***power***	***f^2***
chick T_b below break-point	main	5	23606	0.05	0.8	0.001
	interaction	5	5902	0.05	0.8	0.002
chick T_b above break-point	main	5	21546	0.05	0.8	0.001
	interaction	5	5387	0.05	0.8	0.002
days spent in nest	main	1	29	0.05	0.8	0.271
M_b gain rate	main	1	33	0.05	0.8	0.238
fledge M_b	main	1	30	0.05	0.8	0.262
fledge tarsus	main	1	30	0.05	0.8	0.262
fledge head plus culmen length	main	1	30	0.05	0.8	0.262
tail feather growth rate	main	1	33	0.05	0.8	0.238
tail feather barb density	main	1	30	0.05	0.8	0.262
tail feather CORT conc.	main	1	29	0.05	0.8	0.271

Table S4.2. Model selection table for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chick body temperature (T_b) below and above break-point nest temperatures (T_{nest}) modelled using linear mixed model (LMer) family Gaussian as a function of 1) T_{nest}, 2) breeding season, 3) resource supplementation (hot and dry breeding season [2019/2020] chicks $n_{lowsupp}$ = 2, $n_{highsupp}$ = 4; cool and wet breeding season [2020/2021] chicks $n_{lowsupp}$ = 6, $n_{highsupp}$ = 5), 4) an interaction between T_{nest} and season, and 5) an interaction between T_{nest} and resource supplementation. Models ranked by Akaike's Information Criterion adjusted for small sizes (AICc) with top models (Δ AICc < 2) highlighted in bold. Models were averaged where more than one top model was identified.

			independent variables								
response	**model no.**	**int.**	**T_{nest}**	**season**	**supp.**	**T_{nest} * season**	**T_{nest} * supp**	**df**	**AICc**	**Δ AICc**	**weight**
T_b below break-point	**1**	**39.56**	**-0.11**	**+**	**+**	**+**	**+**	**8**	**28085.9**	**0**	**1**
	3	39.56	-0.09	+	+	+		7	28104.4	18.48	0
	2	39.59	-0.02	+	+		+	7	28784.1	698.20	0
	5	39.49						3	28791.2	705.26	0
	4	39.59	0	+	+			6	28808.1	722.18	0
T_b above break-point	**1**	**40.36**	**0.58**	**+**	**+**	**+**	**+**	**8**	**18248.7**	**0**	**1**
	3	40.37	0.58	+	+	+		7	18267.5	18.87	0
	2	40.38	0.55	+	+		+	7	18929	680.36	0
	4	40.35	0.47	+	+			6	20021.4	1772.71	0
	5	40.13						3	34728.7	16480.05	0

Table S4.3. Model selection table for different growth curve model fits (by fitting Gompertz [G], logistic [L], log-logistic [LL] and Weibull [W] functions) for body mass (M_b) growth curves of Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks which fledged split by breeding season (2019/2020 n = 8; 2020/2021 n = 28). Models ranked by Akaike's Information Criterion (AIC). NAs show where the model type was tested but the data were not suitable to estimate fit.

breeding season	**model type**	**log likelihood**	**AIC**	**lack of fit**	**residual variance**
hot and dry	W1.4	-350.17	710.34	0.24	1192.75
	LL.5	-349.32	710.63	0.25	1182.04
	L.4	-455.76	921.53	0.00	23354.25
	G.4	-456.75	923.50	0.00	24010.19
	L.5	-455.76	923.53	0.00	23708.10
	G.2	-459.04	924.08	0.00	24868.50
	L.3	-459.10	926.20	0.00	25278.95
	L.3	-459.10	926.20	0.00	25278.95
	G.3	-459.43	926.87	0.00	25516.42
	W1.3	NA	NA	NA	NA
	W2.3	NA	NA	NA	NA
	W2.4	NA	NA	NA	NA
	LL.3	NA	NA	NA	NA
	LL.4	NA	NA	NA	NA
cool and wet	W1.4	-1027.86	2065.71	0.07	681.72
	LL.5	-1028.20	2068.41	0.05	687.06
	L.3	-1404.05	2816.09	0.00	20741.97

L.3	-1404.05	2816.09	0.00	20741.97
L.4	-1404.05	2818.09	0.00	20838.00
L.5	-1404.05	2820.09	0.00	20934.92
G.4	-1423.44	2856.87	0.00	24854.71
G.2	-1431.11	2868.22	0.00	26406.19
G.3	-1431.29	2870.57	0.00	26570.28
W1.3	NA	NA	NA	NA
W2.3	NA	NA	NA	NA
W2.4	NA	NA	NA	NA
LL.3	NA	NA	NA	NA
LL.4	NA	NA	NA	NA

Table S4.4. Model selection table of generalised linear models (GLM) family Gaussian of a) the number of days spent in the nest by chicks, b) M_b gain rate, c) fledge M_b, d) fledge tarsus length, e) fledge head plus culmen length, f) tail feather growth rate, g) tail feather barb density, and h) tail feather CORT concentration as functions of 1) breeding season, 2) chick hatch sequence, 3) mean daily maximum T_{nest} from hatch until fledge, 4) resource supplementation, and 5) the null for Southern Yellow-billed Hornbill (*Tockus leucomelas*) chicks. Models ranked by Akaike's Information Criterion adjusted for small sizes (AICc) with top models (Δ AICc < 2) highlighted in bold.

			independent variables							
response	**model no.**	**int**	**hatch order**	**mean max. T_{nest} hatch to fledge / fail / during growth**	**season**	**supp.**	**df**	**AICc**	**Δ AICc**	**weight**
days in the nest	**1**	**53.29**			**+**		**3**	**179.1**	**0**	**0.55**
	5	**50.72**					**2**	**181.0**	**1.89**	**0.22**
	2	50.72	0.5				3	182.9	3.79	0.08
	3	50.72		-0.49			3	182.9	3.82	0.08
	4	50.40				+	3	183.2	4.13	0.07
M_b gain rate	**1**	**4.074**			**+**		**3**	**91.2**	**0**	**0.55**
	5	**4.591**					**2**	**93.0**	**1.85**	**0.22**
	3	4.591		-0.09			3	95.0	3.81	0.08

	2	4.591	0.08				3	95.1	3.89	0.08
	4	4.670				+	3	95.1	3.95	0.08
fledge M_b	**2**	**218.7**	**8.02**				**3**	**316.3**	**0**	**0.34**
	5	**218.7**					**2**	**316.7**	**0.42**	**0.28**
	3	**218.7**		**-6.31**			**3**	**317.4**	**1.11**	**0.20**
	1	213.1			+		3	318.7	2.40	0.10
	4	220.2				+	3	319.1	2.75	0.09
fledge tarsus length	**1**	**41.73**			**+**		**3**	**148.0**	**0**	**0.47**
	3	**43.48**		**-1**			**3**	**148.1**	**0.10**	**0.45**
	5	43.48					2	152.5	4.50	0.05
	2	43.48	0.19				3	154.7	6.71	0.02
	4	43.53				+	3	154.9	6.92	0.02
fledge head plus culmen length	**3**	**96.01**		**-1.55**			**3**	**207.2**	**0**	**0.38**
	5	**96.01**					**2**	**207.7**	**0.46**	**0.30**
	2	96.01	0.82				3	209.3	2.11	0.13
	1	96.66			+		3	209.9	2.73	0.10
	4	96.38				+	3	209.9	2.74	0.10
tail feather growth rate	**1**	**4.33**			**+**		**3**	**59.7**	**0**	**0.44**
	2	**4.68**	**-0.17**				**3**	**60.8**	**1.07**	**0.26**
	5	4.68					2	62.1	2.35	0.14
	4	4.81				+	3	62.6	2.93	0.10

	3	4.68		-0.07			3	63.8	4.07	0.06
tail feather barb density	**1**	**1.39**			**+**		**3**	**-69.3**	**0**	**0.44**
	4	**1.37**				**+**	**3**	**-67.9**	**1.37**	**0.22**
	5	**1.35**					**2**	**-67.7**	**1.54**	**0.20**
	3	1.35		0.01			3	-65.7	3.54	0.07
	2	1.35	-0.01				3	-65.5	3.76	0.07
CORT conc.	**3**	**4.36**		**0.2**			**3**	**23.6**	**0**	**0.94**
	2	4.36	-0.12				3	30.6	7.05	0.03
	5	4.36					2	31.5	7.97	0.02
	1	4.47			+		3	32.9	9.31	0.01
	4	4.33				+	3	33.9	10.32	0.01

5. Collapse of breeding success in desert-dwelling hornbills evident within a single decade

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AEM, SJC, TMFNVDV and myself developed the conceptual framework. LJN, MJF, TMFNVDV and myself collected data. I analysed the data and wrote the manuscript. All the authors contributed to editing and revising the version submitted for publication.

5.1 Abstract

Rapid anthropogenic climate change potentially severely reduces avian breeding success. While the consequences of high temperatures and drought are reasonably well-studied within single breeding seasons, their impacts over decadal time scales are less clear. I assessed the effects of air temperature (T_{air}) and drought on the breeding output of Southern Yellow-billed Hornbills (*Tockus leucomelas*; hornbills) in the Kalahari Desert over a decade (2008 – 2019). I aimed to document trends in breeding performance in an arid-zone bird during a time of rapid global warming and identify potential drivers of variation in breeding performance. Breeding output of the study population collapsed during the monitoring period. Comparing the first three seasons (2008 – 2011) of monitoring to the last three (2016 – 2019), the mean percentage of nest boxes occupied declined from 52% to 12%, nest success from 58% to 17%, and mean fledglings produced per breeding attempt from 1.1 to 0.4. Breeding output was negatively correlated with increasing days on which T_{max} (mean maximum daily T_{air}) exceeded the threshold T_{air} at which male hornbills show a 50% likelihood of engaging in heat dissipation behaviour (i.e. panting [$T_{thresh;}$ T_{air} = 34.5 °C]) and the occurrence of drought within the breeding season, as well as later dates for entry into the nest cavity (i.e. nest initiation) and fewer days post-hatch spent incarcerated in the nest by the female parent. The apparent effects of high T_{air} were present even in non-drought years; of the 115 breeding attempts I recorded, all 18 attempts which had ≥ 72% days during the attempt on which T_{max} > T_{thresh} failed (equivalent to T_{max} during the attempt ≥ 35.7 °C). This suggests global warming was likely the primary driver of the recent, rapid breeding success collapse. Based on current warming trends the T_{max} threshold of 35.7 °C, above which no successful breeding attempts were recorded, will be exceeded during the entire hornbill breeding season by approximately 2027 at my study site. These findings therefore support the prediction that climate change may drive rapid declines and cause local extinctions despite the absence of direct lethal effects of extreme heat events.

5.2 Introduction

Global heating is exacerbating the harsh conditions associated with arid environments by elevating average air temperatures (T_{air}) and increasing the frequency and intensity of heat waves (Pachauri et al. 2014, Mbokodo et al. 2020) and drought (van Wilgen et al. 2016). Possible consequences for animals inhabiting arid regions include increased frequency of mass mortality events (Welbergen et al. 2008, Albright et al. 2017, McKechnie and Wolf 2019, McKechnie et al. 2021b), and disastrous reproductive failures (Bolger et al. 2005, Albright et al. 2010b, Seabrook et al. 2014, McCowan and Griffith 2021, Sharpe et al. 2021). However, heat waves, especially in association with droughts, may also have insidious sublethal effects (Gardner et al. 2016, Conradie et al. 2019, Bourne et al. 2020c, Bourne et al. 2021, Cunningham et al. 2021, Moagi et al. 2021), including loss of body condition (du Plessis et al. 2012, Sharpe et al. 2019), reduced egg or clutch sizes in birds (Albright et al. 2010b, Keynan and Yosef 2010), reduced provisioning rates and compromised offspring quality (van de Ven et al. 2020b, Bourne et al. 2021, Oswald et al. 2021), and the foregoing of breeding altogether (Moreno and Møller 2011, McCreedy and van Riper III 2015, Carstens et al. 2019).

The small size and high mass-specific metabolism of most birds, combined with a diurnal activity period and limited use of underground refugia, make this taxon among the most vulnerable to mismatches between energy and water-balance over short time scales (Wolf 2000, Albright et al. 2017, Conradie et al. 2019, Cooper et al. 2020, Kemp et al. 2020). Arid-zone birds are particularly vulnerable given that they are commonly constrained to breed in response to rainfall, which often occurs during the hottest time of the year (Bolger et al. 2005, Flesch 2014, McCreedy and van Riper III 2015, Mares et al. 2017). Given that birds face the dual threats of dehydration and hyperthermia daily during this period, elucidating the limits of their capacity to cope with the increased resource (food, water, and time) demands associated with breeding is critical for understanding variation in reproductive success under current and future climates (Andreasson et al. 2020, Cunningham et al. 2021). There is a growing body of literature on the impacts of high temperatures and drought on nest success of arid-zone birds at the scale of nesting attempts and seasons (e.g., Catry et al. 2011, Salaberria et al. 2014, Catry et al. 2015, Cruz-McDonnell and Wolf 2016, Bourne et al. 2020a, c, D'Amelio et al. 2022), but fewer studies investigate these impacts on population-level breeding outputs over longer timescales in relation to ongoing climate change trends (however see for e.g., Frederiksen et al. 2013, Hatch 2013, Amélineau et al. 2019, Bourne et al. 2020a, Ridley et al. 2021).

Southern Yellow-billed Hornbills (*Tockus leucomelas*; hereafter hornbills) initiate breeding in response to rainfall in the arid western parts of their southern African range (Kemp 1995, van de Ven et al. 2020b). Like most hornbills, these birds employ an unusual breeding strategy whereby the female seals herself into the nest cavity (Kemp 1995). Nestling hornbills within the sealed nest cavity are therefore largely safe from predators, meaning that breeding success is primarily dependent on other factors

(Moreau and Moreau 1941). In this study population, which has been monitored since 2008, mean maximum daily T_{air} (T_{max}) during the nesting period negatively correlates with fledging probability and fledgling condition (van de Ven et al. 2020b). The reduction in breeding success during hot periods is likely caused by a combination of high nest temperatures (T_{nest}), and reduced provisioning rates by males, due to trade-offs between thermoregulation and parental effort (van de Ven et al. 2019, van de Ven et al. 2020b). Considering a) the mechanistic links between weather conditions and breeding are well-studied in hornbills (van de Ven et al. 2019, van de Ven et al. 2020b, van Jaarsveld et al. 2021), b) *a priori*, the unusual breeding system of hornbills and the fact they are constrained to breed during the hottest time of year in the arid zone, indicates this taxon could be especially vulnerable to global warming, and c) a ten-year monitoring dataset exists for this study population, which resides near the hot, arid south-western edge of the species' distribution, I suggest that this population of hornbills provides an excellent opportunity to test the prediction that lethal and sublethal fitness costs of high T_{max} will lead to increasingly poor reproductive output over time, risking breeding collapse and population extirpation due to climate change (Conradie et al. 2019).

Here, I examined climate trends (1960 – 2020) for the study region and the breeding success of hornbills at both broad (long-term trends 2008 – 2018) and fine (individual breeding attempts) scales. My specific aims were to 1) quantify long-term climate trends in the study region, 2) quantify changes in the breeding success of this population of hornbills over the last decade, and 3) to model the relationships between several extrinsic (metrics of rainfall and temperature) and intrinsic (female entry into the nest cavity date, and days post-hatch the female spent incarcerated in the nest) variables on the breeding success of hornbills. My overall aim was to describe the response of an arid-zone bird to a decade-long period of rapid warming, identify potential drivers of variability in breeding performance, and empirically demonstrate likely mechanistic links between climate change and collapse of breeding output.

5.3 Methods

5.3.1 Study species

Southern Yellow-billed Hornbills are listed as Least Concern by the IUCN, but are thought to be declining (BirdLife International 2022). Their distribution includes most of southern Africa, with a large portion falling within the Kalahari Desert. They are socially monogamous and live up to 23 years in captivity (Strehlow 2001), although the oldest known marked bird at my study site was 8 years old. Hornbills are cavity nesters; once sealed into the nest, females moult all their flight feathers simultaneously. At the study site, pairs usually attempt a single brood per season (though they may be multi-brooded in more mesic areas, Stanback et al. 2021), and the mean duration from first egg lay until the female completes sufficient feather regrowth and breaks out of the nest is 53 ± 6.3 SD days (n = 56, range 36 – 73) in nests that successfully produce at least one fledgling (van de Ven et al. 2020b). After the female breaks out of the sealed cavity, she aids in subsequent provisioning of nestlings.

Research on hornbills at my study site (Kuruman River Reserve in the southern Kalahari Desert, Northern Cape province, South Africa; 26°58′ S, 21°49′ E; hereafter, KRR) has been ongoing since 2008 and breeding data for ten breeding seasons (2008 – 2019, excluding the summer of 2011-12 when no data were collected) were used for this study. The hornbills at KRR typically breed between October and the end of March (van de Ven et al. 2020b). Monitoring allowed us to estimate the number of pairs at the site, and track if and where they bred. Some pairs during the decade monitoring period were recorded breeding in natural cavities. No breeding data was recorded from these attempts. Breeding primarily occurred in nest boxes and breeding data analysed in this study were exclusively from nest boxes. Wooden nest boxes were available at KRR throughout the study period (43 boxes 2008 – 2011, 44 boxes 2012 – 2015, 38 boxes 2015 – 2017, 33 boxes 2017 – 2018, 36 boxes 2019 – 2021). In seasons with low nest box occupancy pairs were observed to still be present at the site but to skip breeding. I defined the hornbill breeding season as 19 October (the earliest recorded date a female entered a box during the decade of the study) – 24 March (the latest recorded fledge / failure date).

5.3.2 Study site and weather data collection

The KRR consists of arid savanna dominated by grasses interspersed with large trees (mainly camelthorn, *Vachellia erioloba*; grey camelthorn, *Vachellia haematoxylon*; shepherds' tree, *Boscia albitrunca*; and buffalo thorn, *Ziziphus 137ucronate*). Rainfall occurs primarily in the Austral spring and summer between October and April (mean annual rainfall 213.9 ± SD 102.0 mm; 1993 – 2020, Van Zylsrus [VZ] weather station, South African Weather Service [SAWS]). The spring and summer are hot; T_{max} (mean maximum daily air temperature [T_{air}]) between October and March is 34.9 ± SD 1.19 °C (1991 – 2020, VZ), which is above the threshold T_{air} at which male hornbills showed a 50% likelihood of engaging in heat dissipation behaviour i.e., panting [$T_{thresh;}$ T_{air} = 34.5 °C] (van de Ven et al. 2019).

In 2011 the study site was equipped with a weather station (Hot Birds Research Project [HBRP] Weather Station; Vantage Pro2, Davis Instruments, Hayward, U.S.A.) set to record T_{air} (°C), wind speed ($m.s^{-1}$), relative humidity (%), and solar radiation ($W.m^{-2}$) at 5-min intervals. To create a continuous weather dataset appropriate to the study site spanning the entire hornbill monitoring period (2008 – 2019), I compared weather data from the HBRP station collected between 2011 and 2020, to those from SAWS stations at VZ, Northern Cape (~30 km from the study site, data available 1992 – 2020), and Twee Rivieren (TR), Northern Cape (~120 km from the study site, data available 1960 – 2020) to validate the use of VZ and TR weather data as proxies for the missing HBRP weather data prior to 2011.

Weather data from all three stations were highly correlated (see supplementary materials; Figures S5.1 & S5.2), but the T_{max} data from VZ and TR were consistently higher than those from the HBRP (VZ mean 1.38 °C ± 1.54 SD higher; TR, mean 2.13 °C ± 1.79 SD higher; Figure S5.1). These values were therefore adjusted (see Supplementary materials; Figure S5.2) before being used to supplement the HBRP weather data collected at the study site. Daily rainfall was not correlated between the three weather stations, but seasonal rainfall was (HBRP~VZ r^2 = 0.97; HBRP~TR r^2 = 0.86; Figure S5.3), allowing me to establish the occurrence / absence of drought at the study site using VZ rainfall data. Mean breeding season rainfall recorded by the VZ weather station was 151.71 mm (average rainfall recorded during the hornbill breeding season 19 October – 24 March each year from 1993 – 2019). I defined 'drought' seasons as those in which rainfall recorded at VZ was < 80% of the long-term seasonal average following Bourne et al. (2020c). Rainfall at the study site has a lagged effect on prey abundance (Doolan and Macdonald 1997), therefore the cumulative rainfall within the two months prior to the start of the breeding season was included in analyses as as a proxy of food availability during breeding (Ridley and Raihani 2007). To analyse long-term weather trends in the southern Kalahari I used unadjusted weather data from all three weather stations.

5.3.3 Statistical analyses

Long-term weather trends

Statistical analyses were conducted in the R statistical environment, version 3.5.1 (R Core Team 2023), using the R Studio platform (R Studio Team 2023). For each weather station (HBRP, TR, VZ) I used generalised linear models (GLMs) to model yearly trends in the T_{max} (TR 1960 – 2020, VZ 1990 – 2020, HBRP 2011 – 2020), cumulative days on which $T_{max} > T_{thresh}$ ($DaysT_{thresh}$; TR 1960 – 2020, VZ 1990 – 2020, HBRP 2011 – 2020), and cumulative rainfall (TR 2007 – 2020, VZ 1995 – 2020, HBRP 2011 – 2020), for each hornbill breeding season (19 October – 24 March annually). Visual inspection of the T_{air} data from TR indicated a non-linear relationship. I therefore used segmented analysis (package segmented, Muggeo 2017) on the dataset with longest record (TR, starting 1960) to investigate whether there was a statistically significant inflection in seasonal T_{max} and cumulative $DaysT_{thresh}$ each season. I also modelled the yearly trends in non-breeding season (25 March – 18 October each year) mean minimum daily T_{air} (T_{min}; TR 1960 – 2020, VZ 1990 – 2020, HBRP 2011 – 2020) and cumulative rainfall (TR 2007 – 2020, VZ 1995 – 2020, HBRP 2011 – 2020). Only breeding and non-breeding seasons with data covering >90% of days were used in analyses (for excluded seasons see Table S5.1). All trends were plotted with linear model predictions (package ggplot2, Wickham 2016).

Seasonal weather conditions and breeding trends

I tested for temporal autocorrelation in all response variables across seasons by assessing the degree of correlation between the model residuals associated with increasing lags within each model. As no temporal autocorrelation between seasons was found for any variables, and sample size in terms of number of seasons was small (n = 10), I used simple Pearson's product-moment correlation coefficient tests to assess the statistical significance of the following long-term trends: (1) seasonal T_{max} and cumulative rainfall for breeding seasons 2008 – 2019; (2) percentage of nest boxes used, percentage of nesting attempts that succeeded in fledging at least one chick (hereafter succeeded), and mean number of fledglings produced per breeding attempt per season 2008 – 2019; (3) relationships between the following weather variables: breeding season (18 August – 18 October annually) cumulative $DaysT_{thresh}$ (this metric used since panting is associated with heavy reductions in foraging success (van de Ven et al. 2019), making $DaysT_{thresh}$ a biologically instructive metric for analyses); breeding season drought occurrence; non-breeding season T_{min}; and the cumulative rainfall within the two months prior to the start of the breeding season, and (a) percentage of boxes used per season (b) percentage of nesting attempts that succeeded, and (c) the mean number of fledglings produced per attempt per season. Simple linear trends were then visualised using *ggplot2* (Wickham 2016). I also performed Welch Two Sample t-tests on each of these dependent variables as a function of drought occurrence.

Individual breeding attempts

A total of 115 breeding attempts were recorded in nest boxes over the study period, of which 91 succeeded. Complete or partial weather data were available for 109 breeding attempts, female entry date was known for 105. Due to these data gaps, final sample sizes for analyses of nest survival in relation to weather conditions were n = 88 for (a) female entry to fledge / fail (hereafter 'entire attempt') and (b) female entry to hatch / fail (hereafter ‘pre-hatch period’). Attempts which had the required combination of known hatch date (n = 91) and complete weather data allowed for a final sample size for analyses n = 88 for (c) hatch to nestling fledge / fail (hereafter ‘nestling period’).

Bayesian generalised linear mixed models (BGLMer) with binomial distribution were used to model the success / failure of (a) each entire attempt, (b) the pre-hatch period, (c) and the nestling period, as a function of: female entry date (coded as the count of days since the start of the breeding season, with 19 October = day 0); the percentage $\text{DaysT}_{\text{thresh}}$ during the attempt; drought occurrence; and the interaction between the percentage $\text{DaysT}_{\text{thresh}}$ and drought occurrence. The number of days post-hatch the female spent incarcerated in the nest was included as an additional explanatory variable for nestling period analyses. I used Bayesian linear mixed models (BLMer) to model the effect of drought occurrence on female entry date and on the number of days post-hatch spent in the nest by the female, with ANOVA (Type II Wald chi-square test) used to test for significant correlations with drought occurrence. Season identity was included in all models as a random effect.

I used variance inflation factors (VIF; package car, Fox and Weisberg 2019) to test for collinearity between explanatory variables and did not fit correlated variables within the same model. I used percentage $\text{DaysT}_{\text{thresh}}$ rather than T_{max} of each nesting period as my ‘temperature’ predictor variable, because these two variables showed notable collinearity in all models (VIF > 10), and models including only percentage $\text{DaysT}_{\text{thresh}}$ outperformed models including only T_{max} according to Akaike Information Criterion adjusted for small sizes (AICc). I used ‘drought occurrence’ (n breeding attempts in drought years = 28, mean rainfall = 75.0 ± 42.8 mm, n breeding attempts in non-drought years = 86, mean rainfall = 257.0 ± 29.1 mm) instead of cumulative rainfall during the attempt as my ‘precipitation’ predictor variable because daily rainfall data were available for only 36 of 115 individual breeding attempts.

Candidate model sets for each analysis included all possible nested models within a biologically sensible global model, including the null model. I used a Bayesian modelling approach since this allowed me to fit a global model with the *a priori* terms of interest while avoiding singularity errors (package blme, Chung et al. 2013). Candidate models were compared using AICc (package MuMIn, Barton 2020). I report on the top performing model, and where more than one top model was identified (those with an Δ AICc < 2), results were reported for the model average of the top models (package MuMIn, Barton 2020). Plots were based on the single model with the lowest AICc (package jtools, Long 2020).

Thermal conditions in nest boxes versus natural cavities

All breeding success data were necessarily collected from birds breeding in nest-boxes (as opposed to natural tree cavities which were sealed and inaccessible). However, between 2012 – 2015 nest temperature (T_{nest}) data were available from occupied natural cavities to compare thermal conditions in these two nest types (collected by TMFNVDV). I analysed T_{nest} data from 27 occupied nest boxes and 9 occupied natural cavities (cumulatively 58 632 hours and 9 816 hours recording at 5-min intervals, respectively) collected between 2012 – 2015 using Thermochron iButtons (DS1923, Maxim, Sunnyvale, CA, USA, resolution = 0.0625 °C, accuracy ± 0.5°C). For nest box measurements, iButtons were mounted within the nests on the underside of the nest box lids in plastic iButton wall holders to minimise bird contact and to avoid interference by the birds. For natural cavity measurements, iButtons were placed in an iButton reader holster which was secured with threading wire at the top of the cavity via the nest opening. I used Bayesian linear mixed models (BLMers) to model T_{nest} as a function of T_{air} as measured by the HBRP weather station, nest type (box vs cavity), and the interaction between those factors. Individual nest identity was included as a random factor. ANOVA (Type II Wald chi-square test) were used to identify factors with significant correlations with T_{nest}.

5.4 Results

5.4.1 Long-term weather trends

In the TR weather data, there was a significant inflection at the summer of 1996 – 1997 after which T_{max} ($t_{54} = 4.58$, $p < 0.001$, ± 3.5 SE years) and the cumulative $DaysT_{thresh}$ ($t_{54} = 3.9$, $p < 0.001$, ± 4.1 SE years) began to increase (Figures 5.1A and 5.1B). Subsequent to summer 1996-1997, TR mean seasonal T_{max} increased by 1.3 °C per decade and cumulative $DaysT_{thresh}$ by 19.7 days per decade. I did not test for an inflection point in the VZ T_{max} data, rather, considering the strong correlation between TR and VZ T_{max} data (*rho.c* = 0.94, $r^2 = 0.89$; Figure S5.1), I applied the same inflection point identified for the TR data to the VZ data. Above the same inflection point the VZ mean seasonal T_{max} increased 1.0 °C per decade, and cumulative days on which $T_{max} > T_{thresh}$ by 19.8 days per decade. Too few years of data were available for the HBRP station to model a trend in T_{max}, however, given the strong correlation between the VZ and HBRP data (*rho.c* = 0.94, $r^2 = 0.94$, Figure S5.1) a similar warming trend of 1.0 °C per decade can be expected for HBRP. No clear long-term pattern in rainfall was identified for either station, however rainfall records only date back to 1993 (Figure 5.1C and 5.1D). No trends or inflection points were apparent in T_{min} or cumulative rainfall during the non-breeding season since 1960 and 1995, respectively, for TR (Figure S5.4).

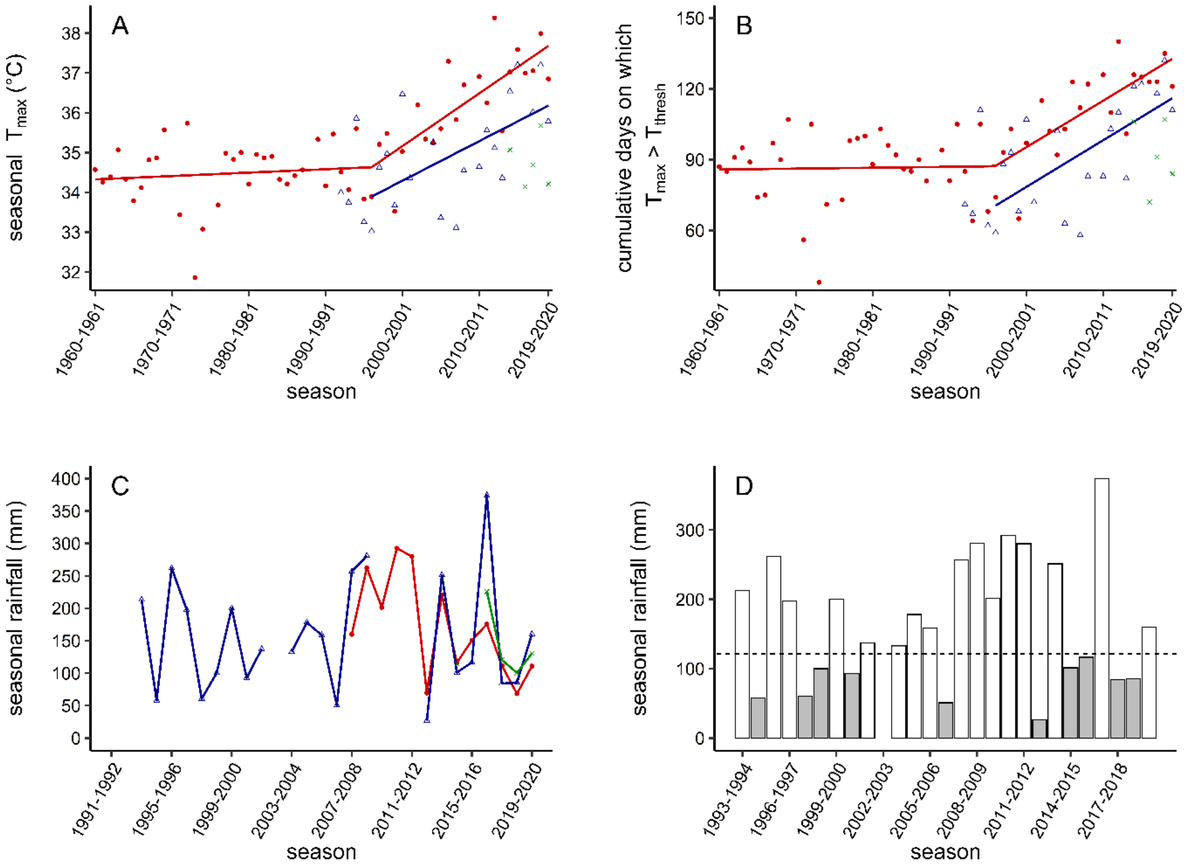

Figure 5.1. (A) Trends in seasonal T_{max} (mean maximum daily air temperature [T_{air}]), (B) cumulative DaysT_{thresh} (days on which $T_{max} > T_{thresh}$ [T_{air} = 34.5 °C]), and (C) cumulative rainfall for each Southern Yellow-billed Hornbill (*Tockus leucomelas*) breeding season (19 October – 24 March each year) modelled from Hot Birds Research Project (HBRP; the on-site weather station, green crosses), Twee Rivieren (red circles, ~120 kms from the study site), and Van Zylsrus (blue triangles, ~30 km from the study site) weather station data. A significant increase in T_{max} (±3.5 SE years) and cumulative DaysT_{thresh} (±4.1 SE years) starting in ~1996-1997 was identified using segmented analysis for the TR weather station. (D) Bar plot for cumulative rainfall from the VZ weather station (data from TR between 2009 – 2012 included where VZ rainfall data were unavailable) with dotted line showing the threshold for drought (grey bars) versus non-drought (clear bars) years.

5.4.2 Long-term breeding trends

The percentage of nest boxes used (r = -0.80, p = 0.005) and the percentage of nesting attempts which succeeded (r = -0.73, p = 0.017) per season declined over the course of the monitoring period (Table 5.1; Figure 5.2). There was a marginally non-significant decline in the mean number of fledglings produced per breeding pair per season (r = -0.63, p = 0.051, Table 5.1). I found no evidence of temporal autocorrelation in the number or percentage of nest boxes used, percentage of nesting attempts which succeeded, or the mean fledglings per attempt, modelled by breeding season.

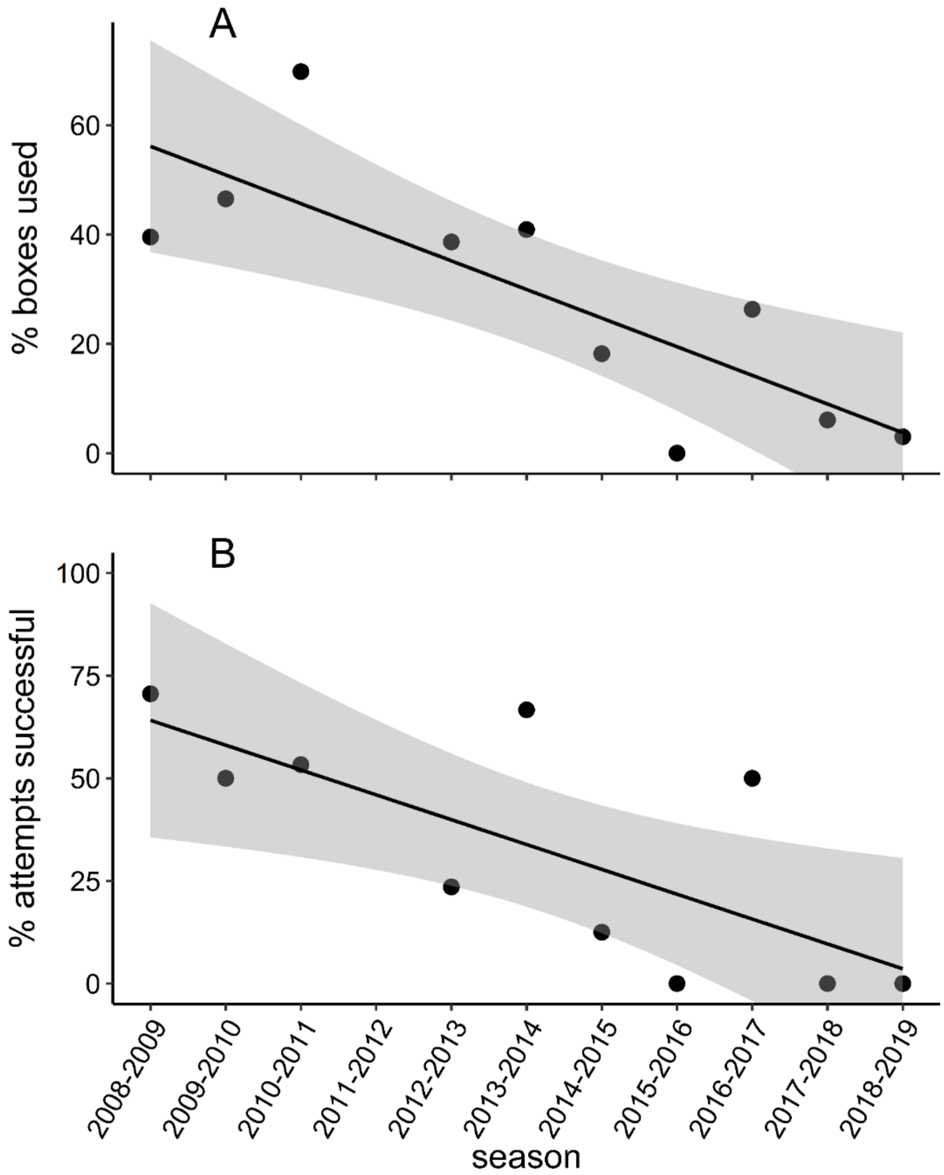

Figure 5.2. (A) The percentage of available nest boxes occupied and (B) the percentage of breeding attempts which succeeded per season in my study population of Southern Yellow-billed Hornbills (*Tockus leucomelas*) between 2008 and 2019. Both trends are significant ($p < 0.05$); 95% confidence intervals (CI) are shown.

The percentage of boxes used ($r = -0.88$, $p < 0.001$), percentage of attempts that succeeded ($r = -0.90$, $p < 0.001$), and mean fledglings per attempt ($r = -0.78$, $p = 0.008$), all declined significantly with increasing cumulative $\mathrm{DaysT}_{\mathrm{thresh}}$ and were all significantly higher in non-drought seasons compared to drought seasons ($p = 0.014$, $p \leq 0.001$, & $p = 0.005$, respectively; Table 5.1; Figure 5.3). However, neither percentage of boxes used ($r = -0.43$, $p = 0.220$; $r = 0.27$, $p = 0.451$), percentage of attempts that succeeded ($r = -0.59$, $p = 0.075$; $r = 0.15$, $p = 0.670$), nor mean fledglings produced per attempt ($r = -0.56$, $p = 0.092$; $r = 0.22$, $p = 0.537$) were significantly related to the cumulative two months' rainfall preceding the start of the breeding season or the T_{min} of the preceding non-breeding season, respectively (Table 5.1).

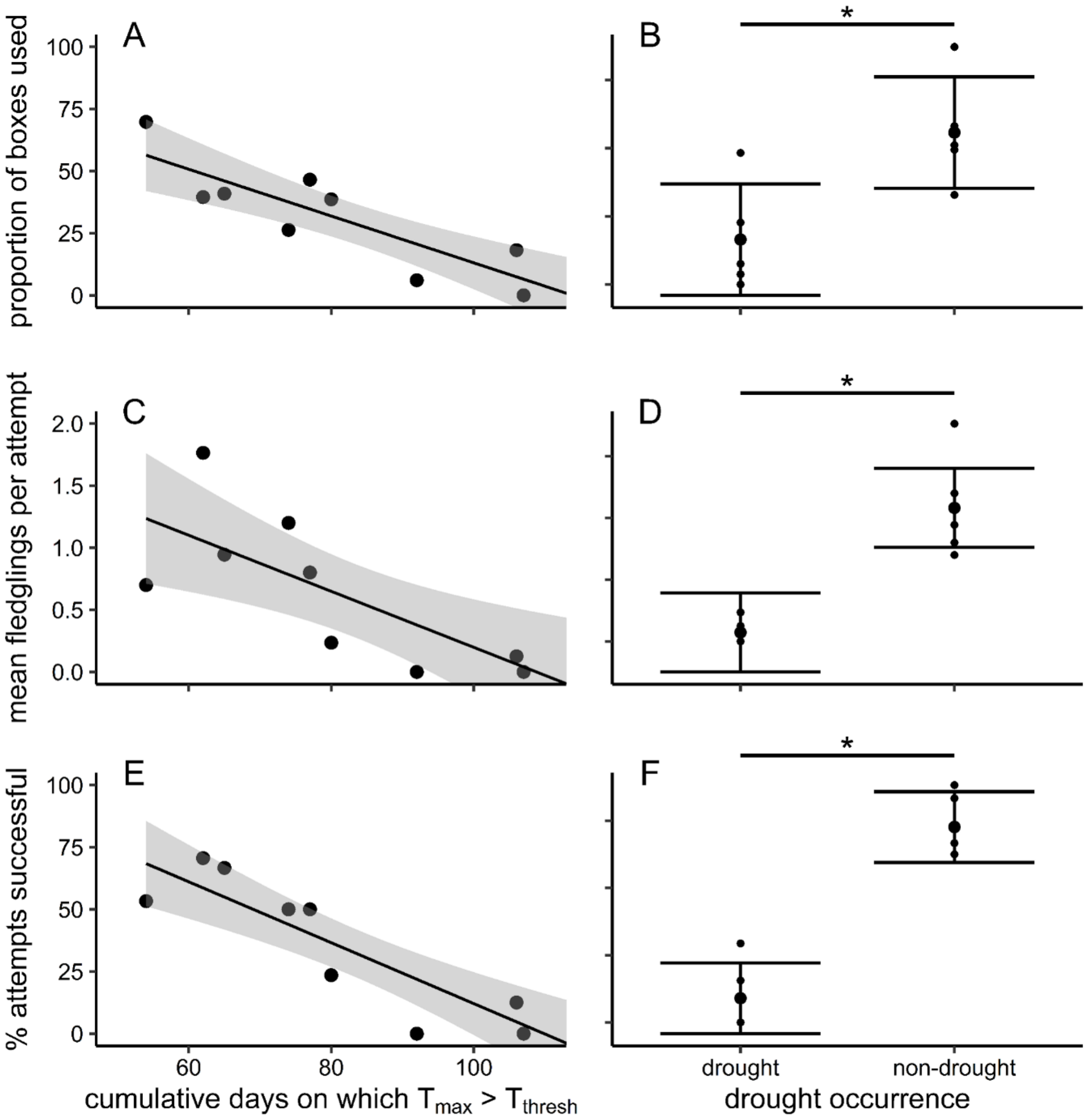

Figure 5.3. (A & B) The percentage of boxes used, (C & D) mean fledglings per attempt, and (E & F) percentage of attempts that succeeded in Southern Yellow-billed Hornbills (*Tockus leucomelas*) as functions of the cumulative DaysT_{thresh} (days on which T_{max} [mean maximum daily air temperature [T_{air}]] > T_{thresh} [T_{air} = 34.5 °C]), and occurrence of drought across the breeding season. All trends are significant ($p < 0.05$), 95% confidence intervals (CI) and means with upper and lower quartiles are shown.

Table 5.1. Pearson's correlation test results for the percentage of boxes used, percentage of attempts fledging at least one chick, and mean fledglings per attempt per season in Southern Yellow-billed Hornbills (*Tockus leucomelas*), correlated with the cumulative DaysT$_{\text{thresh}}$ (days on which T$_{\text{max}}$ [mean maximum daily air temperature [T$_{\text{air}}$]] > T$_{\text{thresh}}$ [T$_{\text{air}}$ = 34.5 °C]) within the breeding season (19 October – 24 March), T$_{\text{min}}$ (mean minimum daily T$_{\text{air}}$), and cumulative rainfall within the two months prior to the start of the breeding season (18 August – 18 October each year). Welch Two Sample t-test results for the same three response variables as function of drought occurrence over the breeding season are also shown. Rows for independent variables with a significant effect are in bold.

Response variable	Independent variables	Pearsons corr. R	t	df	p ≤	Lower 95% CI	Upper 95% CI
% boxes used	**season**	**-0.80**	**-3.82**	**8**	**0.005**	**-0.95**	**-0.35**
	cumulative DaysT$_{\text{thresh}}$	**-0.88**	**-5.32**	**8**	**0.001**	**-0.97**	**-0.57**
	preceding two months' cumulative rainfall	-0.43	-1.33	8	0.220	-0.83	0.28
	drought occurrence		**-3.13**	**8**	**0.014**	**-54.56**	**-8.30**
	T$_{\text{min}}$ (non-breeding season)	0.27	0.79	8	0.451	-0.43	0.77
% success	**season**	**-0.73**	**-3.00**	**8**	**0.017**	**-0.93**	**-0.18**
	cumulative DaysT$_{\text{thresh}}$	**-0.90**	**-5.81**	**8**	**0.001**	**-0.98**	**-0.62**
	preceding two months'	-0.59	-2.05	8	0.075	-0.89	0.07

	cumulative rainfall						
	drought occurrence		**-7.89**	**8**	**0.000**	**-65.82**	**-36.01**
	T_{min} (non-breeding season)	0.15	0.44	8	0.670	-0.53	0.71
mean fledglings per attempt	season	-0.63	-2.29	8	0.051	-0.90	0.00
	cumulative DaysT_{thresh}	**-0.78**	**-3.50**	**8**	**0.008**	**-0.94**	**-0.29**
	preceding two months' cumulative rainfall	-0.56	-1.92	8	0.092	-0.88	0.11
	drought occurrence		**-5.15**	**8**	**0.005**	**-1.53**	**-0.49**
	T_{min} (non-breeding season)	0.22	0.65	8	0.537	-0.47	0.75

5.4.3 Individual breeding attempts

One best-performing model was identified for variation in breeding success (model weight 0.96, Table S5.2). This model indicated that probability of success was negatively correlated with later female entry dates (estimate -1.10 ± 0.41; $p = 0.007$; Table 5.2, Figure 5.4). Additionally, there was a significant interaction between percentage $\text{DaysT}_{\text{thresh}}$ during the attempt and drought occurrence on breeding success (estimate -2.65 ± 1.04; $p = 0.011$, Table 5.2). Post-hoc models of breeding success in drought and non-drought years revealed a significant negative correlation between the percentage $\text{DaysT}_{\text{thresh}}$ during the attempt and breeding success in non-drought seasons (estimate -1.87 ± 0.65; $p = 0.004$), but not in drought seasons (estimate -0.20 ± 0.67; $p = 0.771$, Table 5.2; Figure 5.4). In drought seasons, breeding success was uniformly low; only four of 23 (17.4%) attempts succeeded in fledging at least one chick, compared to 40 of 65 (61.5%) in non-drought seasons. Of the 115 breeding attempts I recorded, all 18 attempts which experienced ≥ 72% days on which $T_{\text{max}} > T_{\text{thresh}}$ (corresponding to T_{max} during the attempt ≥ 35.7°C) failed (Figure 5.4). Based on current warming trends of 1 °C per decade (Figure 5.1), this T_{max} threshold of 35.7 °C will be exceeded over the course of the entire breeding season by approximately 2027 at my study site.

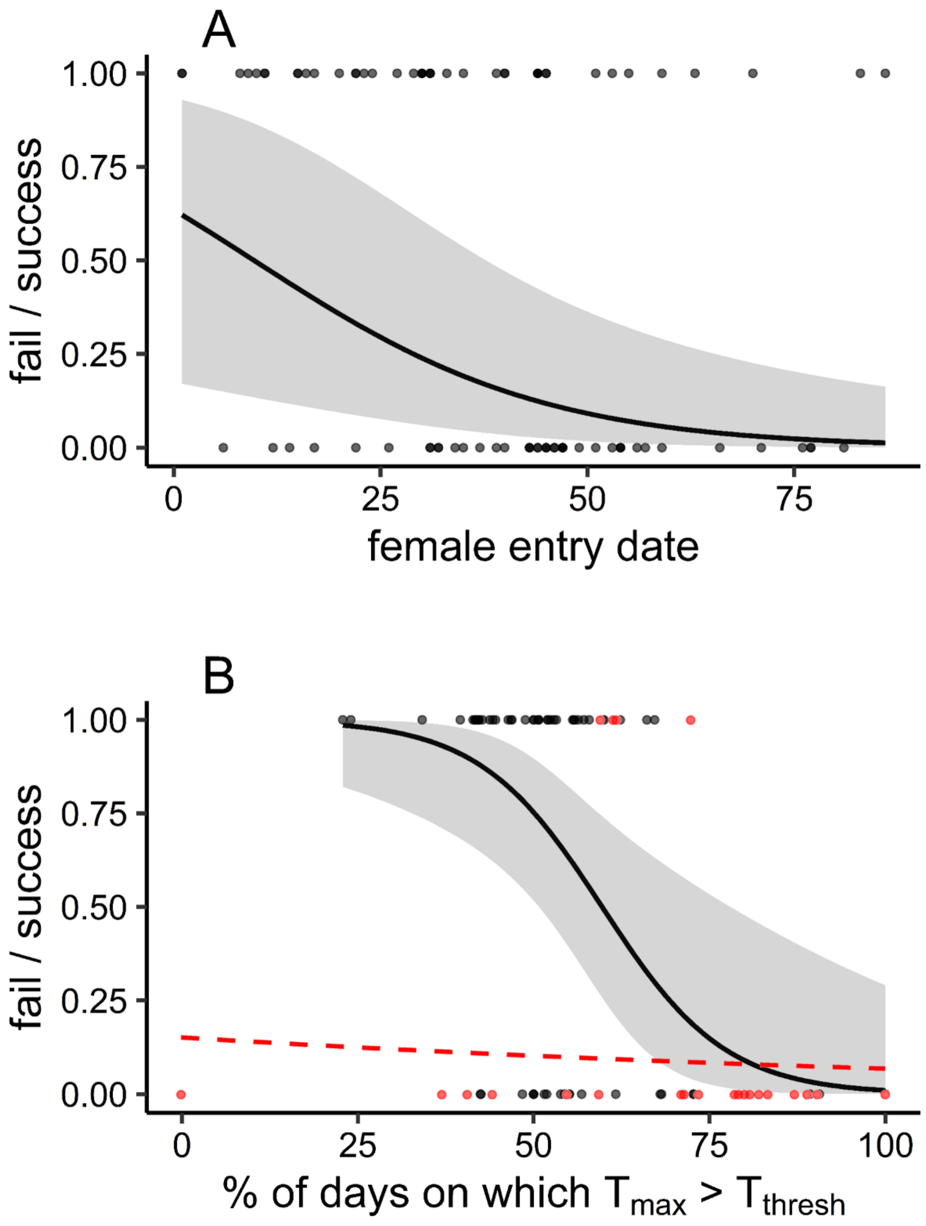

Figure 5.4. The binomial probability of breeding attempt success [0 = fail, 1 = successfully fledging at least one chick)] by Southern Yellow-billed Hornbills (*Tockus leucomelas*) as a function of (A) the female entry date (days since start of season – 19 October), and (B) the percentage DaysT_{thresh} (days during the attempt on which T_{max} [mean maximum daily air temperature [T_{air}]] > T_{thresh} [T_{air} = 34.5 °C]) for drought seasons (red dashed line; not significant) and non-drought seasons (solid black line; significant). The 95% confidence intervals (CI) are shown for significant effects.

One top model was identified for the probability of a breeding attempt successfully progressing from female entry to hatch (model weight 0.66, Table S5.2), with nests significantly less likely to progress to hatching when females entered the nest later (estimate -1.24 ± 0.44; p = 0.005, Table 5.2). The interaction between the percentage DaysT$_{\text{thresh}}$ during the attempt and drought occurrence was significant (estimate -1.55 ± 0.77; p = 0.005, Table 5.2); the probability of a breeding attempt successfully progressing from female entry to hatch declined significantly with increasing percentage DaysT$_{\text{thresh}}$ during the pre-hatch period within non-drought seasons (estimate -1.22 ± 0.00; p = 0.013), but not within drought seasons (estimate -0.91 ± 0.97; p = 0.310; Table 5.2) where successful hatches were low; 15 out of 23 (65.2%) attempts hatched in drought seasons, compared to 56 out of 65 (86.2%) in non-drought seasons.

Four top models were identified for breeding attempt success during the nestling period (model weights 0.30, 0.20, 0.13, & 0.11 respectively; Table S5.2). The model average of these four top models revealed that survival during the nestling period was positively correlated with an increased number of days post-hatch spent in the nest by the female (estimate 1.08 ± 0.38; p = 0.005), and negatively correlated with an increased percentage DaysT$_{\text{thresh}}$ during the nestling period (estimate -0.86 ± 0.37; p = 0.021; Table 5.2; Figure 5.5). The effect of drought occurrence on survival during the nestling period was not significant in the model averaged estimates (estimate 0.71 ± 0.92; p = 0.444, Table 5.2), although four of 15 chicks (26.7%) which hatched in drought seasons fledged, compared to 40 of 56 chicks (71.4%) in non-drought seasons (Figure 5.5).

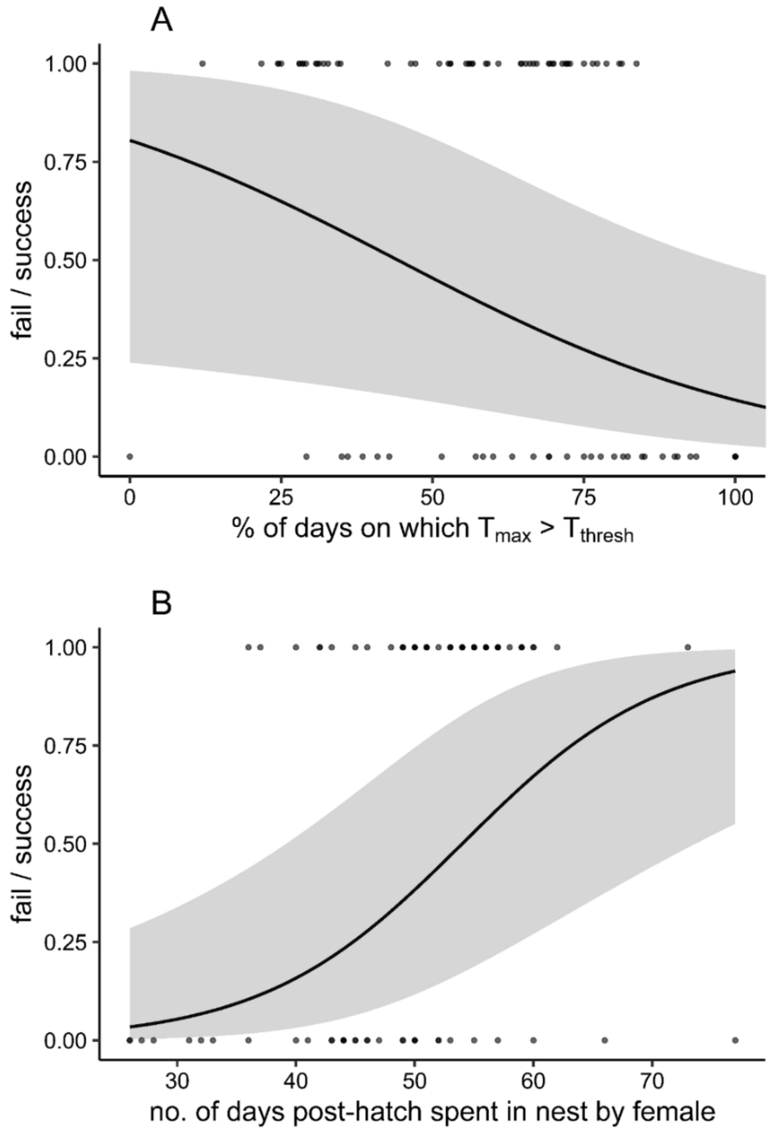

Figure 5.5. The binomial probability of success (0 = fail, 1 = success [fledging at least one chick]) for Southern Yellow-billed Hornbills (*Tockus leucomelas*) nests which hatched at least one chick as a function of (A) the percentage DaysT$_{thresh}$ (days on which T$_{max}$ (mean maximum daily air temperature [T$_{air}$]) > T$_{thresh}$ [T$_{air}$ = 34.5 °C]), and (B) the number of days post-hatch spent in the nest by the female during the period from hatch to success / fail. Both relationships were significant, 95% confidence intervals (CI) are shown.

Two top models were identified for the effect of drought occurrence on female entry date, including the null model (model weights 0.56, 0.44 respectively; Table S5.2), and on the number of days post-hatch spent in the nest by the female, also including the null model (model weights 0.55, 0.45 respectively; Table S5.2). Model averages indicated that drought occurrence did not significantly affect female entry date (estimate -0.07 ± 0.11; p = 0.552), or the number of days post-hatch spent in the nest by the female (estimate -0.03 ± 0.05; p = 0.550) for breeding attempts which hatched at least one chick (Table 5.2).

Table 5.2. Bayesian generalised linear mixed model (BGLMer) of the outcomes of different stages (entire breeding attempt [n = 88], nest survival from female entry until hatch / fail [‘pre-hatch period’; n = 88], and nest survival from hatch until fledge / fail [‘nestling period’; n = 88]) of individual breeding attempts in Southern Yellow-billed Hornbills (*Tockus leucomelas*) as functions of female entry date, percentage $\text{DaysT}_{\text{thresh}}$ (days during the attempt on which T_{max} [mean maximum daily air temperature [T_{air}]] > T_{thresh} [T_{air} = 34.5 °C]), drought occurrence over the breeding season (19 October – 24 March), and the interaction between $\text{DaysT}_{\text{thresh}}$ and drought occurrence. Survival in the nestling period was also modelled as a function of the number of days post-hatch spent in the nest by the female. BGLMer outcomes for female entry date and the number of days post-hatch spent in the nest by the female modelled as functions of drought occurrence also shown. Model outputs are for the single top model, or model averages when there was more than one competing model within 2 ΔAICc (see column ‘Number of top models’). All models contain the random factor ‘season’. For categorical variable “Drought occurrence (drought/non-drought)”, “drought” is set as the intercept. Rows in italics show post-hoc investigations of significant interactions between % $\text{DaysT}_{\text{thresh}}$ and drought occurrence. Rows for independent variables with a significant effect are in bold.

Response variable	Model family	Number of top models	Independent variables	Estimate ± SE (Adj SE for model averaged estimates)	Test statistic (z or t)	df	p ≤	Lower 95% CI	Upper 95% CI
success (1) or failure (0) of the entire breeding	Binomial	1	**female entry date**	**-1.10 ± 0.41**	**-2.72**	**86**	**0.007**	**-1.90**	**-0.31**
			% $\text{DaysT}_{\text{thresh}}$	-0.01 ± 0.58	-0.02	86	0.983	-1.15	1.12

attempt			drought occurrence (non-drought)	1.54 ± 0.94	1.63	86	0.103	-0.31	3.39
			% DaysT_{thresh} * drought occurrence	**-2.65 ± 1.04**	**-2.54**	**86**	**0.011**	**-4.69**	**-0.61**
			% DaysT_{thresh} (drought seasons)	*-0.20 ± 0.67*	*-0.29*	*21*	*0.771*	*-1.50*	*1.11*
			% DaysT_{thresh} (non-drought seasons)	***-1.87 ± 0.65***	***-2.90***	***63***	***0.004***	***-3.14***	***-0.61***
survival (1) or failure (0) during the pre-hatch period	Binomial	1	**female entry date**	**-1.24 ± 0.44**	**-2.81**	**86**	**0.005**	**-2.10**	**-0.37**
			% DaysT_{thresh}	0.16 ± 0.52	0.32	86	0.751	-0.55	6.49
			drought occurrence (non-drought)	2.97 ± 1.80	1.66	86	0.098	-0.85	1.17
			% DaysT_{thresh} * drought occurrence	**-1.55 ± 0.77**	**-2.00**	**86**	**0.045**	**-3.07**	**-0.03**
			% DaysT_{thresh} (drought seasons)	*-0.91 ± 0.90*	*-1.02*	*21*	*0.310*	*-2.67*	*0.85*
			% DaysT_{thresh} (non-	***-1.22 ±***	***-2.48***	***63***	***0.001***	***-2.160***	***-0.251***

			drought seasons)	***0.00***					
survival (1) or failure (0) during the nestling period	Binomial	4	female entry date	-0.11 ± 0.27	0.39	86	0.696	-1.09	0.44
			% DaysT$_{thresh}$	**-0.86 ± 0.37**	**2.30**	**86**	**0.021**	**-1.59**	**-0.13**
			drought occurrence (non-drought)	0.71 ± 0.92	0.77	86	0.444	-0.49	3.04
			days post-hatch spent in the nest by female	**1.08 ± 0.38**	**2.82**	**86**	**0.005**	**0.33**	**1.83**
female entry date	Poisson	2	drought occurrence (non-drought)	-0.07 ± 0.11	0.59	86	0.552	-0.41	0.10
days post-hatch spent in the nest by female	Poisson	2	drought occurrence (non-drought)	0.03 ± 0.05	0.60	86	0.550	-0.05	0.19

5.4.4 Thermal conditions in nest boxes versus natural cavities

One top model was identified for T_{nest}, indicating that T_{nest} inside both nest boxes and natural cavities showed a significant positive relationship with outside T_{air} (estimate 1.03 ± 0.00; p = 0.001), but that there was a significant interaction between T_{air} and type of nest (estimate -0.49 ± 0.00; p = 0.001; Table S5.3 & S5.4). The slope of the relationship between T_{nest} and T_{air} was 0.55 T_{nest} °C.T_{air}^{-1} for natural cavities (estimate 0.55 ± 0.00; p = 0.001), compared to 1.03 T_{nest} °C.T_{air}^{-1} for nest boxes (estimate 1.03 ± 0.00; p = 0.001), suggesting that T_{nest} within natural cavities was buffered against T_{air}, while T_{nest} within nest boxes tracked T_{air} (Table S5.4; Figure 5.6). The difference between T_{nest} within nest boxes and natural cavities was most pronounced at higher T_{air}; at $T_{air} > T_{thresh}$ the mean T_{nest} within nest boxes was 39.65 °C ± 3.23 SD, while the mean T_{nest} within natural cavities was 34.91 °C ± 3.68 SD (Figure 5.6).

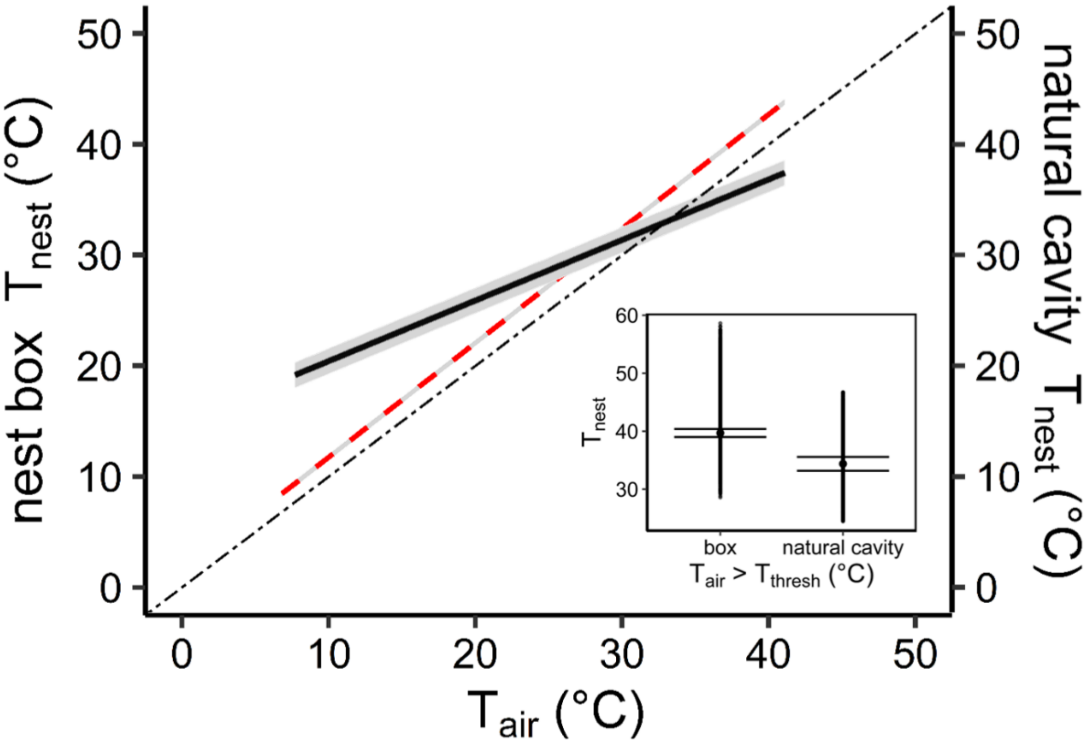

Figure 5.6. Air temperature (T_{air}) within nest boxes (n = 27, red dashed line) and natural cavities (n = 9, solid black line) as a function of T_{air}. Nest temperature (T_{nest}) measured using Thermochron iButtons during Southern Yellow-billed Hornbills (*Tockus leucomelas*) breeding seasons (19 October – 24 March) between 2012 and 2015. T_{nest} within both nest boxes and natural cavities showed a significant positive relationship with T_{air}, but with significantly different slopes. 95% confidence intervals (CI) and 1:1 relationship (two-dash black line) shown. Inset box plot of mean and upper and lower quartiles of T_{nest} within nest boxes and natural cavities at $T_{air} > T_{thresh}$ (T_{air} = 34.5 °C].

5.5 Discussion

The negative impacts of extreme weather events and a rapidly warming climate on survival and reproduction are being recorded worldwide across multiple taxa (Moreno and Møller 2011, Cunningham et al. 2021). Intensive monitoring allowed us to quantify breeding performance of my study population of hornbills over the course of a decade. Breeding effort and performance of hornbills collapsed over the course of my monitoring period, correlating to rapid climate warming in the region. Comparing the first three seasons (2008 – 2011) of monitoring to the last three (2016 – 2019), the percentage of boxes occupied declined from an average of 52% to 12%, the percentage of breeding attempts which succeeded from 58% to 17%, and the mean fledglings produced per attempt from 1.1 to 0.4. Breeding effort and performance were negatively correlated with both extrinsic (higher T_{air} and the occurrence of drought within the breeding season), and intrinsic (later dates of entry into the nest cavity and shorter time periods spent in the nest post-hatch by the female parent) factors. Given the severe negative effects of high T_{air} on both adult condition (van de Ven et al. 2019) and breeding success (van de Ven et al. 2020b, this study) in this population of hornbills, I argue that rapid warming has likely been the primary driver of their recent collapse in breeding success.

5.5.1 Climate and hornbill breeding

The decline in the percentage of nest boxes used over the decade of monitoring could be a result of fewer potential breeding pairs in the study population as the monitoring period progressed (e.g., Rioux Paquette et al. 2014, Cruz-McDonnell and Wolf 2016). However, the number of pairs present was continuously estimated to be around 20 – 25 each year, and in the majority of years since 2012 pairs were seen inspecting nest boxes between October and March, but failed to ultimately breed (N. Pattinson, T. van de Ven unpublished data). Moreover, there was a significant link between higher seasonal T_{air} and reduced nest box occupancy. Therefore, the declining breeding effort likely reflects an increasing number of resident pairs skipping breeding in response to increasingly challenging environmental conditions (i.e., higher T_{air} during the summer breeding season); skipping breeding is common in another southern African bucerotiforme, the Southern Ground-hornbill (*Bucorvus leadbeateri*; Carstens et al. 2019), and is suspected to occur in response to poor breeding conditions in various avian, mammalian, and amphibian taxa (e.g., Pietiainen 1989, Pilastro et al. 2003, Kinkead and Otis 2007, Keynan and Yosef 2010, Cayuela et al. 2014, Griffen 2018). Nesting hornbills experience low rates of predation because the birds seal up the entrance of the nest, leaving only a tiny slit through which food can be passed from the male to the female and chicks inside (Moreau and Moreau 1941), so changes in predation rates with T_{air} or drought are unlikely responsible for variation in breeding performance.

Nest boxes were less buffered against changes in T_{air} compared to natural cavities. My findings may therefore represent a more severe response to high T_{air} than would be evident in birds breeding in natural cavities, especially given the strong effect of T_{nest} on fledging condition (van de Ven et al. 2020b). However, the T_{air} recorded at my field site was consistently lower than that recorded by weather stations in surrounding areas, suggesting that the trends measured are likely at least indicative of what is happening to populations of hornbills breeding in natural cavities in the hottest parts of their range. Moreover, variation in nest success is also driven by the effects of T_{air} on the provisioning behaviour of the parents (van de Ven et al. 2019, van de Ven et al. 2020b) and drought – effects independent of nest type.

Inter-annual and within-season declines in breeding success were strongly associated with both high temperatures and drought. Of the 115 breeding attempts I recorded, none were successful when T_{max} exceeded T_{thresh} ≥ 72 % or more days during an attempt. The hottest period during which an attempt was successful involved 55 of 76 days (72 %) with $T_{max} > T_{thresh}$, but all 18 attempts during hotter conditions failed, indicating the potential for precipitous decline in breeding success at high T_{air}. Additionally, significantly more breeding attempts succeeded (fledged at least one chick) in non-drought seasons (61.5%) compared to during droughts (17.4%). The near ubiquitous nest failure across a range of T_{air} in drought years presumably occurred because low rainfall leads to low food abundance in arid and semi-arid systems, since rainfall drives primary productivity and the energy available through the entire trophic cascade (Mares et al. 2017, Carstens et al. 2019). These results suggest breeding performance in this population of hornbill is susceptible to both low rainfall and high T_{air}

independently, compared to studies suggesting vulnerability only when low rainfall and high T_{air} co-occur (Flesch 2014, Cruz-McDonnell and Wolf 2016, Iknayan and Beissinger 2018, Bourne et al. 2020c). Although my models did not indicate a statistically significant effect of drought during the nestling period, the much lower percent of nestlings which fledged in drought (26.7%, n = 4 out of 15) compared to non-drought (71.4%, n = 40 out of 56) seasons suggested that drought was associated with reduced nest success during both pre-hatch and nestling periods. Indeed, the low number of chicks which hatch or fledge in drought seasons creates a limited sample size for analyses, likely reducing power to statistically demonstrate the effect of drought.

Variation in breeding success within breeding seasons was also correlated with intrinsic factors including female entry date (when the female sealed herself in the nest box) and the number of days post-hatch the female was incarcerated in the nest. Later female entry date and fewer days post-hatch spent incarcerated by the female both correlated with lower breeding success. Delayed nest initiation is associated with drought and low resource availability in some species (McCreedy and van Riper III 2015, Carstens et al. 2019). However, rainfall in the two months preceding the breeding season had no significant effect on seasonal breeding output, and neither female entry dates nor the number of days post-hatch spent in the nest by the female parents were significantly related to the occurrence or absence of drought, suggesting that their effects were likely not artefacts of rainfall and food availability (Harriman et al. 2017). Rather, I suspect that lower quality parents delay the onset of breeding and / or that lower quality females cannot stay incarcerated for extended periods. Fewer stored body reserves in either parent may preclude early breeding or the ability to sustain continuous mass loss during the breeding attempt (van de Ven et al. 2020b). This pattern reflects widespread interactions between the timing of breeding and the quality of the parents (for review, see Verhulst and Nilsson 2008), and supports the well-established concept of earlier breeding and higher parental quality positively affecting reproductive performance (Moreno et al. 2005, Verhulst and Nilsson 2008, de Zwaan et al. 2019).

My analyses of T_{air} and rainfall trends in the southern Kalahari revealed trends consistent with those reported in recent studies (Kruger and Sekele 2013, van Wilgen et al. 2016, Mbokodo et al. 2020); the T_{max} and $DaysT_{thresh}$ during the breeding season of the hornbills have increased by more than 1.0 °C and almost 20 days per decade, respectively, over the last ~25 years, whereas no long-term trend in rainfall / drought recurrence was apparent. This trend indicates that hornbills face severe challenges to their persistence across the seasonally hot, arid parts of their range. The negative effects of high temperatures will increasingly cause reduced breeding success even in non-drought years as global warming advances. Therefore, while the magnitude of population decline is limited by the severity of droughts and heat waves, population recovery and persistence will be limited by a decreasing capacity of the hornbills to breed successfully in non-drought seasons due to increased mean T_{air} (Williams et al. 2016, Albright et al. 2017, Palmer et al. 2017, Conradie et al. 2019). Based on 1) the rapid rate of warming, 2) the fact that no breeding attempts succeeded if ≥ 72% days during the attempt had $T_{max} > T_{thresh}$ (corresponding to a T_{max} during the attempt ≥ 35.7°C, a threshold which will be exceeded across the entire breeding season by ~ 2027 at my study site under current warming trends), and 3) eight years is the longest a wild, colour-ringed hornbill has survived in my study population, I arrive at the grim prediction that this population of hornbills could be extirpated by 2040. Moreover, model predictions suggest that the majority of the hornbill's range will approach the T_{air} threshold above which breeding success is <50% by the turn of the century (Conradie et al. 2019).

5.5.2 Conclusions

Many birds in seasonally hot, summer rainfall, arid zones are constrained to breed in response to, or to coincide with rainfall, making it difficult for them to shift breeding dates outside of the hottest periods of the year when these correspond with the rainfall season (Wolf 2000, McCreedy and van Riper III 2015, Mares et al. 2017, Iknayan and Beissinger 2018, van de Ven et al. 2020b). Therefore, even small increases in summer maximum T_{air} could drive large consequences during breeding (Sinervo et al. 2010, Alagaili et al. 2017, Albright et al. 2017, Riddell et al. 2019, McKechnie et al. 2021b). Moreover, an increase in the frequency and severity of sub-lethal, sub-optimal conditions which reduce parental quality may also reduce fledgling condition, generally resulting in lower survival probability, recruitment, and lifetime fecundity (Dawson et al. 2005, Gardner et al. 2016, de Zwaan et al. 2019, Bourne et al. 2020c, b, Cunningham et al. 2021) (but see McLean et al. 2020). In the case of hornbills, there is evidence that the sub-lethal consequences of high T_{air} (regardless of high rainfall) and drought on the parents affect offspring quality (van de Ven et al. 2020b), and in this study, the probability of successfully fledging offspring or even attempting to breed at all. While the unusual breeding strategy of the hornbills could make them especially vulnerable, high temperatures and drought have negative impacts on breeding output in a variety of taxa across the globe (Welbergen et al. 2008, Sinervo et al. 2010, Gardner et al. 2014a, Andreasson et al. 2020, van de Ven et al. 2020a, Cunningham et al. 2021). Therefore, I suggest that my findings are likely applicable to a range of species, and support the proposition that even for species for which catastrophic heat-related mortality events remain unlikely, climate change can drive rapid declines and potentially local extinctions (Conradie et al. 2019, McKechnie and Wolf 2019, McKechnie et al. 2021b). Indeed, both Iknayan and Beissinger (2018) and Riddell et al. (2019) recently demonstrated that this extirpation process in arid zones is already taking place, and is set to continue under future climate change.

5.5.3 Thesis context

Analysis of variation in breeding success over a decade period indicated that climate warming causing increasingly negative effects of high temperatures (T_{air} and T_{nest}) was the primary cause of the collapse in breeding success. That pattern was partially supported by the negative effects of high T_{air} on male breeding behaviour shown in Chapter 2, reiterating those demonstrated by van de Ven et al. (2019). However, it was strongly contrasted by the findings in Chapter 3, where T_{nest} (and by association T_{air}, see Figure 3.1) had no significant effects on breeding success. The contrast highlighted the importance of the nest box design and its effect on nest microclimate to the hornbills' breeding ecology. Approximately 70% of variation in breeding success was driven by T_{nest} in van de Ven et al. (2020b) study, which used the same nest boxes to inform that conclusion as were used in this chapter. Through insulating and painting the nest boxes, T_{nest} were greatly reduced (maximum >10 °C and average 3.99 °C below those of van de Ven et al. 2020) for the 2019/2020 and 2020/2021 breeding seasons (see Chapter 3). The T_{nest} reduction removed T_{nest} effects on female parent morphology and breeding success (see Chapter 3), and reduced T_{nest} effects on chicks (see Chapter 4). Overall, this suggested that the temperature effects found in this chapter as well as by van de Ven et al. (2020b) may have been exaggerated by unnaturally high T_{nest}, inflated well-above T_{air} and above natural cavity T_{nest}. Moreover, it highlighted the importance of nest box design for conservation purposes, where poor design may create an ecological trap (Larson et al. 2015, Griffiths et al. 2017, Larson et al. 2018, Briggs and Mainwaring 2021, Goldingay and Thomas 2021).

The long-term dataset in this chapter also shows a pronounced negative effect of drought on breeding success. Seasons with drought exhibited near ubiquitous breeding failure (see Figure 5.3), a trend supported by the poorer reproductive success in the near-drought breeding season (2019/2020) compared to the high rainfall season (2020/2021), documented in Chapter 3. Collectively, this suggests that rainfall and the associated resource availability or quality are strong drivers of reproductive success, as shown in various other arid-zone species (e.g., Bolger et al. 2005, Gardner et al. 2016, Mares et al. 2017, Iknayan and Beissinger 2018, Bourne et al. 2020a, c, Riddell et al. 2021). The lack of any significant effects of supplementary food on provisioning rate (see Chapter 2) or breeding success (see Chapter 3) suggests resource availability was not the primary driver of breeding season differences. Rather, the differences in breeding success between breeding seasons could be driven by differences in natural resource quality (Kadin et al. 2012, Coogan et al. 2018), although I did not have the data to test this possibility.

Notably, this chapter shows that breeding success in the hornbills is highly dependent on the birds actually attempting to breed. The percentage of nest boxes used declined with increasing T_{max} and in drought seasons (see Figure 5.3). The negative effects of high temperatures may have been independent of the nest box effects on T_{nest} (unless hotter nest boxes perturbed pairs from using them). If they were independent and higher T_{air} caused pairs to skip breeding, it would indicate a severe negative effect of increasing T_{air} on hornbill breeding success regardless of the thermal qualities of available nesting sites. The negative correlation between percentage of nest boxes used and drought occurrence may also indicate that poor resource availability or quality affects the decision to breed (Reichert et al. 2012, Martin and Mouton 2020). This was not tested by the supplementary feeding experiment in Chapters 2 - 4, which was only conducted on pairs which attempted to breed. This leaves scope for testing whether resource availability or quality affects the decision to breed, as well as if food availability or quality prior to breeding has any carry-over effects on the breeding attempt (Reed et al. 2015).

5.6 Supplementary materials

5.6.1 Results

5.6.1.1 Long-term weather trends

For the period over which data for all three weather stations (Hot Birds Research Project [HBRP], Twee Rivieren [TR], and Van Zylsrus [VZ]) overlapped (2011 – 2020), T_{max} (mean maximum daily air temperature [T_{air}]) from all three weather stations (Lin’s correlation coefficient: VZ~TR, *rho.c* = 0.94, r^2 = 0.89; HBRP~VZ, *rho.c* = 0.94, r^2 = 0.94; HBRP~TR = 0.90, r^2 = 0.92) and T_{min} (mean minimum daily T_{air}) between all three regions (VZ~TR, *rho.c* = 0.95, r^2 = 0.90; HBRP~VZ, *rho.c* = 0.96, r^2 = 0.93; HBRP~TR = 0.94, r^2 = 0.89) were highly correlated (Figure S5.1).

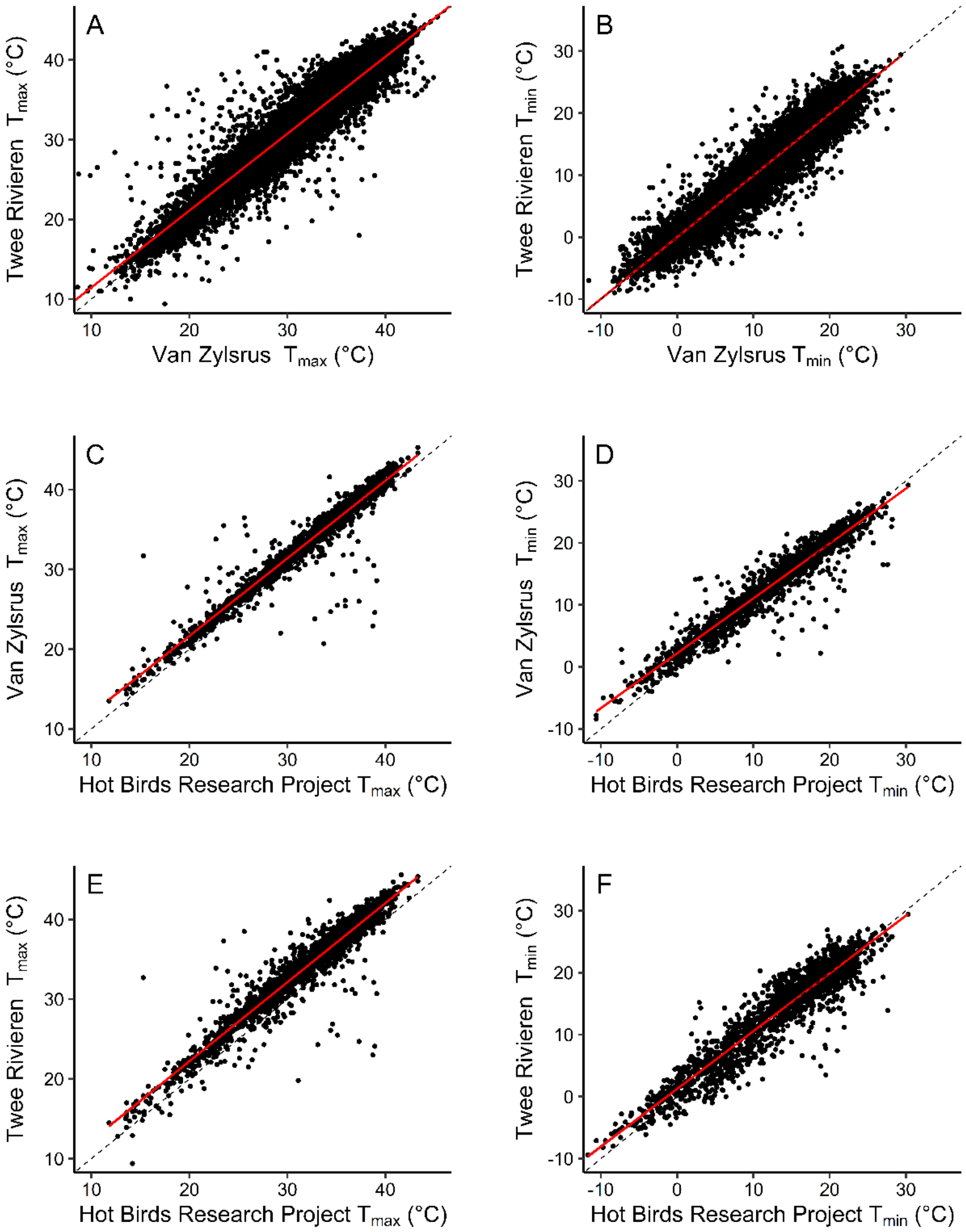

Figure S5.1. Correlation between (A, C, & E) T_{max} (mean maximum daily air temperature [T_{air}]) and (B, D, & F) T_{min} (mean minimum daily T_{air}) for the Hot Birds Research Project (HBRP; the on-site weather station), Twee Rivieren (~120 kms from the study site), and Van Zylsrus (~30 km from the study site) weather stations between 2011 – 2020. Dotted line represents 1:1 relationship.

The T_{max} data from VZ and TR was systematically higher than those from the HBRP (VZ mean 1.38 °C ± 1.54 SD higher; TR, mean 2.13 °C ± 1.79 SD higher; Figure S5.1). To create a single long-term weather dataset for use in further analyses, these values had to be adjusted. VZ and TR T_{max} data were therefore adjusted down by the mean difference between them and the HBRP data. The adjusted values then fell along the 1:1 ratio line, resulting in Lin's correlation coefficients *rho.c* = 0.99 for all three correlations (Figure S5.2).

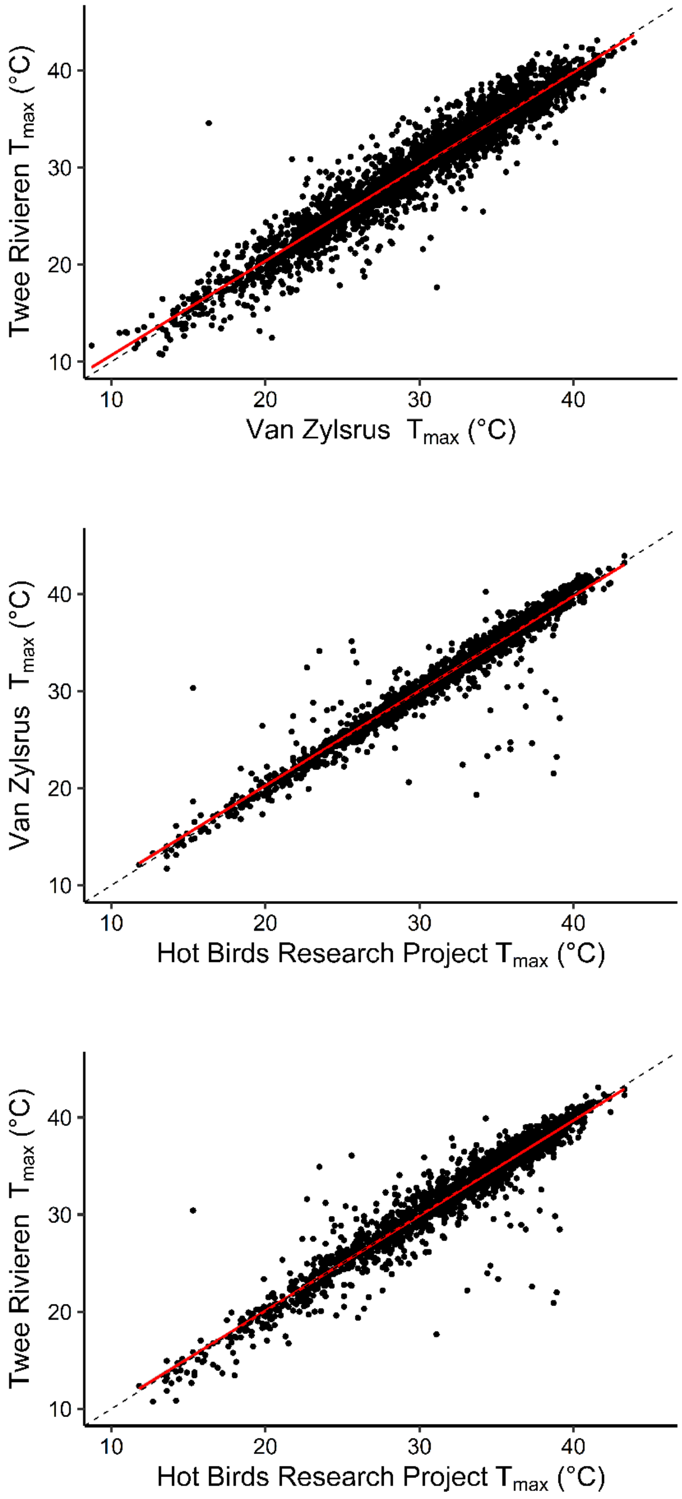

Figure S5.2. Correlation between T_{max} (mean maximum daily air temperature [T_{air}]) data from the Hot Birds Research Project (HBRP; the on-site weather station), Twee Rivieren (~120 kms from the study site), and Van Zylsrus (~30 km from the study site) weather stations between 2011 – 2020. Dotted line represents 1:1 relationship.

Daily rainfall was not correlated between the three weather stations (VZ~TR, *rho.c* = 0.19, r^2 = 0.03; HBRP~VZ, *rho.c* = 0.52, r^2 = 0. 30; HBRP~TR = 0.36, r^2 = 0.14), however, breeding season (19 October – 24 March) rainfall was highly correlated between the HBRP and the VZ (*rho.c* = 0.66, r^2 = 0.97) and TR (*rho.c* = 0.78, r^2 = 0.86) weather stations (Figure S5.3).

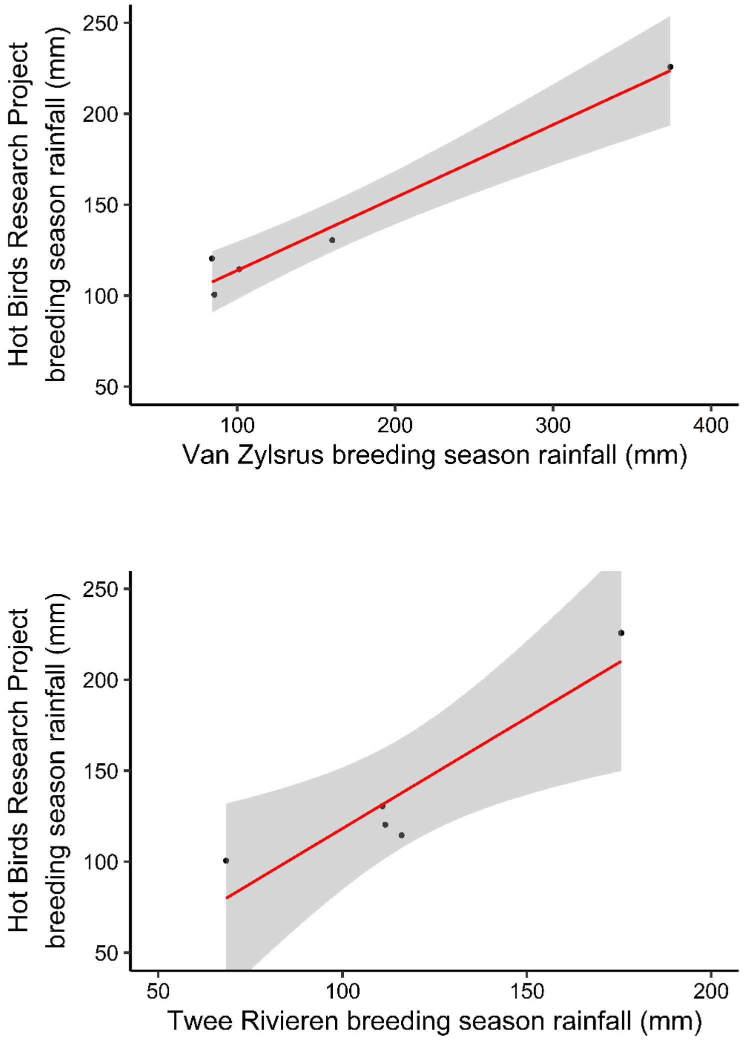

Figure S5.3. Correlations between breeding season (19 October – 24 March) rainfall data from the Hot Birds Research Project (HBRP; the on-site weather station), Twee Rivieren (~120 kms from the study site), and Van Zylsrus (~30 km from the study site) weather stations. 95% confidence intervals (CI) are shown.

No trends were apparent in mean T_{min} or rainfall during the non-breeding season (25 March – 18 October each year; Figure S5.4).

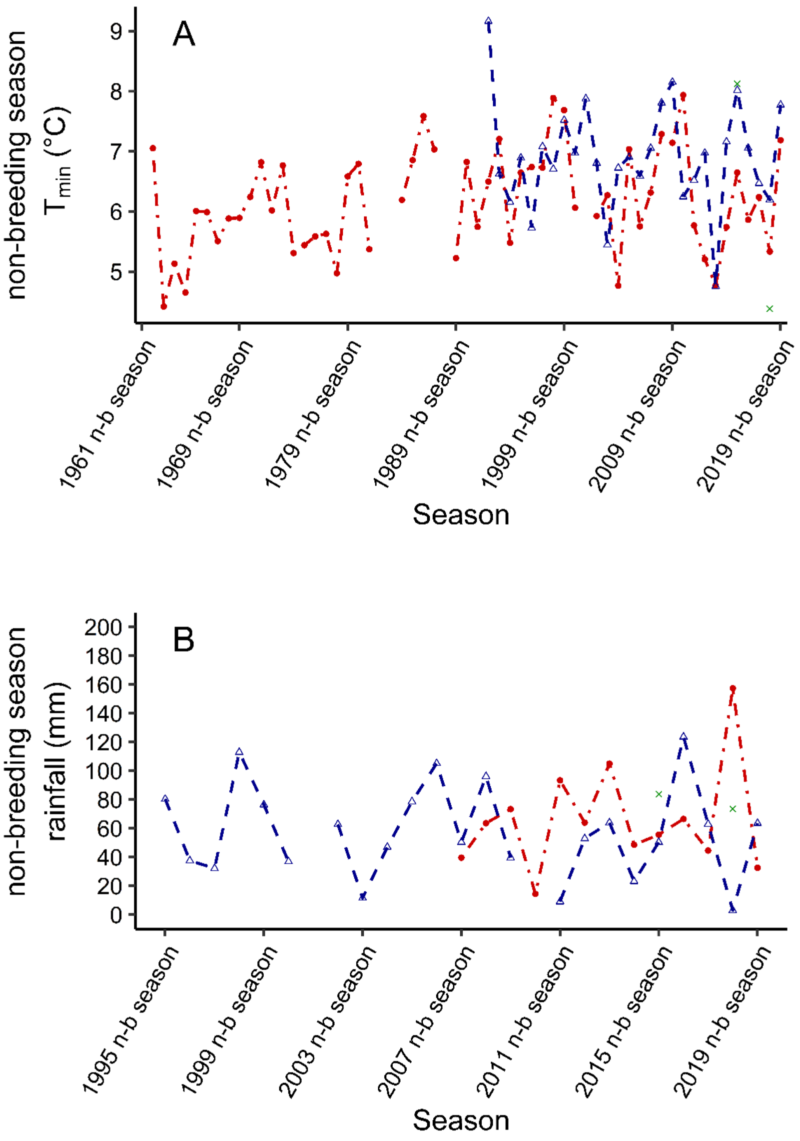

Figure S5.4. Trends in (A) T_{min} (mean minimum air temperature [T_{air}]) and (B) cumulative rainfall during the Southern Yellow-billed Hornbills (*Tockus leucomelas*) non-breeding season (n-b season; 25 March – 18 October) from the Hot Birds Research Project (HBRP; the on-site weather station, green crosses), Twee Rivieren (red circles, ~120 kms from the study site), and Van Zylsrus (blue triangles, ~30 km from the study site) weather stations. Note the difference in axes.

5.6.1.2 Long-term breeding trends

The effect of drought occurrence on survival during the nestling period was not significant in the model averaged estimates (estimate 0.71 ± 0.92; p = 0.444, Table S5.2), although 4 out of 15 (26.7%) of chicks which hatched in drought seasons fledged, compared to 40 out of 56 (71.4%) of chicks in non-drought seasons (Figure S5.6).

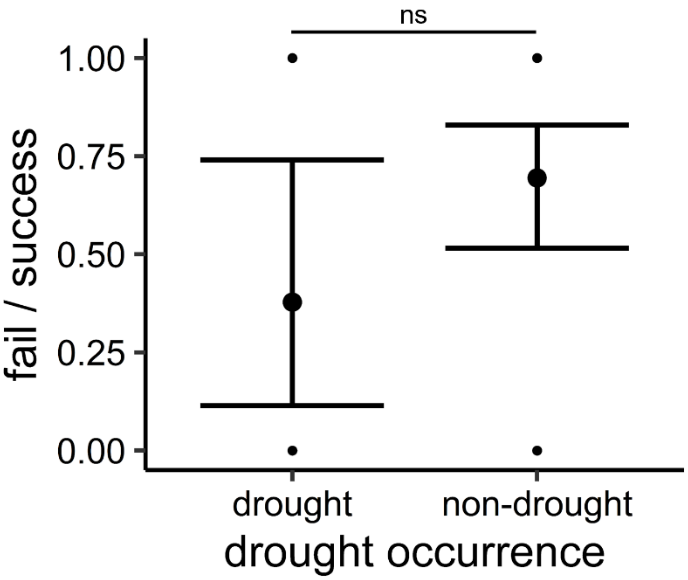

Figure S5.5. The binomial probability of success (0 = fail, 1 = success [fledging at least one chick]) for Southern Yellow-billed Hornbills (*Tockus leucomelas*) nests which hatched at least one chick as a function of the occurrence or absence of drought across the breeding season. Mean and upper and lower quartiles shown.

Table S5.1. Seasons with insufficient (data recorded on <90% of days within the period) T_{max} (mean maximum daily air temperature [T_{air}]), percentage DaysT_{thresh} (days on which $T_{max} > T_{thresh}$ [T_{air} = 34.5 °C]), and rainfall data during breeding seasons (19 October – 24 March) and for insufficient mean minimum daily T_{air} (T_{min}) and rainfall during non-breeding seasons (25 March – 18 October) to be included in analyses listed for each weather station: Twee-Rivieren (TR), Van Zylsrus (VZ), and Hot Birds Research Project (HBRP).

	Weather variable	Weather station	Seasons with insufficient data (<90% of days within period)					
Breeding season	T_{max} & DaysT_{thresh}	TR	1970/1971	1975/1976	1988/1989	2001/02	2009/2010	
		VZ	1991/1992	2002/2003	2003/2004	2006/2007	2009/2010	2016/2017
		HBRP	2011/2012	2012/2013	2013/2014	2015/2016		
	rainfall	TR	2006/2007					
		VZ	2002/2003	2009/2010	2010/2011	2011/2012		
		HBRP	2011/2012	2012/2013	2013/2014	2015/2016		
Non-breeding season	T_{min}	TR	1960	1982	1983	1988	2001	2020
		VZ	2020					
		HBRP	2014	2016	2017	2019	2020	
	rainfall	TR	2020					
		VZ	1993	1994	2001	2010	2011	2020

Table S5.2. Model selection table for Bayesian generalised linear mixed models (BGLMer) for different stages of individual breeding attempts in Southern Yellow-billed Hornbills (*Tockus leucomelas*) as functions of female entry date, percentage $\text{DaysT}_{\text{thresh}}$ (days on which T_{max} (mean maximum daily air temperature [T_{air}]) > T_{thresh} [T_{air} = 34.5 °C]), drought occurrence, and the interaction between $\text{DaysT}_{\text{thresh}}$ and drought occurrence on the binomial success or failure (successfully fledging at least one chick or not) of each entire breeding attempt (n = 88), nest survival from female entry until hatch / fail (‘pre-hatch period’; n = 88), and nest survival from hatch until fledge / fail (‘nestling period’; n = 88). Survival in the nestling period was also modelled as a function of the number of days the female was in the nest. Model selection also shown for BGLMer for female entry date and the number of days spent in the nest by the female as functions of drought occurrence. Model selection was based on Akaike's Information Criterion score adjusted for small sizes (AICc), with the top performing models (Δ AICc < 2) in bold. Where more than one top model was identified, the model average was calculated. *** indicate a significant effect for an explanatory variable within the top models.

Response variable	Model	(Int)	female entry date	% $\text{DaysT}_{\text{thresh}}$	drought occurrence	% $\text{DaysT}_{\text{thresh}}$ * drought occurrence	number of days female in nest	df	AICc	Δ AICc	weight
success (1) or failure (0) of the entire breeding	**1**	**-1.676**	**-1.102*** **	**-0.012**	**+**	**+*** **		**6**	**93.7**	**0**	**0.961**
	4	-1.647		-0.174	+	+		5	100.6	6.84	0.031
	3	-0.164	-0.794	-1.316				4	103.5	9.78	0.007
	6	-0.097		-1.217				3	109.2	15.47	0

attempt	2	-1.567	-0.631		+			4	112.6	18.84	0
	7	-1.673			+			3	115.9	22.16	0
	5	-0.214	-0.723					3	119.7	25.96	0
	8	-0.258						2	124.9	31.2	0
survival (1) or failure (0) during the pre-hatch period	**1**	**0.880**	**-1.240*** **	**0.160**	**+**	**+*** **		**6**	**76.3**	**0**	**0.66**
	3	0.700	-1.060		+			4	79.7	3.41	0.12
	2	2.280	-1.000	-0.620				4	79.8	3.53	0.11
	6	2.100	-1.080					3	80.7	4.41	0.07
	4	0.300		-0.260	+	+		5	82.9	6.65	0.02
	7	1.990		-0.800				3	85.6	9.31	0.01
	5	0.250			+			3	86.7	10.43	0.00
	8	1.790						2	89.2	12.86	0.00
survival (1) or failure (0) during the nestling period	**Avg.**	**-0.021**	**-0.106**	**-0.858*** **	**+**		**1.081*** **	**6**			
	15	**-0.498**		**-0.744*** **	**+**		**1.118*** **	**5**	**101.2**	**0**	**0.295**
	7	**0.534**		**-0.908*** **			**1.135*** **	**4**	**102**	**0.75**	**0.202**
	8	**0.532**	**-0.386**	**-1.044*** **			**0.966*** **	**5**	**102.9**	**1.69**	**0.127**
	16	**-0.389**	**-0.255**	**-0.859*** **	**+**		**1.016*** **	**6**	**103.1**	**1.91**	**0.113**
	31	-0.674		-0.469	+	+	1.125	6	103.5	2.29	0.094

	11	-0.991			+		1.082	4	104.2	2.99	0.066
	32	-0.657	-0.329	-0.419	+	+	0.996	7	105.3	4.13	0.037
	12	-1.029	0.188		+		1.160	5	105.9	4.74	0.028
	6	0.526	-0.817	-1.243				4	107.1	5.94	0.015
	14	-0.036	-0.744	-1.120	+			5	108.6	7.41	0.007
	3	0.428					1.096	3	108.7	7.5	0.007
	30	-0.590	-0.872	-0.326	+	+		6	110.2	8.97	0.003
	4	0.426	0.070				1.124	4	110.9	9.65	0.002
	13	-0.488		-0.742	+			4	111.8	10.59	0.001
	5	0.495		-0.913				3	112.7	11.47	0.001
	29	-0.604		-0.586	+	+		5	114	12.83	0
	9	-1.077			+			3	116.3	15.06	0
	10	-0.984	-0.269		+			4	117.7	16.49	0
	1	0.304						2	121.7	20.49	0
	2	0.342	-0.394					3	121.8	20.6	0
Female entry date	**Avg.**	**3.607**			**+**			**3**			
	2	**3.672**						**2**	**1175.0**	**0**	**0.559**
	1	**3.760**			**+**			**3**	**1175.5**	**0.47**	**0.441**

Days post-hatch spent in the nest by female	**Avg.**	**3.872**	**+**	**3**			
	2	**3.843**		**2**	**665.3**	**0**	**0.551**
	1	**3.895**	**+**	**3**	**665.7**	**0.41**	**0.449**

Table S5.3. Model selection for Bayesian linear mixed models (BLMer) of nest temperature (T_{nest}) of nests occupied by Southern Yellow-billed Hornbills (*Tockus leucomelas*) modelled as function of nest type (natural cavities versus nest boxes), air temperature (T_{air}), and an interaction between them. Model selection was based on Akaike's Information Criterion score adjusted for small sizes (AICc), with the top performing models (Δ AICc < 2) in bold. *** indicate a significant effect for an explanatory variable within the top models.

Response variable	Model	(Int)	Nest type (box versus natural cavity)	T_{air}	T_{air} * Nest type (box versus natural cavity)	df	AICc	Δ AICc	weight
T_{nest}	**1**	**1.443**	**+*** **	**1.032**	**+*** **	**6**	**3454226**	**0**	**1**
	3	3.436		0.961		4	3580761	126534.6	0
	2	3.376	+	0.961		5	3580763	126536.5	0
	5	29.72				3	4895017	1440790.9	0
	4	29.65	+			4	4895018	1440791.9	0

Table S5.4. Model results for nest temperature (T_{nest}) of nests occupied by Southern Yellow-billed Hornbills (*Tockus leucomelas*) modelled as function of nest type (natural cavities versus nest boxes), air temperature (T_{air}), and an interaction between them. Model outputs are for the single top model, or model averages when there was more than one competing model within 2 ΔAICc (see column 'Number of top models'). All models contain the random factor 'season'.

Response variable	Model family	Number of top models	Independent variables	Estimate ± SE (Adj SE for model averaged estimates)	t	df	p ≤	Upper 95% CI	Lower 95% CI
T_{nest}	Gaussian	1	T_{air}	1.03 ± 0.00	2070.98	733733	0.001	1.03	1.03
			nest type (box versus natural cavity)	13.52 ± 0.38	35.89	733733	0.520	14.25	12.78
			T_{air} * nest type (box versus natural cavity)	-0.49 ± 0.00	-371.65	733733	0.001	-0.48	-0.49
			T_{air} (nest type = nest boxes)	1.03 ± 0.00	2214.70	622885	0.001	1.03	1.03
			T_{air} (nest type = natural cavities)	0.55 ± 0.00	347.22	110846	0.001	0.55	0.54

6. General Discussion

Ongoing climate change has resulted in high environmental temperature records being set with increasing regularity worldwide, putting natural systems under severe pressure (Spooner et al. 2018, Stillman 2019). The effects of this warming are manifesting across ecosystems, from the humid tropics and sub-tropics (Tewksbury et al. 2008, McKechnie et al. 2021b, Neate-Clegg et al. 2021, Pollock et al. 2021) to hot deserts (Maestre et al. 2012, Vale and Brito 2015, Hoffmann et al. 2019, Fuller et al. 2021, Riddell et al. 2021), marine systems (Sherley et al. 2012, Ganendran et al. 2016, Jones et al. 2018, Albouy et al. 2020, Piatt et al. 2020, Orgeret et al. 2021), and alpine and polar systems (Rubidge et al. 2012, Dolezal et al. 2021, Frei and Henry 2021, Brambilla et al. 2022). Given that arid regions are often already characterised by thermally and energetically challenging conditions (Wolf 2000), elevated research effort has been dedicated to the ecology of arid-zone organisms (e.g., Lima et al. 2008, Griffis-Kyle et al. 2018, Ribeiro et al. 2019, Aparecido et al. 2020, Chiacchio et al. 2020, van de Ven et al. 2020a, McKechnie et al. 2021a, Moagi et al. 2021, Schoenjahn et al. 2021, Schou et al. 2021).

This thesis contributes to the rapidly growing body of work on the reproductive ecology of desert-dwelling birds, and the thermal ecology of birds facing increasing environmental temperatures more broadly (Andreasson et al. 2020, Conradie et al. 2020, Cunningham et al. 2021, Orgeret et al. 2021, Riddell et al. 2021, Ruuskanen et al. 2021). The knowledge gap that motivated this PhD was that the effects of high environmental temperatures on birds to date have predominantly been studied without explicitly testing for the potential influence of resource availability. However, life history theory suggests that resources should have a significant role in trade-offs between costly traits such as between thermoregulation and activity or development (Kiat and Sapir 2018, de Zwaan et al. 2019). Therefore, this PhD aimed to contribute towards understanding the potential role of resource availability in the relationships between high environmental temperatures and avian ecology. The broad objectives of this thesis, as stated in Chapter 1, were primarily:

“To determine the role of resource availability (both naturally varying and experimentally manipulated) in the established relationships between high environmental temperatures and the behaviour, physiology, morphology, and breeding outcomes of a spring and summer breeding arid-zone bird.”

And secondarily:

“To determine patterns in the breeding success of an arid-zone bird over a decade-long period of rapid climate warming.”

To avoid repetition with previous chapters, this general discussion will be mostly limited to expanding on key findings from each chapter which relate to each other in the context of the overarching objective.

6.1 Breeding season effects: potential shortfalls of supplementary feeding and the case for resource availability or quality effects

As discussed in previous chapters, one would predict an effect of variation in resource availability on reproductive ecology in birds facing high environmental temperatures, especially in arid environments characterised by scarce and unpredictable resources (Riddell et al. 2019, Bourne et al. 2020a, Conradie et al. 2020). Several studies have indicated that high environmental temperatures are significantly more limiting for birds when resources are scarce, such as during droughts (e.g., Cruz-McDonnell and Wolf 2016, Mares et al. 2017, Iknayan and Beissinger 2018, Bourne et al. 2020c, D’Amelio et al. 2022). However, experimental evidence for effects of resources on arid-zone birds’ responses to high environmental temperatures is rare. Acknowledging the potential for publication bias to favour positive results rather than demonstrate an absence of resource supplementation effects, the few studies there are which have provided supplementary food and water in arid zones have also indicated that resource availability has a strong effect on avian physiology and behaviour (Martin 1987, Illera and Díaz 2006, Londoño et al. 2008, Robb et al. 2008, Ruffino et al. 2014). For example, supplying food and water to hoopoe-larks (*Alaemon alaudipes*) in the Arabian Desert led to reduced activity levels, especially during the hottest periods of the day (Tieleman and Williams 2002), and access to *ad libitum* food and water in outdoor aviaries was posited to have reduced the severity of dehydration-thermoregulation trade-offs and facilitated hyperthermia avoidance in several Kalahari Desert species (Thompson et al. 2018). More recently, research on wild zebra finches (*Taeniopygia guttata*) suggested that heatwaves (with air temperature [T_{air}] > 45 °C), even concurrent with drought, were neither stressful nor a challenge for energy and water balance in the presence of *ad libitum* food and water (Cooper et al. 2019, Cooper et al. 2020).

For this general discussion it is important to note that in my study all resources received by incarcerated females and chicks were brought by the free-ranging male parent, which thus acted as a filter for the resource supplementation and breeding season differences to the birds in the nest. Essentially, the characteristics of the food supplied to the nest occupants were dependent on what the male could forage for and decide to bring to the nest. High supp. compared to low supp. males in both breeding seasons, and all males in the cool and wet breeding season compared to the hot and dry breeding season, provisioned more to the nests at all T_{max} (see Chapter 2). Consequently, the birds in the nest did receive more resources from the high supp. treatment and in the cool and wet season, compared to low supp. and the hot and dry season, respectively. Males were observed to almost invariably provision the supplementary food to the nest (see Chapter 2), which meant that high supp. nests received significantly more food, and as such, water, daily than low supp. nests, although high supp. males did reduce the amount of naturally sourced food they provisioned. The improved thermoregulatory performance, manifesting as increased hyperthermia avoidance and more gradual increases in T_b at high T_{air}, in high supp. males suggested that while they provisioned all the supplementary food to the nest, they consumed more of the naturally found prey themselves, benefiting their T_b regulation. Considering that the supplementary system functioned in this way, in conjunction with the patterns shown in the literature outlined above (e.g., Illera and Díaz 2006, Robb et al. 2008, Ruffino et al. 2014), there is a sound theoretical foundation for suspecting that resource availability would mediate environmental temperature effects on, and drive variation in, the hornbills' reproductive ecology. However, the only resource availability associated pattern found in this study consistently corroborated by the supplementary feeding experiment was that high resource availability enabled improved thermoregulation in the form of more gradual increases in T_b and reduced hyperthermia at high T_{air} or T_{nest}. This was evident in the free-ranging male parents (see Chapter 2), incarcerated female parents (see Chapter 3), and incarcerated chicks which fledged (see Chapter 4).

Considering, a) the growing evidence demonstrating the significant effects of supplementary food or food limitation on life-history traits (e.g., Martin 1987, Illera and Díaz 2006, Londoño et al. 2008, Robb et al. 2008, Ruffino et al. 2014, Cooper et al. 2019, Cooper et al. 2020), b) the general lack of evidence for significant nest temperature (T_{nest}) effects on breeding success or morphology in this study, except in terms of chick tarsus length and feather CORT concentrations (see Chapters 3 & 4), c) large breeding season differences in breeding success and morphology of both females and chicks (see Chapters 3 & 4) which would correlate to pronounced differences in natural resource availability or quality (Zann et al. 1995, Lloyd 1999, Dean and Milton 2001, Saunders et al. 2013, Mares et al. 2017, Hidalgo Aranzamendi et al. 2019), and d) the lack of an effect of supplementary feeding in this study, other than on T_b regulation, I suggest three main possibilities:

1) The nutrient and water content (i.e., quality) of the supplementary food was not high enough to elicit detectable responses on the hornbills' reproductive ecology;
2) The amount of supplementary food was not enough to elicit detectable responses on the hornbills' reproductive ecology; and / or
3) The timing of resource supplementation (only once in the early morning) was not suitable to elicit a detectable response on the hornbills' reproductive ecology.

The first possibility was the most likely of the three. Darkling beetle larvae (*Zophobas morio*) themselves are known to be an energy, protein, and water rich food source

(Araújo et al. 2019, Benzertiha et al. 2020, Rumbos and Athanassiou 2021). However, the ideal prey to provision (perhaps, for example, large scorpions, cicadas, or bird eggs which anecdotally appeared more abundant prey in the cool and wet breeding season compared to the hot and dry breeding season) might be important for affecting development, which may not be accounted for by providing a single food supplement (Catto et al. 2021). As stated by Ruffino et al. (2014) "Growing evidence suggests that the ecological impacts of food supplementation can depend on the specific nutritional profile of provisioned foods and that the energetic content of the food (in joules or calories) does not necessarily constitute an indicator of food quality." Therefore, while *Z. morio* present high quality food, they may have lacked specific contents that the hornbills required. Notably, the resource supplementation appeared to have the strongest effects on thermoregulation, which presumably is primarily related to water and energy, while structural growth, which is strongly related to the calcium content of food (Reynolds et al. 2004), appeared unaffected by resource supplementation. *Z. morio* are rich in energy and water, but not in calcium (Andrade et al. 2021), potentially providing some support for this possibility. Moreover, and potentially more importantly, the quality of the natural food available may have been significantly different between the breeding seasons; in the cool and wet breeding season the hornbills possibly had access to much higher quality natural food items than in the hot and dry season when nutrient, water, and energy rich natural prey may have been scarce (Foster 1977, Johnson et al. 2011, Cady et al. 2019). In this case, the hornbills could exhibit prey-switching or increased prey selectivity in the cool and wet season to higher quality prey (Grieco 2002, Tremblay et al. 2005). Again, access to higher quality food (such as scorpions which are protein, energy, fat, and calcium rich prey; Abulude et al. (2006)) could have accounted for the breeding season differences.

The second possibility seemed unlikely based on the fact that the supplemented amount assigned to high resource supplementation breeding attempts was equivalent to approximately 100% of mean daily biomass previously found to be provisioned by male hornbills in this population (van de Ven 2017). However, while biomass provisioned was not estimated in this study, the significant increase (near-doubling) in provisioning rate during the cool and wet breeding season suggested that if more food had been provided in the hot and dry breeding season there was considerable scope for greatly increased provisioning effort (number of provisioning attempts per day = 38.4 ± 19.5 SD and 65.0 ± 32.1 SD in the hot and dry and cool and wet breeding seasons, respectively; see Figure 2.1, Chapter 2). As a corollary to this, the high abundance of presumably high-quality natural food available to both resource supplementation treatments in the cool and wet breeding season may have overwhelmed the majority of potential resource supplementation effects (Tremblay et al. 2005, De Neve et al. 2007, Ruffino et al. 2014).

The third possibility was also significant. Supplementary food (due to logistic and budgetary constraints) was only provided once per day in the morning. Some birds do show the ability to get most of the food or water they need in the night / morning to meet daytime energy and water requirements, e.g., sandgrouse (Cade and Maclean 1967), nightjars (O'Connor et al. 2016, O'Connor et al. 2018), and zebra finches (Cooper et al. 2019). However, other birds (especially those without crops such as hornbills) may require more constant food and water through the day to avoid trade-offs between thermoregulation and other traits, as suggested by the variety of species which continue foraging and drinking even during the hottest parts of the day or at the risk of predation (Sherley et al. 2012, Smit et al. 2016, Abdu et al. 2018b, Czenze et al. 2020, Pattinson et al. 2020, Bourne et al. 2021). Consequently, the hornbills may have required a more constant supplementary food supply to impact breeding success and development or self-maintenance. Food limitation in general (either over the course of a day or over longer timescales) is especially pertinent to breeding success in the hornbills, which is heavily impacted by cannibalism of eggs and small chicks by female parents (Chan et al. 2007, Engelbrecht 2013). If too little food was available at either an hourly, daily, or longer scale, female parents may have resorted to cannibalism to prioritise their own survival and future reproductive potential over current reproductive success (Dehnhard et al. 2015, Jenouvrier et al. 2015, Maron et al. 2015, Nord and Nilsson 2016, Williams et al. 2016). Cannibalism in response to food limitation likely also explained the reducing hatch and fledge probability of later laid eggs; the maximum number of eggs possible to rear under ideal conditions may be laid, with later laid offspring sequentially sacrificed (consumed) to sustain the mother if resources are limited (Martin 1987, Cresswell et al. 2003, Chan et al. 2007, Ng et al. 2011, Decker et al. 2012).

All three of these (non-mutually exclusive) possibilities could explain the fact that the supplementary feeding experiment generally did not corroborate the between breeding season patterns (with the exception of thermoregulatory patterns), which would otherwise be best explained by differences in resource availability. To test if any of these possibilities were responsible for the lack of resource supplementation effects, one could provide *ad libitum* food throughout the day or food of varying quality to the hornbills and repeat the monitoring of their reproductive ecology. Unfortunately, doing so was outside the budgetary and logistic scope of this study, but would be informative going forward. It is also worth noting, as pointed out in the Chapters above, that sample sizes within each resource supplementation treatment within each breeding season were low. As demonstrated by the effect size analyses, this reduced the power to detect some small and medium effect sizes (Cohen’s $f^2 > 0.02$ and > 0.15, respectively) (Cohen 2013). It also meant that some trends were averaged from small sample sizes of individuals, which should be taken into account when considering and interpreting the findings. Statistical power could be improved by performing a resource supplementation experiment on a species or population with more individuals and / or breeding attempts, or during a more climatically stable period with lower natural variation between breeding seasons.

If the supplementary feeding experiment did not strongly affect reproductive ecology for any or all the three reasons above, then the unexplained breeding season differences found throughout this study could be attributed to variation in resource availability or quality. For example, in the cool and wet breeding season a) female post-moult tail feather growth was faster and barb density lower, and b) chick M_b gain and tail feather growth was faster. These breeding season patterns were not significantly affected by T_{nest} or resource supplementation treatment, potentially suggesting that another, unmeasured mechanism acted at the breeding season to breeding season scale to drive variation. However, if supplementary feeding was primarily ineffective or resource quality varied at the breeding season scale, then all of these patterns could be explained by greatly increased resource availability or resource quality in the extremely high rainfall season decreasing the severity of trade-offs between thermoregulation and self-maintenance or development (Pietiainen 1989, Hemborg and Lundberg 1998, Clarke 2001, Moe et al. 2002, De Heij et al. 2006, Ardia and Clotfelter 2007, Vágási et al. 2012, Salaberria et al. 2014, Kiat and Sapir 2018, Møller and Nielsen 2018, Nilsson and Nord 2021). Similarly, hatch and fledge probability, as well as the number of fledglings per female, were significantly greater in the cool and wet breeding season compared to the hot and dry breeding season. However, none of these breeding success metrics were significantly affected by T_{nest} or resource supplementation treatment. Again, while patterns of variation in these traits appeared unexplained in light of a lack of resource supplementation effects to experimentally support a resource availability effect, they would be explained by a large, rainfall-driven increase in resource availability or quality having a positive influence on reproduction (e.g., Bolger et al. 2005, Illera and Díaz 2006, Gardner et al. 2016, Mares et al. 2017, Iknayan and Beissinger 2018, Bourne et al. 2020a, c, Riddell et al. 2021, D'Amelio et al. 2022). The literature that supports this notion includes Chapter 5 of this thesis (recently published; see Pattinson et al. 2022); Chapter 5 showed dramatic negative impacts of drought on breeding success in the hornbills, most likely as a result of severe resource limitations associated with drought in deserts. The fact that resource supplementation did affect thermoregulation suggested that it had tangible effects at least on thermal physiology, but perhaps did not reach a threshold where it could also affect downstream processes of development, self-maintenance, or behaviour. This would be in keeping with life history theory, which would suggest that when facing scarce or low quality food, the limited resources would be primarily allocated to proximate survival (i.e., thermoregulation) instead of current reproductive effort (Flatt and Heyland 2011, Fabian and Flatt 2012).

As a final consideration on the supplementary feeding, it should be noted that sample size constraints precluded an experimental design inclusive of a true control group – an experimental comparison group that received no supplementary food and no disturbance to the males associated with feeding. The amount of food given in the low supp. treatment was designed to be as low (~2% of adult M_b) as possible to be close to an experimental ‘control’, in that the amount of food was theoretically too small to significantly affect the reproductive ecology. The idea was that both treatments should still involve similar disturbance levels (i.e., visiting of feeder, placing worms, alteration of male behaviour associated), such that differences between treatments should have been associated with amount of food provisioned rather than differences in disturbance levels. However, this does not constitute a ‘gold standard’ control comparison. The findings should be considered in this context. This provides another adjustment that can be explored in future work.

6.2 Vastly ameliorated or completely removed temperature effects

Broadly, the results in this thesis supported the growing literature showing negative effects of high environmental temperatures on avian physiology, behaviour, and breeding. For example, the provisioning rate of free-ranging, breeding males decreased with increasing T_{air} in both the hot and dry and cool and wet breeding seasons. This was in keeping with several other studies illustrating the negative effects of high T_{air} on avian behaviour (Thompson et al. 2018, Funghi et al. 2019, Nord and Nilsson 2019, Cook et al. 2020, Pattinson et al. 2020, Bourne et al. 2021, Cunningham et al. 2021, Schoenjahn et al. 2021, Sharpe et al. 2021). Moreover, all hornbills tagged with temperature-sensitive passive integrated transponder (PIT) tags and those with data storage tag heart rate and temperature loggers (DST micro-HRT loggers) displayed hyperthermia in response to high T_{air} or T_{nest}. This reiterated the pervasive effects of high environmental temperatures on T_b regulation, and facultative hyperthermia in response to heat stress (Nilsson and Nord 2018, Gerson et al. 2019, McKechnie and Wolf 2019, Nord and Nilsson 2019, Freeman et al. 2020, Tapper et al. 2020, McKechnie et al. 2021a, Nilsson and Nord 2021, Wojciechowski et al. 2021, Freeman et al. 2022). Chicks also showed reduced tarsi lengths at fledge and elevated feather corticosterone (CORT) levels with increasing T_{nest}. These patterns supported previous studies showing that adverse environmental conditions and heat are stressors (Jessop et al. 2016, Johns et al. 2018, Newberry and Swanson 2018, Moagi et al. 2021, Mentesana and Hau 2022), and that high T_{nest} can compromise development (Andrew et al. 2017, Nord and Giroud 2020, van de Ven et al. 2020b, Corregidor-Castro and Jones 2021, Oswald et al. 2021, Sauve et al. 2021, Ton et al. 2021).

However, despite those patterns, this study found a conspicuous lack of T_{nest} effects on breeding success and adult morphology (see Chapters 3 & 4). In contrast to previous findings in this population of hornbills (van de Ven et al. 2019, van de Ven et al. 2020b), other species (e.g., Hansen 2009, Takahashi 2012, Kingsolver et al. 2013, Bourne et al. 2020b, Cook et al. 2020, Olin et al. 2023), and to the findings of Chapter 5 (showing a strong negative effect of high T_{nest} on breeding success over a decade period), T_{nest} did not significantly affect breeding success or female morphology (see Chapter 3). As discussed in Chapter 3, this potentially suggested that variation in breeding success was unrelated to T_{nest} during the two breeding seasons included in this study. However, the greatly reduced or absent T_{nest} effects could have been driven by two other, non-mutually exclusive possibilities:

1) A difference in modelling approach (including the predictor variables) between Van de Ven et al. (2020b) and the present thesis.
2) Significantly reduced T_{nest} in the present study compared to Van de Ven et al. (2020b).

The first of these is a strong possibility. Because of correlation between the predictor variables used in van de Ven et al. (2020b) for modelling breeding success, only a single predictor was fitted per model. In contrast, this thesis modelled hatch and fledge probability as functions of a predictor variables determined *a priori* to be biologically relevant, including 1) breeding season, 2) egg lay / hatch sequence, 3) mean maximum T_{nest} from lay until hatch / fail or hatch to fledge / fail, and 4) resource supplementation. No model selection was performed; results from this model were reported. Using this approach, this study found that mean T_{nest} from hatch until fledge / fail was not a significant predictor of fledge probability. Cohen's f^2 for these analyses was 0.221, suggesting that the models could detect medium to large effects. However, small effects may not have been detected. This was supported by the fact that if fledge probability was modelled as a function of mean T_{nest} from hatch until fledge / fail as the only predictor variable (as done in van de Ven et al. 2020b) then there was a significant negative effect on fledge probability (estimate -0.94 ± 0.36 SE, $z = -2.61$, $p = 0.009$, lower confidence interval [CI] = -1.74, upper CI = -0.31; analyses not shown). The same was true for the number of fledglings produced, where mean maximum T_{nest} during female incarceration had a significant negative effect (estimate -0.41 ± 0.18 SE, $z = -2.33$, $p = 0.020$, lower CI = -0.77, upper CI = -0.07; analyses not shown) when modelled as the only predictor variable. However, both of these models with T_{nest} as the only predictor variables had higher AIC values (ΔAICc > 2: 21.39 and 2.52, respectively) compared to the top models in the approach used in this study. In combination, these differences suggested that the different modelling approach, as well as the inclusion of different predictor variables which explained significant variation (e.g., breeding season, and hatch or lay sequence), may have partly driven the lack of T_{nest} effects compared to van de Ven et al. (2020b). Additionally, van de Ven et al. (2020b) analysed 49 breeding attempts over three breeding seasons, compared to 20 breeding attempts over two breeding seasons, each spread across two experimental treatments, in the present study. My much smaller sample size (59% reduction) may also have greatly reduced the power to detect similar effects. Small sample sizes in my study also meant that female identity could not be included in the models as a random effect, compared to van de Ven et al. (2020b) who could include it with the larger sample sizes. This may also have led to differences in model outputs; though, as explained in Chapter 3, the number of repeat nest attempts by the same female across both breeding seasons was low (only three individuals), so this is not likely. My much smaller sample size was driven by the fact that fewer hornbills (n = 9 pairs in 2019/2020 and n = 11 pairs in 2020/2021) attempted to breed in either of my breeding seasons compared to van de Ven et al. (2020b) (n = 17 pairs in 2012/2013, n = 20 in 2013/2014, and n = 12 in 2014/2015). I also attempted data collection in a third field season (2018/2019), but none of the hornbills in the study population bred that breeding season, probably due to drought and high T_{air} (see Chapter 5). This lack of breeding effort, even in the exceptionally wet

2020/2021 season, compared to previous years, highlights the potential impacts of climate change on this study population.

The second possibility is also significant (as discussed in Chapters 3 & 4). The new nest box design in the present study (Chapters 2, 3, & 4; not Chapter 5) significantly reduced T_{nest}; nest boxes in the present study showed a T_{nest} maximum >10 °C and an average T_{nest} 3.99 °C below those of van de Ven et al. (2020b), which were also those used in during breeding in Chapter 5. As a result, the T_{nest} in this study may not have been high enough to cross biologically meaningful thresholds for negative impacts which were crossed by the higher T_{nest} in van de Ven et al. (2020b) and in the nest boxes in Chapter 5. This possibility warrants significant attention in terms of conservation management and general study design; nest box design significantly affected the nest microclimate and may have been at least partially responsible for nearly completely mitigating severe negative effects of T_{nest} which may otherwise have been dominant (van de Ven et al. 2020b). This is in keeping with previous studies showing strong effects of nest box design and orientation on life history traits and breeding success, particularly regarding the effects of heat stress (Charter et al. 2010, Larson et al. 2015, Combrink et al. 2017, Maziarz et al. 2017, Sumasgutner et al. 2020, Briggs and Mainwaring 2021, Corregidor-Castro and Jones 2021). Consequently, insulated nest box design, as well as nest box placement in relatively cool microsites, may present significant conservation mechanisms to combat the negative effects of climate warming for birds and other species (Catry et al. 2011, Lei et al. 2014, Griffiths et al. 2017, Bobek et al. 2018, Larson et al. 2018, Goldingay and Thomas 2021, Czenze et al. 2022). It would also be interesting to explore other nest box *versus* natural cavity traits, such as the potential effects of humidity differences and their consequences for heat tolerance (van Dyk et al. 2019, van Jaarsveld et al. 2021). A path analysis also showed a strong direct effect of T_{nest} on breeding success in the van de Ven et al. (2020b) study. The path analysis T_{nest} effect supports the second possibility with much higher T_{nest} strongly driving the environmental temperature effects in the van de Ven et al. (2020b) study.

Importantly, despite the much cooler T_{nest} in the present study compared to van de Ven et al. (2020b) at comparable or slightly cooler T_{air} (average season T_{max} = 34.10 °C during van de Ven et al.'s (2020) study compared to 33.67 °C in the present study) there were still significant T_{nest} effects on chicks. This showed that while the T_{nest} effects on females were mostly removed, chicks remained vulnerable to negative effects of heat stress (Cunningham et al. 2013b, Oswald et al. 2021). In addition, despite abundant resources in the cool and wet breeding season, males still showed T_{air}-limited behavioural patterns. Declines in provisioning rate at high T_{air} could explain T_{nest}-related increases in CORT and declines in growth in the nestlings (30% of the impact of environmental temperatures on nestling growth in the van de Ven et al. (2020b) path analysis was via changes in male provisioning at high T_{max}). This highlights that even high resource availability or quality could not completely mitigate the negative effects of high environmental temperatures on hornbill breeding ecology. On that note, the T_{nest} experienced in nest boxes during breeding (see Chapter 5) prior to the nest box redesign (for the breeding T_{nest} data collected for Chapters 3, and 4) were considerably higher than natural cavities, suggesting a more severe impact of T_{nest} in the nest boxes than birds would naturally experience. However, after the nest box redesign, the T_{nest} profile was considerably more similar to natural cavities (see Chapter 3), suggesting that the findings in Chapters 3 and 4 were likely more closely representative of trends and processes in natural cavities. Despite the increased similarity, this study is based on hornbills that exclusively bred in nest boxes. Therefore, it represents a non-random sample of the population, given that no birds that bred in natural cavities were studied for comparison. Hornbills breeding in natural cavities are essentially impossible to study, given that they seal themselves in the cavity and cannot be accessed. Though populations of birds breeding in nest boxes are commonly used to study reproductive ecology, given the bias in the portion of the population studied, some caution must be taken in extrapolating the findings directly to wild populations.

Lastly, it must be noted that this thesis (other than Chapter 5) is based on a comparison between two breeding seasons. This was not the original intent: total breeding failure in the extreme drought summer of 2018/2019 and the huge differences in weather conditions between the two breeding seasons created a situation which necessitated this comparison. The findings must be interpreted in that context; longer-term studies over multiple seasons provide far more robust inferences regarding seasonal patterns (Lindenmayer et al. 2012; and Chapter 5). There may have been variation between the breeding seasons that could lead to the observed differences that were not measured in this study and could not be definitively isolated in a two year comparison. However, it seems counter-intuitive and in contrast to the literature that variation in resource availability or quality, along with the reduced temperatures and the associated reduction in negative temperature effects, were not the primary driver of seasonal differences (Pietiainen 1989, Hemborg and Lundberg 1998, Clarke 2001, Moe et al. 2002, De Heij et al. 2006, Ardia and Clotfelter 2007, Vágási et al. 2012, Cunningham et al. 2013a, Salaberria et al. 2014, Iknayan and Beissinger 2018, Kiat and Sapir 2018, Møller and Nielsen 2018, Conradie et al. 2019, Riddell et al. 2019, Bourne et al. 2020c, b, McCowan and Griffith 2021, Nilsson and Nord 2021, Riddell et al. 2021). This was supported by the fact that resource supplementation did affect thermoregulation, suggesting that it had tangible effects at least on thermal physiology, but perhaps did not reach a threshold where it could also affect downstream processes of development, self-maintenance, or behaviour. Moreover, the patterns identified in Chapter 5, an analysis of trends in breeding performance over a decade-long period, suggested that the difference between the breeding seasons discussed in Chapters 2-4 were indeed related to resource and temperature differences rather than other, unmeasured forces acting at the breeding season scale.

6.3 Conclusions

This thesis set out to investigate the role of resource availability in the relationships between environmental temperature and reproductive ecology of an arid-zone bird. Despite the possibility that the supplementary feeding experiment may not have been fully effective and that the breeding season differences were largely due to differences in natural resource availability or quality (in addition to slightly cooler environmental temperatures) associated with the unexpected and extreme differences in weather conditions between the seasons, this thesis presents several lines of evidence to meet that objective.

First, higher resource availability in the cool and wet breeding season correlated to significantly increased provisioning rates in breeding male hornbills at all T_{air} (see Figures 2.1 & S2.1, Chapter 2). Increased provisioning rates could reflect that increased resource availability or quality reduced T_{air} limitations on provisioning rate by allowing improved thermoregulation, thus enabling increased activity despite T_{air} (Smit et al. 2013, Czenze et al. 2020). However, it may also have simply been the availability of more food that allowed higher provisioning rates, perhaps at lower effort (e.g., reduced travel distance to foraging patches) under the same T_{air} constraints, rather than that the limiting effects of high T_{air} were lessened (Davoren and Montevecchi 2003, Tremblay et al. 2005). Regardless, while high T_{air} still limited activity, significantly increased daily provisioning rates at all T_{air} presumably correlated to more food and, therefore, water (as all water delivered to the nest was contained within food items), for incarcerated female parents and chicks. Assuming this lessened the severity of trade-offs between investment in different traits (e.g., thermoregulation and development), this resource availability / quality effect on breeding behaviour likely had a strong effect on reproductive ecology (Wiley and Ridley 2016, Tapper et al. 2020, Cauchard et al. 2021). This possibility could then contribute toward explaining the significantly improved breeding success and chick development (i.e., larger tarsi) in the cool and wet breeding season. Generally, this highlights the need for accounting for resource availability / quality effects on behavioural ecology in resource-limited systems. Moreover, this work also contributed more broadly to research demonstrating the importance of behaviour, in endotherms and ectotherms, for both survival and reproduction in the context of climate warming (Kearney et al. 2009, Sinervo et al. 2010, Oswald and Arnold 2012, Abram et al. 2017, Beale et al. 2018, Brivio et al. 2019, Cunningham et al. 2021, Verzuh et al. 2021).

Second, resource availability (including via resource supplementation) significantly affected T_b regulation in male and female parents, as well as incarcerated chicks. This showed that the established relationships between environmental temperature and thermoregulation are influenced by resource availability, presumably via resource availability-driven effects on hydration status (Angilletta et al. 2010, Boyles et al. 2011) and activity patterns (Tieleman and Williams 2002). Enhanced investment in thermoregulation afforded by increased resource availability may have contributed to several important attributes of the hornbills ecology, including a) potentially reducing the costs of breeding to breeding males (van de Ven et al. 2019), b) reducing the costs of incubation for female parents, reducing trade-offs between incubation and self-maintenance (Ardia and Clotfelter 2007, Londoño et al. 2008, Nord and Williams 2015), c) better incubation egg temperatures potentially aiding in avoidance of the deleterious effects of sub-optimal incubation conditions for embryo survival and development (DuRant et al. 2010, DuRant et al. 2012, Carroll et al. 2018, Englert Duursma et al. 2019, Bourne et al. 2021, McCowan and Griffith 2021), and d) mitigating trade-offs between investment in thermoregulation *versus* development in the chicks (Mueller et al. 2019, Nord and Giroud 2020). Generally, these T_b data also provided valuable insights into the thermoregulatory patterns of a free-ranging animal, an area currently lacking data (Smit et al. 2013, McCafferty et al. 2015, Nilsson et al. 2016). These types of remote, bio-logging data are vital for validation of the patterns established during laboratory studies, as well as for understanding the physiology and behaviour of animals in the wild (Ropert-Coudert and Wilson 2005, Fuller et al. 2014, Wilmers et al. 2015). This is especially true considering recent research suggesting that heat dissipation and thermoregulatory limits may be critical factors driving patterns in the behavioural ecology of both ectotherms and endotherms facing high environmental temperatures (Speakman and Król 2010, Terrien et al. 2011, Abram et al. 2017, Nilsson and Nord 2018, Nord and Nilsson 2019, Nilsson and Nord 2021, Tapper et al. 2021). Showing, especially experimentally, that resource availability affects thermoregulation in free-ranging animals is vital to understanding thermoregulatory ecology, as well as the threats posed to animals by increasing environmental temperatures and changing rainfall patterns because of climate change (Smit et al. 2013, Rezende and Bacigalupe 2015, Nilsson et al. 2016, Gerson et al. 2019, Freeman et al. 2020, Nord and Giroud 2020, Mota-Rojas et al. 2021, Freeman et al. 2022).

And third, resource availability and / or quality appeared to strongly influence reproductive success. Both the long-term data (Chapter 5) and breeding season comparison (Chapter 3) indicated that increased rainfall and presumably the associated increase in resources drastically increased breeding performance. This suggests, as demonstrated in several previous studies, that adequate resource availability and / or quality is critical to breeding success, especially in seasonally hot, arid environments (Iknayan and Beissinger 2018, Andreasson et al. 2020, Riddell et al. 2021). However, whether the increased resource availability could offset the negative effects of high environmental temperatures on breeding success was unclear. According to the long-term breeding data (Chapter 5), high environmental temperatures negatively affected breeding regardless of rainfall and resources, with a critical T_{max} limit during a breeding attempt of 35.7 °C, above which no successful attempts were recorded even in high rainfall seasons. However, as discussed above, this may have been partially driven by disproportionate T_{nest} effects associated with poorly insulated nest boxes. A T_{max} of 35.7 °C correlated to an average T_{nest} of ~44 °C before the nest boxes were re-designed (see Figure 3.1, Chapter 3). In the present study, a T_{max} of 35.7 °C correlated to a T_{nest} of ~40 °C, a substantial difference, particularly since the former is well-above normothermic (and approaching potentially lethal) avian T_b, and the latter is below it (Freeman et al. 2022). Therefore, breeding success in the cool and wet, high rainfall season was likely also related to much lower T_{nest}, rather than despite thermally challenging T_{nest}. Consequently, more data are required showing positive fitness effects in the presence of high resource availability or quality (either naturally or experimentally) *and* high environmental temperature conditions known to otherwise reduce fitness, as indicated in southern pied babblers (*Turdoides bicolor*) (Bourne et al. 2020c) and white-plumed honeyeaters (*Ptilotula penicillatus*) (Gardner et al. 2016). I could not test this possibility with the data I had available because most of the items in camera trap videos were not identifiable, meaning I could not quantify the biomass or quality of natural prey provisioned. Furthermore, assessing the true differences in nutritional quality of natural prey available in the hot and dry *versus* cool and wet breeding seasons, and quality of natural prey *versus* the supplemented food, was beyond the scope of this PhD. This possibility therefore remains speculative, and I suggest this as an important avenue for future research.

Overall, this PhD contributes to disentangling the independent effects of high environmental temperatures and resource availability on arid-zone avian ecology. Several key potential effects of resource availability or quality on behaviour, physiology, morphology, and breeding success were identified, which ultimately will hopefully aid in understanding avian ecology and designing future research and conservation interventions in the face of rapid climate warming.

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