Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns?

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Abstract

Quantifying organismal sensitivity to heat stress provides one means for predicting vulnerability to climate change. Birds are ideal for investigating this approach, as they display quantifiable fitness consequences associated with behavioural and physiological responses to heat stress. We used a recently developed method that examines correlations between readily-observable behaviours and air temperature (T_{air}) to investigate interspecific variation in avian responses to heat stress in seasonally hot, arid regions on three continents: the southwestern United States, the Kalahari Desert of southern Africa and the Gascoyne region of western Australia. We found substantial interspecific variation in heat dissipation behaviours (wing-drooping, panting, activity-reduction, shade-seeking) across all three regions. However, pooling the data revealed that little of this interspecific variation was systematically explained by organismal traits (foraging guild, diet, drinking dependency, body mass or activity levels) at the scale we tested. After accounting for phylogeny, we found that larger birds engaged in wing-drooping behaviour at lower T_{air} and had lower activity levels at high T_{air} compared to smaller birds, indicating an effect of body mass on heat dissipation behaviour (HDB). In the Kalahari, reliance on drinking was correlated with significantly lower T_{air} at which panting commenced, suggesting a key role of water acquisition in HDB in that region. Birds also tended to retreat to shade at relatively lower T_{air} when more active, suggesting a behavioural trade-off between activity, heat load and microsite selection. Our results imply that the causes underlying interspecific variation in heat dissipation behaviours are complex. While the variation we observed was not systematically explained by the broad scale organismal traits we considered, we predict that the indices themselves will still reflect vulnerability to potential fitness costs of high air temperatures. Further research is needed on a species-specific basis to establish the functional significance of these indices.

Keywords: birds; climate change; heat dissipation behaviour; heat stress; vulnerability

Introduction

Species living in arid, seasonally hot environments are among those most vulnerable to climate change impacts, given that temperature extremes will become more pronounced in coming decades (Blendinger 2005, Bolger et al. 2005, Cunningham et al. 2013a, Conradie et al. 2019). Birds are ideal models for investigating the effects of increasing temperatures in these environments, as their physiological and behavioural responses to high temperatures have quantifiable consequences for correlates of fitness (Smit et al. 2013, McKechnie et al. 2016). Most birds are diurnal, and generally do not use subterranean thermal refugia during the heat of the day (Dawson 1982, Tieleman and Williams 1999, but see also Williams et al. 1999, McKechnie and Wolf 2010). As a result, to maintain normothermic body temperature (T_b), birds need to dissipate heat generated by activity and metabolism, as well as the heat they gain from their environment (Smit et al. 2013, Smith et al. 2015, O'Connor et al. 2016). The primary means of dissipating heat at environmental temperatures approaching or exceeding normothermic T_b is evaporative water loss (EWL) (Gerson et al. 2014). Therefore, in addition to increasing the threat of lethal hyperthermia, high temperatures may elicit severe water stress, manifested as trade-offs between the risks of hyperthermia and dehydration (Smit et al. 2013). Increasing temperatures under climate change may therefore have severe consequences for the fitness of arid-zone avifauna (McKechnie and Wolf 2010, du Plessis et al. 2012, Cunningham et al. 2013b, van de Ven et al. 2019).

Much of the research on species responses to climate change has used ‘climate envelope’ or other correlative, pattern-based species distribution models to predict changes in distributions and range sizes (Luoto et al. 2005, Gasner et al. 2010, Watling et al. 2012). An assumption implicit in this approach is that species distributions are limited by abiotic climatic variables, and that species–climate relationships will remain constant over time (Pearson and Dawson 2003, Virkkala et al. 2008). While useful, this approach often disregards the functional relationships that species share with their environment (Hampe 2004, Kearney and Porter 2009, Gasner et al. 2010) and with each other (Araújo and Luoto 2007). An increasingly popular alternative approach involves predicting the maximum spatial distribution of a given taxon by integrating its physiology, physical environment and resource availability into a mechanistic distribution model (Hijmans and Graham 2006, Kearney and Porter 2009, Albright et al. 2017, Conradie et al. 2019). A major impediment to using this approach is that the physiological and behavioural data required for these complex models are lacking for most species (Heikkinen et al. 2006, Hijmans and Graham 2006, Milne et al. 2015). Collecting these data is time-consuming and often expensive, as it requires detailed, species-specific studies (Kearney and Porter 2009).

In response to the difficulties of in-depth modelling parameterised using empirical, species-specific data, a method for rapid behavioural assessment of avian species’ potential vulnerabilities to higher maximum temperatures has recently been proposed (Smit et al. 2013, 2016). This method is based on the observation that the temperature-dependence of HDB varies among and within species in a consistent fashion (Smit et al. 2013, 2016). Heat dissipation behaviours either increase EWL to maximise heat loss (e.g. panting, gular flutter or elevation of cutaneous EWL); or minimise heat gain (e.g. shade-seeking, reductions in activity) (Barrows 1981, Davies 1982, Marder and Ben-Asher 1983, Anava et al. 2001, Kelly et al. 2004). Fitting a logistic regression to binomial presence/absence data for visible HDBs in a species provides the basis for estimating indices for species-specific responses to heat stress: *$pant_{50}$* (the air temperature (T_{air}) at which half the individuals of a particular species are expected to pant), *$wing_{50}$* (the T_{air} at which half of a particular species are expected to exhibit wing-drooping), *$rest_{50}$* (T_{air} at which half are expected to be resting/inactive) and *$shade_{50}$* (T_{air} at which half of observed birds are expected to be in shaded microsites) (Smit et al. 2016).

The aims of our study were threefold: first, to quantify variation in HDB indices among arid-zone avian communities from different continents; second, to assess whether, after accounting for phylogeny, this variation is systematically correlated with organismal traits; and third, based on the relationship between HDB indices and organismal traits, to determine if organismal traits can be used to predict behavioural and physiological costs at high T_{air}. We examined the relationships between organismal variables [body mass (M_b), foraging guild, diet, activity levels and drinking dependency] and interspecific variation in HDB indices (*$pant_{50}$*, *$wing_{50}$*, *$rest_{50}$* and *$shade_{50}$*), for bird communities from the Sonoran Desert in the southwestern United States; the Kalahari Desert in north-western South Africa; and the upper Gascoyne region of western Australia. These regions are home to phylogenetically disparate bird assemblages, differing substantially in terms of the families comprising the resident passerines (Morcombe 2003, Poole 2005, Smit et al. 2013, 2016). We tested three non-mutually exclusive hypotheses, the first being that larger species are more sensitive to heat at T_{air} below T_b, manifested as lower HDB index values (Smit et al. 2016) on account of the negative scaling of mass-specific EWL and heat loss with the scaling of the surface area/volume ratio (Whitfield et al. 2015). Second, we hypothesised that high activity levels are correlated with low $pant_{50}$ and $wing_{50}$. Species with high activity levels (e.g. high-activity foraging strategy), are expected to experience elevated heat loads on account of higher endogenous heat production (Wolf 2000, Smit et al. 2016). Third, we hypothesised that species which do not rely on drinking would show higher $pant_{50}$ values than those that do. Species reliant on preformed water in their diet and/or metabolic water should delay behaviours that increase EWL in response to higher air temperatures compared to species that drink, as replacing water would presumably be more difficult for the former species (Smit and McKechnie 2015, Smit et al. 2016).

Materials and methods

Study sites

Data for South African (SA) arid-zone birds were obtained from Smit et al. (2016). These data were collected during the Austral summers of 2009/2010 and 2010/2011 in arid savannas dominated by sparse camelthorn *Vachellia erioloba* woodland growing in deep red sands of the southern Kalahari Desert. Data for southwest United States (US) birds were collected during the boreal summer (22nd June–25th July 2014) in the Kofa National Wildlife Refuge in southwestern Arizona (33°27′N–33°30′N and 114°10′W–113°52′W). The Kofa National Wildlife Refuge (269 300 ha) is situated in the Lower Colorado River Valley. It comprises rocky mountain ranges, interspersed with wide valleys where the hillsides and slopes are dominated by creosote bushes *Larrea tridentata* and cactus (*Carnegiea*, *Cylindropuntia* and *Mammalaria*), and the dry watercourses (washes) are dominated by paloverde *Parkinsonia microphylla*, mesquite *Prosopis velutina*, ironwood *Olneya tesota*, catclaw acacia *Senegalia greggii* and wolfberry (*Lycium sp*.). Australian bird data were collected during the Austral summer (8th February–10th March 2012) in the upper Gascoyne region of western Australia, on a pastoral lease called Glenburgh Station (−25°43′S; 116°11′E). Glenburgh Station is covered by sparse vegetation including small trees (*Acacia*), eucalypt species and shrub varieties (primarily *Eremophila*).

Air temperature measurements

We recorded weather variables in the US using a portable Vantage Vue weather station (Davis Instruments, Hayward, CA) set 1.5 m above the ground. Air temperature (T_{air}) as well as relative humidity were recorded at 10-min intervals. The minimum T_{air} recorded was 25.2°C and the maximum 44.9°C. In Australia, weather data were recorded by a WeatherHawk Signature Series weather station (Model RS232) every 10-min. The minimum T_{air} was 23.5°C, and the maximum 43.1°C. Weather data in SA were obtained using a Vantage Pro weather station (Davis Instruments, Hayward, CA) set up in the centre of each study sites (for details see Smit et al. 2016). For SA the minimum temperature was approximately 7°C, while the maximum was 39°C (Smit et al. 2016).

Behavioural data collection

Our behaviour data protocols for the US and Australian sites followed those of Smit et al. (2016) and involved scan sampling where all birds encountered were identified to species and observed for approximately 30 s. We recorded binary information on any HDBs (panting, gular fluttering, wing drooping: 1 = present, 0 = absent). Binary information (1 = present, 0 = absent) were also recorded for foraging, preening, calling, displaying or behaviour associated with breeding, and exposure to the sun (1 = sun, 0 = shade or partial shade) and activity (mobile = 1 or stationary = 0).

To collect data on behaviour we walked predetermined transects. We observed every bird encountered that (a) was close enough to confidently observe presence or absence of HDB and (b) showed no obvious sign of being disturbed by the presence of an observer. Data recorded for birds that were flushed or otherwise agitated by our presence were not used. Flying birds (such as swallows) and birds that could not be observed for at least 30 s were also excluded. For birds in flocks, a single individual was selected at random and its behaviour recorded along with an estimate of the number of conspecifics in the group. Each observer used binoculars, a stopwatch and an Android mobile device to log observations in real-time using CyberTracker software (Ansell and Koenig 2011).

Transects in both SA and Australia were randomly laid out on a map of the area which could potentially be sampled. In these regions, birds are spread across the landscape, prompting the use of randomised transects. In the US, birds were found almost exclusively in washes, therefore transects were not chosen randomly but were laid out in selected washes. Transects were each sampled repeatedly (necessitated by the small number of accessible, usable washes), but at least two days passed between resampling to minimise the effect of observers on the birds. Repeated sampling of the same transects was accounted for statistically by including ‘transect’ as a random factor in mixed models. We sampled in the US during three periods daily: 07:00–09:00; 11:00–13:00; 16:00–18:00. In Australia, observations were made between 11:00 and 18:00 for the first four weeks and from 08:00 to 19:00 in the final week. About one hour was spent at each sampling location. At all three sites, transects were at least 500 m from the nearest standing water source (to minimise the potentially confounding effect of hydration status), and separated from each other by a minimum of 500 m (to minimise the risk of recording the same individuals in different transects).

Data analysis

All analyses were conducted in R (R Core Team), using the RStudio platform (R Studio Team). We followed the protocols of Smit et al. (2016) to enable comparison of the three datasets. A total of 2365 observations representing 38 species were obtained in the US, the Australian dataset comprised 888 observations representing 47 species, and the Kalahari dataset comprised 11 110 observations representing 76 species.

Humidity has been shown to affect heat load and evaporative cooling capacity (Smit et al. 2013, Gerson et al. 2014). For example, Smit et al. (2013) found higher T_bs in white-browed sparrow-weavers *Plocepasser mahali* at vapour pressure deficits (VPD) < 2 kPa. Observations where the VPD was < 2 kPa made up a small proportion of the data collected from all three regions. Moreover, humidity has no significant effect on $pant_{50}$ values (Smit et al. 2016), and to only significantly affect evaporative cooling capacity at temperatures much higher (~48°C) than those at which birds were observed in this study (Gerson et al. 2014). Therefore, following Smit et al. (2016), we included all observations regardless of humidity levels. We excluded all columbiforms (pigeons and doves; seven species) from our analyses because this taxon relies on increased cutaneous evaporative cooling pathways at high temperatures (McKechnie and Wolf 2004). We also seldom observed columbiforms engaging in respiratory evaporative cooling behaviours. After the exclusion of columbiforms, 18, 30 and 68 species had sufficient observations for analysis (observed a minimum of three times total, and with at least three observations at T_{air} between 35 and 40°C) from the US, Australia and SA respectively.

HDB indices: $wing_{50}$, $pant_{50}$, $rest_{50}$ and $shade_{50}$ values

HDB indices were calculated as the inflection points [intercept value (absolute) divided by beta value (absolute)] of species-specific logistic regressions of the HDB as a function of T_{air}, following Smit et al. (2016). For the Australian dataset, logistic regressions were fitted as generalised linear models (GLM), with family quasibinomial (to account for overdispersion) using nlme (Pinheiro et al. 2016). Due to the repeat sampling design used during observations for the US desert birds, generalised linear mixed models (GLMM) with an added random factor for ‘transect’ were fitted using lme4 (Bates et al. 2015).

Proportion active at high T_{air}: prop_act

We identified all observations made at T_{air} between 35 and 40°C and then calculated the proportion of observations in which birds were active within this T_{air} range for each species. The range was chosen to be consistent with Smit et al. (2016), and because it is a biologically relevant range wherein arid-zone species begin to show deleterious effects of high temperatures on foraging efficiency and reproductive success (Conradie et al. 2019). We then logit-transformed these proportion data for analyses. This logit-transformed value was denoted the prop_act for each species.

Relationship between organismal traits and HDB indices

We compiled a dataset of various traits for each species (Supplementary material Appendix 1 Table A5). These traits included body mass (M_b), foraging guild (on- or off-ground) and diet (predominantly animal, or plant products, or omnivorous) of each bird, as well as whether the birds rely on drinking surface water or obtained water from food (defined as water source; not known to drink at all from open water sources and thus not reliant on drinking 'P' or recorded using open water sources and thus potentially reliant on drinking 'D'). The data for the US species were compiled from the online version of 'The Birds of North America' (Poole 2005), for Gascoyne from the 'Field Guide to Australian Birds' (Morcombe 2003), and for the Kalahari Desert species from Smit et al. (2016) and 'Roberts Birds of Southern Africa' (Hockey et al. 2005). Data from all three regions were pooled, and the relationships between HDB indices and organismal traits were modelled using phylogenetic generalised least squares (PGLS) regression and generalised least squares regression (GLS). For PGLS we followed Smit et al. (2016), and sampled 100 phylogenies from <www.birdtree.org> (Jetz et al. 2012) for the 116 species from all three regions in the dataset, using the Hackett et al. (2008) phylogeny as a back-bone. We then identified the majority consensus tree isolated in the programme Mesquite (Maddison and Maddison 2011). We used Kappa branch length models and used the null models of each trait to establish a phylogenetic signal. We tested phylogenetic signal by running the null model for each variable, as Kappa values significantly greater than '0'. When no phylogenetic signal was identified for a trait we report GLS results only.

For both GLS and PGLS we checked the fixed effects for collinearity using variance inflation factors and the R package car (Fox and Weisberg 2010). Global models $wing_{50}$, $pant_{50}$, $rest_{50}$ and $shade_{50}$ included all fixed effects, including M_b, region, foraging guild, diet, prop_act and water source. All nested models were compared using the dredge function, in the package MuMIn (Barton 2016). We checked for outliers (outliers package, Bonferroni p-value < 0.05; Komsta 2011) and removed these sequentially where justified. The top three models were identified based on Akaike's information criterion score adjusted for small sizes (AIC_c) and summarised using the R package Stargazer (Hlavac 2015). The t-values are reported for the top performing model. Where significant differences between factors were found in global models, we performed post-hoc Tukey HSD tests to establish pairwise differences.

Results

Phylogenetic signal

We found a significant phylogenetic signal for the $wing_{50}$ index (Kappa = 1.13, $p < 0.001$) and prop_act values (Kappa = 0.77, $p < 0.001$), but no phylogenetic signal for $pant_{50}$ (Kappa = 0.53, p = 0.167), $rest_{50}$ (Kappa = 0.2, p = 0.518) or $shade_{50}$ (Kappa = 0.23, p 0.381). We therefore present the outcomes of PGLS analyses for $wing_{50}$ and prop_act only.

Regional comparison

Heat dissipation behaviour indices showed large interspecific variation among the three regions (Table 1). There were significant regional differences in interspecific variation in wing$_{50}$ (GLS, $t_{2,66} = 4.13$, $p < 0.001$; PGLS, $t_{2,62} = 2.22$, $p < 0.05$), rest$_{50}$ (GLS, $t_{2,28} = -3.27$, $p < 0.01$) and prop_act (GLS, $t_{2,109} = -2.63$, $p < 0.01$; PGLS, $t_{1,99} = 0.7$, $p = 0.85$; Fig. 1).

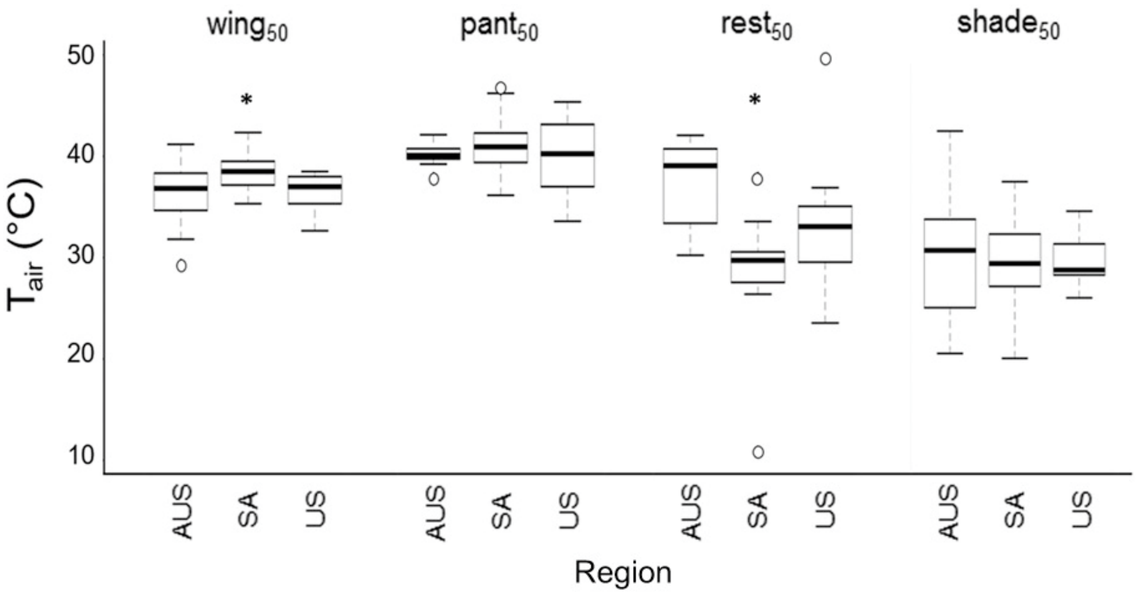
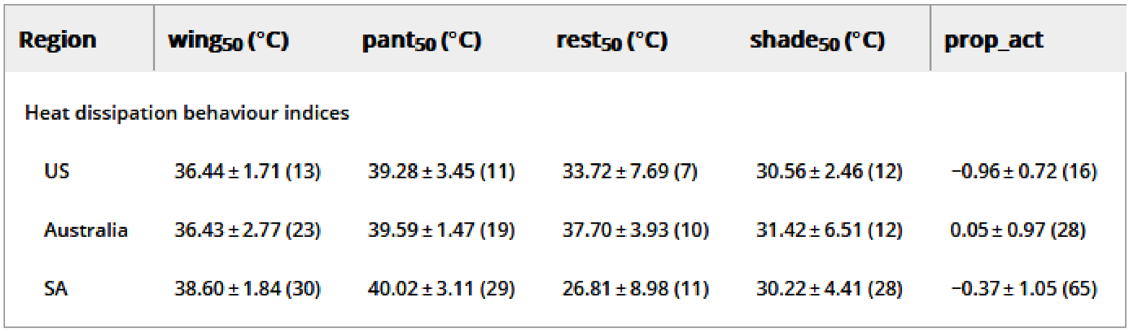


Figure 1. Boxplots showing differences in heat dissipation behaviours between the bird communities from three continents (upper Gascoyne region of western Australia = AUS; Kalahari Desert, South Africa = SA and south-western United States = US). Only wing$_{50}$ (GLS, $t_{2,66} = 4.13$, $p < 0.001$; PGLS, $t_{2,66} = 2.22$, $p < 0.05$) and rest$_{50}$ (GLS, $t_{2,28} = -3.27$, $p < 0.01$) showed significant regional differences. Medians are indicated by bold lines, lower and upper bounds of boxes represent 25 and 75% percentiles, upper and lower caps of whiskers represent maximums and minimums respectively, outliers are shown as clear circles, and significance is indicated by an asterisk.

Table 1. Mean ± standard deviation for each heat dissipation index for each region. Heat dissipation behaviour (HDB) indices *pant*$_{50}$, *wing*$_{50}$, *rest*$_{50}$ and the *shade*$_{50}$ are the T_{air}s at which half the observed birds of a particular species are expected to be in shaded microsites and panting, wing drooping, resting/inactive. Prop_act is the logit-transformed proportion of observations where species were active between 35 and 40°C for all species within each region. The sample sizes (number of species) for each index are indicated in brackets



Region	wing$_{50}$ (°C)	pant$_{50}$ (°C)	rest$_{50}$ (°C)	shade$_{50}$ (°C)	prop_act
Heat dissipation behaviour indices					
US	36.44 ± 1.71 (13)	39.28 ± 3.45 (11)	33.72 ± 7.69 (7)	30.56 ± 2.46 (12)	−0.96 ± 0.72 (16)
Australia	36.43 ± 2.77 (23)	39.59 ± 1.47 (19)	37.70 ± 3.93 (10)	31.42 ± 6.51 (12)	0.05 ± 0.97 (28)
SA	38.60 ± 1.84 (30)	40.02 ± 3.11 (29)	26.81 ± 8.98 (11)	30.22 ± 4.41 (28)	−0.37 ± 1.05 (65)

Heat dissipation behaviour

The top model for both the GLS and the PGLS indicated that interspecific variation in $wing_{50}$ was explained best by region (GLS, $t_{2,66} = 4.13$, $p < 0.001$; PGLS, $t_{2,66} = 2.22$, $p < 0.05$) and body mass (M_b; GLS, $t_{1,66} = -3.73$, $p < 0.001$; PGLS, $t_{1,66} = -2.2$, $p < 0.05$) (Table 2). Post-hoc analyses revealed that the SA birds had significantly higher $wing_{50}$ values, on average, compared to the other two regions (Tukey HSD, $p < 0.05$; Fig. 1). $Wing_{50}$ values scaled negatively with M_b (Fig. 2).

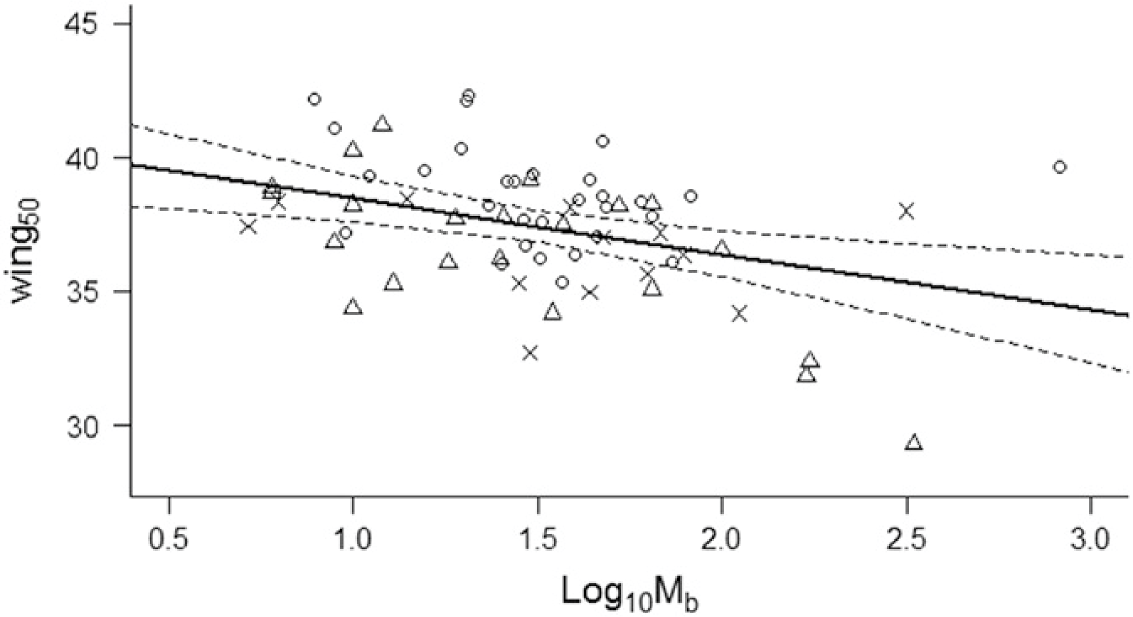


Figure 2. Logistic regression showing the predicted relationship for $wing_{50}$ (n = 66) as a function of $\log_{10}$ transformed body mass ($Log_{10}M_b$) based on pooled data for the three regions. The relationship was significant (GLS, $t_{1,66} = -3.73$, $p < 0.001$; PGLS, $t_{1,66} = -2.2$, $p < 0.05$). 95% confidence limits are shown. Kalahari Desert, South Africa (SA) data are shown as circles, south-western United States (US) as crosses, and upper Gascoyne region of western Australia as triangles.

Drinking dependence was a significant predictor of $pant_{50}$ (Supplementary material Appendix 1 Table A1). Species that relied on drinking displayed significantly lower $pant_{50}$ values than birds that did not (GLS, $t_{1,59} = 2.6$, $p < 0.05$). The mean $pant_{50}$ for species that relied on drinking was 38°C ± 0.8 SE (n = 14) compared to 40°C ± 0.38 SE (n = 45) for species that did not. This relationship was driven by the SA species, as only one species from the US dataset included in analyses drank, and the mean $pant_{50}$ of birds that drank versus birds that did not was similar among Australian species (39.7°C ± 1.04 SE, n = 5, and 39.6°C ± 0.33 SE, n = 14, respectively).

Table 2. Three top weighted models explaining interspecific variation in wing$_{50}$ for phylogenetic generalised least squares (PGLS) analyses. Global models included region, prop_act (logit transformed proportion of observations where a species was mobile between 35 and 40°C), Log$_{10}$ body mass (Log$_{10}$M$_b$), diet, foraging guild and water source. The only variables identified as important are shown ± standard error. Significance is shown: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

	Model		
	1	**2**	**3**
PGLS			
Region (SA)	1.82 ± 0.82*	1.74 ± 0.82*	
Region (US)	0.58 ± 1.01	0.68 ± 1.02	
Prop_act	0.39 ± 0.37		
Log$_{10}$M$_b$	−1.82 ± 0.83*	−1.69 ± 0.84*	−1.81 ± 0.85*
(Intercept)	38.7 ± 1.92***	38.76 ± 1.91***	39.42 ± 1.92***
Observations	66	66	66
AICc	295	296.2	296.8

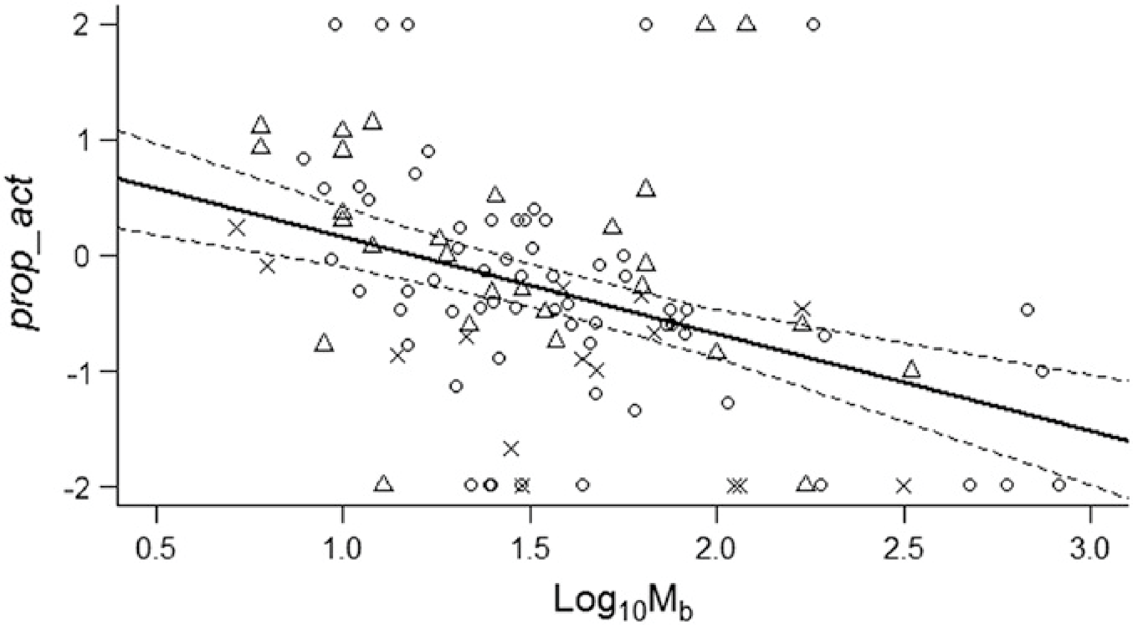


Figure 3. Logistic regression showing the predicted relationship for logit-transformed prop_act (i.e. proportion of observations in which birds were active at $35 < T_{air} < 40°C$; $n = 109$) as a function of log$_{10}$ transformed body mass (Log$_{10}$M$_b$) for the three regions pooled. The relationship was significant (GLS, $t_{1,109} = -5.38$, $p < 0.001$; PGLS, $t_{1,109} = -2.57$, $p < 0.05$). 95% confidence limits are indicated by dashed lines. Kalahari Desert, South Africa (SA) data are shown as circles, south-western United States (US) as crosses, and upper Gascoyne region of western Australia as triangles.

We found significant variation among regions for $rest_{50}$ values (GLS, $t_{2,28} = -3.27$, $p < 0.01$; Supplementary material Appendix 1 Table A2); post-hoc analysis revealed that this was driven by a difference between the SA and Australian species (Tukey HSD, $p < 0.05$; Fig. 1). Interspecific variation in prop_act was significantly related to region (GLS, $t_{2,109} = -3.06$, $p < 0.01$), $Log_{10}M_b$ (GLS, $t_{1,109} = -5.38$, $p < 0.001$) and foraging guild (GLS, $t_{1,109} = 2.33$, $p < 0.05$). Post-hoc analyses showed that mean activity levels at high T_{air} were lower for the US species compared to the Australian species (Tukey HSD, $p < 0.01$; Supplementary material Appendix 1 Table A3). Mean activity levels at high T_{air} also declined significantly with increasing M_b (Fig. 3) and were higher in birds that forage on the ground (Supplementary material Appendix 1 Table A3). However, the top PGLS model only showed a significant effect for $Log_{10}M_b$ on interspecific variation in prop_act (PGLS, $t_{1,109} = -2.57$, $p < 0.05$).

Interspecific variation in $shade_{50}$ was significantly explained by prop_act (GLS, $t_{1,52} = -2.20$, $p < 0.05$; Fig. 4, Supplementary material Appendix 1 Table A4); $shade_{50}$ values declined significantly as the activity levels of species at high air temperatures (between 35 and 40°C) increased.

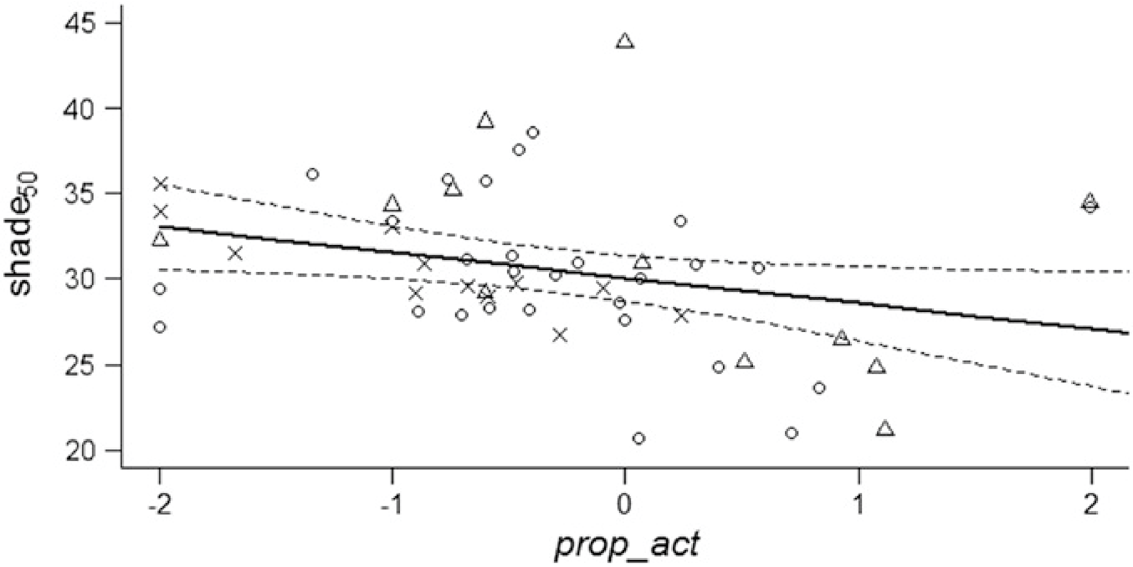


Figure 4. Logistic regression showing the predicted relationship for $shade_{50}$ ($n = 52$) as a function of logit-transformed prop_act (i.e. proportion of observations in which birds were active at $35 < T_{air} < 40°C$; $n = 109$) for the three regions pooled. The relationship was significant (GLS, $t_{1,52} = -2.20$, $p < 0.05$). 95% confidence limits are indicated by dashed lines. Kalahari Desert, South Africa (SA) data are shown as circles, south-western United States (US) as crosses, and upper Gascoyne region of western Australia as triangles.

Discussion

We quantified interspecific variation in heat dissipation behaviour (HDB) across three phylogenetically distinct avian communities. The range of interspecific variation was similar among regions, illustrating the pervasive and consistent influence of temperature on the behaviour of arid-zone birds during hot summers. However, we could predict little of the variation in HDB using organismal traits, including body mass (M_b), drinking dependency, foraging guild, diet and activity levels (prop_act).

Nevertheless, several significant patterns did emerge. Species that drink generally had lower $pant_{50}$ values than those that do not. It has been suggested that non-drinking species are under stronger selective pressure to minimise evaporative cooling requirements, which would presumably delay the onset of panting to higher T_{air} (Smit et al. 2016). However, only one species from the south-western United States (US) study site relied on drinking, and the mean $pant_{50}$ of drinkers and non-drinkers was similar at the Australian study site. Therefore, within our dataset this pattern appears to be specific to the Kalahari region of South Africa (SA).

Body mass was a significant predictor of variation in $wing_{50}$ and prop_act for the pooled dataset. Heavier birds had lower $wing_{50}$ values, and, similarly to Smit et al. (2016), we found that heavier birds tended to be less active at T_{air} between 35 and 40°C. This suggests that behavioural decisions and passive heat dissipation demands vary with M_b. Mass-specific EWL scales negatively with M_b, as does the slope of mass-specific EWL as a function of T_{air} at $T_{air} > T_b$ (Whitfield et al. 2015). Therefore, larger species begin to employ HDB and curtail activity at lower T_{air} than smaller species, presumably reflecting the lower rates of mass-specific EWL (Weathers 1981, Whitfield et al. 2015, McKechnie et al. 2017). Even within species, M_b differences have a significant effect on HDB; for instance, male great bustards *Otis tarda*, which are larger than females, seek shade earlier in the day, show more pronounced reliance on vegetation to escape hot microsites, and engage in different foraging behaviour to females in response to high summer temperatures (Alonso et al. 2015). The fact that $wing_{50}$ values tended to be higher for SA species than for the other two regions is likely due to SA birds having generally lower M_b, with only one species with $M_b > 100$ g in the $wing_{50}$ dataset, compared to three and four in the US and Australian datasets respectively. Therefore, the higher mean $wing_{50}$ of the SA community may simply reflect the higher proportion of smaller species with high $wing_{50}$ values, rather than representing an underlying ecological or phylogenetic pattern.

$Rest_{50}$ values were significantly different between SA and Australian birds. This may represent a functional ecological difference between the regions, where Australian species maintain higher activity levels than the other two regions; but observer effects might also have been involved. Moreover, PGLS analyses found no significant effect of region on prop_act (which is strongly correlated with $rest_{50}$ as they are both measures of activity), suggesting that this relationship is confounded by phylogenetic differences between the regions. Prop_act was also higher for ground foraging species than for off-ground foragers. However, off-ground foragers include ‘sit-and-wait’ foragers, which tend to have low activity, and thus low prop_act values. Excluding ‘sit-and-wait’ foragers from the analyses removes the difference, suggesting that whether or not a bird forages on the ground does not functionally affect its activity levels at high T_{air}. This notion is supported by the fact that no significant effect of foraging guild was evident in the PGLS analyses.

Finally, $shade_{50}$ declined significantly with increasing prop_act. Given that more active birds produce more metabolic heat, they would be expected to confine their activity to relatively cooler, shadier, microsites at lower air temperatures compared to less active species (Smit et al. 2016). In this way active birds can make a thermoregulatory compensation for their activity levels.

Limitations of HDB indices

The methodology of our study had several limitations, which future researchers should consider: First, acquiring a large sample of recordings at high T_{air} was challenging because birds often retreated to microsites that made observations difficult. This may have led to bias in the species observed and the types of behaviour recorded.

Second, the state of individual birds at the time of observation was not known; a bird's the health, hydration status and previous activity levels could have confounded expression the behavioural traits we measured. This is not a limitation per se, since for species observed frequently this inter-individual variation and flexibility would contribute towards a more accurate estimate of the species-specific HDB indices given that a range of individual status would be included in development of the indices. However, for species observed only occasionally, inter-individual variation and trait flexibility should prompt caution when interpreting HDB indices. On a related note, observations of the American and Australian birds were made within a single summer, whereas birds from South Africa were observed over multiple summers. Therefore, potential carry-over effects from previous seasons, and yearly variation, cannot be accounted for with these data. Future research on populations over several consecutive seasons would help in identifying patterns in inter-annual variation, and how individual variation affects the expression of HDB.

Third, the categories used for foraging guild and diet may have been too broad to gain clear insights into the roles of those traits. However, further separation of these categories (i.e. splitting diet into frugivores, nectarivores and granivores etc. and foraging guild into sit-and-wait predators, gleaners, hawkers, etc.) resulted in sample sizes too small for adequate statistical analyses.

Fourth, while the importance of EWL in avian thermoregulation underscores the appropriateness of evaluating variation in heat stress with HDB indices, HDB indices do not take into account the major avenue of EWL (i.e. respiratory versus cutaneous) for each species. They therefore almost certainly underestimate the heat/hydration stress experienced by birds that primarily utilize cutaneous EWL to dissipate heat (Marder and Ben-Asher 1983). This could confound the relationship between HDB indices and organismal traits, such as M_b. However, passerines make limited use of cutaneous EWL at high air temperatures (Wolf and Walsberg 1996), whereas columbids, which primarily use cutaneous EWL at high T_{air} (McKechnie and Wolf 2004), were excluded from our analyses.

And finally, HDB indices as indicators of missed-opportunity costs should be interpreted with caution, primarily because interspecific variation in HDB indices may not systematically correspond to behavioural trade-offs associated with thermoregulation. For instance, a high $rest_{50}$ does not necessarily mean that a species experiences no effect on foraging at high T_{air} (Ricklefs and Hainsworth 1968, du Plessis et al. 2012). Some species, such as southern pied babblers and southern fiscals *Lanius collaris*, likely exhibit high $rest_{50}$ values because they continue to forage at high T_{air}. However, both these species show reduced foraging efficiency at high T_{air} (du Plessis et al. 2012, Cunningham et al. 2015); high T_{air} is therefore likely to adversely impact survivorship and reproductive effort, and hence fitness – despite their high $rest_{50}$ values (Cunningham et al. 2015).

The future of HDB indices

Overall, our analyses reveal there is no fast, easy way to predict behavioural responses to high temperatures using easy-to-measure traits such as M_b or dependence on drinking surface water. Whereas some HDB patterns appear to be phylogenetically conserved, they were not correlated with the ecological traits we assigned to each species. However, our inability to predict interspecific variation in HDB does not detract from the potential usefulness of HDB indices for individual species.

The values of $rest_{50}$ and $shade_{50}$ specifically emphasize the trade-offs between the heat gain associated with activity and the need to maintain T_b below lethal levels (du Plessis et al. 2012, Smit et al. 2013). As temperatures rise in the coming decades, reductions in activity to avoid lethal hyperthermia could lead to a concomitant reduction in the time available for foraging, territorial defence and breeding behaviours (du Plessis et al. 2012, Cunningham et al. 2015, Edwards et al. 2015, Pattinson and Smit 2017). For example, verdins *Auriparus flaviceps* in the Sonoran Desert reduced the amount of time they spent foraging from 75% at $T_{air} = 35°C$, to less than 25% when $T_{air} > 45°C$ (Wolf 2000). These missed-opportunity costs may be significant in terms of fitness and hence could drive demographic change, before any effects of climate warming are manifested more dramatically as mass mortalities or range shifts (du Plessis et al. 2012, Cunningham et al. 2013b, 2015). The $shade_{50}$ values also indicate that the availability of relatively cool microsites within a landscape is likely important for many species that inhabit hot environments (Walsberg 1993, Wolf et al. 1996, Martin et al. 2015, Carroll et al. 2016). In arid regions, species with low $shade_{50}$ values may be especially reliant on thermal refuges provided by larger tree species (e.g. *Boscia albitrunca* in SA, desert mistletoe *Phoradendron californicum* in the US and 'mulga' *Acacia ramulosa* in Australia), to escape high environmental temperatures (Cooney and Watson 2005, Cunningham et al. 2015, Martin et al. 2015).

$Pant_{50}$ values are a potential indicator of EWL demands and the physiological costs of thermoregulation under heat stress. Panting behaviour increases both EWL and oxygen consumption, and produces metabolic heat (Smith et al. 2015). As a result, prolonged panting leads to dehydration, and increases the risk of alkalosis (Dawson 1958, Dawson and Bennett 1973, Smit et al. 2016). For small birds these issues are compounded because they have relatively little stored body water to dissipate before approaching dehydration tolerance limits (Wolf and Walsberg 1996, McKechnie and Wolf 2010, Albright et al. 2017). For example, under dry and hot conditions, white-browed sparrow-weavers *Plocepasser mahali* that spent a significant amount of time panting in response to heat were unable to maintain M_b due to a negative daily water balance (Smit and McKechnie 2015). Moreover, the cost of panting may extend beyond losing water via evaporation, to physically affecting energy and water intake. Panting by southern pied babblers *Turdoides bicolor* and southern yellow-billed hornbills *Tockus leucomelas* may mechanically reduce the efficiency of foraging due to the beak being used for two purposes simultaneously (du Plessis et al. 2012, van de

Ven et al. 2019). Birds with low pant_{50} values are thus likely at greater risk of being adversely affected by rising temperatures.

Future research needs to identify the mechanistic drivers behind interspecific variation in HDB, in order to elucidate how HDB in different species indicate potential vulnerability to heat stress. One avenue worth exploring is the physiological effect of T_b regulation on performance. As T_b rises above optimal levels, we expect behavioural proxies for performance to decline precipitously (Sinervo et al. 2010, Nilsson and Nord 2018). Therefore, we predict that trade-offs between T_b regulation, dehydration and performance might partially drive patterns in respiratory heat loss efforts. However, it is currently unclear how or if T_b regulation affects HDB in birds.

Lastly, the relationship between T_{air} and operative temperature (Bakken et al. 1985, Bakken 1992) varies according to the microsite occupied by the bird. While using operative temperature (or black bulb temperature as a proxy, see Cunningham et al. 2015, Carroll et al. 2016) would be preferable for analyses, correlating the behaviour of wild birds to operative temperature while they are rapidly moving between microsites is extremely challenging. We therefore opted to use T_{air}, which can be a powerful and simple metric for assessing thermally driven patterns (Tieleman and Williams 2002, Kelly et al. 2004, Ashdown and McKechnie 2008, du Plessis et al. 2012, Cunningham et al. 2013a, 2017, Smit et al. 2013, 2016, Villén-Pérez et al. 2013, Pollock et al. 2015, van de Ven et al. 2019). However, correlating behaviour to operative temperatures may be a valuable approach to further understand how behaviour relates to thermoregulation.

Conclusions

While recognising the limitations of HDB indices, we argue there is a strong theoretical foundation for predicting that they indicate physiological and behavioural trade-offs experienced by individual bird species at high temperatures (Smit et al. 2016). Overall, we found considerable interspecific variation in HDB in arid-zone birds experiencing high temperatures in summer, and our data highlight the challenge of understanding if this variation reflects vulnerability of different species to climate warming. Importantly, the use of heat dissipation behaviours by all arid-zone species emphasises that behavioural adjustments are a critical mechanism for survival at high T_{air} (Kelly et al. 2004, Cunningham et al. 2015). However, as temperatures rise in the decades ahead, the energetic and water costs of maintaining T_b within physiological tolerance limits will increase, as will the risk of exposure to lethal heat loads (Boyles et al. 2011, du Plessis et al. 2012, Smith et al. 2015, Noakes et al. 2016). The fitness costs of such responses have already been demonstrated in *Sceloporus* lizards, which have suffered localised extinctions in the hottest areas of their range because the behavioural changes they adopted to survive the heat compromised their reproductive output (Sinervo et al. 2010). Given the variation in HDB that we recorded between phylogenetically and geographically distinct avian communities, and the fact that HDB correlate with missed-opportunity costs at least some of the time (Cunningham et al. 2015, Pattinson and Smit 2017, van de Ven et al. 2019), we believe the data presented here support the value of HDB indices. What remains to be determined is precisely how these indices reflect negative impacts on physiology and behaviour and in turn organismal fitness, and how they might ultimately impact population-level processes.

List of abbreviations

EWL – evaporative water loss, HDB – heat dissipation behaviour, GLS – Generalized linear models, M_b – body mass, $Pant_{50}$ – the air temperature (T_{air}) at which half the individuals of a particular species are expected to pant, PGLS – Phylogenetic generalized linear models, Prop_act – the logit-transformed proportion of observations where species were active between 35 and 40°C for all species within each region, $Rest_{50}$ – T_{air} at which half are expected to be resting/inactive, $Shade_{50}$ – T_{air} at which half of observed birds are expected to be in shaded microsites, T_{air} – air temperature, T_b – body temperature, $Wing_{50}$ – the T_{air} at which half of a particular species are expected to exhibit wing-drooping.

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