Handling the Heat: Managing Microclimates for Nesting Desert Hornbills

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This research was funded by the WWF USA Wildlife Adaptation Innovation Fund. Any opinions, findings, conclusions, and recommendations do not necessarily reflect the views of the funder. The research presented in this thesis was conducted under the ethical clearance from the Science Faculty, University of Cape Town, protocol no(s): 2022/V18/SC; 2022/V17/SC; 2022/V16/SC. The study was also approved by the Department of Agriculture, Land Reform & Rural Development, reference no: 12/11/1/7/1 (2707SR). The study was conducted on private land at Kuruman River Reserve and Leeupan Guest Farm with the permission of landowners and the Northern Cape Department of Environment and Nature Conservation of South Africa (permit no(s): FAUNA 0919/2022; FAUNA 0920/2022).

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Abstract

Anthropogenic climate change poses a major conservation threat to organisms globally, including via negative impacts on breeding success. For example, over the last decade, rising temperatures in the Kalahari Desert, South Africa, have caused serious declines in the breeding success of Southern Yellow-Billed Hornbills *Tockus leucomelas*. Previous research suggests the impact of high air temperatures on hornbill nest success is mediated mostly (70%) through direct negative effects of high nest temperatures on chick growth. To address this, I tested whether an insulated nest box design could buffer negative effects of high air temperatures and improve hornbill chick growth and nest success in the Kalahari. I worked with a study population of hornbills breeding in nest-boxes at Kuruman River Reserve in the southern Kalahari, South Africa. I analyzed a long-term dataset (2008 – 2021) on chick growth and breeding success for this population, during which time nest box design changed from uninsulated (2008 – 2018) to insulated (boxes shaded on all sides with plywood paneling and mounted on the southeast [coolest] side of trees) (2019 – 2021). In this long-term dataset, mean maximum daily air temperature during the nesting period (Tmax), breeding season, and nest box type (insulated/uninsulated) all correlated with chick mass and tarsus length, and nest success; chicks were smaller during hotter weather, and less likely to fledge from uninsulated boxes compared with insulated boxes. However, nest box type, breeding season, and air temperature were also correlated with one another in the long-term dataset, making it difficult to assess the cause of these differences. I therefore also conducted a nest box insulation experiment (2022 – 2024) in which nest boxes were modified to either the insulated or uninsulated design at the time of egg lay (i.e. when hornbills had committed to a nest attempt in the boxes). This ensured both nest box types were used in the same breeding seasons. I collected data on Tmax, and maximum daily nest box temperature (Tbox), chick body mass (g) and tarsus length (mm), and nest success in both box types. I found significant interactions between Tmax and nest box type on chick body mass and tarsus length, such that negative effects of high Tmax were buffered in insulated boxes compared to uninsulated boxes (box type*Tmax interactions: chick body mass: est: 29.72±8.91 g, 95% CI: 12.87 g - 47.90 g; tarsus length: est: 2.83±1.20 mm, 95% CI: 0.55 mm - 5.18 mm). Nest success was also significantly higher (est: 4.19 ±1.50, 95% CI: 1.67 - 7.88); and mean maximum nest box temperatures significantly lower (e.g., by 3±1.09°C in unoccupied insulated nest boxes, 95% CI: 0.89 - 1.10°C) than uninsulated boxes. My findings confirm the importance of nest temperatures in shaping breeding outcomes in this species. My data also suggest nest box temperatures can successfully be manipulated with simple interventions such as using plywood to shade nest boxes and mounting these on the coolest side of trees, and this has significant benefits for breeding birds. These findings are important in a warming climate, especially for conservation projects that provide nest boxes with the intention of improving survival and breeding success of target species.

Introduction

Climate change and habitat loss are among the most important conservation threats globally, and the two drivers might often work in synergy (Larson *et al*., 2015; Segan *et al*., 2016). Climate change has exacerbated extreme weather events globally and will continue to increase their frequency and impact. Additionally, climate change is increasing the frequency of hot days and raising average global temperatures (IPCC 2023). The Intergovernmental Panel on Climate Change (IPCC) estimates that global temperature increases could exceed 1.5 degrees Celsius within the next two decades (IPCC, 2023). Climate change exacerbates impacts of habitat loss. For example, increased heatwaves, droughts and flooding contribute to altered habitats. The loss of habitats further contributes to the decline of and change in distributions of wildlife populations globally (Mawdsley *et al*., 2009). Climate change has impacts on the Earth's ecosystems, including fragmentation of ecosystems, biodiversity declines, reduced genetic diversity, altered interspecific interactions and extinctions (Fahrig, 2003; Fischer and Lindenmayer, 2007; Lorenzen *et al*., 2011; Segan *et al*., 2016).

Birds are a well-researched group of organisms in which impacts of climate change and extreme heat events are increasingly being documented (e.g. Catry *et al*., 2015; Andreasson *et al*., 2020; van de Ven *et al*., 2020; Pattinson *et al*., 2022). For instance, the intensity of extreme hot weather has been shown to cause mass mortality events in avian taxa around the world. For example, heat events can cause mortality via direct impacts of high temperature, for example, in the southeastern region of South Africa's KwaZulu Natal province, mesic savanna birds were found dead when maximum air temperatures reached 43 - 45°C (McKechnie *et al*., 2021). Heat events can also disrupt ecosystems, indirectly causing mortality through changes in species interactions. For example, in the Canadian Pacific Ocean, thousands of Cassin's Auklets *Ptychoramphus aleuticus* were found dead because of widespread starvation due to a marine heat wave event and which reduced mesozooplankton densities in the ocean (Jones *et al*., 2018). In addition to these, climate change is also affecting the timing of animal migrations and breeding through altering habitats and reducing resources, breeding success and population trajectories (Gregory *et al*., 2009; Moore, 2011; Cunningham *et al*., 2013; Stephens *et al*., 2016; Lawrence *et al*., 2022; Pattinson *et al*., 2022).

As well as causing mortalities across age classes, hot weather can negatively affect breeding outcomes. These negative impacts affect species across different ecosystems, from arid zones to high mountains. Pipoly *et al*. (2022) showed that Great Tit *Parus major* nestlings in temperate Hungary suffered higher mortality and had smaller body mass and tarsus length when they experienced frequent hot days. In a seasonal mountain system, the Swiss Alps, high temperatures negatively impacted provisioning rates and biomass provisioned to Ring Ouzel *Turdus torquatus* chicks during the nesting period (Barras *et al*., 2021). In the Mediterranean basin, high maximum temperatures contributed to reduced body mass and high mortality in the Lesser Kestrel *Falco naumanni* nestlings (Catry *et al*., 2015). Hot weather also especially affects birds in arid zones with decreased nestling growth and breeding success, and poor quality of nestlings produced, as is the case for Southern Pied Babblers T*urdoides bicolo*r (Bourne *et al*., 2022), Common Fiscals *Lanius collaris* (Cunningham *et al*., 2013) and Southern Yellow-Billed hornbills *Tockus leucomelas* (van de Ven *et al*., 2020; Pattinson *et al*., 2022).

The interplay between climate change and habitat loss presents further challenges, particularly for species reliant on specific habitat features. For example, habitat loss is an especially important threat for cavity-nesting species because the large, old trees in which they breed are often at particular risk (Stojanovic *et al*., 2016; Ibarra *et al*., 2017). For example, deforestation from selective logging in mature forests, wildfires (increasing in frequency and severity under climate change), and fewer cavities in relatively young secondary growth forests all contribute to reduced nesting sites (Ibarra *et al*., 2017; Stojanovic *et al*., 2016). This is also true in savannah systems, where there is a shorter supply of nesting sites due to the loss of mature trees (Veiga *et al*., 2013). Nest site selection in cavity-nesting birds is further limited by sensitivity to cavity morphologies and thermal properties (Aitken and Martin, 2008; Salaberria *et al*., 2014; Stojanovic *et al*., 2016).

Nest boxes can be an important conservation tool, providing breeding sites for cavity-nesting species living in habitats where natural cavities have become rare (Larson *et al*., 2018). They enhance and improve habitat quality, reproductive success, and population trajectories for cavity-nesting species (McComb and Noble, 1981; Carstens, 2017; Maziarz *et al*., 2017). However, poorly designed and placed nest boxes can become ecological traps, especially under climate change, as they often lack adequate thermal insulation, exposing inhabitants to extreme weather and leading to reduced survival and poor breeding outcomes (Maziarz *et al*., 2017; Larson *et al*., 2018). Understanding how nest box design impacts nest temperatures and breeding success is essential, particularly with rising temperatures (Larson *et al*., 2018; Corregidor-Castro *et al*., 2023). Experimental studies are thus needed to test nest box temperatures and assess the effects of high air temperatures on breeding attempts of cavity-nesting species (Ardia *et al*., 2010; Maziarz *et al*., 2017; Andreasson *et al*., 2018; Corregidor-Castro *et al*., 2023). For example, a study by Corregidor-Castro *et al*. (2023), found that shading nest boxes during extreme heat events improved breeding outcomes for the Lesser Kestrel (*Falco naumanni*), a Mediterranean cavity breeder, as unshaded boxes experienced higher temperatures, leading to high hatching failures and mortality rates, and poorer body condition and growth of nestlings. This underscores the importance of designing nest boxes suited to their environmental conditions to ensure their effectiveness.

Southern Yellow-Billed Hornbills (*Tockus leucomelas*; hornbills) are cavity-nesting birds from southern Africa, including the hot and arid savannas of the Kalahari (Pattinson *et al*., 2022). Hornbills have an unusual breeding strategy where the female seals herself inside a nest cavity, moults all her flight feathers and becomes dependent on the male hornbill to provide food for her and the chicks for much of the nesting period (Kemp, 1995; Pattinson *et al*., 2022). Research on nest success in hornbills breeding in nest boxes in the southern Kalahari shows that nest temperatures are particularly important to determine breeding success (van de Ven *et* al., 2020). High air temperatures negatively affect breeding attempts and were correlated with reduced provisioning rates by the male parent, reduced body mass in the female and nestlings, and thus reduced fledgling success (van de Ven *et al.*, 2020). Temperature effects on nesting success were driven mostly via the effect of air temperature on temperature within nest cavities (nest boxes): 70% of the effect of temperature on nest success was via this pathway, while the other 30% was driven by temperature related declines in provisioning abilities of the male parent (van de Ven *et al*., 2020). During periods of high air temperatures, male provisioning was significantly reduced, as the male undergoes trade-offs between foraging and heat dissipation behaviours such as panting and thus cannot adequately provision for the brood (van de Ven *et al*., 2020).

The southern Kalahari region is warming rapidly, with increases in summer air temperatures of 1°C per decade over the last 20 years (Pattinson *et al*., 2022). The region is already hot and arid, meaning birds like the hornbills may already exist near their physiological limits and be especially vulnerable to further temperature increases (Pattinson *et al*., 2022). In this region, the main cavity-bearing tree in which birds like the hornbills and numerous other cavity-nesting species (e.g. Acacia Pied Barbet *Tricholaema leucomelas*, Scimitarbill *Rhinopomastus*, Lilac-breasted Roller *Coracias caudatus*, African Grey Hornbill *Tockus nasutus*, African Hoopoe *Upupa Africana,* etc) breed, is the camelthorn *Vachellia erioloba*. This tree species is declining (Raimondo *et al.,* 2009), meaning that nest box interventions might become increasingly important in the future for cavity-nesters in the region.

Strong effects of temperature on breeding success, combined with a reliance on cavities for nesting, make the Southern Yellow-Billed Hornbill in the southern Kalahari an excellent model species for studying the impacts of nest box design on nest success in the context of climate change. I therefore used a long-term study population of Southern Yellow-Billed Hornbills breeding at Kuruman River Reserve in the southern Kalahari to assess whether a simple, insulated nest box design could improve breeding success of cavity-nesting species during hot weather conditions.

My research questions were:

(1) Does a thermally insulated nestbox design together with placement on the coolest side of the tree buffer against high nest temperatures during periods of hot weather?
(2) Do chicks in insulated boxes attain higher body mass (g) and size (tarsus length, mm) than chicks in uninsulated boxes, especially during periods of hot weather?
(3) Do nests in insulated nest boxes have a higher probability of success (i.e. fledging at least one chick) than nests in uninsulated nest boxes?

I predicted that high air temperatures would result in low chick growth and therefore low nest success, but that these impacts would be buffered in insulated nest boxes.

Methods

2.1 Study species

Southern Yellow-Billed Hornbills (*Tockus leucomelas,* hereafter ‘hornbills’) are listed as “Least Concern” by the International Union of Conservation of Nature (IUCN, 2016), although the population is thought to be declining (BirdLife International, 2016). The species is widely distributed in southern Africa including the Kalahari Desert (BirdLife International, 2016). Hornbills are socially monogamous cavity nesters. During breeding, the female seals herself into the nest cavity (nests are either in tree cavities or nest boxes), by blocking the entrance with a seal made of mud and faeces, leaving a narrow slit through which the male supplies food. She then moults all her flight and tail feathers immediately after clutch completion and thus relies completely on the male hornbill to provision food for her during incubation and most of the chick-rearing period (Kemp, 1995; Kemp and Boesman, 2020; van de Ven *et al*., 2020; Pattinson *et al*., 2022). The female remains sealed in the nest cavity for most of the nesting period, breaking out once she has regrown her flight feathers, approximately a month after she laid her first eggs (Pattinson *et al*., 2022). Females lay clutches of 2 – 6 eggs, which hatch asynchronously (Hockey *et al*., 2005; van de Ven, 2017).

2.2 Study Area

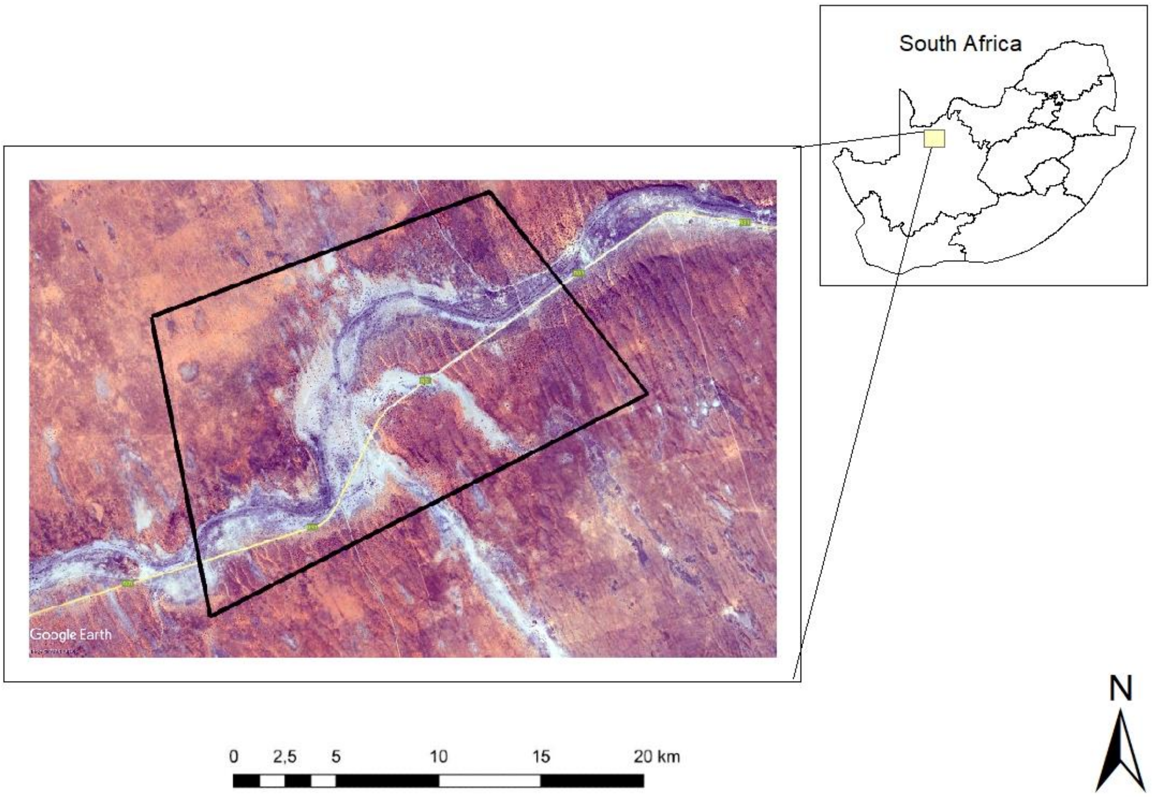

Figure 1: Map of the study site, Kuruman River Reserve (KRR), in the southern Kalahari, Northern Cape Province, South Africa. Southern Yellow-billed Hornbills have been studied on the reserve since 2008.

My study site was the 33-km^2 Kuruman River Reserve (KRR; 26° 58' S, 21° 49' E) located in the southern Kalahari Desert, Northern Cape, South Africa (van de Ven *et* *a*l., 2020). The study area is characterized by dune fields and the dry Kuruman riverbed (Pattinson *et al*., 2022).

The vegetation is arid savanna: composed of grasses, with scattered shrubs including black thorn *Senegalia mellifera*, and driedoring *Rhigozum trichotomum*, and woody trees including camelthorn *Vachellia erioloba*, grey camelthorn *Vachellia haematoxylon*, shepherd's tree *Boscia albitrunca*, and buffalo thorn *Ziziphus mucronata* (van de Ven, 2017; Pattinson *et al*., 2022). The study site receives 202.3 ± 82.4 mm summer rainfall primarily during October to March (van de Ven *et a*l., 2020; Pattinson *et al*., 2022). During summer months (December to March), the average air temperatures are 34.2 ± 9.7°C (van de Ven *et a*l., 2020).

At KRR, hornbills typically nest in cavities of camelthorn trees along the dry riverbed. Since 2008, researchers have provided nest boxes for these hornbills, which they use readily. Hornbills typically initiate breeding in response to summer rain (Finnie, 2012; van de Ven, 2017). The number of hornbill pairs nesting in boxes at KRR has steadily declined over the course of the study 2008 – present (beginning of study, 32 breeding pairs vs 20 – 25 breeding pairs presently), correlated with rapid climate change during this period (> 1°C warming per decade in this area since the summer of 1996-1997, Pattinson *et al*. (2022)).

Weather data for the study were sourced from the Hot Birds Research Project (hereafter HBRP) weather station (Vantage Pro2, Davis Instruments, Hayward, CA, United States), which was deployed at the field site KRR in 2011. The HBRP weather station records air temperature (°C), relative humidity (%), wind speed (m s^{-1}), solar radiation ($W.m^{-2}$) and rainfall (mm) at 5-minute (10 minutes for the nest insulation experiment) intervals (Pattinson *et al*., 2022, van de Ven *et al*., 2020). Weather data were also sourced from the South African Weather Service (SAWS) Van Zylsrus which is ~ 30 km from the study site to fill in missing weather recordings from the HBRP weather station, including from years prior to 2011 (Pattinson *et al*., 2022).

2.3 Study Design

I worked with two datasets, a historic dataset including data on nest success (2008 to 2021) and chick tarsus length (body mass, tarsus length; 2012 to 2021, hereafter "historic dataset") and data on nest success and chick tarsus length collected during a nest-box insulation experiment (2022 to 2024, hereafter "nest insulation experiment dataset") which were analysed separately.

2.3.1 Historic dataset

The historic dataset included data on nest success (where failure = no chicks fledged, and success = at least one chick fledged), collected between 2008 and 2021 (13 years) and data on nestling body mass and tarsus length measured at approximately weekly intervals throughout the nest period, from 2012 – 2021 (9 years). Data were collected by former PhD students Michael Finnie (2008 – 2012), Tanja van de Ven

(2014 – 2017), and Nicholas Pattinson (2018 – 2020), (Finnie, 2012; van de Ven, 2017; Pattinson, 2023).

During each summer breeding season, hornbill nest boxes on KRR were monitored and checked weekly for any breeding activity. A nesting attempt was recorded when there was a full seal on the nest box entrance with the female confined inside (as described by van de Ven et *al*., 2020). Once the female laid eggs, these would be incubated for approximately 3 weeks. From approximately 3 weeks after egg lay, between 2012 and 2021, nest boxes were monitored daily to determine the hatch dates of nestlings. Nestling body mass (M_b, g) and tarsus length (mm) were taken weekly (van de Ven et *al*., 2020; Pattinson, 2023). Nestlings were weighed 0.01g using a top pan balance (Ohaus SCOUT^{TM} PRO SP401 top-pan scale, Ohaus corporation, United States of America), and the tarsus (from the folded toes to the back of the 'heel') measured to 0.1mm with vernier callipers. All nesting attempts 2008 – 2021 were monitored until the nestlings fledged or the nest failed, and the nest outcome was recorded. Nest failures occurred when females cannibalized eggs or chicks, and subsequently abandoned the nest attempt, or in a few cases, died in the nest (Pattinson *et al*., 2022; Pule & Murphy *pers obs*). Because hornbills seal the nest entrance, nest failures almost never occur due to nest predation at this site. Failure was therefore usually determined by an empty nest box prior to the age at which chicks could reasonably be expected to fledge (i.e. younger than ~day 42 after hatch).

During the first part of the study period (2008 – 2018) uninsulated wooden nest boxes were supplied for hornbills at the study site (>40 boxes 2008 – 2010, 43 boxes in 2011, 44 boxes in 2012 – 2015, 38 boxes in 2015 – 2017, 33 boxes in 2017 – 2018). During this period, the nest box design consisted of a simple wooden box with dimensions 25x28x50cm built of 2cm thick pinewood, with a 5.5cm diameter entrance hole. The boxes were placed on camelthorn trees *Vachellia erioloba* at variable heights off the ground, from ~ 1.5 m - 4 m, and at variable orientations on the tree trunks. This was because boxes were initially placed at locations where hornbills had nested in natural cavities before.

During the second part of the study period (2019 – 2021) insulated boxes were provided for the hornbills (50 boxes during the period 2019 – 2021). These nest boxes consisted of the same standard wooden box 25x28x50cm built of 2cm thick pinewood, with a 5.5cm diameter entrance hole, however each box was additionally shaded by 0.2cm thick panels of plywood mounted on all sides (insulation) using 2x2x50cm pine batons, leaving a 2cm air gap on all sides between the box and the plywood shader. All boxes were mounted 1.5 m off the ground on the southeast (coolest) side of the tree-trunks. This box standardization and redesign was conducted by Nicholas Pattinson as part of his PhD (Pattinson, 2023).

2.3.2 Nest-box insulation experiment

There was a clear confound in the historic dataset between box type and placement, and breeding season during which data were collected (uninsulated boxes placed at random compass points on tree trunks in breeding seasons from 2012 - 2018; insulated boxes placed on the southeast side of trees in breeding seasons from 2019 – 2021). Climate variability between seasons, including an especially cool and wet breeding season in summer 2020/21, made it difficult to assess how box type and orientation influenced the nesting success of hornbills. To address this, confound, I conducted a nest box experiment over two breeding seasons (summers of 2022/23 and 2023/24) to assess the effect of box type and orientation on nesting success of hornbills, by including both uninsulated and insulated nest boxes simultaneously in each season.

To address the risk of better-quality birds choosing good quality nest boxes, all nest boxes at the study site were insulated and mounted on the southwest side of the tree trunk before the start of the breeding season, to ensure standardization. Once the female hornbills had sealed themselves within the nest boxes, laid eggs and begun incubating, the active nest boxes were randomly assigned either to the “uninsulated” treatment (this treatment mimics a standard nest box design with no insulation), or to the “insulated” treatment.

Boxes assigned to the “uninsulated” treatment then had insulation panels taken off them and were remounted at a random compass point on the tree, while “insulated” boxes had the front insulation panel taken off and replaced with a new one and were remounted on the southeast side of the tree trunk. The removal and replacement of the front insulation panel of “insulated” boxes ensured that all breeding male hornbills saw a slightly different looking nest box post-modification, whether in a “uninsulated” or "insulated" treatment group. Moving all boxes to a new compass orientation from the original southwest location allowed that "insulated" boxes could be placed on the south-east side of the tree, the most shaded/coolest location of the tree during midday heat, while "uninsulated" boxes were placed at random compass points, simulating the status of nest boxes in other conservation projects (and in the early years of the historic dataset for this site), where box thermal conditions are not always considered (Goldingjay, 2015; Kiss *et al.*, 2017). Starting with a southwest placement ensured all boxes were moved on average 90° around the tree trunk, regardless of whether they were in "uninsulated" or "insulated" group (uninsulated boxes would have moved on average 90°, because 180° rotation are available, and the new compass point was chosen at random for each uninsulated box).

Nest boxes were visited once a week to monitor for hatching, with subsequent weekly visits following the hatching of the first egg (2022/23 – 2023/24 seasons). Data were collected in the same manner as in the historic dataset and were collected by myself and research assistants Benjamin Murphy, Lisa Nupen and Samantha Wagstaff. At each visit, the female (when she was still present in the nest box) and nestlings were weighed to record body mass (M_b) with a Ohaus SCOUT^{TM} PRO SP401 top-pan scale (Ohaus corporation, United States of America) to 0.01g. Tarsus measurements were recorded to 0.1mm with an analogue RS Pro 150mm dial Calliper (RS Components, South Africa, following van de Ven *et al*. (2020). Chicks were weighed and measured once they reached age 7 days and measurements continued for 7 days intervals until they fledged from the nest, which typically occurred at age 42 to 49 days post hatch. Nests were monitored every 2 days following chick measurements at day 42 after hatching, to confirm successful fledging. Nests in which all eggs and chicks disappeared prior to this age were recorded as 'failed' as it is not possible chicks could have successfully fledged prior to day 42.

To monitor nest temperatures, iButton dataloggers (Thermochron iButton, DS1923, Maxim, Sunnyvale, CA, USA) were installed in the nest cavity on the underside of nest box lids. The iButton dataloggers were installed in both occupied nest boxes (presence of eggs, female, chicks) and unoccupied nest boxes (no eggs, female or chicks). Data were collected from occupied nest boxes in the 2022/23 and 2023/24 seasons while for unoccupied nest boxes data were collected only in the 2023/24 season. Weather data were collected from the onsite HBRP weather station.

2.4 Statistical analysis

2.4.1 Historic dataset

2.4.1.1 Nest success

Data on nest success were available for 135 hornbill nest attempts in nest boxes at the KRR over 11 breeding seasons, from 2008/9 – 2020/21 (data not available for seasons 2011/12 and 2015/16). Of these, 113 nests were in uninsulated boxes (breeding seasons 2008/9 – 2017/18) and 22 were in insulated boxes (breeding seasons 2018/19 – 2020/21). Nest success was coded as 1 if at least one chick successfully fledged from the nest, or 0 if the nest failed.

For each nest attempt, I assigned the mean maximum daily air temperature (Tmax) recorded by the weather station, including all days from the date the female sealed herself into the nest box until the date of nest failure or chick fledge. I explored relationships between mean Tmax of nest attempts and breeding season, and mean Tmax of nest attempts and box type (uninsulated, insulated). Because I found significant correlations between all three variables, I could not fit them as predictors within the same models of nest success. I was therefore also unable to model the interaction between mean Tmax and box type on nest success using the historic dataset. I therefore modelled nest success as a function of each of the variables mean Tmax, box type, and breeding season, in separate models. Models were fitted as GLMs with binomial error distribution and a log-link function, and continuous variables (i.e. mean Tmax) were scaled to aid model convergence.

Although each nest box was used only once per breeding season, some boxes were used in more than one season (range 1 attempt – 10 attempts per box, mean = 2.8 ± 2.2 sd attempts per box, 48 boxes). I attempted to fit nest box identity (Box ID) as a random factor in the models, using package lme4 (Bates *et al*., 2015), but the model for breeding season would not converge, as different box types and Box ID were used across the different seasons. I therefore removed the random factor from the models and refitted the models. I compared model Akaike's Information Criteria (AICc) values to determine which variables best explained patterns of nest success or failure.

2.4.1.2 Chick body mass and tarsus length

Data on chick body mass and tarsus length were available for breeding seasons 2012/13 – 2020/21, with total n = 126 chicks and n = 50 nests (n = 60 chicks in uninsulated boxes and n = 66 chicks insulated boxes). Seasons 2012/13, 2015/16, 2016/17, 2017/18 and 2018/19 were excluded from the analysis as data on chick body mass and tarsus length were not available.

I assigned the mean Tmax recorded by the weather station, including all days from the hatch date of each chick to the date of each measurement, e.g. hatch of chick to day 7, hatch to day 14, hatch to day 21 etc. I explored the relationships between explanatory variables: chick body mass (M_b) and tarsus length with predictor variables: box type (insulated, uninsulated), breeding season, chick age, mean Tmax, and individual hatch order. I included the random factors chick identity nested within nest box identity for the chick M_b model. However, this random effects structure resulted in a singular fit for the tarsus length model, so I simplified the random term to just chick identity and refitted the model. The models were linear mixed-effects models (LMMs) with gaussian distribution and an identity-link function, fitted using package lme4 Bates *et al*. (2015) in the R statistical environment (R core team, 2023). I could not fit season, mean Tmax and box type in the same models for chick M_b and tarsus length in the historic dataset because of the correlations between them described in section 2.4.1.1. Therefore, models including each variable were fitted separately and compared using AICc. Brood size was strongly correlated with both Tmax and hatch order, therefore I did not fit it in the model but rather used chick age and hatch order in the models to account for these effects.

2.4.2 Nest box insulation experiment

2.4.2.1 Nest success

For the experimental nest success analysis, I had only 20 nests across the two seasons (2022/23 and 2023/24). For the 2022/23 season, n = 14 nests, with n = 3 in uninsulated boxes and n = 11 in insulated boxes – the discrepancy in sample sizes between box types was due to random allocation between categories and nest failures prior to egg-lay. For the 2023/24 season, n = 6 nests, with n = 4 uninsulated and n =

2 insulated boxes. This small sample size prevented me fitting complex models for nest success to these data. I therefore modelled the effects of mean Tmax (including all days from the date the female sealed herself into the nest box until the date of nest failure or chick fledge) and box type on nest success (0 = failed nest, 1 = nest successfully fledged at least one chick) separately. Models were fitted as GLMs with binomial error distribution and a log-link function, in the R statistical environment (R core team, 2023). Mean Tmax was scaled to aid model convergence. I compared model AICc values to determine which variable best explained patterns of nest success or failure.

2.4.2.2 Chick body mass and tarsus length

Data on chick M_b and tarsus length were available for two breeding seasons 2022/23 and 2023/2024 (n = 206 measurements of 47 chicks in 16 nests – this is fewer than the 20 nests in section 2.4.2.1 because some nests failed before chicks were old enough to measure). I assigned the mean Tmax recorded by the weather station, including all days from the hatch date of each chick to the date of measurement, e.g. hatch of first chick to day 7, hatch to day 14, hatch to day 21 etc to generate the mean Tmax throughout the nestling period. Younger chicks (age < 14) were excluded from the dataset as they experienced cooler Tmax than all other age groups and therefore introduced a chick age ~ Tmax confound. There were also more measurements of nestlings from insulated than uninsulated boxes during cooler weather conditions, due to chance and the small sample size of nests, introducing a box type ~ Tmax confound. To properly assess the effects of box type and whether it could buffer Tmax effects, I therefore subset the chick data to only include chicks that had experienced mean Tmax > 35°C in both box types, to ease the box type ~Tmax confound and enable investigation of the interaction between these variables on chick body mass and tarsus length. Additionally, Tmax = 35°C is the threshold above which Van de Ven et al. (2020) recorded > 50 % probability of nest failure in uninsulated boxes in this study population, and any buffering effect of the insulated nest box design and placement could be particularly important above this temperature. This resulted in a final sample size of n = 109 measurements of 33 chicks in 14 nests.

I modelled chick M_b and chick tarsus length as a function of the interaction between box type and scaled Tmax, including chick age and hatch order as covariates in the model. I could not include the variable “brood size” because of a strong correlation this and chick age. I included the random factors chick identity nested within nest box identity. Models were linear mixed-effects models (LMMs) with gaussian distribution and an identity-link function, fitted using package lme4 (Bates *et al.*, 2015) in the R statistical environment (R core team, 2023).

2.5 Nest box temperature

2.5.1 Unoccupied boxes

Data on temperatures recorded inside unoccupied nest boxes were available for one breeding season, 2023/24 and included data from n = 12 uninsulated boxes and n = 10 insulated boxes. Nest temperature was recorded from the 15th December 2023 until the 31st January 2024 (46 days) for both uninsulated and insulated boxes simultaneously. I initially modelled maximum daily nest box temperature (Tbox) as a function of box type, in interaction with Tmax. There was no interaction ($p = 0.99$) between box type and Tmax so the interaction was taken out and the model refitted. The models were linear mixed-effects models (LMMs) with gaussian distribution and an identity-link function, and Box ID as a random factor, fitted using package lme4 (Bates *et al.*, 2015) in the R statistical environment (R core team, 2023).

2.5.2 Occupied boxes

Data on temperatures inside occupied nest boxes was available for two breeding seasons (2022/23 and 2023/24) and included data from n = 4 uninsulated boxes and n = 12 insulated boxes. Tbox was recorded during the time period 13th November 2022 until 31st January 2024 (150 days); (n = 108 days for the 2022/23 season and n = 42 days for the 2023/24 season). Tbox was not measured on the same days for both box types. Some boxes had incubating females and some chicks or eggs (n = 11 with incubating female and eggs, n = 13 with chicks and female until the time the female leaves the nest; iButton dataloggers failed to record for two nests when the female had eggs only). I modelled Tbox in occupied boxes as a function of box type, in interaction with Tmax. The model was a linear mixed-effects model (LMM) with gaussian distribution and an identity-link function, and Box ID as random factor, fitted using package lme4 (Bates *et al.*, 2015) in the R statistical environment (R core team, 2023).

Data are presented as means ± 1 standard deviation, unless otherwise stated. I used a Type III Anova fitted to the models to evaluate overall significance of each factor within each model. This aided the assessment of overall significance of multi-level factors such as ‘season’ in the historic dataset. Anova output is presented in the text using X^2 and p-values, with $p < 0.05$ taken as statistically significant.

Model estimates for fixed factors are presented in the tables, together with 95% confidence intervals: if these did not contain zero, then I took the result as statistically significant.

Results

3.1 Historic dataset

3.1.1 Nest success

Mean maximum daily air temperature, breeding season (season) and box type were all correlated with one another in the historic dataset (data collected from 2008 until 2021; Tmax & box type: $X^2 = 14.21$ $p < 0.001$, Tmax & season: $X^2 = 170.03$, $p < 0.01$, box type and season: $X^2 = 170.03$, $p < 0.001$) therefore these variables could not be fitted in the same model. I therefore fitted models of nest success (1 = at least one chick fledged, 0 = nest failed) as a function of each of these variables separately. All these variables had significant effects on nest success, however the Tmax model had the lowest AICc (Table 1).

Table 1. Comparison of three linear models explaining variation in nest success of Southern Yellow-billed Hornbills breeding at Kuruman River Reserve between 2008 and 2021, including Akaike's Information Criteria and model weights. (a) Tmax = mean daily maximum air temperature during the nesting attempt, (b) box type = uninsulated or insulated nest boxes, (c) breeding season = the breeding season in which nest attempts took place (e.g. summer 2011/12, 2013/14, etc; between 2008 and 2021).

Model	**df**	**logLik**	**AICc**	**ΔAICc**	**Model weight**
(a) Nest success ~ Tmax	2	-77.00	158.10	0.00	0.99
(b) Nest success ~ box type	2	-84.79	173.7	15.58	0.00
(c) Nest success ~ breeding season	11	-71.68	167.6	9.52	0.01

Nest success declined significantly with increasing Tmax (ANOVA output: $X^2 = 21.43$, $p < 0.01$) and insulated nest boxes had a higher likelihood of successfully fledging at least one chick. There was significant variation in nest success between the breeding seasons in the historic dataset (ANOVA output: $X^2 = 32.09$, $p < 0.01$), with complete breeding failure in some seasons (e.g. 2017/18 and 2018/19), while in others the likelihood of nests successfully fledging at least one chick was > 75% (e.g. 2008/09, 2020/21) (model estimates presented in Table 2; Figure 2)

Table 2: Outputs of linear models of the relationship between nest success of Southern Yellow-billed Hornbills breeding at Kuruman River Reserve between 2008 and 2021, and (a) Tmax during the nesting attempt, (b) nest box type (uninsulated or insulated) and (c) breeding season (the summer during which nest attempts took place, e.g. summer 2011/12, summer 2012/13 etc., between 2008 and 2021). Box type = uninsulated is set as the intercept in the nest box type model; breeding season 2008/09 as the intercept for the breeding season model. Estimates, standard errors, z-values and 95% confidence intervals are presented. Lower 95% confidence intervals were not available for breeding seasons 2017/18 and 2018/19, when the study population suffered complete breeding failure.

(a) Nest success ~ Tmax

Coefficients	Estimate	Std.Error	z value	Lower 95% CI	Upper 95% CI
Intercept	0.30	0.20	1.52	-0.83	0.68
Tmax	-0.92	0.22	-4.16	-1.39	-0.51

(b) Nest success ~ box type

Intercept	0.07	0.19	0.39	-0.30	0.45
Box type: Insulated	1.31	0.59	2.22	0.24	2.61

(c) Nest success ~ breeding season

Intercept	1.10	0.67	1.65	-0.11	2.60
2009/10	-0.99	0.81	-1.23	-2.72	0.53
2010/11	-0.66	0.77	-0.86	-2.32	0.78
2012/13	-2.27	0.87	-2.59	-4.16	-0.46
2013/14	-0.41	0.83	-0.49	-2.16	1.11
2014/15	-3.04	1.26	-2.42	-6.20	-0.88
2016/17	-1.10	0.92	-2.00	-3.02	0.66
2017/18	-18.66	2797.44	-0.01	-	418.54
2018/19	-18.66	3956.18	-0.01	-	786.42
2019/20	-0.59	0.99	-0.59	-2.60	1.39
2020/21	16.47	1192.83	0.01	-33.27	412.36

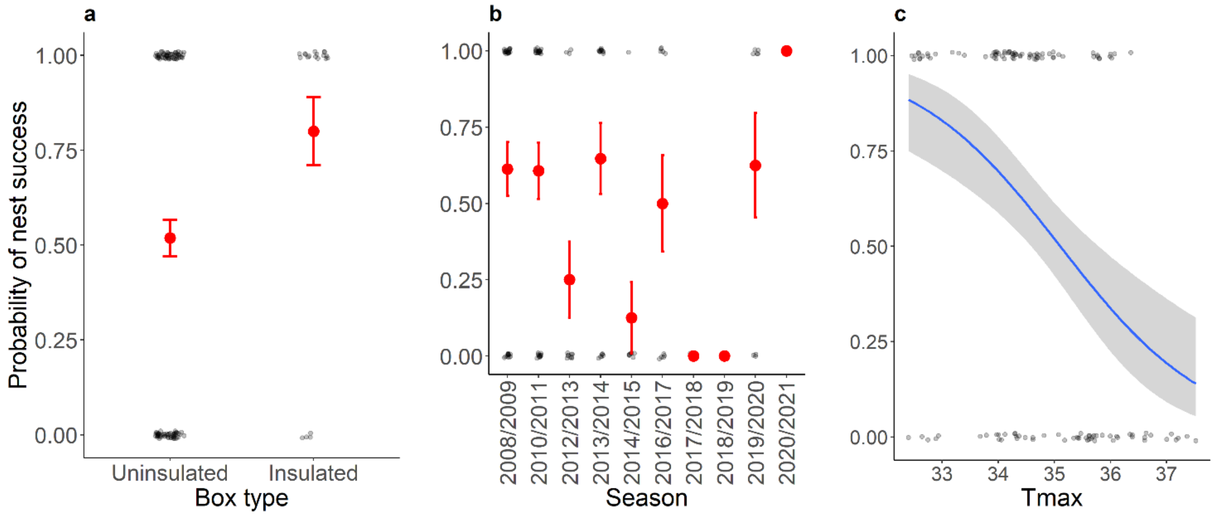

Figure 2: Panel figure showing probability of nest success for Southern Yellow-billed Hornbills in the historic dataset (2008 to 2021), as a function of (a) box type, (b) breeding season and (c) mean maximum daily air temperature (Tmax) during the nesting attempt. Means are shown as red dots (a and b), plus or minus 1 standard error (red error bars; a and b). In (c) the blue line represents the model fit (GLM), and the 95% confidence intervals are shown as grey ribbon. Nest success was significantly higher in insulated boxes (a). There was high variation in nest success between breeding seasons (b) and a significant negative relationship between Tmax and nest success (c).

3.1.2 Chick body mass and tarsus length

As for the nest success analysis, the correlations between Tmax, season and box type meant that these variables could not be fitted in the same models for chick body mass and tarsus length in the historic dataset. I therefore fitted models of chick mass (g) and tarsus length (mm) as a function of Tmax, box type and season separately controlling for age and hatch order. The Tmax model has the lowest AICc for both chick body mass and tarsus length (Table 3; A and B). All had significant effects on both chick body mass and tarsus length.

Table 3. Comparison of three linear mixed effects models explaining variation in (A) chick body mass (g) and (B) tarsus length of Southern Yellow-billed Hornbills breeding at Kuruman River Reserve between 2012 and 2021, including Akaike's Information Criteria and model weights. (a) Tmax = mean daily maximum air temperature during the nesting attempt, (b) box type = uninsulated or insulated nest boxes, (c) breeding season = the breeding season in which nest attempts took place (e.g. summer 2012/13, 2013/14, etc; between 2012 and 2021).

Model	**df**	**logLik**	**AICc**	**ΔAICc**	**Model weight**
(A) Model comparison: Chick body mass (g)					
(a) Chick mass (g) ~ Tmax	7	-2896.62	5907.4	0.00	1
(b) Chick mass (g) ~ box type	7	-3828.87	7671.9	1864.46	0
(c) Chick mass (g) ~ breeding season	10	-3810.44	7641.2	1833.74	0
(B) Model comparison: Chick tarsus length (mm)					
(a) Chick tarsus (mm) ~ Tmax	6	-1016.22	2044.7	0.00	1
(b) Chick tarsus (mm) ~ box type	6	-1367.69	2747.6	702.87	0
(c) Chick tarsus (mm) ~ breeding season	8	-1359.79	2736.0	691.23	0

Chick body mass (g) and tarsus length (mm) declined significantly with increasing Tmax (ANOVA outputs: body mass: X^2 = 43.09, p <0.01; tarsus length: X^2= 10.62, p <0.01). Chicks in insulated nest boxes were heavier and had a longer tarsus than chicks in uninsulated nest boxes ANOVA outputs: (body mass: X^2 = 20.59, p <0.01; tarsus length: X^2 = 16.55, p = <0.01. There was a significant variation of chick body mass and tarsus length between the breeding seasons (ANOVA outputs: body mass: X^2 = 52.60, p <0.01; tarsus length: X^2 = 25.82, p <0.01). (Model estimates presented in Table 4 and 5; Figure 3 and 4).

Table 4: Outputs of linear mixed effects models of Southern Yellow-billed Hornbills chick body mass (g) with gaussian error distribution, and random term chick identity nested within brood identity, for hornbill chicks in nest boxes at the study site (KRR) between 2012 and 2021. All models include fixed factors chick age and hatch order. Model (a) Tmax = mean daily maximum air temperature during the nesting attempt, (b) box type and (c) breeding season. Box type = uninsulated is set as the intercept in (b), and breeding season 2012/13 as the intercept in (c). Estimates, standard errors, z-values and 95% confidence intervals are presented.

Chick body mass (g)					
(a) Chick mass (g) ~ Tmax					
Fixed effects	**Estimate**	**Std. Error**	**T-value**	**Lower 95% CI**	**Upper 95% CI**
Intercept	57.21	10.86	5.27	35.01	78.49
Age	4.89	0.08	58.75	4.73	5.06
Hatch order	-13.34	2.84	-4.70	-18.90	-7.53
Tmax	-11.95	1.82	-6.56	-15.57	-8.36
(b) Chick mass (g) ~ box type					
Intercept	39.13	8.89	4.40	20.89	56.46
Age	4.39	0.07	63.42	4.26	4.53
Hatch order	-9.24	2.10	-4.26	-13.47	-4.73
Box type: Insulated	24.57	5.42	4.50	13.85	35.14
(c) Chick mass (g) ~ breeding season					
Intercept	30.49	9.87	30.9	11.11	49.36
Age	4.38	0.07	63.44	4.25	4.52
Hatch order	-10.25	2.15	-4.77	-14.39	-5.89
Season:					
2013/14	22.49	7.59	2.96	7.98	36.89
2014/15	2.34	8.96	0.26	-14.53	19.30
2019/20	23.36	8.39	2.78	7.50	39.33
2020/21	45.92	7.61	6.03	31.48	60.45

Table 5: Outputs of linear mixed effects models of Southern Yellow-billed Hornbills tarsus length (mm), with gaussian error distribution, and random term chick identity, for hornbill chicks in nest boxes at the study site (KRR) between 2012 and 2021. All models include fixed factors chick age and hatch order. Model (a) Tmax = mean daily maximum air temperature during the nesting attempt, (b) box type and (c) breeding season. Box type = uninsulated is set as the intercept in (b), and breeding season 2012/13 as the intercept in (c). Estimates, standard errors, z-values and 95% confidence intervals are presented.

Chick tarsus length (mm)

(a) Chick tarsus length (mm) ~ Tmax

Fixed effects	**Estimate**	**Std. Error**	**T-value**	**Lower 95% CI**	**Upper 95% CI**
Intercept	29.53	3.91	7.55	21.97	37.19
Age	0.69	0.04	17.63	0.62	0.77
Hatch order	-3.92	1.04	-3.78	-5.94	-1.92
Tmax	-2.18	0.67	-3.26	-3.48	-0.85
(b) Chick tarsus length (mm) ~ box type					
Intercept	14.17	4.19	3.38	5.96	22.33
Age	0.62	0.03	18.89	0.55	0.68
Hatch order	-0.12	1.03	-0.11	-2.12	1.90
Box type: Insulated	7.41	1.82	4.07	3.84	11.01
(c) Chick tarsus length (mm) ~ breeding season					
Intercept	16.32	4.11	3.97	8.55	24.31
Age	0.62	0.03	18.99	0.55	0.68
Hatch order	-0.35	0.99	-0.36	-2.28	1.52
2014/15	-3.13	2.14	-1.46	-7.17	0.91
2019/20	4.32	2.05	2.1	0.32	8.20
2020/21	12.93	3.38	3.83	6.33	19.33

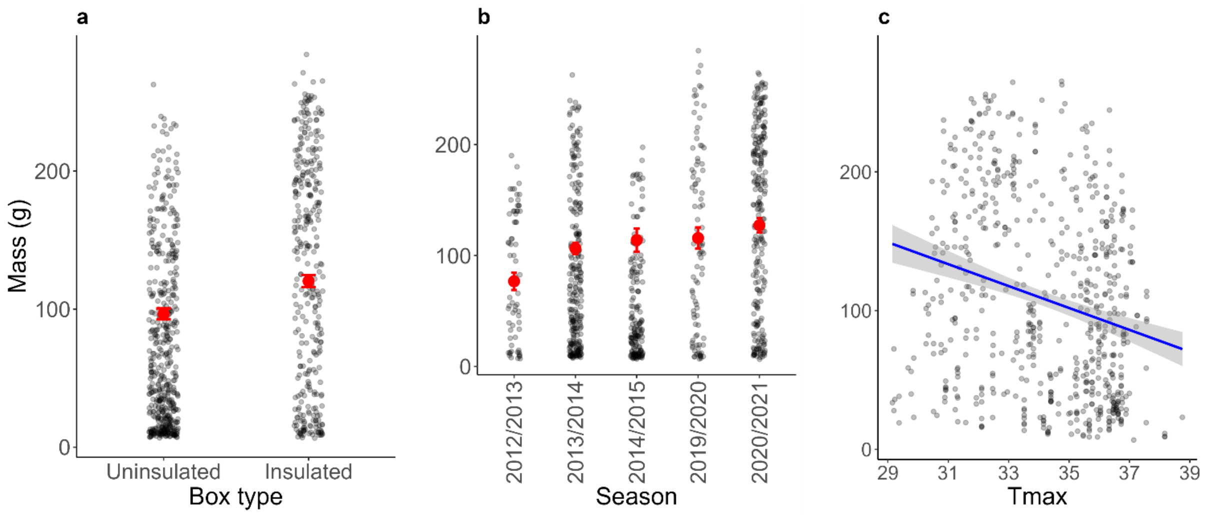

Figure 3: Panel figure showing relationships between chick mass (g) with box type (a), breeding season (b), and mean maximum daily air temperature (Tmax) during the nesting attempt (c), for Southern Yellow-billed Hornbills in the historic dataset (2012 to 2021). Means are shown as red dots (a and b), plus or minus 1 standard error (red error bars; a and b). In (c) the blue line represents the model fit (LMM), and the 95% confidence intervals are shown as grey ribbon. Chicks in insulated boxes have significantly higher body mass than those in uninsulated boxes (a). There is variation in chick body mass between seasons (b) and a negative relationship between Tmax and chick mass. All models account for the effects of chick age and hatch order.

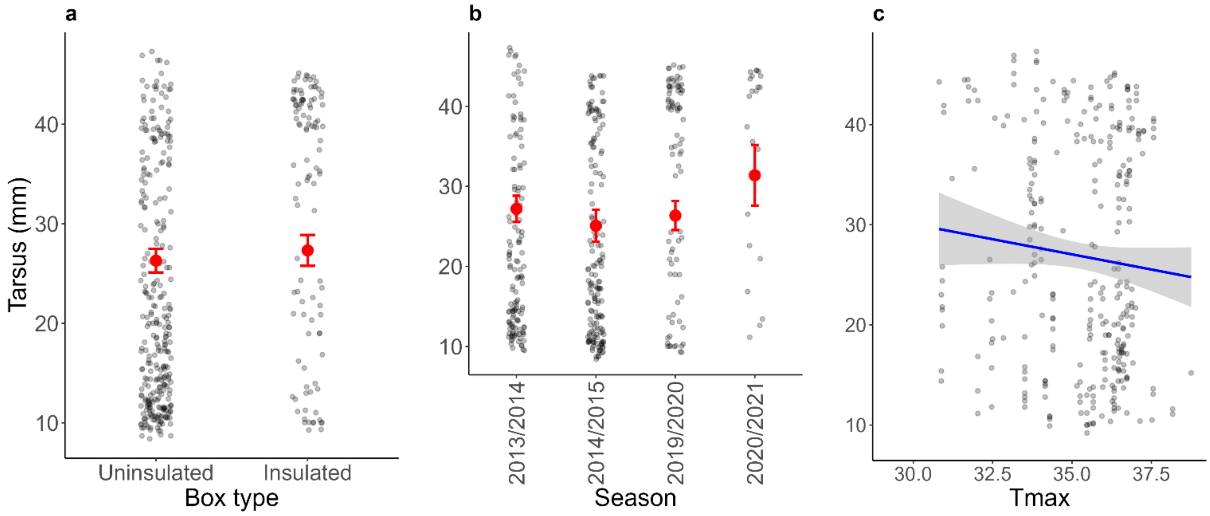

Figure 4: Panel figure showing relationships between chick tarsus length (mm) and box type (a), breeding season (b), and mean maximum daily air temperature during the nesting attempt (Tmax) (c), for Southern Yellow-billed Hornbills in the historic dataset (2012 to 2021, excluding seasons where no chick measurements were collected). Means are shown as red dots (a and b), plus or minus 1 standard error (red error bars; a and b). In (c) the blue line represents the model fit (LLM), and the 95% confidence intervals are shown as grey ribbon. There is variation in chick tarsus length between seasons (b) and a negative relationship between Tmax and chick tarsus length. All models account for the effects of chick age and hatch order.

3.2 Nest box insulation experiment

3.2.1 Nest success

I recorded 20 hornbill nesting attempts over the course of the nest box insulation experiment, n = 13 in insulated boxes, and n = 7 in uninsulated boxes for two breeding seasons (11 insulated and 3 uninsulated in 2022/23 and 2 insulated and 4 uninsulated in 2023/24). The small sample size for nest success meant I had to fit models of Tmax and nest box type separately (Table 6). Insulated boxes had a higher nest success than uninsulated boxes ($X^2 = 12.38$, p = <0.01), and there was a significant negative effect of air temperature on nest success ($X^2 = 4.15$, p = 0.04; Table 7, Figure 5).

Table 6. Comparison of two linear models explaining variation in nest success of Southern Yellow-billed Hornbills breeding at Kuruman River Reserve during the next box insulation experiment (2022 – 2024), including Akaike's Information Criteria and model weights. Tmax = mean maximum daily air temperature during the nesting attempt, box type = uninsulated or insulated nest boxes. Tmax model had the lowest AICc.

Model	df	logLik	AICc	ΔAICc	Model weight
Nest success ~ Tmax	2	-10.43	25.6	8.23	0.12
Nest success ~ box type	2	-6.31	17.40	0.00	0.98

Table 7: Outputs of linear models on the relationship between nest success of Southern Yellow-billed Hornbills breeding at Kuruman River Reserve during the nest box insulation experiment (2022 – 2024), and (a) mean daily maximum air temperature (Tmax) during the nesting attempt, (b) nest box type (uninsulated or insulated). Box type = uninsulated is set as the intercept in the nest box type model.

Nest success ~ Tmax

Coefficients	Estimate	Std. Error	Z-value	Lower 95%CI	Upper 95% CI
Intercept	0.63	0.54	1.17	-0.39	1.79
Tmax	-1.20	0.71	-1.68	-2.96	-0.04

(b) Nest success ~ Box type

Coefficients					
Intercept	-1.79	1.08	-1.66	-4.73	-0.02
Boxtype: Insulated	4.19	1.50	2.79	1.67	7.88

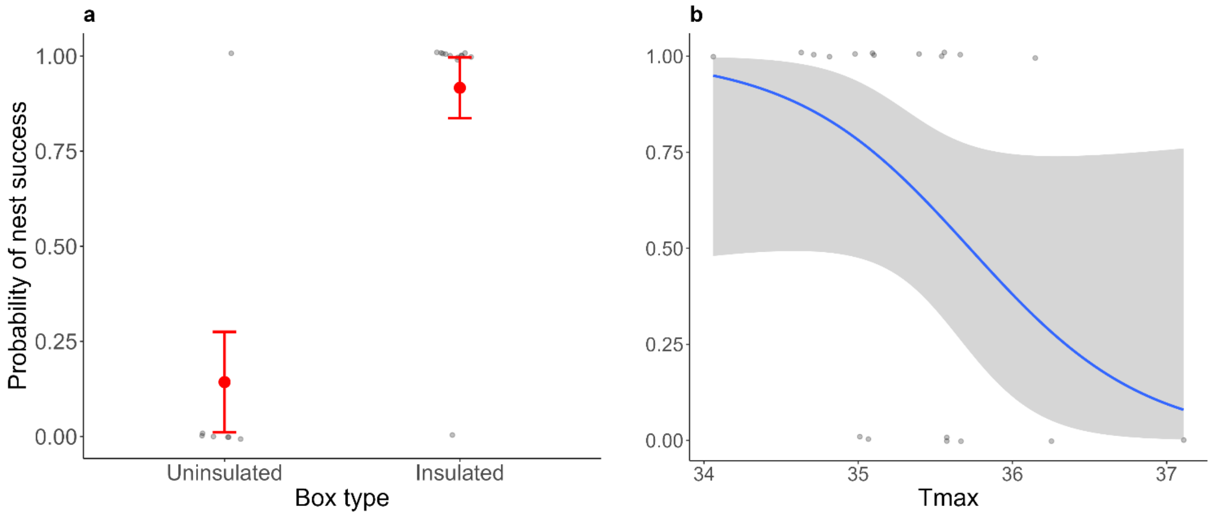

Figure 5: Panel figure showing probability of nest success for Southern Yellow-billed Hornbills at the study site, Kuruman River Reserve, during the nest box insulation experiment (2022 – 2024). Means are shown as red dots, plus or minus 1 standard error (red error bars; a). In (b) the blue line represents the model fit (GLM), and the 95% confidence intervals are shown as grey ribbon. Insulated boxes had a significantly higher probability of successfully fledging at least one chick than uninsulated boxes (a), and nests were less likely to successfully fledge at least one chick as Tmax increased (b) showing a negative significant relationship (95% CI: -2.96, -0.04).

3.2.2 Chick body mass and tarsus length

Age, Tmax and hatch order had significant effects on the Southern Yellow-Billed Hornbill chick mass and tarsus length in the nest box insulation experiment, for chicks that experienced >35°C Tmax (2022-2024). Additionally, there was a significant interaction between box type and Tmax for chick body mass (body mass: $X^2 = 11.12$, $p = <0.01$) such that the negative effects of Tmax on chick mass in uninsulated boxes during hot weather were buffered in insulated boxes (Table 8; Figure 6)

Table 8: Outputs of linear mixed effects models of Southern Yellow-billed Hornbills (a) chick body mass (g) and (b) tarsus length (mm), with gaussian error distribution, and random term chick identity nested within brood identity (for a) or chick identity (for b), for hornbill chicks in nest boxes at the study site (KRR) between 2022 and 2024. All models include the interaction between box type and Tmax, fixed factors chick age and hatch order and random factor chick identity. Box type = uninsulated is set as the intercept in both (a and b). Estimates, standard errors, T-values and 95% confidence intervals are presented.

(a) Body mass

Fixed effects	**Estimate**	**Std. Error**	**T-value**	**Lower 95%CI**	**Upper 95% CI**
Intercept	218.45	32.77	6.67	156.08	282.01
Age	1.95	0.32	6.06	1.33	2.57
Boxtype: Insulated	0.78	26.68	0.03	-50.66	53.85
Tmax	-28.72	8.45	-3.40	-46.18	-12.76
Hatch order	-25.19	4.02	-5.98	-33.23	-15.90
Boxtype Insulated: Tmax	29.72	8.91	3.33	12.87	47.90
(b) Tarsus length					
Intercept	40.50	3.34	12.11	34.14	46.92
Age	0.07	0.05	1.46	-0.02	0.16
Boxtype Insulated	-0.39	1.99	-0.20	-4.21	3.39
Tmax	-2.44	1.17	-2.10	-4.71	–0.20
Hatch order	-0.04	0.45	-0.09	-0.89	0.81
Boxtype Insulated: Tmax	2.83	1.20	2.37	0.55	5.18

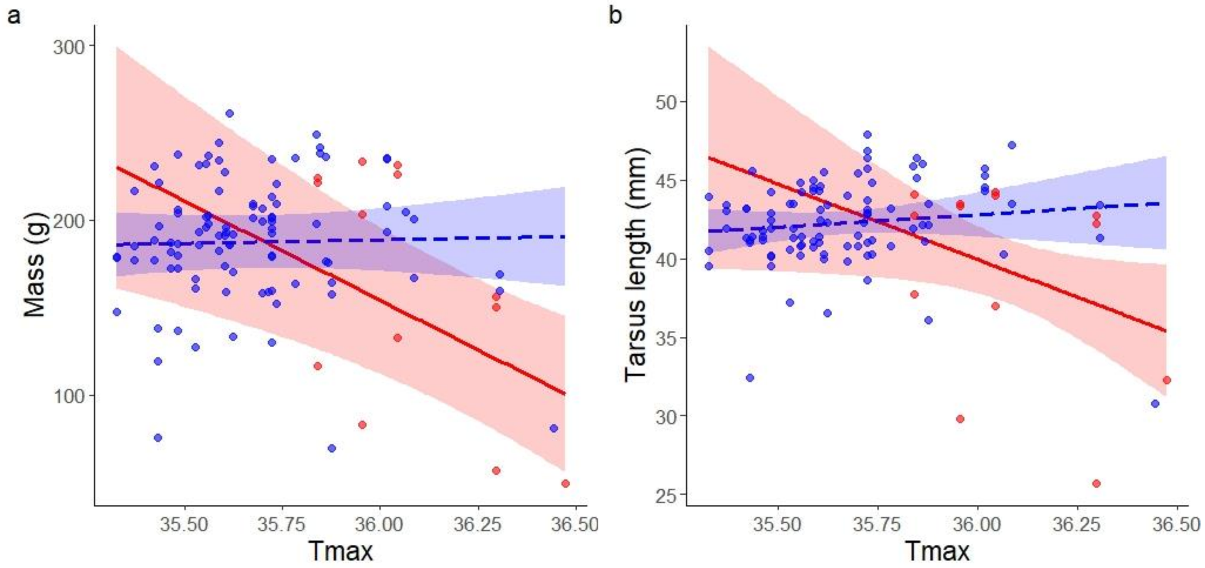

Figure 6: Mean maximum daily air temperature (Tmax) effects on the body mass and tarsus length of the chicks of the Southern Yellow-billed Hornbills at the study site during the nest box insulation experiment (2022 – 2024). Model fits of the linear mixed effect models (LMMs) are shown (a and b) as blue dash line (insulated boxes) and solid red line (uninsulated boxes). 95% CI are shown as the red and blue ribbons (a and b). Red and blue dots show raw datapoints for chicks in uninsulated and insulated boxes, respectively. There was a significant interaction between Tmax and box type, such that negative effects of Tmax on chick mass (a) and tarsus length (b) in uninsulated boxes were not present in insulated boxes.

3.3 Nest temperature

There was a significant interaction between Tmax and box type on maximum daily nest temperature of occupied nest boxes (Tbox) such that birds in uninsulated boxes experienced more rapid increase in Tbox with increasing Tmax than birds in insulated boxes (Table 9; Figure 7). Indeed, Tbox in occupied insulated boxes remained very close to Tmax even as Tmax approached 40°C. However, in occupied uninsulated boxes, mean Tbox approached 50.6°C, the thermal tolerance limit for adult female Southern Yellow-billed Hornbills above which heat-related mortality becomes a high risk (van Jaarsveld *et al*., 2021). I recorded several instances of Tbox > 50.6°C in uninsulated occupied boxes at high Tmax (Figure 7).

There was also a difference in Tbox between insulated and uninsulated unoccupied nest boxes, with insulated boxes experiencing cooler Tbox across all Tmax than uninsulated boxes, but no interaction between box type and Tmax in unoccupied nests. (Table 9, Figure 7).

Table 9. Outputs of linear mixed effects models with Gaussian error distribution, showing relationships between box type and mean maximum daily air temperature (Tmax) on the maximum daily nest temperature recorded in (a) occupied and (b) unoccupied boxes/nests (Tbox). N = 22 unoccupied boxes in which Tbox max was measured for 28 days and N = 16 occupied boxes in which Tbox max was measured for 150 days (n = 150). The model included Tmax, box type, and their interaction, and random effect nest box identity. Non-significant interactions were removed, and the model re-fitted.

Fixed effects	**Estimate**	**Std. Error**	**T-value**	**Lower 95% CI**	**Upper 95% CI**
Intercept	10.46	2.37	4.08	5.46	15.49
Box type insulated	4.17	3.04	1.37	-1.82	10.10
Tmax	0.90	0.07	13.03	0.77	1.04
Boxtype insulated:Tmax	-0.26	0.08	-3.11	-0.42	-0.10

Intercept	6.84	2.04	3.35	2.85	10.82
Box type insulated	-3.00	1.09	-2.75	-5.12	-0.87
Tmax	1.00	0.05	18.89	0.89	1.10

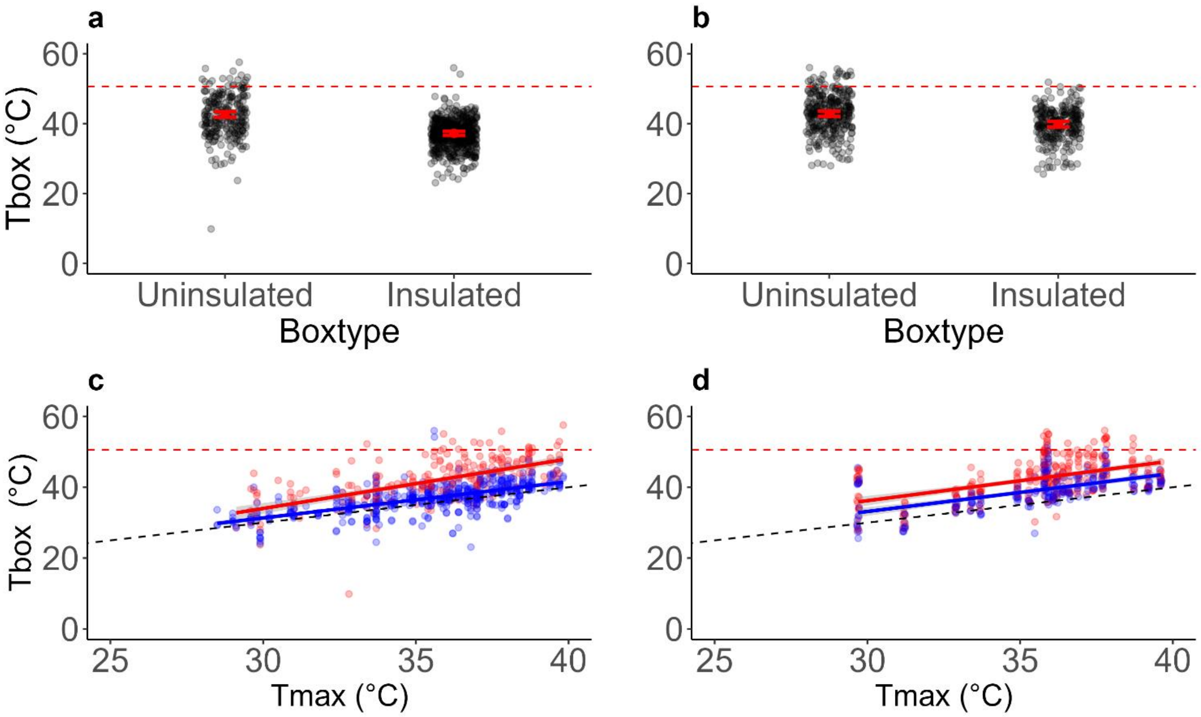

Figure 7. Panel plot showing maximum daily nest temperature (Tbox) for occupied nests and unoccupied nests. From the linear mixed effects model (LMM) the red dots show the means and lines are standard errors in the first two plots (a and b). Insulated boxes are shown as blue lines and uninsulated boxes as red lines, while the grey ribbon represents the 95% confidence interval (CI) in the two bottom plots (c and d). N = 16 occupied boxes in which Tbox was measured for 150 days (a, c) and n = 22 unoccupied boxes in which Tbox was measured for 46 days (b, d). Data were collected at the same time in both box types (insulated and uninsulated) for unoccupied boxes (15/12/2023 to 11/01/2024), but not at the same in occupied boxes (12/11/2022 to 28/02/2023). During the measurement period for occupied boxes, Tmax ranged from 24.3°C to 41.2°C and the mean was 35.21°C ± 0.12 SE. For unoccupied boxes, Tmax ranged from 29.7°C to 41.2°C with the mean 36.14°C ± 0.12 SE. Insulated boxes keep close to the 1 to 1 line with Tmax (black dash line where Tbox equals Tmax) while Tbox in uninsulated boxes rises faster than Tmax rises (c and d). Tbox is higher in uninsulated boxes; both occupied and unoccupied nests (c and d).

Discussion

Across this study, insulated boxes had a higher chance of fledging at least one chick and chicks were heavier and had a longer tarsus in insulated boxes compared to uninsulated boxes. This result was consistent across both the historic dataset and the nestbox insulation experiment, increasing my confidence that the difference was due to the box type and placement, and not just seasonal effects. Ibutton temperature data showed that nest temperatures in occupied insulated boxes were lower than those in uninsulated boxes and stayed closer to air temperature as air temperature increased. The data therefore support my predictions that properly located insulated boxes can buffer against negative effects of high temperature on Southern Yellow-billed Hornbill chick body mass and growth, suggesting that an insulated nest box design could be effective in reducing impacts of climate warming for my study population. The results provide evidence that insulated nest boxes might be an effective intervention for conservation-dependent species that are threatened by climate change via direct temperature-related impacts on reproductive success.

Impacts of nest box insulation on chick survival and growth

Nest success results showed that insulated boxes had a 75% higher likelihood of fledging at least one chick in the historic dataset and 80% likelihood of fledging at least one chick in the nest insulation experiment. These results are in keeping with studies in other species that investigated effects of modifying nestboxes to moderate temperature extremes. For example, Corregidor-Castro *et al*. (2023), found that shaded (insulated) nest boxes reduce chick mortality compared to unshaded (uninsulated) nest boxes in Lesser Kestrels *Falco naumanni* in the Mediterranean, where air temperatures during the breeding season are typically high [i.e. when air temperatures exceed 37°C for more than 2 days, Corregidor-Castro *et al*., 2023]. In both Corregidor-Castro’s study in the Lesser Kestrels and my study in the hornbills, these benefits are likely a result of the nest box modification reducing maximum nest box temperature, with Tbox always being lower in shaded/insulated boxes compared to unshaded/uninsulated boxes. Reducing maximum Tbox likely has beneficial downstream effects on chick survival by allowing nestlings to invest resources into growth rather than heat dissipation in these hot environments. On the other hand, in a temperate-to-cold environment Dawson *et al*. (2005) showed that heating nests improved survival of Tree Swallow chicks, with heated nests more likely to fledge at least one chick and less likely to experience brood reductions compared to unheated nests. This study was conducted in a much cooler habitat than mine or Corregidor-Castro *et al.* (2023), and therefore heating nests likely reduces thermoregulatory costs to chicks of keeping warm, thus increasing their survival chances. At my study site however, thermoregulatory costs of chicks of keeping cool were reduced by nest box insulation as the area is a hot and arid system. Thus, the same results as (Dawson *et al*., 2005) were achieved but via different pathways.

In some circumstances, the impacts of nest box interventions are not as clear cut as in my study, Corregidor-Castro *et al.* (2023) or Dawson *et al*. (2005). For example, Rodríguez and Barba (2016) showed that, in a Mediterranean habitat which experiences warm temperatures during the breeding season, heating nest boxes had no apparent impact on the fledging success for the Great Tit *Parus major* chicks. This is likely because temperatures in the heated nests did not reach lethal thresholds (Rodríguez and Barba 2016). This is at odds with the results of my study in which high nest temperatures often exceeded hornbill thermal threshold of 50.6 °C (Van Jaarsveld *et al*., 2021). Maximum air temperatures at my study site were also higher than maximum air temperatures from Rodríguez and Barba’s (2016) study site. These differences in air and nest temperatures could explain why my results differ from those of Rodríguez and Barba (2016). Taken together, my results and those of Corregidor-Castro *et al*. (2023), Dawson *et al*. (2005) and Rodríguez and Barba (2016) suggest that the impacts of modifying the nest thermal environment either by shading/insulating nest boxes or by heating them will likely depend on background climate conditions.

In addition to surviving better, hornbill chicks in insulated nest boxes in my study were heavier and had a longer tarsus than those in uninsulated nest boxes. This suggests buffering of hot temperature extremes in the nest can mitigate sublethal impacts of high temperatures on chick development as well as improving survival. Similar results were found by Corregidor-Castro *et al*. (2023) in Lesser Kestrel chicks*,* where chicks in shaded (insulated) nest boxes had increased body mass and structural development compared to chicks in unshaded (uninsulated) nest boxes. Also, in support of this, in a warm Mediterranean habitat, experimental heating of nest boxes also resulted in chicks that were lighter and smaller than chicks in unheated nest boxes (Corregidor-Castro and Jones, 2021). On the other hand, in a cool habitat, heating nest boxes resulted in Tree Swallow chicks , that were heavier and had longer ninth primary feathers than those in unheated nest boxes (Dawson *et al*., 2005). Controlling nest box temperatures to minimise both hot and cold extremes may therefore have important impacts on chick growth and mass, as well as on chick survival.

Chicks in uninsulated nest boxes in hot and environments such as the Kalahari and Mediterranean (e.g. this study; Corregidor-Castro *et al*. 2023); or in heated nest boxes in climates that are already warm (e.g. Corregidor-Castro and Jones, 2021; Rodríguez and Barba, 2016) might be lighter because high nest temperatures mean they must invest a lot of resources into thermoregulation, particularly in evaporative water loss to keep themselves cool. Chicks that do not have the ability to regulate their body temperature particularly are not able to thermoregulate well and are sensitive to heat and therefore lose body mass through water loss (Diehl *et al*., 2023). If body temperatures become hyperthermic, this may also directly affect physiological performance (Boyles *et al*., 2011). Taken together, this may compromise body mass gain and structural growth (Corregidor-Castro *et al*., 2023; Diehl *et al*., 2023). At my study site in the Kalahari it is important to keep nests cool as it is already hot (air temperatures are regularly above 35ºC during the breeding season). In a changing climate, characterised by increasing temperatures, negative effects of extreme air temperatures could impair chick growth and create negative carry-over effects in species life histories in many habitats around the world (Salaberria *et al*., 2014; Rodríguez and Barba, 2016; Rodríguez *et al*., 2016; Eastwood *et al*., 2022).

Impacts of nest box insulation on nest box temperatures

Previous work on the hornbills showed that 70% of the negative effect of high temperatures on nest success was via nest box temperature, so a key goal of this study was to test whether the insulated box design and southeast orientation on the tree trunk could successfully bring down maximum daily nest temperatures (Tbox) in insulated boxes compared to uninsulated boxes. The nest box insulation intervention was successful in reducing Tbox for insulated boxes compared to uninsulated boxes.

Insulated boxes remained relatively cool (about 3°C cooler) regardless of whether the boxes were unoccupied or occupied (i.e. no female, eggs, or nestlings). Occupied insulated nest boxes were even cooler compared to occupied uninsulated nests, and temperatures in occupied insulated nest boxes increased more slowly with air temperature than those in occupied uninsulated boxes. This may be because the female and nestlings were able to thermoregulate better in insulated boxes, thus keeping box temperatures lower (Pattinson, 2023). Placing the insulated nest boxes on the southeast side of tree trunks, which is the side that has most shade during midday in the Southern hemisphere (Goldingay, 2015), likely contributed to the much cooler microclimate in the insulated than uninsulated nest boxes. The relative contribution of insulation and orientation on the tree trunk cannot be disentangled with my dataset but could be a useful focus of future studies.

However, my nestbox temperature results are in line with other studies of nest box temperature, for example Corregidor-Castro *et al.*'s 2023 study on Lesser Kestrels showed that shading of nest boxes effectively reduced maximum nest temperatures by approximately 3°C during heat waves. Furthermore, an experimental study on different nest box insulation materials in empty nest boxes in Australia also showed that nest box insulation usually decreased internal temperature of nest boxes (Larson *et al.*, 2018). Taken together, my study and these two other studies suggest that simple interventions in nest-box design and placement can have substantial impacts on nest temperatures, and therefore likely on nest outcomes, especially during hot weather. The differences that exist between these two studies and my study are mainly the location and study design as the Corregidor-Castro *et al.* (2023) study was in the Mediterranean during extreme heat events, and Larson *et al.* (2018) in Australia, tested nest temperatures on empty nests using different materials with insulative or reflective properties i.e. polystyrene, foil batts and reflective paint.

As shown by the results of my study and others (e.g. Dawson *et al.*, 2005; Boyles et al. 2011; Salaberria *et al.*, 2014; Rodríguez *et al.*, 2016; Rodríguez and Barba 2016; Eastwood *et al.*, 2022; Corregidor-Castro *et al.* 2023; Diehl *et al.*, 2023), thermally buffered nest boxes can be very beneficial to nestling survival, development and growth. Natural cavities arecooler and more thermally buffered than nest boxes (McComb and Noble, 1981; Maziarz *et al.*, 2017; Fischer *et al.*, 2018) and this is also true with respect to the uninsulated boxes and natural cavities at my study site

(Pattinson, 2023). However, Pattinson (2023) showed that our insulated boxes mounted on the southeast sides of trees provide very similar thermal environments to natural cavities at the study site. In an age where climate change is influencing avian fauna's laying dates, clutch size, hatching and fledging success, it is very important to provide nest boxes adapted to relevant environmental conditions (i.e. insulated boxes) to improve the reproductive outcomes of cavity-nesting fauna (Bodey *et al.*, 2021). All cavity-nesting and roosting fauna i.e. all vertebrates and invertebrates (especially mammals and birds) could benefit from thermally buffered (insulated) nest boxes especially in hot areas.

Study limitations and recommendations

The main limitation of my study was low sample sizes, especially in the nest box insulation experiment where I was able to collect data on only 20 nest attempts. I had a particularly low number of active uninsulated nests during the nestling stage as most nests failed before hatching. Chance confounds between chick age, air temperature and box type associated with the small sample size further reduced the number of chick measurements I was able to include in the analysis of air temperature * box type impacts on chick size and mass. Although the results of the nest box insulation experiment seem clear despite these limitations, a larger and more balanced sample size would allow more confidence in these results. The low numbers of breeding attempts I was able to study during the nest box insulation experiment is in keeping with the general decline in the study population associated with ongoing climate change, as documented by Pattinson *et al.* (2022), combined with poor rainfall during my study period due to a strong El Nino. This meant fewer breeding pairs, fewer nesting attempts and thus less available breeding success and chick growth data. Effects of climate change make it difficult to get consistent sample sizes at the study site. Increasing nest box supply in the study area and repeating the study for another season should be implemented to try and maximize sample sizes.

Given the findings of this study and other studies that show that thermal properties of nest boxes are important to consider under climate change (Catry and Sutherland, 2011; Larson *et al.*, 2018; Corregidor-Castro *et al.*, 2023), I recommend the widespread usage of insulated thermally buffered nest boxes in conservation projects for nest-box dependant species. The nestbox design and orientation I used in this study was effective, despite the fact that I cannot disentangle what proportion of the effect came from insulation versus orientation – something which requires further research. However, to enhance insulation properties of nest boxes for conservation projects in a warming world, I propose some additional measures. Firstly, material choice can improve nest box thermal properties. Larson *et al*. (2018) showed that different insulation materials had different effects on nest box thermal properties with some insulation materials working better under different scenarios (morning, mid-day, evening) than other materials. For example, foil batts and polystyrene reduced nest temperature during the day while reflective paint caused a small increase in nest temperature in the late afternoon (Larson *et al*., 2018). Materials such as thicker wood or plywood can be used to construct and insulate boxes to simulate thermal properties of natural cavities. Furthermore, household insulation materials such as foam and wool could be applied to insulate nest boxes (Aditya *et al*., 2017). Nest box designs with greater ventilation capabilities are also paramount especially in hot arid areas. For example, constructing nest boxes with double-ventilated walls which are boxes with insulation sleeves around them to create space for air to circulate around the nest box can aid in keeping the nest box cool especially in hot arid area (Ellis and Rhind, 2021). This double-ventilated wall is further cost effective and is environmentally friendly as it uses less materials reducing the footprint of building such nest boxes(Ellis and Rhind, 2021). A combination of the abovementioned could therefore maximize nest insulation properties of nest boxes in the long-term. Therefore, future work needs to fully investigate how different materials and nest box designs will further affect or improve thermal properties of insulated boxes especially in the hot and arid regions where less research has been conducted. There should also be more research to design nest box insulation that will be effective during extreme heat events like heat waves. This means continuous and innovative efforts to insulate nest boxes, which may need to include active cooling mechanisms for extreme heat events. Further conservation work also needs to consider investigating the benefits of nest box orientation in improving thermal properties of insulated boxes for cavity-nesting fauna as orientation may influence nest box microclimates (Ardia *et al*., 2006; Goldingay, 2015).

Conclusions

In conclusion, under current climate warming, global air temperatures are predicted to increase by 1.5°C in just two decades (IPCC, 2023). Habitat loss alongside climate change poses major threats to cavity-nesting species (Larson *et al*., 2015; Segan *et al*., 2016). In the Kalahari Desert the natural cavity-bearing tree camelthorn, in which the Southern Yellow-billed Hornbills and many other cavity-nesting species (such as rollers, woodhoopoes, barbets, etc), nest is in decline as a result (Raimondo *et al.,* 2009). Thus, there is likely to be an increasing need to supplement nesting sites for cavity-nesting species using nest boxes. However, nest boxes under climate change can become ecological traps if they are not well thermally buffered (Maziarz *et al*., 2017; Larson *et al*., 2018). My study investigated the role of insulated nest boxes to increase hornbill breeding success and improve chick body mass and tarsus length under climate change in a hot and arid area. The results of the study showed that these insulated boxes were able to achieve the above-mentioned role and allowed hornbills to overcome the negative effects of high air temperatures. Insulated nest boxes may therefore be important to improve chick growth, development, survival and nesting success of cavity-nesting species, such as the hornbills under climate change (Dawson *et al*., 2005; Rodríguez and Barba, 2016; Larson *et al*., 2018; Corregidor-Castro and Jones, 2021; Corregidor-Castro *et al*., 2023). Therefore, nest box conservation efforts should adopt the widespread use of insulated boxes to reduce mortality, improve nesting success and improve offspring growth of not just avian fauna but of all cavity-nesting species. Insulated boxes can only mitigate effects of climate change to a certain point, thus a change in human activities to reduce anthropogenic climate change should be acted on globally to reduce negative impacts of climate change on all fauna.

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