

Water and energy economy of an omnivorous bird: Population differences in the Rufous-collared Sparrow (*Zonotrichia capensis*)

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Abstract

We investigated the intraspecific variation in basal metabolic rate (BMR) and total evaporative water loss (TEWL) in the omnivorous passerine *Zonotrichia capensis* from two populations inhabiting regions with different precipitation regimes and aridity indices. Values of TEWL in birds from the semi-arid region were significantly lower than those found in sparrows from the mesic region. TEWL in birds from the semi-arid site was 74% of the expectation based on body mass for passerines from mesic areas and similar to the allometric expectation for passerines from arid environments. In sparrows from the mesic area, TEWL was higher than predicted by their body mass for passerines from arid environments (133%), but very close (97%) to the expectation for passerines from mesic areas. BMR values were 25% lower in sparrows from the semi-arid region. The lower TEWL and BMR of birds from the semi-arid region may be a physiological adjustment that allows them to cope with fewer resources and/or water. We propose that the lower endogenous heat production in birds from the semi-arid environment may decrease their water requirements.

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1. Introduction

Organisms can survive and colonize xeric environments through mechanisms acting at cellular, physiological, ecological and/or behavioural levels (Cade et al., 1965; Casotti and Richardson, 1992; Tieleman et al., 1999; Haugen et al., 2003; Bozinovic and Gallardo, 2006; Bozinovic et al., 2003).

Because of their diurnal habits, high mass-specific metabolisms, and high body temperatures, passerines tend to have proportionately high rates of water flux. For xeric-adapted birds, one trait may be possessing low total evaporative water loss (TEWL) rates. Such physiological traits would allow birds to conserve water by reducing insensible water losses (Williams, 1996; McNab, 2002; Tieleman et al., 2003; Vikelski et al., 2003). Some

authors have proposed that the low productivity of desert and semi-desert environments selectively favours animals with lower energy requirements. This hypothesis predicts that animals with a low basal metabolic rate (BMR) are more likely to inhabit xeric environments (Dawson and Bennett, 1973; Schleucher et al., 1991). The scarcity of water in these environments may also be a selective pressure favouring lower BMRs as lower endogenous heat production may decrease water requirements for evaporative cooling (Dawson, 1984).

Recent evidence has shown that energy and water requirements not only vary among species from desert and non desert habitats (see Withers and Williams, 1990; Hinsley et al., 1993; Williams and Tieleman, 2000), but also along an aridity gradient (Tieleman et al., 2004). This suggests that physiology is responsive to and reflects small differences in water availability and temperature. Several studies have examined water conservation in birds at the interspecific level (see also Tieleman et al., 2002, 2003); however, relatively few have sought to understand water conservation at either the intraspecific level (Arieli et al., 2002; Williams and

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Tieleman, 2000) or between populations of the same species that inhabit both mesic and arid environments (Macmillen and Hinds, 1998). However, inter-populational differences in the energy and water economy among birds may be widespread but it is not universal. For example, Macmillen and Hinds (1998) compared the water economy of coastal and desert populations of house finches (*Carpodacus mexicanus*) and reported that birds from the Mojave Desert are more economical in water use (ca. 40% lower TEWL) rather than California coastal forms. By the other hand, Thomas et al. (2001) found no evidence of local adaptation in resting metabolic rates of blue tits (*Parus caeruleus*), in response to hot climates. Intraspecific differences in the physiology of geographically separated populations can provide insight into the evolutionary processes that permit species to cope with environmental variability. These studies are, therefore, important for understanding the origin of physiological diversity and the evolution of physiological tolerance (Garland and Adolph, 1991; Spicer and Gaston, 1999).

To investigate intraspecific variability in energy and water budgets, we measured BMR, TEWL, in the passerine bird, Rufous-collared Sparrow (*Zonotrichia capensis*, Emberizidae). We made these measurements in birds from two localities that varied in both annual precipitation and temperature. We also assessed how the nasal passages affected the capacity to recovery water from expelled air. *Zonotrichia capensis* is an omnivore distributed throughout the neotropics (from southeast México to Cabo de Hornos; Goodall et al., 1951). In Chile, it is nearly ubiquitous, inhabiting areas as different as deserts and rain forests from 0 to more than 3600 m.a.s.l. (Araya, 1996). We predicted that animals from the southern and wet area would have higher levels of energy production (BMR) and water flux (TEWL), than those from the northern xeric area.

2. Materials and methods

2.1. Animals and capture

Sparrows were collected during the austral winter of 2005 from two localities in Chile: (1) La Serena (29° 54' S, 71° 15' W, $n=6$), and (2) Quebrada de la Plata (33° 31' S, 70° 50' W, $n=9$). Our study sites varied in mean annual rainfall: La Serena is semi-arid, and receives 100 mm per year, whereas Quebrada de la Plata is mesic and receives 367 mm per year, and their aridity scores using the index of de Martone, (Martone index = $P/(T+10)$, where P is annual precipitation in mm, and T is mean annual temperature in °C) are 5.13 for La Serena and 14.90 for Quebrada de la Plata (Di Castri and Hajek, 1976; DGA, 2004).

2.2. BMR and TEWL

After capture, we transported the birds to the laboratory in Santiago, Chile (33° 27' S, 70° 42' W) and housed them in individual 35 × 35 × 35 cm plastic-mesh cages. Temperature and photoperiod were held at 22 ± 2 °C and 12 L:12 D respectively. Birds had ad libitum access to mealworms, seeds and water. After an initial laboratory habituation of two days, birds were measured within the first week of capture. We measured rates of

oxygen consumption (VO_2) and total evaporative water loss (TEWL) in post absorptive (four hour fasted), resting birds in the inactive phase, using standard flow-through respirometry and hygrometry methods. Inside dark metabolic chambers (1 L), birds perched on a wire-mesh grid that allowed excreta to fall into a tray containing mineral oil, thus trapping the water from this source. Oxygen consumption was measured using a computerized, open-flow respirometry system (Sable Systems, Henderson, NV, USA) calibrated with a known mix of oxygen (20%) and nitrogen (80%) that were certified by chromatography (INDURA, Chile). Measurements were made at ambient temperatures (T_a) of 25.0, 30.0, and 40.0 ± 0.5 °C at random. We are confident that T_a of 30.0 °C is within the thermo neutral zone for this species (Novoa et al., 1990; Novoa, 1993) as we initially measured VO_2 at temperatures ranging from 15 to 40 °C in four individuals (Fig. 1). To estimate the contribution of turbinates in the water economy of birds, we also determined VO_2 and TEWL at 30 °C in birds with nares occluded by plastic dental resin. We assumed that cutaneous evaporative water loss was not affected by the treatment (see Tieleman et al., 1999). The metabolic chamber received dried air at 500 mL min⁻¹ from a mass flow controller and through Bev-A-Line tubing (Thermo-plastic Processes Inc.). This flow ensured adequate mixing in the chamber. The mass flow meter was calibrated monthly with a volumetric (bubble) flow meter. The excurrent air passed through a RH-200 relative humidity/dewpoint hygrometer (Sable Systems) and through columns of Driedrite, CO₂-absorbent granules of Baralyme, and Drierite before passing through an O₂-analyzer, model FC-10A (Sable System). The complete VO_2 trial lasted 3 h. Output from the H₂O (kPa) and oxygen analyzers (%) was digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using EXPE-DATA data acquisition software (Sable Systems). Our sampling interval was 5 s. Birds remained in the chamber for at least 3 h and visual inspection of the recorded data allowed us to determine when steady-state conditions had been achieved. We averaged water vapour pressure and O₂ concentration of the excurrent airstream over a 20 min period after steady-state was

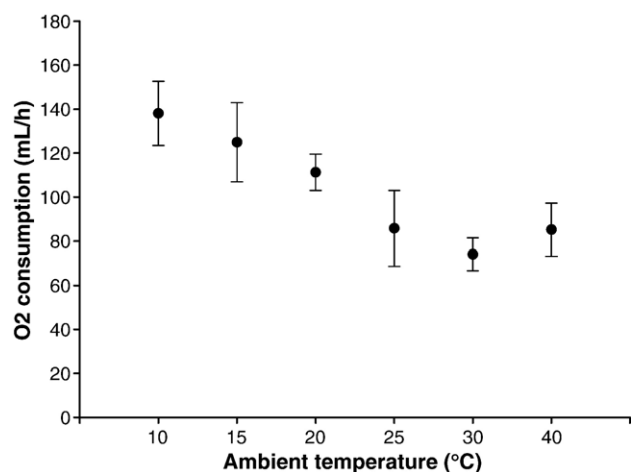


Fig. 1. Profile of oxygen consumption as a function of ambient temperature in *Zonotrichia capensis* from Central Chile. Data are reported as mean ± SD.

Table 1
Body mass, organ masses, body temperature and basal metabolic rate (BMR) in *Zonotrichia capensis* from two localities in central Chile

	La Serena	Quebrada de la Plata
Body mass (g)	20.06±1.13 (6)	20.11±1.17 (9)
Liver mass (g)	0.62±0.08 (6)	0.73±0.22 (9)
Kidney mass (g)	0.22±0.02 (6)	0.24±0.04 (9)
Intestine mass (g)	0.72±0.11 (6)	0.81±0.30 (9)
Heart mass (g)	0.25±0.02 (6)	0.26±0.03 (9)
Body temperature	40.26±0.62 (6)	40.36±0.54 (9)
BMR (mL O ₂ h ⁻¹)	55.85±4.84*(6)	73.08±6.89 (9)

Asterisk denotes significant differences between localities and the number of animals of each treatment is in parenthesis (see text for ANOVA results).

reached (following Tieleman et al., 2002). Because CO₂ was scrubbed before entering the O₂ analyzer, oxygen consumption was calculated as [Withers (1977: p 122)]: $VO_2 = [FR * 60 * (F_i O_2 - F_e O_2)] / (1 - F_i O_2)$, where FR is the flow rate in mL/min after STP correction, F_i and F_e are the fractional concentrations of O₂ entering and leaving the metabolic chamber, respectively. TEWL was calculated as $TEWL = [(V_e \rho_{out} - V_i \rho_{in})]$ where TEWL is in mg/mL. ρ_{in} and ρ_{out} are the absolute humidity in kg/m³ of the inlet air and the outlet air respectively, V_e is the flow rate of the air entering the chamber as given by the mass flow controller (500 mL min⁻¹ after STP correction) and V_e is the flow of exiting air. V_e was calculated following Williams and Tieleman (2000) as $V_e = V_i - [VO_2 (1 - RQ)] + VH_2O$ V_i , and VO_2 (mL min⁻¹) are known. We assumed a respiratory quotient (RQ) as 0.71. Absolute humidity was calculated as $\rho = P / (T * R_w)$, where P is water vapour pressure of the air in Pascal, T is the temperature of the dew-point hygrometer in Kelvin and R_w is the gas constant for water vapour (461.5 J/kg * Kelvin, Lide, 2001). The P_{in} was determining using the average value of the vapour pressure of the air entering the empty chamber (i.e., the baseline period of 15 min) before and after each experiment. Body mass was measured before the metabolic measurements using an electronic balance (±0.1 g) and cloacal body temperature (T_b) was recorded at the end of each measurement with

a Cole–Palmer copper–constantan thermocouple attached to an Digi-Sense thermometer (Model 92800-15).

After metabolic experiments, birds were killed by exposure to CO₂ and all animals were dissected abdominally. We extracted the large and small intestine, and then heart, lungs, liver and kidneys. Organs were weighed immediately (±0.05 g).

2.3. Data analysis

Because our populations did not differ in body mass (m_b) ($F_{1,10}=0.44$, $p=0.52$, Table 1), we analyzed data using a repeated measures ANOVA using individual measurements at each T_a (25, 30 and 40 °C) as repeated measures. Additionally, since TEWL might be affected by oxygen consumption, we performed linear regression analyses with TEWL as the dependent variable and VO₂ consumption as the independent variable in birds measured at each temperature. We estimated the metabolic water production (MWP) of birds using equivalence: 0.567 mL H₂O per liter O₂ consumed (Schmidt-Nielsen, 1997). The ratio between MWP and TEWL was calculated and analyzed for population differences at different temperatures.

3. Results

Values of TEWL in birds from the semi-arid region of La Serena were significantly lower than those found in sparrows from Quebrada de la Plata, which is the mesic region (locality: $F_{1,10}=16.60$, $p=0.002$, Fig. 2). We also found that TEWL increased with increasing T_a (T_a : $F_{2,22}=268.4$, $p<0.001$, Fig. 2). BMR values were 25% lower ($F_{1,20}=27.08$, $p<0.001$, Table 1) in sparrows from La Serena than those of birds from Quebrada de la Plata. Coupled with the increase in TEWL, body temperature was also increased at 40 °C (T_a : $F_{2,22}=87.11$, $p<0.001$) In addition, the MWP/TEWL ratio decreased significantly with T_a (T_a : $F_{2,20}=162.3$, $p<0.001$, Fig. 3) and ranged from ca. 65% at 25 °C to 10% at 40 °C. No significant differences in MWP/TEWL were found between localities ($F_{1,10}=0.32$, $p=0.58$). A

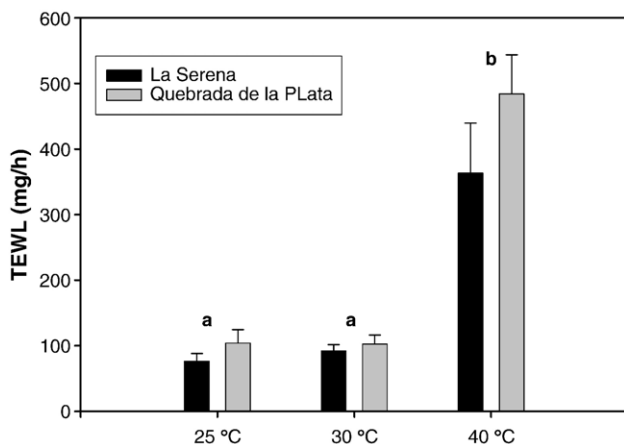


Fig. 2. Total evaporative water loss in *Zonotrichia capensis* from two localities in central Chile at three different temperatures. Letters denote significant differences between temperatures. Data are reported as mean±SD.

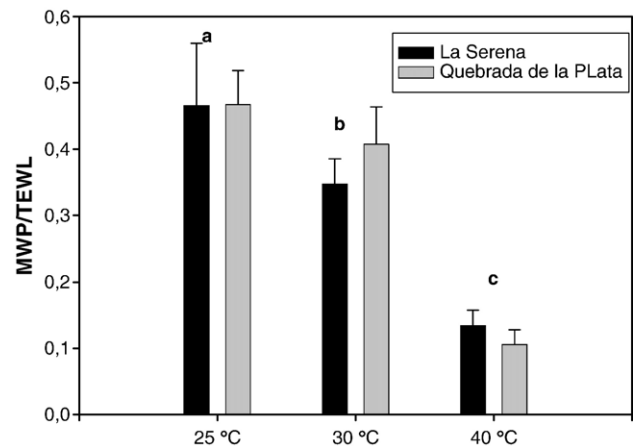


Fig. 3. The ratio between metabolic water production and total evaporative water loss in *Zonotrichia capensis* from two localities in central Chile at three different temperatures. Letters denote significant differences between temperatures. Data are reported as mean±SD.

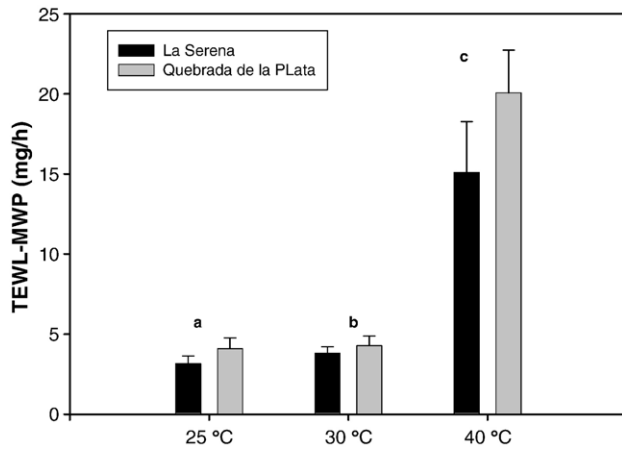


Fig. 4. The difference between total evaporative water loss and metabolic water production in *Zonotrichia capensis* from two localities in central Chile at three different temperatures. Letters denote significant differences between temperatures. Data are reported as mean \pm SD.

significant effect of locality was found in the difference between TEWL and the estimated MWP (locality: $F_{1,10}=14.19$, $p=0.003$, Fig. 4). This difference was higher at Quebrada de la Plata than at La Serena. We found a significant and positive correlation between TEWL and oxygen consumption at 25 °C ($r=0.76$, $p=0.001$) and 30 °C ($r=0.57$, $p=0.005$), but not at 40 °C ($r=0.34$, $p=0.28$).

Birds with occluded nares had significantly greater TEWL compared to birds whose nares were opened ($t_4=7.48$, $p=0.002$ and $t_9=4.50$, $p=0.002$ in La Serena and Quebrada de la Plata populations, respectively). The ratios between TEWL of birds with closed and open nares were 1.33 ± 0.09 and 1.56 ± 0.36 for birds from La Serena and Quebrada de la Plata, respectively. Because the oxygen consumption also increased when birds had their nares occluded ($t_4=4.82$, $p=0.008$ and $t_9=5.66$, $p<0.001$ for La Serena and Quebrada de la Plata, respectively), to assess differences between population in the capacity of recovering water from expired air, we performed an ANCOVA analysis using the ratio of occluded/open TEWL as dependent variable and the ratio of occluded/open VO_2 as covariate (after a correction by the arcsine of the square root of data). This analysis revealed a significant effect of the ratio of VO_2 ($r=0.66$, $F_{1,11}=5.60$, $p=0.03$), but a non significant effect of locality ($F_{1,11}=0.81$, $p=0.39$). In addition, an MANOVA analysis revealed that any organ masses do not differ between populations (Wilks lambda 0.79, $p=0.78$).

4. Discussion

In this paper we tested for intraspecific variability in energy and water budgets, between populations of the passerine bird, Rufous-collared Sparrow. The study of Tieleman et al. (2002) account for interspecific differences in TEWL and BMR in an aridity gradient. In this study, we confirm the effect of climate on the water and energy economy of a granivorous bird at an inter population level. Rufous-collared sparrows from both populations maintain low TEWL when exposed to 25 and 30 °C. However, when exposed to 40 °C, TEWL increases dramatically (460%, Fig. 2). We compared our results obtained at 25 °C with

the expected values from the allometric equations for passerine birds (see Tieleman et al., 2002). TEWL in birds from La Serena was 74% of the expectation based on m_b for passerines from mesic areas and 101% of the allometric expectation for passerines from arid environments. In birds from Quebrada de la Plata, TEWL was higher than predicted by m_b for passerines from arid environments (133%), but very close (97%) to the expectation for passerines from mesic areas. Although no differences were found in the ratio of MWP and TEWL between localities at any temperature (Fig. 3), the total amount of water lost (i.e., the difference between TEWL and MWP) was greater for birds from Quebrada de la Plata (Fig. 4). This indicates that total water requirements (pre-formed water in food and from freshwater drinking) are lower in sparrows from xeric areas. Values of MWP/TEWL in *Z. capensis* are similar to that found among similar size passerines, ca. 0.54–0.46 (Williams, 1996) but very low compared to that found in *Carpodacus mexicanum* (ca. 1.0, Macmillen and Hinds, 1998). However that value was measured at 5 °C, which probably raised the metabolic rate in order to cope the thermoregulatory demands.

Differences in metabolic rate at the inter-population level for *Z. capensis* are comparable to that found at an interspecific levels in birds. Several studies have shown that field metabolic rate and BMR of bird species depend of environmental temperature and rainfall. This has been interpreted as an adaptive feature to cope with low levels of productivity (Tieleman et al., 2004). Generally, increased rainfall increases both the productivity of terrestrial habitats (Lieth, 1978; Polis and Hurd, 1996) and, presumably, the availability of resources (i.e., invertebrates, seeds). For instance, Tieleman et al. (2002) reported that desert and mesic larks (Alaudidae) differ in 43% in BMR, being lower in desert larks. Our results revealed a difference of a 24% in BMR between La Serena and Quebrada de la Plata. The lower difference between our sparrow populations probably reflects the lower gradient in temperature and rainfall between Chilean localities.

The mechanism we suggest that *Z. capensis* has evolved to cope with semi-arid environments by reducing TEWL remains to be tested. Yet, several studies have reported that the morphology of the nasal passages in birds can contribute to a decrease in evaporative water loss through a countercurrent heat exchange mechanism present in the turbinates (Geist, 2000). Our findings support the hypothesis that nasal passages can reduce evaporative water loss. Birds with occluded nares exhibited an elevated TEWL (33–56%), which is in accord with Tieleman et al. (1999) who found that TEWL was elevated by 27% in Crested larks (*Galerida cristata*) with occluded nares at 15 °C, but the effects of the turbinate disappears at elevated temperatures (e.g., 40 °C) when birds were panting. Interestingly, these authors did not found any effect of nasal passages on TEWL in the Desert lark *Ammomanes deserti*. Contrary to the results of Tieleman et al. (1999), we found the increase in VO_2 consumption in birds with occluded nares was significant. The significant and positive correlation between the increment of TEWL and the increment of VO_2 we report in this study revealed that roughly 44% of the variation in TEWL is explained by the increment in VO_2 . The remaining 56% of variation may be explained by the condensation of the exhaled air stream on the cooled membranes of the nasopharynx (Schmidt-Nielsen et al., 1970). This is also supported by our finding that the

ratio between the MWP/TEWL was higher in birds with open nares (Fig. 3). However, because there was no difference in the ability of the two populations to recover water from expired air, our findings suggest that the structure of nasal passages is similar between them. This observation is consistent with results of investigation in several bird species that demonstrated no main differences in turbinates-mediated water savings (Geist, 2000). In addition, our regression analysis indicates that oxygen consumption may explain 30% to 56% of water loss at moderate temperatures. Therefore, one factor influencing TEWL between our populations appears to be energy expenditure. Besides, Haugen et al. (2003) demonstrated that adjustments in ratios of lipids in the skin are associated with changes in cutaneous water loss (see also Muñoz-García and Williams, 2005; Williams and Tieleman, 2005). Hence, additional tests are needed to determine whether populations of *Z. capensis* show differences in skin permeability and what the relative contributions of respiratory and cutaneous water losses are to TEWL.

The physiological mechanisms responsible for differences in BMR of birds from both populations are unknown. Several alternatives have been proposed to explain a reduction in BMR, including a reduction in the amount of metabolically active tissue and lower rates of metabolism of specific tissues (Daan et al., 1990; Konarzewski and Diamond, 1995; Piersma and Lindström, 1997; Kersten et al., 1998; Merkt and Taylor, 1994, but see Burnes et al., 2005). In addition, it has been demonstrated that birds may acclimate their organ masses. For example Klaassen et al. (2004) found differences in organ masses and BMR in cold- and warm-acclimated garden warblers (*Sylvia borin*). Our results do not support the first alternative, i.e., a reduction in the size of organs as heart, liver, and kidneys (Table 1). The second alternative appears as plausible but further efforts are needed to evaluate this hypothesis in *Z. capensis*.

In summary, the lower TEWL and energy expenditures in sparrows from the semi-arid locale could be interpreted as an adaptive feature to cope with fewer resources and/or water (Williams and Tieleman, 2005). However, as pointed out by Garland and Adolph (1994) that the “two species comparison” approach is limiting, the two-population comparisons can only be used with caution to infer adaptation. It is probably that two populations (or species) may differ in several physiological or morphological traits just because they are different populations (Garland and Adolph, 1994). Besides, physiological adjustments to climatic conditions may be the result of phenotypic plasticity (the modification of phenotype according to environmental cues; see Pigliucci, 2001; Hammond et al., 2001). Physiological and morphological features related to water economy in birds may be modified by acclimation (i.e., phenotypic flexibility; see Williams and Tieleman, 2000; Haugen et al., 2003; Tieleman et al., 2003) and by the exposition to different environments during early development (or developmental plasticity sensu Piersma and Drent, 2003; McKechnie et al., 2006). For example, Hudson and Kimzey (1966) found that the sparrow (*Passer domesticus*) from Houston, Texas, had a lower BMR than sparrows from more mesic latitudes. Authors attribute the reduction in BMR in the Houston form to an adaptive feature to cope with warm climates. However, the efforts to obtain increases in BMR by cold accli-

mation in this species have been unsuccessful; suggesting that lower BMR in this population may be genetically programmed. It seems that *Z. capensis* can be considered as a physiologically flexible bird. For example, Castro and Wunder (1991) reported differences in BMR of cold acclimated and warm acclimated *Z. capensis* from Peru; Sabat et al. (2004) and Sabat et al. (1998) found a morphological and biochemical responses in kidney and gut traits when fed on different diets, and Novoa et al. (1994) found seasonal adjustments in thermal conductance of *Z. capensis* of a population from a seasonal locality of central Chile. It is likely that *Z. capensis* populations can adjust their physiology to meet different environmental conditions. Chronic temperature acclimation during the development of birds (i.e., months) and measurements of TEWL, are needed to evaluate these hypotheses. Besides, as many authors suggest, plasticity of physiological and morphological traits may be constrained in specialist individuals, and might have an adaptive value in those that experience larger temporal variation in their physical and biotic environment (Schlichting and Pigliucci, 1998). For example the White-browed scrubwrens (*Sericornis frontalis*) from Australian deserts (which exhibits more temporal variation than mesic habitats) reduced BMR during summer, but a population in a more mesic area did not show such seasonal adjustment (Ambrose and Bradshaw, 1988). However, Tieleman et al. (2003) found no evidence for the hypothesis that species from desert environments display larger phenotypic flexibility than those from mesic areas. In this sense, *Z. capensis* dwell in a great range of habitats with a broad seasonal variation. Hence, some potential variation in the availability of water and temperature regime that individuals experience is expected through time. To what extent the ability to modify metabolic capacities and water fluxes depends on the ecological habits of species or populations are a question yet to be assessed.

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