Climate Change Responses

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Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming

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Abstract

Background: Temperature increases associated with climate change pose a substantial threat to arid-zone bird species. However, predicting vulnerability to high temperatures using species-specific, mechanistic data, and assessing how this varies within and among species, is complex, time consuming and expensive. Using the bird community of the southern Kalahari Desert, we investigated whether interspecific variation in heat dissipation behaviour (HDB) thresholds could provide an index of vulnerability to high temperatures. We fitted logistic regression models to presence/absence data for behaviours as a function of air temperature (T_{air}) in order to determine, for each species, the T_{air} at which panting and gular flutter ($pant_{50}$), wing-drooping ($wing_{50}$), resting ($rest_{50}$) and shade-seeking ($shade_{50}$) responses occurred in 50 % of instances.

Results: We show that $pant_{50}$ ($n = 30$ species) is higher in species that 1) are smaller, 2) maintain low activity levels at high T_{air}s, and 3) rely mostly on food as their water source (i.e. non-drinking species) — the only predictor variable to remain significant in phylogenetically-independent analyses. Like $pant_{50}$, $wing_{50}$ ($n = 30$ species) was negatively correlated with body mass, but did not vary systematically with other organismal traits. There was no systematic variation in $shade_{50}$ ($n = 33$ species) or $rest_{50}$ ($n = 14$ species) values.

Conclusions: Our findings suggest that evaporative cooling demands are relatively higher in larger birds and could limit activities (such as foraging) at T_{air}s exceeding 30 °C, while the trade-off between thermoregulation and sustaining activity levels appears less pronounced in smaller species. Kalahari species that do not drink regularly show a relatively greater dependence on wing-drooping compared to panting/gular flutter, probably resulting from selective pressures to reduce evaporative cooling demands in an arid environment with scarce surface water. Two key questions remain to be answered to confirm whether variation in HDB thresholds provides an opportunity for rapid assessment of vulnerability to high temperatures in avian species from hot, arid environments. First, what are the relationships between HDB patterns and body temperature regulation? Second, is heat dissipation effort indicative of dehydration risk?

Background

A key challenge facing researchers seeking to predict the impacts of climate change on animals concerns the trade-off between single-species models based on in-depth studies of physiological and behavioural processes, versus more generalised correlative models that can yield predictions for entire communities. Recent decades have seen substantial conceptual development in both these fields. Bioclimatic envelope models (BEMs) have rapidly become a popular prediction tool for large scale changes in the distributions of organisms in response to climate warming [1–4]. BEMs rely on quantifying the climate envelope currently inhabited by a species, then using outputs from global circulation models to predict where, geographically, suitable climate conditions for the species will occur in future. The attractiveness of this method and its popularity over the last two decades [1, 5, 6] is due in no small measure to the relative ease and rapidity with which predictions for multiple species can be generated.

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In contrast to BEMs, mechanistic models predict species' niches based on detailed understanding of ecological and physiological processes. Detailed parameterisation of mechanistic models relies on intensive and time-consuming sampling of focal taxa. To date, this approach has focussed predominantly on single species [7–10], limiting inference over the potential impact of climate change on communities. Despite the difficulties of building and parameterising complete mechanistic models, empirical mechanistic studies have provided convincing insights into how particular species and populations are affected by climate, particularly in response to high temperatures (e.g., [11–19]).

Birds inhabiting hot, arid environments provide a useful model system for developing novel approaches to predicting species' vulnerabilities to increasing temperatures, combining mechanistic underpinnings with the potential to rapidly and cheaply generate predictions for entire communities. In these habitats, operative temperatures (a measure of the overall environmental heat load experienced by an animal [20]) routinely approach or exceed avian body temperature (T_b) [21]. This creates conditions where the need to conserve water and avoid dehydration is in direct conflict with reliance on evaporative cooling to avoid lethal hyperthermia [17, 22–25]. Occasionally, periods of extremely hot weather cause catastrophic mass mortality events, sometimes involving thousands of individuals [26, 27]. Even at air temperature (T_{air}) below avian T_b, metabolic heat gain, or heat gained from solar radiation, means that birds must frequently dissipate excess heat via evaporative and non-evaporative mechanisms, such as panting/gular flutter and wing-drooping, respectively [14, 28–30]. The demands of heat dissipation behaviour (HDB) can lead to trade-offs that have potentially far-reaching implications for body condition, survival and reproduction [13, 31, 32].

Recent studies in southern Africa's Kalahari Desert highlight the links between easily-observable patterns of behaviour and variables that directly impact survival and reproduction [13–16, 31]. For example, du Plessis et al. [13], found a negative correlation between T_{air} and body mass (M_b) gain of Southern Pied Babblers (*Turdoides bicolour*) during summer, such that on hot days (i.e. maximum $T_{air} > 35.5$ °C) the birds' M_b gain during the day was insufficient to balance typical overnight M_b loss. Reduced M_b gain appeared to be driven by reduced foraging efficiency on hot days resulting from conflicts between dissipating heat by panting and simultaneous foraging [13].

Relatively little is known about the effects of high T_{air} on behavioural and physiological responses in free-ranging birds [13, 14, 16, 33], and more specifically, how these vary at an inter-specific level with organismal variables such as M_b and ecological attributes (e.g. behaviour, diet and microhabitat use) [34]. Although we expect the time allocated to heat dissipation to increase at high T_{air}, we can also make several predictions regarding interspecific variation in HDB.

First, larger birds have been shown to initiate evaporative cooling responses at lower temperatures compared to smaller birds [35], presumably reflecting their lower surface area-volume ratios and increasing thermal inertia with increasing M_b. Hence, we might predict that during hot weather, trade-offs between HDB and time allocated to activities, such as foraging and maintenance behaviours, should be more pronounced in larger species.

Second, we expect that the ecological significance of such trade-offs is greater in species with overall higher activity levels. For example, species that are active gleaners, and whose foraging mode involves near-constant activity, presumably generate a greater metabolic heat load per unit time while foraging, compared to sit-and-wait foragers.

Third, respiratory HDB, in particular panting and gular flutter, is associated with high evaporative water loss (EWL) requirements. We may therefore expect species relying solely on food as a water source to depend to a lesser extent on respiratory EWL and more on passive heat loss mechanisms such as wing-drooping. These species may also show lower activity levels and spend less time in the sun to reduce evaporative cooling demands.

We test whether HDB varies in a predictable manner among bird species from the southern Kalahari. Should HDB thresholds vary predictably (as outlined above), then we believe behaviour is likely to be both a good proxy for investigating the ecological significance of thermal physiological trade-offs, and useful in understanding ecological and evolutionary determinants of species persistence in hot, arid landscapes.

Methods

Study sites

Data were collected at three different sites within the southern Kalahari: Tswalu Kalahari Reserve (S27°19′, E22°25′), Dreghorn Game Ranch (S26°52′, E20°43′) and Kuruman River Reserve (S26°58′, E21°49′). All sites were located within the arid savannah biome of the Northern Cape Province of South Africa. Mean annual rainfall data values were obtained from private rangeland owners. At Tswalu Kalahari Reserve, mean annual rainfall over a 30-year period was 295 ± 172 mm (coefficient of variation, CV = 58.3 %) (D.N. MacFadyen, unpublished data). Mean annual rainfall at a ranch near Kuruman River Reserve and Dreghorn Game Ranch was lower at ~190 ± 125 mm (CV = 66 %) over a 60-year period (G. Scholtz, unpublished data). Long-term T_{air} data were not available for these sites. Habitat type at all three study sites was savannah on red sand dunes with

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no natural free-standing surface water sources, although there were artificial water troughs in the reserves/ranches.

Weather data
During our study we obtained weather data using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA), set 2 m above the ground at a central location within each study site. The T_{air} recorded during our study ranged from 18.9 to 38.9 °C (record maximum T_{air} was 37–38.9 °C at all the sites during the study).

Behavioural observations
Behavioural observations of birds were conducted during austral summers (November-March) of 2009/2010 and 2010/2011. We collected a total of 11,110 observations during the study at all the sites; 4673 observations at Tswalu Kalahari Reserve during the first summer, and 4243 during the second. We also collected 2148 observations at Dreghorn Game Ranch and 62 at Kuruman River Reserve during the second summer. The small numbers of observations from Kuruman River Reserve were included to boost observations for a few target species (e.g. Crimson-breasted Shrike, *Laniarius atrococcineus*). Behavioural observations were conducted during the warmer part of the day (between 10:00 h and 18:00 h) when bird behaviour was likely to be affected most by high temperatures. We conducted observations by searching for birds while walking, or from a vehicle. Walking observations were conducted in 426 plots (approximately 800 m × 100 m in size) that we selected at random within the landscape. These plots were separated by at least 500 m, and were a minimum of 500 m from the nearest surface water source. The majority of the plots were sampled only once (414 plots, 3545 observations), and plots sampled on the same day were always more than 1 km apart. A subset of 12 plots at Tswalu Kalahari Reserve were surveyed 18 times each, at varying times of day and on days of varying maximum air temperature (total of 5546 observations); during repeated sampling of these plots there may have been some degree of pseudoreplication as some individual birds may have been observed more than once. Within each plot, we searched for birds over a period of 30 min to 1 h by moving from one end to the other at an average speed of ~0.5 kmh^{-1} stopping regularly to scan the surroundings for birds. Driving observations were obtained ad-hoc while driving in a motor vehicle along an un-surfaced track (a total of 235 tracks, 2019 observations) between 1 and 10 kmh^{-1} for 30 min to 1 h; each track was only sampled once. We stopped the motor vehicle at regular intervals and scanned for birds; birds were generally more conspicuous when approached from the vehicle than by foot.

During observation periods, each bird seen was identified to species level, and we recorded the presence (=1) or absence (=0) of HDB; if HDB could not be assessed = NA (Not Applicable). Heat dissipation behaviours were categorised as either respiratory HDB, or non-respiratory HDB. Panting (defined as gaping when breathing) and gular flutter (rapid movement of the gular area) behaviours are well known avian respiratory HDBs associated directly with evaporative cooling and increased EWL rates [23, 28–30, 36, 37]. Wing-drooping behaviour (defined as holding the wings away from the body) is often recorded as a mechanism to increase the surface area of the body to enhance radiative and convective dry heat loss by exposing thermal windows under the wing [28, 37]. Both these categories of behaviours are easily observable in the field [13, 14, 31]. In addition we recorded activity state (mobile = 1, resting = 0) and exposure (full sun = 1, associated with vegetation shade = 0) during the observation event. Behavioural assessment of each individual generally lasted around 30 s.

With the exception of ambush flights (sallying or pouncing), birds in flight were not recorded, and aerial foragers, such as swifts and swallows, were therefore excluded from the study. In addition, birds were not recorded if their behaviour appeared to have been altered by the presence of the observer, or if the bird was observable for too short a time for behaviours to be determined with certainty. If more than one individual of the same species was encountered and it was considered that the behaviour of each individual was not independent of the other birds in the group (e.g. they were foraging together as a flock) then a judgement of the predominant behaviour of the group was made.

Statistical analyses
Analysis of heat dissipation behaviour
We calculated two types of indices for heat dissipation behaviour:

(1) We determined the relationships between T_{air} and binomial behaviour data for each species separately by performing logistic regression analyses, using a *logit* link-function and quasi-binomial probability density function to account for over-dispersion, in R [38]. In cases where the beta estimate was significant at the 95 % confidence level, or approached significance (i.e. fell between 95 and 90 % confidence level), we used model predictions to determine, for each species, the T_{air} at which the behavioural response was present in 50 % of observations, i.e. median T_{air}. Median T_{air} values of panting and gular flutter ($pant_{50}$), wing-drooping ($wing_{50}$), resting ($rest_{50}$) and shade-seeking ($shade_{50}$) were calculated as the intercept value (absolute) divided by the beta value (absolute).

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(2) For each species we extracted all the data recorded at hot T_{air}s (35–40 °C) during our study. We then counted all the instances where each species was panting, wing-drooping, mobile, and in full sun, and calculated proportional values from the total number of observations at hot temperatures for each species; hereafter referred to as *prop_pant*, *prop_wing*, *prop_act*, and *prop_sun*, respectively. These proportional values provided us with a supplementary index of behaviour in each species.

Previous studies have found a link between humidity, heat load and the demands for evaporative cooling in birds [14, 39]. Specifically, Smit et al. [14] found that White-browed Sparrow-Weavers had higher T_bs when vapour pressure deficits were below 2 kPa. During the current study, vapour pressure deficits were sometimes below 2 kPa during rainy periods. Observations associated with vapour pressure deficits below 2 kPa made up a very small proportion of our data, and prevented us from conducting adequate statistical analyses to account for humidity. Excluding data associated with low vapour pressure deficits (<1kPa, <2 kPa, <3 kPa, in a step-wise manner) did not affect our $pant_{50}$ estimates. We therefore included all observations in this study, regardless of vapour pressure deficit and did not include humidity as a variable in our analyses.

Interspecific analyses

We performed both generalized linear models (GLS) and phylogenetic generalized linear models (PGLS) in R—the latter using the *ape* [40] and *caper* [41] packages, to test for systematic differences in median T_{air} values of behaviour ($pant_{50}$, $wing_{50}$, $shade_{50}$ and $rest_{50}$). In PGLS analyses we used Kappa transformations to estimate phylogenetic signal in the null models for each dependent factor. We included $\log_{10}$ body mass ($\log_{10} M_b$), diet, foraging location, drinking dependency, *prop_act*, and *prop_sun* (defined above) as independent variables in the global models (*prop_act* and *prop_sun* were excluded from $rest_{50}$ and $shade_{50}$ models, respectively). Foraging location was grouped into arboreal versus terrestrial foragers; diet was grouped into frugivores, granivores, omnivores and insectivores (insectivores and carnivores pooled); and drinking dependency was grouped into non-drinking or drinking species based on their reliance on free-standing surface water. All above groupings were based on Hockey et al. [42]. We included *prop_act* and *prop_sun* as independent variables since we expected high levels of activity and sun exposure to be associated with heat dissipation behaviours.

We sampled 100 phylogenies for all the species in our dataset from http://www.birdtree.org [43] using the Hackett et al. [44] phylogeny as a back-bone. We used the majority consensus tree identified using the programme Mesquite [45]. For each dependant variable we initially ran a global model with all the independent variables as listed above. We then used multi-model inference [46], using the R package "MuMIn" [47] to select the top three models. We based our model selection on Akaike Information Criteria corrected for small sample sizes (AICc) values. We calculated the variance inflation factors for all independent factors in the global models. Although variance inflation factors were never >5, we found that $\log_{10}M_b$ and *prop_act* were correlated (Pearson's correlation coefficient = 0.72). We therefore tested the effect of $\log_{10}M_b$ on *prop_act* using both GLS and PGLS. In these analyses we performed a logit-transformation on *prop_act* values, following Warton and Hui [48]. In addition, "diet" was slightly collinear with drinking dependency (variance inflation factor = 4) and was subsequently excluded from most global models.

To test our hypothesis that non-drinkers avoid evaporative cooling to conserve water, we calculated the differences between $pant_{50}$ and $wing_{50}$ ($wing_{50} - pant_{50}$) values for 17 species and tested if the magnitude and direction of $wing_{50} - pant_{50}$ differences were explained by drinking dependency, including $\log_{10} M_b$ and *prop_act* as covariates in GLS and PGLS analyses.

Results

We obtained data from 76 species during the study (see Additional file 1: Table S1 and Additional file 2), and were able to calculate statistically significant estimates of median T_{air} values for $pant_{50}$, $wing_{50}$ and $shade_{50}$ for 33 species, and $rest_{50}$ values for 13 species (see Additional file 1: Table S2 and Additional file 3). Kappa values in $pant_{50}$ and $shade_{50}$ were 1.00 and 0.762, respectively, but only approached significance from zero ($p = 0.064$ and $p = 0.051$, respectively). The Kappa value of $wing_{50}$ was not significantly different from zero ($K = 0.571$, $p = 0.196$). Our sample size for $rest_{50}$ values was smaller than the minimum number of species needed to obtain a phylogenetic signal [49]. In contrast, we found significant phylogenetic signals in *prop_act* ($K = 0.843$, $p < 0.01$), and $\log_{10} M_b$ ($K = 0.673$, $p < 0.05$).

Median T_{air} values for different categories of HDB varied widely: $pant_{50}$ values ranged from 31.3 to 46.0 °C (mean 39.3 °C), whereas $wing_{50}$ values ranged from 35.3 to 44.6 °C (38.9 °C) (Figs. 1 and 2). For 19 species, we were able to obtain estimates of both $pant_{50}$ and $wing_{50}$ (Fig. 2.). For a further six species, we found a significant response in only $wing_{50}$, but not $pant_{50}$, and vice versa for another six (Additional file 1: Table S2; Fig. 2). We found that $rest_{50}$ and $shade_{50}$ values were generally lower than $pant_{50}$ and $wing_{50}$, and ranged from 6.7 to 38 °C (mean = 24.6 °C) in $rest_{50}$, and 14.2 to 54 °C (30.3 °C) in $shade_{50}$ (Fig. 3).

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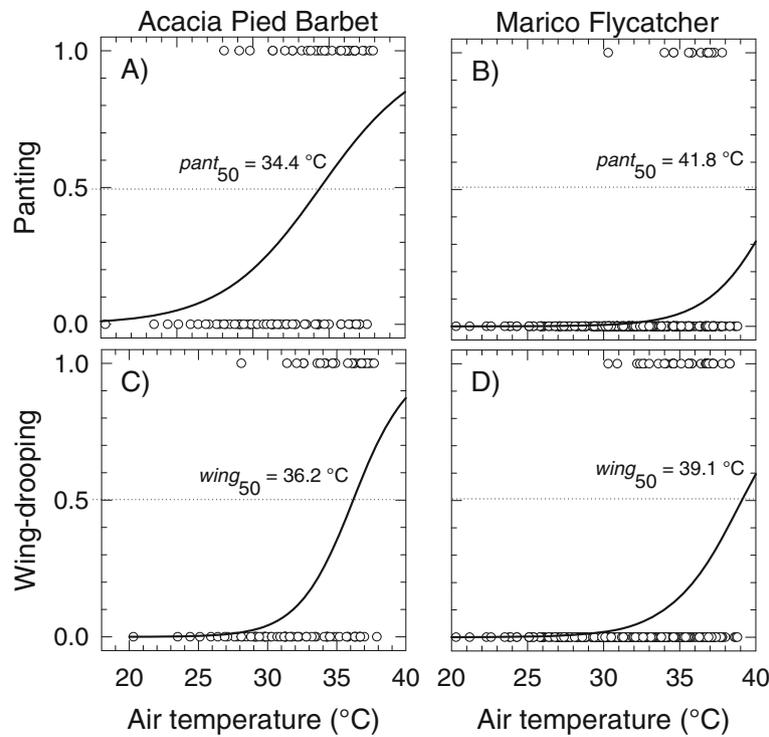
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Fig. 1 Heat dissipation behaviour representing presence/absence of (**a** & **b**) panting, and (**c** & **d**) wing-drooping as a function of air temperature (T_{air}) in two avian species in the Kalahari Desert; Acacia Pied Barbet, *Tricholaema leucomelas* (32 g), and Marico Flycatcher, *Bradornis mariquensis* (26 g). Presence of the behaviour = 1, and absence of the behaviour = 0. The logistic regressions represent predicted proportion of heat dissipation. Significant ($p < 0.05$) relationships are indicated by *solid trendlines*. Median T_{air} values where panting ($pant_{50}$) or wing-drooping ($wing_{50}$) was likely to occur in 50 % of cases are shown in each panel. These species illustrate the variation observed in their heat dissipation responses to T_{air} (see Additional file 1: Table S2, for statistics); whereas Acacia Pied Barbet showed relatively low $pant_{50}$ and $wing_{50}$ values, Marico Flycather showed relatively high $pant_{50}$ and $wing_{50}$ values
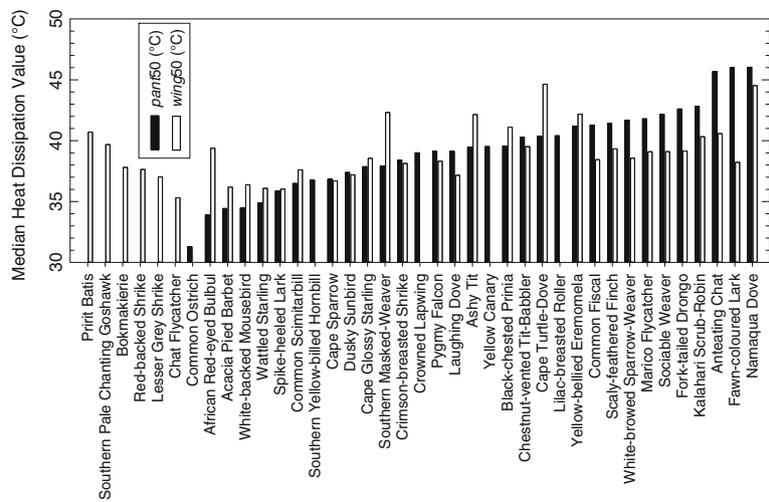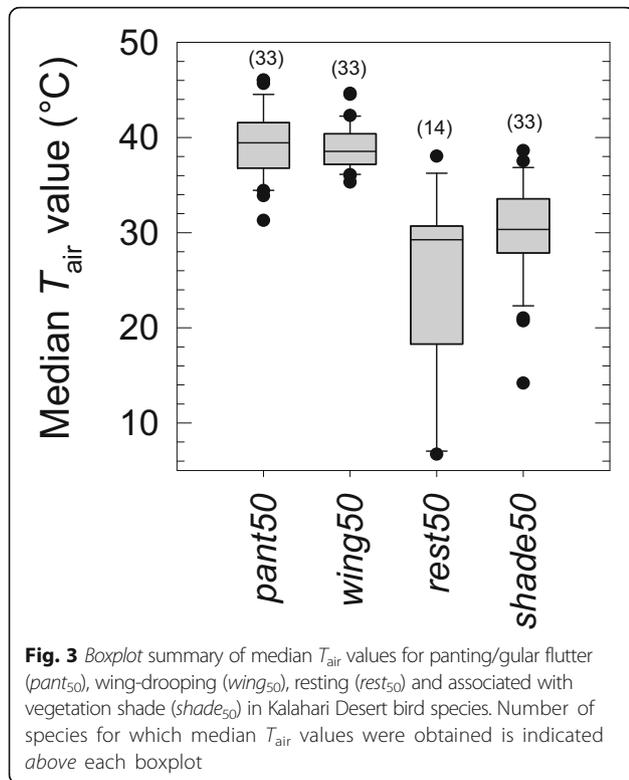

Fig. 2 Median T_{air} values where panting ($pant_{50}$, *black bars*) or wing-drooping ($wing_{50}$, *white bars*) was likely to occur in 50 % of cases in Kalahari Desert bird species

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Fig. 3 *Boxplot summary of median T_{air} values for panting/gular flutter (pant$_{50}$), wing-drooping (wing$_{50}$), resting (rest$_{50}$) and associated with vegetation shade (shade$_{50}$) in Kalahari Desert bird species. Number of species for which median T_{air} values were obtained is indicated above each boxplot*

We excluded data from Common Ostrich (*Struthio camelas*, $M_b > 60$ kg) from our multi-species analyses because this species is several orders of magnitude larger than the remaining species from which we obtained HDB data (9 to ~800 g). We also excluded Namaqua Dove (*Oena capensis*) and Spike-heeled Lark (*Chersomanes albofusciata*) from pant$_{50}$ analyses; Namaqua Dove, Cape Turtle Dove (*Streptopelia capicola*) and Southern Pale Chanting Goshawk (*Melierax canorus*) from wing$_{50}$; and Ant-eating Chat (*Myrmecocichla formicivora*) from shade$_{50}$ analyses, as their respective median values were highly influential outliers based on Cook's distance.

Models for pant$_{50}$

A conventional GLS analysis identified $\log_{10}M_b$, prop_act and drinking dependency as important explanatory variables in the top three most highly weighted models of pant$_{50}$ (Table 1). We found that pant$_{50}$ was significantly negatively correlated with $\log_{10}M_b$ $t_{1,25} = -3.62$, $p < 0.01$) and prop_act ($t_{1,25} = -4.05$, $p < 0.001$), and significantly higher in non-drinking species (mean pant$_{50}$ ± SD, 40.7 ± 2.6 °C, $n = 20$) compared to drinking species (36.9 ± 2.4 °C, $n = 10$) $t_{1,25} = 3.86$, $p < 0.001$) (Fig. 4). Whereas both foraging location and prop_sun were influential in some of the top models, these variables did not show a significant effect on pant$_{50}$ ($p > 0.1$)

Table 1 Three top-weighted models explaining median T_{air} values in panting/gular flutter behaviour (pant$_{50}$) using both generalized linear models (GLS) and phylogenetic independent analyses (PGLS). The global model included: $\log_{10}$ body mass ($\log_{10} M_b$); proportion of observations where birds were mobile (prop_act), and exposed to full sun (prop_sun) at air temperature between 35 and 40 °C (see methods for details); drinking dependency; foraging location; and diet as independent variables. Only the variables that were influential in the three top-weighted models are shown. For each variable we provide the contrast (± standard error), and significance level (see note below Table)

	Model		
	1	2	3
	GLS		
$\log_{10} M_b$	−5.62 ± 1.56**	−5.06 ± 1.57**	−5.29 ± 1.56**
prop_act	−7.69 ± 1.91**	−7.79 ± 1.97**	−6.73 ± 2.02**
Drinking dependency (non-drinking)	3.12 ± 0.81**	2.94 ± 0.83**	3.12 ± 0.80**
Foraging location (terrestrial)	1.32 ± 0.79		1.54 ± 0.79
prop_sun			2.86 ± 2.20
Intercept	48.30 ± 3.15**	48.20 ± 3.26**	46.57 ± 3.38**
Observations	30	30	30
AICc	136.4	136.4	137.8
	PGLS		
prop_act			−1.56 ± 2.20
Drinking dependency (non-drinking)	4.08 ± 1.06**	4.04 ± 1.15*	3.95 ± 1.09*
prop_sun	5.07 ± 2.42		−4.59 ± 2.55
Intercept	34.44 ± 2.72**	36.07 ± 4.04**	35.05 ± 2.88**
Observations	30	30	30
AICc	159.7	161.7	161.8

Note: *$p < 0.05$; **$p < 0.01$

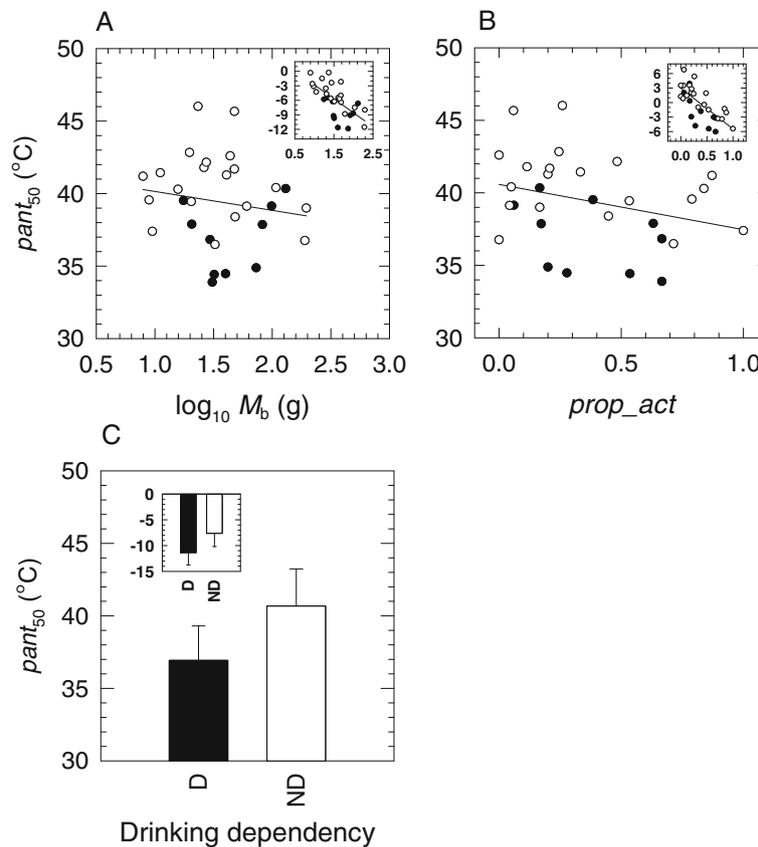Smit *et al. Climate Change Responses* (2016) 3:9

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Fig. 4 Median T_{air} values for panting/gular flutter ($pant_{50}$) were significantly related to (**a**) $\log_{10}$ body mass ($\log_{10}M_b$) (negative relationship), **b** *prop_act* (negative relationship), and **c** drinking dependency (D: drinking species; ND: non-drinking species); $pant_{50}$ was lower in species that rely on surface water. The *insets* represent partial residuals of the model including all three above-mentioned variables. The *filled* and *clear circles* represent drinking and non-drinking species, respectively

(Table 1). A PGLS analyses showed that drinking dependency was the most important explanatory variable in all the top weighted models, and non-drinking species had significantly higher $pant_{50}$ values compared to drinking species ($t_{1,28} = 3.86$, $p < 0.001$) (Table 1). The top performing model included a positive correlation with *prop_sun* as an explanatory variable that approached significance ($t_{1,28} = 2.10$, $p = 0.051$).

Models for wing$_{50}$

A conventional GLS showed that $\log_{10}M_b$ best explained variation in $wing_{50}$ in the top three most influential models (Table 2); $wing_{50}$ was significantly negatively correlated with $\log_{10}M_b$ ($t_{1,28} = -2.85$, $p < 0.01$; Fig. 5). Although drinking dependency and *prop_act* were important in models 2 and 3, neither of these had a significant effect on $wing_{50}$ (all $p > 0.7$) (Table 2). In contrast, a PGLS analysis showed that $\log_{10}M_b$ and *prop_sun* were influential in some of the models, but did not perform better than the null model; none of these factors had a significant effect on $wing_{50}$ ($\log_{10}M_b$: $p = 0.08$; *prop_sun*: $p > 0.30$) (Table 2).

Comparing pant$_{50}$ and wing$_{50}$

For species for which both $pant_{50}$ and $wing_{50}$ could be calculated, drinking species showed mean $pant_{50}$ and $wing_{50}$ values of 37.6 ± 3.7 °C ($n = 10$) and 39.2 ± 3.4 °C ($n = 10$), respectively, and these were correlated (Pearson correlation coefficient = 0.752). Non-drinking species showed mean ($\pm$ SD) $pant_{50}$ and $wing_{50}$ of 40.7 ± 2.6 °C ($n = 18$) and 39.2 ± 1.5 °C ($n = 18$), respectively, and these values were not correlated (Pearson correlation coefficient = 0.244). Both a GLS and PGLS showed that *prop_act* and drinking dependency significantly predicted the magnitude and direction of $wing_{50} - pant_{50}$ (Fig. 6). Proportion activity was significantly positively correlated with $wing_{50} - pant_{50}$ (GLS: $t_{1,25} = 3.33$, $p < 0.01$; PGLS: $t_{1,25} = 2.52$, $p < 0.05$); species with high activity demands showed $wing_{50}$ values higher than $pant_{50}$ values (Fig. 6). Non-drinking species showed a greater difference between $wing_{50}$ and $pant_{50}$ values than drinkers (GLS: $t_{1,25} = -3.94$, $p < 0.001$; PGLS: $t_{1,25} = -3.55$, $p < 0.01$); non-drinkers initiated panting at higher T_{air}s than wing-drooping (Fig. 6).

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Table 2 Three top-weighted models explaining median T_{air} values in wing-drooping behaviour ($wing_{50}$) using both generalized linear models (GLS) and phylogenetic independent analyses (PGLS). The global model included: $\log_{10}$ body mass ($\log_{10} M_b$); proportion of observations where birds were mobile ($prop\_act$), and exposed to full sun ($prop\_sun$) at air temperatures between 35 and 40 °C (see methods for details); drinking dependency; foraging location; and diet as independent variables. Only the variables that were influential in the three top weighted models are shown. For each variable we provide the contrast (± standard error), and significance level (see footnote below Table)

	Model		
	1	2	3
	GLS		
$\log_{10} M_b$	-3.18 ± 1.12**	-3.03 ± 1.12**	-3.43 ± 1.38**
Drinking dependency (non-drinking)		0.26 ± 0.76	
prop_act			-0.42 ± 1.31
Intercept	43.24 ± 1.69**	42.83 ± 2.08**	43.78 ± 2.42**
Observations	30	30	30
AICc	120.4	122.3	122.3
	PGLS		
$\log_{10} M_b$	-2.60 ± 1.47		
Proportion sun			-1.73 ± 1.71
Intercept	41.99 ± 3.21***	37.60 ± 2.15***	37.98 ± 2.18***
Observations	30	30	30
AICc	129.7	130.4	131.6

Note: **$p < 0.01$; ***$p < 0.001$

Models of $rest_{50}$ and $shade_{50}$

Our small sample size of significant $rest_{50}$ values precluded detailed interspecific analyses. In both GLS and PGLS analyses, $shade_{50}$ was best explained by the null models (see Additional file 1: Table S3). Although *prop_act* and forage location appeared to be influential in the top three models, none of these were significant (all $p > 0.2$).
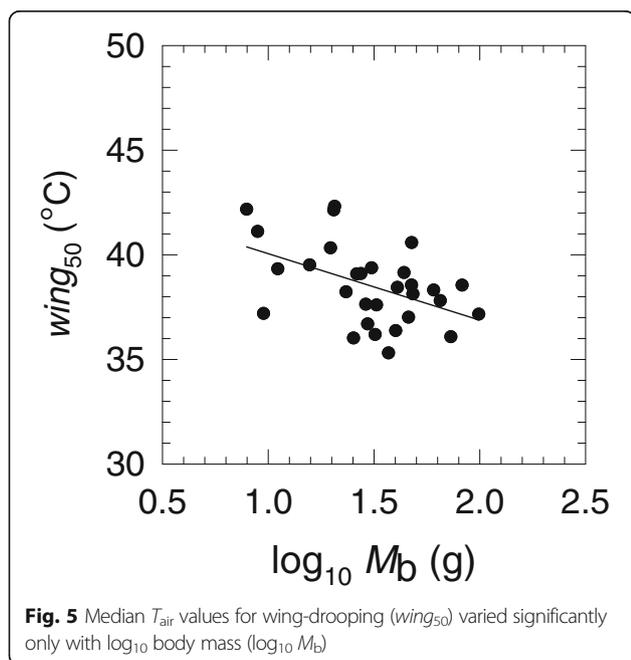
Fig. 5 Median T_{air} values for wing-drooping ($wing_{50}$) varied significantly only with $\log_{10}$ body mass ($\log_{10} M_b$)
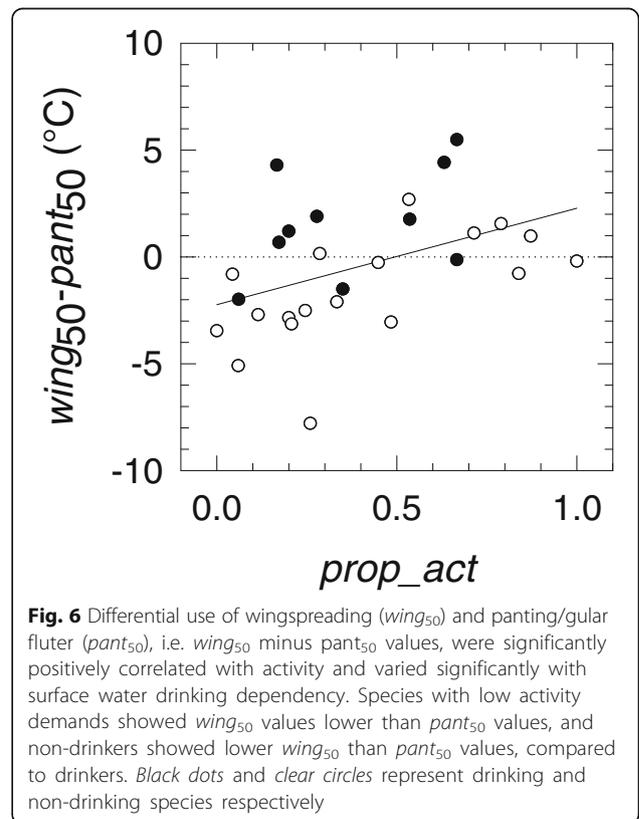
Fig. 6 Differential use of wingspreading ($wing_{50}$) and panting/gular fluter ($pant_{50}$), i.e. $wing_{50}$ minus $pant_{50}$ values, were significantly positively correlated with activity and varied significantly with surface water drinking dependency. Species with low activity demands showed $wing_{50}$ values lower than $pant_{50}$ values, and non-drinkers showed lower $wing_{50}$ than $pant_{50}$ values, compared to drinkers. *Black dots* and *clear circles* represent drinking and non-drinking species respectively

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The relationship between prop_act and body mass

Most species were active (mobile) in less than 50 % of the observations (mean *prop_act* = 0.37), but 11 species were active in more than 50 % of observations (*prop_act* = 0.5 to 1.0). A GLS showed that *prop_act* (logit-transformed) was significantly negatively related with $\log_{10} M_b$ (GLS: $t_{1,30} = -5.64$, $p < 0.001$); large species were less active (Fig. 7). Similarly, a PGLS analyses revealed that *prop_act* was significantly negatively correlated with $\log_{10} M_b$ (PGLS: $t_{2,30} = -4.17$, $p < 0.001$).

Discussion

We found considerable interspecific variation in the temperature dependency of HDB, activity patterns and shade-seeking among the common bird species of the Kalahari Desert. Most species increased HDB at high temperatures, although reliance on respiratory HDB (i.e., *pant_50*) versus non-respiratory HDB (*wing_50*) differed between drinking and non-drinking species. In conventional analyses, respiratory HDB thresholds varied systematically with body mass, activity levels and drinking dependency, while only M_b influenced non-respiratory HDB thresholds. After accounting for phylogeny however, drinking dependency was the only remaining variable that explained variation in respiratory HDB. In contrast, after accounting for phylogenetic effects, non-respiratory HDB was not explained by any of the variables in our global analyses.

Importantly, non-drinking species used panting/gular flutter at higher T_{air}s compared to wing-drooping. Birds may face a trade-off between reducing their heat load through evaporative cooling (which requires water) and acquiring this water (an activity that in turn increases heat load or may incur other costs); our data suggest that drinking species afford water-costly HDB at lower a T_{air} threshold, whereas non-drinking species may rely more on passive heat loss to conserve water. To the best of our knowledge, this study is the first to report on interspecific variation in HDB of free-living birds, with previous studies focusing only on single species, for example, Heermann's Gull *Larus heermanni* [28]; Southern Pied Babbler *Turdus bicolor* [13]; White-browed Sparrow-Weaver *Plocepasser mahali* [14]; Common Fiscal *Lanius collaris* [15]; Australian Magpie *Cracticus tibicen* [31]; and Great Knots *Calidris tenuirostris* [50].

Conventional and phylogenetic analyses

Our phylogenetic independent analyses provide strong support for the notion that higher *pant_50* values have evolved in non-drinking species. Although $\log_{10} M_b$ and *prop_act* were correlated with most categories of HDB, we found no statistical support for these relationships after taking phylogenetic relatedness into account. Both $\log_{10} M_b$ and *prop_act* showed significant phylogenetic signals, suggesting these traits are phylogenetically constrained. It is therefore not clear whether the effects of $\log_{10} M_b$ and *prop_act* on HDB are the result of mechanistic differences, or simply because closely related taxa are similar in mass and activity patterns. In contrast, the relationship between *prop_act* and $\log_{10} M_b$ was strong, and here the effect remained important after accounting for phylogeny. We believe that the scaling effect of *prop_act* is linked to the scaling effects of energy-, water-, and heat balance observed in endotherms, regardless of phylogeny. We therefore argue that the correlations of HDB with $\log_{10} M_b$ and *prop_act* that emerged in the conventional analyses are functionally important for understanding how species of varying M_b respond to hot conditions.

Effects of body mass and activity levels on heat dissipation behaviour

After accounting for activity levels and drinking dependency in conventional analyses, the negative relationship between *pant_50* and $\log_{10} M_b$ (albeit limited to species <200 g) observed in our study corroborates laboratory studies of avian thermoregulation at high temperatures. These studies typically show that the T_{air} thresholds for initiation of panting/gular flutter and elevated EWL rates scale negatively with body mass [18, 19, 35, 51]. It was hypothesized that the smaller surface area-volume ratio of larger birds should result in higher thermal inertia, and therefore, as T_{air} approaches T_b the windows for passive heat
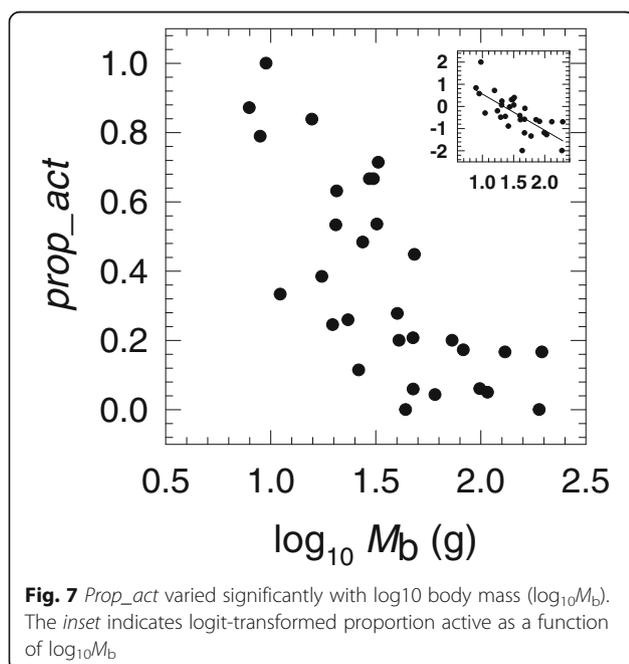

Fig. 7 *Prop_act* varied significantly with log10 body mass ($\log_{10} M_b$). The *inset* indicates logit-transformed proportion active as a function of $\log_{10} M_b$

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loss become smaller for larger birds compared to small birds [35, 52]. Under these conditions, larger birds will dissipate metabolic heat more slowly via passive avenues, compared to smaller birds, and will either need to store the excess heat (i.e. facultative hyperthermia) or make use of evaporative cooling to minimise hyperthermia. Our $pant_{50}$ data, which show that larger birds pant/gular flutter at lower T_{air}s, support the latter point. The former option of storing excess heat in long bouts of hyperthermia has been shown to be less beneficial in large birds, as net water savings are decreased by increased pulmonary water loss at a high T_b [53]. We found a significant reduction in activity with increasing T_{air} in 4/7 commonly observed species >100 g (mean 159.1 g). In contrast, only 9/39 species <100 g (mean 64.7 g) showed this same pattern of reduced activity. Reduced activity translates into reduced metabolic heat load, so this finding suggests that larger birds may rely less on facultative hyperthermia and heat storage than smaller birds, perhaps for the above reasons proposed by Tieleman and Williams [53]. More detailed studies on the relationships between M_b, hyperthermia and EWL, involving concurrent records of T_b patterns and HDB behaviour in birds under natural/semi-natural conditions, will be required to test these hypotheses.

It is important to note that the pattern of lower activity levels and greater heat dissipation effort that we observed in larger birds, which may imply that larger birds are at a disadvantage under climate warming, is likely linked to situations where $T_{air} < T_b$ (as was the case in our study). At extremely high T_{air} ($T_{air} > T_b$), when activity is suspended in all birds regardless of M_b, a different picture will emerge. Under these conditions, smaller birds, despite regulating T_b at higher levels, will still rapidly reach dehydration limits (11 to 20 % of M_b) while attempting to maintain T_b below lethal limits [51]. Larger birds, on the hand, may be less at risk during extreme heat waves as their lower mass-specific EWL, lower rates of environmental heat gain, and larger body-water pool afford them the critical window of extra survival time.

In our data set, few small species showed significant reductions in activity levels ($rest_{50}$) at high T_{air}: in total 11 species sustained high levels of activity (*prop_act* between 0.5 and 1.0) at hot T_{air}s, often while engaging in HDB. Here the relative use of respiratory versus passive heat loss, and degree of facultative hyperthermia used (discussed below) may be critical. Most active behaviour involves foraging, and high foraging effort under hot conditions may indicate strong temperature-related trade-offs [13]. Maintaining high foraging effort is likely important in arid habitats, due to the associated lower overall food availability compared to more mesic habitats [54].

The role of surface water dependency in the initiation of heat dissipation behaviour

The major pattern emerging from our data is that species that are independent of surface water showed higher thresholds for the initiation of panting and gular flutter compared with drinking species. The majority of the drinking species in our study are granivores and most non-drinkers are insectivores. The few non-drinking granivore and omnivore species (e.g. Scaly-feathered Finch *Sporopipes squamifrons*, and White-browed Sparrow-weaver *Plocepasser mahali*) also fit the above pattern, with consistently higher $pant_{50}$ values compared to granivore and omnivore drinking species (e.g. Cape Sparrow *Passer melanurus* and Southern Masked Weaver *Ploceus velatus*). For example, mean $pant_{50}$ values were on average 5 °C higher in non-drinking omnivores (40.8 ± 3.8 °C, $n = 5$) compared to drinking omnivores (35.8 ± 1.9 °C, $n = 5$).

Our findings also indicate that most non-drinking species depend on wing-drooping behaviour as the dominant form of HDB at T_{air} between 30 and 40 °C, postponing the initiation of panting/gular flutter (to higher T_{air}s). This pattern is consistent among the non-drinkers and suggests behavioural and physiological responses are functionally centred on reducing evaporative water loss. Non-drinking species acquire most of their water by foraging, and therefore run the risk of expending more water on evaporative cooling while active, than they obtain through their food [17, 33, 54], particularly if foraging efficiency is reduced at high T_{air} [13]. Wing-drooping enhances dry heat loss through convective and radiative cooling [28, 37], and while it is unlikely to be as efficient as evaporative cooling, it is less costly in terms of water demands.

We suggest two probable reasons for the link between drinking dependency and high levels of panting and gular flutter. First, drinking species may have more water available than non-drinking species, and consequently are able to expend more water on regulating T_b. According to this scenario, we expect the expression of HDB in these species to be very sensitive to reduced water availability; i.e. HDB in drinking species should be reduced when water sources are scarce. For example, when deprived of drinking water, Emus (*Dromaius novaehollandiae*) reduced respiratory heat dissipation and elevated T_b compared to when water was available [55]. However, it is important to note that increased EWL is not the only cost associated with panting and gular flutter: sustained panting carries a risk of alkolosis, i.e. increased build-up of blood CO_2 to dangerous levels [56, 57]. Therefore we hypothesize that birds should make use of panting or gular flutter only when the costs of hyperthermia outweigh the physiological costs associated with respiratory HDB. Species with low thresholds for panting

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or gular flutter might be more sensitive to elevations in T_b, which lead to decreases in thermal performance or risk physiological damage [58]. These species will have higher evaporative cooling demands to defend stable T_b, which could explain their reliance on drinking water.

We propose that T_b patterns at high T_{air}, in particular facultative hyperthermia, play a key role in activity and evaporative cooling trade-offs. Studies relating HDB directly to short-term changes in T_b are limited [14]. Smit et al. [14] showed that panting was initiated when T_b was above modal active-phase levels in free-ranging White-browed Sparrow-weavers (*Plocepasser mahali*). Because panting and gular flutter appear to represent a response to increasing T_b, potentially approaching lethal limits (44–46 °C, [22]), we hypothesise that variation in thresholds of panting/gular fluttering is related to variation in tolerance of a raised T_b. We predict that non-drinking species likely make use of facultative hyperthermia [14] under free-living conditions to a greater extent than drinking species.

Considerations when undertaking this approach

In our study we identified a number of limitations in using heat dissipation and behavioural patterns as a proxy for thermoregulatory demands in bird communities. First, the utility of the method presented here is likely to be limited to relatively open habitat, such as arid regions, where birds can be observed when they are inactive. Second, collecting data at a community level requires that most species are fairly abundant in the community, i.e. species evenness should be high. In many cases workers will need to increase search effort for less abundant species to obtain a community level data set. Third, in cases where a median T_{air} value for HDB cannot be established, an alternative metric for behavioural responses would therefore be to simply use proportional values. In all cases, *prop_pant* or *prop_wing* values were highly correlated with their respective median T_{air} values of HDB (see Additional file 1: Figure S1). Median values seem a good predictor of the percentage of time a behaviour is expressed during hot temperatures and represent functional differences in activity time-budgets.

Finally, some avian taxa, such as the order Columbiformes, are expected to make substantial use of cutaneous evaporative cooling [59–61]. Panting or gular flutter behaviour will greatly underestimate evaporative heat dissipation efforts in these taxa. In our study we found that the *pant_{50}* values for two species of dove, Namaqua Dove and Cape Turtle Dove, were higher than for similar sized passerines in our data-set, and represented influential outliers. The low incidence of panting and gular flutter observed in doves could be explained by the highly efficient evaporative cooling rates recently shown for this taxon [62, 63]. In contrast, the order Passeriformes have a limited capacity for cutaneous evaporative cooling at high temperatures [64–66]. We argue that, with the exception of the Columbiformes, cutaneous evaporative cooling is unlikely to be an important avenue of heat loss at high temperatures in most of the species observed in our study, especially the non-drinking species, since cutaneous evaporative cooling will be expensive when water sources are scarce.

Heat dissipation behaviour as a proxy for vulnerability

Many regions in South Africa have shown sustained climate warming over the past few decades, i.e. 1990s to 2010s [67, 68]. Moreover, globally, the years of 2015/2016 have been the warmest on record. During the austral summer of 2015/2016 most of the semi-arid and arid-zone regions of South Africa experienced record monthly maximum temperatures (in some cases 3 to 5 °C above average) and all-time record maxima were observed country wide (https://www.wunderground.com). It seems evident that over the next few decades many avian populations will more frequently experience T_{air}s that will elevate water demands and behavioural trade-offs. Our data show that species vary in their behavioural and thermoregulatory responses to high temperatures. Some of the species included in our study have already been shown to experience challenging trade-offs at T_{air}s between 30 and 40 °C. For example, Common Fiscals (*Lanius collaris*) show changes in shade-seeking behaviour leading to reduced prey capture and provisioning rates, compromising breeding success [15, 16] and White-browed Sparrow-weavers show elevated T_b [14] and mismatches between daily water intake and water loss [17]. Common Fiscals and White-browed Sparrow-weavers have relatively high *pant_{50}* values of 40 and 46 °C, respectively, whereas 58 % of species in our data set had *pant_{50}* values below 40 °C. We therefore predict that most of the latter species are already vulnerable to increasing T_{air}s.

Conclusion

This study presents a novel method for large-scale and low-cost assessment of variation in behavioural patterns of heat stress in bird communities. Our study shows that systematic inter-specific variation in panting and gular flutter is related to the drinking ecology of species, and to some extent, their body mass and activity patterns. We propose that this approach could greatly supplement integrative studies on the trade-offs between energy and water demands, foraging effort and thermoregulation under hot conditions. We further propose that this method could be developed as a proxy for investigating community-level response to high temperatures, and that it would be particularly relevant to predict vulnerability to climate warming scenarios. However, to fully understand the thermal physiological trade-offs

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associated with heat dissipation thresholds we still need to determine if variation in $pant_{50}$ is associated with species-level physiological differences, other than those driven by intrinsic factors such as body mass and activity demands. A small number of studies have already demonstrated that HDBs represent behavioural trade-offs with potential fitness consequences [13]. However, to further understand links between HDB and thermal physiological trade-offs that may underpin vulnerability, further investigation should address the following questions: 1) what are the relationships between heat dissipation patterns and T_b regulation? We predict that lower $pant_{50}$ and $wing_{50}$ values could be related to lower tolerance of T_b elevations; 2) is heat dissipation effort indicative of dehydration risk? We predict species with low $pant_{50}$ values to show greater daily water demands and a greater risk of dehydration on hot days; 3) How flexible are temperature-related HDB, activity and T_b patterns as a result of food and water supply? We predict that there will be variation in species' capacity to adjust their thermoregulatory patterns and this may be linked to adaptation to arid environments. In conclusion, our study shows that interspecific variation in HDBs, together with information on body size, physiology and ecology has the potential to provide community-level assessments of the thermoregulatory trade-offs that species confront at high T_{air}s. We hope that, together with further research on the relationships between HDBs, T_b regulation and dehydration risk, these findings will form a foundation for using low-cost field-based observational studies to assess vulnerability to climate change.

Additional file

Additional file 1: Summary of heat dissipation observations and statistics. (DOCX 82 kb)

Additional file 2: Behavioural observation data of birds collected during the austral summers (November-March) of 2009/2010 and 2010/2011. (XLSX 1.09 mb)

Additional file 3: Raw data as presented in Table S1 and Table S2. (XLSX 63 kb)

Abbreviations
BEMs: Bioclimatic envelope models; EWL: Evaporative water loss; GLS: Generalized linear models; HDB: Heat dissipation behaviour; M_b: Body mass; $pant_{50}$: Air temperature where panting behaviour occur in 50 % of cases; PGLS: Phylogenetic generalized linear models; prop_act: Proportion of observations where birds were mobile at air temperatures between 35 and 40 ℃; prop_pant: Proportion of observations where birds were panting at air temperatures between 35 and 40 ℃; prop_sun: Proportion of observations where birds were exposed to full sun at air temperatures between 35 and 40 ℃; prop_wing: Proportion of observations where birds were wing-drooping at air temperatures between 35 and 40 ℃; $rest_{50}$: Air temperature where resting behaviour occur in 50 % of cases; $shade_{50}$: Air temperature where shade-seeking behaviour occur in 50 % of cases; T_{air}: Air temperature; T_b: Body temperature; $wing_{50}$: Air temperature where wing-drooping behaviour occur in 50 % of cases

Availability of data and material
All raw data are available in Aditional file 2.

Authors' contributions
BS, ROM, SJC, AEM and PARH developed the conceptual framework. BS, ROM and GZ collected data. BS analysed conducted data analyses. BS and AEM wrote the manuscript. ROM and SJC edited the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare that they have no competing interests.

Consent for publication
We have obtained consent to publish the data collected by Tom Flower at KRR. We declare there are no further contents of this manuscript that require consent to be published.

Ethics approval and consent to participate
Not applicable.

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