

RESEARCH ARTICLE

Avian thermoregulation in the heat: evaporative cooling capacity and thermal tolerance in two Australian parrots

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ABSTRACT

Avian orders differ in their thermoregulatory capabilities and tolerance of high environmental temperatures. Evaporative heat loss, and the primary avenue whereby it occurs, differs amongst taxa. Although Australian parrots (Psittaciformes) have been impacted by mass mortality events associated with extreme weather events (heat waves), their thermoregulatory physiology has not been well characterized. We quantified the upper limits to thermoregulation under extremely hot conditions in two Australian parrots: the mulga parrot (*Psephotellus varius*; ~55 g) and the galah (*Eolophus roseicapilla*; ~265 g). At air temperatures (T_a) exceeding body temperature (T_b), both species showed increases in T_b to maximum values around 43–44°C, accompanied by rapid increases in resting metabolic rate above clearly defined upper critical limits of thermoneutrality and increases in evaporative water loss to levels equivalent to 700–1000% of baseline rates at thermoneutral T_a . Maximum cooling capacity, quantified as the fraction of metabolic heat production dissipated evaporatively, ranged from 1.71 to 1.79, consistent with the known range for parrots, similar to the corresponding range in passerines, and well below the corresponding ranges for columbids and caprimulgids. Heat tolerance limit (the maximum T_a tolerated) ranged from 44 to 55°C, similar to the range reported for passerines, but lower than that reported for columbids and caprimulgids. Our data suggest that heat tolerance in parrots is similar to that in passerines. We argue that understanding how thermoregulatory capacity and heat tolerance vary across avian orders is vital for predicting how climate change and the associated increase in frequency of extreme weather events may impact avian populations in the future.

KEY WORDS: Body temperature, Evaporative water loss, Hyperthermia, Psittaciformes, Respiratory evaporative water loss, Resting metabolic rate

INTRODUCTION

Arid environments dominate the Australian landscape, covering almost half of the continent's total land area (Fisher et al., 1972). These environments present significant physiological and life

history challenges for organisms. High air temperatures combined with intense solar radiation and limited surface water mean that use of evaporative cooling to defend normothermic body temperatures (T_b) must be balanced against the risk of dehydration (Dawson, 1954; Dawson and Bartholomew, 1968; Dawson and Schmidt-Nielsen, 1964; Serventy, 1971). Birds living in subtropical deserts may need to defend a T_b setpoint 15°C or more below their operative temperature (Bakken, 1976; Williams and Tieleman, 2005; Wolf and Walsberg, 1996; Wolf et al., 2000). They accomplish this using a combination of evaporative heat loss assisted by associated behaviors such as panting and gular fluttering, avoiding heat loads by reducing activity and seeking cooler microclimates, and tolerating mild hyperthermia (Albright et al., 2017). Even at moderate environmental temperatures, the demands of thermoregulation may constrain multiple components contributing to fitness, including foraging and body condition (du Plessis et al., 2012), nestling provisioning and growth rates (Cunningham et al., 2013), and nest predation risk (Tieleman et al., 2008).

The potential impacts of anthropogenic climate change on the thermoregulatory demands of birds, and thus population persistence and biodiversity, is a question of considerable conservation interest (McKechnie et al., 2012; McKechnie and Wolf, 2010). Aside from the potential sub-lethal impacts on life history mentioned above, extreme heat events can cause large-scale mortality events in bird populations. Current climate models predict that heat waves will become longer, more frequent and more intense as global surface temperatures increase, and the deserts of Australia are expected to warm by >4°C by the end of this century (IPCC, 2011). Deaths of birds during extremely hot weather are not a new occurrence in Australia, having been reported as early as the late 18th century (reviewed by McKechnie et al., 2012); however, projected warming scenarios will result in higher frequency of these events (McKechnie and Wolf, 2010). More recent events have included the deaths of thousands of budgerigars (*Melopsittacus undulatus*) and zebra finches (*Taenopygia guttata*) at the Overlander Roadhouse ~500 km north of Perth, Western Australia, during a 2009 heat wave that was associated with $T_a > 45^\circ\text{C}$ for several consecutive days (McKechnie et al., 2012), and the deaths of hundreds of endangered Carnaby's black cockatoos (*Calyptorhynchus latirostris*) during a single-day 2010 heat wave in Western Australia with T_a exceeding 47°C (Saunders et al., 2011). Low (2011) cites other recent reports of bird mortality events in other areas of Australia, including deserts in southwestern Queensland. Populations of mammals have also experienced heat-related mortality events, with more than 30,000 flying foxes (*Pteropus* spp.) having perished in heatwaves since 1994 in colonies along the eastern coast of Australia (Welbergen et al., 2008). These reports make it clear that a better picture of how heat tolerance and evaporative cooling capacity vary among and within avian taxa is vital for predicting how arid-zone avifauna will respond to a hotter and drier environment.

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Parrots (order Psittaciformes) represent a major element in the avifauna of the vast arid interior of Australia, where these mostly diurnal birds cope with maximum summer air temperatures that may reach 47–52°C (Serventy, 1971). There is a long history of ecophysiological studies of metabolism and evaporative water loss in parrots, including a number of Australian species, but many of these studies were focused on thermoregulation at moderate T_a within and below the thermoneutral zone (Burton et al., 2008; Dawson, 1965; Macmillen and Baudinette, 1993; Williams et al., 1991; Zungu et al., 2013), or designed to measure these parameters during exercise (Tucker, 1968). There have been fewer studies of metabolism and evaporative water loss in parrots at high T_a (Dawson and Fisher, 1982; Greenwald et al., 1967; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976). These studies reveal that parrots respond to high T_a with the increases in evaporative water loss and metabolic rate typical of many birds, using panting and lingual flutter (analogous to gular flutter in other taxa) to augment rates of evaporative water loss (Dawson and Fisher, 1982; Greenwald et al., 1967; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976). However, it is not clear whether these studies elicited maximum heat tolerance and evaporative cooling capacities in the study individuals used, or whether greater heat tolerance is possible under different experimental conditions. In Dawson and Fisher's (1982) study of galahs, for instance, the dewpoint of air in chambers varied between 14 and 18°C, potentially impeding evaporative heat loss from birds exposed to high T_a (Gerson et al., 2014; Lasiewski et al., 1966; Smith et al., 2017).

Here, we examined the thermoregulatory capacities of two species of desert-dwelling Australian parrots exposed to levels of heat stress typical of their natural habitats. We quantified heat tolerance and evaporative cooling capacity using the same methods as those employed in a number of recent studies spanning several avian orders (McKechnie et al., 2017, 2016a,b; O'Connor et al., 2017; Smith et al., 2015, 2017; Talbot et al., 2017; Whitfield et al., 2015). We used heat-acclimatized, wild birds to ask: (1) what are the metabolic and evaporative water loss rates in these parrot species and how do they respond to increasing air temperatures and during extreme heat stress; (2) what is the maximum thermal gradient ($T_a - T_b$) that these species can maintain during heat exposure; (3) what is the magnitude of hyperthermic responses and what are the limits of heat tolerance in these parrot species; and (4) to what degree does panting enhance the efficiency of heat dissipation?

MATERIALS AND METHODS

Study species and site

We measured heat tolerance and evaporative cooling capacity in two Australian parrot species: the mulga parrot [*Psephotellus varius* Clark 1910, Psittaculidae; mean±s.d. body mass (M_b)=54.6±4.4 g, $n=17$, 7 female, 10 male] and the galah [*Eolophus roseicapilla* (Vieillot 1817), Cacatuidae; $M_b=266.3±30.2$ g, $n=7$, sex not determined].

The study took place at BirdLife Australia's Gluepot Reserve, South Australia (33°46'S, 140°07'E), between 30 January and 16 March 2014. Birds were captured using mist nets and were initially held in cloth bags before being transported to a field laboratory. All birds used in the study were adults and appeared to be in good condition. Sample sizes used depended on the number of birds captured. No individuals showing evidence of a brood patch were used. Measurements took place on the same day as each individual was captured. Birds were held in cages constructed of shade cloth with water available *ad libitum*. Birds were always offered water before and after experimental measurements, and a feeding tube

attached to a syringe was used to introduce 1–10 ml of water directly into the crop if the birds did not drink while in cages (administered to one mulga parrot before measurements, and four mulga parrots and one galah after measurements). Measurements typically lasted 2–3 h, resulting in M_b loss (expressed as a percentage of initial M_b at the start of measurements) of 2.9±2.4% in mulga parrots and 6.3±1.1% in galahs. Time in captivity did not exceed 24 h, after which birds were released at the site of capture.

Habitats at Gluepot Reserve consist of summer, red and yorrell mallee scrub and black oak woodland. The climate is hot and arid, with a mean annual precipitation of 276±96 mm. Maximum T_a during January (the hottest month) averages 33.8±5.7°C, and maximum T_a exceeds 40°C on 12.9±5.2 days year⁻¹ (weather records for 2000–2016 obtained from Bureau of Meteorology, www.bom.gov.au).

All experimental procedures were approved by the Animal Ethics Committees of the University of Adelaide (S-2013-151A) and the University of Pretoria (EC054-16), and the Institutional Animal Care and Use Committee of the University of New Mexico (12-1005370-MCC). Birds were captured under a permit issued by the Department of Environment, Water and Natural Resources of South Australia (E26141-2), and work on the Gluepot Reserve was done with permission from BirdLife Australia.

Measurements of metabolism, evaporative water loss and body temperature

Rates of CO₂ production (\dot{V}_{CO_2}) and evaporative water loss (EWL) were determined using a flow-through respirometry system. The respirometry chamber was a transparent plastic container (5 liters with maximal external dimensions of approximately 22×25×12 cm) modified by the addition of ports for incurrent and excurrent air flow and a thermocouple. The bird rested on a plastic mesh platform 5 cm above a 2 cm layer of medium weight mineral oil, an arrangement that trapped excreta and prevented oiling of feather surfaces. The chamber was housed in an insulated ice chest in which air temperature was controlled to within ±0.5°C with a Peltier unit (AC-162 Peltier-Thermoelectric Air Cooler and TC-36-25-rs232 controller, TE Technology, Traverse City, MI, USA). Dry air was produced by pushing compressed air through a membrane air dryer (Champion® CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA) or a calcium sulfate desiccant column (W. A. Hammond Drierite Co., Xenia, OH, USA). The dry air stream pushed into the respirometry chamber was regulated using mass flow controllers [50 or 100 SLPM (standard liters per minute) range] with an accuracy of ±0.8% of the reading ±0.2% of the full scale (Alicat Scientific Inc., Tucson, AZ, USA). Mean flow rate at which samples were obtained was 25.8±13.5 SLPM, but ranged from 10 to 65 SLPM. Sub-samples of incurrent and excurrent air were directed through a CO₂/H₂O analyzer (model LI-840A, LICOR, Lincoln, NE, USA) calibrated as described in Whitfield et al. (2015). Prior to placement in the chamber, each bird was hooded and briefly restrained (approximately 20 s) while a temperature-sensitive passive integrated transponder (PIT) tag (model TX1411BBT, Biomark, Boise, ID, USA) was injected into the abdominal cavity through an antiseptically prepared skin site (McKechnie et al., 2017, 2016b; Smith et al., 2015, 2017; Talbot et al., 2017). A droplet of cyanoacrylate adhesive closed the needle puncture site and the bird was released bearing the tag. The technique involving brief restraint was deemed less stressful to the bird than employing anesthesia. Body mass was measured to ±0.1 g (scale model V31XH2, Ohaus, Parsippany, NJ, USA). An infrared light and video camera allowed continuous observation of the

subject bird in the darkened ice chest. A bird was considered to have tolerated this intervention well if it demonstrated escape attempts while being placed into the chamber, engaged in exploration of the chamber, then settled into quiet, but alert posture with eyes open and only shifted position slightly or moved the head to look about the chamber. Core body temperature (T_b) was recorded every 10 s from a transceiver (Biomark FS2001, Boise, ID, USA), placed within the ice chest, that interrogated the PIT tag. Chamber temperature (T_a) was continuously monitored with a type T thermocouple (TC-2000 thermocouple reader, Sable Systems International, Las Vegas, NV, USA). Respirometry chamber CO_2 and humidity values were recorded once each second via an A-D converter (UI-2, Sable Systems International) and data were captured on a laptop computer using Expedata (version 1.4.15, Sable Systems International).

During each trial the bird was exposed initially to a T_a (30–35°C) approximating thermoneutrality as defined in earlier studies (Dawson and Fisher, 1982; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976; Williams et al., 1991). When the bird was calm, as indicated by $\text{CO}_2/\text{H}_2\text{O}$ values that had reached a nadir and T_b and T_a were stable for approximately 10 min, the bird was then exposed to higher T_a from 40°C or higher upward in 2°C increments over a period of 1–3 h. Dry air flow rate was adjusted to maintain chamber water vapor values <5.0 ppt (dew point <−5°C) to avoid impairing evaporative water loss because of increased chamber humidity (Lasiewski et al., 1966) and help to keep the bird calm. Flow rates of up to 65 SLPM were required to maintain acceptable water vapor pressure levels as the birds increased evaporation with rising T_a . Calculation of metabolic rate from CO_2 production rather than O_2 utilization is more reliable with higher flow rates. The data used for analysis were taken after 5–10 min of stable T_b at a stable T_a and from birds at rest showing no evidence of flight attempts or escape behavior at the time. A trial was terminated if the bird demonstrated continuous active escape behavior or evidence of neurological impairment by loss of balance or righting reflex. Trials were also terminated if a heat tolerance limit (HTL) was reached, which we defined as a T_b approaching 45°C, close to the lethal limits of ~46°C (Lutterschmidt and Hutchison, 1997), or if this T_b was approached at a rate of T_b increase greater than 0.1°C min^{−1} (McKechnie et al., 2017, 2016b; Smith et al., 2015, 2017; Talbot et al., 2017). The bird was then removed from the chamber, cooled, given additional water by gavage, and observed for thermoneutral T_b and normal behavior before release. No mortality occurred during the course of these experiments. During measurements, the behavior of birds while in the chamber was scored on a scale from 0 to 5, where 0 corresponded to a completely calm individual sitting immobile and 5 corresponded to a highly agitated bird exhibiting sustained escape behavior. Data analyses were restricted to data corresponding to an activity score of 0–3.

Calculations and statistical analysis

In order to ensure comparability among studies, we analyzed our data in the same way as in our other recent studies (McKechnie et al., 2017, 2016b; Smith et al., 2015; Whitfield et al., 2015). \dot{V}_{CO_2} was calculated using eqn 10.5 from Lighton (2008). Metabolic heat production (MHP; W) was calculated as in Walsberg and Wolf (1995) assuming a respiratory exchange ratio (RER) of 0.71. MHP as so calculated is herein also referred to as the resting metabolic rate (RMR). Rates of EWL were calculated using eqn 10.9 from Lighton (2008) assuming 0.803 mg H₂O ml^{−1} of water vapor. The calculation for evaporative heat loss was based on 2.406 J mg^{−1} H₂O. We used broken-stick linear regression models fitted in the R package segmented (Muggeo, 2008) to identify inflection points for the

relationships between EWL, RMR, the ratio of evaporative heat loss to metabolic heat production (EHL/MHP) and T_b as a function of T_a . We then fitted linear mixed-effects models that included individual identity as a random factor in the R package nlme (Pinheiro et al., 2018). R (v3.4.0) was run inside RStudio (v1.0.143). Changes in evaporative heat loss variables before and after the onset of panting were assessed using repeated-measures ANOVA in SPSS (v24.0.0.0). Values for variables are given as means±s.d. and values for slopes are given with 95% confidence intervals.

RESULTS

Body temperature and thermal endpoints

From the lowest test T_a (~30°C), T_b increased significantly to the HTL (Table 1, Fig. 1). Above the inflection point ($T_a=35.3^\circ\text{C}$ in mulga parrots and 41.4°C in galahs), the rates of increase in T_b approximately doubled in mulga parrots and increased by 1.7-fold in galahs (Table 1). In galahs there was a second inflection point apparent at $T_a=51.9^\circ\text{C}$, above which the rate of increase in T_b increased by threefold relative to the rate between the inflection points. In mulga parrots there was no second inflection point evident. Breadth of the regression line confidence limits ranged between 0.05 and 0.3°C °C^{−1} (Table 1). At the HTL, an average T_b of 43.4±0.6°C in mulga parrots and 44.1±0.3°C in galahs was maintained with stable RMR and EWL values for at least 10 min. In mulga parrots, the HTL was reached in two individuals at $T_a=44^\circ\text{C}$, one individual at $T_a=48^\circ\text{C}$ and one individual at $T_a=49^\circ\text{C}$. In galahs, the HTL was reached in one individual at $T_a=53^\circ\text{C}$, five individuals at $T_a=54^\circ\text{C}$ and one individual at $T_a=55^\circ\text{C}$.

Resting metabolic rate

Minimum RMR values averaged 0.65±0.10 W at $T_a=35^\circ\text{C}$ in mulga parrots and 2.07±0.41 W at $T_a=30^\circ\text{C}$ in galahs and increased significantly with increasing T_a (Table 1, Fig. 2). Segmented regressions indicated inflection points at $T_a=40.8^\circ\text{C}$ in mulga parrots and at $T_a=40.2^\circ\text{C}$ in galahs, which represent the upper critical temperatures (T_{uc}) for each species. RMR as a function of T_a increased above the T_{uc} from near zero to 0.05 W °C^{−1} in mulga parrots and from 0.02 to 0.07 W °C^{−1} in galahs, an increase of ~3.5-fold (Table 1, Fig. 2). In galahs there was a second inflection point apparent at $T_a=50.7^\circ\text{C}$, above which the rate of increase in RMR was 0.37 W °C^{−1}, an increase of ~5.3-fold relative to the rate between the inflection points. In mulga parrots there was no second inflection point apparent. Breadth of regression line confidence intervals ranged between 0.01 and 0.30 W °C^{−1} (Table 1). Maximum average RMR values coincided with the HTL in both species and were 1.38±0.12 W in mulga parrots and 4.40±0.60 W in galahs, approximately double the minimum RMR values.

Evaporative water loss

Minimum EWL values occurred at the lowest test T_a (~30°C) in both species (0.37±0.21 g h^{−1} in mulga parrots and 1.15±0.32 g h^{−1} in galahs) and increased significantly with increasing T_a (Table 1, Fig. 3). Above single inflection points, which were at $T_a=40.2^\circ\text{C}$ in mulga parrots and at $T_a=41.3^\circ\text{C}$ in galahs, the rate of EWL increase with T_a increased approximately fivefold to 0.23 g h^{−1} °C^{−1} in mulga parrots and 0.66 g h^{−1} °C^{−1} in galahs (Table 1). Breadth of the regression line confidence intervals ranged from 0.01 to 0.09 g h^{−1} °C^{−1}. Maximum EWL occurred at each species' HTL and were equivalent to approximately sevenfold minimum values in mulga parrots and 10-fold minimum values in galahs. Average maximum EWL values were 2.66±0.07 g h^{−1} in mulga parrots and 11.64±1.36 g h^{−1} in galahs.

Table 1. Variables (\pm s.d.) related to thermoregulation at high air temperature (T_a) in two Australian parrot species

Variable	Mulga parrot <i>Psephotellus varius</i>	Galah <i>Eolophus roseicapilla</i>
Body mass (g)	54.6 \pm 4.4 (17)	266.3 \pm 30.2 (7)
Body temperature (T_b)		
Min. T_b ($^{\circ}$ C)	40.1 \pm 0.7 (7)	39.8 \pm 0.33 (3)
T_a at T_b minimum ($^{\circ}$ C) ^a	30	30
Inflection T_a ($^{\circ}$ C)	35.3	41.4, 51.9
T_b vs T_a slope below inflection 1 ($^{\circ}$ C $^{\circ}$ C ⁻¹) ^b	0.13 [-0.02, 0.29]	0.10 [0.03, 0.18]
T_b vs T_a slope above inflection 1 ($^{\circ}$ C $^{\circ}$ C ⁻¹) ^b	0.25 [0.20, 0.30]	0.17 [0.08, 0.26]
T_b vs T_a slope above inflection 2 ($^{\circ}$ C $^{\circ}$ C ⁻¹) ^b	no second inflection	0.51 [0.21, 0.81]
Max. T_b ($^{\circ}$ C)	43.4 \pm 0.6 (4)	44.1 \pm 0.3 (7)
T_a at T_b maximum ($^{\circ}$ C) ^a	48	54
Heat tolerance limit ($^{\circ}$ C) ^a	44 (2), 48 (1), 49 (1)	53 (1), 54 (5), 55 (1)
Resting metabolic rate (RMR)		
Min. RMR (W)	0.65 \pm 0.10 (7)	2.07 \pm 0.41 (3)
Min. RMR (mW g ⁻¹) ^c	11.96 \pm 2.80 (7)	7.55 \pm 1.36 (3)
T_a at RMR minimum ($^{\circ}$ C) ^a	35	30
Inflection T_a ($^{\circ}$ C)	40.8	40.2, 50.7
RMR slope below inflection 1 (W $^{\circ}$ C ⁻¹) ^b	0.0004 [-0.0075, 0.0082]	0.02 [0.05, 0.09]
RMR slope above inflection 1 (W $^{\circ}$ C ⁻¹) ^b	0.05 [0.03, 0.08]	0.07 [-0.01, 0.15]
RMR slope above inflection 2 (W $^{\circ}$ C ⁻¹) ^b	no second inflection	0.37 [0.09, 0.65]
Max. RMR (W)	1.38 \pm 0.12 (3)	4.40 \pm 0.60 (7)
Max. RMR (mW g ⁻¹) ^c	24.40 \pm 3.04 (3)	16.52 \pm 2.76 (7)
T_a at RMR maximum ($^{\circ}$ C) ^a	48	54
Max. RMR/min. RMR	2.14	2.12
Evaporative water loss (EWL)		
Min. EWL (g h ⁻¹)	0.37 \pm 0.21 (7)	1.15 \pm 0.32 (3)
Min. EWL (mg h ⁻¹ g ⁻¹) ^c	6.69 \pm 3.96 (7)	4.16 \pm 1.05 (3)
T_a at EWL minimum ($^{\circ}$ C) ^a	30	30
Inflection T_a ($^{\circ}$ C)	40.2	41.3
EWL slope below inflection (g h ⁻¹ $^{\circ}$ C ⁻¹) ^b	0.04 [0.03, 0.05]	0.13 [0.09, 0.18]
EWL slope above inflection (g h ⁻¹ $^{\circ}$ C ⁻¹) ^b	0.23 [0.18, 0.28]	0.66 [0.58, 0.75]
Max. EWL (g h ⁻¹)	2.66 \pm 0.07 (3)	11.64 \pm 1.36 (7)
Max. EWL (mg h ⁻¹ g ⁻¹) ^c	47.09 \pm 4.69 (3)	43.44 \pm 3.97 (7)
T_a at EWL maximum ($^{\circ}$ C) ^a	48	54
Max. EWL/min. EWL	7.13	10.15

Numbers of individuals are in parentheses and 95% confidence intervals for slopes are in brackets.

^aTest $T_a \pm 0.5^{\circ}$ C.

^bSlopes are derived from linear mixed models.

^cMass-specific values.

Panting and evaporative heat dissipation

Minimum EHL/MHP values occurred at the lowest test T_a ($\sim 30^{\circ}$ C) in both species (0.35 \pm 0.12 in mulga parrots and 0.37 \pm 0.03 in galahs) and increased significantly with increasing T_a (Table 2, Fig. 4). In mulga parrots there was a single inflection point at $T_a = 37.8^{\circ}$ C, above which the slope of the relationship of EHL/MHP with T_a increased approximately 10-fold to 0.10 $^{\circ}$ C⁻¹. In galahs there were two inflection points apparent: above the first, the slope of the relationship of EHL/MHP with T_a increased 5.5-fold to 0.11 $^{\circ}$ C⁻¹; above the second, the slope decreased by 3.7-fold relative to the slope between the inflection points, to 0.03 $^{\circ}$ C⁻¹. Breadth of the regression line confidence intervals ranged from 0.01 to 0.25 $^{\circ}$ C⁻¹. At the highest T_a in mulga parrots, which also corresponded to this species' HTL, EHL/MHP was $\sim 24\%$ lower than it was at its maximum at $T_a = 46^{\circ}$ C (1.71 \pm 0.18; Table 2). Maximum EHL/MHP in galahs occurred at this species' HTL of $T_a = 54^{\circ}$ C and was 1.79 \pm 0.27. Maximum EHL/MHP was ~ 5 -fold higher than minimum in both species. It should be noted, however, that these values are based on the assumption that RER=0.71, i.e. the metabolic substrate during gas exchange measurements consisted entirely of lipids. If this assumption is incorrect, the actual EHL/MHP values could be higher, ranging from 2.16 in mulga parrots to 2.45 in galahs if the metabolic substrate consisted solely of carbohydrates (i.e. RER=1.00; see dashed lines in Fig. 4).

In some cases the onset of panting coincided with an increasing T_a as the chamber temperature was adjusted to the next test T_a ; however, in 10 individual mulga parrots and four individual galahs we were able to observe the onset of panting during a period of stable T_a . Thus, we have a record of the changes in RMR, EHL and EHL/MHP that occurred abruptly as panting commenced (Table 2, Fig. 5). The onset of panting occurred at $T_a = 40.9 \pm 1.1^{\circ}$ C in mulga parrots and $T_a = 42.7 \pm 2.5^{\circ}$ C in galahs. RMR did not increase significantly at the onset of panting in either species ($F_{1,9} = 3.27$, $P = 0.104$ and $F_{1,3} = 1.15$, $P = 0.362$ for mulga parrots and galahs, respectively), but increased linearly thereafter. EHL increased significantly at the onset of panting in both species ($F_{1,9} = 85.61$, $P < 0.001$ and $F_{1,3} = 26.44$, $P = 0.014$ for mulga parrots and galahs, respectively), approximately doubling. The proportion of metabolic heat dissipated by evaporation (EHL/MHP) increased significantly in both species ($F_{1,19} = 41.72$, $P < 0.001$ and $F_{1,3} = 116.52$, $P = 0.002$ for mulga parrots and galahs, respectively), increasing by 1.6-fold in mulga parrots and 1.8-fold in galahs (Table 2).

DISCUSSION

Both species of parrots in the present study showed patterns of thermoregulation at high T_a broadly similar to those of other parrots, including previous measurements in galahs (Dawson and Fisher, 1982), with T_b increasing from normothermic values of $\sim 40^{\circ}$ C to

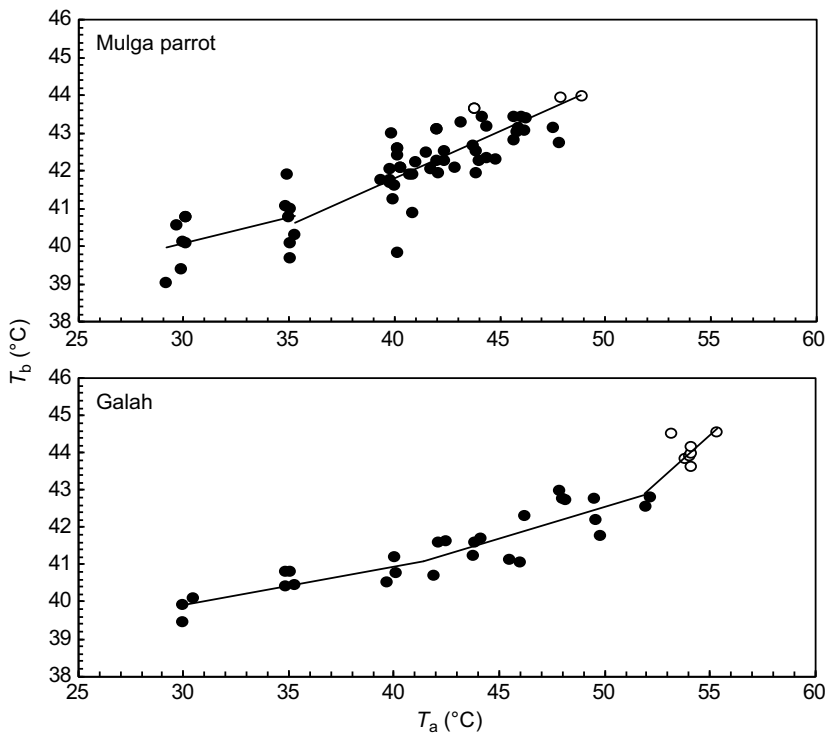


Fig. 1. Body temperature (T_b) in mulga parrots ($N=17$) and galahs ($N=7$) over a range of air temperatures (T_a). Open circles indicate individuals that reached thermal endpoints. Segmented regressions were used to estimate the inflection point(s) in the relationship between T_b and T_a , and the slopes were calculated using linear mixed-effects models. These data represent only calm birds.

maxima around 43–44°C. The regulation of T_b below T_a was achieved via large increases in rates of evaporative heat dissipation, with EWL increasing to 700–1000% of resting values at thermoneutral T_a . Both species showed clearly defined upper critical limits of thermoneutrality. At the highest T_a values in galahs, cooling mechanisms could not compensate for rapid increases in T_b , leading to a plateau in evaporative heat dissipation that corresponded with the HTL of this species.

Body temperature and heat tolerance limits

The normothermic T_b of the two species investigated here (~40°C) increased to maximum T_b values around 43–44°C at HTLs. The T_a inflection points above which T_b began to increase rapidly in the present study were in the same range as those reported for five species of passerines measured at the same study site (McKechnie et al., 2017). In galahs, a second T_a inflection occurred at $T_a=51.9^\circ\text{C}$, above which the rate of T_b change increased by an additional ~3-fold

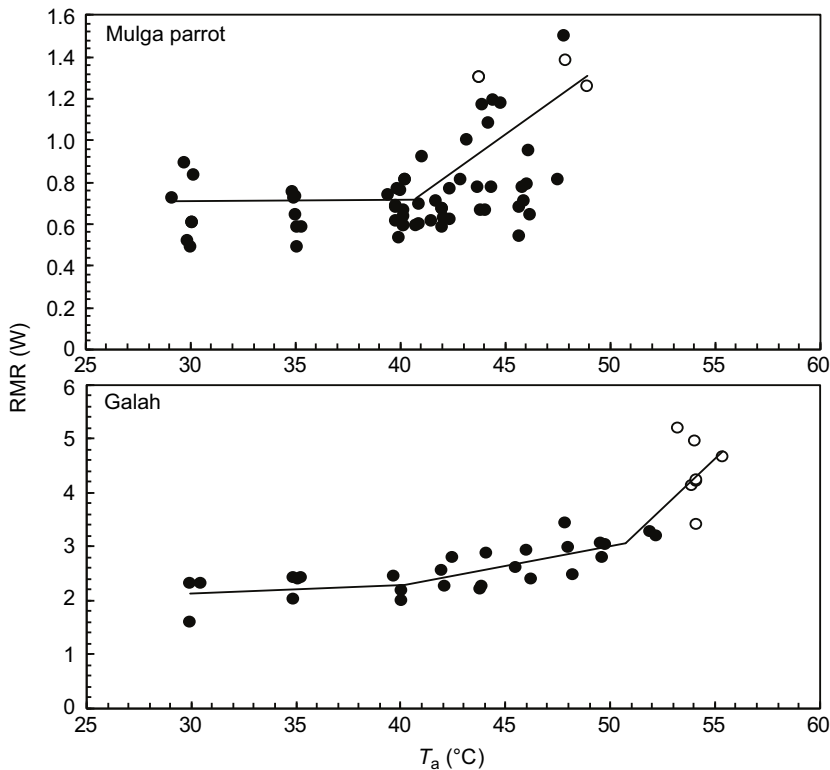


Fig. 2. Resting metabolic rate (RMR) in mulga parrots ($N=17$) and galahs ($N=7$) over a range of T_a . Open circles indicate individuals that reached thermal endpoints. Segmented regressions were used to estimate the inflection point(s) in the relationship between RMR and T_a , and the slopes were calculated using linear mixed-effects models. These data represent only calm birds.

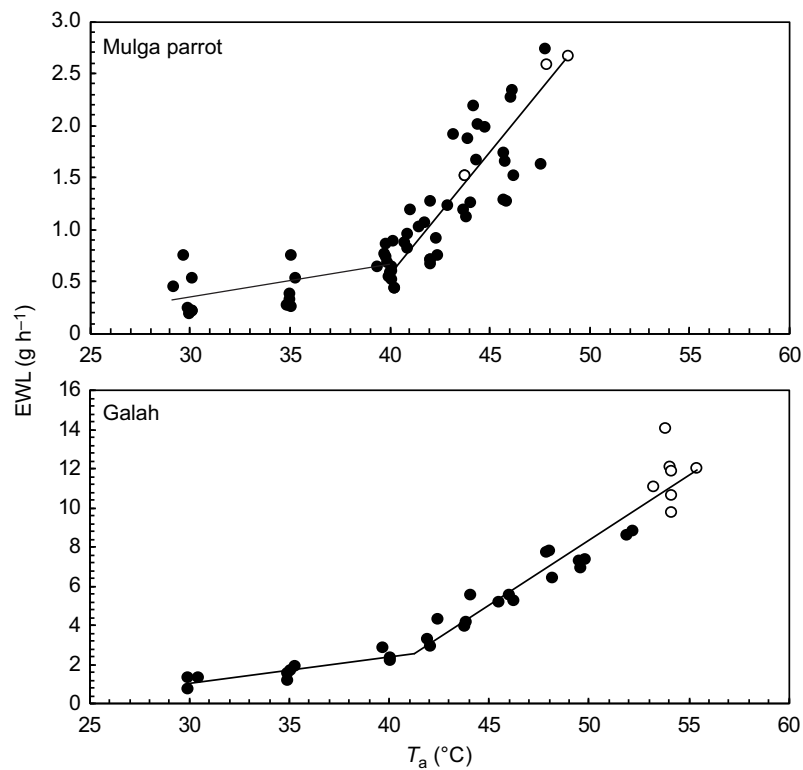


Fig. 3. Evaporative water loss (EWL) in mulga parrots ($N=17$) and galahs ($N=7$) over a range of T_a . Open circles indicate individuals that reached thermal endpoints. Segmented regressions were used to estimate the inflection point(s) in the relationship between EWL and T_a , and the slopes were calculated using linear mixed-effects models. These data represent only calm birds.

and most birds reached their thermal endpoints (i.e. HTL), suggesting a failure of thermoregulatory mechanisms. In contrast, Dawson and Fisher (1982) reported a single T_b inflection point for the same species at $T_a \sim 34^\circ\text{C}$ for summer-acclimatized birds based on cloacal temperatures (2-cm insertion) upon removal from metabolic chambers, although maximum T_a values were lower than in the present study.

Maximum T_b values associated with acute heat stress in the two parrot species in the present study were comparable to previously reported values in other taxa. Dawson and Fisher (1982) reported maximum T_b of $43\text{--}44.2^\circ\text{C}$ in galahs held at $T_a=47\text{--}48^\circ\text{C}$ for 6–8 h;

these birds were held at lower T_a values for much longer periods compared with the present study, but exhibited similar maximum T_b values. Maximum T_b values recorded in the present study were within the same range as those recently reported for southern African passerines (Whitfield et al., 2015), columbids from southern Africa and North America (McKechnie et al., 2016b; Smith et al., 2015) and a southern African sandgrouse (McKechnie et al., 2016a), with all these studies involving the same methods as we used here. The present study therefore confirms that the approximate upper T_b limit to physiological function in psittaciform birds under acute heat exposure conditions is similar to that in most

Table 2. Variables (\pm s.d.) related to the efficiency of evaporative cooling in two Australian parrot species

Variable	Mulga parrot <i>Psephotellus varius</i>	Galah <i>Eolophus roseicapilla</i>
Min. EHL/MHP	0.35 ± 0.12 (7)	0.37 ± 0.03 (3)
T_a at EHL/MHP minimum ($^\circ\text{C}$) ¹	30	30
Inflection T_a ($^\circ\text{C}$)	37.8	38.1, 48.1
Slope of EHL/MHP vs T_a below inflection 1 ^b	0.01 [−0.02, 0.05]	0.02 [−0.02, 0.06]
Slope of EHL/MHP vs T_a above inflection 1 ^b	0.10 [0.08, 0.13]	0.11 [0.08, 0.14]
Slope of EHL/MHP vs T_a above inflection 2 ^b	No second inflection point	0.03 [−0.01, 0.06]
Max. EHL/MHP	1.71 ± 0.18 (3)	1.79 ± 0.27 (7)
T_a at EHL/MHP maximum ($^\circ\text{C}$) ^a	46	54
T_b at onset of panting ($^\circ\text{C}$)	42.0 ± 0.8 (12)	41.3 ± 0.4 (4)
T_a at onset of panting ($^\circ\text{C}$)	40.9 ± 1.1 (12)	42.7 ± 2.5 (4)
Change in RMR with panting (W) ^c	(a) 0.65 ± 0.14 (10) (b) 0.73 ± 0.10 (10)	(a) 2.32 ± 0.23 (4) (b) 2.50 ± 0.44 (4)
Change in EHL with panting (W) ^c	(a) 0.32 ± 0.16 (10) (b) 0.55 ± 0.18 (10)	(a) 1.26 ± 0.64 (4) (b) 2.51 ± 0.98 (4)
Change in EHL/MHP with panting ^c	(a) 0.47 ± 0.22 (10) (b) 0.76 ± 0.21 (12)	(a) 0.53 ± 0.22 (4) (b) 0.98 ± 0.22 (4)

Numbers of individuals are in parentheses and 95% confidence intervals for slopes are in brackets.

^aTest $T_a \pm 0.5^\circ\text{C}$.

^bSlopes are derived from linear mixed models.

^cChange in variables with onset of panting: (a) before panting and (b) after the onset of panting (bold font indicates a significant difference in b relative to a by repeated-measures ANOVA).

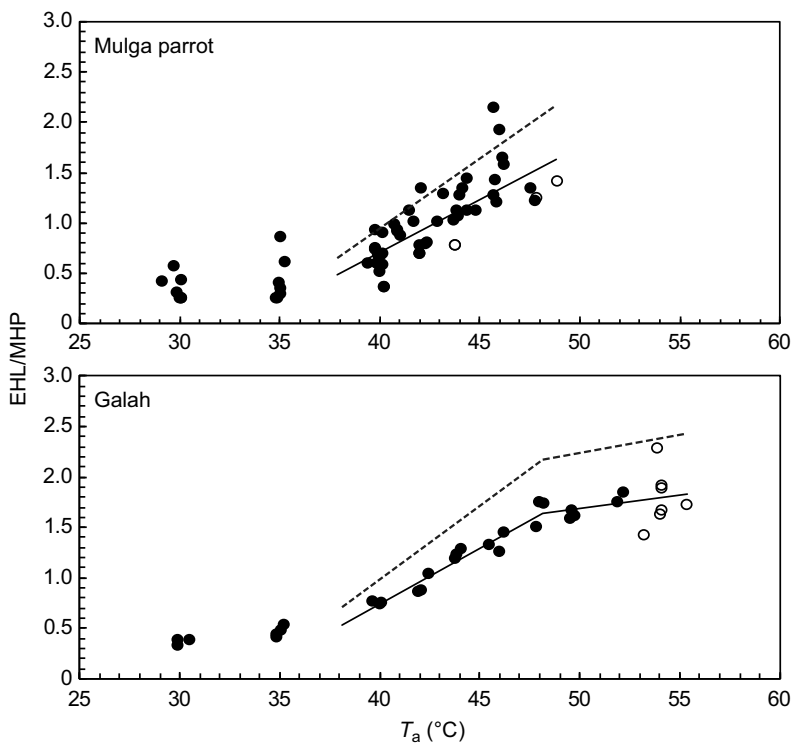


Fig. 4. The ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) in mulga parrots ($N=17$) and galahs ($N=7$) over a range of T_a . Open circles indicate individuals that reached thermal endpoints. Segmented regressions were used to estimate the inflection point(s) in the relationship between EHL/MHP and T_a , and the slopes were calculated using linear mixed-effects models (solid lines). The dashed lines show the relationship if EHL/MHP is recalculated assuming carbohydrate metabolism, i.e. respiratory exchange ratio=1.0. These data represent only calm birds.

avian taxa. As discussed by McKechnie et al. (2017), the fact that these values are slightly more conservative than some reported in the earlier literature may reflect the fact that we actively avoided exposing birds to lethal T_b .

The range of HTL for parrot species in the present study ($T_a=44$ – 55°C) is similar to the range reported for passerines (46 – 54°C ; McKechnie et al., 2017; Whitfield et al., 2015), both of which are lower than the ranges reported for caprimulgids (52 – 62°C ; O'Connor et al., 2017; Talbot et al., 2017) and columbids (56 – 62°C ; McKechnie et al., 2016b). At their HTL, mulga parrots maintained $T_b \sim 4.6^\circ\text{C}$ below T_a and galahs maintained $T_b \sim 9.9^\circ\text{C}$ below T_a ; comparable data are not available for other parrot species. Passerines show a similar positive correlation of T_a – T_b values with M_b at HTL, ranging from ~ 1 – 3°C at $M_b=10$ – 15 g to $\sim 6^\circ\text{C}$ at $M_b=117$ g (McKechnie et al., 2017; Whitfield et al., 2015). In columbiforms, T_a – T_b values at HTL are generally higher, ranging from $\sim 11^\circ\text{C}$ at $M_b=37$ g to $\sim 14^\circ\text{C}$ at $M_b=186$ g (McKechnie et al., 2016b), and in caprimulgiforms values are higher still, ranging from ~ 8 to $\sim 19^\circ\text{C}$ in species with $M_b=44$ to 50 g (Talbot et al., 2017).

Resting metabolic rate

Both species showed a clear T_{uc} above which RMR increased linearly, occurring at $T_a \sim 40^\circ\text{C}$ and closely matching T_a at the onset of panting. This close link between the onset of panting and increases in RMR above thermoneutral values is consistent with recent data for Burchell's sandgrouse (*Pterocles burchelli*) (McKechnie et al., 2016a), but contrasts with data for five passerines at Gluepot Reserve, in which there was no clear relationship between the T_{uc} and the onset of panting (McKechnie et al., 2017). Previously reported T_{uc} values for monk parakeets (38.5°C ; Weathers and Caccamise, 1975) and budgerigars (41°C ; Weathers and Schoenbaechler, 1976) were very similar to the T_{uc} values observed for the two species in the present study. In galahs we observed a second inflection point in the relationship between RMR and T_a at 50.7°C , which closely matches the second inflection

point observed in the T_b data (51.9°C), presumably because birds were attempting to counter rapid increases in T_b .

The fractional increases in RMR observed in this study between thermoneutral and maximum values were ~ 2 -fold in both mulga parrots and galahs. Taking all available psittaciform data into account (four species), the mean ratio of RMR at $T_a=48^\circ\text{C}$ compared with $T_a=35^\circ\text{C}$ is 1.77 ± 0.28 (present study, Dawson and Fisher, 1982; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976) compared with 1.38 ± 0.22 in seven species of passerines (McKechnie et al., 2017; Tieleman et al., 2002; Whitfield et al., 2015; Wolf and Walsberg, 1996) and 1.07 ± 0.09 in seven species of columbids (Hoffman and Walsberg, 1999; McKechnie et al., 2016b; McKechnie and Wolf, 2004; Withers and Williams, 1990). The relatively larger fractional changes in RMR at high T_a in passerines and in the four species of psittaciform birds studied to date likely reflect the metabolic cost of muscle contractions involved in panting or gular fluttering (Dawson, 1982; Richards, 1970) to increase respiratory evaporative water loss (REWL), whereas the smaller increases in columbiform birds seem to be functionally linked to less energetically demanding cutaneous evaporative water loss in those taxa (McKechnie et al., 2016b).

Evaporative water loss

In both mulga parrots and galahs, EWL increased gradually with increasing T_a at moderate values, and then increased rapidly and linearly above $T_a \sim 40^\circ\text{C}$, again corresponding very closely to the temperature at onset of panting. Dawson and Fisher (1982) found an identical pattern in their earlier study on the galah; however, their inflection temperature at which EWL began to increase rapidly was lower at $T_a \sim 32.5^\circ\text{C}$, possibly reflecting the higher chamber humidities in the latter study compared with ours, and/or different acclimation/acclimatization histories. Weathers and Caccamise (1975) and Weathers and Schoenbaechler (1976) reported similar patterns in monk parakeets and budgerigars, respectively. The inflection T_a for EWL appears to be at $\sim 36^\circ\text{C}$ in the monk parakeet

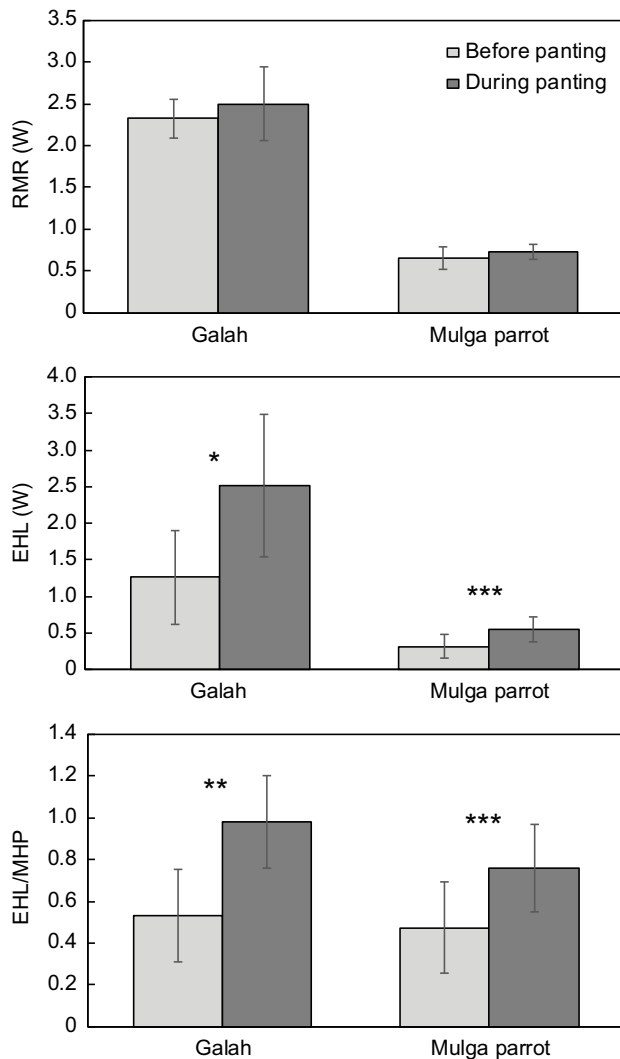


Fig. 5. Effect of panting on RMR, EHL and the ratio of EHL to MHP in mulga parrots ($N=10$) and galahs ($N=4$). Data represent values before and immediately after the onset of panting in birds, where panting commenced at a stable T_a . Asterisks indicate a significant effect of panting for a given parameter within each species (* $P<0.05$, ** $P<0.005$, *** $P<0.001$).

(Weathers and Caccamise, 1975) and at $\sim 39^\circ\text{C}$ in the budgerigar (Weathers and Schoenbaechler, 1976). Greenwald et al. (1967) described a similar pattern of EWL with T_a in the budgerigar, with an inflection point at $\sim 34^\circ\text{C}$.

Maximum EWL rates in the present study were ~ 7 -fold higher than minimum EWL rates in mulga parrots, and ~ 10 -fold higher in galahs. Dawson and Fisher (1982) reported a 40-fold increase in EWL in summer-acclimatized galahs between T_a of 20 and 48°C . Extrapolating their data to EWL at $T_a=30^\circ\text{C}$ (the minimum T_a used in the present study, at which minimum EWL occurred for galahs) provides an estimate of $\sim 0.42\text{ g h}^{-1}$, which is ~ 2.8 -fold lower than that of birds measured in the present study. This equates to a ~ 14.5 -fold increase in EWL between $T_a=30^\circ\text{C}$ and their maximum measurement $T_a=48^\circ\text{C}$. This maximum T_a is lower than that in the present study, and the proportional increase in EWL higher, although the galahs in that study were exposed to this temperature for several hours, losing $\sim 10\%$ of starting M_b and $\sim 15\%$ of body water. By way of comparison, birds in the present study lost between 3% and 6% of starting M_b . Weathers and Schoenbaechler (1976)

reported that maximum EWL in budgerigars was 16-fold higher at $T_a=45^\circ\text{C}$ relative to thermoneutral T_a . Similarly, Weathers and Caccamise (1975) reported that maximum EWL in monk parakeets increased by 12-fold between thermoneutral T_a and $T_a=46^\circ\text{C}$. On balance, these findings suggest that parrots have a high capacity to increase EWL.

Panting and evaporative heat dissipation

The metabolic cost of cooling in galah began to rise rapidly above a T_a inflection point of $\sim 50^\circ\text{C}$ in order to counter a rapid increase in T_b . Because EWL continued increasing at the same rate, evaporative heat dissipation (EHL/MHP) appears to plateau above $T_a\sim 48^\circ\text{C}$. Galahs above $T_a\sim 50^\circ\text{C}$ were reaching their HTL, suggesting that cooling mechanisms were beginning to fail. Maximum EHL/MHP in galahs was 1.79, assuming $\text{RER}=0.71$ (lipid catabolism) in post-absorptive birds. Dawson and Fisher (1982) reported EHL/MHP values of 1.4–1.7 in galahs exposed to $T_a\sim 48^\circ\text{C}$. Weathers and Caccamise (1975) reported EHL/MHP values of 1.53 for monk parakeets exposed to $T_a=44^\circ\text{C}$, and Weathers and Schoenbaechler (1976) reported EHL/MHP values of 1.56 for budgerigars exposed to $T_a=45^\circ\text{C}$. These latter two studies were not designed to test HTLs, so it is not clear whether these are maximum EHL/MHP values for these species. Passerines in general appear to have maximum cooling efficiencies similar to those of the parrot species in the present study, equivalent to $\text{EHL/MHP}<2.0$ even in larger species (Marder, 1973; McKechnie et al., 2017; Whitfield et al., 2015).

The metabolic cost of cooling (RMR) increased linearly after T_{uc} and the onset of panting in both species in the present study. Evaporative heat loss increased significantly at the onset of panting, approximately doubling, in both species. EHL/MHP increased significantly in both species (1.6-fold in mulga parrots and 1.8-fold in galahs). Dawson and Fisher (1982) reported extensive panting by galahs exposed to high T_a , describing vigorous thoracic movements and also pumping of the fleshy tongue (coincident with breathing movements) that appeared to foster increased movement of the gular area. These authors also reported galahs at high T_a using wing drooping, where the wings are held away from the body surface to augment convective heat loss. Weathers and Caccamise (1975) reported open-mouthed panting including tongue movements in monk parakeets at high T_a , referring to these latter movements as ‘lingual flutter’, and Weathers and Schoenbaechler (1976) similarly reported panting and tongue movements synchronized with thoracic movements in budgerigars. We did not record observations of tongue movements in the present study, but it may be a common strategy in parrots to increased movement of the gular area and thus increase EWL rate.

Conclusions

Our data on thermoregulation at environmental temperatures above T_b in two Australian parrot species suggest that evaporative cooling in Psittaciformes is generally less efficient than in orders such as Columbiformes and Caprimulgiformes, but similar to that in Passeriformes. Increases in EWL, RMR and T_b with increasing T_a in the parrot species in the present study were similar to increases in five species of Australian passerines studied at the same Gluepot Reserve field site (McKechnie et al., 2017). Maximum heat dissipation capacity measured as maximum EHL/MHP in parrots ranges from 1.5 to 1.8 (present study; Dawson and Fisher, 1982; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976), which is comparable to the range in passerines of 1.2–2.2 (McKechnie et al., 2017; Whitfield et al., 2015), and lower than the range in columbids of 2.3–4.7 (McKechnie et al., 2016b; Smith

et al., 2015) and in caprimulgids of 3.0–5.2 (Dawson and Fisher, 1969; O'Connor et al., 2017; Talbot et al., 2017). It is likely that this variation in evaporative cooling efficiency arises from variation amongst orders in the primary avenues of heat dissipation. Columbids appear to use cutaneous evaporative water loss extensively (reviewed by McKechnie et al., 2016b; McKechnie and Wolf, 2004), whereas passerines rely primarily on respiratory evaporative water loss augmented by panting (McKechnie et al., 2017; Wolf and Walsberg, 1996). Caprimulgids also rely on respiratory evaporative water loss, using a comparatively massive buccal surface area to maximize evaporation (Talbot et al., 2017). Data from the present study and other studies of parrot species thermoregulating at high T_a show the importance of panting (and potentially lingual flutter augmented by tongue movements coincident with breathing) for maximizing EWL in psittaciform birds; presently it is not known the extent to which parrots are able to rely on cutaneous evaporative water loss.

These taxonomic differences in evaporative heat dissipation and HTL are reflected in differences in behavior and microsite selection in both wild and captive birds. At Gluepot Reserve, wild Australian ring-necked parrots (*Barnardius zonarius*) were observed on very hot days ($T_a \geq 44^\circ\text{C}$) to sit in deep shade under trees, wing venting and pressing their bellies to the soil to lose heat (W.A.T., personal observation). Captive parrots spend more time resting and retire to shaded microsites on extremely hot summer days, whereas doves may increase activity and feeding behavior during the hottest periods, often doing so in full solar exposure (Xie et al., 2017). Fisher et al. (1972) reported observations of wild Australian arid-zone birds and found that drinking patterns differed greatly amongst orders at high T_a , with parrots visiting water points only in the early morning and at sunset, and doves continuing to visit water points throughout the day. The potential links between avian heat tolerance physiology and drinking behavior patterns remain unexplored. One prediction, for instance, is that at unshaded waterholes exposed to intense solar radiation, the very high operative temperatures small birds experience at midday may favor drinking at cooler times of the day in taxa that lack highly efficient evaporative cooling pathways.

Parrots are widespread in the arid interior of Australia and have featured conspicuously in reports of large-scale mortality events associated with heat waves (reviewed by McKechnie et al., 2012). These events have recently impacted a threatened parrot species, the Carnaby's black cockatoo (Saunders et al., 2011), and are likely to occur much more frequently in the coming decades than they have in the past (McKechnie and Wolf, 2010). Our results, along with those of the few other studies of thermoregulation in parrots exposed to high T_a , indicate that they may be more vulnerable than taxa such as Columbiformes and Caprimulgiformes to extreme weather events. However, additional data are needed across a broad range of parrot families and body sizes to effectively model the heat tolerance and hydration status of free-ranging birds in natural habitats, which is vital for predicting how climate change and extreme weather events may impact parrot populations in the future.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.E.M., B.O.W.; Methodology: A.E.M., B.O.W.; Formal analysis: T.J.M.; Investigation: T.J.M., A.R.G., W.A.T., E.K.S.; Writing - original draft: T.J.M.; Writing - review & editing: T.J.M., A.R.G., W.A.T., E.K.S., A.E.M., B.O.W.

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