

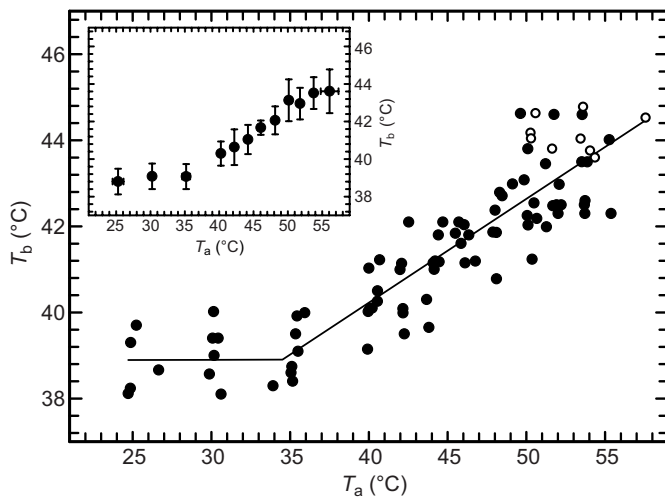
## CORRECTION

# Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*)

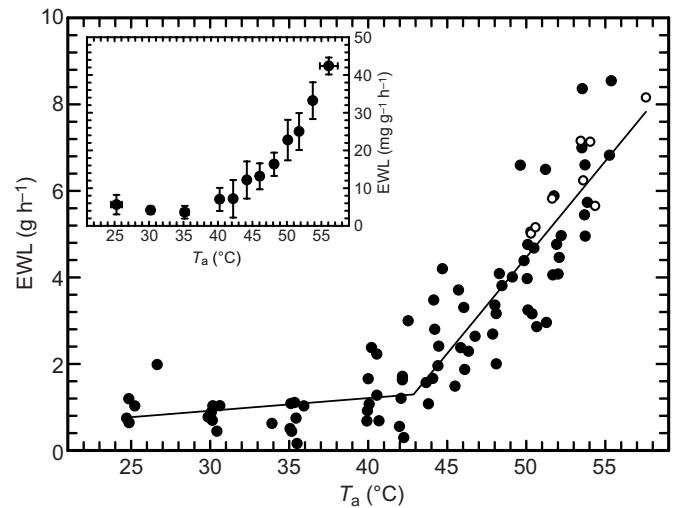
Andrew E. McKechnie, Ben Smit, Maxine C. Whitfield, Matthew J. Noakes, William A. Talbot, Mateo Garcia, Alexander R. Gerson and Blair O. Wolf

There was an error published in *J. Exp. Biol.* **219**, pp. 2137-2144.

The scaling of the y-axes in the insets of Figs 2 and 3 is incorrect. The corrected figures are printed below.



**Fig. 2.** Body temperature ( $T_b$ ) of Burchell's sandgrouse (*Pterocles burchelli*) as a function of air temperature ( $T_a$ ). Data for individuals that reached their thermal endpoint are shown as open circles. The solid line is the segmented linear regression model that provided the best fit; the relationship between  $T_b$  and  $T_a > 34.5^\circ\text{C}$  is  $T_b = 0.241T_a + 30.58$  ( $r^2$  for segmented regression model = 0.818). Inset shows mean  $\pm$  s.d.  $T_b$  for  $T_a$  bins of  $2^\circ\text{C}$ . For each bin,  $n = 5-12$ , except at  $T_a \sim 56^\circ\text{C}$ , where  $n = 3$ .



**Fig. 3.** Evaporative water loss (EWL) in Burchell's sandgrouse (*Pterocles burchelli*) increased rapidly above an inflection point at an air temperature ( $T_a$ ) of  $42.9^\circ\text{C}$ . Data for individuals that reached their thermal endpoint are shown as open circles. The solid line is the segmented linear regression model that provided the best fit; the relationship between EWL and  $T_a > 42.9^\circ\text{C}$  is  $\text{EWL} = 0.445T_a - 17.76$  ( $r^2$  for segmented regression model = 0.843). Inset shows mean  $\pm$  s.d. mass-specific EWL for  $T_a$  bins of  $2^\circ\text{C}$ . For each bin,  $n = 5-12$ , except at  $T_a \sim 56^\circ\text{C}$ , where  $n = 3$ .

We apologise to the authors and readers for any inconvenience this may have caused.

## RESEARCH ARTICLE

# Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*)

Andrew E. McKechnie<sup>1,\*</sup>, Ben Smit<sup>2</sup>, Maxine C. Whitfield<sup>1</sup>, Matthew J. Noakes<sup>1</sup>, William A. Talbot<sup>3</sup>, Mateo Garcia<sup>3</sup>, Alexander R. Gerson<sup>4</sup> and Blair O. Wolf<sup>3</sup>

## ABSTRACT

Sandgrouse (Pterocliiformes) are quintessential examples of avian adaptation to desert environments, but relatively little is known about the limits to their heat tolerance and evaporative cooling capacity. We predicted that evaporative cooling in Burchell's sandgrouse (*Pterocles burchelli*) is highly efficient and provides the basis for tolerance of very high air temperature ( $T_a$ ). We measured body temperature ( $T_b$ ), resting metabolic rate (RMR) and evaporative water loss (EWL) at  $T_a$  between 25°C and ~58°C in birds exposed to successive increments in  $T_a$ . Normothermic  $T_b$  averaged 39.0°C, lower than typical avian values. At  $T_a > 34.5^\circ\text{C}$ ,  $T_b$  increased linearly to a maximum of 43.6°C at  $T_a = 56^\circ\text{C}$ . The upper critical limit of thermoneutrality ( $T_{uc}$ ) was  $T_a = 43.8^\circ\text{C}$ , closely coinciding with the onset of panting and gular flutter. Above the  $T_{uc}$ , RMR increased 2.5-fold to 2.89 W at  $T_a = 56^\circ\text{C}$ , a fractional increase far exceeding that of many other species under comparable conditions. Rates of EWL increased rapidly at  $T_a > 42.9^\circ\text{C}$  to  $7.84 \pm 0.90 \text{ g h}^{-1}$  at  $T_a = 56^\circ\text{C}$ , an 11-fold increase above minimal levels. Maximum evaporative cooling efficiency (ratio of evaporative heat loss to metabolic heat production) was 2.03, but could be as high as 2.70 if our assumption that the birds were metabolising lipids is incorrect. Thermoregulation at very high  $T_a$  in *P. burchelli* was characterised by large increases in RMR and EWL, and is much less efficient than in taxa such as columbids and caprimulgids.

**KEY WORDS:** Body temperature, Critical thermal maximum, Evaporative water loss, Hyperthermia, Pterocliiformes, Upper critical limit of thermoneutrality

## INTRODUCTION

Deserts represent some of the most inhospitable and physiologically challenging habitats occupied by terrestrial organisms. Extremes of air temperature combined with desiccating conditions and highly unpredictable water and food resources impose severe constraints on the maintenance of energy and water balance (Dawson and Bartholomew, 1968; Dawson and Schmidt-Nielsen, 1964; Serventy, 1971). The challenges of avoiding lethal hyperthermia are

especially pronounced in birds because of their small body size, typically diurnal activity and limited use of thermally buffered microsites such as burrows; the adaptations that permit birds to occupy even the hottest deserts remain one of the most enduring fields of inquiry among ecological and evolutionary physiologists (Austin, 1976; Dawson and Bartholomew, 1968; Keast, 1960; Maclean, 1984; Williams and Tieleman, 2005). Thermoregulation under extremely hot conditions, when intense solar heat loads may result in birds experiencing operative temperatures 15°C or more above normothermic body temperature ( $T_b$ ) (Bakken, 1976; Robinson et al., 1976; Wolf and Walsberg, 1996b), involves consequential trade-offs between hyperthermia avoidance via evaporative heat dissipation and dehydration avoidance through the conservation of body water.

Sandgrouse (Pterocliiformes) are the quintessential arid-adapted avian taxon. Consisting of 16 species distributed across the Afrotropics and Palaearctic, sandgrouse possess a suite of physiological and behavioural traits with clear functional links to desert environments (de Juana, 1997), such as the unique feather morphology and behaviours that allow adult birds to transport water in their belly feathers to their chicks (Cade and Maclean, 1967; Maclean, 1983; Meade-Waldo, 1896). Sandgrouse have a pronounced capacity to tolerate extremely hot conditions (Thomas, 1984; Thomas and Maclean, 1981; Thomas and Robin, 1977). Several of these authors have noted that the onset of heat dissipation behaviours such as panting occurs at a much higher air temperature ( $T_a$ ) in sandgrouse than in most other birds. Moreover, behavioural responses of sandgrouse to  $T_a > T_b$  include piloerection and huddling, a behaviour that may reduce environmental heat loads and that becomes significantly more pronounced when birds are dehydrated (Thomas and Maclean, 1981).

In laboratory studies of thermoregulation, four species of sandgrouse were found to have comparatively low resting metabolic rates (RMR), high upper critical limits of thermoneutrality ( $T_{uc}$ ) and pronounced evaporative cooling capacities (Hinsley, 1992; Hinsley et al., 1993; Marder et al., 1986). However, with the exception of the study by Marder et al. (1986), in which spotted sandgrouse (*Pterocles senegallus*) were exposed to  $T_a = 60^\circ\text{C}$  for 120 min, little is known about the upper limits to heat tolerance and evaporative cooling in this group of birds.

We investigated the heat tolerance limits and evaporative cooling capacity of sandgrouse in the context of their distinctive behaviour and ecology by measuring  $T_b$ , RMR and evaporative water loss (EWL) during acute heat stress in Burchell's sandgrouse (*Pterocles burchelli* Sclater 1922), a species endemic to the arid regions of southern Africa (Lloyd, 2005). We predicted that *P. burchelli* has a pronounced capacity for evaporative cooling and can tolerate higher

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**List of symbols and abbreviations**

|                  |  |
|------------------|--|
| CEWL             | cutaneous evaporative water loss         |
| EHL              | evaporative heat loss                    |
| EWL              | evaporative water loss                   |
| $M_b$            | body mass                                |
| MHP              | metabolic heat production                |
| RER              | respiratory exchange ratio               |
| REWL             | respiratory evaporative water loss       |
| RMR              | resting metabolic rate                   |
| PIT              | passive integrated transponder           |
| $T_a$            | air temperature                          |
| $T_b$            | body temperature                         |
| TEWL             | total evaporative water loss             |
| $T_{uc}$         | upper critical limit of thermoneutrality |
| $\dot{V}_{CO_2}$ | carbon dioxide production                |
| $\dot{V}_{O_2}$  | oxygen consumption                       |

$T_a$  values than many other arid-zone species, and furthermore that evaporative cooling in this species is very efficient, with comparatively shallow increases in EWL and RMR with increasing  $T_a$  above normothermic  $T_b$ . Because sandgrouse begin panting only at very high  $T_a$  (Thomas and Maclean, 1981; Thomas and Robin, 1977), we also predicted that an inflection point in RMR indicating the  $T_{uc}$  occurs only at a  $T_a$  greater than normothermic  $T_b$ .

**MATERIALS AND METHODS****Study species and site**

The study took place in the southern Kalahari Desert in the Northern Cape province of South Africa, an arid area with a mean annual rainfall of ~200 mm and summer daily maximum temperatures ranging from approximately 20 to 43°C (Whitfield et al., 2015). Seventeen Burchell's sandgrouse (*P. burchelli*) with a mean±s.d. body mass ( $M_b$ ) of 192.9±12.2 g were caught early in the morning on the property Gemsbok (27°06' S, 22°04' E) using mist nets set up around waterholes where the birds regularly drink. Following capture, birds were transported in cloth bags approximately 40 km by road to a field laboratory set up at Leeupan Ranch (26°58' S, 21°50' E; see Whitfield et al., 2015). The study took place during the austral summer in late January 2013.

Sandgrouse were used for measurements the same day they were captured. They were held in cages constructed of shade cloth with grain (crushed maize, millet and sunflower seeds) and water available *ad libitum*, but were never observed to feed while in captivity. Birds were always offered water before experimental measurements, and a feeding tube attached to a syringe was used to introduce 5–10 ml of water directly into the crop if they were unwilling to drink, which was the case for most individuals. Measurements typically lasted 2–3 h, a period that typically limited  $M_b$  loss to <5% of initial  $M_b$  (mean  $M_b$  loss during measurements was 4.0±1.8% of initial values) and time in captivity did not exceed 24 h, after which they were released at the site of capture.

All experimental procedures were approved by the Animal Ethics Committee of the University of Pretoria (protocol EC071-11) and the Institutional Animal Care and Use Committee of the University of New Mexico (12-1005370-MCC). A permit to trap the birds was issued by the Northern Cape Department of Environmental Affairs (ODB 008/2013).

**Gas exchange and temperature measurements**

$T_a$  and  $T_b$  were measured using the same methods and equipment described by Whitfield et al. (2015). Briefly,  $T_b$  was measured using

calibrated temperature-sensitive passive integrated transponder (PIT) tags (Biomark, Boise, ID, USA) injected intraperitoneally into the abdominal cavity. During gas exchange measurements,  $T_b$  was monitored using a reader and transceiver system (model FS2001, Biomark). Carbon dioxide production ( $\dot{V}_{CO_2}$ ) and EWL were measured over the  $T_a$  range of 25–58°C, also using the same experimental setup as described by Whitfield et al. (2015) for their measurements during the 2013 season. Sandgrouse were placed individually in 9-litre plastic chambers, within which they stood on a platform of plastic mesh 10 cm above a 1-cm layer of mineral oil to trap excreta. We used flow rates between 15 and 75 l min<sup>-1</sup> depending on the experimental  $T_a$  in order to keep chamber humidity below 5 ppt so that humidity within the chamber remained similar to values the birds experience naturally. As was the case in the study by Whitfield et al. (2015), we found that increasing flow rate during the course of measurements (and thereby reducing chamber humidity) usually kept birds calm even at very high  $T_a$ .

**Experimental protocol**

Experiments took place during the day using the same protocol as described by Whitfield et al. (2015), with birds exposed to progressively higher  $T_a$  using a stepped profile with 5°C increments at  $T_a$  between 25 and 40°C, and 2°C increments at  $T_a$  between 40 and 58°C. Birds spent a minimum of 10 min, and on average ~30 min, at each  $T_a$  value. Birds were continually monitored during measurements using a video camera and an infrared light source (Whitfield et al., 2015). As was the case in Whitfield et al. (2015), measurements were terminated when a bird (1) was obviously stressed (sustained escape behaviour such as agitated jumping, pecking and/or wing flapping), or (2) showed signs of extreme heat stress such as loss of coordination or balance, or a sudden decrease in EWL, RMR and/or an uncontrolled increase in  $T_b$ . In the last instance, the bird was considered to have reached its upper limit of heat tolerance, and the  $T_a$  associated with the onset of these signs of heat stress and/or  $T_b$  approaching 45°C was considered the thermal endpoint for that individual. Any bird that reached its thermal endpoint was removed from the chamber and held in front of an air conditioner producing chilled air, with a cotton pad soaked in ethanol rubbed on the bird's body in order to aid in heat loss (Whitfield et al., 2015).

**Data analyses**

Data were analysed following Whitfield et al. (2015). We present whole-animal values, although in the case of EWL we calculated the slope of mass-specific EWL versus  $T_a$  to facilitate comparisons with the allometric equation presented by McKechnie and Wolf (2010). Rates of EWL were converted to rates of evaporative heat loss (W) assuming a latent heat of vaporisation of water of 2.406 J mg<sup>-1</sup> at 40°C (Tracy et al., 2010). We suspect that birds were post-absorptive at the time of measurements, but were unable to confirm this. Birds were captured early in the morning, with measurements typically starting at mid-morning the same day. Although food was offered, they were never observed feeding in captivity. Each bird's crop was palpated before measurements and in all instances appeared to be empty. Hence, we assumed a respiratory exchange ratio (RER) of 0.71, representative of lipid metabolism in post-absorptive birds (Walsberg and Wolf, 1995), and converted rates of  $\dot{V}_{CO_2}$  to metabolic rate (W) using 27.8 J ml<sup>-1</sup> CO<sub>2</sub> (Withers, 1992).

Broken-stick linear regression models fitted in the R package segmented (Muggeo, 2009) were used to identify inflection points in physiological variables, and linear mixed effects models that included individual identity as a random factor were fitted in the R package nlme (Pinheiro et al., 2009). In the case of RMR, values at

$T_a=25^\circ\text{C}$  were excluded when we fitted a model to identify the inflection point, as visual inspection of the data suggested that this  $T_a$  value fell below the lower critical limit of thermoneutrality (Fig. 1). Values are presented as means $\pm$ s.d.

## RESULTS

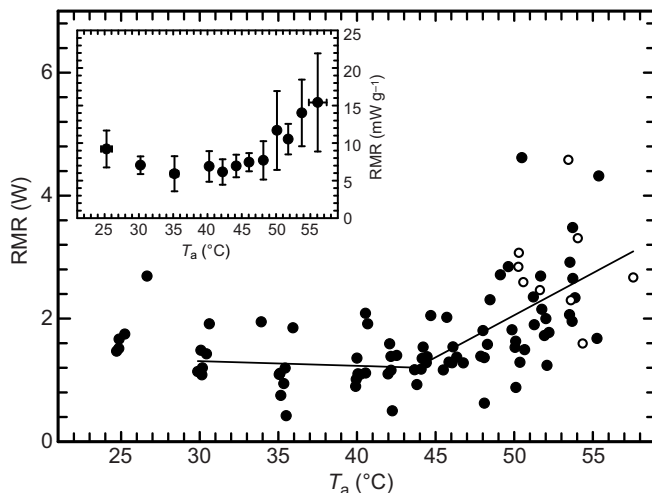
### Body temperature and thermal endpoints

The normothermic  $T_b$  of *P. burchelli* ranged from  $38.80\pm 0.68^\circ\text{C}$  ( $n=5$ ) at  $T_a\sim 25^\circ\text{C}$  to  $39.07\pm 0.67^\circ\text{C}$  ( $n=8$ ) at  $T_a\sim 35^\circ\text{C}$  (Fig. 2), with an overall mean  $T_b$  of  $39.00\pm 0.65^\circ\text{C}$  ( $n=5-8$ ) in the range  $25^\circ\text{C}\leq T_a\leq 35^\circ\text{C}$ . An inflection point in  $T_b$  occurred at  $T_a=34.5^\circ\text{C}$ , above which  $T_b$  increased linearly and significantly ( $t=21.48$ ,  $P<0.001$ ) to a maximum of  $43.61\pm 1.16^\circ\text{C}$  ( $n=3$ ) at  $T_a\sim 56^\circ\text{C}$ . The single highest  $T_b$  value (i.e. mean  $T_b$  over a 5-min period) was  $44.78^\circ\text{C}$ , measured in an individual experiencing  $T_a=53.60^\circ\text{C}$ . There was no significant relationship between  $T_a$  and the rate of  $T_b$  increase during the last 5 min at each  $T_a$  value ( $t=0.23$ ,  $P=0.820$ ). However, mean rates of increase tended to be higher at  $T_a>40^\circ\text{C}$  ( $0.02-0.05^\circ\text{C min}^{-1}$ ) than at  $T_a<40^\circ\text{C}$  ( $0.002-0.01^\circ\text{C min}^{-1}$ ).

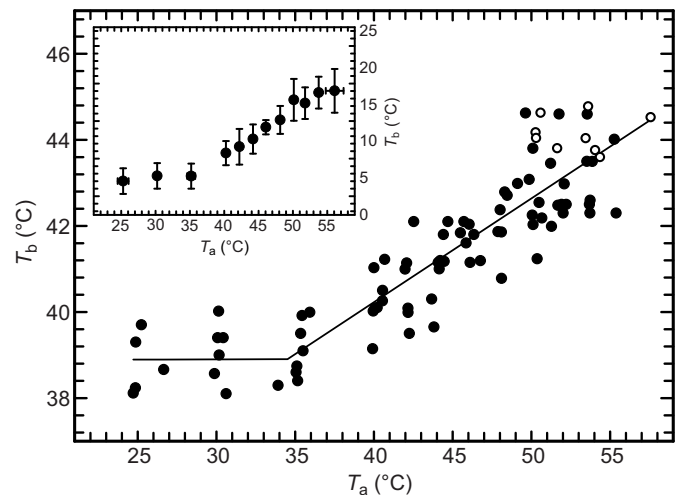
All individuals that reached thermal endpoints did so at  $T_a>50^\circ\text{C}$  (Fig. 2). The  $T_b$  of individuals that reached their thermal endpoint was  $44.15\pm 0.41^\circ\text{C}$ , significantly higher ( $F_{1,18}=7.44$ ,  $P=0.014$ ) than that of individuals that did not ( $42.91\pm 0.89^\circ\text{C}$ ).

### Resting metabolic rate

The minimum RMR within the thermoneutral zone was  $1.162\pm 0.515\text{ W}$  ( $n=8$ ) at  $T_a\sim 35^\circ\text{C}$  (Fig. 1). The inflection point above which RMR increased occurred at  $T_a=43.8^\circ\text{C}$ , which we interpret as the  $T_{uc}$  (Fig. 1). At  $T_a>T_{uc}$ , RMR increased linearly and significantly ( $t=6.19$ ,  $P<0.001$ ) to a maximum of  $2.887\pm 1.335\text{ W}$  ( $n=3$ ) at  $T_a\sim 56^\circ\text{C}$ , equivalent to 2.5 times the minimum thermoneutral RMR. Visual inspection of the data suggests that RMR began to increase with decreasing  $T_a$  at  $T_a\sim 25^\circ\text{C}$  (Fig. 1), but there were



**Fig. 1.** Resting metabolic rate (RMR) of Burchell's sandgrouse (*Pterocles burchelli*) showed an inflection point at an air temperature ( $T_a$ ) of  $43.8^\circ\text{C}$ , corresponding to the upper critical limit of thermoneutrality for this species. Data for individuals that reached their thermal endpoint are shown as open circles. The solid line is the segmented linear regression model that provided the best fit; the relationship between RMR and  $T_a>43.8^\circ\text{C}$  is  $\text{RMR}=0.137T_a-4.800$  ( $r^2$  for segmented regression model=0.414). RMR data measured at  $T_a\sim 25^\circ\text{C}$  were excluded from the regression model-fitting procedure, as this  $T_a$  appeared to fall below the thermoneutral zone. Inset shows mean $\pm$ s.d. mass-specific RMR for  $T_a$  bins of  $2^\circ\text{C}$ . For each bin,  $n=5-12$ , except at  $T_a\sim 56^\circ\text{C}$ , where  $n=3$ .



**Fig. 2.** Body temperature ( $T_b$ ) of Burchell's sandgrouse (*Pterocles burchelli*) as a function of air temperature ( $T_a$ ). Data for individuals that reached their thermal endpoint are shown as open circles. The solid line is the segmented linear regression model that provided the best fit; the relationship between  $T_b$  and  $T_a>34.5^\circ\text{C}$  is  $T_b=0.241T_a+30.58$  ( $r^2$  for segmented regression model=0.818). Inset shows mean $\pm$ s.d.  $T_b$  for  $T_a$  bins of  $2^\circ\text{C}$ . For each bin,  $n=5-12$ , except at  $T_a\sim 56^\circ\text{C}$ , where  $n=3$ .

insufficient data at  $T_a<30^\circ\text{C}$  to fit a segmented regression model and reliably estimate the lower critical limit of thermoneutrality.

The estimated  $T_{uc}$  of  $43.8^\circ\text{C}$  corresponded closely with the onset of panting and gular flutter, which commenced at  $T_a=44.4\pm 1.7^\circ\text{C}$  ( $n=8$ ). Observations of the sandgrouse during measurements revealed that both panting and gular flutter occurred. However, because the surveillance camera was positioned for monitoring overall behaviour during measurements, it was often not possible to distinguish between panting and gular flutter (e.g. when birds were facing away from the camera), and so we were unable to quantify these heat dissipation behaviours separately.

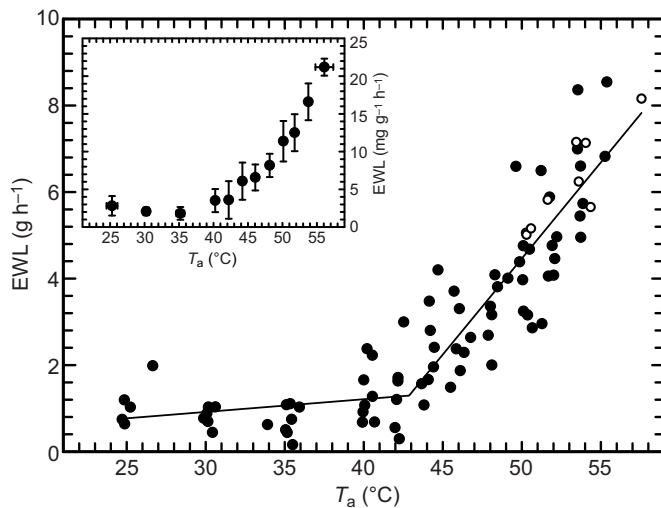
### Evaporative water loss

Rates of EWL were minimal at  $T_a\sim 30^\circ\text{C}$  and  $\sim 35^\circ\text{C}$ , with values of  $0.808\pm 0.225\text{ g h}^{-1}$  ( $n=6$ ) and  $0.710\pm 0.343\text{ g h}^{-1}$  ( $n=8$ ), respectively. An inflection point in EWL occurred at  $T_a=42.9^\circ\text{C}$ , above which EWL increased with increasing  $T_a$  to a maximum of  $7.842\pm 0.903\text{ g h}^{-1}$  ( $n=3$ ) at  $T_a\sim 56^\circ\text{C}$ , equivalent to an 11.0-fold increase over the value at  $T_a\sim 35^\circ\text{C}$  (Fig. 3). EWL at  $T_a\sim 56^\circ\text{C}$  was equivalent to  $4.30\pm 0.23\%$   $M_b\text{ h}^{-1}$ . Above the inflection  $T_a$ , the relationship between mass-specific EWL ( $\text{EWL}_{MS}$ ;  $\text{mg g}^{-1}\text{ h}^{-1}$ ) and  $T_a$  was described by the relationship  $\text{EWL}_{MS}=2.354T_a-94.523$  ( $r^2=0.745$ ).

The mean ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) remained below 1.00 at all  $T_a<44^\circ\text{C}$ , increased to  $1.139\pm 0.302$  ( $n=8$ ) at  $T_a\sim 44^\circ\text{C}$  and reached a maximum value of  $2.029\pm 0.699$  ( $n=3$ ) at  $T_a\sim 56^\circ\text{C}$ . When EHL/MHP was plotted as a function of the  $T_a-T_b$  gradient (Fig. 4), an inflection point was evident at  $T_a-T_b=-3.54^\circ\text{C}$ . Above this inflection point, the  $y$ -intercept of the linear regression model was 0.77; in other words, on average, 77% of MHP was dissipated by evaporation when  $T_b=T_a$ .

## DISCUSSION

Thermoregulation at high  $T_a$  in *P. burchelli* is characterised by relatively low normothermic  $T_b$ , a relatively high  $T_{uc}$  that closely coincides with the onset of panting and gular flutter, rapid increases

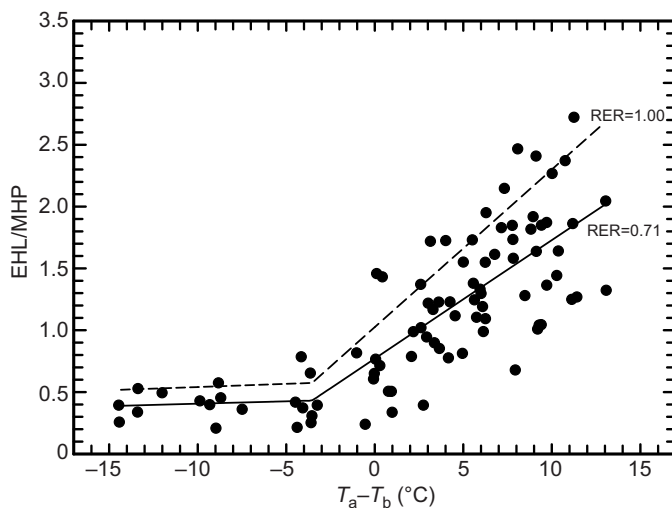


**Fig. 3.** Evaporative water loss (EWL) in Burchell's sandgrouse (*Pterocles burchelli*) increased rapidly above an inflection point at an air temperature ( $T_a$ ) of 42.9°C. Data for individuals that reached their thermal endpoint are shown as open circles. The solid line is the segmented linear regression model that provided the best fit; the relationship between EWL and  $T_a > 42.9^\circ\text{C}$  is  $\text{EWL} = 0.445T_a - 17.76$  ( $r^2$  for segmented regression model = 0.843). Inset shows mean  $\pm$  s.d. mass-specific EWL for  $T_a$  bins of 2°C. For each bin,  $n = 5$ –12, except at  $T_a \sim 56^\circ\text{C}$ , where  $n = 3$ .

in both EWL and RMR with increasing  $T_a$ , and a maximum evaporative cooling capacity within the range typical for other birds investigated to date.

#### Body temperature

The  $T_b$  of *P. burchelli* was relatively stable at  $T_a$  below normothermic  $T_b$ . In contrast, in black-bellied sandgrouse (*P. orientalis*), the



**Fig. 4.** Relationship between the ratio of evaporative heat loss (EHL) and metabolic heat production (MHP) in Burchell's sandgrouse (*Pterocles burchelli*) as a function of the gradient between air temperature ( $T_a$ ) and body temperature ( $T_b$ ). Values were calculated assuming a respiratory exchange ratio (RER) of 0.71, corresponding to lipid metabolism. The solid line is the segmented linear regression model that provided the best fit; the relationship between EHL/MHP and  $T_a - T_b > -3.5^\circ\text{C}$  is  $\text{EHL/MHP} = 0.096(T_a - T_b) + 0.771$  ( $r^2$  for segmented regression model = 0.636). The dashed line is the regression model when the data were recalculated assuming RER = 1.00, corresponding to carbohydrate metabolism. In this case, the relationship is  $\text{EHL/MHP} = 0.128(T_a - T_b) + 1.025$ .

daytime cloacal  $T_b$  of birds in respirometry chambers was linearly related to  $T_a$  between 12 and 43°C, with predicted  $T_b$  of 39.2 and 40.6°C at  $T_a = 25$  and 35°C, respectively (Hinsley et al., 1993). Thomas and Maclean (1981) measured cloacal  $T_b$  of double-banded (*P. bicinctus*) and Namaqua (*P. namaqua*) sandgrouse held in cardboard boxes placed in outdoor aviaries at a site in the Namib Desert. Compared with *P. burchelli*, both of these species maintained higher  $T_b$  at  $T_a \sim 35^\circ\text{C}$  ( $\sim 39.0^\circ\text{C}$ ) [*P. bicinctus*:  $40.0 \pm 0.6^\circ\text{C}$  ( $n = 11$ ); *P. namaqua*:  $40.4 \pm 0.4^\circ\text{C}$  ( $n = 5$ ); Thomas and Maclean, 1981]. The active-phase  $T_b$  of six spotted sandgrouse (*P. senegallus*) at  $T_a = 27^\circ\text{C}$  was  $41.4 \pm 0.6^\circ\text{C}$ , measured in birds in the hand using a hypodermic needle probe inserted into the lower intestinal region (Marder et al., 1986).

The active-phase normothermic  $T_b$  values we recorded in *P. burchelli* are lower than those of four other sandgrouse species. These differences may represent genuine interspecific variation, but we suspect that they instead arise from methodological differences among studies. Data for the four species listed above were all collected using cloacal probes (or hypodermic needle probes in the case of *P. senegallus*), whereas our data were collected using PIT tags injected into the abdominal cavity. Sandgrouse are notorious for being nervous and highly strung study subjects, and in several cases cloacal measurements of  $T_b$  have proven impossible on account of the birds' behaviour (Hinsley, 1992; Hinsley et al., 1993). In light of the nervous disposition of these birds, we suspect the lower  $T_b$  of *P. burchelli* compared with the species investigated previously reflects the fact that in our study birds were unrestrained within respirometry chambers, and did not have cloacal thermocouples inserted and secured to their plumage. It is striking that the highest mean  $T_b$  recorded in sandgrouse at moderate  $T_a$  ( $41.4 \pm 0.6^\circ\text{C}$  in *P. senegallus*) was associated with a measurement protocol likely to be highly stressful, with birds held in the hand and a hypodermic needle probe inserted into their intestinal region (Marder et al., 1986).

The active-phase normothermic  $T_b$  of *P. burchelli* ( $\sim 39.0^\circ\text{C}$ ) is lower than typical avian values; Prinzinger et al. (1991) reported a mean active-phase  $T_b$  for all birds of  $41.02 \pm 1.3^\circ\text{C}$ , and  $T_b = 39^\circ\text{C}$  is well below the typical range for taxa other than ratites (Clarke and Rothery, 2008). However, in view of the potential methodological variation discussed above, it is not possible at this stage to rigorously compare the  $T_b$  values of sandgrouse in general with those of other avian taxa.

At  $T_a$  approaching or exceeding normothermic  $T_b$ , the  $T_b$  of *P. burchelli* increased linearly to maximum values in the 43–45°C range, a response qualitatively similar to other species exposed to the same heat tolerance experimental protocol employed in the present study (Smith et al., 2015; Whitfield et al., 2015). Compared with the  $T_b$  values reported in other sandgrouse at high  $T_a$ , those we measured in *P. burchelli* were relatively high. For instance, at  $T_a \sim 50^\circ\text{C}$ , the mean  $T_b$  of 43.1°C in *P. burchelli* compares with 41.6°C in *P. bicinctus* and 41.0°C in *P. namaqua* (Thomas and Maclean, 1981), and 42.6°C in *P. senegallus* (Marder et al., 1986).

The  $T_b$  values (44–45°C) associated with thermal endpoints in *P. burchelli* are in the same range as those reported for three southern African ploceid passerines (Whitfield et al., 2015) and southern African and Australian doves (McKechnie et al., 2016), but slightly lower than those of one North American quail and two doves (45–46.1°C; Smith et al., 2015). The significantly higher  $T_b$  in sandgrouse that reached thermal endpoints compared with those that did not is consistent with the argument that these  $T_b$  values are close to the birds' critical thermal maxima. As was the case for the

passerines examined by Whitfield et al. (2015), patterns of  $T_b$  in *P. burchelli* appear to conform approximately to generalized biphasic models of heat stroke during acute heat stress (Leon, 2006), where initial increases in  $T_b$  of 2–4°C are followed by the regulation of approximately constant hyperthermic  $T_b$ , after which thermoregulatory breakdown is associated with rapid, unregulated increases in  $T_b$  toward lethal levels. A visual examination of the trajectory of  $T_b$  during acute heat stress in *P. burchelli* reinforces this impression, as  $T_b$  appears to reach a plateau at  $T_a > 50^\circ\text{C}$  (Fig. 2 inset).

### Resting metabolic rate

The  $T_{uc}$  of 43.8°C we observed in *P. burchelli* is higher than typical avian  $T_{uc}$  values (e.g. Calder and Schmidt-Nielsen, 1967; Dawson and Bennett, 1973; McNab and Bonaccorso, 1995; Tieleman and Williams, 2002; Weathers, 1981). The fact that in *P. burchelli* the thermoneutral zone extends to several degrees above normothermic  $T_b$  confirms the findings of workers who previously investigated the thermal physiology of sandgrouse: Hinsley and colleagues were unable to reliably define daytime  $T_{uc}$  values for *P. orientalis*, *P. alchata* or *P. burchelli* based on measurements of RMR over a  $T_a$  range extending up to ~43°C (Hinsley, 1992; Hinsley et al., 1993). Moreover, these results are also consistent with behavioural data indicating that heat dissipation behaviours commence only at  $T_a$  well above  $T_b$  (Thomas and Maclean, 1981; Thomas and Robin, 1977).

The inflection in RMR that defined the  $T_{uc}$  of *P. burchelli* coincided very closely with the mean  $T_a$  at which birds began to pant and/or gular flutter within respirometry chambers. This observation suggests strongly that the increase in RMR at high  $T_a$  primarily reflects the energetic cost of these processes, and that patterns of RMR at high  $T_a$  in this species conform well to the classic Scholander–Irving model of endothermic homeothermy (Scholander et al., 1950a,b). A combination of panting and gular flutter has also been reported in other sandgrouse species (Marder et al., 1986).

Contrary to our prediction that evaporative cooling in *P. burchelli* is highly efficient, fractional increases in RMR at  $T_a > T_{uc}$  were relatively large: RMR increased by ~150% above thermoneutral values at  $T_a = 56^\circ\text{C}$ . This increase is substantially greater than those of 30%, 35% and 60% in three ploceid passerines that reached  $T_a$  values of 48–54°C under similar experimental conditions (Whitfield et al., 2015), or the corresponding increases in RMR at  $T_a$  values of 56–62°C in Gambel's quail (*Callipepla gambelli*) and six species of columbids from North America, Australia and southern Africa (Smith et al., 2015; McKechnie et al., 2016).

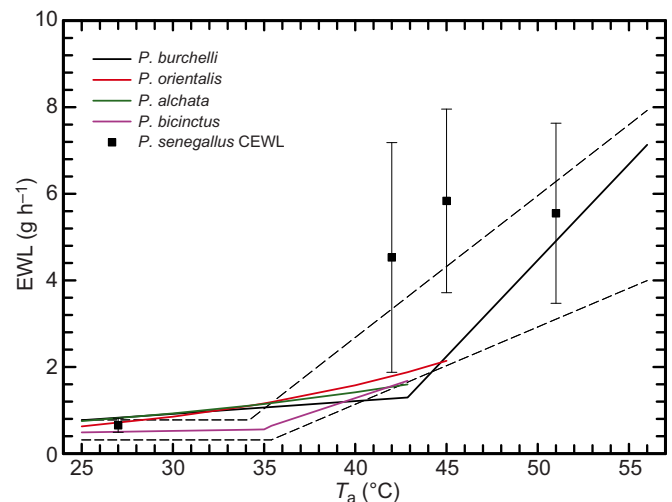
Increases in avian RMR at  $T_a$  above the thermoneutral zone presumably comprise the effect of increasing  $T_b$  on metabolism plus the energetic cost of evaporative cooling mechanisms. Within the thermoneutral zone of *P. burchelli*, the  $Q_{10}$  for RMR (calculated from mean RMR and  $T_b$  values at  $T_a = 35$  and 44°C) was 2.2. Assuming the same  $Q_{10}$  at  $T_a > T_{uc}$ , we estimate that just 17% of the increase in RMR between  $T_a = 46$  and 54°C was attributable to increases in  $T_b$ . This relatively small contribution of temperature effects is consistent with the argument that increases in RMR above the thermoneutral zone primarily reflect the energetic cost of evaporative cooling pathways such as panting. In general, the temperature dependence of avian RMR during hyperthermia remains unclear; whereas the  $Q_{10}$  for RMR in *P. burchelli* is similar to those expected for biological processes in general (Withers, 1992), data for other species suggest lower  $Q_{10}$  values, which in some cases may be close to 1 (i.e. independent of  $T_b$ ; e.g. see table 3 of Smith et al., 2015).

The minimum daytime RMR of the 193-g *P. burchelli* is similar to the corresponding values reported for other similar-sized sandgrouse: 0.731 W (*P. burchelli*; 197 g) to 0.981 W (*P. alchata*; 243 g; Hinsley, 1992; Hinsley et al., 1993). As our measurements took place during the day (i.e. active phase), we could not estimate the basal metabolic rate of this species.

### Evaporative water loss

Minimal EWL at thermoneutrality in *P. burchelli* (0.710 g h<sup>-1</sup> at  $T_a \approx 35^\circ\text{C}$ ) is equivalent to 187% of the value predicted by Williams' (1996) conventional equation for arid-zone birds, and 183% of the value predicted by his phylogenetically independent equation for all birds. Compared with the predictions of Williams' conventional equation, in other sandgrouse species EWL at  $T_a = 25^\circ\text{C}$  varies from close to expected to well above expected (*P. orientalis*: 98%; *P. alchata*: 166%). Thus, there appears to be no clear pattern among the sandgrouse for which data are currently available in terms of how EWL at moderate  $T_a$  compares with allometrically expected values.

The inflection point in EWL in *P. burchelli* occurred at  $T_a \approx 43^\circ\text{C}$ , nearly 4°C above normothermic  $T_b$  and at a much higher value than would be expected for a 193-g bird (35.1°C; McKechnie and Wolf, 2010, see their supplementary material). This high inflection in EWL is surprising, but consistent with the relatively modest increases in EWL above baseline levels observed in other sandgrouse at  $T_a$  values of 40–45°C (Hinsley, 1992; Hinsley et al., 1993) (Fig. 5). A high inflection  $T_a$  for EWL could also explain why the relationships between EWL and  $T_a$  in *P. orientalis* and *P. alchata* were best described by logarithmic curves (Hinsley et al., 1993), although Hinsley (1992) documented an inflection point at  $T_a = 35^\circ\text{C}$  in *P. burchelli*.



**Fig. 5. Evaporative water loss (EWL) as function of air temperature ( $T_a$ ) in four species of sandgrouse.** Data are shown for *Pterocles burchelli* (black line; present study), *P. orientalis* (red line; Hinsley et al., 1993), *P. alchata* (green line; Hinsley et al., 1993) and *P. burchelli* (pink line; Hinsley, 1992). Also shown are cutaneous evaporative water loss (CEWL) rates measured in *P. senegallus* (squares; mean  $\pm$  s.d.; Marder et al., 1986). The area between the dashed lines shows the range of EWL predicted for birds with body masses ( $M_b$ ) between 150 and 500 g (the approximate  $M_b$  range of sandgrouse; de Juana, 1997). These rates of EWL are based on predicted rates at moderate  $T_a$  (conventional equation for arid-zone birds; Williams, 1996), predicted inflection points at which EWL begins to rapidly increase (McKechnie and Wolf, 2010) and the predicted slopes of EWL versus high  $T_a$  (McKechnie and Wolf, 2010).

Above  $T_a=43^\circ\text{C}$ , the slope of mass-specific EWL versus  $T_a$  in *P. burchelli* was much steeper than predicted by a recent analysis of the scaling of avian EWL (McKechnie and Wolf, 2010, see their supplementary material). The observed slope of  $2.354\text{ mg g}^{-1}\text{ h}^{-1}\text{ }^\circ\text{C}^{-1}$  is equivalent to 224% of the expected slope for a 193-g bird, at odds with our expectation that this species should show a relatively shallow slope and hence small increases in EWL. In sharp contrast, the slopes for *P. orientalis*, *P. alchata* and *P. bicinctus* were all well below (29–70%) allometrically expected values (McKechnie and Wolf, 2010). However, this comparison likely reflects the much higher  $T_a$  values to which birds were exposed in the present study compared with previous work; Hinsley (1992) and Hinsley et al. (1993) exposed birds to maximum  $T_a$  of  $42\text{--}45^\circ\text{C}$ , temperatures at which EWL in *P. burchelli* was only just beginning to increase (Fig. 5). The lower maximum  $T_a$  in the latter two studies is probably the major reason for this difference in slopes.

The maximum evaporative cooling capacity of *P. burchelli* (i.e. the maximum EHL/MHP ratio) was estimated as 2.029, with a  $y$ -intercept of 0.770 for EHL/MHP versus  $T_a$  (Fig. 4). These calculations are based on an assumed RER=0.71, corresponding to lipid metabolism. However, if we recalculate RMR assuming RER=1.00 [i.e. a thermal equivalence of  $20.9\text{ J ml}^{-1}\text{ CO}_2$  (Withers, 1992), in which case estimated RMRs are 24.8% lower than reported above], the maximum EHL/MHP increases to 2.699, and the  $y$ -intercept increases to 1.025 (Fig. 4). The latter value is almost exactly that expected in theoretical grounds (the defence of a  $T_b$  setpoint equal to  $T_a$  requires that 100% of metabolic heat production is dissipated evaporatively). Whereas we are confident that the sandgrouse were post-absorptive during measurements and hence likely metabolising lipids, the latter result raises the possibility that this assumption is incorrect. Previous work on the thermal physiology of sandgrouse does not shed any light; EHL/MHP in *P. orientalis* was well below 1.0 when  $T_a$  was approximately equal to  $T_b$ , but was approximately equal to 1.0 in *P. alchata* and *P. bicinctus* (Hinsley, 1992; Hinsley et al., 1993). This uncertainty regarding maximum EHL/MHP and the  $y$ -intercept illustrates a largely unavoidable limitation of our approach to measuring avian heat tolerance at extremely high  $T_a$ : the high flow rates required to keep chamber humidity low preclude accurate measurements of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ) and hence RER. The potential error associated with converting  $\dot{V}_{\text{CO}_2}$  to metabolic rate in the absence of accurate RER measurements is almost threefold greater than is the case for  $\dot{V}_{\text{O}_2}$  (Walsberg and Wolf, 1995).

One factor critical in interpreting relationships between avian EWL and RMR at high  $T_a$  is the primary avenue of evaporative heat dissipation. Birds generally rely on either respiratory evaporative water loss (REWL) or cutaneous evaporative water loss (CEWL) as the primary mode of evaporative heat dissipation when  $T_a>T_b$  (Hoffman and Walsberg, 1999; Marder and Arieli, 1988; McKechnie and Wolf, 2004; Ro and Williams, 2010; Tieleman and Williams, 2002; Wolf and Walsberg, 1996a). A comparison of passerines and columbids suggests that the primary mode of evaporative heat dissipation has important consequences for heat tolerance and evaporative cooling capacity, with CEWL-dominated cooling allowing for more efficient cooling and the capacity to handle higher maximum  $T_a$  compared with REWL-dominated cooling (McKechnie et al., 2016).

To the best of our knowledge, the only investigation of the relative importance of REWL versus CEWL in sandgrouse is that of Marder et al. (1986), who combined measurements of the diffusive resistance of breast skin in spotted sandgrouse (*P. senegallus*) with temperature data to estimate area-specific rates of CEWL. However,

when these CEWL estimates for *P. senegallus* are converted to whole-animal rates (using a predicted surface area of  $408\text{ cm}^2$ ; Walsberg and King, 1978), they prove puzzling. Marder et al. (1986) reported an almost sevenfold increase in CEWL between  $T_a=27^\circ\text{C}$  and  $T_a=42^\circ\text{C}$  to a value that is between twofold and threefold higher than total evaporative water loss (TEWL) in other sandgrouse at comparable  $T_a$  values (Fig. 5). Estimated CEWL for *P. senegallus* then increases to values approximately threefold higher than TEWL for congeners at  $T_a=45^\circ\text{C}$ , before decreasing slightly at  $T_a=51^\circ\text{C}$  (Marder et al., 1986) (Fig. 5). Because of these quantitative discrepancies between CEWL in *P. senegallus* and TEWL in other sandgrouse, we suspect that Marder et al. (1986) may have greatly overestimated rates of cutaneous evaporation.

On the basis of their reported rates of CEWL in *P. senegallus*, Marder et al. (1986) argued that sandgrouse are similar to columbids in that CEWL is the primary mode of heat dissipation at very high  $T_a$ . However, our data for *P. burchelli* suggest the opposite: the close match between the upward inflection in RMR at the  $T_{uc}$  and the onset of panting and gular flutter, together with the rapid increases in RMR with increasing  $T_a$  to rates equivalent to  $\sim 2.5$  times the thermoneutral RMR, comprise the pattern expected if respiratory evaporation is the primary mode of heat dissipation at  $T_a>T_b$ .

## Conclusions

Several authors have noted that sandgrouse tolerate heat loads that are among the most extreme faced by any birds (reviewed by Thomas, 1984), and the behavioural and physiological mechanisms sandgrouse use to thermoregulate under very hot conditions have received considerable attention (Dixon and Louw, 1978; Thomas and Maclean, 1981; Thomas and Robin, 1977). Our data on heat tolerance and evaporative cooling in *P. burchelli* reveal that, during acute heat stress, this species can tolerate  $T_a$  up to  $\sim 56^\circ\text{C}$ . They also suggest that sandgrouse may have lower normothermic  $T_b$  than many other birds, and likely cannot tolerate  $T_b$  exceeding  $45^\circ\text{C}$ . Increases in EWL and RMR occur at higher  $T_a$  than typical for birds, with the thermoneutral zone extending to  $43.8^\circ\text{C}$  in *P. burchelli*, also the approximate  $T_a$  at which panting and gular flutter commence. These findings may explain the observations of several authors who found that heat dissipation behaviours in sandgrouse are delayed to  $T_a$  well above  $T_b$  (Thomas, 1984; Thomas and Maclean, 1981; Thomas and Robin, 1977). These high inflection points for EWL and RMR may also be related to ptiloerection and huddling, behaviours characteristic of sandgrouse at  $T_a>T_b$  (Thomas and Maclean, 1981).

We exposed sandgrouse to  $T_a$  much higher than was the case in most previous studies (Hinsley, 1992; Hinsley et al., 1993). One unexpected pattern to emerge is that the metabolic costs of thermoregulation at  $T_a>T_{uc}$  are substantial in *P. burchelli*; RMR at the highest  $T_a$  tolerated was equivalent to  $\sim 250\%$  of minimal thermoneutral values, a much greater fractional increase than in passerines or columbids (Smith et al., 2015; Whitfield et al., 2015; McKechnie et al., 2016). Moreover, the slope of the relationship between EWL and  $T_a$  was much steeper than expected. These observations were surprising because, *a priori*, we expected sandgrouse to possess very efficient evaporative cooling mechanisms. These data also suggest that REWL is probably the major avenue of evaporative heat loss at high  $T_a$ , contrary to the arguments of Marder et al. (1986). Sandgrouse hence appear to lack evaporative cooling mechanisms comparable in efficiency to those found in taxa such as columbids and caprimulgids. In these groups, increases in metabolic rate at  $T_a>T_b$  are very small, with RMR often remaining indistinguishable from thermoneutral values until

$T_a > 50^\circ\text{C}$  (Dawson and Fisher, 1969; Smith et al., 2015; McKechnie et al., 2016; R. S. O'Connor, B.O.W., R. M. Brigham and A.E.M. unpublished data).

We can only speculate as to why similarly efficient CEWL-dominated cooling seems not to have evolved in sandgrouse. One possibility is that the water demands for CEWL-dominated cooling are not sustainable for birds that typically forage far from water and visit water sources to drink only once a day, usually in the early morning (de Juana, 1997), and in the case of *P. burchelli* typically 2–3 h after sunrise (Lloyd, 2005). When foraging during the heat of the day, sandgrouse therefore likely experience strong trade-offs between activity, heat storage and EWL. We hypothesise that evaporative cooling dominated by REWL facilitates delaying the initiation of rapid evaporative heat dissipation. According to this reasoning, as  $T_a$  exceeds  $T_b$ , sandgrouse initially minimise heat loss via mechanisms such as ptiloerection and huddling, and only commence gular flutter and panting when  $T_a$  is well above  $T_b$ . It is perhaps relevant that columbids with very high evaporative cooling capacities, such as Namaqua doves (*Oena capensis*), in which EHL/MHP ratios can approach 5 (McKechnie et al., 2016), are seldom seen far from water during the hottest part of the day (Dean, 2005).

In summary, the heat tolerance of Burchell's sandgrouse is impressive, with individuals tolerating  $T_a$  up to  $\sim 56^\circ\text{C}$  when exposed to acute heat stress under laboratory conditions. However, tolerance of very high  $T_a$  involves large fractional increases in rates of evaporation and metabolism, making evaporative cooling in this species considerably less efficient than in groups such as columbids and caprimulgids. The high rates of EWL required for thermoregulation under extremely hot conditions, combined with maximum  $T_b$  limits that are not above the typical avian range, may partly explain the strong dependence of sandgrouse on often-distant water sources.

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#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

B.O.W. and A.E.M. designed the study. B.S., M.C.W., M.J.N., W.A.T., M.G. and B.O.W. collected data. A.R.G., A.E.M. and M.C.W. analysed the data. A.E.M. and B.O.W. wrote the manuscript.

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