

# ECOGRAPHY

## Research article

### Integrating fine-scale behaviour and microclimate data into biophysical models highlights the risk of lethal hyperthermia and dehydration

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Climate change threatens biodiversity by compromising the ability to balance energy and water, influencing animal behaviour, species interactions, distribution and ultimately survival. Predicting climate change effects on thermal physiology is complicated by interspecific variation in thermal tolerance limits, thermoregulatory behaviour and heterogeneous thermal landscapes. We develop an approach for assessing thermal vulnerability for endotherms by incorporating behaviour and microsite data into a biophysical model. We parameterised the model using species-specific functional traits and published behavioural data on hotter (maximum daily temperature,  $T_{\max} > 35^{\circ}\text{C}$ ) and cooler days ( $T_{\max} < 35^{\circ}\text{C}$ ). Incorporating continuous time-activity focal observations of behaviour into the biophysical approach reveals that the three insectivorous birds modelled here are at greater risk of lethal hyperthermia than dehydration under climate change, contrary to previous thermal risk assessments. Southern yellow-billed hornbills *Tockus leucomelas*, southern pied babbler *Turdoides bicolor* and southern fiscal *Lanius collaris* are predicted to experience a risk of lethal hyperthermia on ~ 24, 65 and 40 more days year<sup>-1</sup>, respectively, in 2100 relative to current conditions. Maintaining water balance may also become increasingly challenging. Babblers are predicted to experience a 57% increase (to ~186 days year<sup>-1</sup>) in exposure to conditions associated with net negative 24 h water balance in the absence of drinking, with ~ 86 of those days associated with a risk of lethal dehydration. Hornbills and fiscals are predicted to experience ~ 84 and 100 days year<sup>-1</sup>, respectively, associated with net negative 24 h water balance, with ≤ 20 of those days associated with a risk of lethal dehydration. Integrating continuous time-activity focal data is vital to understand and predict thermal challenges animals likely experience. We provide a comprehensive

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thermal risk assessment and emphasise the importance of thermoregulatory and drinking behaviour for endotherm persistence in coming decades.

Keywords: behaviour, ecophysiology, hyperthermia, NicheMapR, thermal physiology

## Introduction

Biodiversity is threatened by rapid anthropogenic global warming, increasingly pushing species toward rapid decline (Urban 2015, Conradie et al. 2019, Pattinson et al. 2022). Animals are directly affected by increasing air temperatures ( $T_{\text{air}}$ ), which over time scales of decades may lead to morphological changes (Gardner et al. 2019) and restructuring or even collapse of communities (Riddell et al. 2019). Avian responses to high environmental temperatures span changes in both behaviour (e.g. panting, shade-seeking; Cunningham et al. 2021) and physiology (e.g. increased evaporative water loss, facultative hyperthermia; Dawson 1954, McKechnie et al. 2021a). The need to maintain body temperature ( $T_b$ ) below lethal limits (Dawson 1954, Boyles et al. 2011, McKechnie et al. 2021a) gives rise to tradeoffs between behavioural thermoregulation and activities such as foraging, with associated missed opportunity costs (Cunningham et al. 2021). Understanding the behavioural and physiological mechanisms underlying these tradeoffs, and the limits to behavioural and physiological thermoregulation, is vital for predicting species-specific climate vulnerability (Conradie et al. 2019).

Several authors have modelled species' exposure and sensitivity to weather conditions associated with risks of lethal dehydration and/or hyperthermia (Albright et al. 2017, Conradie et al. 2020, Ma et al. 2023) or sublethal fitness costs (Conradie et al. 2019) under recent and anticipated future conditions. However, models of dehydration and hyperthermia risk often assume that endotherms are resting in completely shaded microsites where operative environmental temperature ( $T_e$ ), which represents the thermal load experienced by an organism, is approximately equal to  $T_{\text{air}}$  (McKechnie and Wolf 2010, Albright et al. 2017, Conradie et al. 2019, 2020). Whether these assumptions are correct is unclear, and assuming  $T_e \approx T_{\text{air}}$  may underestimate the likelihood of acute heat exposure for active individuals experiencing  $T_e > T_{\text{air}}$  (Wolf and Walsberg 1996, Wolf 2000). For this reason, incorporating observed patterns of behaviour into risk assessment models for dehydration or hyperthermia may provide a better understanding of the risks that free-ranging species experience when average and maximum  $T_{\text{air}}$  increases.

When  $T_e$  exceeds body temperature ( $T_b$ ), birds rely on evaporative heat loss as the primary effective mechanism to maintain thermal homeostasis (Dawson 1954, Robinson et al. 1976), with maximum rates of evaporative heat loss under dry conditions in desert birds varying among taxa from  $< 150\%$  to  $> 500\%$  of metabolic heat production (McKechnie et al. 2021a). Rapid evaporative heat loss during extremely hot weather incurs substantial costs: small

birds may lose water equivalent to  $> 5\%$  of their body mass ( $M_b$ ) per hour via evaporative cooling, even while inactive in completely shaded microsites (Wolf and Walsberg 1996, McKechnie and Wolf 2010). Thus, a fundamental trade-off exists between avoiding hyperthermia by increasing evaporative water loss (EWL), and avoiding dehydration by conserving body water under high  $T_e$  (Dawson 1954, 1964). During extreme heat waves, birds may be exposed to conditions associated with lethal dehydration or hyperthermia, occasionally resulting in mass mortality events (Finlayson 1932, Saunders et al. 2011, McKechnie et al. 2021b).

Even under milder conditions, when  $T_{\text{air}}$  remains in the  $30\text{--}40^\circ\text{C}$  range, behavioural changes related to microsite use and activity can incur sublethal costs (du Plessis et al. 2012, Cunningham et al. 2015, van de Ven et al. 2019). On hot days, birds may seek shaded microsites, where foraging returns are lower (van de Ven et al. 2019, Orolowitz et al. 2023) or trade off foraging against heat dissipation behaviours such as panting, resulting in progressive  $M_b$  loss during periods of sustained hot weather (du Plessis et al. 2012, Gardner et al. 2016, Sharpe et al. 2019). In most species investigated so far, behavioural and foraging tradeoffs related to  $M_b$  maintenance generally become apparent when  $T_{\text{air}} \geq 35^\circ\text{C}$  (Cunningham et al. 2013b, Wiley and Ridley 2016, Bourne et al. 2020c, van de Ven et al. 2020), and may lead to sublethal fitness costs including reduced breeding success (Gardner et al. 2016, Sharpe et al. 2019, Kemp et al. 2020). Although less dramatic than mass mortality events, these sublethal fitness costs can result in population declines (Conradie et al. 2019, Ridley et al. 2021, Pattinson et al. 2022).

Drinking behaviour in desert birds depends on their ecology, with  $\sim 50\%$  of species inhabiting southern Africa's Kalahari Desert seldom (if ever) drinking, instead obtaining water from their diet and metabolic processes (Macleay 1984, Smit et al. 2019). Here, we aimed to improve dehydration and hyperthermia risk models for desert birds by incorporating empirical behaviour data for the entire diurnal cycle. This represents a significant shift from previous modelling efforts that have focused on the hottest period of the day and often assume that birds consistently rest in deep shade during hot periods (McKechnie and Wolf 2010, Albright et al. 2017, Conradie et al. 2019, 2020). We also evaluated how drinking dependence will change with increasing  $T_{\text{air}}$  and whether currently non-drinking species will be able to persist without changing their behaviour during very hot weather. We modelled EWL and  $T_b$  for three bird species widespread in the southern African arid zone under natural conditions in mid-summer. Two of the species typically do not drink, while the third can persist in the absence of drinking but regularly drinks when water is available. Species-specific biophysical

properties and published data on microsite use and other behaviours were used to inform a daily assessment of lethal dehydration and hyperthermia risk under recent and projected future climates.

## Methods

### Study system

Southern yellow-billed hornbills *Tockus leucomelas* (hereafter, hornbills), southern pied babblers *Turdoides bicolor* (hereafter, babblers) and southern fiscals *Lanius collaris* (hereafter, fiscals) are common and widespread bird species in the southern Kalahari Desert. The region is arid savanna, dominated by sparsely distributed camelthorn *Vachellia erioloba* trees and driedoring *Rhigozum trichotomum* bushes (Steenkamp et al. 2008). The Kalahari experiences hot summers (average daily summer maximum  $T_{\text{air}}$  of  $34.2 \pm 9.7^\circ\text{C}$ , December–March) and cool, dry winters with mean annual rainfall of  $\sim 186.2 \pm 87.5$  mm (van de Ven et al. 2019). The Kalahari Desert is warming rapidly, with the frequency of very hot days ( $T_{\text{air}} \geq 40^\circ\text{C}$ ) increasing over the last 20 years (Kruger and Sekele 2013, van Wilgen et al. 2016, Pattinson et al. 2022).

Hornbills and babblers forage predominantly on the ground (Kemp 1995, Ridley 2022), although hornbills occasionally hawk insects and both species glean in trees (Kemp 1995, Hunt et al. 2023). In contrast, fiscals are ‘perch-and-pounce’ hunters, seldom spending more than a few seconds at a time on the ground (Dean 2005). These distinct foraging behaviours are linked to different thermal landscapes, likely influencing the thermal risks experienced. Foraging locations for all three species were categorised as low (0 m: babblers and hornbills, 0.5–1.5 m: fiscals) or high perches ( $\geq 2$  m above ground). Babblers are able to obtain all their required water from their diet, but will readily drink when water is available and did so during the period over which the behaviour data included in this study were collected (Bourne et al. 2021a, b). Fiscals and hornbills, however, rarely drink even when water is available (Smit 2013).

### Behaviour and physiology data

Conradie et al. (2023) validated *NicheMapR* biophysical predictions of thermal responses for our three study species under standard metabolic chamber conditions, confirming the model adequately captures the sequence of physiological responses to heat exposure ( $T_{\text{air}} = 10\text{--}50^\circ\text{C}$ ). Here, we extended the validated *NicheMapR* models for these species to the complex thermal environments experienced by free-ranging individuals in their natural habitats. Similarly, biophysical models have previously been demonstrated to accurately predict field-active body temperature in other endotherms (Mathewson et al. 2020).

We used published behaviour data obtained from continuous time-activity focal observations of individual free-living birds over multiple breeding seasons (October–January) at

moderate to high  $T_{\text{air}}$  for breeding babblers (years: 2016–2019, Bourne et al. 2020c, 2021a), fiscals (years: 2011–2012, Cunningham et al. 2013a, b, 2015) and hornbills (years: 2012–2015, van de Ven 2017, van de Ven et al. 2019). These data were all collected at various times of the day, where an observer continuously recorded exposure (sun versus shade), location (low versus high perches) and behaviour (active versus resting), with the duration of each observed behaviour recorded to the nearest second. Concurrent measurements of  $T_{\text{air}}$  were obtained from weather station data at each site and averaged for each focal hour. The associated probability and duration of exposure and location were calculated across daily  $T_{\text{air}}$  and times of day (sunrise–10:59, 11:00–14:59, 15:00–sunset; Fig. 1). These data were subset into hotter (daily maximum  $T_{\text{air}}$ :  $T_{\text{max}} > 35^\circ\text{C}$ ) and cooler ( $T_{\text{max}} < 35^\circ\text{C}$ ) days, as a  $T_{\text{max}}$  of  $\sim 35^\circ\text{C}$  is associated with biologically important temperature thresholds above which sublethal fitness costs become apparent in all three species (Cunningham et al. 2013b, Wiley and Ridley 2016, Bourne et al. 2020a, b, c, van de Ven et al. 2020). Full descriptions of behaviour data collection, analysis and incorporation into the biophysical model are provided in the Supporting information.

The outputs of these behaviour calculations were used to assign hourly location and exposure combinations in our model, and the associated  $T_c$  values obtained from the microclimate model described below. The species-specific models developed here differ from previous biophysical models incorporating behaviour (Briscoe et al. 2016) by including detailed, continuous observations of behaviour in free-living individuals under natural conditions, rather than predicting behaviour based on an individual’s state and an associated predefined set of responses for that state (Briscoe et al. 2016).

### Microclimate model

To model the  $T_c$  likely experienced by each species, we employed a microclimate model using the *micro\_ncep* function of the ‘microclima’ and ‘NicheMapR’ biophysical modelling packages (version 3.0) in the R programming environment ([www.r-project.org](http://www.r-project.org)) using the R Studio (ver. 3.2.3) interface. Simulations were run for each of the two sites in the Kalahari Desert region where behaviour data had been collected, namely Kuruman River Reserve ( $26^\circ 58'S$ ,  $21^\circ 49'E$ ; babblers and hornbills) and Tswalu Kalahari Reserve ( $27^\circ 17'S$ ,  $22^\circ 23'E$ ; fiscals) under sun ( $\sim 10\%$  shade available) and shade (50–90% shade available) conditions and a combination of low (0 m: babblers and hornbills, 0.5–1.5 m: fiscals) and high perch ( $\geq 2$  m) scenarios. The shaded category simulated changes in the level of shadiness throughout the day based on the position of the sun and therefore the amount of sunlight striking the ground. The microclimate model derived using the *micro\_ncep* function integrates gridded climate data ( $\sim 200 \times 200$  km) interpolated from the NOAA-NCEP reanalyses program, downscaled to hourly resolutions between  $\sim 30$  cm and 3 m using digital elevation data and applying lapse corrections for each spatial coordinate independently (Kearney et al. 2019, Maclean et al.

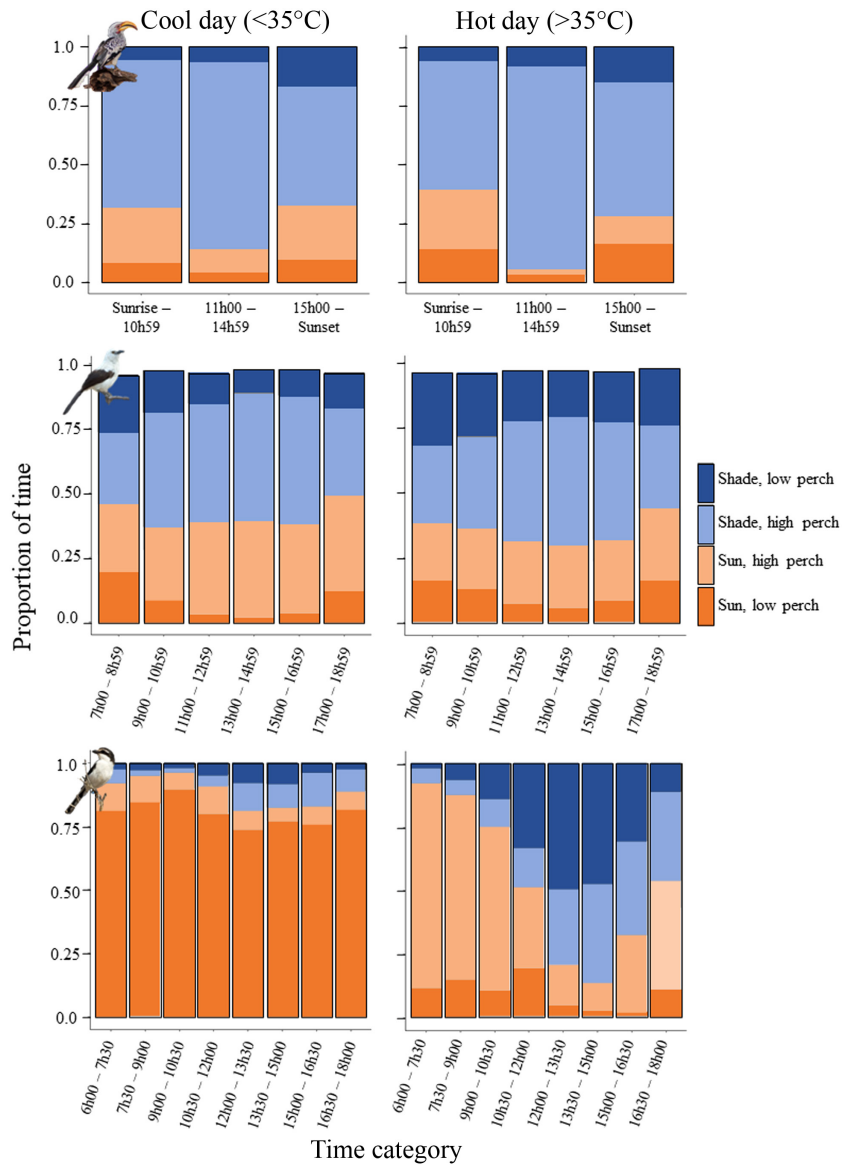


Figure 1. Time allocation to microsite use by southern yellow-billed hornbills *Tockus leucomelas* (van de Ven et al. 2019), southern pied babblers *Turdoides bicolor* (Bourne et al. 2020a, b, c, 2021a, b) and southern fiscals *Lanius collaris* (Cunningham et al. 2015) on cool [daily maximum air temperature ( $T_{\max}$ ) < 35°C] versus hot ( $T_{\max}$  > 35°C) days. Microsite categories were split into sun (< 10% shade), shade (> 50% shade), low perches (0 m: hornbills and babblers, 0.5–1.5 m: fiscals) and high perches (> 2 m). Babbler data included an out-of-sight category resulting in the proportions occasionally not summing to 1. Bird images courtesy of Warwick Tarboton.

2019). The microclimate outputs for each exposure/location combination included  $T_{\text{air}}$  (°C), surface temperature (°C), wind speed ( $\text{m s}^{-1}$ ) and relative humidity (%) which we used to model hourly  $T_c$  experienced by each species under recent conditions (2015–2020) and incorporated  $T_c$  into the respective species-specific biophysical models described below. Detailed description of the climate variables included in the microclimate model are provided by Maclean et al. (2019).

Future microclimate conditions (2080–2100) were modelled using an adjusted *micro\_ncep* function for a moderate-warming (~1.5°C increase in  $T_{\text{air}}$  globally, RCP 4.5, Supporting information) and high-warming future scenario (~ 4°C increase in  $T_{\text{air}}$  globally, RCP 8.5). Models were

adjusted using the forcing fields described by Mbokodo et al. (2020). These authors used an ensemble of conformal cubic atmospheric model downscalings from six global climate model projections under two emission scenarios (RCP 8.5 and RCP 4.5) across South Africa at ~ 50 km resolution. Projections for the southern Kalahari region were consistent with previous multi-modal forecasts for 2100 (IPCC 2014, Engelbrecht et al. 2015).

### Biophysical model

We used the endotherm component (Kearney et al. 2021) of *NicheMapR* to model EWL and  $T_b$  under likely  $T_c$  conditions

based on species-specific exposure-location predictions and  $T_{\text{air}}$ . The biophysical model uses museum measurements and first principles of thermodynamics to simultaneously solve for metabolic heat production and skin and feather temperature as required to balance the heat budget for a specified core  $T_b$  given conductive, convective, radiative and evaporative heat exchange with the surrounding environment (Kearney et al. 2021). We used museum specimens obtained from the Ditsong Museum of Natural History, Pretoria, South Africa ( $n=10$  per species, comprising 5 adult males and 5 adult females), to measure plumage characteristics and body dimensions following the methods described by Kearney et al. (2016) and Conradie et al. (2023). The model was adjusted from the default version which runs behaviour (i.e. posture) and physiological responses in a step-wise sequence, to simultaneously increase EWL and  $T_b$ . We further adjusted the model using *endoR\_devel* following Conradie et al. (2023), which starts with the bird in a heat-loss minimising posture and ptiloerect feathers and continues to heat-loss maximizing responses as skin temperature increases (Supporting information).

Once EWL, RMR and  $T_b$  were computed for each species in each respective exposure-location category, the behaviour model was used to inform the daily patterns of landscape use. The probability that each species was in one of the exposure-location combinations was multiplied by the predicted EWL or  $T_b$  for each time category over daytime hours (Supporting information).

For the purposes of modelling, we assumed that none of the three study species drank water (although babblers were observed drinking) and restricted water intake to preformed (dietary) water and metabolic water. Preformed water intake was estimated using information on average daily biomass of prey captured, where available, per microsite and time category (Supporting information, van de Ven et al. 2019, Bourne et al. 2021b). We used measured values of daily metabolic water production for babblers across a range of  $T_{\text{air}}$  (Bourne et al. 2021a, b), and allometrically estimated values for hornbills and fiscals using a similar approach to Kearney et al. (2016) (Supporting information). Net 24 h water loss was calculated for each species by including published overnight  $M_b$  loss values for hornbills (4.5%; van de Ven et al. 2019) and babblers (3.8%; du Plessis et al. 2012), whereas a value of 4% was assumed for fiscals based on their body mass. We assumed that individuals begin each day fully hydrated and do not carry over the effects of the 24 h water loss from the day before. Following Albright et al. (2017), we used a lethal dehydration threshold value of 15%  $M_b$  lost over  $\leq 5$  h. Although apparently severe dehydration was observed in the field for babblers (Bourne et al. 2021a), no instances of lethal dehydration or hyperthermia were reported in any of the published studies.

## Results

Exposure to lethal dehydration was predicted on  $\sim 8$  days year<sup>-1</sup> under recent conditions for babblers (assuming no

drinking), whereas the risk for lethal dehydration was zero for hornbills and minimal for fiscals (Fig. 2). By 2100, under unmitigated climate change conditions (RCP 8.5 2080 – 2100), babblers and fiscals are predicted to be at risk of lethal dehydration for  $\sim 86$  and  $\sim 20$  more days year<sup>-1</sup>, respectively (Fig. 2 and 4). In contrast, the risk of lethal dehydration is predicted to remain low for hornbills, with no days exceeding the lethal dehydration threshold under anticipated future conditions (RCP 8.5, Fig. 2).

Babblers and fiscals faced  $\sim 118$  and 59 days year<sup>-1</sup>, respectively, of negative 24-h water balance under recent conditions, assuming no drinking (Fig. 2). By 2100, exposure to net negative 24-h water balance is predicted to increase by 57% to  $\sim 186$  days year<sup>-1</sup> for babblers,  $\sim 115$  days year<sup>-1</sup> for fiscals and  $\sim 84$  days year<sup>-1</sup> for hornbills. To avoid lethal dehydration, babblers need to gain water (including dietary and metabolic water) equivalent to  $\sim 10\%$   $M_b$  per day currently, increasing to  $\sim 12\%$   $M_b$  per day by 2100.

Defending  $T_b$  at sublethal levels is predicted to become increasingly challenging and poses a greater risk than lethal dehydration for all three species over the coming decades. Under recent conditions, only babblers (assuming no drinking) are predicted to experience mean  $T_b$  approaching their maximum  $T_b$  ( $T_{b,\text{max}} = 44.8^\circ\text{C}$ ; Fig. 3), whereas fiscals and hornbills are predicted to maintain mean  $T_b$  at sublethal levels throughout the heat of the day during summer months (October–February; Fig. 3). By 2100, lethal hyperthermia risk during the hottest part of the day is predicted to increase, with all three species predicted to experience  $> 20$  days per summer with mean  $T_b > 44.5^\circ\text{C}$  during at least one time category (Fig. 3). Hornbills and fiscals are predicted to experience  $\sim 24$  and 40 more days year<sup>-1</sup>, respectively, where  $T_b > 44.5^\circ\text{C}$  by 2100 (Fig. 3 and 4). Fiscals are predicted to experience substantial variation in mean  $T_b$  in the future due to strong behavioural shifts on hot compared to cool days (Fig. 1 and 3c). Combined risk, where cumulative EWL reaches dehydration tolerance limits and  $T_c$  exceeds maximum  $T_{\text{air}}$  tolerated before the onset of severe hyperthermia, is predicted to increase substantially for babblers but to remain low for hornbills and fiscals, likely due to higher patterns of activity in exposed sites on hot days in babblers (Fig. 4).

## Discussion

Our inclusion of continuous time-activity observations of behaviour into a mechanistic model suggests that previous models (primarily assuming inactive birds in shaded sites) may underestimate thermal risks under natural conditions. Our analysis reveals substantial variation in exposure to acute lethal risk, assuming no drinking, in three desert birds under recent and projected future climates. Babblers and fiscals are predicted to already occasionally encounter conditions associated with negative 24 h net water balance, the consequences of which have been observed for babblers in the field (Bourne et al. 2021a). Only babblers are predicted to experience conditions associated with lethal dehydration (15%  $M_b$

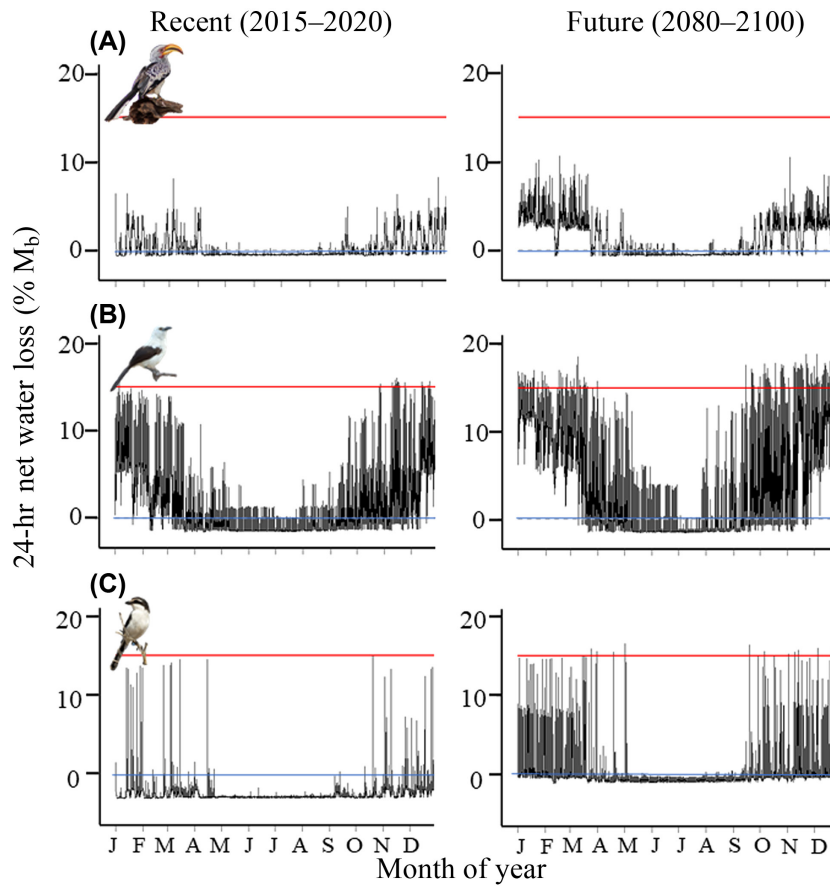


Figure 2. Predicted 24 h water loss ( $\% M_b$ ) assuming no drinking as a function of predicted evaporative water loss and water influx (dietary and metabolic water) for southern yellow-billed hornbills *Tockus leucomelas* (A), southern pied babblers *Turdoides bicolor* (B) and southern fiscals *Lanius collaris* (C) estimated from modelled environmental temperature under recent (2015–2020) and a high-risk future scenario (RCP 8.5; 2080–2100). Environmental temperatures were modelled based on the probability of exposure (sun versus shade) and location (low perch versus high perch) throughout the day (7–18 h) using the ‘NicheMapR’ package. Red lines indicate lethal dehydration risk (cumulative EWL  $\sim 15\% M_b$ ), and blue lines indicate 24 h net zero water loss. Bird images courtesy of Warwick Tarboton.

loss) currently. Our behaviourally informed model revealed a greater risk of lethal hyperthermia than dehydration, for all three species, contrary to previous thermal risk assessment models (Conradie et al. 2020). We note that neither mass loss to this extent nor death of adult birds as a result of dehydration or hyperthermia have been observed in the field to date (Du Plessis et al. 2012, Bourne et al. 2021a). The absence of hydration-related mortality reported by Bourne et al. (2021a) during their study of free-living babblers likely reflects that most individuals in the study population used in our model were observed drinking water daily.

### Predicting thermal and hydric exposure

Access to water may influence thermoregulation (i.e. evaporative cooling) and behaviour (i.e. shade use), potentially mitigating the impacts of high heat loads. Increasing water dependence may result in higher predation pressure at water sources (Cade 1965, Sirot et al. 2016), possibly changing population dynamics within the Kalahari system. In the absence of drinking, facultative drinkers may adjust their

behaviour, using the thermal landscape differently to select cooler microsites and reduce thermal risks, whereas conspecifics with access to water may engage in riskier thermal behaviour (e.g. panting) than would be sustainable under hot conditions if they were unable to drink (A.R Bourne pers. comm. 2019, Orolowitz et al. 2023).

Among the species modelled here, babblers are predicted to experience the greatest increase in acute dehydration risk ( $\sim 57\%$  by 2100), because of increased water demands associated with riskier thermal behaviour (e.g. foraging activity in exposed sites). We expect that they were able to engage in these riskier behaviours because the babblers for which we had detailed behaviour data had access to water and were therefore able to drink and mitigate water loss in that way. Species that are currently non-drinkers may be forced to drink under conditions where evaporative cooling demands exceed metabolic water available for thermoregulation in already hot systems. For instance, fiscals have been recorded drinking water on days where  $T_{\max} > 35.3^\circ\text{C}$  (Smit 2013). Similarly, several small insectivorous birds such as grey tit-flycatcher *Myioparus plumbeus* and willow warbler *Phylloscopus*

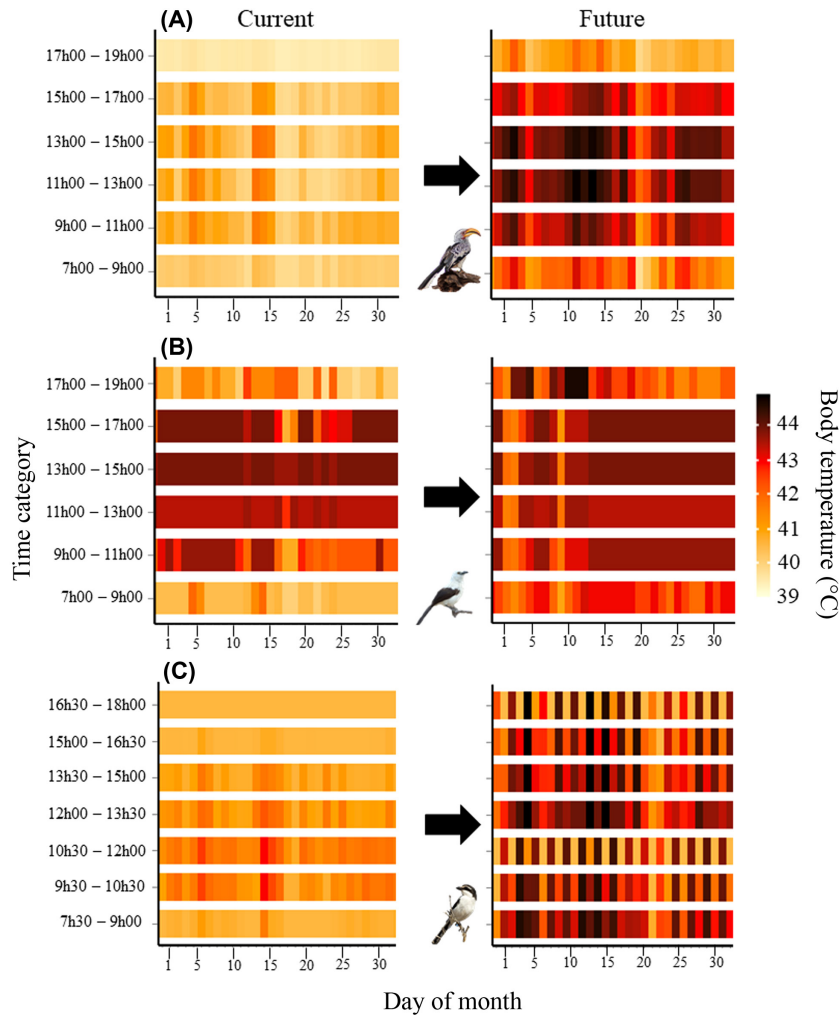


Figure 3. Predicted average body temperature ( $T_b$ ) in southern yellow-billed hornbills *Tockus leucomelas* (A), southern pied babblers *Turdoides bicolor* (B) and southern fiscals *Lanius collaris* (C) for each day of an average month in summer (averaged over October–February) as a function of modelled microsite conditions under recent (2015–2020) and a high-risk future scenario (RCP 8.5; 2080–2100). Microsite conditions were modelled based on the behavioural probability of exposure (sun versus shade) and location (low perch versus high perch) throughout the day (07–19 h) using the ‘NicheMapR’ package. The bar code-like pattern, evident particularly for fiscals under future conditions, arises from the sharp contrast in behavioural repertoire assigned for days on which  $T_{max} > 35^\circ\text{C}$  compared to cooler days. Bird images courtesy of Warwick Tarboton.

*trochilus*, which are typically described as non-drinking birds, were observed drinking on an extremely hot day in northern Kwa-Zulu Natal, South Africa (A.S. Riley pers. comm. 2019). In contrast, red larks *Calendulauda burra* under conditions of extreme heat never drank even when offered water in captivity (M.T. Freeman and R. Kemp pers. comm. 2019).

As hot days become more frequent, birds are predicted to be less able to maintain  $M_b$  and water intake due to compromised foraging success and increased EWL (Conradie et al. 2019). Our model predicts that all three species will experience an increase in the number of days with  $\sim 8\text{--}10\%$  net 24 h  $M_b$  loss by 2100. These  $M_b$  loss conditions may not result in acute mortality, but repeated exposure could be lethal unless individuals alter their behaviour and/or have continuous access to ad libitum food and water. Reduced  $M_b$  has been associated with reduced survival in adult birds (Gardner et al.

2019) and nestlings (Todd et al. 2003, Schwagmeyer and Mock 2008, Bourne et al. 2020b), and lower likelihood of attaining breeding status in babblers (Raihani et al. 2010), exacerbating sublethal fitness consequences by negatively affecting recruitment. Additionally, there are documented mass mortality events linking drinking behaviour to elevated risks of lethal hyperthermia (Finlayson 1932, Towie 2009), presumably due to metabolic heat production associated with activity such as flight. Similarly, behaviours such as nest building, provisioning and incubation may increase  $T_b$  (Bourne et al. 2021a, b), presenting an additional tradeoff between activity and hyperthermia avoidance.

Our model predicts more frequent exposure to conditions under which lethal hyperthermia, rather than dehydration, is possible compared to previous models (Conradie et al. 2019). The model of Conradie et al. (2019) differs from ours by

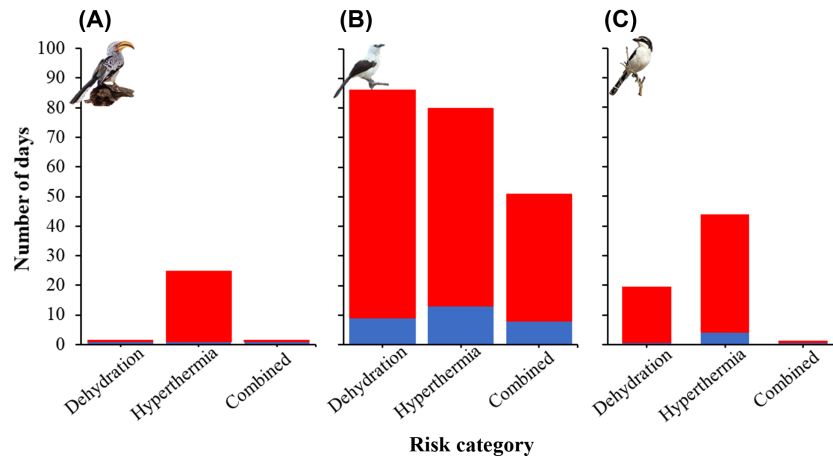


Figure 4. Predicted number of days per summer on which environmental conditions, behaviour and water intake result in a meaningful risk of dehydration, hyperthermia or both for southern yellowbilled hornbills *Tockus leucomelas* (A), southern pied babblers *Turdoides bicolor* (B) and southern fiscals *Lanius collaris* (C) under recent climate conditions (2015–2020, blue) and a high-risk future climate scenario (RCP 8.5 2080–2100, red). Bird images courtesy of Warwick Tarboton.

assuming that  $T_{\text{air}} \approx T_c$  for free-ranging birds and modelled thermal risks during the hottest time of day. In contrast, we incorporate empirical behaviour data collected throughout the day, including observations of birds being active and occupying exposed sites, during the hottest part of the day. Incorporating microsite use throughout the day allowed us to model  $T_c$  experienced by free-ranging birds and better characterize thermal landscapes used.

### Assumptions and limitations

Our model is based on several assumptions, including that all species obtain all their water through diet. While hornbills and fiscals likely meet this assumption, babblers will drink water and did so in the behaviour data used here (Bourne et al. 2021a). Access to water likely influences thermoregulatory behaviours (e.g. shade use, Smit et al. 2016, Orolowitz et al. 2023), and may explain the high modelled thermal risks predicted for babblers despite death by hyperthermia or dehydration not being observed in the field. The high frequency of days with predicted net negative 24 h water balance suggest that babblers may not survive on dietary water alone in the future, in the absence of significant behaviour adjustments (e.g. shifting activity to cooler times of day).

We assumed that the behaviour data used here represent the full suite of behavioural responses to high  $T_{\text{air}}$  available to the modelled species and will be representative of future behaviours under climate change. Temperatures exceeding core  $T_b$  are predicted to become increasingly common in the Kalahari (Engelbrecht et al. 2015) and may lead to behavioural changes previously not recorded due to the limited sample size of days with  $T_{\text{air}} > 40^\circ\text{C}$  in the observational data used here (babblers and hornbills: < 10 days, fiscals: zero days). For example, babblers could spend more time at the base of trees or in cooler burrows than in the low perch shade category used here (Bourne and Soravia 2023). Affected

species may reduce breeding effort (Bourne et al. 2020a), forgo breeding (Pattinson et al. 2022) or become increasingly crepuscular (Moore et al. 2018). Behavioural plasticity in physiological heat tolerance may alter exposure to high heat loads and result in a different suite of thermal risks associated with foraging under high  $T_{\text{air}}$ . Our understanding of behavioural plasticity in relation to thermoregulation is limited, but there is evidence of behavioural flexibility in individuals within the same study population depending on group size, surface water availability and shade available (Whyte 2023). Additionally, traits relating to heat tolerance show flexibility in acclimation and acclimatization studies (McKechnie and Wolf 2004, Mariette and Buchanan 2016, Noakes et al. 2016). Behavioural flexibility may be enough to withstand increases in average conditions, but will likely be insufficient for extreme events (Papalexioiu et al. 2018).

Lastly, we assumed that the biophysical model adequately represents the relationship between thermoregulation and other environmental factors such as humidity, wind speed and solar radiation. The biophysical model was validated under respirometry conditions with low humidity, no wind and no solar radiation (Conradie et al. 2023), although the package can account for these environmental factors, as we have shown here. Including these factors has not been critically evaluated and tested in natural conditions, and our understanding about the interactions between evaporative cooling,  $T_b$  and humidity remains limited (but see van Dyk et al. 2019, Freeman et al. 2024). Additionally, it is important to note that the *NicheMapR* microclimate model is not spatially explicit, as simulations are run independently at each spatial coordinate through time. The model outputs are therefore limited in their ability to fully capture how landscape heterogeneity and habitat features influence the microclimates experienced by an organism moving across the landscape.

Our analysis provides mechanistic insights into desert birds' sensitivity and exposure to heat, accounting for

physiological tolerances, observed behaviour under natural conditions and the thermal landscape. We argue that the inclusion of continuous time-activity focal observations of behaviour provides more realistic predictions of lethal risks associated with acute heat exposure than previous models (Albright et al. 2017, Conradie et al. 2019). In coming decades, prolonged exposure to hyperthermic conditions coupled with rapid EWL is potentially unsustainable, and may contribute to extinctions in areas with significant anthropogenic warming.

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#### Author contributions

**Shannon R. Conradie:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Writing - original draft (lead); Writing - review and editing (equal). **Blair O. Wolf:** Conceptualization (equal); Supervision (supporting); Writing - review and editing (equal). **Susan J. Cunningham:** Conceptualization (equal); Data curation (equal); Supervision (supporting); Writing - review and editing (equal). **Amanda Bourne:** Data curation (equal); Writing - review and editing (equal). **Tanja van de Ven:** Data curation (equal); Writing - review and editing (equal). **Amanda R. Ridley:** Data curation (equal); Writing - review and editing (equal). **Andrew E. McKechnie:** Conceptualization (equal); Funding acquisition (lead); Supervision (lead); Writing - review and editing (equal).

#### Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/ecog.07432>.

#### Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.zgmsbccnh> (Conradie et al. 2024).

The NicheMapR release relevant to this study (v3.0.0) and the endotherm component are both available via Zenodo (Kearney 2021).

#### Supporting information

The Supporting information associated with this article is available with the online version.

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