An evaluation of a biophysical model for predicting avian thermoregulation in the heat

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Summary Statement

We present an evaluation of a biophysical model's performance, sensitivity and usability for predicting avian thermoregulation in the heat, improving on previous models' performance across temperatures linked to sublethal fitness costs.

Abstract

Survival and reproduction of endotherms depend on their ability to balance energy and water exchange with their environment, avoiding lethal deficits and maximising gains for growth and reproduction. At high environmental temperatures, diurnal endotherms maintain body temperature (T_b) below lethal limits via physiological and behavioural adjustments. Accurate models of these processes are crucial for predicting effects of climate variability on avifauna.

We evaluated a biophysical models' performance (NicheMapR) for predicting evaporative water loss (EWL), resting metabolic rate (RMR) and T_b at environmental temperatures approaching or exceeding normothermic T_b for three arid-zone birds: Southern Yellow-billed Hornbill (*Tockus leucomelas*), Southern Pied Babbler (*Turdoides bicolor*) and Southern Fiscal (*Lanius collaris*). We simulated metabolic chamber conditions and compared model outputs to thermal physiology data collected at air temperatures (T_{air}) between 10 °C and 50 °C. Additionally, we determined the minimum data needed to accurately model diurnal birds' thermoregulatory responses to T_{air} using sensitivity analyses. Predicted evaporative water loss, metabolic rate and T_b corresponded tightly with observed values across T_{air}, with only minor discrepancies for EWL in two species at $T_{air} = \sim 35$ °C. Importantly, the model captured responses at $T_{air} = 30 – 40$ °C, a range spanning threshold values for sublethal fitness costs associated with sustained hot weather in arid-zone birds. Our findings confirm how taxon-specific parameters together with biologically relevant morphological data can accurately model avian thermoregulatory responses to heat. Biophysical models can be used as a non-invasive way to predict species sensitivity to climate, accounting for organismal (e.g., physiology) and environmental factors (e.g., microclimates).

Introduction

For diurnal endotherms inhabiting hot environments, rapid anthropogenic global heating is exacerbating the challenges of maintaining energy and water balance (Parmesan, 2006; Urban et al., 2016). During hot conditions, endotherms maintain body temperature (T_b) below lethal limits via physiological and behavioural processes (Dawson, 1964, 1954; McKechnie et al., 2021a). Increasingly intense heat waves exert direct pressure on water budgets (Albright et al., 2017; Riddell et al., 2019), occasionally exceeding the physiological ability of endotherms to avoid lethal dehydration and/or hyperthermia (Albright et al., 2017; McKechnie et al., 2021b; McKechnie and Wolf, 2010; Ratnayake et al., 2019), as illustrated by a number of recent heat-related mass mortality events (Holt and Boersma, 2022; McKechnie et al., 2021b; Quintana et al., 2022; Sloane et al., 2022). Additionally, the increased duration and frequency of sustained hot weather places indirect pressure on endotherms through missed-opportunity costs arising from trade-offs between thermoregulation and activities such as foraging (Cunningham et al., 2021). Among birds, functional links between hotter conditions and fitness costs are becoming increasingly apparent for a handful of well-studied species [e.g., Carroll et al., 2015; du Plessis et al., 2012; Edwards et al., 2015; Kemp et al., 2020; Sharpe et al., 2019; van de Ven et al., 2019] but remain unexplored for most species.

Physiological thermoregulatory responses (e.g., evaporative cooling) to changing environmental conditions have been studied by extrapolating empirical laboratory data to the field via regression models (e.g., McKechnie & Wolf, 2010). Such approaches are limited by challenges of translating results from simple laboratory thermal environments to complex natural ones, and because the accuracy and applicability of the model is a direct function of the amount of data and range of conditions studied. Alternatively, thermoregulatory responses can be predicted using biophysical models that integrate functional traits of organisms and their environment via heat exchange models to predict T_b, metabolic rates and water loss in response to complex and often variable natural conditions (Porter and Gates, 1969; Porter et al., 1973; Tracy, 1976). The exchanges of heat and water are tightly coupled and can be defined mathematically based on universal physical and biological principles (Porter and Gates, 1969) and used to predict species' environmental responses given their functional traits (Kearney et al., 2021). Biophysical models have been used to understand the role of thermoregulation in buffering species from increasingly extreme conditions associated with climate change (Kearney et al., 2009, 2013; Kearney and Porter, 2017; Malishev et al., 2017; Mathewson et al., 2016), and to evaluate the cost of increased cooling requirements (Riddell et al., 2021, 2019). Additionally, biophysical models have been shown to predict metabolic rate better than allometric models in White-footed Sportive Lemurs (*Lepilemur leucopus*; Stalenberg, 2019). However, empirical data are needed to test and parameterise these models to appropriately capture species-specific behavioural and physiological responses, particularly under environmental conditions on the upper edge of the thermoneutral zone. Once tested, these models can be used to predict species responses under any given combination of environmental conditions, or to explore the thermoregulatory responses available to organisms within the constraints of thermodynamics.

Although biophysical models have a long history (Briscoe et al., 2022), they have often been challenging to apply because of limited documentation, closed-source code and convoluted pipelines for integrating data on traits and environments. The recently developed NicheMapR biophysical modelling package, is an open-source program which aims to provide ecologists with an accessible and flexible suite of tools for analysing, visualizing and predicting energy and mass budgets of species, including endotherms. The package is based on the original work of Porter and his colleagues for modelling heat balance across taxa by solving steady-state heat budgets (Kearney and Porter, 2017; McCullough and Porter, 1971; Porter et al., 1973). The release of the NicheMapR endotherm model (Kearney et al., 2021) resolves previous accessibility issues and provides new opportunities to understand and predict responses of birds and mammals to their environments. The model operates under user-specified microclimate conditions and is based on species' morphological and physiological functional traits. Appropriate functional trait data are therefore essential, and can either be obtained directly or inferred from species that are phylogenetically-closely related and/or ecologically similar (e.g. Kearney et al., 2016).

Here, we evaluate the endotherm model of NicheMapR for predicting evaporative water loss (EWL), resting metabolic rate (RMR) and T_b for three southern African arid-zone birds, Southern Yellow-billed Hornbill (*Tockus leucomelas*), Southern Pied Babbler (*Turdoides bicolor*) and Southern Fiscal (*Lanius collaris*). These species differ in patterns of behavioural thermoregulation, foraging mode and use of cool microsites in their arid savanna habitats. Biologically-important daily maximum air temperature (T_{air}) thresholds exist in the 30 – 40 °C range, above which sublethal fitness costs related to body mass maintenance and breeding success have been documented for all three species (Cunningham et al., 2013; du Plessis et al., 2012; van de Ven et al., 2019). Moreover, physiological adjustments, including changes in thermal conductance, T_b and EWL, begin to occur within this range of T_{air} values, and upper critical limits of thermoneutrality are often within this same range (McKechnie et al., 2021a). We thus focused on 1) evaluating NicheMapR's ability to adequately predict thermal responses of birds by comparing the accuracy of the respective model outputs to empirically collected thermal physiology data at T_{air} values between 30 and 40 °C and under very hot conditions when $T_{air} > T_b$, and 2) evaluating the sensitivity of the model to parameter changes and assessing whether accurate predictions can still be obtained with limited empirical data and biophysical modelling knowledge. We used a combination of measurements from museum specimens (e.g., plumage depth, body length) and published physiological information on thermal responses (e.g., heat tolerance limit, basal metabolic rate) to parameterise biophysical models for these three species. The model was set up to represent simulated metabolic chamber conditions, which were then tested against empirical EWL, RMR and T_b data collected under laboratory conditions.

Materials and methods

Study system and species

All three species are widespread and common in the southern Kalahari Desert. The area experiences hot summers and cool, dry winters with a mean annual rainfall of ~221 mm and average daily summer maximum T_{air} of ~ 33 - 37 ˚C (Fick and Hijmans, 2017). The southern Kalahari region is experiencing rapid warming, making it particularly vulnerable to the negative effects of climate change. For instance, the Kgalagadi Transfrontier Park spanning South Africa and Botswana has experienced warming of 0.039 ± 0.007 SE ˚C year^{-1} and annual mean maximum temperatures have increased by 1.95 ˚C since 1960 (Moise and Hudson, 2008; van Wilgen et al., 2016).

Southern Yellow-billed Hornbills (hornbills, *Tockus leucomelas*) and Southern Pied Babblers (babblers, *Turdoides bicolor*) forage predominantly on the ground, with hornbills occasionally hawking flying insects and gleaning in trees (Kemp, 1995). In contrast, Southern Fiscals (fiscals, *Lanius collaris*) hunt for their prey by perching predominantly on exposed posts or branches and pouncing on invertebrates and small vertebrates (Dean, 2005; Hockey et al., 2005). Data on interactions between metabolic heat production, evaporative heat loss and the consequent patterns of T_b at moderate to high T_{air} are available for these three species (Czenze et al., 2020; van Jaarsveld et al., 2021). Data were collected using standardized respirometry methods involving exposure to stepped series of progressively higher T_{air} at very low chamber humidities (Czenze et al., 2020). We collected additional data for hornbills at T_{air} = 10 – 25 °C during summer (October – November 2020, n = 10), near the south-eastern edge of the Kalahari Desert [Radnor Farm (26˚6'23''S, 22˚52'54''E)] in South Africa. We used a flow-through respirometry system as described by van Jaarsveld et al. (2021) to measure oxygen consumption, carbon dioxide production and EWL at T_{air} values between 10 ˚C and 25 ˚C. Birds were fasted for 24 h and individually placed in a ~17-L airtight chamber positioned inside a ~195-L modified chest freezer used as a temperature control unit. In brief, atmospheric air from an oil-free compressor was filtered through a membrane dryer (Champion®CMD3 air dryer and filter, Champion Pneumatic, Quincy IL, USA) to remove any water vapour present. The filtered atmospheric air was regulated using a mass flow controller (0-30 SLPM, Alicat Scientific Inc., Tuscon, AZ, USA), entering the chamber through an inlet fitted near the top of the chamber. Birds were exposed to each T_{air} value (T_{air} = 10, 15, 20, 25 ˚C) for ~ 1.5 hours during daytime runs where flow rates were regulated at 6 – 11 L min^{-1} (usually ~7 L min^{-1}) depending on the bird's behaviour and chamber humidity (< 1 kPa). All experimental protocols were approved by the University of Pretoria Animal Ethics committee (protocol NAS058/2020), the Animal Research and Scientific Ethics Committee of the South African National Biodiversity Institute (protocol P18-12) and the Northwest Parks Board (permit 26026).

Museum measurements

We obtained measurements from museum specimens at Ditsong Museum of Natural History, Pretoria, South Africa (n = 10 per species, comprising 5 adult males and 5 adult females) following the methods described by Kearney et al., (2016). Specifically, we measured the depth of plumage at multiple locations (~ 20) on the dorsal and ventral sides (~ 10 per side) from the top of the shoulder to the base of the tail, as well as the length of feathers (~ 3 per side) for all three species. These measurements were collected using a standard measuring tape, measuring rod and string. Shape estimates for each species were derived by measuring relative dimensions (length from the beak to the base of the body, width, and depth at the shoulder).

Avian biophysical model

To model EWL, RMR and T_b under standard metabolic chamber conditions (i.e., operative temperature equivalent to T_{air}) we used the endotherm model (function endoR_devel) of the NicheMapR biophysical modelling package (version 3.1) in the R programming environment (Version 1.2.5033, (Team, 2015) using the R Studio (version 3.2.3) interface. The model setup has been described in detail elsewhere (Kearney et al., 2021) but, in brief, consists of a suite of subroutines to solve coupled heat and water budgets given a set of physiological and morphological traits that can be configured to match species-specific behavioural thermoregulatory sequences under specific environmental conditions for every hour of the day. The model computes the RMR and EWL necessary to maintain T_b given conductive, convective, radiative and evaporative heat exchange with the surrounding environment by calling a set of routines from a Fortran library using the endoR_devel interface in R (Kearney et al., 2021). The endoR_devel function allows the user to code behaviour and thermoregulatory responses configured for a species from the default version in R (Kearney et al., 2021). As described below, we adjusted the endoR_devel code to represent the general behavioural and physiological requirements of a bird, which was then used as the baseline model for all three species. The species-specific input biophysical traits (e.g., body dimensions, Table 1) and physiological responses (e.g., respiratory rate, Table 1) were then used to~~to modify the~~ parameterise the general bird model for each species (Table S1 & 2). Thereafter, we compared the outputs from the default endoR_devel code with the outputs from the aforementioned adjusted endoR_devel code (online appendix: https://github.com/ShannonConradie1/NicheMapR-endoR_devel_edited.git).

Thermoregulatory response parameterization

Our main objective was to examine model performance and establish whether predicted relationships between environmental temperature and thermoregulatory responses were consistent with observed thermal physiology. We predicted EWL, RMR and T_b for hornbills, babblers and fiscals at rest under standard metabolic chamber conditions [i.e. incremental increases in T_{air} (0 – 55 °C), low relative humidity (5%) and wind speed (0.01m/s^{-1}), no solar heat gain (Lustick, 1969)] and compared the model output to thermal physiology data collected here and previously (Czenze et al., 2020; Cunningham et al., unpublished data; van Jaarsveld et al., 2021). Model performance was determined based on the agreement between model outputs and thermal physiological data, where we considered good agreement if 95% of model output values across T_{air} fell within the range of observed values. The default model parameterisation has been described by Kearney et al., (2021) but, in brief, begins with physiological settings anticipated under cold conditions and simultaneously solves for metabolic heat production, skin and feather/fur temperature that balances the heat budget for a specified core T_b. If predicted metabolic heat production is lower than the specified minimum (e.g., basal metabolic rate for a resting individual), a series of species-specific behaviours and physiological responses are invoked such as altering posture, increasing flesh thermal conductivity, panting and allowing core T_b to rise. The main adjustments we made to the base endoR_devel model involved allowing for ptiloerection of feathers at T_{air} values below the thermoneutral zone, where feather depth begins at feather length and is progressively sleeked to normal as T_{air} increases (Fig. S1). Here we also adjusted the sequence of behavioural responses to start with an endotherm in a heat-loss minimising posture, with ptiloerect feathers and proceed to heat-loss maximizing responses as skin temperatures increase (see Github: https://github.com/ShannonConradie1/NicheMapR-endoR_devel_edited.git for full code):

1. flatten feathers to normal position,
2. change posture (uncurl),
3. increase conductivity of flesh,
4. simultaneously increase T_b and EWL.

This sequence contrasts that of the default model parameterization which initiates a stepwise sequence of behavioural responses (Fig. S1). Allowing changes in T_b and EWL to occur simultaneously resulted in a more gradual increase in T_b, accounting for interactions between EWL, RMR and T_b. We modelled thermoregulation for each of the three bird species following the aforementioned sequence of responses, and only changed input parameters relating to morphology (measured), target core and maximum T_b, respiratory rate and skin wetness (inferred from empirical data) to species-specific values (see Table S1 & 2 for full parameter descriptions).

Hornbill model sensitivity analysis

We ran a sensitivity analysis for the hornbill model only, because the empirical dataset for this species spans a wide range of diurnal T_{air} values (T_{air} = 10 – 50 °C) likely experienced by the species, whereas the other two species' datasets are only for $T_{air} > 30$ °C. We used the hornbill model to evaluate whether accurate predictions of avian thermoregulation can still be obtained with limited species-specific empirical data and biophysical modelling knowledge. We quantified the sensitivity of the hornbill model to input variables by adjusting morphological and physiological values to determine their effect on the predicted EWL, RMR and T_b inflection points (i.e. T_{air} above which each variable dramatically increased) and slopes (i.e. relationship between T_{air} and each variable, for T_{air} above the respective inflection points). Additionally, we determined the hornbill model's sensitivity to low (100 W m^{-2}) and high (900 W m^{-2}) short wave solar radiation by changing the QSOL input parameter in NicheMapR, assuming all other variables remain the same. We fitted a piecewise linear regression model (*Sizer* package, Sonderegger 2021) to model outputs (EWL, RMR and T_b) in order to identify changes in predicted inflection points and segmented general linear models (*lme4* package, (Bates et al., 2015) to identify changes in the predicted relationship between EWL, RMR, T_b and T_{air} in hornbills (i.e. slopes). Specifically, sensitivity of the predicted relationship between EWL, T_b and T_{air} to input parameters were assessed because of the importance of variation in these parameters in predicting species vulnerability to lethal dehydration and hyperthermia (Albright et al., 2017; Conradie et al., 2020). Cohen's *d* values (*effsize* package, (Torchiano, 2020) were used to assess the effect sizes of the change in the response variable (i.e. EWL, RMR and T_b) for over- and under-estimating biophysical input variables (Cohen, 1992, 1977). Here, deviations in predictions were scaled using the residual variation in the empirical dataset. These analyses were conducted under the simulated metabolic chamber conditions described above, minimising the effects of environment and bird behaviour. All user-specified variables were held constant except for the one being evaluated, which was varied within biologically realistic values based on observed among-individual variation and known maximum and minimum values for hornbills (van de Ven, 2017; van de Ven et al., 2020; van Jaarsveld et al., 2021).

Results

Species-specific NicheMapR models, with our adjusted sequence of behavioural responses (e.g. flattened feathers to normal position, increase T_b and EWL in parallel but independently etc.), accurately predicted evaporative water loss, metabolic rate and body temperature in all three study species at T_{air} between 30 °C and 52 °C (Fig. 1), with predictions greatly improved compared to those under the default NicheMapR model parameterisation (i.e. stepwise sequence of behavioural responses, Fig. S2). The greatest discrepancy between the species-specific NicheMapR predicted and observed values was an overestimation of hornbill and babbler EWL at T_{air} = 35 °C (hornbills: predicted_{EWL}= 0.95 g h^{-1}, observed_{EWL}= 0.31 – 0.73 g h^{-1}; babblers: predicted_{EWL}= 0.53 g h^{-1}, observed_{EWL}= 0.27 – 0.52 g h^{-1}). At T_{air} > 40 °C, however, model predictions fell well within the range of empirically observed values. Body temperature predictions were also slightly above the mean observed values for hornbills (observed-predicted = 0.13 – 0.8 °C), but within the upper limit of observations. In contrast, the default model T_b predictions all fell outside of the limit of observations for T_{air} = 30 – 50 °C, and overestimated T_b by ~ 2 °C (Fig. S2).

Sensitivity analysis: hornbill biophysical model

The hornbill biophysical model accurately predicted EWL and T_b, with correlation coefficients between observed and predicted values of 0.86 and 0.97 for T_{air} above the respective predicted inflection points (Fig. 2). The model-predicted inflections in EWL and T_b at T_{air} = 38.3 °C and T_{air} = 30.3 °C, respectively, both fell within 95% confidence intervals for observed values (95% CI_{EWL}: T_{air} = 38.2 – 41.1 °C, R^2 = 0.86 and CI_{Tb}: T_{air} = 28.3 – 35.0 °C, R^2 = 0.97, Fig. 2).

The NicheMapR endotherm model was most sensitive to changes in water budget parameters, particularly base and maximum skin wetness (i.e. area of skin that can act as a free-water surface), respiratory rate and the increments by which the panting multiplier (i.e. effect of panting on basal metabolic rate) increased (Fig 3 & S2; Table 1). Under- or overestimation of biophysical traits which produced the greatest effect on predicted EWL had negligible effects on predicted T_b and *vice versa*. For example, underestimating maximum skin wetness had the greatest effect on EWL (Cohen's *d* = 0.61), but negligible effect on T_b (Cohen's *d* = 0.03; Fig 3). In contrast, underestimation of respiratory rate had the greatest effect on T_b (Cohen's *d* = 0.5), and a negligible effect on EWL (Cohen's *d* = 0.1; Fig 3). Under standard, near black body, metabolic chamber conditions, the model was least sensitive to morphometric data, with variables such as feather length exerting negligible influence (Cohen's *d* < 0.2; Table 1). However, species-specific estimates of size and shape had small effects on EWL and T_b predictions (Cohen's *d* = ~ 0.2 – 0.4, Table 1). Including low solar radiation (100 W m^{-2}) had negligible effects on the overall predicted EWL and T_b (EWL: Cohen's *d* = 0.11; T_b: Cohen's *d* = 0.07, Table S3). However, under high solar radiation (900 W m^{-2}) these effect sizes increased for the overall predictions of EWL and T_b to large and medium, respectively (EWL: Cohen's *d* = 0.94; T_b: Cohen's *d* = 0.78, Table S3). The model remained sensitive to changes in water budget variables under high solar radiation, and the sensitivity of the model to morphometric data increased with feather length, plumage depth and feather reflectivity having the greatest overall effect sizes (Fig. S3; Table S3).

Discussion

This study demonstrates that the NicheMapR endotherm model, when parameterised appropriately, can be used to accurately predict thermoregulatory responses of birds to hot conditions. In three arid-zone species, the predicted species-specific patterns of evaporative heat dissipation, metabolic heat production and T_b were very similar to those observed under laboratory conditions. This strong correspondence between predicted and observed values spans the range of T_{air} over which consequential behavioural and physiological thresholds occur in most species investigated to date (T_{air} = 30 – 40 °C) and extends up to T_{air} ~ 10 °C above normothermic T_b. In contrast, the default NicheMapR endotherm thermoregulatory sequence overestimated T_b by ~ 2 °C within this critical range of T_{air} (30 – 40 °C), highlighting the importance of appropriately customising thermoregulatory responses for the modelled taxa.

Predicting thermoregulatory responses

Evaporative heat dissipation is the only physiological mechanism whereby birds can avoid lethal hyperthermia when environmental temperature exceeds normothermic T_b (reviewed by McKechnie et al., 2021) and the NicheMapR endotherm model accurately predicted rates of EWL for all three species. The only noteworthy differences between predicted and observed values occurred at T_{air} = 35°C, where EWL was overestimated by 51 % in hornbills and 24 % in babblers. Our analysis suggests that these differences will not meaningfully reduce the overall predictive power of the models, for two reasons. First, in both hornbills and babblers, the observed-predicted differences in EWL at T_{air} = 35°C are equivalent to < 0.25 % of body mass and likely too small to significantly affect predictions of variables such as time to dehydration during extreme heat events, with predicted values closely matching observed values at all $T_{air} > 40$°C. Second, inflection points and slopes of EWL are accurately predicted (Fig. 2) and the predicted T_b and RMR values all fall well within the range of observed values, as did the predicted T_{air} at which each species reached their known maximum T_b (McKechnie et al., 2021a; van Jaarsveld et al., 2021).

Parameterizing NicheMapR endotherm models as we have done here improves the accuracy of predictions for the effects of high environmental temperatures on energy and water balance compared to previous applications of this approach to species in hot, arid environments (e.g., Kearney et al., 2016). One obvious improvement compared to previous models concerns predicted T_b within the $T_{air} = 30 – 40$ °C range, as well as when $T_{air} > T_b$. For example, in a study of budgerigars by Kearney et al., (2016), predicted T_b differed substantially from actual values in the 30 – 40 °C range, with the model underestimating T_b at $T_{air} = 30$ °C by ~2 °C and overestimating the T_{air} at which T_b reaches 40 °C by 3-4 °C (Figure A1.1, Figure 2b of Kearney et al., 2016). Accurate predictions of T_b are critical for predicting patterns of behavioural thermoregulation, such as the environmental temperatures at which endotherms retreat to shaded microsites or the onset of panting, which can lead to large reductions in foraging efficiency (van de Ven et al., 2019).

Model sensitivity: southern yellow-billed hornbills

The hornbill model sensitivity analysis revealed model outputs were most sensitive to changes in water budget variables (e.g., respiratory rates and skin wetness) with the strongest effects (Cohen's $d > 0.5$) on biologically realistic input values for these parameters under conditions of low solar radiation (≤ 100 W·m^2). Over- or underestimating morphological input variables has small or negligible effects on the EWL, T_b and RMR predictions provided the values are within the natural range experienced by the species. Our findings are consistent with those of Peterman and Gade (2017), who found respiratory rate to be the most important parameter in their biophysical modelling approach affecting energy balance in salamanders (*Plethodon jordani*).

In contrast, under conditions of high solar radiation (900 W m^{-2}), model water budget outputs become increasingly sensitive to changes in morphological variables (especially feather properties). Several authors have reported that fur depth and solar reflectivity were the most important parameters affecting model predictions of metabolic rate and T_b in mammals (Mathewson et al., 2020; Moyer-Horner et al., 2015; Ratnayake, 2018). Thus, pelage and feather properties are likely to be more important for biophysical models under environmental conditions where solar heat gain plays a crucial role, unlike the standard black-body chamber conditions presented here (Wolf et al., 2000; Wolf and Walsberg, 2000).

Limitations

One limitation of this study is that it focussed on birds experiencing low metabolic chamber humidities. These conditions are likely representative of hot summer days in the southern African arid zone but, in more mesic, humid environments, evaporative cooling efficiency is likely to be lower (Gerson et al., 2014; Weathers, 1997). Although relatively few studies have empirically quantified the relationships between humidity and thermoregulation at T_{air} approaching or exceeding T_b under metabolic chamber conditions (Gerson et al., 2014; Powers, 1992; van Dyk et al., 2019), NicheMapR accounts for the effects of ambient humidity. Specifically, the model increases rates of EWL, RMR and T_b more rapidly at higher humidities, with maximum T_b reached at lower T_{air} compared to drier conditions. We are unaware of avian studies that have used empirical data to validate the predictions of biophysical models over a range of humidities (but see Briscoe et al., 2021), although the physical principles are well-understood, and such validations are a prerequisite to applying a biophysical modelling approach to species occupying humid environments.

A second limitation of the present study is that it involved laboratory conditions under which $T_{air} \approx T_e$, rather than natural thermal environments in which heat exchange involves more complex combinations of radiative, forced convective and conductive fluxes (Bakken, 1976; Robinson et al., 1976). Our sensitivity analysis, for instance, is based on conditions birds experience in metabolic chambers, including predominantly free convection and limited radiative fluxes. Under natural conditions, additional avenues of heat transfer may influence the sequence of physiological responses (Wolf et al., 2000) and the sensitivity of the model to specific input variables. NicheMapR has a microclimate subroutine that can be used to predict the fine-scale thermal landscape experienced by a species (Kearney and Porter, 2017), which in turn can be linked to the model used here to predict heat and water exchanges in individuals experiencing natural thermal environments and including behavioural thermoregulation. For example, Mathewson et al. (2020) demonstrated that a similar biophysical modelling approach can predict vervet monkey T_b within 0.5 °C of actual values measured in free-living animals for specific behaviour categories (e.g., huddled, inactive, uncurled etc.). Integrated with models or empirical data on behaviour, biophysical modelling approaches can provide predictions that account for time-activity budgets and animals' movements through landscapes (Malishev et al., 2018).

Our model did not account for excess heat loss via appendages such as the beak or when holding the wings open. Heat loss via beaks has been shown to be an important contributor to avian thermoregulation, particularly in species with disproportionately large beaks relative to body size such as hornbills (Tattersall et al., 2009; van de Ven et al., 2016). Vasodilation in a highly vascularised beak, such as those of hornbills or toucans, can cause beak surface temperature to increase, reducing the need for evaporative heat dissipation (Tattersall, 2016; van de Ven et al., 2016). However, the capacity for non-evaporative heat dissipation via the beak is most effective when $T_{air} < T_b$, with the T_b - T_{air} gradient declining to zero at $T_b = T_{air}$ (van de Ven et al., 2016). Our predictions for heat loss under high T_{air}, specifically when $T_{air} \geq T_b$, are thus unlikely to be altered by heat loss via the beak.

Conclusion

Biophysical model predictions can provide a mechanistic understanding of species sensitivity to climate change, accounting for physiological tolerances and the environment (Cunningham et al., 2021). Accurate predictions of species' energy and water fluxes under hot conditions, in addition to improving our understanding of their ecology and evolution, provide the basis for modelling exposure to several categories of risk associated with climate change. Models of the risks of lethal dehydration or lethal hyperthermia have, in the past, been based on either species-specific empirical data (Albright et al., 2017; Conradie et al., 2019; Conradie et al., 2020; Wolf, 2000) or allometrically predicted values (McKechnie and Wolf, 2010). The former method is restricted to species for which suitable physiological data exist, whereas the latter approach fails to capture inter- and intraspecific variation in traits such as the primary avenue of evaporative heat dissipation, which can result in over- or underestimation of exposure to potentially lethal conditions (McKechnie et al., 2021). Biophysical approaches have the potential to overcome these limitations and accurately predict exposure to acute, lethal risks in species for which thermal physiology and behavioural data are limited, but exist for ecologically similar species and/or can be allometrically predicted. Moreover, key functional traits may be phylogenetically conserved [e.g., whether the primary avenue for evaporation is respiratory or cutaneous (McKechnie et al., 2021)], increasing the potential to make inferences for data deficient taxa. Our sensitivity analysis also provides insight into which functional traits (i.e., respiratory rate and skin wetness) should be prioritised in empirical studies.

Additionally, the model can be used in a hypothetico-deductive approach to understand thermal adaptation or the underlying mechanisms of a system. For example, mismatches between model predictions and observations can potentially provide insight into physiological adaptations. The model can also be used to test hypotheses about thermal constraints on species occurrence, based on universal physical principles and functional trait data. However, although the model is widely applicable and general taxon-nonspecific values can often be used, caution is sometimes needed in extrapolating data from the literature to unstudied species. For example, Red-billed Queleas (*Quelea quelea*) have recently been shown to tolerate extreme hyperthermia with maximum T_b averaging 48.0 °C (Freeman et al., 2020), values ~3 °C higher than the maximum T_b of most small passerines. The exceptionally high ceiling to T_b of this species underscores the importance of empirical evidence in ground-truthing model predictions.

Quantifying thermoregulatory responses of endotherms to more complex thermal environments in the lab is difficult and time consuming and likely produces species-specific results (Wolf et al., 2000; Wolf and Walsberg, 1996). Our study shows that biophysical models can capture the complex physiological responses of birds to thermal extremes, increasing confidence in the ability of such models to infer thermoregulatory performance in endotherms under the more complex conditions found in nature. In principle, biophysical models permit rapid assessment of species and population responses to a rapidly changing climate without the challenge of collecting and extrapolating respirometry data to free-ranging species. However, users still need a general understanding of the underlying physical principles, and how these processes are implemented in biophysical models, to generate appropriate predictions (Briscoe et al., 2022). Biophysical models are not meant to replace empirical data but, as they provide insight into the underlying mechanisms of a system, should be used to complement and interpret empirical data and focus data collection. For instance, the NicheMapR endotherm model or other similar models for threatened or data-deficient species can provide a credible basis for evaluating physiological constraints and risks associated with climate change or human alteration of thermal landscapes, information that is often vital for conservation and evaluation of potential management interventions.

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Author contributions

S.R.C, A.E.M, B.O.W and S.J.C designed the study; S.R.C and M.R.F collected and analysed data. S.R.C and R.K ran the models with contributions from M.R.K. M.R.K developed the NicheMapR package and endotherm component; S.R.C wrote the first draft of the manuscript with contributions from all authors. All authors contributed critically to the manuscript and gave their final approval for publication.

Data availability statement

The NicheMapR release relevant to this study (v3.0.0) and the endotherm component are both available via Zenodo (Kearney 2020). Additionally, the changes made to the endoR_devel code made here are available via Github (https://github.com/ShannonConradie1/NicheMapR-endoR_devel_edited.git).

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Figures and Table

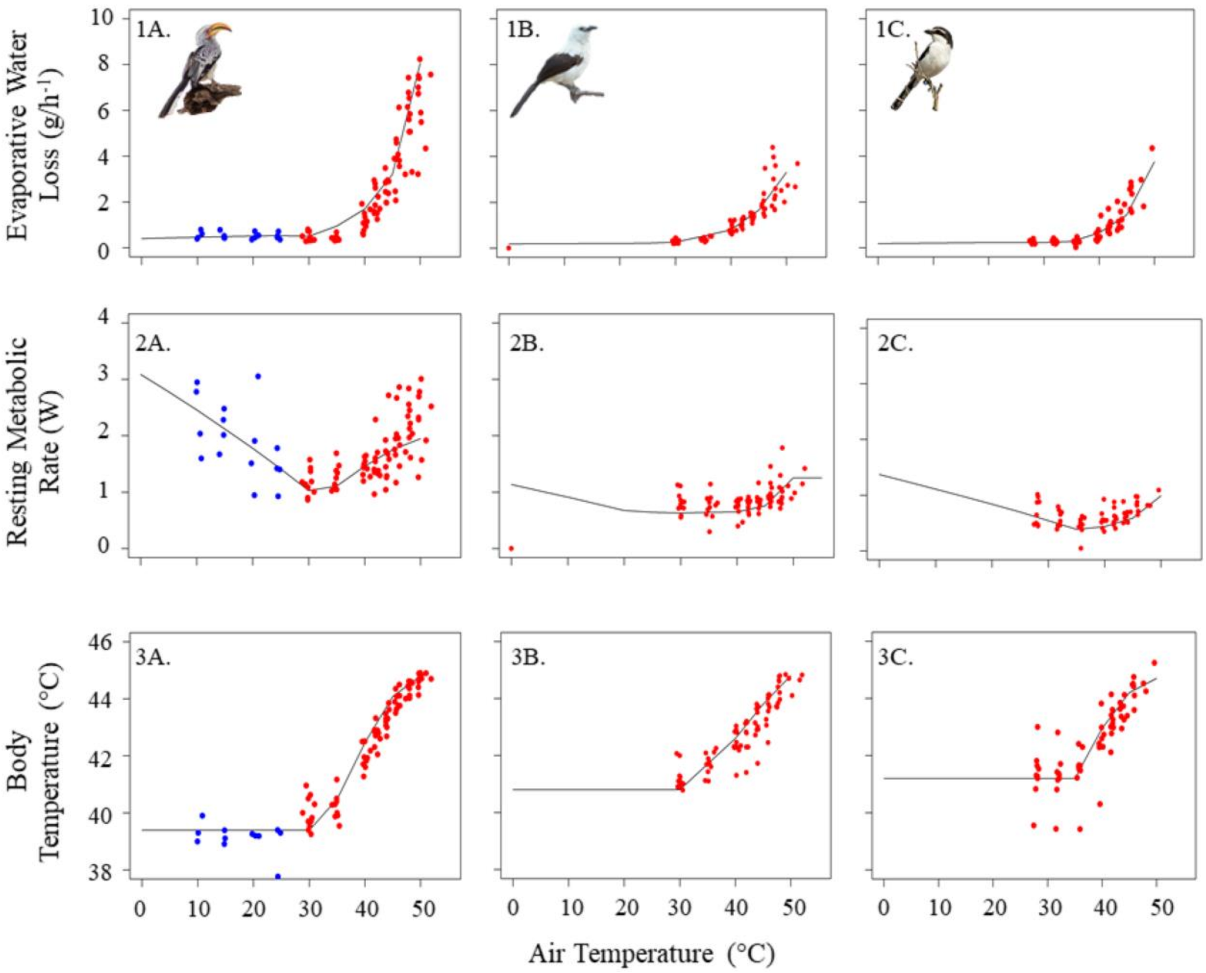

Fig. 1. Evaporative water loss [1: EWL (g/h^{-1})], resting metabolic rate [2: RMR (W)] and body temperature [3: T_b (°C)] of Southern Yellow-billed Hornbills (*Tockus leucomelas*, A), Southern Pied Babblers (*Turdoides bicolor*, B) and Southern Fiscals (*Lanius collaris*, C) as a function of air temperature [T_a (°C) red dots: T_{air} > 30 °C, and blue dots: T_{air} < 30 °C]. The black lines are the relationships predicted using the NicheMapR endotherm model (Kearney et al., 2021) and the dots represent empirical data.

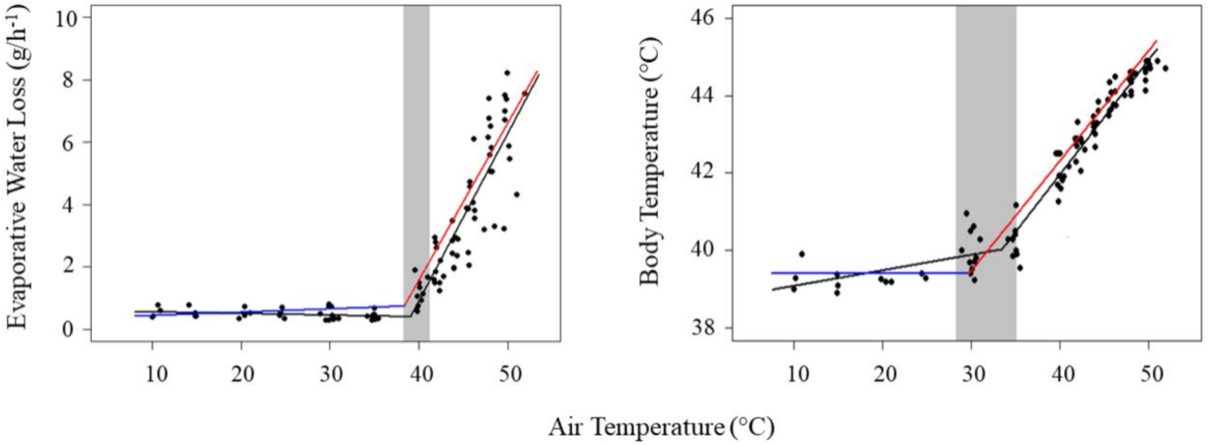

Fig. 2. Predicted relationships between air temperature and evaporative water loss (EWL, left) and body temperature (T_b, right) in Southern Yellow-billed Hornbill (*Tockus leucomelas*) generated using the NicheMapR endotherm model. Red and blue lines show the model predictions, whereas black lines are linear-mixed effects regression models fitted to empirical data (black dots) measured using flow-through respirometry. The grey bars represent the 95% confidence limits for the observed inflection points within the empirical data. Correlation coefficients for EWL and T_b between observed and predicted values were 0.86 and 0.97 respectively for T_{air} above the predicted inflection points.

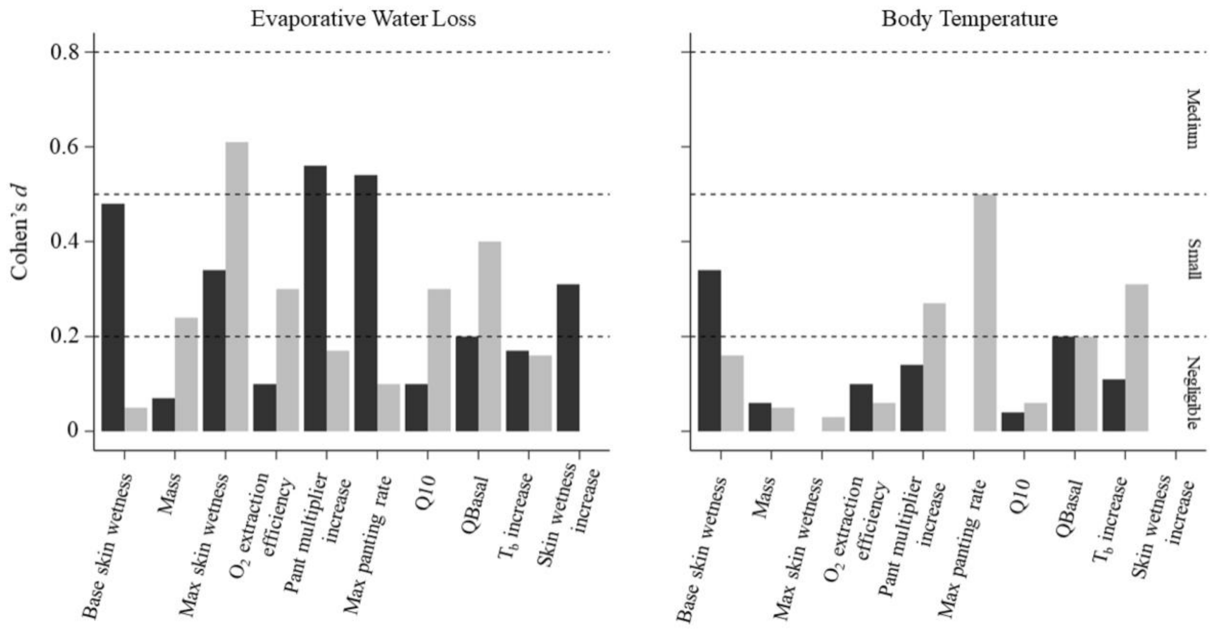

Fig. 3. Cohen's *d* values reflecting the effect size of model predictions for evaporative water loss (left) and body temperature (right) associated with over- (maximum biologically realistic value, black) and under-estimating (minimum biologically realistic value, grey) the biophysical parameters used in the NicheMapR endotherm model. Dashed lines correspond to negligible (0 – 0.2), small (0.2 – 0.5) and medium (0.5 – 0.8) effect (Cohen, 1992) on evaporative water loss and / or body temperature predictions.

Table 1. Biophysical parameters for the NicheMapR endotherm model for avian thermoregulatory responses to air temperature. Summarized sensitivity analysis results are shown as the range of EWL and T_b slope (i.e. relationship between a thermoregulatory variable and T_{air}) and inflection points (i.e. T_{air} where the thermoregulatory variable rapidly increases, Fig. 1). Linear regression models were fitted and the value of Cohen's *d* for the minimum and maximum changed parameters are shown. Cohen's *d* values correspond to negligible (normal, 0 – 0.2), small (italics, 0.2 – 0.5), medium (bold, 0.5 – 0.8) and large (> 0.8, not observed) effects on EWL and T_b. Values are shown for the hornbill model.

	Variable	**Modelled value**	**Sensitivity range**	**EWL slope**	**EWL inflection**	**T_b slope**	**T_b inflection**	**EWL Cohen's *d***	**T_b Cohen's *d***
Morphometrics	Mass (kg)[a,f]	0.20	0.17 – 0.26	0.48 – 0.54	37.96 – 38.35	0.28 – 0.30	29.74 – 32.66	*0.24*, 0.07	0.05, 0.06
	Target normothermic T_b (°C)[c]	39.4	37.0 – 41.0	0.44 – 0.47	37.81 – 41.84	0.29 – 0.18	27.42 – 30.32	0.14, 0.07	0.12, 0.07
	Maximum T_b (°C)[c]	45	44.0 – 45.5	0.48 – 0.48	38.24 – 39.0	0.20 – 0.26	28.34 – 29.43	0.06, 0.17	0.12, 0.07
	Increments to increase T_b (°C)[b]	0.2	0.10 – 0.25	0.39 – 0.44	34.04 – 38.2	0.20 – 0.23	27.46 – 31.52	0.16, 0.17	*0.31*, 0.11
	Body density (kg/m^3)[d]	1000	800 – 1200	0.40 – 0.50	38.38 – 42.4	0.21 – 0.23	28.3 – 29.04	0.01, 0.19	0.01, 0.04
	Feather diameter (m)[d]	30E-06	10E-06 – 50E-06	0.55 – 0.50	38.98 – 42.43	0.27 – 0.21	31.53 – 27.98	0.001, 0.2	0.1, 0.05

	Feather length (m)[f]	0.03	0.01 – 0.10	0.53 – 0.47	38.69 – 42.27	0.25 – 0.20	30.14 – 25.80	0.0, 0.21	0.09, 0.09
	Plumage depth (m)[f]	0.01	0.001 – 0.1	0.62 – 0.44	39.3 – 38.21	0.27 – 0.25	32.14 – 29.83	0.05, 0.14	0.12, 0.04
	Plumage density $(1/m^2)$[f]	15 000000	10 000000 – 80 000000	0.50 – 0.48	38.26 – 48.35	0.21 – 0.21	29.62 – 26.69	0.01, 0.2	0.04, 0.1
	Feather reflectivity[d]	0.25	0.1 – 0.5	NE	NE	NE	NE	0	0
Heat budget	Q_{10}[c]	2	1 – 3.5	0.41 – 0.47	38.10 – 42.92	0.2 – 0.24	28.3 – 29.75	*0.3.* 0.1	0.06, 0.04
	Q_{Basal} (W)[c]	1.19	0.5 – 1.43	0.47 – 0.43	41.69 – 33.447	0.28 – 0.21	32.97 – 27.98	*0.4, 0.2*	*0.2, 0.2*
	Δ inhaled vs exhaled air (°C)[d]	5	2 – 8	0.49 – 0.50	38.05 – 38.44	0.21 – 0.22	28.24 – 28.74	0.0, 0.0	0.03, 0
	O_2 extraction efficiency (%)[d]	25	24 – 26	0.44 – 0.46	37.83 – 37.86	0.20 – 0.21	27.60 – 27.91	*0.3,* 0.1	0.06, 0.1
	Flesh conductivity (W/mK)[e]	0.41 – 2.8	0.41 – 2.8	NE	NE	NE	NE	0	0

Water budget	Base skin wetness (%)[d]	1.8	0.5 – 5	0.22 – 0.49	33.80 – 38.21	0.16 – 0.27	25.77 – 34.10	0.05, **0.48**	0.16, *0.34*
	Maximum skin wetness (%)[f]	50	10 – 80	0.11* – 0.50	29.90* – 38.36	0.22 – 0.23	28.74 – 28.95	**0.61**, 0	0.03, 0
	Skin wetness increase (%)[f]	10	0.5 – 15	0.26 – 0.63	33.86 – 38.98	0.22*	28.74*	*0.34*, *0.31*	0
	Respiratory rate[f]	7.5	4 – 10	0.40 – 0.72	34.02 – 38.58	NE	NE	0.1, **0.54**	**0.5**, 0
	Pant multiplier[f]	1	0 – 1	0.49 – 0.50	33.40 – 38.36	0.19 – 0.22	27.40 – 28.7	0, 0.17	0, 0.1
	Increments to increase pant multiplier[f]	0.014	0.05 – 1	0.18 – 0.46	32.08 – 37.58	0.14 – 0.28	24.62 – 36.40	0.17, **0.56**	**0.27**, 0.14

[a]van Jaarsveld et al., 2021; [b]Clarke & Rothery, 2008; [c]McKechnie & Wolf, 2004; [d]Kearney et al., 2016; [e]Chato, 1969 and [f]estimated/this study

Materials and Methods

The NicheMapR endotherm model consists of a set of subroutines which are called to iteratively solve an organism's heat balance (equation 1) given a set of functional traits and an environment (adapted from Kearney et al., 2021):

$$Q_{gen} - Q_{resp} - Q_{evap} = Q_{fur} = Q_{rad} + Q_{conv} + Q_{cond} + Q_{evap,feathers} - Q_{sol} \qquad [1]$$

where, Q_{gen} is the heat generated from the metabolism, Q_{resp} is heat lost via respiration, Q_{evap} is cutaneous heat lost, Q_{fur} is the heat lost which passes through the pelage, which all needs to balance heat exchange via thermal radiation Q_{rad}, convection Q_{conv}, conduction Q_{cond} and evaporation from the feathers $Q_{evap,feathers}$, and solar heat gain Q_{sol}. Each of these heat exchange terms contains functional traits and 'functional environments' that must be provided as input parameters. A brief introduction of this can be found in Kearney et al. (2021) and full model descriptions, equations and tutorials are available (https://github.com/mrke/NicheMapR/tree/3.1.0/vignettes). The model finds the unique value of Q_{gen} and of the skin and feather temperature that satisfies this equation such that it sums to zero (the first law of thermodynamics). Under conditions of heat stress, this may result in a predicted Q_{gen} that is below the permissible metabolic rate of the organism (it could even be negative, which is of course physically impossible). The endotherm model thus invokes a series of behavioural and physiological adjustments that increase overall heat loss (e.g., by altering surface areas for convective and radiative exchange, increasing respiration rate or skin wetness to enhance evaporative cooling) until the heat balance equation is satisfied for the specified minimum possible metabolic rate. Parameterisation of the model involves both obtaining the functional trait values (e.g. solar absorptivity, surface area, pelage properties) as well as adjusting the sequence of physiological and behavioural responses.

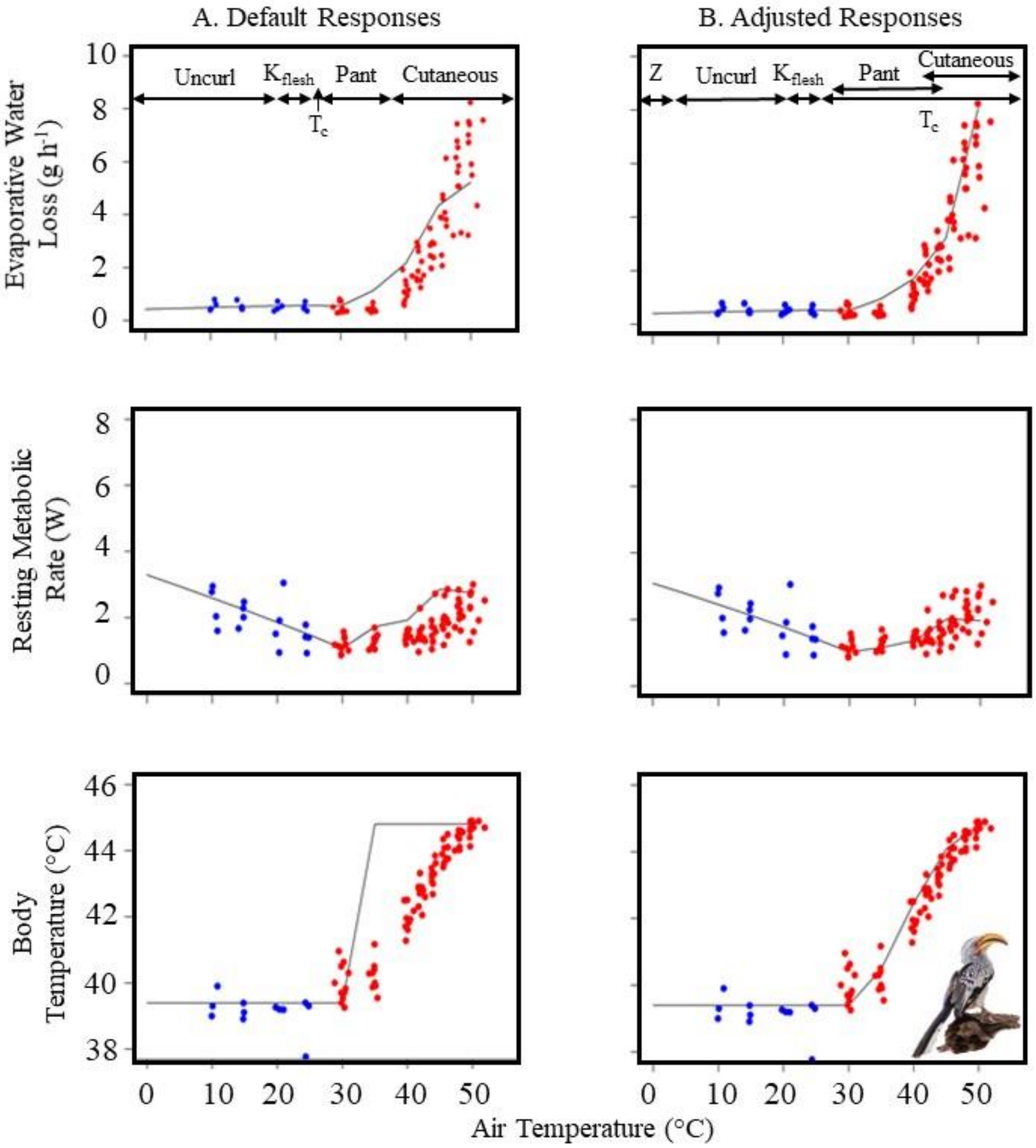

Fig. S1. NicheMapR model predictions of evaporative water loss [EWL (g h^{-1})], resting metabolic rate [RMR (W)] and body temperature [T_b (°C)] using A) the default endoR_devel sequence of behavioural responses or B) the adjusted sequence of behavioural responses described here for Southern Yellow-billed Hornbills (*Tockus leucomelas*). The black lines are the relationships predicted using the NicheMapR endotherm model (Kearney *et al.,* 2021) and the dots represent empirical data.

Importantly, the adjusted sequence incorporates ptiloerect feathers (Z) at cool temperatures which flatten as skin temperature warms. Additionally, the adjusted sequence allows body temperature changes and evaporative cooling to occur in parallel.

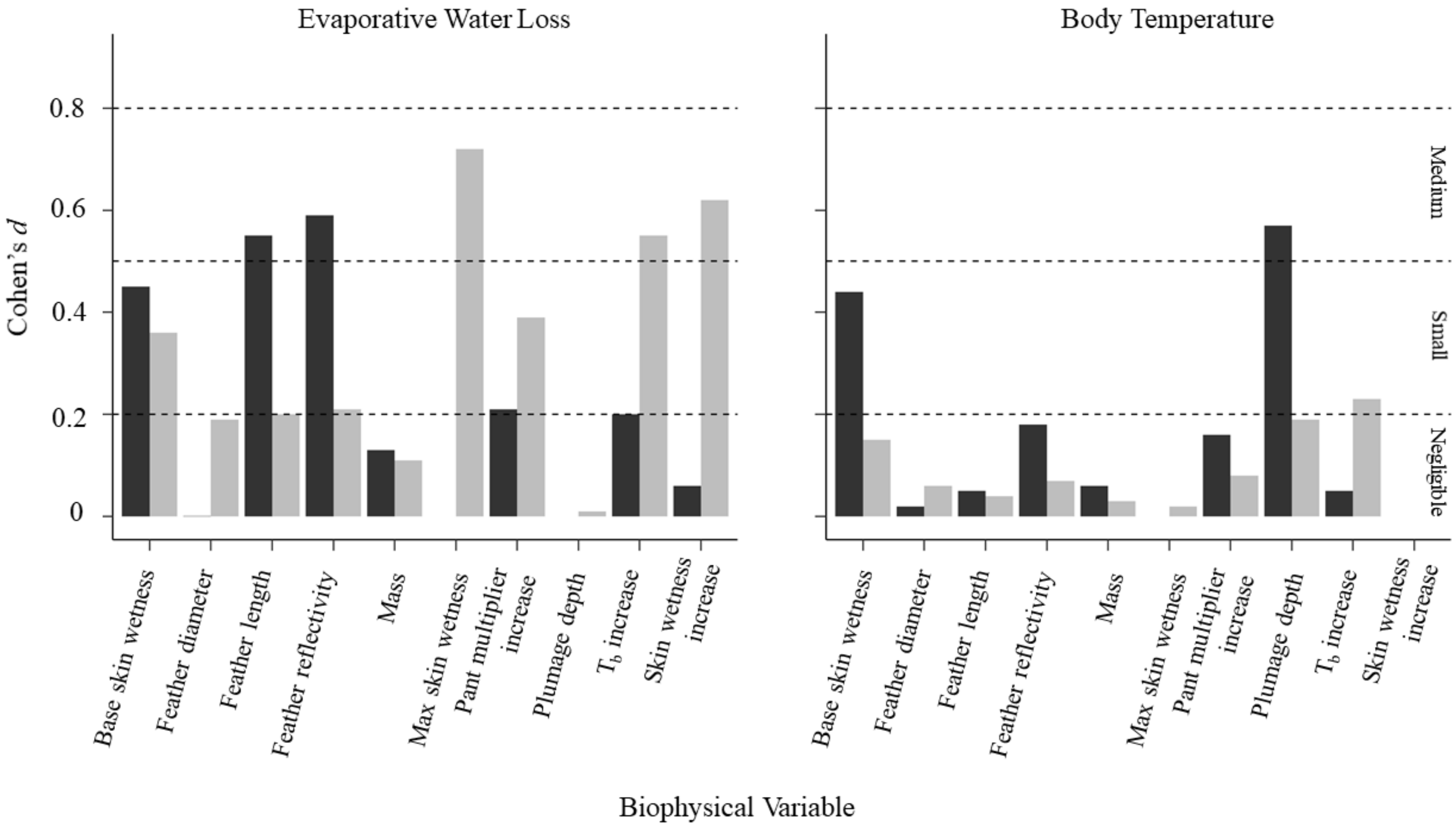

Fig. S2. Cohen's *d* values used to assess effect size of model predictions under high solar radiation (900 W m^{-2}) for evaporative water loss (left) and body temperature (right) associated with over- (maximum biologically realistic value, black) and under-estimating (minimum biologically realistic value, grey) the biophysical parameters used in the NicheMapR endotherm model. Dashed lines correspond to negligible (0 – 0.2), small (0.2 – 0.5) and medium (0.5 – 0.8) effect (Cohen, 1992) on evaporative water loss and / or body temperature predictions.

Table S1. Detailed description of the parameters used in the endotherm component on NicheMapR to evaluate thermoregulatory responses in three arid-zone bird species Southern Yellow-billed Hornbills (Hornbill, *Tockus leucomelas*), Southern Pied Babblers (Babbler, *Tudoides bicolor*) and Southern Fiscals (Fiscal, *Lanius collaris*). Full variable descriptions are available at https://github.com/mrke/NicheMapR/blob/master/vignettes/endotherm-components-tutorial.Rmd.

	Variable	Description	Values	Hornbill	Babbler	Fiscal	Reference
Environment (Metabolic chamber)	TAs (°C)	Air temperature (approximating operative temperature) regulated in the metabolic chamber	**0 - 55**	0 – 55	0 – 55	0 - 55	Czenze et al., 2020
	VEL (m/s^{-1})	Wind speed	**0.01**	0.01	0.01	0.01	Czenze et al., 2020
	RH (%)	Relative humidity	**5**	5	5	5	Czenze et al., 2020
	EMISAN	Animal emissivity	**0.99**	0.99	0.99	0.99	Kearney et al. (2021)
Morphometrics	AMASS (kg)^{a,f}	Average mass of living individuals	**Species-specific**	0.199	0.076	0.0373	Czenze et al., 2020; van Jaarsveld et al., 2021

SHAPE	Ellipsoid shape	**4**	4	4	4	Kearney et al. (2021)
TC (°C)[b]	Target normothermic body temperature for optimal performance	**Species-specific**	39.4	40.8	41.2	Czenze et al., 2020; van Jaarsveld et al., 2021
TC_MAX (°C)[b]	Maximum voluntary T_b before reaching potentially lethal T_b	**Species-specific**	45	45	45	Czenze et al., 2020; van Jaarsveld et al., 2021
TC_INC (°C)[f]	Increments by which TC is increased	**0.2**	0.2	0.2	0.2	Clarke & Rothery (2008)
ANDENS (kg/m^3)[d]	Body density	**1000**	1000	1000	1000	Kearney et al. (2016)
DHAIR (m)[d]	Feather diameter, set for ventral and dorsal sides respectively	**Species-specific**	30E-06	30E-06	30E-06	This study, museum measurement

	LHAIR (m)^f	Feather length, set for ventral and dorsal sides respectively	**Species-specific**	0.03	0.025	0.025	This study, museum measurement
	ZFUR (m)^f	Plumage depth, set for ventral and dorsal sides respectively	**Species-specific**	0.01	0.008	0.007	This study, museum measurement
	RHO (1/m^2)^f	Plumage density, set for ventral and dorsal sides respectively	**15000000**	15000000	15000000	15000000	Estimate
	REFL^d	Feather reflectivity (fractional, 0-1)	**Species-specific**	0.25	0.25	0.25	This study, museum measurement
	SAMODE	Bird skin surface area allometry from Walsberg & King (1978)	**1**	1	1	1	Kearney et al. (2021)
Heat budget	Q_{10}^{c}	Effect of T_b on metabolic rate when T_b > core T_b	**Species-specific**	2.5	2	2	McKechnie & Wolf (2004)
	Q_{Basal} (W)^c	Basal heat production	**Species-specific**	1.19	0.66	0.39	McKechnie & Wolf (2004)
	DELTAR (°C)^d	Respiratory heating of breath, when	**5**	5	5	5	Kearney et al.

		$T_b > T_{air}$. Otherwise air leaving lunges were assumed to be the same as T_b.					(2016)
	EXTREF	O_2 extraction efficiency (%)[d]	**25**	25	25	25	Kearney et al. (2016)
	AK2 (W/mK)	Conductivity of fat	**0.230**	0.230	0.230	0.230	Chato (1969)
	AK1 & AK1_MAX (W/mK)[e]	Range of thermal conductivities of flesh.	**0.412 – 2.8**	0.412 – 2.8	0.412 – 2.8	0.412 – 2.8	Chato (1969)
Water budget	PCTBAREVAP (%)	Surface area for evaporation that is skin (i.e. bare skin, where cutaneous evaporation can occur)	**Species-specific**	0.5	0.5	0.5	Estimated from museum measurements
	PCTWET (%)[d]	Part of skin that acts as a free-water surface	**Species-specific**	1.8	1.5	1.5	Inferred from observed base water loss rate (respirometry data)
	PCTWET_MAX (%)[f]	Maximum surface area acting as a	**50**	50	50	50	Estimated

		free-water surface					
	PCTWET_INC (%)[f]	Intervals by which skin wetness is increased	**Species-specific**	10	10	17.5	Estimated
	PANT_MAX[f]	Maximum respiratory rate, defined as the multiplier on air flow through the lungs to simulating panting. Determined by metabolic rate.	**Species-specific**	5	5	5.5	Estimated from Kearney et al., 2016
	PANT_MULT[f]	Maximum possible increase in basal metabolic rate due to panting (i.e. 0.5 would result in 1.5 x BMR when panting is at the max value)	**1**	1	1	1	Kearney et al. (2021)
	PANT_INC[f]	Increment for multiplier on breathing rate to simulate panting	**Species-specific**	0.14	0.14	0.14	

Table S2. Summarized sensitivity analyses values under conditions of low and high solar radiation respectively for predicted EWL and T_b. The value of Cohen's *d* for the minimum and maximum changed parameter are shown. Cohen's *d* values correspond to negligible (normal, 0 – 0.2), small (italics, 0.2 – 0.5), medium (bold, 0.5 – 0.8) and large (bold and italics, > 0.8) effects on EWL and T_b. Values are shown for the hornbill model. Similar trends were observed in the babbler and fiscal models.

				Low Radiation (100 W m^{-2})		**High Radiation (900 W m^{-2})**	
	Variable	**Modelled value**	**Sensitivity range**	**EWL Cohen's *d***	**T_b Cohen's *d***	**EWL Cohen's *d***	**T_b Cohen's *d***
	Overall prediction	-	-	0.11	0.07	0.94	0.78
Morphometrics	Mass (kg)	0.20	0.17 – 0.26	0.03, 0.04	0.01, 0.02	0.11, 0.13	0.03, 0.06
	Core T_b (°C)	39.4	37.0 – 41.0	0.13, 0.03	**0.71, 0.60**	**0.55,** 0.19	*0.37, 0.27*
	Maximum T_b (°C)	45	44.0 – 45.5	0.04, 0.14	0.05, 0.03	0.19, *0.26*	0.16, 0.14
	Increments to increase T_b (°C)	0.18	0.10 – 0.25	*0.26,* 0.09	0.19, 0.07	**0.55,** *0.20*	*0.23,* 0.05
	Body density (kg/m^3)	1000	800 – 1200	0.07, 0.003	0.01, 0.01	*0.21,* > 0.001	0.03, 0.03
	Feather diameter (m)	30E-06	10E-06 – 50E-06	0.05, 0.01	0.01, 0.02	0.19, 0.001	0.06, 0.02
	Feather length (m)	0.03	0.01 – 0.10	0.09, 0.01	0.02, 0.07	*0.2,* **0.55**	0.04, 0.05
	Plumage depth (m)	0.01	0.001 – 0.1	0.05, *0.48*	0.06, *0.41*	0.01, ***0.93***	0.19, **0.57**

	Plumage density (feathres/m^2)	15 000000	10 000000 – 80 000000	0, 0	0, 0	0, 0	0, 0
	Feather reflectivity	0.25	0.1 – 0.5	0.01, 0.03	0.01, 0.02	*0.21,* **0.59**	0.07, 0.18
Heat budget	Q10	2	1 – 3.5	0.18, 0.09	0.03, 0.02	0.04, *0.22*	0.09, 0.03
	QBasal	1.19	0.5 – 1.43	*0.29, 0.22*	0.11, 0.13	0.05, *0.25*	0.18, 0.17
	Δ inhaled vs exhaled air	5	2 – 8	0.01, 0.01	0.03, 0	*0.20, 0.23*	0.02, 0.05
	O_2 extraction efficiency (%)	25	24 – 26	0.02, 0.12	0.04, 0.06	0.19, 0.19	0.01, 0.03
Water budget	Base skin wetness (%)	1.8	0.5 – 5	0.13, 0.04	0.14, *0.22*	*0.36, 0.45*	0.15, *0.44*
	Maximum skin wetness (%)	50	10 – 80	*0.2,* 0	0.01, 0	**0.72,** 0	0.02, 0
	Skin wetness increase (%)	10	0.5 – 15	0.11, 0.05	0, 0	**0.62,** 0.06	0, 0
	Maximum panting rate	5	4 – 10	0.06, 0.19	0.02, 0	0.04, 0.17	0.03, 0
	Pant multiplier	0.01	0 – 1	0.002, 0.19	0, 0.04	0, *0.25,*	0, 0.09
	Increments to increase pant multiplier	0.14	0.05 – 1	*0.42,* 0.16	0.15, 0.16	*0.39, 0.21*	0.08, 0.16