

Interspecific variation in avian thermoregulatory patterns and heat dissipation behaviours in a subtropical desert

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Highlights

- Avian setpoint body temperatures were higher than expected.
- Body temperature responses to increasing air temperature varied greatly among species.
- Most species avoided prolonged periods of hyperthermia.
- Seeking shade and reducing activity are important for thermoregulation in many species.
- Linking behaviour to physiological thermoregulation requires species-specific data.

Abstract

Deserts are physiologically challenging environments for birds, with scarce, unpredictable water resources combined with air temperatures (T_{air}) regularly exceeding avian body temperature (T_{b}). For arid-zone birds, mismatches between water supply and demand are a constant threat, yet interspecific variation in trade-offs between hyperthermia avoidance and dehydration avoidance remain poorly understood, particularly for free-ranging individuals. We examined behavioural and physiological responses to high T_{air} in nine species representing three orders that vary substantially in their heat dissipation thresholds, specifically pant_{50} , the T_{air} at which panting behaviour is present in 50 % of observations. Birds housed during mid-summer in large free-flight aviaries in the Kalahari Desert each received a surgically-implanted T_{b} logger, and we quantified shade-seeking, activity and panting behaviours to examine relationships between species-specific pant_{50} and T_{b} regulation. Overall, species setpoint T_{b} values were higher (range: $41.4 \pm 0.5^{\circ}\text{C}$ to $43.1 \pm 0.4^{\circ}\text{C}$) than expected with maximum T_{b} values of $43.4 - 45.5^{\circ}\text{C}$. Interspecific variation in T_{b} patterns at high T_{air} was substantial, with T_{b} increasing with T_{air} in most species, whereas in others no pattern or a negative relationship between T_{b} and T_{air} was evident. Most species avoided prolonged hyperthermia, with reductions in activity and increased shade-seeking evidently adequate to manage heat load without resorting to hyperthermia in several of our study species. Access to drinking water and food resources in captivity may have affected T_{b} patterns. Our data reveal that thermoregulation varies substantially among species, and suggest that free-ranging birds in hot, arid environments may maintain higher T_{b} than currently thought.

Keywords: *hyperthermia,, thermal physiology, trade-off, Passeriformes, Columbiformes, Coliiformes.*

1. Introduction

In hot, arid environments daily air temperatures can routinely exceed avian normothermic body temperatures. One major physiological challenge facing desert birds, therefore, is the maintenance of stable core body temperature (T_{b}) and avoidance of lethal hyperthermia (Dawson & Bartholomew 1968, Prinzinger *et al.* 1991, Tieleman & Williams 1999, Møller 2010). Birds respond to increases in T_{b} via physiological and behavioural adjustments that return T_{b} to a normothermic range, which often involve costs related to increased water and/or energy demands (Dawson & Bartholomew 1968). During hot weather, when T_{air} approaches or exceeds the normothermic setpoint T_{b} (T_{bset}), passive heat loss ceases (Wolf 2000, Nilsson *et al.* 2016) and birds need to actively dissipate heat via evaporation to avoid T_{b} reaching lethal limits ($\sim 46-48^{\circ}\text{C}$; Dawson & Schmidt-Nielsen 1964, Tieleman & Williams

1999, Whitfield *et al.* 2014). Birds increase rates of evaporative heat loss via a combination of respiratory and cutaneous evaporative heat loss (REWL and CEWL, respectively). The contribution of these two avenues to evaporative cooling varies among taxa (Wolf & Walsberg 1996, McKechnie *et al.* 2016). Elevated CEWL promotes heat loss without the metabolic heat production associated with the muscle contractions required for panting (REWL), and therefore appears to be the more efficient mechanism of evaporative heat dissipation (Marder & Arieli 1988, McKechnie & Wolf 2004).

Irrespective of the pathways involved, high rates of evaporative cooling are problematic in desert environments where dehydration risk is high and surface water scarce (Dawson 1954, Bartholomew & Cade 1956). For example, at very high T_{air} small birds can lose > 5% of body mass per hour via evaporation (Wolf & Walsberg 1996). To reduce water loss through evaporative cooling in hot environments, birds may show regulated, reversible increases in T_b (facultative hyperthermia; reviewed by Tieleman & Williams 1999). However, the potential benefits of hyperthermia also vary with body mass and among avian taxa (Tieleman & Williams 1999, Whitfield *et al.* 2015, McKechnie *et al.* 2016) and even among populations within species (Smit *et al.* 2013). For instance, a desert population of White-browed Sparrow-Weavers (*Plocepasser mahali*) maintained higher T_{bset} than individuals from milder semi-desert sites, favouring a reduction in the use of hyperthermia (Smit *et al.* 2013).

Birds use behavioural adjustments such as reducing activity and increasing shade-seeking behaviour to reduce physiological costs of thermoregulation at high T_{air} (Calder & King 1974, Wolf 2000, Dawson 1982, Wolf 2000). However, the conflict between actively foraging to maintain energy and water budgets, and hyperthermia avoidance by reducing activity and seeking shade can be expensive in terms of lost opportunity costs (Cunningham *et al.* 2013, 2015). Additionally, high T_{air} can reduce overall fitness, as the aforementioned

behaviours coupled with increases in heat dissipation behaviour (HDB, such as panting and wing-drooping) reduce foraging efficiency, causing short-term losses of body condition (Du Plessis *et al.* 2012, van de Ven 2017) and reduced parental care (Cunningham *et al.* 2013, van de Ven 2017). Furthermore, there is considerable interspecific variation in the temperature dependence of HDB as well as activity and shade-seeking behaviours (Smit *et al.* 2016). The latter authors showed that the T_{air} associated with 50 % of a population panting or wing-drooping varies by > 21 °C among species in the Kalahari. Such interspecific differences in the T_{air} associated with the onset of HDB may provide a basis for using HDB thresholds to assess species vulnerability to high temperatures in hot environments, which consequently could be important for modelling avian responses to climate change (Smit *et al.* 2016). However, it is first necessary to establish whether functional links exist between inter- and intraspecific variation in HDB and T_{b} regulation (Smit *et al.* 2016).

Most data on avian thermoregulation at high T_{air} originate from laboratory studies in which T_{b} is measured concomitantly with metabolic rates and evaporative water loss (e.g., Smith *et al.* 2015, Whitfield *et al.* 2015; McKechnie *et al.* 2016). However, laboratory studies may not accurately reflect thermoregulation under natural conditions, as ambient conditions are controlled, and activity restricted (Smit *et al.* 2013). The few studies that have examined diurnal T_{b} patterns in free-ranging birds during hot weather typically focus on just one or two species (Smit *et al.* 2013, O'Connor *et al.* 2017). These studies confirm that T_{b} patterns can differ substantially between free-ranging individuals and individuals held in respirometry chambers (O'Connor *et al.* 2017). Yet, despite the importance of thermoregulation and associated trade-offs in the ecology of desert birds, very little is known about interspecific differences in thermoregulatory patterns in free-ranging birds (Smit *et al.* 2013) or how these relate to species traits, including variation in the temperature-dependence of HDB.

Recent years have seen an increasing interest in the notion that thermal performance of endotherms represents a continuum from thermal specialisation to generalisation, akin to that found in ectotherms (Angilletta *et al.* 2010, Boyles *et al.* 2011a). This view posits that thermoregulation is co-adapted with thermal sensitivity of performance, such that trade-offs occur whereby some species maintain high performance over only a narrow T_b range, responding strongly to changes in T_b (thermal specialists) whereas others tolerate a wider range of T_b but at lower performance levels and respond less to T_b changes (thermal generalists; Angilletta *et al.* 2010, Boyles *et al.* 2011a). Different environmental pressures likely alter the benefits of being either a thermal specialist or generalist. Yet, little is known about how much variation there is in the thermal performance breadth of specialists and generalist thermoregulators in specific environments, or whether species can shift from being a thermal specialist to a thermal generalist when heat stressed.

Here, we hypothesised that interspecific variation in HDB is functionally linked to body temperature regulation. We tested this hypothesis by examining patterns of T_b and behaviour in nine species that differ widely in the temperature dependence of panting, focussing specifically on panting thresholds, i.e. the T_{air} at which panting behaviour is present in 50 % of observations ($pant_{50}$). Thus, we selected our nine study species on the basis of $pant_{50}$; which varied by $> 10^\circ\text{C}$ with a range from $34.5 - 45.5^\circ\text{C}$ (Smit *et al.* 2016). We, 1) quantified interspecific variation in T_{bset} , 2) tested the prediction that T_b patterns correspond with $pant_{50}$ in terms of how T_b responds to increasing T_{air} , and 3) quantified hyperthermia use/avoidance across these species. 4.) We also tested the prediction that $pant_{50}$ is related to activity patterns and shade-seeking behaviours at high T_{air} . Due to the onset of active evaporative cooling when T_{air} approaches normothermic T_b , we expected $pant_{50}$ to be correlated with T_{bset} ,

with species that pant at lower T_{air} defending lower T_{bset} and showing a lower degree of heterothermy.

2. Methods & Materials

2.1. Study animals and housing

Table 1: Kalahari desert bird species used to compare variation in body temperature parameters. Each species has a unique abbreviation (Abb.) used for referral in figures and text. Species belong to three orders, passeriformes (PASS), columbiformes (COLU) and Coliiformes (COLI). Summer seasons where species were sampled are indicated by Season (2014 refers to Austral summer: i.e. Nov 2013-March 2014 *etc*). Species are categorised according to dominant dietary guild; i.e. frugivores (FRU), insectivores (INS), granivores (GRA), omnivores (OMN) using diet information from Hockey *et al.* 2005. Sample sizes for physiological (N_{Tb}) and behavioural data (N_{behav}) included.

Abb.	Order	Species	Season	Diet	N_{Tb} (N_{behav})	Body mass
WBM	COLI	White-backed Mousebird (<i>Colius colius</i>)	2016	FRU	5(10)	34.5 ± 1.7
CGS	PASS	Cape Glossy Starling (<i>Lamprotornis nitens</i>)	2015(2016)	OMN	8(16)	74.5 ± 7.1
REB	PASS	African Red-eyed Bulbul (<i>Pycnonotus nigricans</i>)	2014	FRU	7(10)	29.3 ± 2.2
WBS	PASS	White-browed Sparrow Weaver (<i>Plocepasser mahali</i>)	2015	OMN	6(10)	35.8 ± 2.6
CTD	COLU	Cape Turtle-Dove (<i>Streptopelia capicola</i>)	2015(2016)	GRA	11(16)	129.5 ± 11.3
LAD	COLU	Laughing Dove (<i>Streptopelia senegalensis</i>)	2015	GRA	8(11)	89.6 ± 9.9
SOW	PASS	Sociable Weaver (<i>Philetairus socius</i>)	2014	OMN	8(9)	24.0 ± 1.0
FCL	PASS	Fawn-coloured Lark (<i>Calendulauda africanoides</i>)	2014	OMN	6(8)	23.9 ± 0.7
NAD	COLU	Namaqua Dove (<i>Oena capensis</i>)	2015(2016)	GRA	8(19)	36.9 ± 2.3

We examined thermoregulation in nine bird species resident in the southern Kalahari Desert, representing three orders (Passeriformes, Columbiformes and Coliiformes). These species have a ~6-fold range in body mass and represent a variety of foraging guilds (Table 1). Birds were caught using species-appropriate trapping methods including mist-netting, spring traps baited with mealworms and walk-in traps baited with seed. Individual morphometric data including body mass were recorded upon capture, and birds were assigned a unique colour ring combination for individual identification while in captivity. Each species was kept separately for a single two-month period during either of the austral summers of 2014–2016 in one of three large outdoor aviaries (each 3 m high x 3 m wide x 8 m long). The aviaries were

erected at Murray Game Ranch (26°59'S, 20°51'E), a private farm ~ 12 km east of the town of Askham in the Northern Cape province of South Africa. Birds were habituated to the aviaries for at least six days before experimentation began. Within the aviaries, birds experienced natural daily ambient temperature cycles. Shade was provided by covering one-third of the aviary roof with sheets of corrugated steel. Perches were placed at various heights and positions inside the aviaries, and a comparable range of perching locations was available in each aviary. Birds were fed species-specific diets; columbids were fed a diet of wild birdseed, omnivorous passerines were also maintained on a diet of wild birdseed with daily supplements of mealworms and occasional supplements of freshly caught insects (predominantly lacewings and moths) trapped around domestic light sources in the evenings. Frugivorous species were fed seasonal fresh fruit mixed with ProNutro breakfast cereal (Bokomo, Pioneer Foods Groceries (Pty) Ltd, Tygervalley, Western Cape, South Africa) occasionally supplemented with mealworms. All birds received water *ad libitum* during the measurements reported here.

2.2. Body and air temperature measurements

Measurements of T_b for the two larger species, Laughing Dove (hereafter LAD) and Cape Turtle-Dove (hereafter CTD), were obtained using miniature temperature loggers (Thermochron iButton, model 1922L, Maxim Dallas Semiconductors, Sunnyvale, California, USA) programmed to record T_b every five minutes. For the remaining seven species (African Red-eyed Bulbul, Cape Glossy Starling, Fawn-coloured Lark, Namaqua Dove, Sociable Weaver, White-browed Sparrow-Weaver, White-backed Mousebird hereafter REB, CGS, FCL, NAD, SOW, WBS and WBM, respectively), we used surgically implanted temperature-sensitive radio transmitters (model BD-2TH, Holohil Systems Ltd., Carp, Ontario, Canada). A

data logging station consisting of a VHF radio receiver / data logger (Lotek SRX_400 receiver, Lotek Wireless Inc., Newmarket, Ontario, Canada) was set up outside the aviaries. The logging station included a multiplexor to accommodate three Yagi antennae (one per aviary) with the receiver continuously cycling through transmitter frequencies in such a way that the T_b of individuals was recorded at roughly four-minute intervals. Signal interference in the shaded areas of the aviaries was common and often interrupted the continuous recording of T_b . Individuals with intermittent T_b traces were omitted from the T_b analyses but data from all individuals were included in the behavioural analyses. The mass of loggers and transmitters mass was $\leq 5\%$ of body mass of all birds, excepting SOW and FCL where mass was $< 7.5\%$ of body mass. Loggers and transmitters were coated with surgical wax before being implanted intraperitoneally into the abdominal cavities of the birds under inhalation anaesthesia by a qualified veterinarian (Dr A Lategan, SAVC reg. no. D90-3031). To allow a full recovery the surgery took place at least a week before data collection. All loggers/transmitters were precalibrated over a temperature range of 0–45°C in a circulating water bath against a mercury-in-glass thermometer with NIST-traceable accuracy. Drift in radio transmitters required T_b traces to be corrected (see Data analysis section).

Air temperature, dew point, rainfall and other weather variables were recorded at five-minute intervals using a portable weather station (Vantage Pro2, Davis Instruments, Haywood, California, USA) placed within 400 m of the aviaries. Air temperature inside the aviaries (T_{aviary}) was also measured using temperature data loggers (TidbiT v2 temperature data logger UTBI-001, Onset Computer Corporation, Bourne, Massachusetts, USA) placed 2 m above the ground at perch level, in the shade at the back of each aviary. Each TidbiT was suspended inside a hollow plastic PVC tube (20 cm long x 5 cm diameter) with holes drilled into the sides for ventilation. TidbiTs were synched with the weather station and recorded

T_{aviary} every five min. TidbiTs were also precalibrated following the same procedure as T_b devices.

2.3. Behavioural observations

Behavioural data were collected by an observer seated far enough from the aviary that bird behaviour was not influenced by the observer's presence. The distance varied according to observed vigilance and alarm thresholds of the different species but generally ranged between 5-10 m from the aviary. We made instantaneous behavioural observations (Altmann 1974) per individual between 07:00–12:00 h and 14:00–17:30 h daily. This was done by observing an individual for a short time period (~20 seconds) and recording basic binomial data on panting behaviour (none = 0, panting = 1), shade-seeking (sun = 0, shade = 1) and activity (inactive = 0, active = 1). During these periods, individuals were sampled between 2–5 times depending on the ease of individual identification. Numbers of individuals per species included for behavioural data are generally higher than for T_b , reflecting the exclusion from the analyses of individuals with poor T_b traces.

2.4. Data analysis

All statistical analyses were conducted in the R environment (R Core Team 2016).

2.4.1. Transmitter drift correction

The Holohil temperature-sensitive radio transmitters used in this study have been previously shown to exhibit signal drift (Williams et al. 2009, Cunningham et al. 2017), and we encountered the same issue during the present study. To correct for drift, we examined T_b traces to identify where transmitters began to drift (break point) by running segmented models using the package *segmented* (Muggeo 2008) in R and, following the procedure of

Cunningham et al. (2017), corrected each individual T_b trace. Transmitters that did not start drifting immediately typically had break points between 8-15 days after implantation. The magnitude of drift in all transmitters varied anywhere between 0.02 – 0.13 °C/day.

2.4.1. Model fitting and selection

We fitted a global model including all terms that we hypothesised could have an effect on the response variable. The best model was selected by comparing AICc (Akaike's Information Criteria, adjusted for small samples) between all possible models nested within the global model using the dredge function in R package MuMIn (Barton 2010), and selecting the model with the lowest AICc score. All top models had Δ AICc > 2 points lower than the next best models. For all analyses, we visually inspected residuals of global and final models to ensure model assumptions were met. Statistical significance of the effects of retained predictor variables was inferred if 95% confidence intervals (CIs) excluded zero.

2.4.1. Body temperature analyses

Due to the failure of a number of T_b data loggers in the 2014–15 season, experiments for three species (number of failures: NAD = 7, CTD = 6, CGS = 10) were repeated during the 2015–16 summer (Table 1). For these species, T_b data from different years were pooled.

Analyses focused on T_b patterns across the whole day, hereafter 'diurnal' as well as looking at during the hottest period of the day (12:00-19:20), hereafter referred to as 'hot'. Diurnal (07:00-19:20) variation in T_b was analysed using a simple comparative metric, the Heterothermy Index (HI), which quantifies the extent of heterothermy for each individual bird by examining variation in T_b around the modal diurnal normothermic T_b (Boyles et al. 2011b), and is calculated as:

$$HI = \sqrt{\frac{\sum(T_{b\text{mod}} - T_{bi})^2}{n - 1}}$$

where $T_{b\text{mod}}$ is the modal normothermic T_b of an individual, T_{bi} is the T_b at time i , and n is the number of times T_b is sampled (Boyles *et al.* 2011b).

In all analyses, we included individual as a random effect to account for repeated measures per individual. Differences in $T_{b\text{mod}}$ and HI between species were modelled using linear mixed models (LMM) with fixed factors species and mass run with the package *lme4* (Bates *et al.* 2015). Body mass for each species was calculated as the mean mass of all study individuals. Tukey post-hoc tests using *multcomp* (Hothorn 2008) were used to identify significant differences between species and correlations between $T_{b\text{mod}}$ and HI were tested using Pearson's product-moment correlation. Following Smit *et al.* (2013) $T_{b\text{mod}}$ was determined by pooling all T_b recorded in the early morning (07:00–10:00), when birds were active but unlikely to be heat stressed.

For each species, we then modelled diurnal T_b and hot T_b as a function of T_{aviary} , controlling for time of day (diurnal T_b only) and body mass using LMM. Time of day (TOD) was divided into three periods, early: 07:00–10:00 when birds are active but not heat stressed, midday: 10:00–14:00, and afternoon: 14:00–19:20 where T_{aviary} peaked. Tukey post-hoc tests were used to examine differences in diurnal T_b , $T_{b\text{mod}}$ and HI with time of day (early: 07:00–10:00, midday: 10:00–14:00, afternoon: 14:00–19:20).

2.4.1. Behavioural analyses

Individual was included as a random factor in all behavioural analyses. For activity, panting and shade-seeking behaviour, T_{aviary} was the only significant predictor present in top models. We used model predictions for each species to determine the T_{aviary} at which panting behaviour was present in 50 % of observations (pant₅₀) following Smit *et al.* (2016).

Additionally, following the same methodology, we also calculated the T_{aviary} at which shade-seeking behaviour was present in 50 % of observations (shade_{50}) and the T_{aviary} at which species were active in 50 % of observations (activity_{50}). Activity_{50} models for CTD and REB did not converge. The removal of a single CTD individual for which no active observations were recorded resolved convergence issues for CTD. For REB, removal of any individual resolved convergence issues, with similar model outputs (all non-significant), regardless of the individual removed. The inability to identify which individual to remove ultimately meant REB model convergence issues remained unresolved. Further, Pearson's product-moment correlations were calculated to establish whether pant_{50} correlated with T_{bset} and mass.

3. Results

3.1. *Body temperature*

Diurnal T_{bmod} varied among the nine species from $41.4 \pm 0.5^{\circ}\text{C}$ in WBM to $43.1 \pm 0.4^{\circ}\text{C}$ in REB (Table 2, Figure 1). Variation in diurnal T_{b} , quantified as HI values, was similar among most species (Table 2). NAD had higher HI (i.e., T_{b} was more variable) in comparison

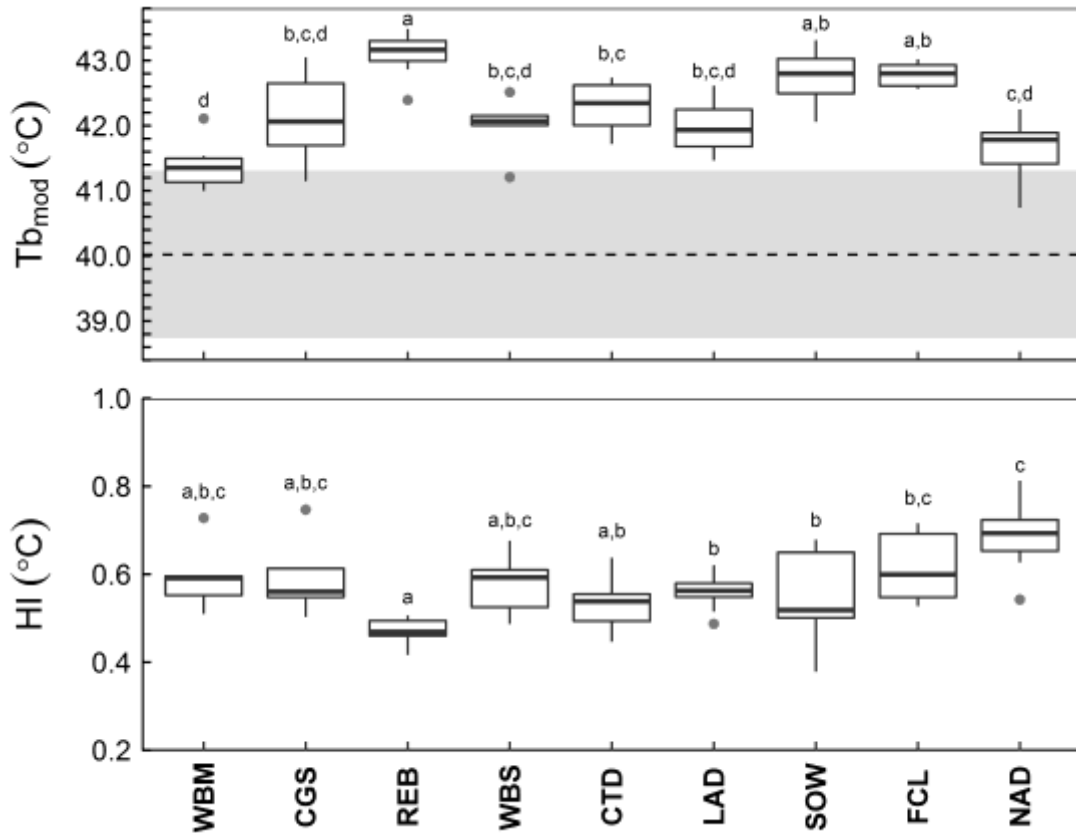


Figure 1: Interspecific differences in $T_{b_{mod}}$ and heterothermy index (HI) for nine species. Boxes represent means of individual $T_{b_{mod}}$ and HI. Species are arranged in order of heat dissipation thresholds ($pant_{50}$), from lowest (left) to highest (right; see Table 1). The dashed line in $T_{b_{mod}}$ panel indicates the mean (\pm sd = grey ribbon) active phase T_b for 724 bird species taken from Prinzing *et al.* (1991). Diurnal $T_{b_{mod}}$ generally fell above mean active phase T_b for all birds. Differences between species are indicated by letters above boxes. If species share a letter, 95% CIs include zero, and values do not differ. WBM = White-backed Mousebird, CGS = Cape Glossy Starling, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove. to REB LAD, CTD and SOW. FCL also showed greater variation in T_b than REB (Figure 1).

Among species $T_{b_{mod}}$ and HI were not correlated, although REB had the highest $T_{b_{mod}}$ and the lowest HI, whereas NAD had low $T_{b_{mod}}$ and the highest HI (Figure 1).

Diurnal T_b was predicted by T_{aviary} in most species, but effect sizes were very small (Table 3; Figure 8, Appendix). In most species (CGS, WBS, CTD, SOW and NAD) T_b increased with T_{aviary} . In comparison, the T_b of LAD, FCL and WBM showed small but significant decreases with increases in T_{aviary} (Table 3). The magnitude of the effect of T_{aviary} on T_b was influenced by the interaction of T_{aviary} and mass in CGS and NAD, where smaller

Table 2: Body temperature (T_b , °C) summaries for species across a range of aviary air temperatures (T_{aviary} , °C). Sample sizes differ for T_b data (N_{Tb}) and behavioural data (N_{behav}) however, the number of days used (N_{days}) is the same for both physiological and behavioural data collection. For the three species that were repeated, N values are presented as Season 1 (Season 2) values. Data for T_{aviary} and T_b variables for these species were pooled. $Pant_{50}$ was calculated using panting observations observed across the range of T_{aviary} . The most frequent T_b during the time of day when birds are active but not thermally stressed, i.e. using all T_b recorded during early morning (7:00-10:00) when T_{aviary} is lower, represents T_{bmod} . T_{bmean} was calculated using T_b recorded throughout diurnal period whilst T_{bmax} was the maximum T_b recorded for the species during the hottest period (12:00-19:20). Heterothermy index ($HI_{diurnal}$) expresses variation in T_b accounting for deviation from T_{bmod} and time spent away from T_{bmod} .

pecies	pant ₅₀	N_{Tb} , N_{behav}	N_{days}	T_{aviary} range	Body temperature variables (°C)			
					T_{bmod}	T_{bmean}	T_{bmax}	$HI_{diurnal}$
WBM	36.3	6, 10	7	16.0-41.8	41.4 ± 0.5	41.1 ± 0.7	43.4	0.58 ± 0.16
CGS	36.6	1(4), 11(10)	4(9)	14.6-44.3	42.1 ± 0.7	42.0 ± 0.7	43.9	0.59 ± 0.21
REB	37.4	7, 10	12	17.6-40.5	43.1 ± 0.4	43.0 ± 0.5	45.4	0.47 ± 0.10
WBS	38.3	6, 10	8	17.3-44.3	42.0 ± 0.4	42.1 ± 0.6	44.6	0.59 ± 0.25
CTD	39.1	5(6), 10(6)	8(12)	8.8-41.2	42.4 ± 0.4	42.3 ± 0.7	44.7	0.54 ± 0.12
LAD	43.8	8, 11	12	10.5-40.8	42.0 ± 0.4	42.0 ± 0.6	44.2	0.56 ± 0.12
SOW	44.7	8, 9	13	16.1-40.5	42.8 ± 0.4	42.8 ± 0.6	45.5	0.56 ± 0.19
FCL	46.1	6, 6	12	17.6-40.5	42.8 ± 0.2	42.1 ± 0.5	44.7	0.61 ± 0.16
NAD	–	3(5), 3(5)	8(7)	12.8-41.8	41.6 ± 0.4	41.9 ± 0.8	45.4	0.67 ± 0.22

Table 3: Effect sizes, ([95% lower - upper CIs], t-values) of predictor variables retained in the top model for T_b for each species. Models were fitted to data for the entire diurnal period (07:00-19:20) and for the hottest period of the day (12:00-19:20). Global models tested the effect of aviary temperature (T_{aviary}), mass, time of day (TOD; only for diurnal models) and the interactions between T_{aviary} *mass and T_{aviary} *TOD on T_b . If factors were not present in the top model cells were left blank. Values in bold indicate that 95% CIs do not include zero.

Species	Model	N	T_{aviary} (°C)	Mass (g)	TOD	T_{aviary} *Mass	T_{aviary} *TOD
White-backed Mousebird	diurnal	6	-0.01 [-0.02--0.00] t = 2.29		+		+
	hot	6	0.72 [0.47-0.97] t = 5.63	0.79 [0.43-1.14] t = 4.08		-0.02 [-0.03--0.01] t = -5.72	
Cape Glossy Starling	diurnal	5	0.16 [0.13-0.19] t = 11.10	0.04 [-0.04-0.13] t = 0.99	+	-0.00 [-0.00--0.00] t = -7.8	
	hot	5	0.05 [0.05-0.06] t = 15.36				
African Red-eyed Bulbul	diurnal	7			+		
	hot	7	0.21 [0.14-0.27] t = 6.27	0.23 [0.13-0.34] t = 4.17		-0.01 [-0.01--0.00] t = -5.70	
White-browed Sparrow-Weaver	diurnal	6	0.02 [0.01-0.02] t = 5.39		+		+
	hot	6	0.01 [0.01-0.02] t = 5.13				
Cape Turtle-Dove	diurnal	11	0.02 [0.01-0.02] t = 19.4		+		
	hot	11	0.02 [0.02-0.02] t = 16.66				
Laughing Dove	diurnal	8	-0.01 [-0.02--0.01] t = -6.76		+		+
	hot	8	-0.01 [-0.0--0.00] t = -4.33				
Sociable Weaver	diurnal	8	0.03 [0.02-0.03] t = 9.59		+		+
	hot	8	0.03 [0.03-0.04] t = 13.79				
Fawn-coloured Lark	diurnal	6	-0.02 [-0.03--0.02] t = -7.4		+		+
	hot	6					
Namaqua Dove	diurnal	8	0.16 [0.12-0.20] t = 7.95	0.26 [0.15-0.36] t = 4.64	+	-0.00 [-0.01--0.00] t = -8.97	
	hot	8	0.55 [0.42-0.69] t = 8.42	0.62 [0.47-0.78] t = 7.49		-0.01 [-0.02--0.01] t = -8.45	

birds increased T_b more than larger birds as T_{aviary} increased (Table 3). During the hottest part of the day (12:00-19:20), T_{aviary} was the only significant predictor of T_b for CGS, WBS, SOW, CTD and LAD. No factors emerged as good predictors of T_b for FCL during the hottest portion of the day (Table 3). During the hottest part of the day all species increased T_b with increasing T_{aviary} , except LAD, in which T_b decreased with T_{aviary} ; as with the diurnal analyses, the

Table 4: Differences in T_b between three time of day (TOD) categories (early: 07:00-10:00, mid: 10:00-14:00, aft: 14:00-19:20). Mean $T_b \pm sd$ for the three TOD categories are included. Model outputs* are presented as effect sizes, [95% lower - upper CIs], t-statistic. Values in bold indicate 95% CIs that exclude zero.

Species	mean $T_b \pm sd$			Model output		
	early	mid	aft	early – aft	mid – aft	mid – early
White-backed Mousebird	41.3 ± 0.7	41.2 ± 0.6	41.1 ± 0.6	0.34 [0.27-0.41] t = 10.76	0.06 [0.02-0.10] t = 3.09	-0.28 [-0.33--0.23] t = -10.49
Cape Glossy Starling	42.0 ± 0.7	42.1 ± 0.7	42.2 ± 0.7	0.25 [0.2-0.31] t = 10.82	-0.05 [-0.1--0.01] t = -2.49	-0.31 [-0.36--0.25] t = -13.00
African Red-eyed Bulbul	43.0 ± 0.6	42.8 ± 0.4	43.0 ± 0.4	-0.02 [-0.04-0.01] t = -1.40	-0.20 [-0.27--0.21] t = -17.00	-0.22 [-0.24--0.14] t = -14.50
White-browed Sparrow-Weaver	42.2 ± 0.7	42.0 ± 0.6	42.3 ± 0.5	-0.19 [-0.24--0.13] t = -7.56	-0.33 [-0.38--0.28] t = -14.87	-0.14 [-0.2--0.1] t = -6.06
Cape Turtle-Dove	42.5 ± 0.6	42.1 ± 0.6	42.4 ± 0.7	0.15 [0.12-0.19] t = 11.28	-0.36 [-0.39--0.34] t = -31.23	-0.52 [-0.55--0.49] t = -37.94
Laughing Dove	42.1 ± 0.7	41.7 ± 0.6	42.1 ± 0.6	-0.13 [-0.17--0.9] t = -7.49	-0.42 [-0.46--0.4] t = -29.85	-0.3 [-0.34--0.26] t = -17.91
Sociable Weaver	42.8 ± 0.7	42.5 ± 0.6	42.9 ± 0.6	0.09 [0.04-0.15] t = 3.86	-0.31 [-0.35--0.28] t = -23.3	-0.41 [-0.46--0.36] t = -19.75
Fawn-coloured Lark	42.9 ± 0.6	42.2 ± 0.5	42.7 ± 0.5	-0.32 [-0.38--0.27] t = -13.97	-0.62 [-0.66--0.58] t = -39.41	-0.3 [-0.35--0.25] t = -13.4
Namaqua Dove	41.8 ± 0.8	41.6 ± 0.6	42.3 ± 0.7	-0.68 [-0.73--0.62] t = -28.78	-0.72 [-0.77--0.68] t = -39.1	-0.04 [-0.09-0.01] t = -2.02

* Derived from Tukey post-hoc test using $T_b \sim TOD + T_{aviary}$

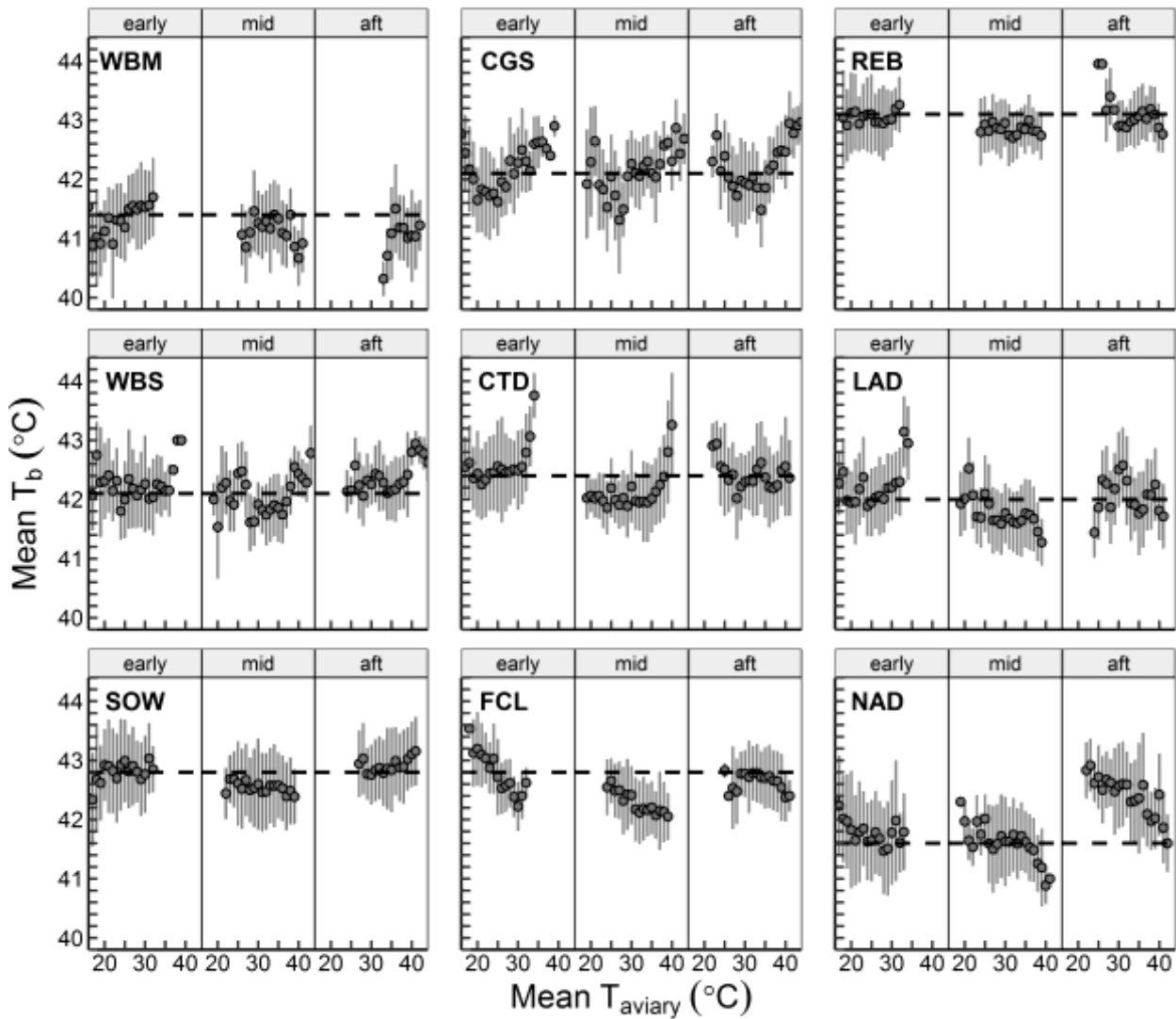


Figure 3: Changes in Mean T_b with increases in mean daily T_{aviary} during 3 times of day (TOD) categories (early: 07:00-10:00, mid: 10:00-14:00, aft: 14:00-19:20). Mean T_b was calculated from all values binned in 1°C intervals of T_{aviary} . Error bars indicate standard deviation. WBM = White-backed Mousebird, CGS = Cape Glossy Starling, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.

magnitude of effect sizes was small with changes of no more than 0.4°C per 10°C increase in T_{aviary} (Table 3). For WBM and NAD mass and the interaction between mass and were also important predictors of T_b with smaller birds increasing T_b more than larger birds as T_{aviary} increased. When this interaction term was removed, T_{aviary} and mass were no longer significant predictors of T_b . The highest T_b recorded during the hottest part of the day was in

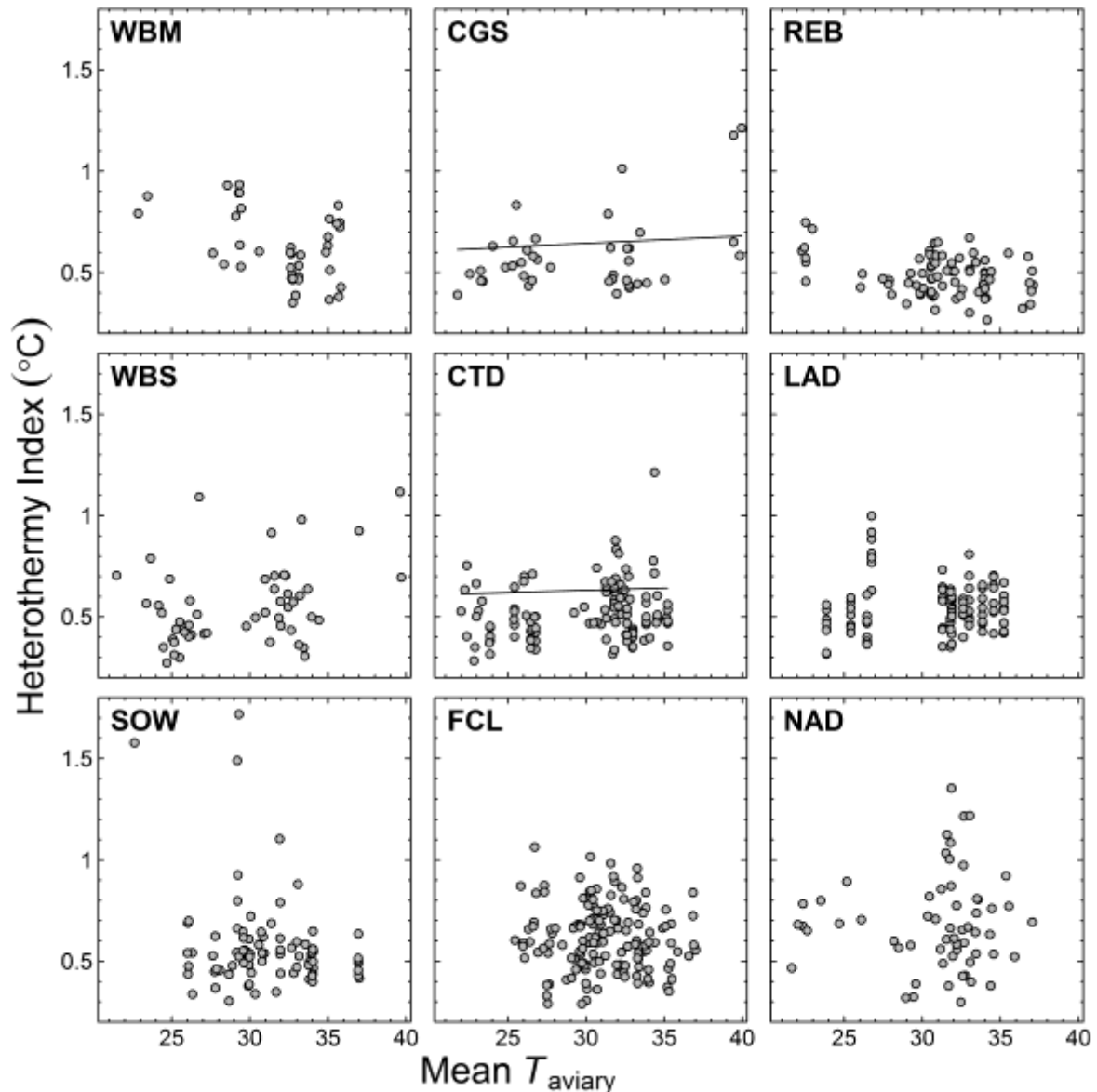


Figure 3: Variation in T_b reflected as heterothermy index (HI) with increases in mean daily T_{aviary} . CGS and CTD were the only species to increase HI with increases in mean T_{aviary} . If the outlier in CTD is removed, the relationship is no longer significant. WBM = White-backed Mousebird, CGS = Cape Glossy, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.

NAD (45.4°C) resulting in the greatest deviation of T_b from T_{bmod} ($T_{bmax} - T_{bmod} = 3.8^\circ\text{C}$; Table 2). In all other species $T_{bmax} - T_{bmod} < 2.8^\circ\text{C}$.

For all species time of day was a significant predictor of T_b . However, diurnal patterns in T_b were species-specific and the magnitude of the difference in T_b between the three TOD categories was small (Table 4). Higher early morning T_b s were maintained by WBM compared to the afternoon. During midday T_b decreased below early morning T_b , with small but significant differences in T_b between midday and afternoon periods (Table 4, Figure 2). A decrease in T_b during midday compared to early mornings and the afternoons was observed in CGS, WBS, SOW, LAD, CTD and FCL (Table 4, Figure 2). During the afternoon, T_b in WBS, LAD and FCL was significantly higher than in the morning, whilst CGS, CTD and SOW had highest T_b early in the morning (Table 4). The T_b of Namaqua doves did not differ between early mornings and midday, but T_b was significantly higher ($\sim 1^\circ\text{C}$ higher than T_{bmod}) during the afternoons (Table 4, Figure 2). There was an important interaction between T_{aviary} and TOD in WBM, WBS, SOW, LAD and FCL (Figure 2). WBS and SOW showed increases in T_b with increasing afternoon temperatures, whilst WBM, LAD and FCL decreased T_b with increasing afternoon temperatures (Figure 2). For most species, HI was independent of T_{aviary} (Figure 3). CGS and CTD showed a significant increase in HI with increasing T_{aviary} , however removal of the outlier for CTD resulted in the relationship no longer being significant in this species. In CGS, the magnitude of the effect was small with only a $\sim 0.2^\circ\text{C}$ change in HI over a 10°C increase in mean T_{aviary} (LMM: 0.02°C , [0.01-0.03], $t = 3.2$; Figure 3).

3.2. Behaviour

Unexpectedly, activity was not correlated with T_{aviary} in most species (Figure 4). WBM, CGS and SOW significantly decreased time spent active as T_{aviary} increased, while LAD increased activity as T_{aviary} increased. In contrast, panting behaviour increased with

increasing T_{aviary} for most species (Figure 5). Heat dissipation thresholds ranged from $\text{pant}_{50} = 36.3^{\circ}\text{C}$ for WBM up to $\text{pant}_{50} = 46.1^{\circ}\text{C}$ in FCL. NAD were only observed panting twice, at $T_{\text{aviary}} > 38.8^{\circ}\text{C}$. Thus, there were too few panting data to describe the relationship

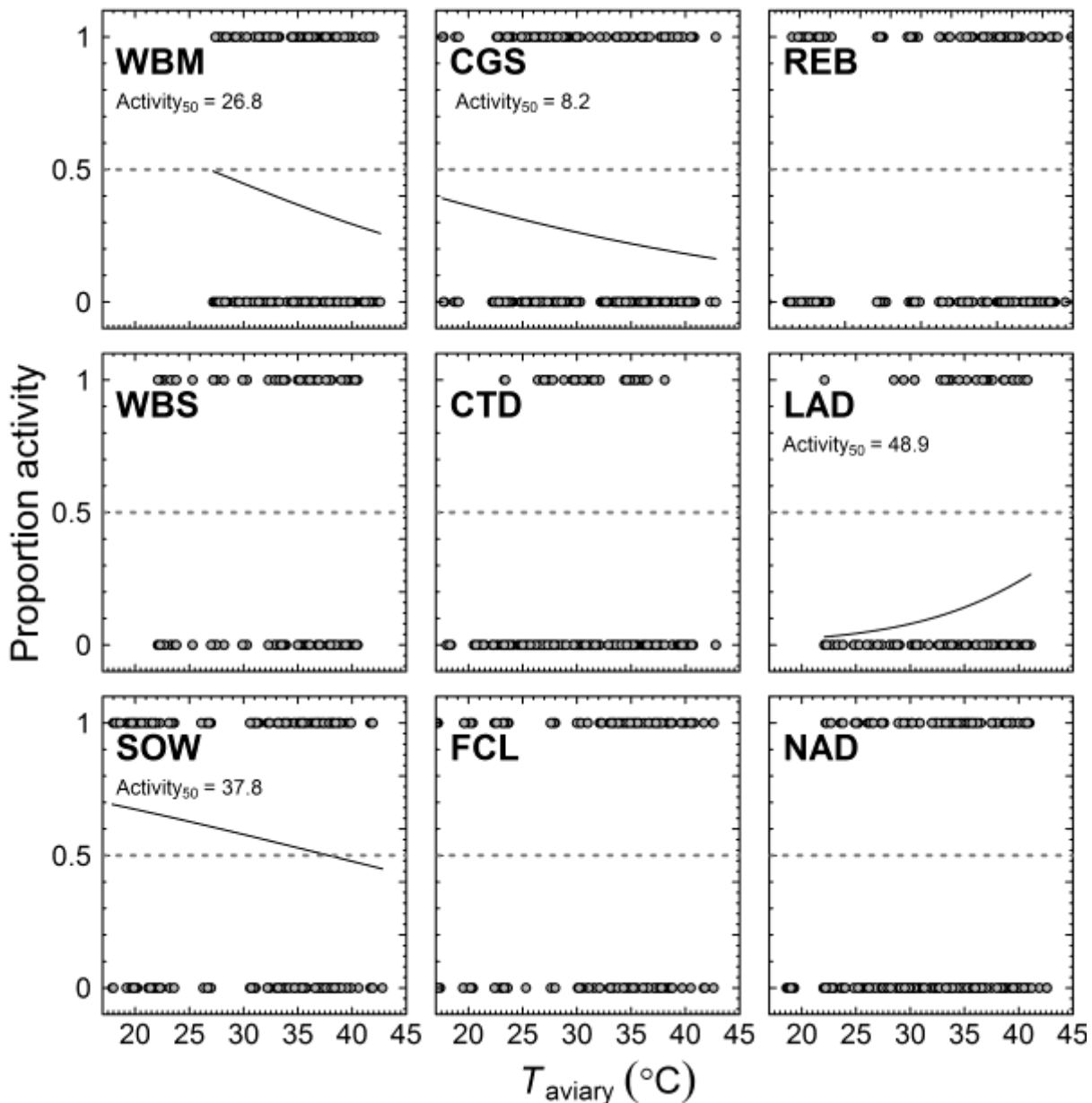


Figure 4: Proportion of time spent active as T_{aviary} increases, where 1 = active and 0 = inactive. Activity_{50} , the T_{aviary} at which 50% of observed individuals are active, is displayed for species where the logistic regression models are significant. Models for REB did not converge. In most species activity is independent of T_{aviary} . Several species (WBM, CGS, SOW) decrease time spent active as T_{aviary} increases while LAD increase activity as T_{aviary} increases. WBM = White-backed Mousebird, CGS = Cape Glossy, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.

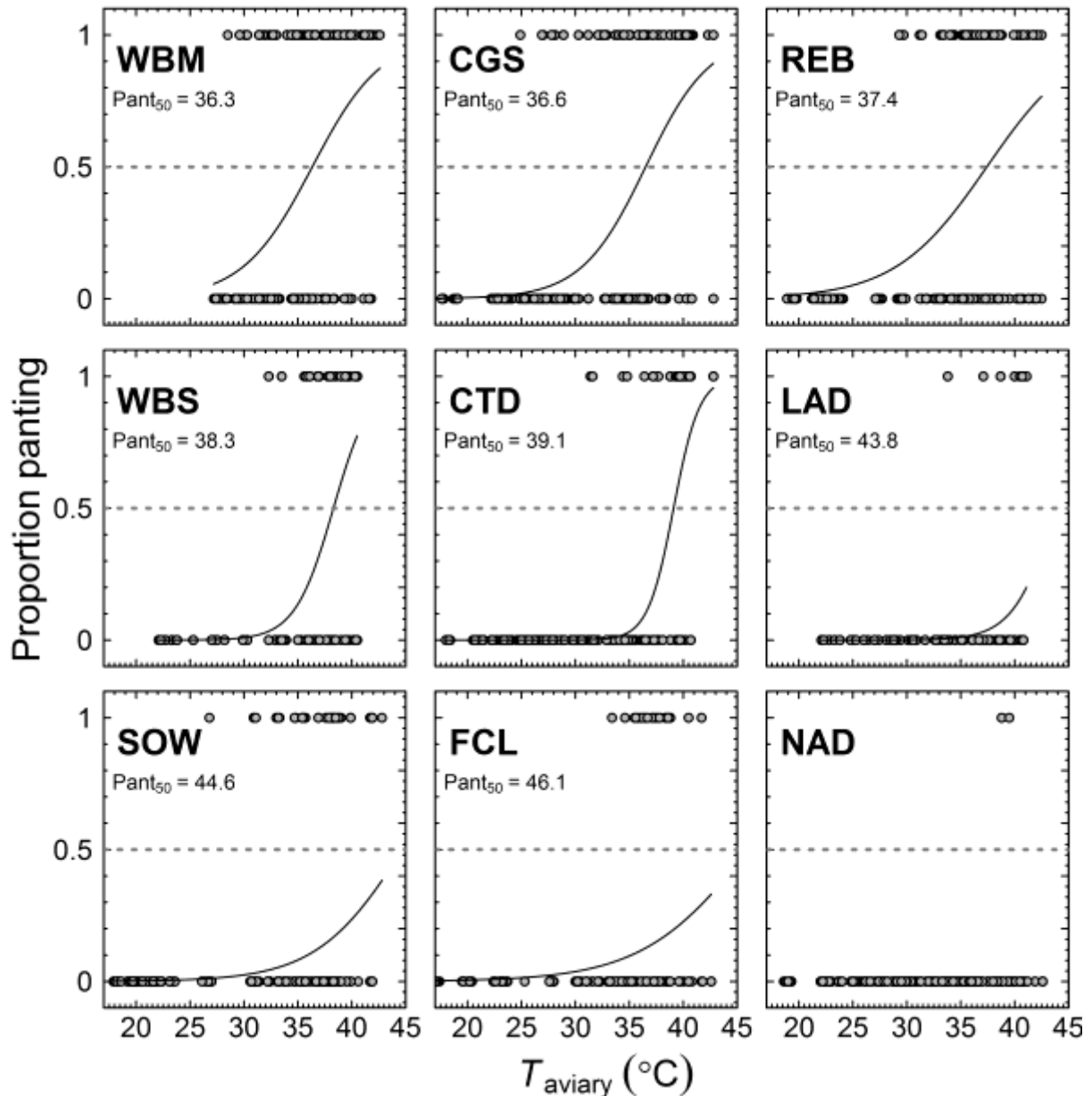


Figure 5: Proportion of time spent heat dissipating with increases in T_{aviary} . $Pant_{50}$ is calculated as the T_{aviary} at which 50% of observed individuals are displaying panting/gular fluttering. Gular fluttering observations in NAD were insufficient to calculate a significant $pant_{50}$. WBM = White-backed Mousebird, CGS = Cape Glossy, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.

between panting and T_{aviary} for this species (Figure 5). Moreover, neither T_{bmod} nor mass correlated significantly with $pant_{50}$. Shade-seeking behaviour was strongly temperature-dependent in all species excepting CTD and LAD, which were mostly confined to shady microsites in aviaries regardless of T_{aviary} . However, the inflection points and slopes of the binomial regressions varied widely between species (Figure 6).

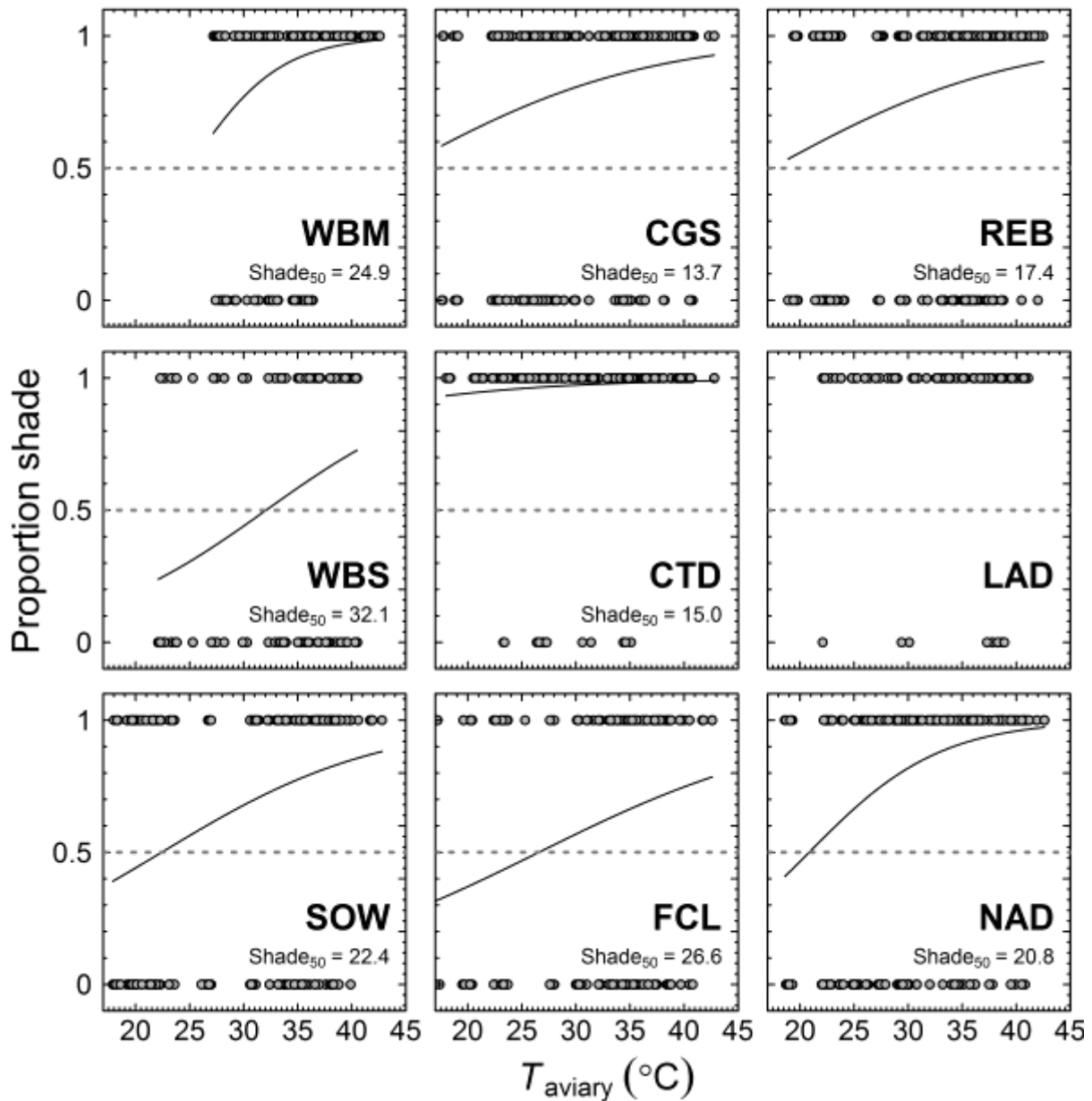


Figure 6: Proportion of time spent in the shade with increases in T_{aviary} , where observations of birds in 1 = dappled or full shade and 0 = sun. Shade use increase with T_{aviary} in all species except CTD and LAD, which spent most of the time in the shade. WBM = White-backed Mousebird, CGS = Cape Glossy, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.

4. Discussion

Our results reveal that arid-zone birds held under semi-natural conditions show considerable interspecific variation in T_b patterns at high T_{air} , with small but significant increases in T_b with T_{air} in most species, but some showing the opposite pattern. In addition, although shade-seeking and panting behaviour increased with T_{air} in almost all

species, the slopes were variable. Our data suggest patterns of thermoregulation that are strongly species-specific, with each species modulating behavioural and physiological aspects of thermoregulation differently.

Our study species generally had higher $T_{b\text{mod}}$ than typical avian active $T_{b\text{mean}}$ values (Prinzinger *et al.* 1991, Figure 1). Passerines in general appear to have slightly higher $T_{b\text{mod}}$ than columbids ($42.6 \pm 0.6^\circ\text{C}$ and $42.0 \pm 0.6^\circ\text{C}$, respectively), also consistent with the conclusions of Prinzinger *et al.* (1991). One potential functional basis for the higher $T_{b\text{mod}}$ of passerines may concern their basal metabolic rates being 12% higher than those of non-passerine orders (Londoño *et al.* 2015). Of the nine species we investigated, free-ranging T_b patterns during hot weather have been examined previously in only WBS (Smit *et al.* 2013), work demonstrating that T_b patterns may vary both within and between populations under changing environmental conditions. In the present study, WBS showed higher summer $T_{b\text{mod}}$ ($42.0 \pm 0.4^\circ\text{C}$) than previously recorded in free-ranging desert ($41.5 \pm 0.2^\circ\text{C}$) and semi-desert ($40.2 \pm 0.3^\circ\text{C}$) populations (Smit *et al.* 2013) despite our study population being only ~60km west from the desert population studied by the latter authors. The higher $T_{b\text{mod}}$ value for WBS in the present study could reflect inter-population variation in $T_{b\text{set}}$; but an alternative explanation is that in our study, captive conditions resulted in stress-induced hyperthermia [SIH; elevated T_b in response to stress (Bakken *et al.* 1999, Carere *et al.* 2001, Keeney *et al.* 2001)] compared to free-ranging populations. Particularly for species that naturally exist solitarily or in pairs, captivity may encourage more frequent SIH due to stressful forced interactions (Cunningham *et al.* 2017). This may explain the higher $T_{b\text{mod}}$ in several of our species, not only WBS. Regardless, our $T_{b\text{mod}}$ data are still more likely to reflect $T_{b\text{set}}$ values of free-ranging birds as they are calculated from continuous T_b records from birds experiencing natural fluctuations in T_{air} , whereas most previous T_b data were collected during laboratory studies.

Across our sample of species, thermoregulatory patterns appear to be species-specific. In most species, there were small but significant increases in T_b with increasing T_{air} , but in three species T_b decreased. In most species, T_b responses to increasing T_{air} were also dependent on time of day, but the direction varied among species. This variability, together with the observation that in some species, T_b showed no obvious response to increasing T_{air} (e.g. FCL) whereas in others T_b decreased with increasing T_{air} (e.g. LAD) during the hottest part of the day, leads to several non-mutually exclusive explanations for the large interspecific variation in observed responses.

First, most species did not make prolonged use of facultative hyperthermia (defined here as T_b exceeding T_{bmod} by 2°C or more) over the range of T_{air} experienced during this study (Figure 7, Appendix). Increasing T_b with T_{air} is a common physiological response in birds, thought to reduce evaporative water loss at high T_{air} (Tieleman & Williams 1999). Some species, e.g. SOW, CGS and WBS, did show small increases in T_b above T_{bmod} , but only NAD made use of facultative hyperthermia in the afternoons. The high afternoon T_b of NAD illustrates the importance of time of day as a predictor of hyperthermia, as in most species there was little overall response in T_b to increasing T_{air} (Figure 7, Appendix). The more frequent hyperthermia in NAD is the pattern expected for a species closer to the generalist end of the thermal specialist/generalist continuum, where deviations in T_b from T_{bset} are thought to have fewer negative effects on performance. However, this is confounded by hyperthermia shown in NAD being restricted to lower afternoon T_{air} , suggesting an avoidance of high T_b during the hottest times when hyperthermia would, theoretically, be most beneficial.

Tolerance of T_b values well above T_{bmod} also does not appear to be restricted to species with low T_{bmod} . For example, of the two species with the lowest T_{bmod} values in this study, WBM avoided hyperthermia, but NAD showed facultative hyperthermia during the afternoons. Species in which T_b exceeded T_{bmod} also generally had higher HI, but

again NAD was the only species to show significantly higher variation in T_b compared to other species. However, the distinct lack of response in HI to increasing T_{air} in most species suggests that the range of T_{air} s experienced in this study, or the free availability of water (see below), did not require the species we examined to allow a large variation of T_b , complicating the process of evaluating links between hyperthermia use and shifts in thermal performance breadth. Despite the small magnitude of effect sizes in T_b patterns, these effects are still likely to be biologically meaningful at very high T_{air} when T_b approaches lethal limits, affecting rates of biochemical reactions and enzymatic structure (Hochochka & Somero 2002, Angilletta *et al.* 2010). The overall variation in T_b patterns between species highlights how complex and poorly understood is the ecological significance of avian facultative hyperthermia.

A second potential explanation for the large interspecific variation in observed responses is that behavioural adjustments accompanying changes in T_b with increasing T_{air} were also variable, and species differed in their combinations of hyperthermia tolerance and behavioural changes in activity, panting and shade-seeking associated with thermoregulation. At high T_{air} all species sought out shady microsites in the aviaries, however T_{air} values at which shade-seeking took place varied widely (shade₅₀ range: 13.7 – 32.1°C) and were clearly species-specific (Figure 7). Similarly, activity patterns between species differed (activity₅₀ range: 8.2 – 48.9°C). Three species (WBM, CGS and SOW) reduced activity with increasing T_{air} , but most species showed no change in activity levels. Generally, shade-seeking and reductions in activity buffer against physiological costs associated with evaporative cooling and hyperthermia by reducing exposure to higher heat loads (Dawson 1954, Wolf 2000, Angilletta *et al.* 2010; Boyles *et al.* 2011a). During hot weather birds either reduce foraging effort, limiting activity to the shade to avoid lethal hyperthermia, or continue foraging and thereby increase exposure to lethal hyperthermia and dehydration (Williams *et al.* 1999, Cunningham *et al.* 2015). We might therefore

expect hyperthermia-avoiding species to adjust behaviour to a greater extent at high T_{air} . While this may be true for some species, (i.e. WBM), it is clearly not the case for all. For example, LAD avoided hyperthermia, despite increasing activity with increasing T_{air} and only initiating panting at $T_{air}s > 37^{\circ}C$ (Figure 6). One possible explanation for the ability of LAD to maintain T_b around T_{bmod} at high T_{air} concerns the mechanism of evaporative cooling. Previous studies suggest that predominance of CEWL may provide a more efficient physiological basis to maintain T_b below T_{air} , compared to taxa relying on panting (e.g. passerines) to dissipate heat (Marder & Arieli 1988, McKechnie & Wolf 2004). For example, under laboratory conditions columbids show more gradual increases in T_b at high T_{air} (McKechnie *et al.* 2016) than passerines (Whitfield *et al.* 2015). In our study, the lower T_{bmod} during hot weather of the two smaller dove species may reflect the greater efficiency of CEWL compared to panting in the passerines, as more efficient evaporative cooling pathways may result in lower T_b s in general. The lack of reduction in activity with T_{air} in most species is, however, supported by previous observations in the Kalahari, where few species have been shown to reduce activity significantly at high T_{air} $39^{\circ}C$ compared to milder T_{air} of $29^{\circ}C$, with most species reducing activity by only 10-20% at high T_{air} (Smit 2013).

Finally, freely available drinking water during the course of the study may have ameliorated physiological trade-offs between increasing evaporative cooling to maintain T_b below lethal limits and avoiding dehydration by conserving water (Dawson 1954), thereby creating a situation where T_b was regulated more precisely than it might have been in free-ranging conspecifics. The *ad libitum* water supply may partially explain the negative or absent T_b response to increasing T_{air} in some species and only small increases in T_b with T_{air} in the remaining species (Table 3). During the present study, water and food was easily accessible and the energy needed to acquire it presumably a fraction of that under natural conditions for free-ranging birds. Consequently, birds may have drunk more

frequently, permitting more evaporative cooling to take place compared to conditions with higher dehydration risk. This notion is supported by the observation that even species generally relying on preformed water as their main water source were regularly observed drinking water in the aviaries (WBM, WBS, SOW and FCL). Therefore, we argue that the provision of *ad libitum* water likely relaxed the dehydration-thermoregulation trade-off usually faced by free-living arid zone birds. Importantly, this easy access to water also explains the general lack of hyperthermia despite $T_{\text{air}} > 40^{\circ}\text{C}$. We were thus unable to identify any links between pant_{50} and the use of hyperthermia. Species with high pant_{50} did not necessarily show high T_{bmod} or an aversion for tolerating hyperthermia compared to species with low pant_{50} . Smit et al 2016 suggested that larger birds, which have significantly lower pant_{50} , should make more extensive use of evaporative cooling to avoid hyperthermia. However, freely available water may have influenced the relative use of evaporative cooling among species in this study, such that the relationship between pant_{50} and body mass was absent. Overall this suggests that, across the T_{air} range investigated here, pant_{50} may not be a good indicator of physiological heat stress.

In conclusion, the variation in T_{bset} among our study species and the difficulty in drawing any general patterns from behavioural and physiological responses to increasing T_{air} emphasises the need for species-specific studies to understand a species' T_{b} regulation. Many factors influence regulation of T_{b} in free-living birds, including factors we were not able to consider in this study. For example, recent research indicates that social status influences T_{b} patterns, with dominant birds regulating more stable T_{b} than subordinate individuals as T_{air} increases (Cunningham *et al.* 2017). Additionally, the freely available water and food resources birds had access to during this study greatly underestimate the challenges free-ranging desert birds face in terms of balancing water and energy. As such, despite our attempts to make captive conditions as natural as possible, thermoregulatory patterns are likely to vary to an even greater extent

intraspecifically between captive and wild populations. Further, interspecific thermoregulatory patterns will likely also vary more as unequal foraging-dehydration trade-offs persist among wild species due to variation in their dependency on free-standing water and/or preformed dietary water.

Despite the difficulties of extrapolating data from captive birds to free-ranging individuals, captive studies do offer certain benefits including the opportunity for close and continuous behavioural and physiological observations and the practicability to experimentally manipulate resource availability. Little is currently known about how avian thermoregulation is adjusted when water availability is reduced. Captive studies may be the only way to effectively investigate and answer questions such as these and therefore are key to evaluating the usefulness of HDB thresholds to assess species vulnerability to increasing T_{air} , and to further understand the complexities of thermoregulation in hot, arid environments.

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Appendix

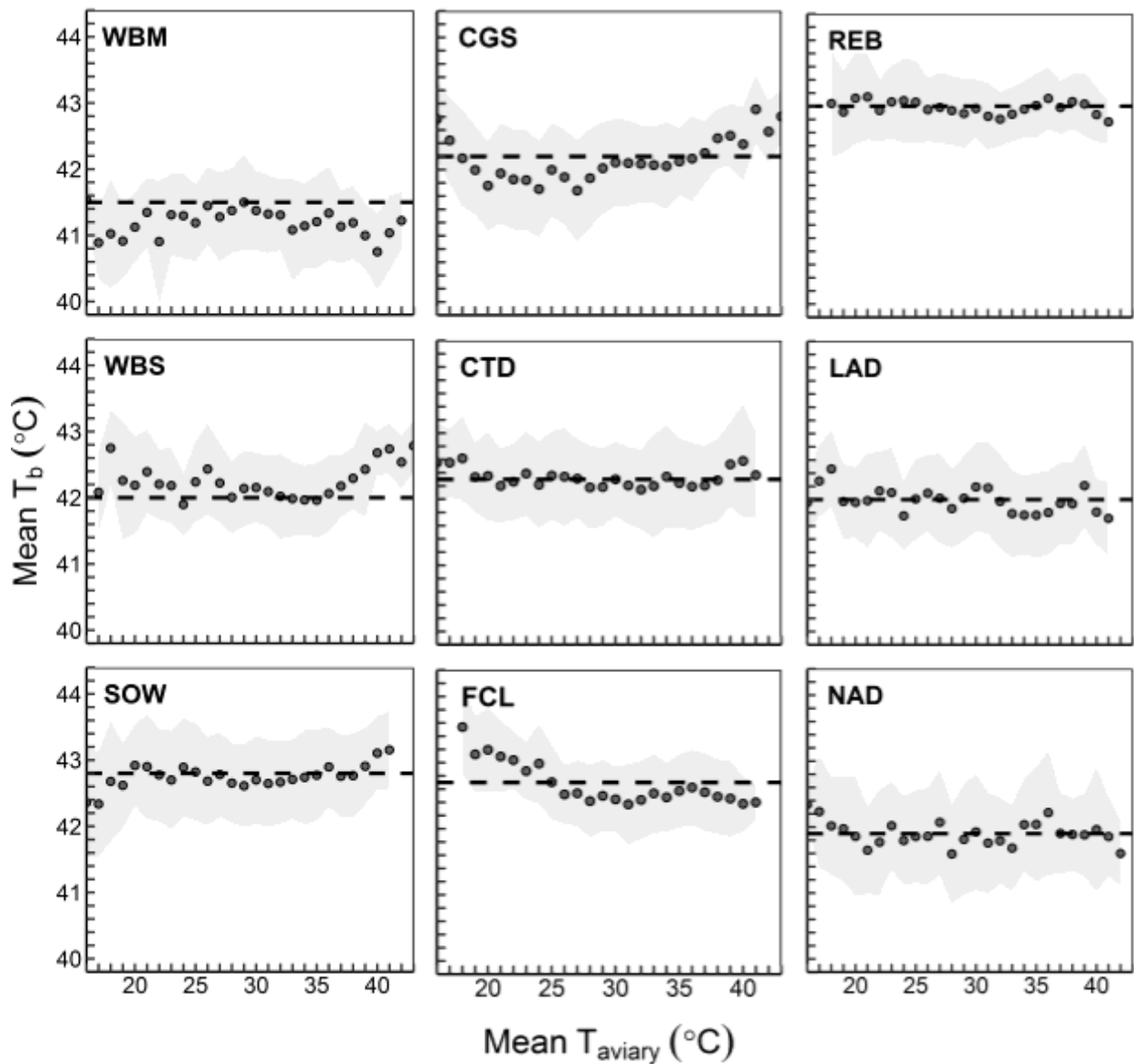


Figure 7: Mean increases in T_b per degree (°C) increase in T_{aviary} for each species observed. White-backed Mousebirds (WBM), Laughing Doves (LAD) and Fawn-coloured Larks (FCL) decreased T_b with increasing T_{aviary} whilst Cape Glossy Starling (CGS), White-browed Sparrow-Weaver (WBS), Cape Turtle-Dove (CTD), Sociable Weaver (SOW) and Namaqua Dove (NAD) increased T_b with increasing T_{aviary} . African Red-eyed Bulbul (REB) did not adjust T_b with increasing T_{aviary} . Grey ribbons represent standard deviation while dashed lines represent species $T_{b\text{mod}}$.

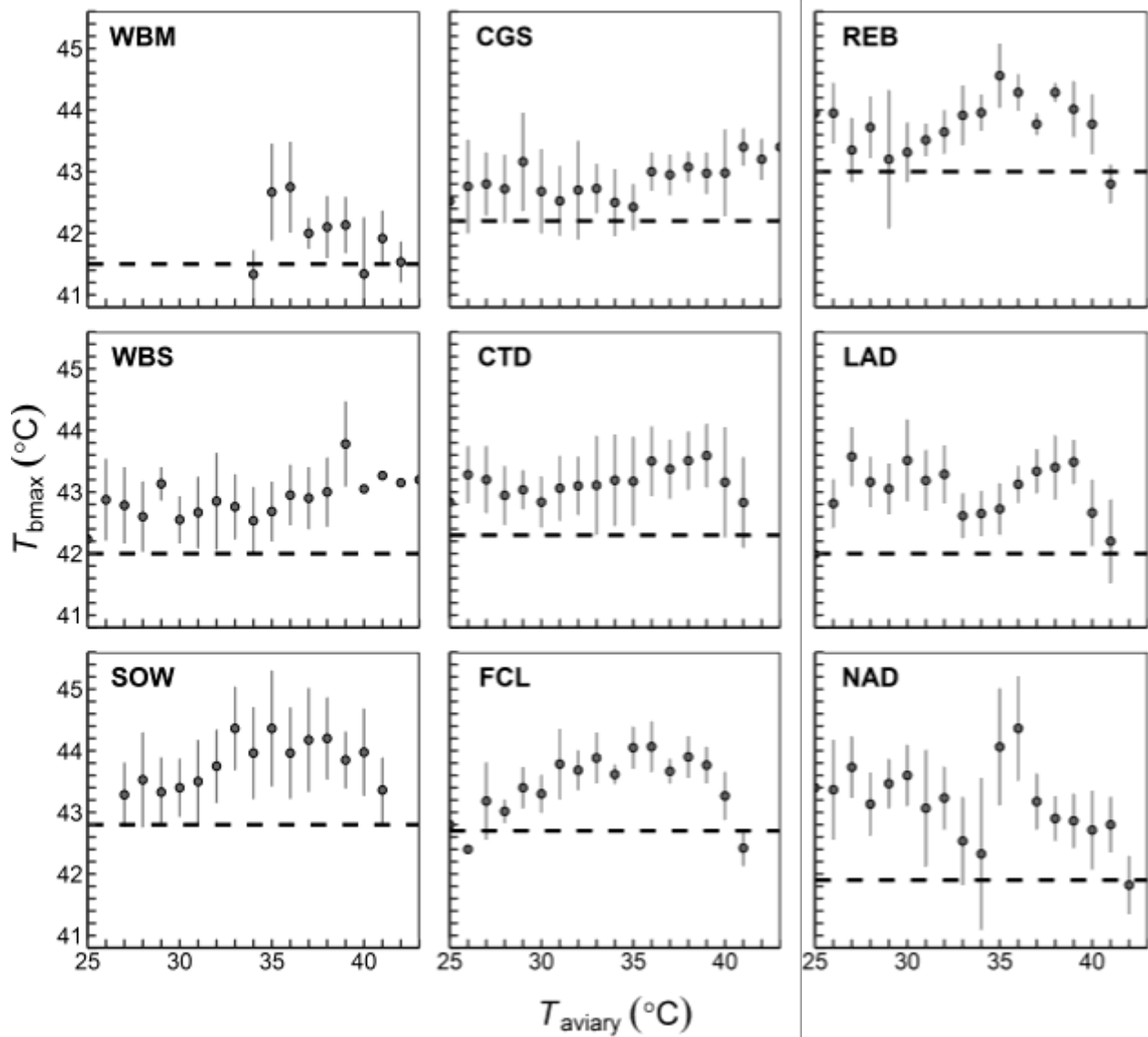


Figure 8: Mean increases in T_{bmax} per degree (°C) increase in T_{aviary} for each species observed. Error bars represent standard deviation while dashed lines represent species T_{bmod} . WBM = White-backed Mousebird, CGS = Cape Glossy Starling, REB = African Red-eyed Bulbul, WBS = White-browed Sparrow-Weaver, CTD = Cape Turtle-Dove, LAD = Laughing Dove, SOW = Sociable Weaver, FCL = Fawn-coloured Lark, NAD = Namaqua Dove.