A heat-sensitive songbird's risk of lethal hyperthermia increases with humidity

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ABSTRACT

Frequent and intense heatwaves are causing heat-related avian mass mortality events to become more common, but the role of elevated humidity as a contributing factor remains unclear. Here, we quantified the effect of humidity on risks of lethal hyperthermia for blue waxbills (*Uraeginthus angolensis*), the species most common among the victims of South Africa's first documented heat-related mass mortality event involving wild bird populations. We quantified blue waxbill's body temperature (T_b), metabolic heat production and evaporative heat loss at air temperatures (T_{air}) approaching and surpassing normothermic T_b in dry (1.1 ± 0.9 g m^{-3}) and humid (21.3 ± 0.4 g m^{-3}) air. The humid treatment was correlated with significant declines in evaporative cooling capacity, and maximum heat tolerated by waxbills was T_{air} ~2 ºC lower (45.7 ºC) compared to the dry air treatment (47.9 ºC). A model of end-Century exposure for the waxbills reveals that elevated humidity will increase the risks of lethal hyperthermia 3- to 7-fold in some parts of southern Africa.

Keywords: climate change, evaporative heat dissipation, heat tolerance limit, heatwave, passerine, upper thermal limits

INTRODUCTION

Anthropogenic climate change has resulted in extreme heat events becoming more intense and frequent over time [1] and can result in mass mortality among wildlife [2–6]. Heat-related mass mortality events can have serious consequences for populations; for instance, Australia is thought to have lost ~33 % of its population of spectacled flying foxes (*Pteropus conspicillatus*) during a 2-day extreme heat event in late 2018 [7]. Although their body temperature (T_b) is higher than that of mammals, birds are vulnerable to extreme heat on account of their small body size, high activity during the heat of the day, and reduced use of thermally buffered microsites such as burrows [8]. Heat-related avian mass mortality events appear to have become more frequent in recent years [5,9–11], underscoring the importance of predicting conditions that exacerbate lethal hyperthermia or lethal dehydration risks, particularly for threatened species [12–15].

Models that investigate climate change impacts on the likelihood of avian heat-related mortality events have largely focused on arid-zone species [5,8,13,14]. However, in some mesic environments elevated humidity impedes evaporative heat dissipation [16,17], reducing evaporative cooling efficiency and causing birds and other animals to approach their heat tolerance limits at lower air temperature (T_{air}) in humid relative to dry conditions [18–21]. Among Australasian pteropodid bats, for instance, elevated humidity is a predictor of heat-related mass mortality events [6,22]. There is evidence that humidity has shaped bird thermal physiology, whereby birds occupying hot, humid lowlands having evolved more prominent hyperthermia tolerance compared to their counterparts occupying habitats characterised by drier conditions [20–23].

In November 2020, a heatwave in Phongolo Nature Reserve (PNR) in eastern South Africa, involving maximum air temperature (T_{max}) of 45 ºC and humidity of 12.4 – 13.9 g m^{-3} (equivalent to relative humidity = ~21 %), resulted in at least 47 birds dying in a ~45-ha search area [6]. The majority (94 %) of these deaths involved passerines, reflecting the reliance of this taxon on panting for heat dissipation (reviewed by McKechnie *et al.* 2021 [24]), with blue waxbills (= southern cordonbleu, *Uraeginthus angolensis*; Passeriformes, Estrildidae) representing 43 % of carcasses observed. The prominence of this species among the mortalities identifies it as an appropriate model for evaluating whether lethal hyperthermia was likely the proximate cause of death during the PNR mortality event and how humidity influences this risk.

We hypothesised the risk of lethal hyperthermia for blue waxbills is strongly dependent on humidity and tested the following predictions: 1) T_{air} = 45 °C combined with elevated humidity represents lethal conditions for free-ranging waxbills, 2) waxbills' heat tolerance limits (HTL, the maximum T_{air} tolerable before the start of severe, irreversible hyperthermia) are significantly reduced by elevated humidity and 3) the spatial extent and incidence of waxbill exposure to environmental conditions associated with lethal hyperthermia risk under climate warming is substantially higher when humidity is taken into account.

METHODS AND MATERIALS

Study area and species

We captured 20 blue waxbills (hereafter 'waxbills') during February 2022 at Mfuleni Nature Reserve (27°52'59.5"S 32°21'41.7"E) and along Old Hluhluwe Road, KwaZulu-Natal province, South Africa. The area is characteristically hot and humid, experiencing mean summer (October – March) T_{max}, absolute humidity and precipitation of 29.98 ± 1.85 °C, 17.07 ± 1.44 g m^{-3} and 628 ± 123.94 mm respectively [25]. Waxbills are small estrildids (body mass = 9.4 ± 0.57 g) that occur from north-eastern South Africa into Angola and Tanzania [26,27].

Temperature and gas exchange measurements

We measured carbon dioxide production ($\dot{V}_{CO_2}$), evaporative water loss (EWL) and T_{b} in dry air in 10 waxbills following the method of Freeman *et al.* (2022). For measurements, waxbills were placed individually in 3-L metabolic chambers (20 cm high x 15 cm wide x 10 cm deep). Incurrent flow rates ranged between 3.00 and 5.00 L min^{-1}, with flow rates regularly adjusted to maintain chamber humidity < 3 g m^{-3} (mean ± SD = 1.12 ± 0.85 g m^{-3}). Flow rates were typically adjusted during transitions between successive T_{air} values; after each adjustment, adequate time (2.8 to 4.6 min) was allowed for the chamber air to reach 99 % equilibrium, calculated following Lasiewski *et al.* (1966) [16].

Gas exchange and T_{b} were also measured in 10 waxbills (different individuals to those in the dry air treatment) at a chamber humidity of 21.28 ± 0.41 g m^{-3}, hereafter referred to as 21 g m^{-3}. Humidity was regulated by mixing dry air with humid air upstream of the chamber. The humid air was generated by passing air through three bubblers in series, each consisting of a 3-L plastic screw-top bottle filled to within ~10 cm of the top with water. Each bubbler was equipped with an air inlet and outlet, with incurrent air passed through an aquarium stone positioned at the bottom of the water column. The first bubbler was maintained at room temperature (T_{air} = 35 ºC), whereas the second and third were placed in a temperature-controlled chamber (PELT-5, Sable Systems, Las Vegas, NV, USA) in which T_{air} was maintained 2-3 ºC above the desired dew point temperature. Flow rates for the dry and humid air streams were regulated using mass flow controllers and regularly adjusted to maintain approximately constant chamber humidity values despite variation in the bird's EWL. Downstream from the dry air / humid air merge, a needle valve was used to route a subset of the mixed air through a baseline channel. The remainder of the air passed through a 0-10 L min^{-1} mass flow meter (Alicat Scientific Inc., Tuscon AZ, USA) set to its maximum flow rate and hence acting as a mass flow meter to measure in-current flow rates to the chamber. For the humid treatment, flow rates of 1.52 - 2.49 L min^{-1} were used, with 99 % equilibrium times [16] of 5.5 – 9.1 min.

In both the dry and humid treatments, birds experienced a stepped T_{air} profile, following Freeman *et al.* (2022). At the start of measurements, each bird was placed in a chamber at T_{air} = 28 ºC for 1 h to habituate to experimental conditions. For individuals in the dry air treatment, physiological measurements commenced at T_{air} = 28 ºC following the habituation period, with chamber T_{air} subsequently increased in 4-ºC increments at $T_{\mathrm{air}} \leq 40$ ºC and then in 2-ºC increments at $T_{\mathrm{air}} > 40$ ºC. For individuals in the humid treatment, a chamber humidity of 7 – 10 g m^{-3} was maintained during the 1-h habituation period at T_{air} = 28 ºC, whereafter it was increased to 21 g m^{-3}. Initial measurements revealed no differences in $\dot{V}_{CO_2}$, EWL or T_{b} between birds in the dry and humid treatments at T_{air} = 28 – 36 ºC (similar to findings for other species of similar body mass [16]), and for subsequent measurements of individuals in the humid treatment we increased T_{air} to 34 ºC over ~30 min following habituation. We commenced measurements for birds in the humid treatment at T_{air} = 34 ºC, whereafter we increased the chamber T_{air} in 2-ºC increments at all $T_{\mathrm{air}} > 34$ ºC. Starting the measurements for individuals in the humid treatment at T_{air} = 34 ºC instead of T_{air} = 28 ºC and using 2- rather than 4ºC increments in T_{air} below as well as above 40 ºC reduced the total time bird spent in the chamber and ensured a more gradual increase in chamber temperature compared to birds in the dry treatment.

Birds were continuously monitored during the experiments using CCTV camera and infrared light source. Following Whitfield et al. (2015) [28], birds were removed from the chambers when they reached thermal endpoints characterised by loss of balance, uncoordinated movement or abrupt decreases in $\dot{V}_{CO_2}$ or EWL or uncontrolled increases in T_{b}. Birds were also removed if they showed sustained agitation and escape behaviour. Data were only included in analyses if they were obtained from calm birds resting quietly in the chamber [28]. After removal from the chamber, birds were offered water while in the hand using a syringe, then placed in a quiet dark environment at room temperature to recover with water available *ad libitum* and finally, offered water again before release at their site of capture.

Data Analysis

All analyses were conducted in R version 4.1.2 [29]. Inflection T_{air} values, above which T_{b}, resting metabolic rate (RMR), EWL and EHL/MHP rapidly increased with T_{air} were determined using the *segmented.lme* [30] package with bird identity included as a random factor. Linear mixed-effects models (LMM) were then fitted separately to data above and below inflection T_{air} values following Freeman *et al*. (2022) with the addition of treatment (i.e., dry vs humid air) and the T_{air} : treatment interaction term as predictors, using the *lme4* [31] and *lmerTest* [32] packages. We compared the rate of increase in T_{b} with T_{air} (T_{b}slope) and maximum T_{b}, RMR, EWL and EHL/MHP (T_{b}max, $\mathrm{RMR}_{\mathrm{max}}$, $\mathrm{EWL}_{\mathrm{max}}$ and $\mathrm{EHL/MHP}_{\mathrm{max}}$, respectively) at experimental endpoints between treatments using paired t-tests.

Lethal hyperthermia risk assessment

To quantify the frequency and geographical extent of conditions associated with lethal hyperthermia under future climate scenarios within waxbills' southern African range, we mapped waxbill exposure to $T_{\mathrm{air}} \geq$ HTL for 2090-2100. To ensure projections reflected the lowland, humid areas occupied by waxbills, mapping was restricted to elevations < 500 m in eastern southern Africa (South Africa, Eswatini, Zimbabwe and Mozambique). We applied a high-risk future climate change scenario (RCP 8.5) to reanalyse data obtained from ERA5 daily aggregates [30-km grid spatial resolution, Copernicus Climate Change Service (C3S) (2017)]. The climate change scenario was derived from an ensemble of CCSM downscalings from six global climate model (GCM) projections, following Mbokodo *et al.* 2020 [33]. Projections were consistent with previous multimodal forecasts for the end of the century across southern Africa [1,34,35].

RESULTS

Heat tolerance limits were significantly lower ($t = 6.07$, $p < 0.001$) in the humid treatment (45.7 ± 0.99 °C) compared to the dry treatment (47.9 ± 0.95 °C). An inflection point for T_{b} was identified at $T_{\mathrm{air}} = 38.5$ °C in the dry air treatment. Neither T_{b}max ($t = 0.73$, $p = 0.49$) nor

$T_b$slope at $T_{air} > 38.5$ °C ($t = 2.07$, $p = 0.07$) differed significantly between treatments. However, the T_{air} : treatment interaction emerged as significant ($F = 4.40$, $p = 0.04$), revealing the relationship between T_b and T_{air} varied with humidity. RMR_{max} did not differ significantly between treatments ($t = 1.17$, $p = 0.27$). However, EWL_{max} was 42% higher ($t = 3.89$, $p = 0.004$) in dry air (0.57 ± 0.17 g h^{-1}) compared to humid conditions (0.40 ± 0.12 g h^{-1}). The T_{air} : treatment interaction was significant for both RMR ($F= 12.54$, $p < 0.001$) and EWL ($F = 8.50$, $p = 0.005$). Waxbills' EHL/MHP_{max} ($t = 4.524$, $p = 0.001$) was significantly higher under dry conditions (1.37 ± 0.41) compared to humid conditions (0.94 ± 0.28), due to reduced EWL_{max} under humid conditions.

The reduced HTL under humid conditions substantially increases the frequency and spatial extent of waxbills' lethal hyperthermia risk under RCP 8.5 climate predictions (Figure 2) the mesic eastern lowlands of southern Africa (Figure 2). In southern Mozambique and parts of northern Kruger Park (indicated by lower in Figure 2), exposure to $T_{air} >$ HTL will occur on 2.92 ± 0.69 d y^{-1} (maximum = 4 d y^{-1}), whereas under humid conditions average exposure increases to 19.3 ± 6.43 d y^{-1} (maximum = 23 d y^{-1}). In the Zambezi River valley (upper oval in Figure 2), the corresponding projected values for dry and humid conditions are 9.9 ± 2.87 d y^{-1} (maximum = 13 d y^{-1}) and 30.9 ± 13.1 d y^{-1} (maximum = 47 d y^{-1}), respectively.

DISCUSSION

The effects of humidity on waxbills' heat tolerance supported our first prediction: under humid conditions, the waxbills' heat tolerance limit decreased by > 2 °C from $T_{air} = 47.9$ °C to $T_{air} = 45.7$ °C, a value similar to the maximum T_{air} on the day of the mass mortality event. However, vegetation in the area where the mortality event occurred consists primarily of fine-leafed woodland with several tree species (e.g., *Vachellia*, *Senegalia*) characterised by generally sparse canopies, making it likely that the operative temperatures birds experienced during the mortality event were higher than $T_{air} = 45$ °C. Our model also supported the third prediction, that exposure to conditions associated with lethal hyperthermia risk by the end of this century will be considerably higher under humid compared to dry conditions.

Although our experimental humidity treatment (21 g m^{-3}) was higher than prevailing humidity during the mortality event (12.4 - 13.9 g m^{-3}), for many regions of the world relative humidity is anticipated to remain approximately constant (and thus absolute humidity will increase) with advancing climate change [36,37]. Maximum summer (January – February) humidity at our study site is ~18.7 g m^{-3} [25]; assuming unchanged relative humidity, a 4-°C

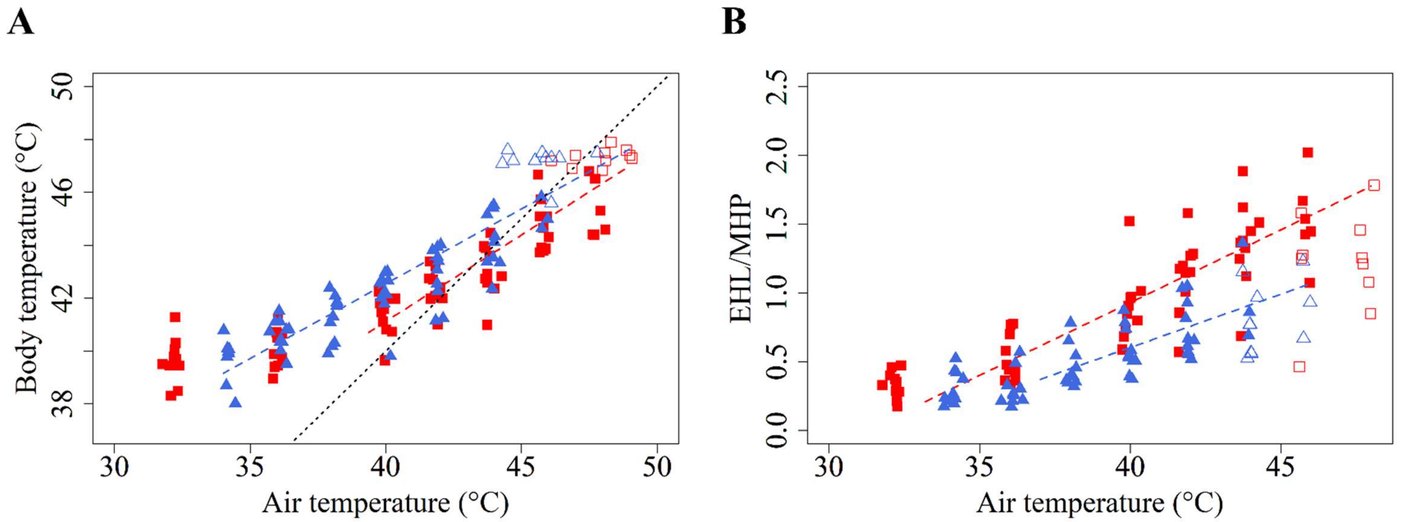

Figure 1. Blue waxbill (*Uraeginthus angolensis*) body temperature (**A**), and evaporative heat loss / metabolic heat production (EHL/MHP, **B**)) as a function of air temperature under dry (1.12 ± 0.85 g m^{-3}; red squares) or humid (21.28 ± 0.41 g m^{-3}; blue triangles) conditions. Individuals that reached thermal endpoints are depicted as open symbols. The black dashed line in A depicts $T_b = T_{air}$. Dashed blue and red lines show regression models fitted data at $T_{air} >$ inflection points [(A) dry air: 38.4 ºC, humid air: 34 ºC; (B) : dry air: 32.6 ºC, humid air: 37.0 ºC)].

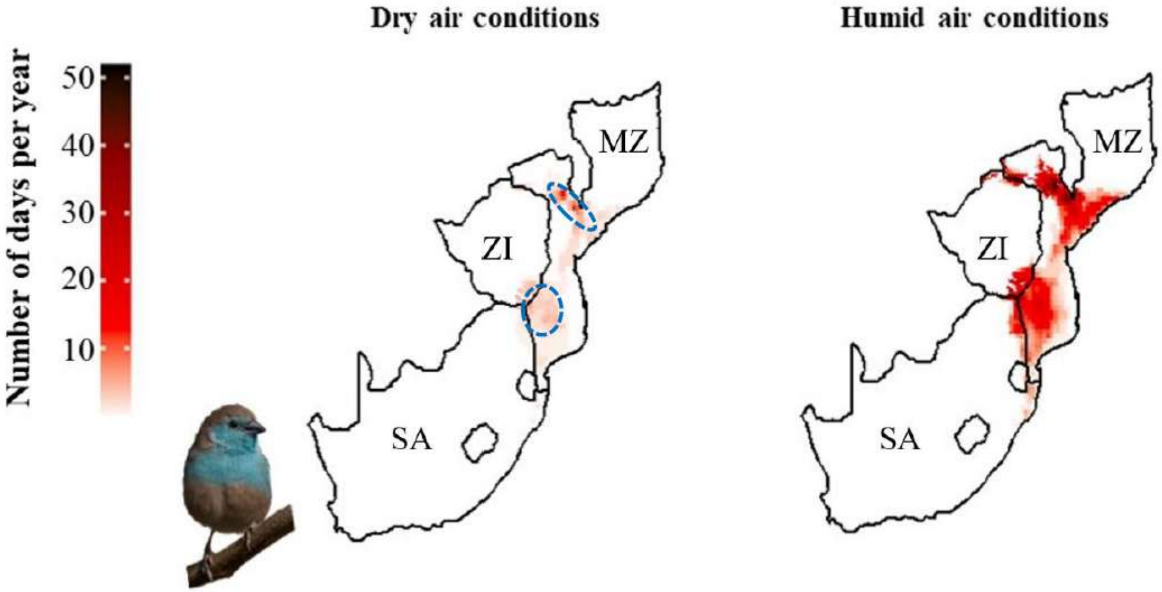

Figure 2. Days per year on which blue waxbills (*Uraeginthus angolensis*) are projected to be at risk of lethal hyperthermia (i.e., T_{air} exceeding heat tolerance limits) in the eastern lowlands (< 500 m elevation) of southern Africa under dry conditions (left) and humidity of 21 g m^{-3} (right) during 2090-2100 (RCP 8.5 Climate Change Scenario 2100). The model assumes birds are inactive and completely shaded from solar radiation, and is therefore likely conservative. The blue ovals in the dry air map indicate the two regions referred to in the text, one in southern Mozambique (MZ) and including parts of northern Kruger National Park in South Africa (SA), the second in the Zambezi River valley in central Mozambique

increase in extreme maximum T_{air} to 49 ºC by 2100 would be associated with maximum humidity of ~22.5 g m^{-3}, slightly above our experimental value.

Our data add to the evidence that that avian evaporative cooling capacity and heat tolerance are reduced by elevated humidity [16,18,20,21]. In addition, the maximum T_{b} tolerated by the waxbills (47.5 ºC and 47.2 ºC under dry and humid conditions, respectively) is ~ 3 ºC higher than those tolerated by arid-zone passerines, supporting arguments that birds in humid environments have evolved pronounced hyperthermia tolerance [20,23,38]. However, employing hyperthermia as a thermoregulatory strategy is only beneficial if birds can sustain hyperthermia until conditions allow for passive or evaporative heat dissipation (e.g. humidity decreases, or T_{air} declines), or they risk their T_{b} increasing towards lethal limits. Hence, prolonged heat exposure at T_{air} approaching and exceeding 45 ºC and humidity of 21 g m^{-3} dramatically elevates the risk of lethal hyperthermia. During the PNR mortality event T_{air} was > 40 ºC for ~4 hours, which likely amplified lethal hyperthermia risks in birds [6].

The combination of T_{air} and humidity experienced by the waxbills at their heat tolerance limit in the humid treatment is equivalent to a wet bulb temperature (T_{W}; calculated following Stull 2011 [39]) of 30.7 ºC, just 1 ºC below the maximum tolerable T_{W} ($T_{\mathrm{W\text{-}max}}$) for trumpeter hornbills (*Bycanistes bucinator*), a forest frugivore [21]. The T_{W} = 30.7 ºC tolerated by the waxbills is likely close to the species' $T_{\mathrm{W\text{-}max}}$, since most individuals were no longer able to maintain $T_{\mathrm{b}} < T_{\mathrm{air}}$ (Figure 1A) and EHL/MHP was < 1.0 (Figure 1B). However, hornbills exhibited EHL/MHP < 0.5 at their $T_{\mathrm{W\text{-}max}}$ [21], suggesting that waxbills may be able to reach slightly higher T_{W} values.

Projected increases in the frequency of days per annum on which T_{air} will exceed the waxbills' heat tolerance limits by the end of the Century are 3- to 7-fold greater under humidity of 21 g m^{-3} compared to dry conditions (Figure 2). These observations reiterate that increases in wet-season humidity will elevate risks of avian lethal hyperthermia to a greater extent than increasing T_{air} alone [21] and that, as is the case for humans [40,41] increases in exposure to moist heat pose a major risk under climate change. The areas that are likely to rendered uninhabitable for blue waxbills during hot, humid conditions include much of Mozambique, central and northern Kruger National Park and southeastern Zimbabwe including Gonarezhou National Park. It is likely that the range of this species will contract substantially as exposure to lethal combinations of heat and humidity increase in the eastern parts of its range.

Our results also have broader implications for other small passerines occupying hot, humid tropical zones globally, which may be more vulnerable to heat-related mass mortality events than previously thought. These findings also highlight how the relative risks of lethal hyperthermia and lethal dehydration (e.g., [8,14]) might vary along aridity gradients. On extremely hot days in humid environments, impeded evaporative heat loss will delay cumulative dehydration reaching lethal levels (the major risk for many arid-zone birds; [8,14]), but reduced HTL under humid conditions will increase the likelihood of lethal hyperthermia. Interventions like the provision of artificial water may thus be expected to be less effective at ameliorating the effects of extreme heat waves in humid regions compared to arid regions, a notion supported by the observation that the mortality event in PNR occurred despite the proximity of a large body of water [24].

In addition to increasing the likelihood of lethal hyperthermia, high humidity likely intensifies fitness costs arising from behavioural trade-offs between heat dissipation and activities such as foraging [15,42–44], exacerbating the consequences of sustained hot weather. Waxbills are less likely to incur sublethal costs under dry conditions, as they have a greater thermal safety margin for increases in T_b resulting from activity-associated heat production (e.g., [45]). Such fitness costs are not restricted to waxbills: other species that share similar body size, habitats, life histories and feeding guilds might also encounter exacerbated sublethal fitness costs and mortality risks during humid heat events. Waxbills and other small granivores that typically forage on the ground in the sun [27] are likely to experience greater sublethal fitness costs compared to frugivores foraging in shady tree canopies [46,47].

Our estimation of exposure of blue waxbills to lethal hyperthermia risk under future climate is likely conservative. First, our models simulated inactive birds occupying completely shaded microsites where operative temperature is equivalent to T_{air}, a situation likely rare for free-ranging waxbills. Operative temperatures during the heat of the day will often exceed T_{air} on account of radiative heat fluxes arising sources that include solar radiation penetrating into tree and shrub canopies and reflected radiation [42,48]. Moreover, in some of the modelled areas future humidity may exceed the 21 g m^{-3} we have modelled here, potentially resulting in waxbill HTL values lower than our assumed value of 45.7 ^{o}C.

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ETHICS STATEMENT

All experimental procedures performed in this study approved by the University of Pretoria's Animal Ethics Committee (NAS036/2022 and NAS141/2020). The study took place under permit OP 164/2022 and OP42-2022 issued by Ezemvelo KZN Wildlife.

REFERENCES

1. Masson-Delmotte V *et al.* 2021 IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. (doi:10.1017/9781009157896)

2. Finlayson HH. 1932 Heat In The Interior of South Australia: holocaust of bird-life. *South Australia Ornithology* **11**, 158–160.

3. Welbergen JA, Klose SM, Markus N, Eby P. 2008 Climate change and the effects of temperature extremes on Australian flying-foxes. *Proceedings of the Royal Society B: Biological Sciences* **275**, 419–425. (doi:10.1098/rspb.2007.1385)

4. Pruvot M, Cappelle J, Furey N, Hul V, Heng HS, Duong V, Dussart P, Horwood P. 2019 Extreme temperature event and mass mortality of insectivorous bats. *European Journal of Wildlife Research* **65**, 41. (doi:10.1007/s10344-019-1280-8)

5. McKechnie AE, Hockey PAR, Wolf BO. 2012 Feeling the heat: Australian landbirds and climate change. *Emu - Austral Ornithology* **112**, i–vii. (doi:10.1071/MUv112n2_ED)

6. McKechnie AE, Rushworth IA, Myburgh F, Cunningham SJ. 2021 Mortality among birds and bats during an extreme heat event in eastern South Africa. *Austral Ecology* **46**, 687–691. (doi:10.1111/aec.13025)

7. Sharnie K, Stephan A. 2018 Extreme heat wipes out almost one third of Australia's spectacled flying fox population. *ABC News*. See https://www.abc.net.au/news/2018-12-19/heat-wipes-out-one-third-of-flying-fox-species/10632940 (accessed on 29 April 2025).

8. McKechnie AE, Wolf BO. 2010 Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters* **6**, 253–256. (doi:10.1098/rsbl.2009.0702)

9. Holt KA, Boersma PD. 2022 Unprecedented heat mortality of Magellanic Penguins. *Ornithological Applications* **124**. (doi:10.1093/ORNITHAPP/DUAB052)

10. Quintana F, Uhart MM, Gallo L, Mattera MB, Rimondi A, Gómez-Laich A. 2022 Heat-related massive chick mortality in an Imperial Cormorant Leucocarbo atriceps colony from Patagonia, Argentina. *Polar Biology* **45**, 275–284. (doi:10.1007/S00300-021-02982-6/FIGURES/5)

11. Sloane SA, Gordon A, Connelly ID. 2022 Bushtit (Psaltriparus minimus) nestling mortality associated with unprecedented June 2021 heatwave in Portland, Oregon. *The Wilson Journal of Ornithology* **134**. (doi:10.1676/21-00080)

12. Saunders DA, Mawson P, Dawson R. 2011 The impact of two extreme weather events and other causes of death on Carnaby's Black Cockatoo: A promise of things to come for a threatened species? *Pacific Conservation Biology* **17**, 141–148. (doi:10.1071/PC110141)

13. Albright TP, Mutiibwa D, Gerson AlexanderR, Smith EK, Talbot WA, O'Neill JJ, McKechnie AE, Wolf BO. 2017 Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences* **114**, 2283–2288. (doi:10.1073/pnas.1613625114)

14. Conradie SR, Woodborne SM, Wolf BO, Pessato A, Mariette MM, McKechnie AE. 2020 Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology* **8**. (doi:10.1093/conphys/coaa048)

15. Conradie SR, Woodborne SM, Cunningham SJ, McKechnie AE. 2019 Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 14065–14070. (doi:10.1073/pnas.1821312116)

16. Lasiewski RC, Acosta M, Acosta AL, Bernstein MH. 1966 Evaporative Water Loss In Birds - I. Characteristics Of The Open Flow Method Of Determination, And Their Relation To Estimates of Thermoregulatory Ability. *Comparative Biochemistry and Physiology* **19**, 445–457.

17. Powers DR. 1992 Effect of Temperature and Humidity on Evaporative Water Loss in Anna' s Hummingbird (Calypte anna). *J Comp Physiol B* **162**, 74–84.

18. Gerson AR, Smith EK, Smit B, McKechnie AE, Wolf BO. 2014 The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology* **87**, 782–795. (doi:10.1086/678956)

19. van Dyk M, Noakes MJ, McKechnie AE. 2019 Interactions between humidity and evaporative heat dissipation in a passerine bird. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **189**, 299–308. (doi:10.1007/s00360-019-01210-2)

20. Freeman MT, Coulson B, Short JC, Ngcamphalala CA, Makola MO, McKechnie AE. 2024 Evolution of avian heat tolerance: The role of atmospheric humidity. *Ecology* **105**. (doi:10.1002/ecy.4279)

21. Coulson B, Freeman MT, Conradie SM, McKechnie AE. In review. Hyperthermia risk for a frugivorous bird inhabiting humid lowland forests will increase greatly by the end of the Century. *Conservation Physiology*

22. Ratnayake HU, Kearney MR, Govekar P, Karoly D, Welbergen JA. 2019 Forecasting wildlife die-offs from extreme heat events. *Animal Conservation* **22**, 386–395. (doi:10.1111/ACV.12476)

23. Freeman MT, Czenze ZJ, Schoeman K, McKechnie AE. 2022 Adaptive variation in the upper limits of avian body temperature. *Proceedings of the National Academy of Sciences* **119**. (doi:10.1073/pnas.2116645119)

24. McKechnie AE, Gerson AR, Wolf BO. 2021 Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *Journal of Experimental Biology* **224**. (doi:10.1242/jeb.229211)

25. Fick SE, Hijmans RJ. 2017 WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* **37**, 4302–4315. (doi:10.1002/JOC.5086)

26. Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ. 1997 THE ATLAS OF SOUTHERN AFRICAN BIRDS.

27. Chittenden H, Davies G, Weiersbye I. 2016 *Roberts Bird Guide: Illustrating Nearly 1000 Species in Southern Africa*. The John Voelcker Bird Book Fund.

28. Whitfield MC, Smit B, McKechnie AE, Wolf BO. 2015 Avian thermoregulation in the heat: Scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *Journal of Experimental Biology* **218**, 1705–1714. (doi:10.1242/JEB.121749/-/DC1)

29. R Core Team. 2022 R: A Language Environment for Statistical Computing.

30. Muggeo VMR. 2017 Interval estimation for the breakpoint in segmented regression: a smoothed score-based approach. *Australian & New Zealand Journal of Statistics* **59**, 311–322. (doi:10.1111/anzs.12200)

31. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* **67**. (doi:10.18637/jss.v067.i01)

32. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software* **82**. (doi:10.18637/jss.v082.i13)

33. Mbokodo I, Bopape M-J, Chikoore H, Engelbrecht F, Nethengwe N. 2020 Heatwaves in the Future Warmer Climate of South Africa. *Atmosphere* **11**, 712. (doi:10.3390/atmos11070712)

34. IPCC. 2014 Climate Change 2014 Synthesis Report. Contribution of working groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

35. Engelbrecht F *et al.* 2015 Projections of rapidly rising surface temperatures over Africa under low mitigation. *Environmental Research Letters* **10**. (doi:10.1088/1748-9326/10/8/085004)

36. Sherwood SC, Meyer CL. 2006 The General Circulation and Robust Relative Humidity. *Journal of Climate* **19**, 6278–6290. (doi:10.1175/JCLI3979.1)

37. Willett KM, Gillett NP, Jones PD, Thorne PW. 2007 Attribution of observed surface humidity changes to human influence. *Nature* **449**, 710–712. (doi:10.1038/nature06207)

38. Weathers WW. 1997 Energetics and thermoregulation by small passerines of the humid, lowland tropics. *The Auk* **114**, 341–353.

39. Stull R. 2011 Wet-Bulb Temperature from Relative Humidity and Air Temperature. *Journal of Applied Meteorology and Climatology* **50**, 2267–2269. (doi:10.1175/JAMC-D-11-0143.1)

40. Sherwood SC, Huber M. 2010 An adaptability limit to climate change due to heat stress. *Proceedings of the National Academy of Sciences* **107**, 9552–9555. (doi:10.1073/pnas.0913352107)

41. Vecellio DJ, Kong Q, Kenney WL, Huber M. 2023 Greatly enhanced risk to humans as a consequence of empirically determined lower moist heat stress tolerance. *Proceedings of the National Academy of Sciences* **120**. (doi:10.1073/pnas.2305427120)

42. Cunningham SJ, Martin RO, Hockey PAR. 2015 Can behaviour buffer the impacts of climate change on an arid-zone bird? *Ostrich* **86**, 119–126. (doi:10.2989/00306525.2015.1016469)

43. van de Ven TMFN, McKechnie AE, Cunningham SJ. 2019 The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia* **191**, 205–215. (doi:10.1007/s00442-019-04486-x)

44. Bourne AR, Cunningham SJ, Spottiswoode CN, Ridley AR. 2020 High temperatures drive offspring mortality in a cooperatively breeding bird. *Proceedings of the Royal Society B: Biological Sciences* **287**, 20201140. (doi:10.1098/rspb.2020.1140)

45. Nilsson J-Å, Nord A. 2018 Testing the heat dissipation limit theory in a breeding passerine. *Proceedings of the Royal Society B: Biological Sciences* **285**, 20180652. (doi:10.1098/rspb.2018.0652)

46. Strydom LH, Conradie SR, Smit IPJ, Greve M, Boucher PB, Davies AB, McKechnie AE. 2024 Mapping tree canopy thermal refugia for birds using biophysical models and LiDAR. *Int J Biometeorol* (doi:10.1007/s00484-024-02833-z)

47. Martin RO, Cunningham SJ, Hockey PA. 2015 Elevated temperatures drive fine-scale patterns of habitat use in a savanna bird community. *Ostrich* **86**, 127–135. (doi:10.2989/00306525.2015.1029031)

48. Bakken G, Santee W, Erskine D. 1985 Operative and standard operative temperature: tools for thermal energetics studies. *American Zoologist* **25**, 933–943.