

Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species

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ABSTRACT

1. Surface water is a critical resource for many birds inhabiting arid regions, but the implications of regular drinking and dependence on surface water for the evolution of thermal physiology remain largely unexplored.
2. We hypothesized that avian thermoregulation in the heat has evolved in tandem with the use of surface water and predicted that (a) regularly drinking species have a greater capacity to elevate rates of evaporative water loss (EWL) compared to non-drinking species, and (b) heat tolerance limits (HTLs) are higher among drinking species. To test these predictions, we quantified thermoregulatory responses to high air temperature (T_a) in 12 species of passerines from the South African arid zone and combined these with values for an additional five species. We categorized each species as either: (a) water-dependent, regularly drinking, or (b) water-independent, occasional-/non-drinking.
3. In support of our predictions, both conventional and phylogenetically independent analyses revealed that evaporative scope (the ratio of maximum EWL to minimum thermoneutral EWL) during acute heat exposure was significantly higher among drinking species. Moreover, evaporative scope was significantly and positively related to HTL (i.e. maximum air temperature tolerated before the onset of severe hyperthermia).
4. These findings offer new insights into the co-evolution of water dependence, movement ecology and thermal physiology in the context of trade-offs between dehydration avoidance and resistance to lethal hyperthermia in hot desert habitats.

KEYWORDS

Thermoregulation, metabolism, evaporative cooling, heat tolerance, drinking behaviour, birds, arid zone, physiology

INTRODUCTION

The coupling of animals' water and heat balance is most apparent in desert habitats, where high air temperatures, intense solar radiation and low humidity are combined with scarce and unpredictable water and food resources (Dawson & Schmidt-Nielsen, 1964). Under these conditions, individuals may face frequent trade-offs between water conservation and dehydration tolerance *versus* high evaporative cooling requirements to avoid lethal hyperthermia (Dawson & Bartholomew, 1968). These trade-offs are most apparent in small, diurnal endotherms, for which a combination of exposure to high operative temperatures and high mass-specific energy and water requirements constrains survival and reproduction (Cunningham, Martin, Hojem, & Hockey, 2013; McKechnie & Wolf, 2010; Serventy, 1971; Williams & Tieleman, 2005).

Surface water is a critical resource for many animals inhabiting arid environments, particularly those taxa whose diets contain little preformed water (e.g., dry seeds) (Bartholomew & Cade, 1963; Fisher, Lindgren, & Dawson, 1972; MacMillen & Hinds, 1998). Within desert bird communities there is considerable variation in dependence on surface water, with some species drinking regularly, others drinking occasionally, and some species apparently never drinking (Fisher et al., 1972; Lynn, Chambers, & Rosenstock, 2006; Lynn, Rosenstock, & Chambers, 2008; Smit, Woodborne, Wolf, & McKechnie, 2019; Smyth & Coulombe, 1971). Dependence on drinking water may vary within closely related taxa; among southern African larks (Alaudidae), for instance, some species are entirely independent of drinking (e.g., Dune lark [*Calendulauda erythrochlamys*], Red lark [*Calendulauda burra*]; (Dean & Ryan, 2005b, 2005a)) whereas others drink daily (Grey-backed sparrow lark [*Eremopterix verticalis*], Stark's lark [*Spizocorys starki*]; (Lloyd, 2005b, 2005a)). Even in arid areas where surface water is available, selection may favour drinking-independence on account of factors such as the cost of travelling daily to distant water sources, and high predation risk at isolated water holes (Aulie,

1971; Cade, 1965; Engel, Biebach, & Visser, 2006; Fisher et al., 1972; Rosenstock, Ballard, & Devos, 1999; Torre-Bueno, 1978; Tucker, 1968).

Recent investigations of avian heat tolerance limits and maximum evaporative cooling capacities have revealed considerable variation among and within taxa. Among arid-zone passerines, heat tolerance limits (HTL; maximum air temperature tolerated before the onset of severe hyperthermia) varies by $\sim 10^{\circ}\text{C}$ among species, evaporative scope [the ratio of maximum evaporative water loss (EWL) to minimum EWL] varies from ~ 6.7 to ~ 18.4 , and maximum ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) vary from ~ 1.2 to ~ 2.2 (McKechnie et al., 2017; Whitfield, Smit, McKechnie, & Wolf, 2015). Some of this variation appears to reflect broad biogeographic differences (McKechnie et al., 2017; Smith et al., 2017), but ecological correlates of evaporative cooling capacity have yet to be explored.

Species that drink on a daily basis have the opportunity to predictably replenish their body water pools whereas non-drinking species that rely only on dietary and metabolic water may face increased risk of dehydration, particularly during very hot weather (Smit & McKechnie, 2015). Furthermore, water budgets are strongly influenced by diet. Granivorous species, particularly in arid environments, may be under stronger pressure to drink standing water compared to insectivorous species because of the much lower water content of air-dried seeds ($\sim 6\%$ by mass) compared to insects (70-90%; Bartholomew & Cade, 1963; Cade, 1962; MacMillen, 1990; MacMillen & Baudinette, 1993). We hypothesized that use of surface water has shaped the evolution of avian evaporative cooling capacity at high environmental temperatures so that regularly-drinking species are able to invest proportionately larger amounts of water in thermoregulation. Therefore, we predicted that regularly-drinking species have a greater capacity to elevate rates of evaporative water loss above minimal levels (i.e., greater evaporative scope) compared to non-drinking species. Because the extent to which EWL can be increased above baseline levels may, *a priori*, be expected to determine the maximum environmental temperature at which body temperature can be defended, we further predicted that HTL is positively correlated with evaporative scope.

To test these predictions, we took advantage of the high diversity of larks (Alaudidae) and other passerines in the southern African arid zone to quantify variation in heat tolerance and evaporative cooling capacity among species that

vary in ecological traits including diet and reliance on free-standing water. Using the same techniques involving high flow rates and very low chamber humidities as employed for a number of recent studies examining the comparative physiology of avian thermoregulation at high T_a (e.g., Smit et al., 2018; Smith et al., 2015; Whitfield et al., 2015), we quantified HTL, evaporative scope and related parameters in five species of larks and representatives of seven hitherto-uninvestigated passerine families in southern Africa's Nama Karoo biome.

MATERIALS AND METHODS

Study site and species

We quantified thermoregulatory performance in the heat in 12 species (this study) that vary in ecological traits including diet and reliance on surface water, but are of broadly similar body mass (M_b ; range= ~8-46g; Table 1). Data on these species were obtained at two sites during the austral summer. Between 1 October - 23 November 2018 and 21 February - 1 March 2019 we captured Marico flycatchers (MF; *Melaenornis mariquensis*: Muscicapidae; n=5), fork-tailed drongos (FTD; *Dicrurus adsimilis*: Dicruridae; n=3), and crimson-breasted shrikes (CBS; *Laniarius atrococcineus*: Malaconotidae; n=9) at Radnor farm (26°6'S23", 22°52'54"E) near Vorstershoop, North West Province, South Africa. The vegetation of this region is characterised as Molopo Bushveld; an open woodland to closed shrubland dominated with *Vachellia erioloba* and *Boscia albitrunca* trees and *Lycium cinereum*, *L. hirsutum* and *Rhigozum trichotomum* shrubs.

Between 2 December 2018 and 4 February 2019 we captured grey-backed sparrow-larks (GBSL; *Eremopterix verticalis*: Alaudidae; n=10), Karoo long-billed lark (KLBL; *Certhilauda subcoronata*: Alaudidae; n=10), spike-heeled lark (SHL; *Chersomanes albofasciata*: Alaudidae; n=10), fawn-coloured lark (FCL; *Calendulauda africanoides*: Alaudidae; n=7), Stark's lark (SL; *Spizocorys starki*: Alaudidae; n=10), lark-like buntings (LLB; *Emberiza impetuani*: Emberizidae; n=10) at Black Mountain Mine Conservation Area (29°18'S, 18°51'E) near the town of Aggeneys, Northern Cape, South Africa. The study site is arid with a mean annual rainfall of ~ 100 mm and daily maximum T_a that ranged from 26.4 - 40.3°C during the study. This area consists of scattered *Rhizogum trichotomum* and grasses. We also caught red-eyed bulbuls (REB; *Pycnonotus nigricans*: Pycnonotidae; n=10), Orange River white-eyes (ORWE; *Zosterops*

pallidus: Zosteropidae; n=10), and southern fiscals (SF; *Lanius collaris*: Laniidae; n=9) around the town of Aggeneys in irrigated gardens and green spaces. All individuals were captured using spring traps baited with superworms (*Zophobas morio*). Captured birds were held in cloth bags and transported by road (approximately 20 min trip) to an animal holding room. Birds were then housed individually in indoor cages (0.8 m³) for no more than 12 h and were provided with ad libitum supply of water and food (superworms), before being transferred to a field laboratory.

We also included published EWL and HTL data from five additional passerine species: red larks (RL; *Calendulauda burra*) studied by Kemp and McKechnie (2019) at Aggeneys between 11 January and 10 February 2018, scaly-feathered weavers (SFW; *Sporopipes squamifrons*: Ploceidae), sociable weavers (SW; *Philetairus socius*: Ploceidae) and white-browed sparrow-weavers (WBW; *Plocepasser mahali*: Ploceidae) studied by Whitfield et al. 2015, and Southern pied babbler (SPB *Turdoides bicolor*: Leiothrichidae; S.J. Cunningham et al. unpubl. data). All the above species have $M_b < 70\text{g}$ and occupy the sandy arid regions of western Southern Africa where the availability of surface water is limited. We used observations from the literature to categorize each species as either a “regular drinker” (significant numbers of the species have been observed drinking from surface water sources), or a non-drinker (not observed drinking from surface water even when available in their habitat) following Abdu, McKechnie, Lee, & Cunningham, 2018; Smit, Woodborne, Wolf, & McKechnie, 2019; van der Merwe & Smit, 2019. Some species were considered opportunistic drinkers (e.g. sociable weaver and white-browed sparrow-weaver) as they drink regularly when water is available (Smit et al., 2019); because most work was carried out on rangelands where these species had access to surface water we classified them as regular drinkers.

Air and body temperature

We measured T_b by injecting temperature-sensitive passive integrated transponder (PIT) tags (Biotherm, Biomark, Boise ID, USA) into the abdominal cavity of each individual. We placed individual PIT-tagged birds in a metabolic chamber (below) within the receiving range of an antenna linked to a portable transceiver system (HPR+, Biomark, Biose ID, USA). We calibrated PIT tags in a circulating water bath (model F34, Julabo, Seelbach BW, DE) over temperatures

ranging 35 to 50 °C against a thermistor probe (TC-100, Sable Systems, Las Vegas, NV, USA). Temperatures measured by PIT tags deviated 0.02 ± 0.09 °C ($n = 20$) from actual values. To measure T_a during the gas exchange measurements, we inserted a thermistor probe (TC-100, Sable Systems, Las Vegas, NV, USA) sealed with a rubber grommet through the side of each metabolic chamber.

Gas exchange

We used an open flow-through respirometry system to measure carbon dioxide production (V_{CO_2}) and EWL during measurements. We used two metabolic chambers that consisted of a 4 or 12.8 L airtight container outfitted with a plastic mesh platform elevated ~ 10 cm above a ~ 1 cm layer of mineral oil to trap excreta. These chambers have been previously shown to not absorb water vapour (Whitfield et al., 2015). The chambers were placed in a controlled-temperature box constructed from either an ice chest (~ 100 L) or custom-built aluminum box (~ 640 L). The T_a within both chambers was regulated using a Peltier device (AC-162 Thermoelectric Air Cooler, TE Technology, Traverse City MI, USA) mounted in one of the walls and controlled via a digital controller (TC-36-25-RS485 Temperature Controller, TE Technology, Traverse City MI, USA).

Atmospheric air, supplied by an oil-free compressor, was scrubbed of water vapour using a membrane dryer (Champion[®]CMD3 air dryer and filter, Champion Pneumatic, Quincy IL, USA). The dried air was provided to both systems and split into a baseline and experimental channel. A needle valve (Swagelok, Solon, OH, USA) was used to regulate the flow rate in the baseline channel, and a mass flow controller (Alicat Scientific Inc., Tuscon AZ, USA), calibrated using a soap-bubble flow meter (Giliberator 2, Sensidyne, St Petersburg, FL, USA), regulated the experimental flow rates. The air inlet was placed close to the top of each metabolic chamber with an elbow joint facing the top (to minimize any potential convective cooling at higher flow rates) and the air outlet below the mesh platform to maximize air mixing. Flow rates ranged from $1.1 - 30.7$ L min^{-1} , depending on T_a , M_b , and individual behaviour, and were adjusted to maintain water vapour pressures as low as possible (i.e., < 4 parts per thousand) within the chamber while allowing for the accurate measurements of differences in water vapour and CO_2 between incurrent and excurrent air.

Excurrent air from the chamber and baseline air were subsampled sequentially using a respirometry multiplexer (model MUX3-1101-18M, Sable Systems) in manual mode and an SS-3 Subsampler (Sable Systems). Subsampled air was pulled through a CO₂/H₂O analyzer (model LI-840A, LI-COR, Lincoln, NE, USA), which was regularly zeroed using nitrogen, and spanned for CO₂ using a certified calibration gas with a known CO₂ concentration of 2000 ppm (AFROX, Johannesburg, South Africa). The H₂O sensor of the Li-840A was regularly zeroed using nitrogen and spanned using a dewpoint generator (DG-4, Sable Systems, Las Vegas NV). All tubing in the system was Bev-A-Line IV tubing (Thermoplastic Processes Inc., Warren, NJ, USA). Voltage outputs from the analyzers and thermistor probes were digitized using an analog-digital converter (model UI-3, Sable Systems, Las Vegas NV, USA) and recorded with a sampling interval of 5 s using Expedata software (Sable Systems).

Experimental Protocol

To allow individuals to acclimatize and ensure they were post-absorptive, we estimated the food passage rate for each species using the scaling equation provided by Karasov (1990), and individuals were held without food for at least one hour in the metabolic chamber before commencing measurements. Trials occurred during the day, during which V_{CO_2} , and EWL were recorded over a stepped series of progressively higher T_a values. Measurements commenced with a baseline air subsample until water and CO₂ readings were stable (5 min). Subsequently, chamber excurrent air was subsampled when T_a had stabilized at the target value, and CO₂ and H₂O traces were stable for at least 5 min, followed by another 5 min baseline. Trials began at T_a of 28 °C with 4 °C increases until 40 °C and then 2 °C increases until reaching a thermal endpoint (i.e., when $T_b > 45.3$ °C), or when individuals exhibited prolonged escape behavior.

During measurements, individuals were continuously monitored using an infrared video camera. Trials were terminated and individuals immediately removed from the chamber if they displayed sustained escape behaviour (i.e., agitated jumping), they exhibited a loss of coordination or balance, showed sudden decreases in EWL or resting metabolic rate (RMR), and/or exhibited rapid increases in $T_b > 45$ °C. After an individual was removed from the chamber we placed it immediately in front of an air conditioner producing chilled air, and dabbed its underparts with ethanol to facilitate more rapid cooling. Once T_b

stabilized at normothermic levels (40 – 42 °C), the bird was offered water using a syringe, placed back in its cage at room temperature to rest with ad libitum water and food. The bird was later released at the site of capture. This experimental protocol has been used previously and, in one instance with opportunistic monitoring for several weeks post-release, no adverse effects were observed (Kemp & McKechnie, 2019).

Data Analysis

We corrected for analyzer drift and lag using the relevant algorithms in Expedata software (Sable Systems, Las Vegas NV, USA). Equations 9.5 and 9.6 from Lighton (2008) were used to calculate V_{CO_2} and evaporative water loss (EWL) from the lowest stable 5 min periods of CO_2 and water vapour at a given T_a , assuming $0.803 \text{ mg H}_2\text{O mL}^{-1}$ vapour. As individuals were likely post-absorptive, we calculated RMR from V_{CO_2} assuming respiratory exchange ratio (RER) = 0.71 (Walsberg & Wolf, 1995) and converted rates of V_{CO_2} to metabolic rate (W) using $27.8 \text{ J mL}^{-1} CO_2$ (Withers, 1992). The rates of EWL were converted to rates of evaporative heat loss (EHL, W) assuming a latent heat of vaporization of water of 2.406 J mg^{-1} at 40 °C (Tracy, Welch, Pinshow, & Porter, 2010).

Intraspecific analyses

To identify inflection points for EWL, RMR, T_b , EHL/MHP, we used the package 'segmented' (Muggeo, 2008) and performed a broken-stick regression analysis in R 3.5.2 (R Core Team, 2018). We created subsets that only included data above inflection points to estimate the slopes for the relationships of EWL, RMR, EHL/MHP, T_b and rate of T_b increase as functions of T_a . To test for an effect of T_a above inflection points on the above parameters, we performed generalized mixed-effect models with the R package 'nlme' (Pinheiro, Bates, DebRoy, Sarkar, & Team., 2009). We accounted for pseudoreplication (due to multiple measurements from individuals) by including individual identity as a random factor in all analyses. We included M_b as a covariate in all above models; however, it did not improve the model fit and so was discarded in all analyses. We assessed significance at $\alpha < 0.05$ and values are presented as mean \pm s.d.

Interspecific analyses

We used both generalized linear models (GLM) and phylogenetic generalized least squares (PGLS) to test the effects of drinking habits on evaporative scope, minimum EWL, and maximum EWL. We further tested the effects evaporative scope on the HTL. For phylogenetic analyses, we downloaded 100 phylogenies from <http://www.birdtree.org> (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012), using the Ericson et al. (2006) phylogeny as a back-bone. We built a majority rule consensus tree (specified fraction, $p > 0.5$), using the program Mesquite (Maddison & Maddison, 2014), and subsequently ran our PGLS models in R using the package *ape* (Paradis & Schliep, 2019) We used the null models (trait ~ 1) of each organismal trait to test for phylogenetic signal. We considered Kappa values significantly greater than "0" indicative of phylogenetic signal. In both GLM and PGLS analyses we included drinking habits ("drinker", or "non-drinker") and M_b as fixed effects, but sequentially removed non-significant terms ($p > 0.05$).

RESULTS

Body temperatures, metabolic rates and evaporative water loss

Normothermic T_b at thermoneutrality varied by ~ 2.6 °C among species (39.6 ± 1.04 °C in GBSL to 42.2 ± 0.7 °C in FTD; Sup. Fig. 1, 2, Table 2, 3). Maximum T_b varied from 43.9 ± 0.6 °C in REB ($n = 4$) to 45.2 °C in MF ($n = 1$), SF ($n = 1$), and FTD ($n = 2$) (Table 2, 3). The maximum T_a reached by all birds varied from 46 °C in ORWE to 54 °C in a single GBSL and KLBL (Table 2, 3). All birds' thermal endpoints (i.e., when $T_b > 45.3$ °C), or when individuals exhibited prolonged escape behavior, ranged from $T_a = 46 - 54$ °C.

Minimum resting metabolic rate values within the TNZ varied from 0.19 W in ORWE to 0.59 W in CBS (Fig 1.; Table 2, 3). All species showed a clear upper critical limit to thermoneutrality (T_{uc}) above which RMR increased linearly (Sup. Fig. 3, 4). The T_{uc} ranged from $T_a = 28.4$ °C in LLB to $T_a = 42.3$ °C in FTD. Above the T_{uc} , RMR for all species increased to maximum values equivalent to $141 - 266\%$ of minimum values. Panting commenced at $T_a = 39.0 - 42.3$ °C and $T_b = 39.6 - 43.6$ °C (Table 2, 3).

Minimum EWL within the TNZ varied from 0.08 g h⁻¹ in SL to 0.26 g h⁻¹ in SF and FTD (Fig. 1; Table 2, 3; Sup. Fig. 5, 6). For all species, EWL increased

rapidly above a clear inflection point that varied between $T_a = 36.1$ °C in RL to $T_a = 42.2$ °C in FTD (Table 2, 3). Maximum rates of EWL ranged from 0.83 g h^{-1} in MF to 3.04 g h^{-1} in SF, and evaporative scope (i.e., the ratio of maximum EWL to minimum thermoneutral EWL) ranged from ~ 5.53 for MF to ~ 15.3 for SL (Table 2, 3). Maximum evaporative cooling capacity, expressed as maximum EHL/MHP, ranged from 1.32 for MF to 2.35 in KLBL (Sup. Fig. 7, 8). However, we based these values on the assumption that $\text{RER} = 0.71$ (i.e., individuals catabolized entirely lipids), and they could be higher if individuals used carbohydrates (MF = 1.76 to KLBL = 3.04).

Correlations between water-dependence and thermal physiology

We did not find significant phylogenetic signal in EWL traits or body mass in our data set of passerine species from the southern African arid zone (M_b : Kappa = 0.69, $p = 0.22$; evaporative scope: Kappa = 0.60, $p = 0.33$; HTL: Kappa = 0.54, $p = 0.39$; min EWL: Kappa = 0.25, $p = 0.64$; max EWL: Kappa = 0.29, $p = 0.59$). Although evaporative scope did not scale with M_b ($p > 0.05$), it differed between regular drinkers and non-drinkers (GLM: $F_{1,15} = 8.3$, $p = 0.01$, $R^2 = 0.31$; PGLS: $F_{1,15} = 16.2$, $p < 0.01$, $R^2 = 0.52$; Fig. 1). In the GLM, both minimum and maximum EWL were correlated with both M_b (MaxEWL: $F_{1,15} = 31.6$, $p < 0.01$, $R^2 = 0.66$; MinEWL: $F_{1,15} = 44.2$, $p < 0.01$, $R^2 = 0.73$), but not drinking habits. Similarly, in the PGLS, both minimum and maximum rates of EWL were not correlated with drinking habits (all $p > 0.05$), although both were positively correlated with M_b (min EWL: $F_{1,15} = 70.0$, $p < 0.001$, $R^2 = 0.82$; max EWL: $F_{1,15} = 53.9$, $p < 0.001$, $R^2 = 0.78$).

Our data supported the notion of a functional link between evaporative scope and HTL, with these variables were positively correlated in both GLM and PGLS analyses (GLM: $F_{2,14} = 17.6$, $p < 0.01$, $R^2 = 0.57$; PGLS: $F_{2,14} = 26.4$, $p < 0.001$, $R^2 = 0.79$; Fig. 1). Heat tolerance limit was also positively correlated with body mass (GLM: $F_{2,14} = 5.3$, $p = 0.04$, $R^2 = 0.57$ PGLS: $F_{2,14} = 27.1$, $p < 0.001$, $R^2 = 0.79$).

DISCUSSION

Our data reveal an apparent functional link between the drinking behaviour of arid-zone species and their thermoregulatory capacity, with greater evaporative cooling capacity (maximum EHL/MHP) observed in species that regularly drink

surface water. Larger evaporative scopes (the ratio of maximum EWL to minimum thermoneutral EWL) were, in turn, correlated with higher heat tolerance limits. Below, we highlight how these data provide an improved understanding of the potential coevolution of avian behaviour and thermal physiology in the context of trade-offs between dehydration avoidance and resistance to hyperthermia in hot deserts.

In the present study, the evaporative scopes of regularly-drinking species were approximately 50% greater than those of non-drinking species, indicating variation in evaporative cooling capacity is attributable to the contribution of surface water to overall water balance. For southern African arid-zone passerines, maximum evaporative scopes during heat exposure varied from 5.5 - 15.3. These data suggest that species with ready access to surface water and that drink frequently more readily expend water to dissipate larger heat loads than species that rely solely on dietary water. We note, however, that there remain broad biogeographic differences in avian evaporative scope globally, with values averaging 7.3 ± 0.8 in five Australian passerines (McKechnie et al., 2017) representing both drinkers and nondrinkers (Fisher et al., 1972).

Our finding that the maximum T_a birds can tolerate is correlated with evaporative scope suggests a mechanistic basis for the ~ 8 °C variation in HTL reported for the passerines (McKechnie et al., 2017; Smith et al., 2017; Whitfield et al., 2015; this study). Assuming metabolic costs of evaporative heat dissipation via panting are approximately constant among similarly-sized species, those capable of higher evaporative scopes would be expected to maintain larger $T_a - T_b$ gradients (Dawson, 1982), an argument supported by our data. These observations also support the notion that broad biogeographic variation in avian HTLs may reflect interspecific variation in evaporative scopes (McKechnie et al., 2017; Smith et al., 2017; Whitfield et al., 2015).

The relationships between drinking, evaporative cooling capacity and heat tolerance documented here are relevant to understanding several aspects of the ecology of birds in arid regions and the coevolution of their diets, behavioural ecology and thermal physiology. Interspecific variation among desert birds in terms of dependence on surface water is strongly related to dietary water content, with regular drinking far more prevalent among granivorous species compared to insectivores or omnivores (Fisher et al., 1972; Serventy, 1971; Smit et al., 2019). Water dependence, in turn, has a strong influence on

movement ecology, with water-dependent species often flying considerable distances daily to water sources in order to drink (e.g., Willoughby & Cade, 1967). Indeed, Smit et al. (2019) showed that a small passerine, the violet eared waxbill (*Uraeginthus granatinus*), would travel over 2 km daily to reach water. The analysis we present here suggests that the thermal physiology of desert birds has co-evolved with aspects of their ecology related to water dependence, raising new questions about the evolution of avian heat tolerance.

First, what are the adaptive benefits of greater heat tolerance for granivorous, water-dependent species? We speculate that more pronounced heat tolerance may permit longer foraging bouts in sunlit microsites, where operative temperatures (*sensu* Bakken, 1980; Robinson, Campbell, & King, 1976), may exceed air temperature by 10-15 °C in small species (e.g., Wolf & Walsberg, 1996b). Under these conditions, the capacity for large increases in evaporative heat dissipation likely increases foraging time and efficiency compared to individuals less able to maintain T_b at sublethal levels. The notion that predictable replenishment of body water stores through drinking allows birds to increase EWL more readily than non-drinking species is supported by the observation that, among Kalahari birds, panting commences at lower T_a values among drinking species compared to non-drinking species (Smit et al., 2016).

Second, why should comparable evaporative cooling capacity and heat tolerance limits not have evolved in non-drinking species that are reliant on dietary water? In species where insects or other animal prey are the primary source of water, water gains are subject to strong temperature-mediated trade-offs between foraging efficiency and thermoregulatory behaviours such as panting, wing-drooping and use of shaded microsites (Cunningham et al., 2013; du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; van de Ven, McKechnie, & Cunningham, 2019). We suspect the answer to this question involves dehydration risk and water conservation; species for which daily water intake is constrained by prey acquisition rates and is generally less predictable are likely under strong selection for water conservation, as manifested among our study species as relatively modest evaporative scopes and associated lower HTL values. Kemp and McKechnie (2019), for example, noted that a red lark resting in the shade during the heat of the day showed a number of behaviours (e.g., wing drooping and selection of shaded microsites) that appear directed at water conservation.

We can evaluate the functional consequences of differences in heat tolerance limits and evaporative cooling capacity between drinking and non-drinking species and their relative vulnerability to extreme heatwaves via a comparison of threshold daily maximum air temperature (T_{\max}) values associated with lethal dehydration risk (survival time < 5 hr; Albright et al. 2017; Conradie et al. 2019) and lethal hyperthermia risk (Figure 2). We find that dehydration T_{\max} thresholds for lethal dehydration are slightly higher among non-drinking species compared to drinking species (Figure 2). When combined with higher HTLs, the lower dehydration T_{\max} thresholds of drinking species result in larger differences between thresholds for lethal hyperthermia and lethal dehydration. Drinking species may thus exceed their limits of dehydration tolerance at lower T_{\max} values than non-drinking species if surface water is absent or they spend long periods inactive in shaded microsites during the heat of the day. Drinking species, in contrast, if we assume visits to water during the heat of the day, will be able to tolerate higher T_{\max} than non-drinking species and are better equipped to cope with extreme heat events with T_{\max} approaching or exceeding 50 °C (Figure 2).

In a recent study exploring the processes underlying the collapse of bird communities in North America's Mojave Desert over the last century (Iknayan & Beissinger, 2018), Riddell et al. (2019) found that the probability of species persistence was lowest at hot, dry sites and those lacking surface water. These authors attributed the declines to interspecific variation in increased thermoregulatory water demands, estimated using a biophysical model predicting evaporative cooling requirements for resting birds. Increases in cooling requirements were correlated with declines in occupancy for insectivores and carnivores whereas no correlation was evident for granivores and frugivores, supporting the argument that, in areas with surface water, in general insectivores will be more vulnerable than granivores to lethal risks of acute heat exposure (Riddell, Iknayan, Wolf, Sinervo, & Beissinger, 2019). Our present analysis, however, reveals that this higher vulnerability also extends to lethal hyperthermia, because of the lower heat tolerance limits of non-drinking species and the smaller differences between threshold values for lethal dehydration and hyperthermia.

We restricted this analysis to passerines to avoid patterns of interspecific physiological variation being confounded by differences in the primary

mechanism of evaporative cooling. Passerines rely on panting, whereas among non-passerines gular flutter and rapid cutaneous evaporation may replace panting as the primary cooling mechanism (Bartholomew, Hudson, & Howell, 1962; Bartholomew, Lasiewski, & Crawford, 1968; Lasiewski & Bartholomew, 1966; Webster & Bernstein, 1987; Webster & King, 1987; Wolf & Walsberg, 1996a). Both gular flutter and cutaneous evaporation dissipate heat evaporatively with minor metabolic costs thus allowing for more efficient heat dissipation compared to high metabolic heat loads associated with panting and tend to be associated with greater heat tolerance (Calder & Schmidt-Nielsen, 1966; Dawson, 1958; McKechnie et al., 2016; Smith, O'Neill, Gerson, & Wolf, 2015b; but see Lasiewski & Seymour, 1972; Smit et al., 2018). Moreover, both these mechanisms require less energy than panting and trade-offs between foraging and thermoregulation can *a priori* be expected to be less severe, particularly in the case of cutaneous evaporation. Overall, however, we predict similar functional links between surface water use and thermoregulation in the heat among non-passerines as those we report here for passerines; irrespective of the relative metabolic cost of the primary avenue of evaporative cooling, species that can regularly replenish body water reserves by drinking should be better-suited to elevate EWL far above baseline levels for thermoregulation.

Our analysis was also restricted to southern African species. Fewer data on heat tolerance limits and evaporative cooling capacity exist for the avifaunas of other arid regions, but those that do exist suggest that the findings we report here should not yet be extrapolated to other continents for several reasons. First, as noted above, the evaporative scopes of five Australian passerines (including several regular drinkers) were much lower than in many southern African species (McKechnie et al., 2017; Whitfield et al., 2015; this study). Second, seven species from the hotter Sonoran Desert showed high HTLs with little variation compared to southern African and Australian species from cooler sites (Smith et al., 2017). Hence, more data from these regions are needed to evaluate functional links similar to those we have demonstrated here for southern African species.

Conclusions

A substantial component of the variation in heat tolerance and evaporative cooling capacity within a desert bird community can be linked to interspecific

differences in dependence on surface water. Among passerines, the capacity for increases in evaporative heat dissipation appears to have evolved in response to the relative importance of drinking as a source of water input in such a way that drinking species are capable of higher evaporative scopes and greater heat dissipation capacities. The functional significance of this variation is directly related to heat tolerance limits, such that drinking species can tolerate higher environmental temperatures before the onset of unregulated hyperthermia. These findings reveal novel functional linkages between avian diet, movement ecology and thermal physiology, and have implications for understanding the ecology of arid-zone taxa under both current and future climates.

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Author contributions

ZJC, RK, BvJ, and MTF collected data

ZJC, RK, BvJ, MTF, BS analysed data

ZJC, BS, BOW, and AEM led the writing of the manuscript

All authors contributed critically to the drafts and gave final approval for publication

DATA AVAILABILITY STATEMENT

Data are available at <https://doi.org/10.5061/dryad.sn02v6x1k> (Czenze et al. 2020)

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Table 1. Variation in body mass, drinking behaviour and diet of 17 species of passerine from the arid zone of southern Africa.

Species	Mass	Regular drinking?	Diet	Source
Orange River white-eye (ORWE)	7.7±0.6 (10)	Y*	Insects and fruit	This study
Scaly-feathered weaver (SFW)	10.4±0.7 (16)	N [†]	Seeds	Whitfield et al. 2015
Lark-like bunting (LLB)	14.2±2.0 (10)	Y [†]	Seeds	This study
Grey-backed sparrow-lark (GBSL)	16.0±1.1(10)	Y [†]	Seeds	This study
Stark's lark (SL)	17.9±1.7(10)	Y*	Seeds	This study
Marico flycatcher (MF)	21.8±2.2 (7)	N [†]	Insects	This study
Fawn-coloured lark (FCL)	22.7±2.2(7)	N [†]	Insects and seeds	This study
Sociable weaver (SW)	24.9±1.0 (25)	Y [†]	Insects and seeds	Whitfield et al. 2015
Spike-heeled lark (SHL)	25.0±2.7(10)	N*	Insects and seeds	This study
Red-eyed bulbul (REB)	30.1±3.7 (10)	Y [†]	Insects and fruit	This study
Southern fiscal (SF)	37.3±2.2 (9)	N [†]	Vertebrates and insects	This study
Red lark (RL)	38.3±2.1(52)	N*	Insects and seeds	Kemp & McKechnie (2019)
Fork-tailed drongo (FTD)	43.7±3.5 (3)	Y*	Insects	This study
White-browed sparrow-weaver (WBSW)	39.4±2.9 (30)	Y [†]	Insects and seeds	Whitfield et al. 2015
Karoo long-billed lark (KLBL)	40.0±2.7(10)	N [‡]	Insects	This study
Crimson-breasted shrike (CBS)	46.2±2.7 (9)	N [†]	Insects	This study
Southern pied babbler (SPB)	69.9±3.8 (10)	Y*	Insects	S.J. Cunningham et al. unpubl. data

Drinking observations from *(Bowie, 2005; Dean, 2005a, 2005b, 2005c; Dean & Ryan, 2005b; Lloyd, 2005b);

[†](Smit et al., 2019); [‡](van der Merwe and Smit, unpublished data)

Table 2. Summary of thermoregulatory performance as a function of chamber air temperature (T_a) in six lark species from the arid zone of southern Africa. T_b = body temperature, T_a = ambient temperature, RMR = resting metabolic rate, EWL = evaporative water loss, EHL= evaporative heat loss, MHP = metabolic heat production. Means, SD and N are reported. Data for red larks are from Kemp & McKechnie (2019).

Variable	Grey-backed sparrow-lark (GBSL)	Stark's lark (SL)	Fawn-coloured lark (FCL)	Spike-heeled lark (SHL)	Red lark (males; RL)	Karoo long-billed lark (KLBL)
Body mass (g)	16.0±1.1 (10)	17.9±1.7 (10)	23.0±2.2 (8)	25.0±2.7 (10)	38.3±2.1 (52)	40.0±2.7 (10)
Body temperature						
Min. T_b (°C)	39.6±1.0 (10)	40.7±1.0 (10)	40.5±0.6 (6)	40.9±1.2 (10)	40.6±0.5 (8)	40.5±0.6 (9)
Inflection T_a (°C)	33.3	34.4	34.8	33.8	36.2	33.5
T_b versus T_a slope (°C)	0.34	0.25	0.32	0.3	0.25	0.24
Max T_b (°C)	44.8 (2) 45.1 (1)	45 (2)	44.5±0.4 (3)	44.9±0.1 (4) 45.0 (1)	44.7±0.3 (5)	44.5±0.3 (3) 44.9 (1)
Max T_a (°C)	52 (2) 54 (1)	52 (2)	48 (3) 50 (1)	50 (4) 52 (1)	50 (5)	52 (3) 54 (1)
T_b at onset of panting (°C)	43.2 (2)	42.7±0.8 (6)	43.2±0.9 (3)	43.6±0.7 (8)	41.9 (17)	42.5±1.3 (10)
T_a at onset of panting (°C)	40.5 (2)	40.4±3.5 (6)	41.8±2.4 (3)	41.9±2.5 (8)	38.0±1.7 (19)	41.8±2.1 (10)
95 th percentile $T_b > T_a$ (°C)	44.2	43.6	43.99	44.4	42.9	43.4
Resting metabolic rate						
Min. RMR (W)	0.25±0.05 (9)	0.25±0.04 (10)	0.31±0.05 (6)	0.36±0.11 (10)	0.31±0.06 (9)	0.49±0.06 (9)
T_{uc} (°C)	36.0	37.8	35.2	37.2	36.6	38.9

RMR slope (mW °C ⁻¹)	11.90	10.39	9.76	9.56	9.0	13.87
Max. RMR (W)	0.39±0.13 (7)	0.43 (2)	0.44±0.13 (3)	0.49±0.06 (4)	0.53±0.08 (5)	0.69±0.06(7)
				0.51 (1)		
Max. RMR/min. RMR	1.56	1.72	1.42	1.42	1.71	1.41
Evaporative water loss						
Min. EWL (g h ⁻¹)	0.09±0.04 (10)	0.08±0.03 (10)	0.15±0.08 (7)	0.16±0.04 (10)	0.24±0.11 (9)	0.22±0.07 (9)
Inflection T_a (°C)	38.6	38.4	37.1	40.2	36.1	39.1
EWL slope (g h ⁻¹ °C ⁻¹)	0.08	0.10	0.09	0.11	0.08	0.16
Max. EWL (g h ⁻¹)	1.08 (2)	1.24±0.44 (4)	0.88±0.23 (3)	1.34±0.52 (4)	1.48±0.11 (5)	2.34±0.87 (3)
			1.05 (1)			
Max. EWL/min. EWL (evaporative scope)	12.00	15.33	7.00	8.40	6.16	10.64
Min. EHL/MHP	0.21±0.09 (10)	0.21±0.07 (10)	0.33±0.19 (6)	0.3±0.15 (10)	0.33±0.16 (8)	0.29±0.08 (9)
EHL/MHP inflection T_a - T_b	-3.9	-5.5	-5.4	-3.0	-7.0	-2.9
EHL/MHP slope	0.17	0.19	0.16	0.19	0.08	0.20
Max. EHL/MHP	1.89 (2)	2.0±0.56 (4)	1.77±0.40 (3)	1.87±0.47 (4)	1.58±0.25 (5)	2.35±0.77(3)
			1.97 (1)			

Table 3. Summary of thermoregulatory performance as a function of chamber air temperature (T_a) in seven passerine species from the southern African arid zone. T_b = body temperature, T_a = ambient temperature, RMR = resting metabolic rate, EWL = evaporative water loss, EHL= evaporative heat loss, MHP = metabolic heat production. Means, SD and N are reported.

Variable	Orange River white-eye (ORWE)	Lark-like bunting (LLB)	Marico flycatcher (MF)	Red-eyed bulbul (REB)	Southern fiscal (SF)	Fork-tailed drongo (FTD)	Crimson-breasted shrike (CBS)
Body mass (g)	7.7±0.6 (10)	14.2±2.0 (10)	21.8±2.2 (7)	30.1±3.7 (10)	37.3±2.2 (9)	43.7±3.5 (3)	46.2±2.7 (9)
Body temperature							
Min. T_b (°C)	40.2±1.0 (10)	40.4±1.0 (9)	40.1±1.0 (7)	40.4±1.2 (10)	41.2±0.9 (9)	42.2±0.7 (3)	40.4±0.6 (9)
Inflection T_a (°C)	35.3	28.3	34.7	40.1	35.8	31.3	35.5
T_b versus T_a slope (°C)	0.44	0.28	0.38	0.26	0.32	0.21	0.3
Max T_b (°C)	44.7±0.3 (4)	44.4±0.6 (4)	45.0±0.3 (3) 45.2 (1)	43.9±0.6 (4)	44.4 (2) 45.2 (1)	45.2 (2)	44.3±0.3 (3)
Max T_a (°C)	46 (4)	48 (4) 50 (1)	46 (3) 48 (1)	52 (4)	48 (2) 50 (1)	50 (2)	48 (3)
T_b at onset of panting (°C)	42.7±0.6 (10)	42.4±0.7 (10)	42.5±1.5 (4)	41.6±0.8 (5)	42.9±0.6 (8)	39.6±0.6 (3)	40.8±1.7 (8)
T_a at onset of panting (°C)	40.0±1.2 (10)	39.3±2.9 (10)	39.9±0.2 (4)	39.8±2.0 (6)	40.0±2.2 (8)	42.3±0.2 (3)	40.6±1.3 (8)
95 th percentile $T_b > T_a$ (°C)	44.8	43.8	44.5	42.6	43.9	43.4	43.6
Resting metabolic rate							

Min. RMR (W)	0.19±0.03 (10)	0.24±0.06 (10)	0.32±0.15 (7)	0.45±0.11 (9)	0.50±0.09 (8)	0.53±0.07 (3)	0.59±0.07 (3)
T_{uc} (°C)	35.7	28.4	30.6	37.5	37.8	42.3	38.2
RMR slope (mW °C ⁻¹)	12.46	10.4	9.4	25.4	49.5	56.0	57.9
Max. RMR (W)	0.30±0.04 (4)	0.39±0.04 (4)	0.41±0.09 (3)	0.86±0.18 (7)	0.83±0.12 (7)	1.12 (2)	1.1±0.49 (9)
		0.41 (1)	0.45 (1)		1.09 (1)		
Max. RMR/min. RMR	1.58	1.71	1.41	1.91	2.18	2.66	1.86
Evaporative water loss							
Min. EWL (g h ⁻¹)	0.12±0.05 (10)	0.11±0.05 (10)	0.15±0.05 (7)	0.22±0.08 (9)	0.26±0.07 (9)	0.26±0.05 (3)	0.23±0.05 (3)
Inflection T_a (°C)	38.4	37.9	39.9	38.1	40.6	42.2	40.1
EWL slope (g h ⁻¹ °C ⁻¹)	0.07	0.11	0.09	0.17	0.34	0.21	0.28
Max. EWL (g h ⁻¹)	0.85±0.08 (4)	1.14±0.15 (4)	0.80±0.08 (3)	2.61±0.66 (4)	2.39 (2)	2.21 (2)	1.91±0.75 (9)
			0.92 (1)		4.35 (1)		
Max. EWL/min. EWL (evaporative scope)	7.08	10.36	5.53	11.86	11.7	8.5	8.3
Min. EHL/MHP	0.37±0.15 (10)	0.29±0.12 (10)	0.31±0.15 (7)	0.29±0.06 (9)	0.27±0.1 (9)	0.28±0.05 (3)	0.23±0.05 (9)
EHL/MHP inflection T_a - T_b	-4.4	-6.2	-3.9	-4.3	-3.2	-5.2	-2.7
EHL/MHP slope	0.27	0.21	0.14	0.15	0.25	0.11	0.20
Max. EHL/MHP	1.92±0.2 (4)	1.97±0.29 (4)	1.31±0.15 (3)	2.27±0.54 (4)	1.96 (2)	1.74 (2)	1.58±0.24 (3)
			1.35 (1)		2.67 (1)		

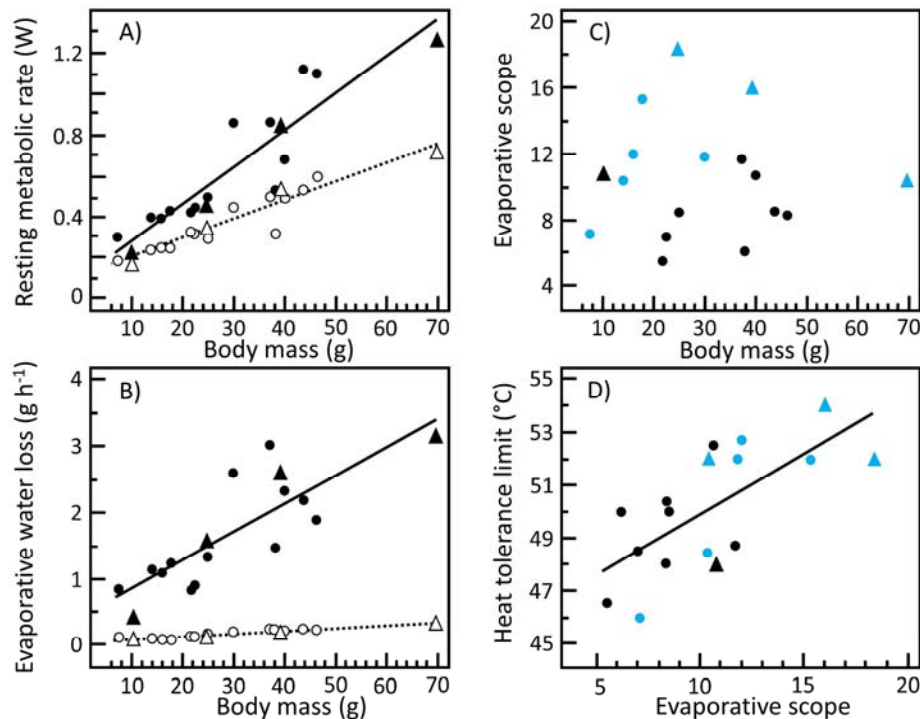


Figure 1. Scaling of heat tolerance and evaporative cooling parameters in seven passerine species from the arid zone of southern African. (A) Circles represent data from the present study, triangles represent other southern African passerines (Whitfield et al. 2015; Smit et al. 2018; S.J. Cunningham et al. unpubl. data), filled symbols represent maximum resting metabolic rate (Max RMR; W), open symbols represent minimum resting metabolic rate (Min RMR; W). The solid line represents the ordinary least squared regression of Max RMR and body mass (M_b); Max RMR scaled positively with body mass ($t=8.6$, $F_{1,15}=73.9$, $p<0.001$, $R^2=0.82$; Max RMR= $0.02M_b + 0.09$). The dashed line represents the ordinary least squared regression of Min RMR and M_b ($t=11.1$, $F_{1,15}=122.7$, $p<0.001$, $R^2=0.88$; Min RMR= $0.01M_b + 0.1$). (B) Filled circles represent maximum evaporative water loss (Max EWL), open circles represent minimum evaporative water loss (Min EWL). Solid line represents the ordinary least squared regression of Max EWL and M_b ($t=5.6$, $F_{1,15}=31.6$, $p<0.001$, $R^2=0.66$; Max EWL= $0.043M_b + 0.40$). Dashed line represents the ordinary least squared regression of Min EWL and M_b ($t=6.6$, $F_{1,15}=44.2$, $p<0.001$, $R^2=0.73$; Min EWL= $0.004M_b + 0.045$). (C) Evaporative scopes (the ratio of minimum thermoneutral evaporative water loss (EWL) to maximum EWL) of each species. Circles represent data from this study, triangles represent data from four other southern African passerines (as above), blue symbols represent regular drinkers, and black symbols represent non-drinkers. Species that regularly drink have higher evaporative scopes than non-drinking species (D) Heat tolerance limits of passerines in relation to evaporative scope. Species with greater evaporative scopes had higher heat tolerance limits ($t=4.6$, $F_{2,15}=11.1$, $p<0.01$, $R^2=0.54$; HTL= 0.49 (Evaporative scope) + 43.8).

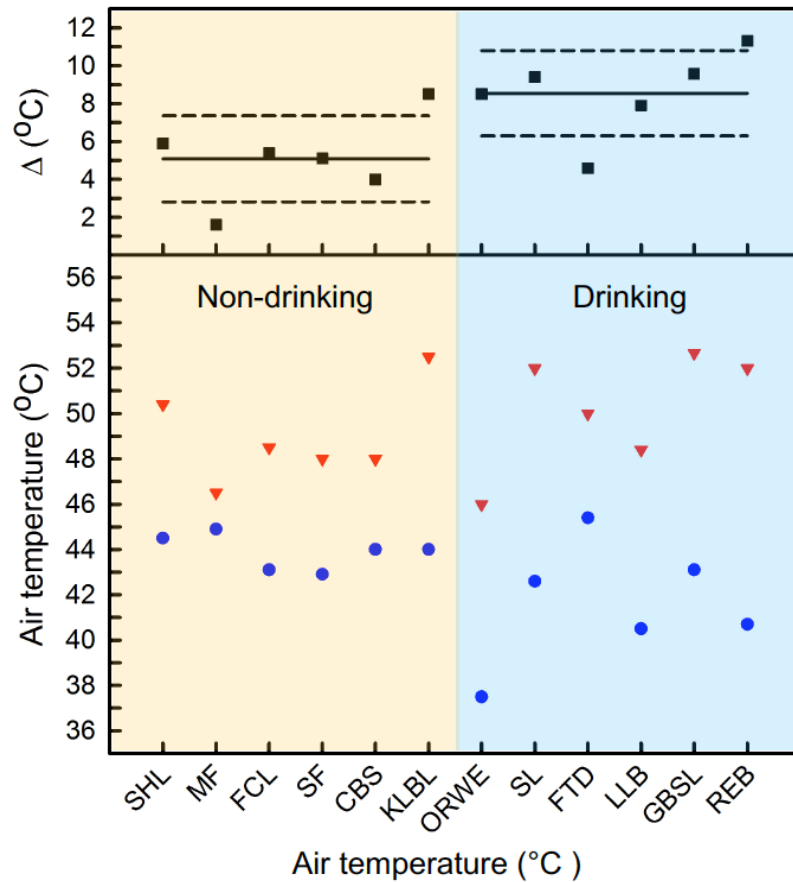


Figure 2. Threshold daily maximum air temperature (T_{\max}) for risk of lethal dehydration (blue circles) and heat tolerance limits (HTL; red triangles) for southern African arid-zone passerines [red-eyed bulbuls (REB; *Pycnonotus nigricans*), Orange River white-eyes (ORWE; *Zosterops pallidus*), lark-like buntings (LLB; *Emberiza impetuani*), southern fiscals (SF; *Lanius collaris*), grey-backed sparrow-larks (GBSL; *Eremopterix verticalis*), Karoo long-billed lark (KLBL; *Certhilauda subcoronata*), spike-heeled lark (SHL; *Chersomanes albofasciata*), fawn-coloured lark (FCL; *Calendulauda africanoides*), Stark's lark (SL; *Spizocorys starki*), Marico flycatchers (MF; *Melaenornis mariquensis*), fork-tailed drongos (FTD; *Dicrurus adsimilis*), and crimson-breasted shrikes (CBS; *Laniarius atrococcineus*)] broadly divisible into regular drinkers and occasional/non-drinkers. A threshold T_{\max} value for each species was estimated following the approach of Conradie et al. (2019), by fitting a polynomial curve to hourly air temperature (T_a) on the ten hottest days between 2000 and 2010 in the southern Kalahari, and estimating cumulative evaporative water losses (EWL) between 12:00 and 17:00. For each species, the generic T_a curve was shifted upwards until cumulative EWL reached 15 % of body mass, with the corresponding T_{\max} value considered the threshold for lethal dehydration for that species. The top panel shows the difference between HTL and the threshold T_{\max} (i.e., the difference between thresholds for lethal hyperthermia and dehydration), revealing that, on average, the difference is larger for drinking compared to non-drinking species. The solid horizontal lines show the mean values and the dashed lines ± 1 SD.