

Water and energy fluxes during summer in an arid-zone passerine bird

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Endothermic animals resident in hot, arid terrestrial environments are likely to face a trade-off between their ability to obtain water and elevated thermoregulatory water requirements. We assessed whether daily water flux (DWF) is higher on hot days, reflecting increases in evaporative cooling demands, in an arid-zone bird that obtains its water through food intake. We obtained measurements of DWF (partitioned into water influx and efflux rates) in 71 White-browed Sparrow-Weavers *Plocepasser mahali* at a desert site and a semi-desert site, during summer in the Kalahari Desert of southern Africa. We found no evidence that DWF varied with maximum daily air temperature (T_{air} , range = 27.6–39.2 °C). Instead, DWF was lower during dry periods than in the wet season at the semi-desert site. Furthermore, birds showed deficits in water balance (water influx/water efflux) during the dry periods at both sites. Our data show that DWF is low in a non-drinking bird that obtains its water through food, and that demands for evaporative water loss on very hot days (maximum T_{air} of 40–44 °C) may exceed water intake rates during hot and dry periods. Species that do not have opportunities to drink will experience strong trade-offs between thermoregulation, hydration state and activity levels as temperatures increase.

Keywords: climate change, evaporative water loss, field metabolic rate, foraging, *Plocepasser mahali*, water turnover, White-browed Sparrow-Weaver.

Mismatches between the demand and supply of critical resources, such as water and energy, may have deleterious effects on survival and fitness. For endothermic animals living in arid terrestrial environments, the trade-off between resource acquisition and expenditure can be severe (Tieleman & Williams 2000, Tieleman *et al.* 2003). Resource bottlenecks can be driven strongly by temperature, with extremes of cold and heat typically affecting energy and water budgets, respectively (Carmi-Winkler *et al.* 1987, Kam *et al.* 1987, Wolf & Martinez del Rio 2000, Ehrhardt *et al.* 2005). Information on how endotherms acquire and allocate

water and energy is thus vital for understanding how they inhabit arid environments.

Diurnal birds that live in subtropical deserts often need to forage under very hot conditions, potentially trading off dietary water intake against elevated thermoregulatory water requirements (Tieleman *et al.* 2003, du Plessis *et al.* 2012). The demands for evaporative cooling constitute the greatest thermoregulatory cost during hot weather, and resting rates of evaporative water loss (EWL) in small birds can exceed 5% of their body mass (m_b) per hour during periods of high air temperature (T_{air}) and intense solar radiation (Wolf & Walsberg 1996). Under these conditions, total water losses may exceed dehydration tolerance limits within just a few hours (Wolf 2000, McKechnie & Wolf 2010). Bartholomew and Cade (1956) showed that under conditions of moderate heat stress (*c.* $T_{\text{air}} = 39$ °C), House Finches *Carpodacus mexicanus* typically drink volumes of water equiva-

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lent to 40% (but sometimes exceeding 100%) of their body mass daily. To fulfil a daily water intake of similar magnitude, species that rely on preformed or metabolic water are likely to incur greater energetic and evaporative cooling costs associated with foraging, and consequently experience poorer body condition when energy and water intake are reduced during hot weather (Bartholomew & Cade 1956, du Plessis *et al.* 2012). Moreover, species that rely on preformed water in their food could easily lose more water searching for food than they gain from eating it (Kotler *et al.* 1998).

Under laboratory conditions, EWL begins to increase with increasing T_{air} within the thermoneutral zone (TNZ; Dawson 1954, Weathers 1981, Tieleman *et al.* 2002), and the rate of increase scales negatively with body mass (McKechnie & Wolf 2010). In contrast, little is known about how daily water flux (DWF, defined as influx and efflux of body water) varies with increasing T_{air} in free-ranging birds inhabiting hot, arid habitats. When T_{air} exceeds body temperature (T_b), water demands are relatively straightforward to predict, as birds under these conditions are generally inactive in the coolest microsites available and resting EWL may make up a major component of DWF. Measurements of EWL in birds resting in metabolic chambers may therefore provide a reasonable approximation of EWL demands in resting free-ranging individuals.

However, predicting water demands at high T_{air} (30–40 °C) below avian T_b is more complex, as birds may show signs of heat stress such as gular flutter and/or panting but nevertheless continue to forage actively instead of retreating to shade and curtailing activity (Tieleman & Williams 2002, Tieleman *et al.* 2003, du Plessis *et al.* 2012, Smit *et al.* 2013). Under these conditions, birds can also experience periods in which operative temperature (T_e , defined as an integrated temperature that reflects the overall thermal environment that individuals experience; Bakken 1992) exceeds T_b , for example when foraging in full sun (Wolf & Walsberg 1996). Birds in desert environments that need to optimize food intake can allow their T_b to increase above the normothermic range while active (thereby reducing the demands for panting), but this may come at the cost of T_b approaching its lethal limit (Smit *et al.* 2013). Therefore, within this temperature range, birds may experience the strongest trade-off between foraging and

thermoregulation (EWL and high T_b), especially when the intake of water-rich food decreases as T_{air} approaches T_b (du Plessis *et al.* 2012). A recent study on Southern Pied Babbblers *Turdoides bicolor* showed that foraging efficiency, but not foraging effort, decreased significantly when the need to augment heat dissipation increased above $T_{\text{air}} = 30$ °C. When maximum daily T_{air} exceeded 36 °C, the birds did not eat enough food to compensate for overnight mass loss; this threshold has major implications for body condition and fitness (du Plessis *et al.* 2012).

There are thus two opposing predictions that can be made concerning the relationship between DWF and temperature when maximum T_{air} is in the 30–40 °C range. First, thermoregulatory EWL demands drive daily water intake (Weathers 1981, Tieleman *et al.* 2002) and DWF increases with increasing T_{air} , especially when birds can compensate for their water loss by drinking or eating water-rich food. Alternatively, if DWF is limited by factors such as reduced intake of food with a high water content at high T_{air} , we predict that birds will experience mismatches between water influx vs. water efflux on hotter days. The latter relationship would be most likely in non-drinking species, which do not have access to free-standing water but instead obtain their water from food that must be actively searched for (Tieleman & Williams 2002, du Plessis *et al.* 2012).

We tested these alternate predictions in two resident populations of an arid-zone passerine, the White-browed Sparrow-Weaver *Plocepasser mahali*, in the Kalahari Desert – one population at a comparatively arid site and the other at a semi-arid site. Sparrow-Weavers are largely independent of drinking water, drinking only when water is available, and can obtain most of their water through eating insects (du Plessis 2005). Smit *et al.* (2013) found that at high T_{air} (> 35 °C), White-browed Sparrow-Weavers from these Kalahari Desert sites largely maintained foraging effort (although activity was decreased during midday on hot days), but they also panted more (Fig. 1). Given the persistent foraging efforts observed at high T_{air} in sparrow-weavers, we expected that they would increase DWF on hot days to compensate for increased EWL demands. Alternatively, if foraging efficiency is not increased, or even reduced, at high T_{air} we expect that these birds will experience dehydration, which will result in reduced capacity to cool evaporatively as T_{air} approaches T_b .

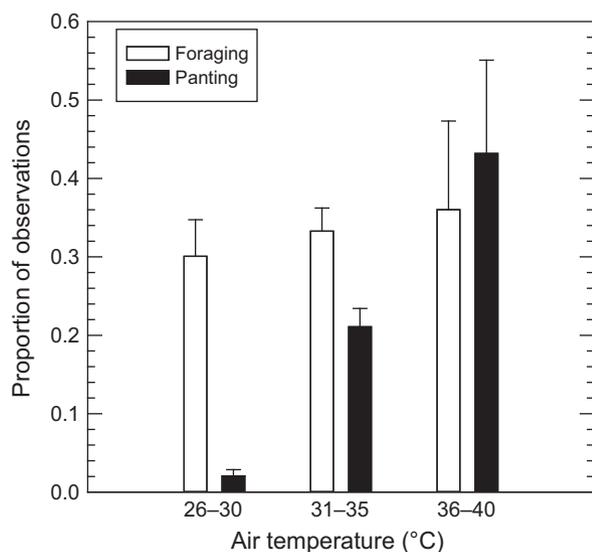


Figure 1. Mean (± 1 sd) proportion of time spent foraging (white bars) and panting (black bars) as a function of air temperature (grouped at intervals of 4 °C) representing 109 focal observations of 26 White-browed Sparrow-Weavers (modified from Smit *et al.* 2013).

METHODS

Study sites and measurement of air temperature

We collected DWF and daily energy expenditure (DEE) measurements from birds at a semi-desert site from 11 December 2010 to 15 March 2011 (austral summer) at Tswalu Kalahari Reserve (TKR, *c.* 1100 m asl, 27°19'S, 22°25'E), and from 21 November 2011 to 18 December 2011 at a more arid site, Wildsgenot Game Ranch (WGR, *c.* 890 m asl, 27°04'S, 21°23'E; *c.* 100 km due west of TKR). The vegetation at both sites is arid savanna on deep, red sand forming parallel fossil dunes. There are no natural free-standing or free-flowing water sources at these sites.

Precipitation at both sites occurs mainly during summer (December to March), and the region is classified as desert given the highly unpredictable nature of significant rainfall events (Lovegrove 1993, Usman & Reason 2004, Reason *et al.* 2006). Mean annual rainfall is higher at TKR than at WGR, mainly because TKR lies within the western boundaries of the inter-tropical temperate troughs that bring regular summer rain to eastern South Africa (Usman & Reason 2004, Reason *et al.* 2006). Mean (± 1 sd) annual rainfall at TKR was

295 \pm 172 mm (coefficient of variation, CV = 58.3%) over a 30-year period (D.N. MacFadyen, unpubl. data). Mean annual rainfall at WGR was 190 \pm 125 mm (CV = 66%) over a 60-year period (G.H.D. Scholtz unpubl. data). Hereafter we refer to TKR and WGR as the 'semi-desert' and 'desert sites', respectively.

We measured T_{air} as a crude estimate of the T_e birds experienced in shaded locations in the field. Standard T_{air} measurements are generally correlated highly with T_e , and typically match temperature measured in shaded microsites very closely (Bakken 1992, Tieleman & Williams 2002, Tieleman *et al.* 2003). Standard T_{air} and humidity (actual vapour pressure, kPa) were obtained at both sites using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA, USA), set 2 m above ground at a central location at each study site. We validated temperature readings of the weather station against an NIST-traceable mercury thermometer for T_{air} , and the humidity readings using a CO₂/H₂O gas analyser (LI-840A, LI-COR Inc., Lincoln, NE, USA), regularly calibrated using pure nitrogen or saturated air at a known T_{air} . We calculated the water vapour pressure deficit (VPD, kPa) as the difference between actual vapour pressure and saturated vapour pressure at the respective T_{air} .

Warm and dry conditions prevailed at the semi-desert site during December 2010, but after 1 January 2011 significant rainfall events were frequent and primary productivity increased dramatically (Table 1). At the desert site, rainfall was overall much less but T_{air} was comparable to the dry sampling period at the semi-desert site; daily maxima were slightly higher (Table 1). Sampling periods at the semi-desert site therefore represented distinct dry and wet periods, with most of the data at the semi-desert site (85%) collected during a wet period. We sampled at the desert site before the end of the annual dry cycle. There was no significant rainfall at either site at least 7 months before we began sampling. The few months before the rains are generally characterized by extremely low primary productivity and very low insect activity (B. Smit pers. obs.).

Study species

White-browed Sparrow-Weavers ($m_b = 35$ –50 g) live in highly territorial family groups (2–10 individuals) and occur throughout the arid savanna

Table 1. Weather during the study period at Tswalu Kalahari Reserve (semi-desert) and Wildsogenot Game Ranch (desert).

	Semi-desert (dry)	Semi-desert (wet)	Desert (dry)
Minimum temperature (°C)	18.7 ± 2.6 (14.2 to 23.5)	20.1 ± 1.7 (16.7 to 23.7)	15.8 ± 4.4 (6.6 to 23.1)
Maximum temperature (°C)	34.6 ± 3.0 (25.2 to 38.3)	31.7 ± 2.1 (28.3 to 35.1)	34.2 ± 3.2 (27.6 to 39.2)
Dew point (°C) ^a	4.9 ± 6.8 (−12.1 to 16.6)	17.0 ± 2.3 (11.1 to 21.1)	3.4 ± 4.1 (−8.5 to 18.5)
Total rainfall (mm)	20.3	244.1	11.2

Daily water flux (DWF) measurements at the semi-desert site were collected during a dry summer period (December 2010) and wet summer period (January to February 2011), and at the desert site during a dry summer period (November to December 2011). Daily energy expenditure (DEE) data were obtained at the semi-desert site during the wet season and at the desert site during the dry season. Values represent mean ± 1sd (range: minimum–maximum). Both ‘dry season’ data collection periods were at the end of typical annual austral dry cycles, which last from April to December, and neither site received any significant rainfall for at least 7 months prior to the sampling periods. Sample sizes for DLW and DEE measurements are included. ^aMean measurements at 14:00 h.

regions of southern and eastern Africa (du Plessis 2005). These birds are omnivorous and feed on insects (80% of diet), seeds and seasonal fruit (du Plessis 2005). At our study sites, only individuals with home-ranges surrounding a free-standing water source drink (i.e. < 200 m from water source; unpubl. data). We therefore obtained DWF and DEE measurements from individuals that we caught more than 2 km from artificial water sources, to ensure that our study birds would not drink. Because wild sparrow-weaver groups take a number of days to habituate to the presence of observers in their territories, we did not make behavioural observations on the birds in this study while obtaining DWF and DEE measurements. Therefore in interpreting our data we rely on the behavioural patterns observed by Smit *et al.* (2013) on the same species at the same sites during a parallel study on thermoregulation and behaviour.

Water flux and energy expenditure measurements

We measured DWF and DEE in White-browed Sparrow-Weavers using the doubly labelled water (DLW) technique (Nagy & Costa 1980, Speakman 1997). All our procedures were approved by the University of Pretoria Animal Use and Care Committee (#EC055-10), under sampling and blood collection permits issued by the Department of Environment and Nature Conservation, Northern Cape, South Africa (# FAUNA 720/2010 and # FAUNA 1031/2011). We trapped birds at night (21:00–23:00 h; UTC + 2 h) in their respective roost chambers and obtained a blood sample (50–100 µL) by venipuncture, using a sterile

27-gauge hypodermic needle, from the left brachial vein of each individual to establish background ratios (BG) of stable hydrogen and oxygen isotopes in the body water. Each individual then received an intramuscular injection, using a sterile 27-gauge needle, of DLW, consisting of approximately one part 99.9 at.% deuterium oxide and five parts 97.0 at.% ¹⁸O (Sigma-Aldrich, Kempton Park, SA, USA). However, during the study at the semi-desert site, some birds were injected with only 99.9 at.% deuterium oxide because we ran short of ¹⁸O; deuterium oxide enriches the body water $\delta^2\text{H}$ but not $\delta^{18}\text{O}$. The birds were injected with a dose of 65 µg per 100 g body mass for DLW, or 10 µg per 100 g body mass for deuterium oxide, estimated to enrich body water $\delta^2\text{H}$ by approximately 1000‰ VSMOW (Vienna Standard Mean Ocean Water) and $\delta^{18}\text{O}$ by approximately 400‰ VSMOW. Whereas the DLW was used to determine both DWF and DEE, the deuterium was used to estimate DWF only. Approximately 1 h (equilibration time = 1 h ± 7 min; see Williams & Nagy 1984 and Tieleman *et al.* 2003) after injection, we obtained another blood sample (i.e. first enriched sample, S1; 50–100 µL) from the right brachial vein of each bird to estimate initial isotope enrichments. Birds were then released back into the same roost chambers of capture. However, at the desert site, roost nests were often too high above ground for us to reach and c. 35% of the individuals were kept for the remainder of the night (from approximately 24:00 to 05:00 h) in cloth bags suspended under a sheltered veranda, and released at dawn at the roost tree. Given the short time the birds spent in holding bags (during which they were calm), it is unlikely that this procedure perturbed subsequent DWF and DEE

measurements. This is supported by subsequent analysis that showed no statistical difference in mean DWF and DEE between individuals that slept in cloth bags and those that were placed back into their roosts.

The initial enrichments of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ were used to estimate the isotope dilution space which reliably estimates total body water (TBW; Degen *et al.* 1981, Speakman 1997). Each individual was re-trapped approximately 23.5 h after initial injection, weighed, and a final blood sample (S2) collected as described above (mean time between S1 and S2 = 23 h 50 min, range 22 h 41 min to 24 h 58 min). Immediately following collection, we transferred each blood sample to a 150- μL micropipette and flame-sealed both ends (Speakman 1997). The blood was stored between 2 °C and 5 °C in a portable domestic fridge until further analysis. All water extraction for analyses was conducted at the Council for Scientific and Industrial Research (CSIR), Pretoria, South Africa. We separated pure water from blood samples by cryogenic vacuum distillation, and measured the δD and $\delta^{18}\text{O}$ of the water samples using a PAL autosampler and DLT-100 liquid water isotope analyser (Los Gatos Research, Mountain View, CA, USA). Samples were bracketed with standards spanning -79.00 to 1950.69‰ VSMOW (δD) and -11.54 to 466.72‰ VSMOW ($\delta^{18}\text{O}$). A minimum of 10 1- μL replicates were analysed per sample or standard, with values for the first five replicates being discarded to avoid isotopic memory effects.

The respective washout rates for labelled hydrogen and oxygen were then used to estimate DWF and CO_2 production (Lifson & McClintock 1966, Nagy 1980). From the isotope dilution space measurements, we estimated TBW using blood samples from 85 individuals (34 and 51 from the semi-desert and desert sites, respectively) obtained at S1. We did not re-inject birds with isotopes to obtain a second measure of TBW on the second night of capture. One of the main assumptions of the DLW method is that birds maintain water and energy balance, and body mass during the period of measurement (Nagy & Costa 1980, Degen *et al.* 1981, Speakman 1997). Birds in our study, on average, lost $2.5 \pm 2.5\%$ of m_b during the *c.* 24-h period between S1 and S2 blood samples; we tested for statistical relationships between % m_b loss and daily temperature, *VPD* and sampling periods (see Results). Because of the changes in m_b during the measurement period in most of our

birds, we used equations 4 and 6 of Nagy and Costa (1980) to calculate water influx and efflux, respectively (these equations assume mass changes linearly with time). In birds that had identical m_b between sampling periods, DWF estimated through equations 4 and 6 was identical (Nagy & Costa 1980). We assumed TBW changed as a constant % of m_b over the measurement period following Speakman (1997); this is a reasonable assumption for a small passerine and a number of studies have shown that TBW as a % of m_b is generally maintained in birds under chronic negative water balance (Dawson *et al.* 1979, Carmi-Winkler *et al.* 1994, Klaassen 2004, Gerson & Guglielmo 2011). We used equation 2 of Nagy (1980), assuming linear change in TBW over the measurement period, to estimate CO_2 production. Rates of CO_2 production were converted to energy expenditure assuming an 80% insect- and 20% seed-based diet for White-browed Sparrow-Weavers (du Plessis 2005). We assumed that seeds contained 13.5% protein, 5.1% lipid and 81.4% carbohydrate (MacMillen 1990) and that an insect contains 62.0% protein, 14.9% lipid and 15.0% carbohydrate (Williams & Prints 1986). We calculated a conversion factor of 24.59 kJ per litre CO_2 based on the conversion factors of protein, fat and carbohydrate metabolism (Gessaman & Nagy 1988).

Data analysis

All statistical analyses were done with R (R Development Core Team 2011). We tested for the effect of sex and m_b on DWF (both influx and efflux estimates) and DEE using general linear models. When DEE or DWF varied significantly with m_b , we extracted partial residuals of these variables accounting for m_b for subsequent analyses. We could not reliably account for the effect of maximum daily T_{air} or *VPD* on DWF and DEE during the study at the semi-desert site because rainfall fell on most days when maximum $T_{\text{air}} < 30$ °C; the temperature range over which the remaining samples were collected was small (< 5 °C). Rainfall occurred on four of our sampling days and all 17 samples collected on these days were excluded from analyses, unless otherwise stated. In contrast, weather conditions at the desert site remained dry, with no significant rain having fallen for 9 months. For this sampling period we used a general linear model to test for the

effect of maximum daily T_{air} and VPD on DWF and DEE. We tested for differences in DWF and DEE between the sampling periods that we grouped into four periods: desert, semi-desert during wet season, semi-desert during dry season and days on which precipitation occurred; we used a Kruskal–Wallis test because of small sample sizes and unequal variances. Finally, we obtained resting EWL data as a function of T_{air} , measured under laboratory conditions, for White-browed Sparrow-Weavers (Whitfield *et al.* 2015), to estimate daily EWL requirements. We used daily profiles of air temperature (maximum T_{air} range 25–44 °C) measured in the Kalahari Desert to determine expected hourly rates of EWL. We then calculated cumulative EWL based on daily traces of T_{air} over 24-h periods. This allowed us to estimate how much of the daily water intake will be allocated to resting EWL requirements.

RESULTS

We obtained DWF measurements for days varying in maximum T_{air} from 27.5 °C to 37.4 °C at the semi-desert site ($n = 31$), and 27.6 °C to 39.0 °C at the desert site ($n = 40$). We obtained DEE measurements on days varying from 27.5 °C to 34.9 °C at the semi-desert site ($n = 9$), and 27.6 °C to 39.2 °C at the desert site ($n = 40$). Humidity varied greatly at both sites during our study. Mean daily absolute humidity ranged from 3.9 to 12.6 g/m³ at the desert site and from 8.2 to 22.6 g/m³ at the semi-desert site.

Body mass varied significantly between sites ($F_{1,94} = 6.240$, $P < 0.05$) and with sex ($F_{1,94} = 8.90$, $P < 0.01$); the interaction between site and sex was not significant and was subsequently removed from the model. Body mass was significantly higher in males than females ($P < 0.05$). Whereas m_b of female birds at the semi-desert site (42.9 ± 3.2 g) was significantly higher compared with females at the desert site (40.8 ± 2.8 g), there was no significant difference in mass of male birds between sites (semi-desert males = 44.0 ± 2.6 g; desert males = 43.1 ± 2.7 g). TBW as a % of m_b was significantly higher in the semi-desert birds than in those from the desert site ($F_{1,77} = 13.4$, $P < 0.001$): $71.9 \pm 3.6\%$ in the semi-desert birds and $68.7 \pm 3.30\%$ in the desert birds. The m_b of individual birds at S2, expressed as a % of m_b at S1, was lower in birds from the desert site and semi-desert site during the dry season than in birds at

the semi-desert site during the wet season (Kruskal–Wallis $\chi^2 = 9.91$, $P < 0.01$). During the wet season at the semi-desert site, m_b as a % of initial m_b in birds was, on average, 0.8% lower. In contrast, during the dry periods at the desert site and semi-desert site, m_b was 3.2% and 3.5% lower, respectively. We found no statistically significant relationship between m_b loss, and maximum T_{air} and VPD (all P -values > 0.7).

DWF (both water influx and water efflux) did not differ between sexes. DWF was not significantly related to m_b , maximum T_{air} or VPD in the desert site birds (all $P > 0.2$; Supporting Information Figs S1 & S2). Mean daily water influx rates varied significantly amongst sampling periods (Kruskal–Wallis $\chi^2 = 22.45$, $P < 0.001$); influx rates were significantly lower in the desert birds and semi-desert birds during the dry season (mean \pm sd, range, for desert site = 10.3 ± 2.5 , 6.2–16.1 mL/day; semi-desert during dry season = 9.8 ± 1.4 , 7.9–11.3 mL/day) compared with the wet sampling period (semi-desert during wet season = 16.4 ± 3.4 , 11.1–23.1 mL/day; Fig. 2a). Similarly, mean daily water efflux varied significantly among sampling periods (Kruskal–Wallis $\chi^2 = 19.35$, $P < 0.001$); efflux rates were significantly lower during the dry sampling periods (desert site = 11.2 ± 2.4 , 7.5–17.0 mL/day; semi-desert during dry season = 10.9 ± 1.5 , 8.5–12.2 mL/day) compared with the wet sampling period (16.7 ± 3.4 , 11.2–23.5 mL/day). On days when rain occurred during DWF measurements, water influx (18.2 ± 3.8 , 13.6–24.1 mL/day) and efflux (18.5 ± 3.4 , 13.8–23.9 mL/day) rates were slightly higher, but not significantly so, than measurements at the semi-desert site obtained during the wet season (Fig. 2).

To assess whether the above differences in m_b loss, and apparent mismatches between estimates of influx and efflux rates could represent differences in water balance over the measurement periods, we determined ratios of water influx/water efflux for each individual (hereafter referred to as proportional water balance). Mean proportional water balance approximated to a ratio of 1.00 in birds at the semi-desert site during the wet season (mean = 0.99, range = 0.91–1.05), and on days when rainfall occurred (mean = 0.98, range = 0.93–1.03). In contrast, proportional water balance was significantly lower in the desert site birds (mean = 0.91, range = 0.70–1.06) and semi-desert site birds during the dry season (mean = 0.90,

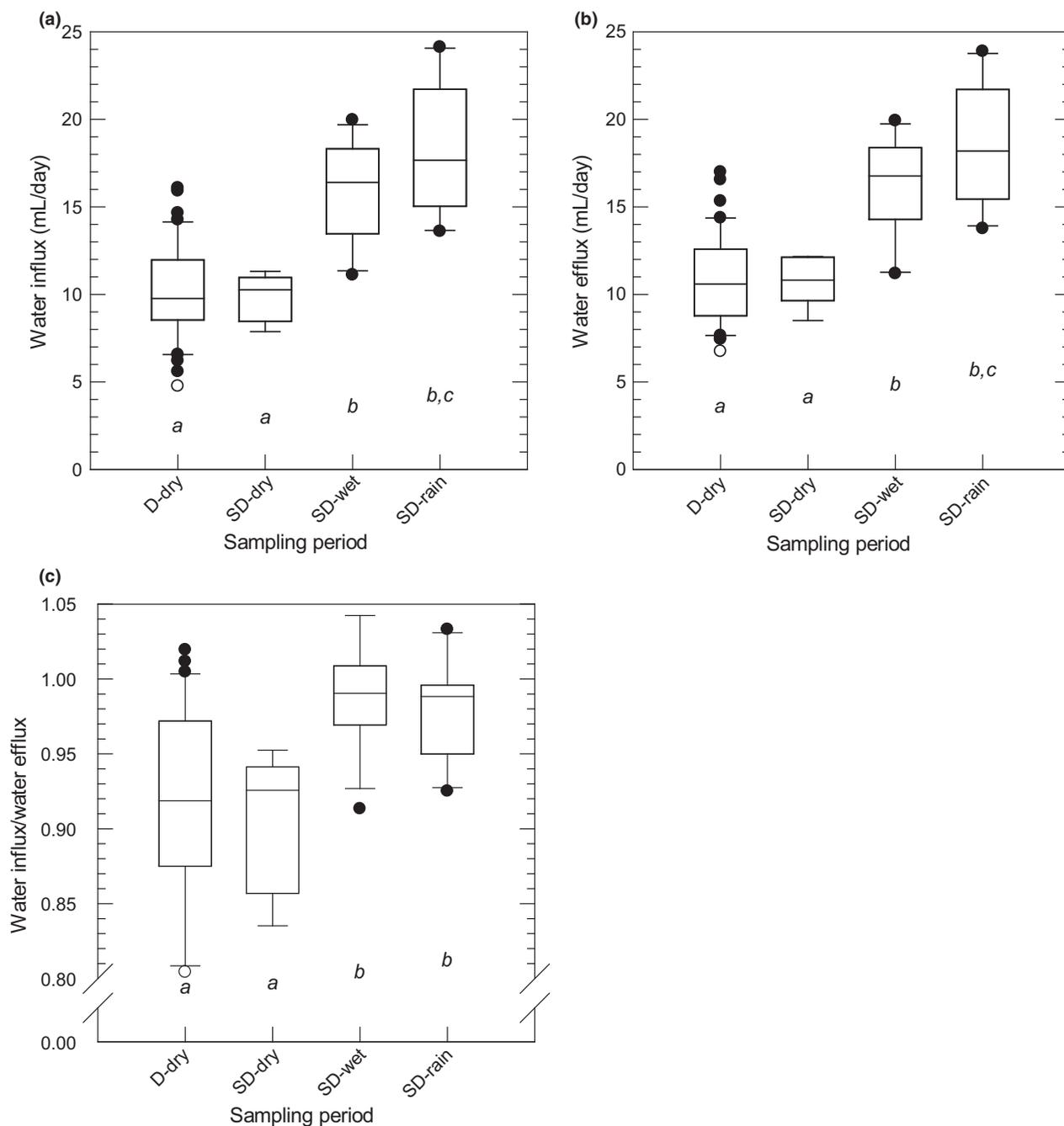


Figure 2. (a) Daily water influx rates, (b) daily water efflux rates and (c) proportional water balance (water influx/water efflux) in White-browed Sparrow-Weavers as a function of sampling period. A Kruskal–Wallis post hoc test was used to test for significant differences ($P < 0.05$ indicated by letters). Acronyms represent the desert site (D-dry), semi-desert site during the dry season (SD-dry), semi-desert site during the wet season (SD-wet) and the days on which rain was observed (SD-rain).

range = 0.84–0.95; Kruskal–Wallis $\chi^2 = 13.52$, $P < 0.01$; Fig. 2c). We interpret these results as individuals being in negative water balance during the dry sampling periods, compared with birds at

the semi-desert site during the wet season. Proportional water balance was not significantly related to maximum T_{air} , VPD or m_b (all $P > 0.4$; Figs S1 & S2).

DEE was significantly positively related to m_b at both sites ($F_{1,38} = 18.34$, $P < 0.001$; Fig. 3a). Partial residual DEE was not significantly related to maximum T_{air} in the desert site birds ($F_{1,35} = 3.41$, $P = 0.073$; Fig. 3b), although on the hottest day (39 °C) DEE was on average 7%

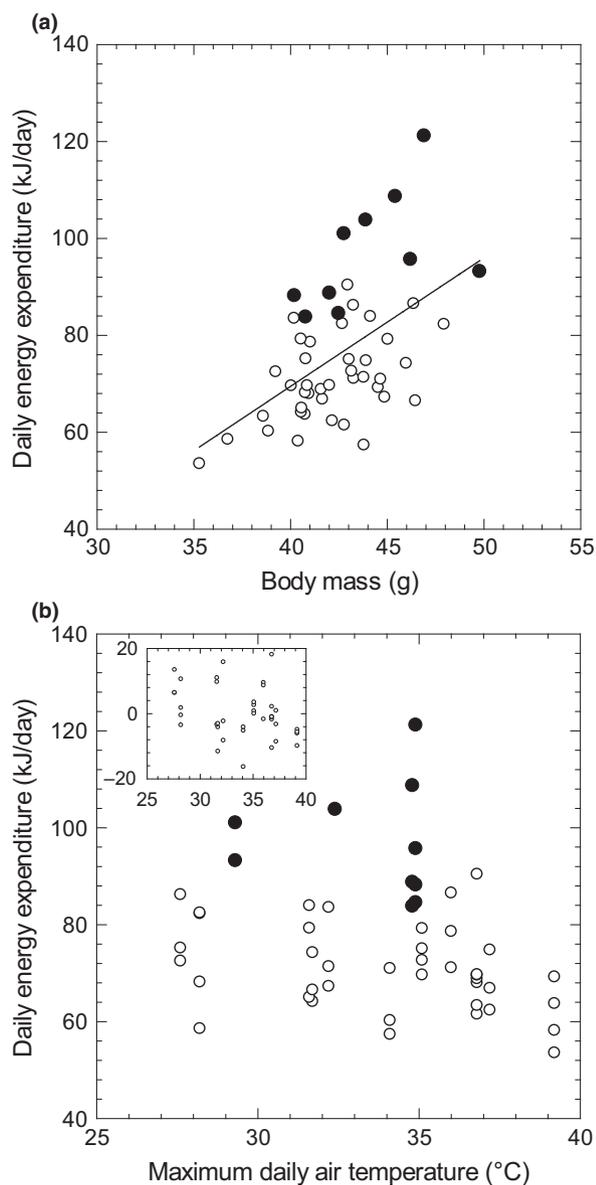


Figure 3. Daily energy expenditure (DEE) as a function of (a) body mass and (b) maximum daily air temperature in two populations of White-browed Sparrow-Weavers. The black dots and open circles represent measurements made at the semi-desert and desert sites, respectively. The inset graph represents mass-corrected partial residuals of DEE in the desert site birds.

below mean DEE. Over a comparable range of maximum T_{air} (34–36 °C), DEE was significantly higher in semi-desert birds ($n = 6$, 95.8 ± 14.1 kJ/day) than desert birds ($n = 4$, 74.1 ± 4.1 kJ/day; Kruskal–Wallis $\chi^2 = 9.00$, $P < 0.01$).

DISCUSSION

Our results reveal limited variation in DWF and DEE with daily T_{air} in an arid-zone passerine. Instead, we found that DWF and DEE varied significantly at both a temporal and a spatial scale, driven perhaps by an increase in the availability of water-rich food resources, such as insects or succulent vegetation (Alkon *et al.* 1982). The period of high rainfall coinciding with our sampling period at the semi-desert site precluded us from drawing firm conclusions regarding temperature-dependency. We further showed that during dry sampling periods, many sparrow-weavers were not maintaining body mass over the 24-h measurement period. These results suggest that during hot and dry desert conditions, water gains in sparrow-weavers through foraging or oxidative water formation were typically not sufficient to balance water losses. A combination of low overall food availability and high rates of EWL could explain these patterns.

On the hottest days during our study, DEE was slightly lower (7% on average), probably reflecting reduced activity. The trend of decreasing DEE at high T_{air} could reflect greater periods spent resting, observed in a concurrent study during the middle of the day, to avoid excessive heat gain (Smit *et al.* 2013). However, sparrow-weavers resumed foraging later in the day (after 14:00 h), even when T_{air} approached 40 °C, and this was combined with significantly more time spent panting (Smit *et al.* 2013). Collectively, these findings suggest that sparrow-weavers experience a trade-off between the avoidance of elevated body temperatures (through increased panting) and foraging to maintain water and energy (Smit *et al.* 2013). The elevation in T_b observed in sparrow-weavers at high T_{air} in the latter study could play an important role in reducing thermoregulatory EWL to aid in water balance under conditions when water-rich food is scarce; for example, a 2.3 °C increase in T_b can facilitate thermoregulatory water savings of up to 50% at $T_{\text{air}} = 38$ °C (Weathers 1981). The effect of experimental water supplementation on T_b , DWF and foraging effort would be an important

avenue for future research investigating this apparent trade-off.

During the dry periods in our study, many birds appeared to be in negative water balance. We cannot rule out the effect of capture and handling stress on the observed mass deficits but it is noteworthy that mass deficits were significantly greater in dry periods than in a wet period, during which birds maintained m_b . As White-browed Sparrow-Weavers live in groups with strong dominance hierarchies, and defend exclusive territories from neighbouring groups (Harrison *et al.* 2013, Cram *et al.* 2014), we suspect that social status and territory quality will be important determinants of the ability of individuals to maintain water and energy balances. Moreover, these deficits resemble the patterns of mass loss observed during dry summers in the Kalahari Desert in another cooperative breeding bird with a similar social system, the Southern Pied Babbler (Ridley *et al.* 2008, Golabek *et al.* 2012, du Plessis *et al.* 2012).

The differences in m_b and TBW (as a percentage of m_b) observed between White-browed Sparrow-Weavers are more complex to interpret. We cannot establish whether the smaller size of females at the desert site than at the semi-desert site represents genotypic divergence or phenotypic plasticity. We suspect, however, that this represents a phenotypic reduction in mass related to low food and water availability. Many small arid-zone birds have reduced body sizes under environmental conditions where food and water are scarce, and lost m_b is usually regained during periods when food and water abundance increases (Anava *et al.* 2002, Golabek *et al.* 2012). Estimates of TBW between 65 and 75% as a percentage of m_b are common in birds (Alkon *et al.* 1982, Speakman 1997, Anava *et al.* 2002), although values over 70% are normally indicative of low body fat content (Alkon *et al.* 1982). In our study, birds had significantly higher TBW as a percentage of mass during the wet season at the semi-desert site (*c.* 72%), which could represent reductions in total body fat (Alkon *et al.* 1982), possibly through the allocation of energy reserves to reproduction.

Our findings that DWF and DEE increased significantly during the wet season at the semi-desert site are likely to be explained by birds taking in more food with higher content while also gaining more oxidative water from the increased feeding. Insect activity is generally greatly increased during periods of significant rainfall (Louw & Seely 1982,

Smit 2008), and sparrow-weavers were often observed eating one to two large caterpillars during a 30-min focal observation under these conditions (B. Smit pers. obs.). Many of the sparrow-weaver groups were also breeding during the wet season at the semi-desert site; we observed a number of females with brood patches between January and March 2011. White-browed Sparrow-Weavers generally breed opportunistically at the onset of wet periods (du Plessis 2005) and breeding activity combined with increased food availability could explain the higher DWF and DEE values observed during wet periods at the semi-desert site. Other DLW studies on arid-zone passerines also showed higher DEE and daily water intake rates during the breeding season when food was more abundant, compared with the dry, non-breeding season in summer (72.5 g, Arabian Babbler *Turdoides squamiceps*, Anava *et al.* 2002; 40.7 g, Hoopoe Lark *Alaemon alaudipes*, Tieleman *et al.* 2003). During our sampling period at the desert site, none of the White-browed Sparrow-Weaver groups showed any evidence of breeding activity. Both mean DWF and DEE measured in the White-browed Sparrow-Weavers during dry periods (for birds that maintained m_b) were similar (within 2%) to the expected values for an arid-zone bird (Tieleman & Williams 2000). In contrast, DEE and DWF in the sparrow-weavers during the wet season were 4 and 15% higher, respectively, than expected for a 43-g desert bird (Tieleman & Williams 2000).

Considering the strong positive relationship between EWL and T_{air} typically observed in endothermic animals exposed to high T_{air} under laboratory conditions (Weathers 1981, Dawson 1982), we expect EWL to become a substantial component of DWF at T_{air} approaching T_b . White-browed Sparrow-Weavers at our study sites pant most of the time when T_{air} approaches 40 °C (Smit *et al.* 2013), which would result in increased respiratory EWL. The elevated demands for panting under natural conditions are probably slightly higher than under laboratory conditions because birds are gaining heat through activity, and they are likely to experience T_e above T_b , even at $T_{air} < 40$ °C (Wolf & Walsberg 1996). Under these situations, sparrow-weavers may be expected to be less able to conserve water as they start spending more energy on EWL than they might gain through their foraging efforts.

To conserve water, desert birds with limited water sources should use the minimum amount of

water possible to maintain energy balance (Tielemann & Williams 2000). Nagy and Peterson (1988) developed the water economy index (WEI) for animals that maintain water balance, measured as the water (mL) used per kJ of energy metabolized (i.e. DWF/DEE), to quantify the effectiveness of an animal's water conservation mechanisms. We calculated WEI for White-browed Sparrow-Weaver individuals whose body mass varied by 1% or less over the sampling period. Our limited sample size precluded us from testing for a relationship between WEI and maximum T_{air} or VPD . WEI was, on average, lower in birds from the desert site (0.155 ± 0.030 mL/kJ, $n = 8$) than in birds from the semi-desert site during the wet season (0.214 ± 0.028 mL/kJ, $n = 3$). The different ratios indicate that the diets of the birds were likely to be different during the two sampling periods. These ratios are also remarkably similar to the mean ratios reported by Nagy (2004) for desert (0.150 mL/kJ) and non-desert birds (0.195 mL/kJ), respectively. The lower rate of water flux relative to energy expenditure facilitated the capacity of sparrow-weavers at the dry desert site to maintain water balance.

The findings we report here have important implications for predicting the vulnerability of desert birds to climate change, particularly small non-drinking species. During dry periods, sparrow-weavers at our study sites take in *c.* 28% of their body mass in water on hot days where T_{air} approaches typical avian T_b . Daily water loss comprises a combination of excretory water losses as well as respiratory and cutaneous EWL, and on hot days birds must allocate a greater proportion of daily water intake to thermoregulatory EWL. We estimated that on a typical hot day in the Kalahari Desert, when maximum $T_{\text{air}} = 40$ °C, birds will need to allocate 85% of mean DWF to daily resting EWL (i.e. estimated total EWL over 24 h, Fig. 4). The points where the curve of daily resting EWL bisects the lower and upper limits of DWF (Fig. 4) represent the maximum daily T_{air} range where we expect individuals to spend their entire DWF on resting EWL. Assuming birds cannot increase daily water intake further on hotter days, the maximum daily T_{air} of 39.5–44.4 °C (mean = 41.9 °C) could represent threshold temperatures for maintaining water balance of White-browed Sparrow-Weavers in the Kalahari Desert (Fig. 4). Coincidentally, this range of maximum T_{air} currently represents the hottest conditions

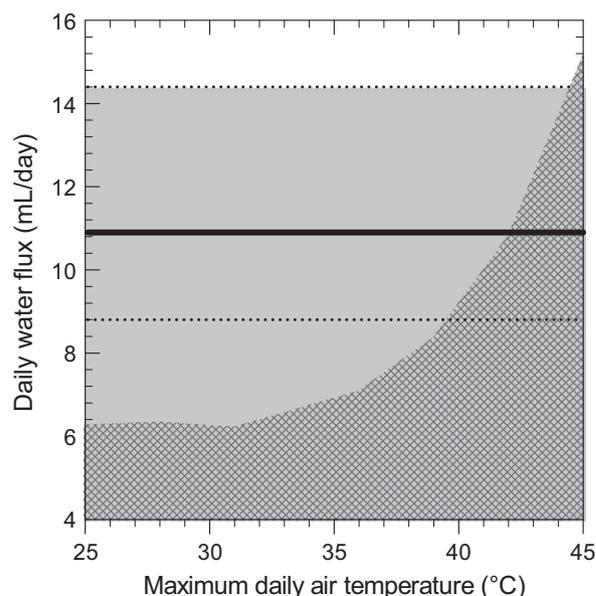


Figure 4. Daily water flux (mL/day) represented by the grey area (the solid and dotted lines represent mean and range, respectively) as a function of maximum daily air temperature in non-drinking White-browed Sparrow-Weavers under dry desert conditions, assuming the highest rate of DWF is maintained on hotter days. These values were obtained in the present study from birds that maintained body mass ($< 1\%$ mass change over the measurement period). The hatched area represents evaporative water loss rates predicted from lab-based measures (Whitfield *et al.* 2015) for temperatures corresponding to the 24-h profile associated with a given thermal maximum.

experienced by White-browed Sparrow-Weavers across their range in southern Africa (the recorded maximum T_{air} was *c.* 44 °C for Twee Rivieren weather station, South Africa, obtained from www.wunderground.com). Given that respiratory water lost through activity (e.g. high foraging effort) will probably further elevate daily EWL demands on hot days, these birds are likely to undergo severe pressure to maintain water balance in these environments over the next few decades. Although some birds are nomadic and can avoid conditions when food is scarce, a surprisingly large number of small bird species are highly sedentary and territorial year-round (Harrison *et al.* 1997), especially cooperative breeders such as White-browed Sparrow-Weavers and Southern Pied Babblers (Ridley *et al.* 2008, Golabek *et al.* 2012, Harrison *et al.* 2013, Cram *et al.* 2014). We predict, therefore, that resident birds would need to drink free-standing water under increasingly hot conditions to maintain water balance.

It has been predicted that the frequency distribution of current maximum temperatures, as well as record maximum temperatures, will shift upwards over the next few decades (see fig. SPM. 3 of IPCC 2011). Whereas acute, short-term mismatches in water supply and demand during hot extremes could result in large-scale die-offs such as those documented in Australian birds (Finlayson 1932, Towie 2009, Saunders *et al.* 2011), overall higher temperatures could result in longer-term, chronic mismatches. Although these chronic mismatches, such as those predicted here for White-browed Sparrow-Weaver, might not be lethal, they could be manifested as reduced body condition when, for example, foraging efficiency and water acquisition are compromised at T_{air} approaching T_b (du Plessis *et al.* 2012), or they could significantly compromise reproductive fitness (Cunningham *et al.* 2013).

In summary, we found that during dry and hot conditions, an arid-zone passerine has low water intake and many individuals do not maintain m_b . Our results are widely applicable to arid-zone birds across the globe; White-browed Sparrow-Weavers are comparable in body size and ecology to many other ground-foraging passerine birds inhabiting arid environments (Harrison *et al.* 1997, Barrett *et al.* 2003), and most avian communities inhabiting the subtropical deserts of the world are dominated by small non-drinking, insectivorous species (Cade & Greenwald 1966, Fisher *et al.* 1972). We predict that non-drinking species that do not have opportunities to increase water intake will experience strong trade-offs between thermoregulation, hydration state and activity levels as temperatures increase. Many of these non-drinking species may become more dependent on free-standing water sources.

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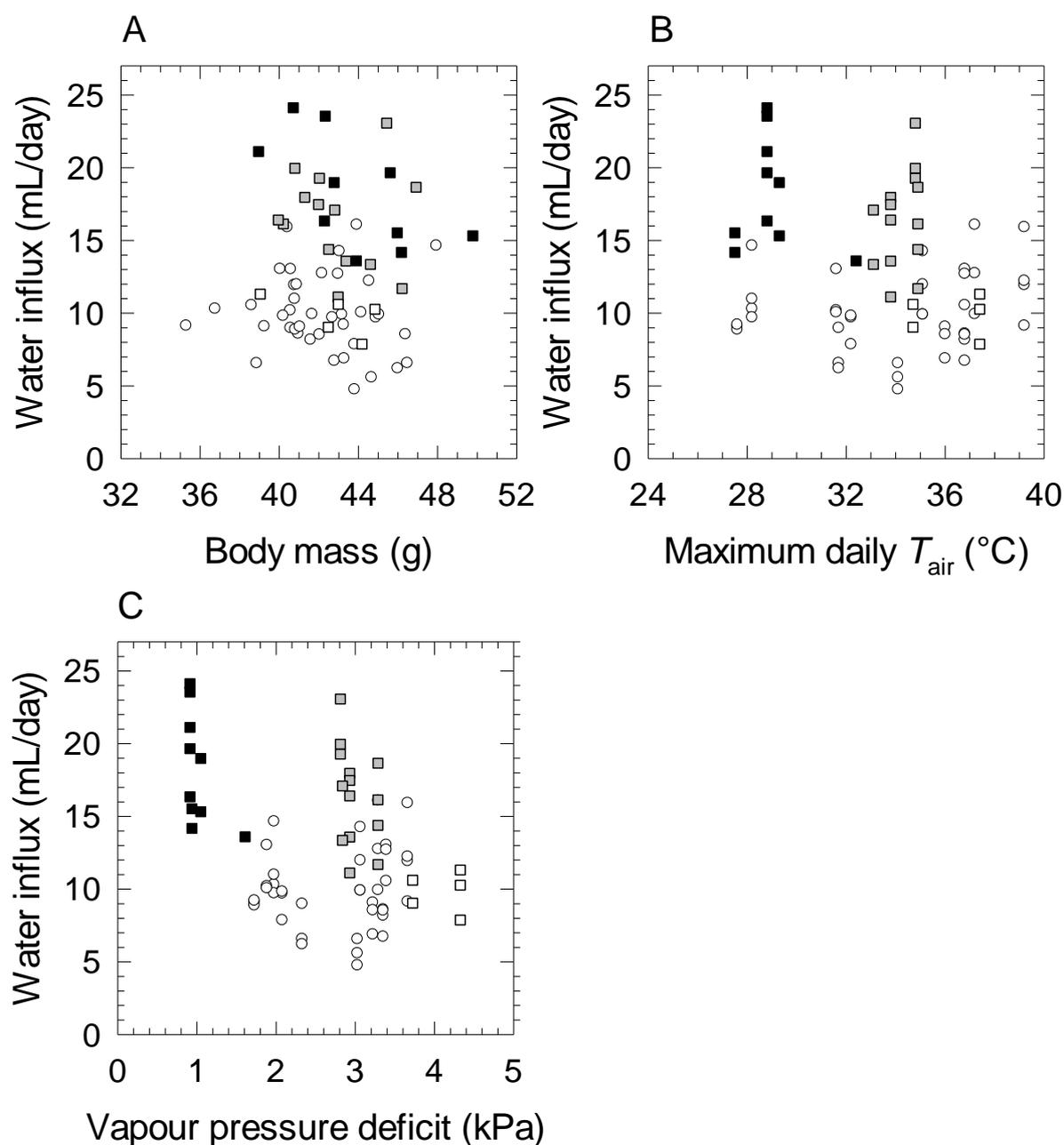
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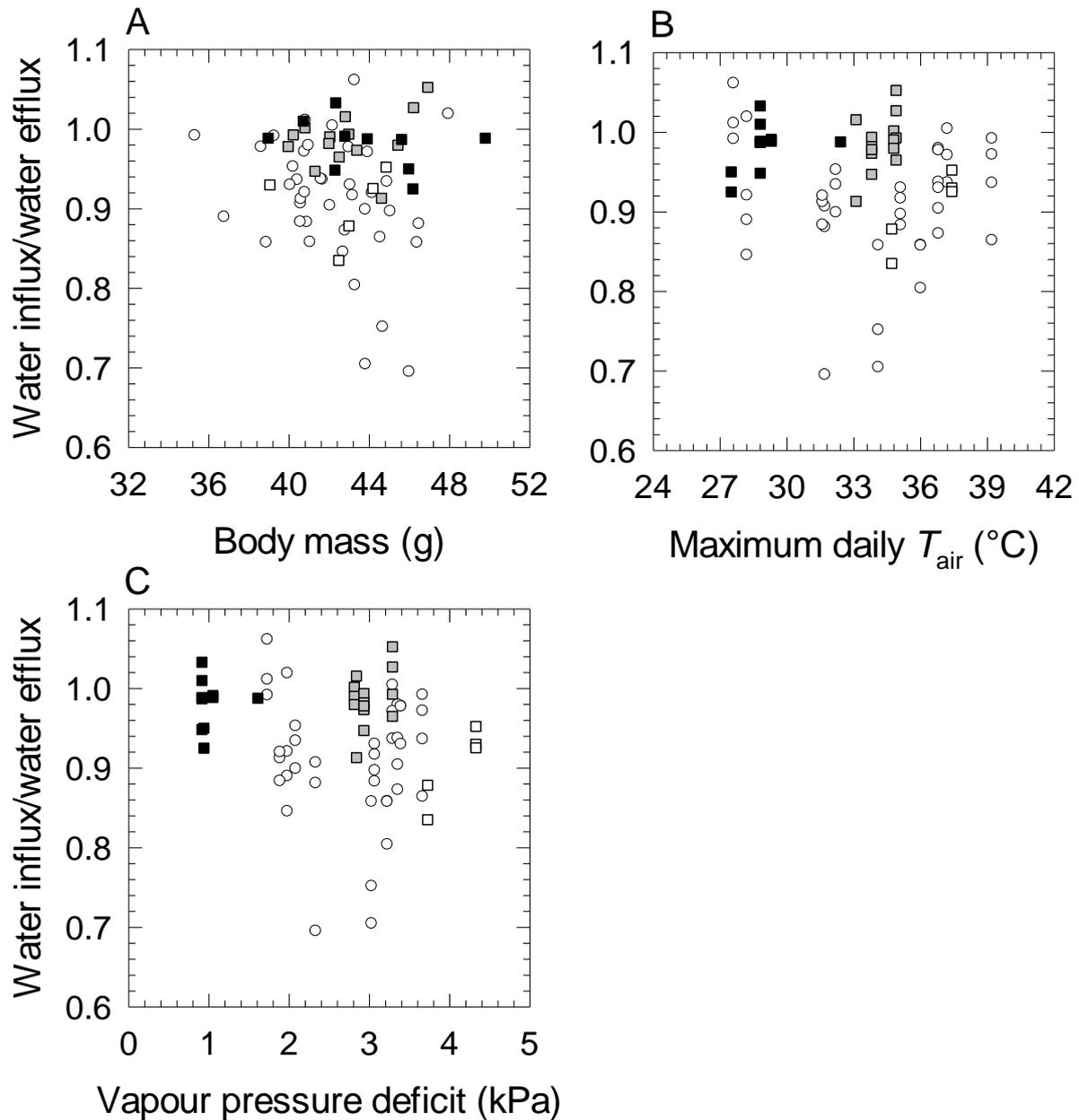
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Supporting Information



Supporting Figure S1: Daily water influx as a function of A) body mass, B) maximum daily air temperature (T_{air}), and C) water vapour pressure deficit, in White-browed Sparrow-Weavers (*Plocepasser mahali*). The clear circles represent measurements obtained at the desert site (Wildsgenot Game Ranch, South Africa). Squares represent measurements obtained at the semi-desert site (Tswalu Kalahari Reserve, South Africa) during the dry (clear squares) and wet seasons (grey squares), and samples obtained on rainy days (black squares), respectively. Samples obtained during rainy days were excluded from statistical analyses. There was no relationship between DWF and body mass, maximum daily T_{air} , or water vapour pressure deficit, within each respective sampling period. Daily water flux varied significant with sampling period (see main text for details).



Supporting Figure S2: Figure S1: Water influx/ water efflux rates (indication of daily water balance) as a function of A) body mass, B) maximum daily air temperature (T_{air}), and C) water vapour pressure deficit, in White-browed Sparrow-Weavers (*Plocepasser mahali*). The clear circles represent measurements obtained at the desert site (Wildsgenot Game Ranch, South Africa). Squares represent measurements obtained at the semi-desert site (Tswalu Kalahari Reserve, South Africa) during the dry (clear squares) and wet seasons (grey squares), and samples obtained on rainy days (black squares), respectively. Samples obtained during rainy days were excluded from statistical analyses. There was no relationship between DWF and body mass, maximum daily T_{air} , or water vapour pressure deficit, within each respective sampling period. Daily water flux varied significant with sampling period (see main text for details).