RESEARCH ARTICLE

Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines

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ABSTRACT

Many birds can defend body temperature (T_b) far below air temperature (T_a) during acute heat exposure, but relatively little is known about how avian heat tolerance and evaporative cooling capacity varies with body mass (M_b), phylogeny or ecological factors. We determined maximum rates of evaporative heat dissipation and thermal end points (T_b and T_a associated with thermoregulatory failure) in three southern African ploceid passerines, the scaly-feathered weaver (*Sporopipes squamifrons*, $M_b \approx 10$ g), sociable weaver (*Philetairus socius*, $M_b \approx 25$ g) and white-browed sparrow-weaver (*Plocepasser mahali*, $M_b \approx 40$ g). Birds were exposed to a ramped profile of progressively increasing T_a, with continuous monitoring of behaviour and T_b used to identify the onset of severe hyperthermia. The maximum T_a birds tolerated ranged from 48°C to 54°C, and was positively related to M_b. Values of T_b associated with severe heat stress were in the range of 44 to 45°C. Rates of evaporative water loss (EWL) increased rapidly when T_a exceeded T_b, and maximum evaporative heat dissipation was equivalent to 141–222% of metabolic heat production. Fractional increases in EWL between $T_a < 40°C$ and the highest T_a reached by each species were 10.8 (*S. squamifrons*), 18.4 (*P. socius*) and 16.0 (*P. mahali*). Resting metabolic rates increased more gradually with T_a than expected, probably reflecting the very low chamber humidity values we maintained. Our data suggest that, within a taxon, larger species can tolerate higher T_a during acute heat stress.

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

INTRODUCTION

The ability to maintain body temperature (T_b) below lethal levels when exposed to environmental temperatures that exceed T_b is a prerequisite for the occupancy of hot, arid habitats by diurnal animals. Daytime air temperatures (T_a) in many deserts routinely exceed the normothermic T_b of mammals and birds (Dawson and Schmidt-Nielsen, 1964; Serventy, 1971) and even when T_a remains below T_b, the additional heat load associated with exposure to solar radiation can result in operative temperatures (*sensu* Bakken, 1976; Robinson et al., 1976) far above T_b, particularly in small species (King and Farner, 1961; Wolf and Walsberg, 1996b). Birds provide

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some of the most striking examples of organisms that survive and breed in extremely hot, inhospitable environments (Grant, 1982; Tieleman et al., 2008).

Evaporative heat dissipation is the only avenue of heat flux that permits the defence of a T_b set point substantially below environmental temperature (Dawson and Whittow, 2000). At present, relatively little is known about avian upper thermoregulatory limits and capacities for evaporative cooling during acute exposure to T_a far above T_b. Several authors have measured rates of evaporative water loss (EWL) and T_b during acute heat exposure at $T_a \geq 50°C$ (Dawson and Fisher, 1969; Tieleman et al., 2002b; Wolf and Walsberg, 1996a; Marder, 1973) and occasionally, $T_a \approx 60°C$ (Marder and Arieli, 1988). Although these studies show that some birds can successfully defend T_b at levels 15–20°C below T_a, it remains largely unknown how heat tolerance scales with body mass, varies across taxa, and/or correlates with ecological variables.

Avian lethal body temperatures are generally thought to be in the 46–48°C range (Arad and Marder, 1982; Brush, 1965; Dawson, 1954; Randall, 1943), although many of these data are from domestic chickens rather than wild birds. Considerably less information is available on the T_b at which normal behaviors (e.g. the capacity for coordinated movement) become compromised, which in towhees (*Piplio* spp.) occurred at $T_b > 45°C$ (Dawson, 1954). Interactions between T_b and behaviour at very high T_a remain largely unexplored in birds.

A priori, body mass (M_b) may be expected to have a strong influence on upper thermoregulatory limits. At T_a values approaching or exceeding normothermic T_b, the slope of EWL as a function of T_a scales negatively with M_b, such that EWL increases much more rapidly with increasing T_a in small birds compared with larger species (McKechnie and Wolf, 2010). The latter observation leads to the prediction that small birds should be better able to cope with extremely high T_a, on account of the larger fractional increases in EWL. However, the negative scaling of mass-specific EWL also means that, in the absence of water intake, small birds may reach dehydration tolerance limits sooner, giving rise to a second prediction in the opposite direction. Moreover, resting metabolic rate (RMR) increases more rapidly with temperatures above the upper critical values in small species (Weathers, 1981).

Another factor that is likely to have a strong influence is the relative contribution of respiratory and cutaneous pathways to overall EWL. Increases in respiratory evaporative water loss (REWL) at high T_a usually involve muscle contractions (and hence increased heat production) for panting and/or gular flutter (Calder and Schmidt-Nielsen, 1967; Dawson, 1982) and so may be a less efficient cooling mechanism than cutaneous evaporative water loss (CEWL). This notion is supported by lower resting metabolic rate (RMR) at $T_a \approx 45°C$ in heat-acclimated white-winged doves (*Zenaida asiatica*) with elevated CEWL compared with

List of symbols and abbreviations

EHL	evaporative heat loss
EWL	evaporative water loss
M_b	body mass
MHP	metabolic heat production
RER	respiratory exchange ratio
RMR	resting metabolic rate
T_a	air temperature
T_b	body temperature
$T_{b,max}$	maximum body temperature
$\dot{V}_{CO_2}$	rate of CO_2 production

cool-acclimated conspecifics (McKechnie and Wolf, 2004). However, systematic comparisons of the efficiency of evaporative heat dissipation across taxa varying in the relative contributions of REWL and CEWL are lacking.

In this study, we investigated the scaling of upper thermal limits and maximum evaporative cooling capacity during acute heat exposure in three passerine birds representing approximately four-fold variation in M_b. Evaporative heat dissipation in passerines experiencing high T_a is dominated by REWL associated with panting (Ro and Williams, 2010; Tieleman and Williams, 2002; Wolf and Walsberg, 1996a). The available literature (1944–2014) on thermoregulation in heat-stressed passerine birds, defined here as exposure to $T_a>40°C$, encompasses approximately 31 species, and varies widely in methodologies and scope. The responses of most species (26) have been measured at $T_a=40–45°C$ and only four species have been exposed to $T_a=47–52°C$ (e.g. Williams, 1999; Wolf and Walsberg, 1996a,b). The measurement conditions, sample sizes and activity states of the individuals also vary greatly among studies. Sample sizes vary from 4 to 71 individuals, with most species acclimated to $T_a=18–25°C$ for weeks or months (e.g. Rising, 1969; Tieleman and Williams, 2002), although 11 species were acclimated to warm/hot summer temperatures prior to experiments (e.g. Hinds and Calder, 1973; Weathers and Greene, 1998). About two-thirds of the species were measured during the rest phase of their daily cycle, and the sequence and number of exposure temperatures are unstated in most studies. Metabolic chamber humidity is also of considerable importance during measurements of thermoregulatory performance because of its effects on rates of water loss and increase of T_b (Lasiewski et al., 1966; Gerson et al., 2014); chamber relative humidity was <20% for 13 species and 21–65% for the remainder.

In light of the limited sampling of passerines (only 31 of 6000+ extant species) at $T_a>40°C$, and the variability in the methods and conditions used in prior studies, we made an effort to provide standardized conditions appropriate for birds living in hot deserts during summer. We restricted the study to members of a single passerine family, namely the Ploceidae. All individuals were captured in a single habitat in summer, in an effort to minimize the effects of variables other than M_b on our results and ensure that birds were maximally heat-acclimatized. To ensure comparability among species, we measured variables in birds experiencing a standardized ramped T_a profile in combination with very low chamber absolute humidities that provided minimal impediment to evaporative heat dissipation.

RESULTS

Scaly-feathered weavers

The RMR of *S. squamifrons* decreased from 24 ± 1.1 mW g^{-1} at $T_a=25°C$ to 15.4 ± 4.2 mW g^{-1} at $T_a=30°C$ (Fig. 1A). Above $T_a=35°C$, RMR increased linearly and significantly ($t_{1,24}=6.95$,

$P<0.001$) to 19.9 ± 3.5 mW g^{-1} at $T_a=48°C$ (Fig. 1A, Table 1). At $25<T_a<39°C$, EWL was consistently low, averaging 4.0 ± 2.9 mg g^{-1} h^{-1} (Fig. 2A). Above $T_a=40°C$, EWL increased linearly and significantly ($t_{1,18}=16.14$, $P<0.001$) with increasing T_a to 43.2 ± 6.2 mg g^{-1} h^{-1} at $T_a=48°C$, representing a 10.8-fold increase (Fig. 2A, Table 1).

Above $T_a=40°C$, the percentage of metabolic heat production (MHP) dissipated evaporatively increased linearly and significantly from $15\pm13\%$ to $141\pm39\%$ at $T_a=48°C$ ($t_{1,18}=9.95$, $P<0.001$, Fig. 3A, Table 1). Evaporative capacity in calm scaly-feathered weavers appeared to reach a maximum at high T_a values, with evaporative dissipation as a percentage of MHP increasing by 34% between $T_a=44$ and 46°C, but by only 14% between $T_a=46$ and 48°C.

Mean T_b averaged $40.1\pm0.74°C$ at all $T_a<35°C$, but began to increase significantly ($t_{1,17}=9.9$, $P<0.001$) at a rate of 0.37°C per
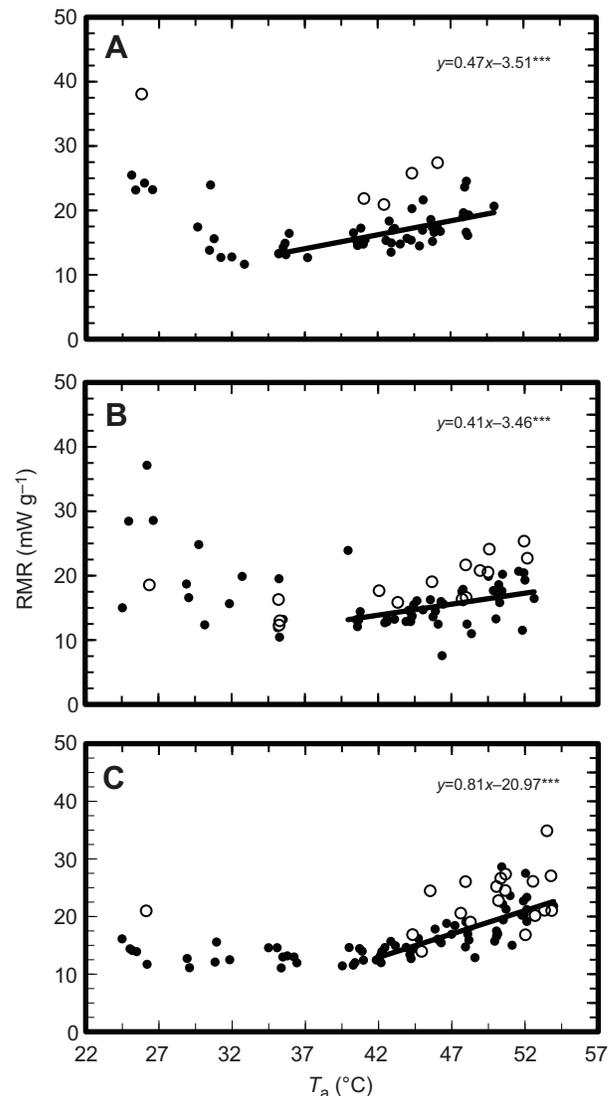
Fig. 1. Resting metabolic rate (RMR) in three species of African weavers over a range of air temperatures (T_a). (A) Scaly-feathered weavers ($N=15$). (B) Sociable weavers ($N=25$). (C) White-browed sparrow-weavers ($N=31$). Data from calm and active birds are shown by filled and open circles, respectively. Segmented regressions were used to estimate the inflection point in the relationship between RMR and T_a for calm birds only. Statistical analyses were performed on data from calm birds to determine coefficients for the linear relationships above inflection points. **$P\leq0.01$, ***$P\leq0.001$.

Table 1. Data for calm African weavers at the highest shared air temperature (T_a) at which all species were tested (~48°C)

	White-browed sparrow-weaver	Sociable weaver	Scaly-feathered weaver
N	8	6	6
T_b (°C)	43.0±0.5	44.1±0.4	44.7±0.6
$T_{b,max}$ (°C)	43.2±0.5	44.3±0.3	44.9±0.8
Rate of increase of T_b (°C min^{-1})	0.034±0.024	0.030±0.022	0.056±0.047
EWL (mg g^{-1} h^{-1})	38.51±4.80	37.47±3.76	43.22±6.24
RMR (mW g^{-1})	16.78±2.14	15.24±2.84	19.93±3.50
EHL/MHP	1.46±0.23	1.61±0.44	1.41±0.39

T_b, body temperature; $T_{b,max}$, maximum body temperature; EWL, evaporative water loss; RMR, resting metabolic rate; EHL, evaporative heat loss; MHP, metabolic heat production. Rate of increase of T_b is given over ~10 min period. All data are means±s.d.

1°C increase in T_a at $T_a \approx 35$°C (Fig. 4A). At T_a=48°C, mean T_b was 44.7±0.6°C (Fig. 4A, Table 1). The relationship between T_a and the rate of T_b increase was not significant ($t_{1,5}$=0.97, P=0.38), with no consistent pattern over the ~10 min period before removal from the chamber (Fig. 5). Between T_a=44 and 48°C, however, a number of birds displayed higher rates of T_b increase (up to 0.12°C min^{-1}), compared with those observed at lower T_a (Fig. 5). At T_a=48°C, rate of T_b increase averaged 0.06±0.05°C min^{-1} (Fig. 5A, Table 1).

For scaly-feathered weavers, when T_a was 3–5°C lower than T_b, evaporative heat loss (EHL) was 2.6±0.4 mW g^{-1}. EHL increased as T_a approached T_b, averaging 14±1.2 mW g^{-1} when $T_a \approx T_b$ and increasing significantly at a rate of 3.78 mW g^{-1} °C^{-1} ($t_{1,15}$=8.49, P<0.001). EHL averaged 25.3±2.1 mW g^{-1} when T_a exceeded T_b by 3–4°C (i.e. when $T_a \approx 48$°C).

Thermal end point was reached at T_a=44°C by 11% of individuals, increasing to 14% at T_a=46°C and 57% at T_a=48°C (Fig. 6). We were unable to experimentally determine the T_a at which 100% of scaly-feathered weavers reached their thermal end point, and can therefore only estimate that it would probably have occurred by $T_a \approx 50$°C (Fig. 6). Among the birds that reached their thermal end point, mean T_b was 44.6±0.6°C, mean maximum body temperature ($T_{b,max}$) was 45.5±0.6°C and mean EHL/MHP was 1.32±0.36 (Table 1).

Sociable weavers

Between T_a=25 and 35°C, the RMR of *P. socius* generally decreased, although there was considerable variation among individuals (Fig. 1B). At T_a>35°C, RMR increased linearly and significantly ($t_{1,22}$=3.25, P<0.01) from 13.2±0.8 mW g^{-1} at T_a=40°C to 17.7±3.8 mW g^{-1} at T_a=52°C (Fig. 1B). At T_a<40°C, EWL was low and stable, averaging 3.4±1.8 mg g^{-1} h^{-1} (Fig. 2B). Above T_a=40°C, EWL increased linearly and significantly ($t_{1,14}$=10.37, P<0.001) to 62.6±16.1 mg g^{-1} h^{-1} at T_a=52°C, an 18.4-fold increase above the levels at T_a<40°C (Fig. 2B, Table 1). Above T_a=40°C, the percentage MHP dissipated evaporatively increased linearly and significantly ($t_{1,22}$=9.85, P<0.001) to 222±26% at T_a=52°C (Fig. 3B, Table 1). The latter variable increased by 41% between T_a=48 and 50°C, and by 20% between T_a=50 and 52°C.

Mean T_b averaged 41.3±1.1°C at T_a<40°C and increased significantly ($t_{1,19}$=11.19, P<0.001) when T_a>40°C at a rate of 0.32°C per 1°C increase in T_a (Fig. 4B). At T_a=48°C, mean T_b was 44.3±0.3°C (Fig. 4B, Table 1), compared with 44.7±0.5°C when T_a=52°C (Fig. 4B). Over ~10 min at a given T_a, T_b remained fairly constant with a mean change of 0.003±0.033°C min^{-1} when T_a<48°C (Fig. 5B). However, the rate of change in T_b increased significantly at T_a>48°C ($t_{1,4}$=4.37, P<0.05), reaching a maximum of 0.12±0.04°C min^{-1} at T_a=52°C (Fig. 5B).
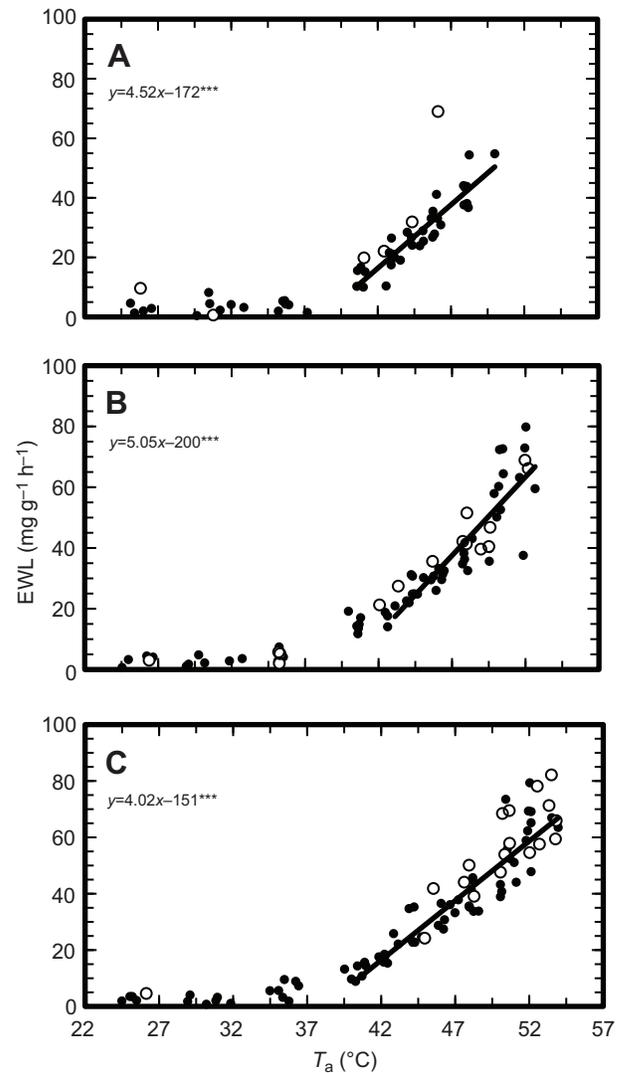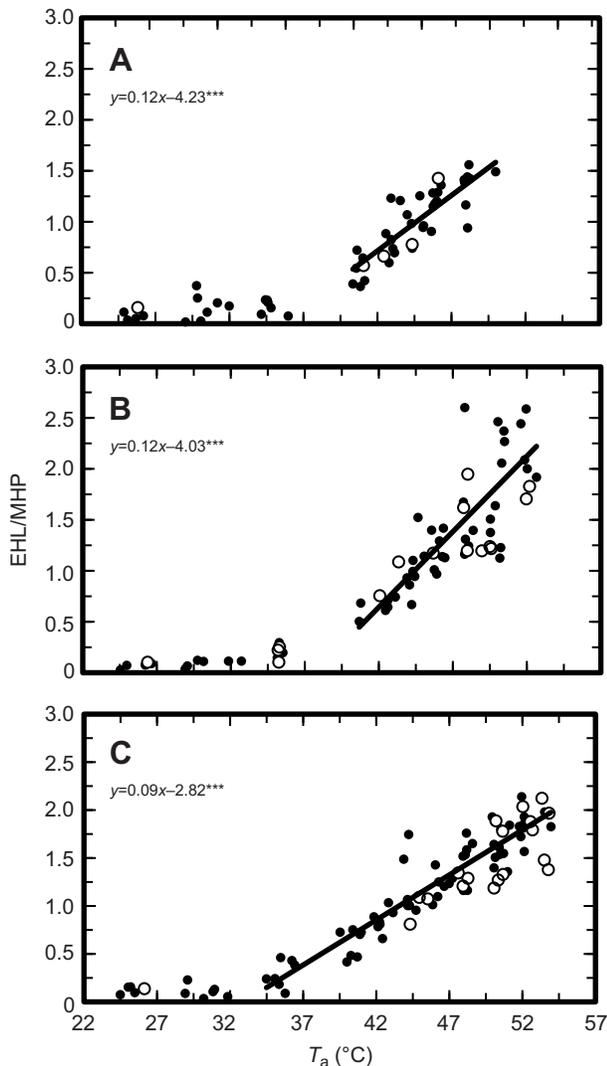

Fig. 2. Evaporative water loss (EWL) in three species of African weavers over a range of air temperatures (T_a). (A) Scaly-feathered weavers (N=15). (B) Sociable weavers (N=25). (C) White-browed sparrow-weavers (N=31). Data from calm and active birds are shown by filled and open circles, respectively. Segmented regressions were used to estimate the inflection point in the relationship between EWL and T_a for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. ***P≤0.001.

EHL in sociable weavers began to increase significantly ($t_{1,9}$=8.48, P<0.001) from 3.96 mW g^{-1} °C^{-1} when $T_a \approx T_b$ to 24.1±2.0 mW g^{-1} to a maximum of 39.3±10.1 mW g^{-1} when T_a exceeded T_b by 6–9°C at T_a=52°C. Thermal end points were reached by 67% of sociable weavers at T_a=50°C, increasing to 100% at T_a=52°C (Fig. 6). For the birds that reached their thermal end point at T_a=52°C, mean T_b, mean $T_{b,max}$ and EHL/MHP were 44.5±0.5°C, 45.3±0.4°C and 2.09±0.30, respectively.

White-browed sparrow-weavers

At 25<T_a<40°C, the RMR of *P. mahali* remained approximately constant, averaging 13.4±1.4 mW g^{-1} (Fig. 1C). Above T_a=40°C, RMR increased linearly and significantly ($t_{1,19}$=7.55, P<0.001) to 21.3±0.4 mW g^{-1} at T_a=54°C (Fig. 1C). At 25<T_a<39°C, EWL was consistently low, averaging 4.1±2.5 mg g^{-1} h^{-1} (Fig. 2C). Above T_a=40°C, EWL increased linearly and significantly

Fig. 3. The ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) in three species of African weavers over a range of air temperatures (T_a). (A) Scaly-feathered weavers (N=15), (B) sociable weavers (N=25) and (C) white-browed sparrow-weavers (N=31). Data from calm and active birds are shown by filled and open circles, respectively. Segmented regressions were used to estimate the inflection point in the relationship between EHL/MHP and T_a for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. ***P≤0.001.

Fig. 4. Mean body temperature (T_b) in three species of African weavers over a range of air temperatures (T_a). (A) Scaly-feathered weavers (N=15). (B) Sociable weavers (N=25). (C) White-browed sparrow-weavers (N=31). Data (means±s.d.) from calm and active birds are shown by filled and open circles, respectively. Segmented regressions were used to estimate the inflection point in the relationship between mean T_b and T_a for calm birds only. In the case of white-browed sparrow-weavers, two inflection points were found. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. ***P≤0.001.

($t_{1,24}$=16.65, P<0.001) to 65.5±1.8 mg g^{-1} h^{-1} at T_a=54°C, a 16.0-fold increase (Fig. 2C, Table 1). Above T_a=35°C, the percentage MHP that was dissipated evaporatively increased linearly and significantly ($t_{1,33}$=23.6, P<0.001) from 14±6% to 193±8% at T_a=54°C (Fig. 3C, Table 1). This variable increased by 17% between T_a=50 and 52°C, and 14% between T_a=52 and 54°C.

Mean T_b averaged 41.2±0.9°C at T_a<40°C, but increased significantly ($t_{1,12}$=7.18, P<0.001) at T_a>40°C to 43.0±0.5°C at T_a=48°C (Fig. 4). A second significant inflection point in T_b occurred at T_a=49.3°C ($t_{1,68}$=8.47, P<0.001), above which the slope of mean T_b increased to 0.53°C per 1°C increase in T_a. At T_a=54°C, mean T_b was 44.8±0.2°C (Fig. 4C). Over ~10 min at a given T_a, change in T_b remained fairly constant, averaging 0.001±0.027°C min^{-1} when T_a<48°C (Fig. 5C). The rate of change of T_b increased significantly at T_a>48°C ($t_{1,7}$=6.2, P<0.001) (Fig. 5C). At T_a=48°C, the rate of increase of T_b averaged

0.03±0.02°C min^{-1}, increasing to 0.1±0.03°C min^{-1} at T_a=54°C (Fig. 5C, Table 1).

For white-browed sparrow-weavers, EHL began to increase significantly at a rate of 3.17 mW g^{-1} °C^{-1} when T_a−T_b≈−1.5°C, ($t_{1,22}$=12.98, P<0.001), to a maximum of 35.3±5.0 mW g^{-1} at T_a=54°C, when T_a exceeded T_b by 6–9°C. Thermal end point was reached by 10% of white-browed sparrow-weavers at T_a=48°C, increasing to 14% at T_a=50°C, 60% at T_a=52°C and 100% at T_a=54°C (Fig. 6). Of the birds that reached their thermal end point at T_a=54°C, mean T_b, mean $T_{b,max}$ and EHL/MHP were 44.4±0.9°C, 45.5±0.1°C and 1.79±0.30, respectively.

Patterns of interspecific variation

At T_a=48°C, the highest T_a at which we obtained data for all three species, both mean and maximum T_b were negatively related to M_b, with the ~10 g scaly-feathered weavers showing the highest values and the ~40 g white-browed sparrow-weavers the lowest
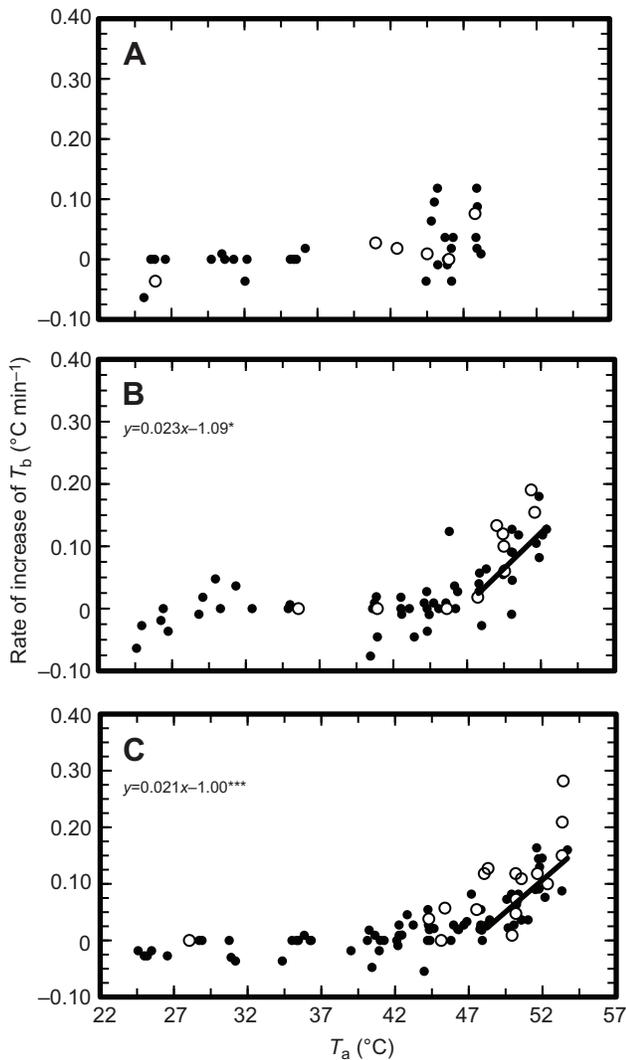
Fig. 5. Rate of increase of body temperature (T_b) over ~10 min in three species of African weavers over a range of air temperatures (T_a). (A) Scaly-feathered weavers (N=15). (B) Sociable weavers (N=25). (C) White-browed sparrow-weavers (N=31). Data from calm and active birds are shown by filled and open circles, respectively. Segmented regressions were used to estimate the inflection point in the relationship between the rate of T_b increase and T_a for calm birds only. Statistical analyses were performed on calm birds to determine coefficients for the linear relationships above inflection points. In the case of scaly-feathered weavers, the relationship was not statistically significant, and so is not shown. *P≤0.05, ***P≤0.001.

(Table 1). Similarly, the rate of increase of T_b during the final 10 min before removal from the chamber was greatest in *S. squamifrons*, whereas the two other species showed similar values (Table 1). This variation was manifested in nearly half of the scaly-feathered weavers tested reaching their thermal end points at T_a=48°C, whereas almost no individuals of the two larger species did so (Table 1). Mean rates of mass-specific EWL and RMR were strikingly similar for *P. mahali* and *P. socius*, despite the substantial difference in M_b between these species (40 g vs 25 g, respectively), whereas corresponding values for *S. squamifrons* were substantially higher (Table 1). In contrast, mean EHL/MHP at T_a=48°C was substantially higher in *P. socius* compared with either of the other species (Table 1), suggesting more effective evaporative cooling in this species as a result of the lower rates of heat production.
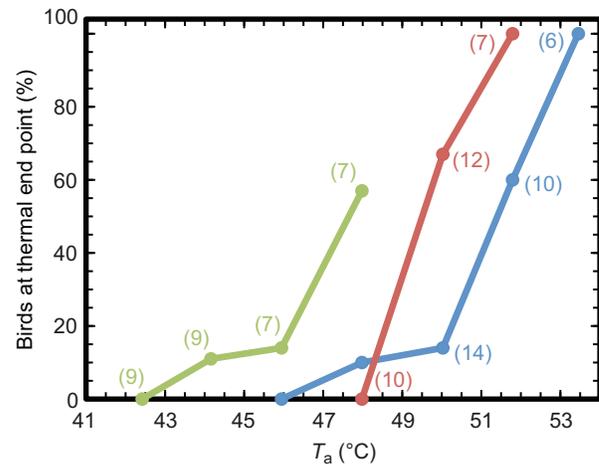
Fig. 6. Percentage of individual African weavers that reached their thermal end point over a range of air temperatures (T_a). (A) Scaly-feathered weavers (N=15, green). (B) Sociable weavers (N=25, red). (C) White-browed sparrow-weavers (N=31, blue). Numbers in brackets indicate the total birds tested at each T_a.

The slopes describing the relationships between evaporative heat loss and the T_a–T_b gradient varied from 3.17 mW g^{-1} °C^{-1} in *P. mahali* to 3.96 mW g^{-1} °C^{-1} in *P. socius*. Comparisons of the slopes for RMR, EHL/MHP, EWL and T_b as functions of T_a did not reveal any obvious patterns of interspecific variation other than (1) a higher mass-specific RMR in *S. squamifrons* compared with the two larger species, and (2) a negative relationship between M_b and the slope of T_b as a function of T_a, as was expected from the direction of the interspecific variation in T_b values at T_a=48°C (Table 1).

DISCUSSION

Our data on heat tolerance and maximum evaporative cooling capacity in three southern African ploceids suggest that the highest T_a values these birds can tolerate during acute heat exposure are in the 48–54°C range, and are positively related to M_b. Maximum evaporative heat dissipation ranges from approximately 140% to 220% of resting metabolic heat production. Body temperatures associated with severe heat stress appeared to be between 44°C and 45°C for all three species, with absolute maximum values about 1°C higher.

Our experimental protocol involved ramped profiles of T_a during which birds experienced progressively hotter conditions after a short period at each T_a value, together with high flow rates to minimize chamber humidity. This approach could be criticized on the basis of not providing steady-state physiological data, but these aspects of the experimental protocol reflect our intention to quantify upper thermoregulatory limits in a manner directly comparable among species. The interacting effects of evaporative heat loss and dehydration make it impossible to expose birds to T_a>T_b for periods similar to those used for measurements of RMR at moderate T_a (e.g. Jacobs and McKechnie, 2014; Page et al., 2011). Furthermore, our observations indicate that birds do not respond well if exposed to very high T_a immediately after being placed in a respirometry chamber, and they hence require an initial period of moderate T_a for habituation to the experimental conditions (B.O.W. and A.E.M., personal observations). The experimental protocol we used here is in many ways analogous to the sliding cold-exposure protocol widely used for determination of summit metabolism at low T_a (Swanson et al., 1996). Moreover, our approach of visually assessing when steady-state conditions

were attained during measurements at high T_a follows that of several other authors (e.g. Tieleman et al., 2002b).

The high flow rates we used to keep chamber absolute humidity low may have resulted in observed rates of EWL modestly higher than those likely to occur under most conditions in wild, free-ranging individuals. Again, however, our goal was to measure maximum evaporative cooling capacity in such a manner as to facilitate comparisons among species, and these values are broadly representative of humidity values experienced by birds living in hot subtropical deserts where dew point temperatures often range from 1 to 5°C (e.g. http://www.bom.gov.au/; see humidity maps for January–February 2015). Measurements using a hot-wire anemometer placed in the centre of a 4 litre chamber at a flow rate of 30 l min^{-1} yielded a wind speed of 0.3 m s^{-1}. Rates of EWL at very high T_a can be strongly affected by humidity levels (Gerson et al., 2014), and we frequently observed that, at a given T_a, the behaviour of birds in the chamber was highly sensitive to humidity, with even small decreases via increased flow rates resulting in reduced levels of escape behaviour.

Body temperature and thermal end points

Gradual, regulated increases in T_b when T_a exceeds normothermic T_b are a widespread avian response to heat stress (Dawson and Fisher, 1969; Marder et al., 1986; Weathers, 1981) and may have significant consequences for water conservation (Tieleman and Williams, 1999). Birds in the present study typically showed stable T_b elevated above normothermic levels, which increased in a step-wise fashion with each increment in T_a, as indicated by the rate of change in T_b at each experimental T_a value (Fig. 5). The increase in rate of change of T_b at very high T_a supports our conclusion that birds had indeed reached the highest T_a that they could tolerate, and were no longer able to regulate a stable T_b.

The changes in T_b with exposure to progressively higher T_a in this study are broadly consistent with those of generalized biphasic models of heat stroke (Leon, 2006). In these models, acute heat exposure leads to (1) initial rapid increases in T_b by 2–4°C above the normothermic setpoint; (2) a phase of 'thermoregulatory equilibrium' during which hyperthermic T_b is regulated at approximately constant levels, or gradually increases; and finally (3) thermoregulatory breakdown marking the onset of rapid, unregulated increases in T_b towards lethal levels (Leon, 2006). The patterns of T_b we documented in heat-stressed birds suggest that such models are applicable to birds as well as mammals, and moreover support our interpretation that thermal end points as identified here provide a good indication of the absolute maximum T_a values that can be tolerated and T_b values approaching critical thermal maxima (CT$_{max}$) – the minimum T_b values that are lethal to organisms. Values of CT$_{max}$ are widely used in the ectotherm literature, but are seldom estimated for endotherms. The T_b maxima we observed here are close to known avian lethal T_b values (Arad and Marder, 1982; Brush, 1965; Dawson, 1954; Dmi'el and Tel-Tzur, 1985).

Avian tolerance of high T_a appears to vary phylogenetically, with passerines apparently tolerating lower temperatures compared with taxa such as caprimulgids and columbids. Fatal hyperthermia has been documented in towhees at T_a=39–43°C (Dawson, 1954), Baltimore orioles (*Icterus galbula*) at T_a=44°C (Rising, 1969) and zebra finches (*Taeniopygia guttata*) at T_a=45–46°C (Cade et al., 1965), although some species can tolerate T_a≥50°C (Wolf and Walsberg, 1996a; present study). In contrast, spotted nightjars and houbara bustards tolerated T_a values of 55–57°C (Dawson and Fisher, 1969; Tieleman et al., 2002b), and heat-acclimated rock

doves survived and even bred when daytime T_a was 60°C (Marder and Arieli, 1988; Marder and Gavrieli-Levin, 1986).

Evaporative water loss

The fractional increases in EWL associated with increasing T_a in the three species we examined here fall within the range of those documented previously. For instance, verdins (*Auriparus flaviceps*; ∼7 g) exposed to T_a=50°C exhibited a 13.7-fold increase in EWL relative to values at T_a=30°C (Wolf and Walsberg, 1996a) and spotted nightjars (*Eurostopodus argus*) exposed to T_a=56.5°C increased EWL to approximately 20-times baseline values (Dawson and Fisher, 1969).

The slope of the relationship between EWL and T_a at high T_a scales negatively with M_b among birds in general (McKechnie and Wolf, 2010). In this regard, it is noteworthy that in both *P. socius* and *P. mahali*, the slopes were considerably steeper when regressions were fitted to data for all T_a (Fig. 2) compared with when they were fitted to data for T_a≤48°C – an observation that is relevant for interspecific comparisons. In the data set compiled by McKechnie and Wolf (2010; see their supplementary material), the maximum T_a at which EWL was measured varied among studies from 42.5–56.5°C. The variation in maximum T_a may have influenced the estimated slopes, with shallower slopes in species exposed to relatively low maximum T_a and vice versa. For instance, the slopes for black-bellied sandgrouse (*Pterocles orientalis*) and pin-tailed sandgrouse (*Pterocles alchata*) that experienced maximum T_a=45°C (Hinsley et al., 1993) are 68 and 48% lower, respectively, than allometrically expected values, whereas the slope for *E. argus*, based on maximum T_a=56.5°C (Dawson and Fisher, 1969) is approximately equal to the value predicted by McKechnie and Wolf (2010). These observations suggest that analyses of the scaling of avian EWL may need to be restricted to data sets involving EWL measurements over similar ranges of T_a.

Compared with the EWL slopes predicted by the equation of McKechnie and Wolf (2010), the observed slope for *S. squamifrons* was virtually identical, whereas the slopes for *P. socius* and *P. mahali* were considerably steeper (172.4 and 171.7% of predicted values, respectively). Compared with other arid-zone species of similar M_b, EWL at T_a=44°C in scaly-feathered weavers was similar to that of the ∼12 g spinifexbird (*Eremiornis carteri*) at the same T_a (Ambrose et al., 1996), the EWL at T_a=48°C of sociable weavers was approximately half that of 27 g dune larks (*Calendulauda erythrochlamys*) (Williams, 1999) and at T_a=50°C, white-browed sparrow-weavers exhibited EWL similar to that of the 38 g greater hoopoe lark (*Alaemon alaudipes*) (Tieleman et al., 2002a).

Resting metabolic rate

The RMR of all three species conformed to the classic model of endotherm thermoregulation (Scholander et al., 1950), with a clear upper critical limit of thermoneutrality above which metabolic rate increased linearly. The slope of the relationship between avian RMR and T_a above thermoneutrality scales negatively with M_b (Weathers, 1981), but among our study species the slope was greatest in *P. mahali*, the largest species, and lowest in the intermediate-sized *P. socius*. Moreover, all three species we studied here showed much more gradual increases in RMR than predicted by Weathers' (1981) equation for the scaling of 'coefficient of heat strain'. Observed slopes (mW g^{-1} °C^{-1}) in *S. squamifrons*, *P. socius* and *P. mahali* were equivalent to 17.2, 26.5 and 70.6%, respectively, of predicted values (Weathers, 1981). This variation may reflect the effects of absolute humidity on chamber activity levels: restlessness and escape behaviour was pronounced when birds experienced a

combination of high T_a and high absolute humidity, and we therefore maintained very low chamber humidities during measurements by increasing flow rates. Many of the studies reviewed by Weathers (1981) did not report chamber water vapour pressures and the flow rates used in many of these studies suggest that chamber humidity may have been much higher than in ours.

Comparisons of RMR with similarly sized species at comparable T_a values also reveal substantial variation. At T_a=44°C, scaly-feathered weavers exhibited an average RMR ∼37% lower than that of spinifexbirds (Ambrose et al., 1996). At T_a=48°C, RMR in dune larks was almost double that of sociable weavers (Williams, 1999), whereas white-browed sparrow-weavers exhibited an RMR 14% lower than that of greater hoopoe larks (Tieleman et al., 2002a). These data suggest considerable variation in the metabolic costs associated with heat dissipation in desert passerines. Some of this variation may, however, also potentially arise from variation in chamber absolute humidity levels; Gerson et al. (2014) found some evidence for interacting effects of T_a and humidity on RMR at high T_a.

Scaling of heat tolerance

Our comparison of heat tolerance and evaporative cooling capacity among three ploceids suggests that the maximum T_a tolerated during acute heat stress scales positively with M_b. Most scaly-feathered weavers (∼10 g) reached thermal end points by T_a=48°C, whereas for sociable weavers (∼25 g) and white-browed sparrow-weavers (∼40 g), the T_a values associated with 100% of birds reaching thermal end points were 52°C and 54°C, respectively. A positive correlation between thermal end point and M_b might be expected if dehydration is the major factor involved; during exposure to ramped T_a profiles used in this study, small birds presumably approach dehydration tolerance limits faster on account of higher mass-specific rates of EWL (McKechnie and Wolf, 2010). We estimated hourly rates of water loss during our measurements and found that the largest species (*P. mahali*) showed greater total water loss rates (∼6.5% of M_b h^{-1}) at thermal end points, compared with the two smaller species (*P. socius*=3.1%, *S. squamifrons*=4.0%). These data suggest that responses to acute heat stress were driven primarily by an inability to defend T_b at very high T_a, rather than chronic heat stress where small species are expected to dehydrate sooner on account of higher mass-specific rates of EWL.

In contrast, we did not find a clear effect of M_b on evaporative cooling capacity among the three ploceids. At T_a=48°C, scaly-feathered weavers had, as expected, higher mass-specific RMR and EWL than sociable weavers or white-browed sparrow-weavers (Table 1). Sociable weavers at T_a=52°C exhibited a lower mass-specific RMR, and a similar mass-specific EWL to the much larger white-browed sparrow-weavers. It is tempting to speculate that the comparatively low mass-specific RMR and EWL of *P. socius*, together with the steeper increase in EWL with increasing T_a (Fig. 2), is related to it being the only one of the study species whose distribution is restricted to the southern African arid zone (Hockey et al., 2005).

Maximum observed ratios of EHL/MHP in our study species (1.41–2.22) are similar to those reported for other species exposed to high T_a. For instance, the EHL/MHP of white-browed sparrow-weavers at T_a=44°C (∼1.15) was very similar to values for three of four species with M_b≈40 g examined by Lasiewski and Seymour (1972). In our study, EHL/MHP showed indications of reaching plateaux in the two smaller species, with smaller increases associated with increments in T_a as T_a approached the birds' thermal limits. In contrast, EHL/MHP showed no indication of reaching maximum values in *P. mahali*, our largest study species.

The data we have presented here were collected under laboratory conditions intended to elicit maximum evaporative cooling capacity and facilitate the identification of thermal end points, and may or may not be directly applicable to free-ranging birds experiencing more gradual changes in T_a and higher humidity. For birds living in hot deserts, the humidity conditions maintained during our trials (dew point<5°C) are representative of those experienced by free-ranging birds during the summer, and thus provide relevant information on avian thermoregulatory performance for desert birds. For tropical species at lower air temperatures and higher humidity the thermal endpoints may be significantly lower (Weathers, 1997). Studies of wild birds in arid habitats have identified important threshold T_a values in the 30–40°C range for variables related to body condition (du Plessis et al., 2012) and provisioning rates during breeding (Cunningham et al., 2013), suggesting that in many cases, detailed models of specific determinants of survival and/or reproduction will be necessary to predict the effects of climate change. However, catastrophic mortality events during extreme heat waves in the arid zones of Australia and elsewhere (reviewed by McKechnie et al., 2012; McKechnie and Wolf, 2010), combined with predicted increases in the frequency and intensity of heat waves (IPCC, 2011), underscore the relevance of models of avian survival over time scales of hours during acute heat exposure, and the need for comparative data on the upper limits of avian heat tolerance.

In the latter regard, no firm conclusions can be drawn from the patterns we have documented here, other than that, within closely related taxa, larger species may be able to handle slightly higher environmental temperatures during acute heat exposure than smaller species. Rather, we see this study involving three passerines as an initial step in examining comparative variation in avian heat tolerance. Comparable data for taxa that rely on increases in CEWL rather than REWL for evaporative heat dissipation will permit testing of the hypothesis that elevating CEWL is a more energetically efficient mode of dissipating heat than increasing REWL, and birds in which CEWL is the dominant model of EHL may be better able to tolerate periods of extremely hot weather.

MATERIALS AND METHODS
Study sites

The study was conducted at two sites in the southern Kalahari Desert in South Africa, over two consecutive summers. We collected data at Wildsgenot Game Ranch (27°04′S, 21°23′E) between 26 January and 1 April 2012, and at Leeupan Ranch (26°58′S, 21°50′E) from 27 December 2012 to 3 March 2013. These sites are both situated along the dry Kuruman River and are ∼50 km apart. Mean annual rainfall is similar at both sites (190–210 mm $year^{-1}$), as were the ranges of daily maximum air temperatures during the study periods (20–42.7°C and 20–42.5°C at Wildsgenot and Leeupan, respectively). Habitat and vegetation are virtually identical between the sites, consisting of woodland dominated by *Acacia erioloba* and sparse grassland on red sand dunes.

Study species

We measured EWL, RMR and T_b in the scaly-feathered weaver (*Sporopipes squamifrons* Smith 1836), sociable weaver (*Philetairus socius* Latham 1790) and white-browed sparrow-weaver (*Plocepasser mahali* Smith 1836) (Hockey et al., 2005). All are members of the Ploceidae, with *S. squamifrons* and *P. socius* endemic to the arid savannah regions of southern Africa, and *P. mahali* occurring in the arid savannahs of both southern and East Africa. All three species are resident year-round in the Kalahari Desert, with the two larger species exhibiting a high degree of site fidelity and *S. squamifrons* being locally nomadic (Hockey et al., 2005). Both *P. socius* and *P. mahali* are omnivorous, consuming both seeds and insects, whereas *S. squamifrons* is predominantly granivorous.

Birds were captured using mist nets or spring traps at various times of the day, and initially held in cloth bags. All birds used in the study were adults and appeared to be healthy. The mean body masses of *S. squamifrons* *P. socius* and *P. mahali* were 10.4±0.7 g (mean±s.d.; *N*=16), 24.9±1.0 g (*N*=25) and 39.4±2.9 g (*N*=30) respectively. Birds were either used for measurements immediately following capture, or held for 1–24 h in cages constructed of shade cloth, with seed and/or mealworms as well as water available *ad libitum*. Birds were always offered water before the experiment, but if they were unwilling to drink, a feeding tube attached to a syringe was used to introduce water directly into the crop. Each individual was subjected to measurement of at most three T_a values per day, and time in captivity did not exceed 24 h.

All experimental procedures were approved by the Animal Ethics Committee of the University of Pretoria (protocol EC071-11) and animals were captured under permits issued by Northern Cape Department of Environmental Affairs (ODB 008/2013).

Air and body temperature measurements
Air temperatures within the chambers used for gas exchange measurements were measured using a thermistor probe (model TC-100, Sable Systems, Las Vegas, NV, USA) inserted through the lid of each chamber via a small hole sealed with a rubber grommet. A temperature-sensitive passive integrated transponder (PIT) tag (Biomark, Boise, ID, USA) was injected into each bird's abdominal cavity. During gas exchange measurements, T_b was monitored using a PIT tag reader and portable transceiver system (model FS2001, Destron Fearing, St. Paul, MN, USA). At the beginning of the study, a representative sample of 70 PIT tags were calibrated in a circulating water bath over temperatures from 39 to 46°C against a digital thermocouple reader (model RDXL12SD, Omega, Stamford, CT, USA) with Cu–Cn thermocouples (Physitemp, Clifton, NJ, USA). The temperatures measured by the PIT tags deviated from actual values by 0.02±0.09°C (mean±s.d., *N*=70).

Gas exchange measurements
Carbon dioxide production ($\dot{V}_{CO_2}$) and EWL were measured over T_a between 25 and 54°C using an open flow-through respirometry system. Birds were placed in plastic chambers with a volume of 1.9 litres (*P. socius* and *S. squamifrons*) or 4 litres (*P. mahali*). Before measurements, we tested the chambers for water vapour absorption by comparing the rates of change for CO_2 and water vapour when switching between air streams that differed substantially in CO_2 and water vapour content. A 1 cm layer of mineral oil was placed at the bottom of each chamber to prevent evaporation from urine and faeces, with a plastic mesh platform positioned approximately 10 cm above the oil layer. The chambers were placed in a modified ice chest (~75 litres) in which T_a was regulated via a Peltier device (model AC-162, TE Technology Inc., Traverse City, MI, USA) and a custom-built controller. This system permitted rapid changes in T_a (~1°C min^{-1}) as well as precise regulation of a setpoint value (typically ±0.1°C).

During the 2012 season, atmospheric air was supplied by a pump with a maximum capacity of approximately 30 l min^{-1} (model DOA-P13- BN, Gast Air Pumps, Benton Harbour, MI, USA) before being dried by columns of silica gel and drierite connected in series. During the 2013 season, compressed air provided by a compressor was pushed through a membrane dryer (Champion® CMD3 air dryer and filter, Champion Pneumatic, Quincy IL, USA). During both seasons, the airstream was then split into two channels, namely the baseline and chamber, with flow rate in the baseline channel regulated by a needle valve (Swagelok, Solon, OH, USA) and that to the chamber by mass flow controllers (Alicat Scientific Inc., Tuscon, AZ, USA). To maximize mixing of air within the chamber, the air inlet was positioned near the top of the chamber and the outlet near the bottom. Incurrent flow rates were recorded manually from the readout of the mass flow controller, whereas flow rates for the baseline channel were maintained at approximately 1.5 l min^{-1}, verified using a flow meter (SS-3 subsampling unit, Sable Systems). Flow rates were selected so as to maintain absolute humidity levels within the chamber as low as possible (<1 kPa), while still maintaining an accurately measurable difference in [CO_2] and water vapour between the incurrent and excurrent air. Depending on T_a and M_b, flow rates of 2–40 l min^{-1} were used. Birds tended to remain calmer when flow rates were higher and chamber humidity lower (<5 ppt water vapour).

Birds were held without food for at least 1 h before commencing an experimental run, and we assumed a respiratory exchange ratio (RER)= 0.71, representative of lipid metabolism in post-absorptive birds (Walsberg and Wolf, 1995). Excurrent air from the chamber and baseline air were sequentially subsampled using a respirometry multiplexer (model MUX3-1101-18M, Sable Systems) in manual mode. At the start of each set of measurements, baseline air was subsampled until water and CO_2 readings were stable (typically ~5 min). Subsequently, chamber excurrent air was subsampled when T_a had stabilized at the target value, and CO_2 and H_2O traces were stable for at least 5 min. Thereafter, baseline air was subsampled again. Subsampled air was pulled through a CO_2/H_2O analyser (model LI-840A, LI-COR, Lincoln, NE, USA), which was regularly zeroed using nitrogen, and spanned for CO_2 using an analytically certified gas with a known CO_2 concentration of 2000 ppm (AFROX, Johannesburg, South Africa) and for H_2O using the oxygen dilution technique (Lighton, 2008). All tubing in the system was Bev-A-Line IV tubing (Thermoplastic Processes Inc., Warren, NJ, USA). Voltage outputs from the analysers and thermistor probes were digitized using an analog-digital converter (model UI2, Sable Systems) and recorded with a sampling interval of 5 s using Expedata software (Sable Systems).

Experimental protocol
Experimental trials were made during the day, and birds were exposed to progressively higher T_a values using a ramped profile with 5°C increments at T_a between 25 and 40°C and 2°C increments at T_a of 40–54°C. Each individual was exposed to one or two low T_a values (25–35°C) and three high (>40°C) T_a values, selected randomly on the day, for a minimum of 10 min and an average of approximately 30 min per T_a value. Measurements involving T_a between 40 and 50°C started with birds placed in the chamber at T_a=35°C for at least 30 min to habituate to the experimental setup, whereas for measurements at T_a>50°C birds were started at T_a=40°C. Each set of measurements typically lasted <3 h. The chamber in which the bird was placed was completely dark, but we monitored birds using a video camera with an infrared light source.

During measurements, T_b and activity were continuously monitored. Measurements were terminated and a bird was immediately removed from the chamber when it displayed prolonged escape behaviour such as agitated jumping, pecking and/or wing flapping, or if there were signs of distress such as loss of coordination or balance or a sudden drop in EWL, RMR and/ or an uncontrolled increase in T_b to >45°C. In the latter 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>45°C was considered the thermal end point for that individual. A bird that had reached its thermal end point was removed immediately from the chamber and held in front of an air conditioner producing chilled air, and a cotton pad soaked in ethanol was rubbed on the bird's body to aid in rapidly lowering T_b. Once T_b stabilized at normothermic levels (40–42°C), the bird was offered water and placed in a cloth bag at room temperature to rest. The bird was later released at the site of capture, after checking that behaviour appeared normal. In almost all cases individuals lost less than 5% of their body mass in faeces and water during a trial.

Data analyses
Rates of $\dot{V}_{CO_2}$ and EWL were calculated using eqns 10.5 and 10.9, respectively, from Lighton (2008) assuming 0.803 mg H_2O ml vapour^{-1}. MHP (mW) was calculated assuming RER=0.71 following Walsberg and Wolf (1995). EHL (mW) was calculated assuming 2.26 J mg H_2O^{-1}. RMR and rates of EWL were calculated from steady-state traces of $\dot{V}_{CO_2}$ and $\dot{V}_{H_2O}$ in Expedata, with the lowest 1 min mean values considered resting values. Rate of T_b increase (°C min^{-1}) was calculated from the change in T_b during the final 10 min of exposure to a given stable T_a value. Mean T_b and $T_{b,max}$ were taken as the average and single highest values respectively during each 10 min period.

Broken-stick regression analyses were performed in R 3.0 (R Development Core Team, 2011) using the package 'segmented' (Muggeo, 2009) to identify inflection points for EWL, RMR, T_b, rate of change of T_b and EHL/MHP. All data points associated with agitation or activity in the metabolic chambers were excluded from these analyses. We did not test for the effect of activity on response parameters as we seldom had enough data

for active birds to conduct reliable comparisons, and because of difficulty in interpreting and quantifying activity among individuals. Data for T_a values above inflection points were used to estimate slopes for the relationships of EWL, RMR, EHL/MHP, T_b and rate of T_b increase as functions of T_a. For these subsets of the data, we performed generalized mixed-effect models with the R package 'nlme' (Pinheiro et al., 2009) to test for an effect of T_a on the above parameters. To account for measurements at multiple T_a values in the same individuals, individual identity was included as a random factor in all analyses.

Some uncertainty exists regarding the most appropriate regression models for avian EWL data (see e.g. Weathers, 1997). We followed McKechnie and Wolf (2010) and fitted segmented linear models to facilitate comparisons among species. However, to verify the validity of this approach, we also fitted second-order polynomial models to EWL data over the entire range of T_a, and compared Akaike Information Criterion (AIC) values for the two models within each species. Polynomial AIC values were lower than those for segmented linear models for *P. mahali* (polynomial AIC=464.6; linear AIC=469.4) and *P. socius* (polynomial AIC=395.0; linear AIC=396.8), but the opposite was true for *S. squamifrons* (polynomial AIC=298.8; linear AIC=295.9). In light of the small differences in AIC values, and the lack of a consistent direction, we used segmented linear models in all further analyses.

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