

Research



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Physiological regulation of evaporative water loss in endotherms: is the little red kaluta (*Dasykaluta rosamondae*) an exception or the rule?

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It is a central paradigm of comparative physiology that the effect of humidity on evaporative water loss (EWL) is determined for most mammals and birds, in and below thermoneutrality, essentially by physics and is not under physiological regulation. Fick's law predicts that EWL should be inversely proportional to ambient relative humidity (RH) and linearly proportional to the water vapour pressure deficit (Δwvp) between animal and air. However, we show here for a small dasyurid marsupial, the little kaluta (*Dasykaluta rosamondae*), that EWL is essentially independent of RH (and Δwvp) at low RH (as are metabolic rate and thermal conductance). These results suggest regulation of a constant EWL independent of RH, a hitherto unappreciated capacity of endothermic vertebrates. Independence of EWL from RH conserves water and heat at low RH, and avoids physiological adjustments to changes in evaporative heat loss such as thermoregulation. Re-evaluation of previously published data for mammals and birds suggests that a lesser dependence of EWL on RH is observed more commonly than previously thought, suggesting that physiological independence of EWL of RH is not just an unusual capacity of a few species, such as the little kaluta, but a more general capability of many mammals and birds.

1. Introduction

Understanding the effects of relative humidity (RH) on physiological parameters, particularly evaporative water loss (EWL), is important because of the theoretical effect of RH on EWL and consequent effects on other physiological variables (e.g. body temperature, T_b ; metabolic rate, MR and thermal conductance, C), especially for mammals and birds. It is a central paradigm of comparative physiology, for mammals and birds at T_a in and below thermoneutrality and over the short-term (i.e. hours), that EWL is determined essentially by physics [1–3], and not by physiological regulation, although EWL is often actively enhanced for thermoregulation at high ambient temperature (T_a) and can be modified in the longer term by development and acclimatization.

Based on Fick's law of diffusion [1–3], EWL depends on the difference in water vapour concentration (χ) between the body surface (χ_{sat} ; assumed to be saturated, RH = 100%) and ambient air (χ_o) i.e. $EWL \propto (\chi_{sat} - \chi_o)$. Ambient water vapour concentration depends on RH and χ_{sat} ; $\chi_o = (RH/100)\chi_{sat}$. EWL and χ_{sat} are expected to increase exponentially with T_a ($^{\circ}K$), e.g. $\chi_{sat} = 9.16 \cdot 10^8 e^{-(5218/T_a)}$ [4]. Water vapour pressure (wvp) is an equivalent measure of water potential to χ [1], so EWL should be inversely and linearly related to ambient wvp and positively linearly related to water vapour pressure deficit ($\Delta wvp = wvp_{sat} - wvp_o$). Various studies have reported that EWL changes inversely with RH and wvp, or linearly with Δwvp , for various small endotherms at and below thermoneutrality [5–13], as expected from physical principles. However, a few studies have reported a lower or even opposite relationship between EWL and RH,

wvp or Δwvp [12–14]. This raises the important question of whether these endotherms have physiological regulation of EWL at low and moderate T_a , which could confer substantial advantages for balancing their water budget. However, complexities with these studies, such as use of RH, wvp or Δwvp , heterothermy [13], postural adjustments [14], measurement method and protocols [13,15], and use of skin or ambient temperature to calculate Δwvp [16] make it difficult to interpret these patterns.

Here, we measure the effect of varying ambient T_a and RH on hygric, metabolic and thermal physiology for the little red kaluta (*Dasykaluta rosamondae*). This small (35 g) dasyurid marsupial has several physiological characteristics of arid-habitat mammals, including a low and thermolabile T_b , low basal metabolic rate and EWL, high point of relative water economy and ready use of torpor [17]. We might expect the EWL of little red kaluta to deviate from a theoretical linear relationship with Δwvp , if such deviation has adaptive value such as water conservation. We explore the effects of RH and Δwvp on EWL for the kaluta and other small endotherms in comparison with biophysically predicted expectations, then we consider the implications of effects of RH on EWL for thermal and metabolic physiology.

2. Material and methods

(a) Study animals

Eight little red kalutas (seven males, one female) were collected in northern Western Australia [see 17]. They were housed individually at T_a approximately 20°C, with a 12 L:12 D cycle, and were fed mince, tinned cat food and mealworms, with ad libitum water.

(b) Respirometry

MR (oxygen consumption, VO_2 ; carbon dioxide production, VCO_2) and EWL were measured by flow-through respirometry [18]. An Aalborg GFC17 mass flow controller regulated compressed air flow through a 265 ml chamber at 350 ml min^{-1} , inside a temperature-controlled room at a T_a of 25°C, 30°C and 35°C. RH was controlled at each T_a (approx. 17%, 36%, 56% and 78% RH) by saturating inlet air at known temperatures, using a Lauda K-2/R refrigerated water bath, then warming to T_a ; RH was calculated from saturation wvp at the water bath temperature and T_a , using standard equations [19]. Excurrent RH and T_a were measured with a Vaisala HMP45A probe, and a subsample was drawn through a column of drierite then a Servomex OA174 or A184 O_2 analyser and a Hereus–Leybold Binos or Hartmann and Braun Uras 10E CO_2 analyser. Analysers were interfaced to a PC via digital multimeters and serial ports. Excurrent O_2 , CO_2 , RH and T_a were recorded every 20 s throughout the experiment, using custom-written software (VISUAL BASIC v. 6). T_b was measured immediately at the end of each experiment using a RadioSpares 611–234 thermocouple meter, with a plastic-tipped thermocouple inserted approximately 2 cm into the cloaca.

The O_2 analysers were two-point calibrated with compressed nitrogen (BOC Gases) and dry ambient air (20.95%). The CO_2 analysers were calibrated with compressed N_2 and a certified gas mix (0.53% CO_2 ; BOC Gases). The RH probes were calibrated over a wide range (using air saturated at a known temperature then warmed to ambient T_a as described above), and calibration was routinely confirmed using 1% RH air (dried with Drierite) and 100% RH air (saturated; by breathing on the RH probe). Flow meters were calibrated using a Sensidyne Gilibrator 2.

Kalutas were fasted for 24 h before commencement of experiments, then measured for no less than 6 h at each T_a and RH

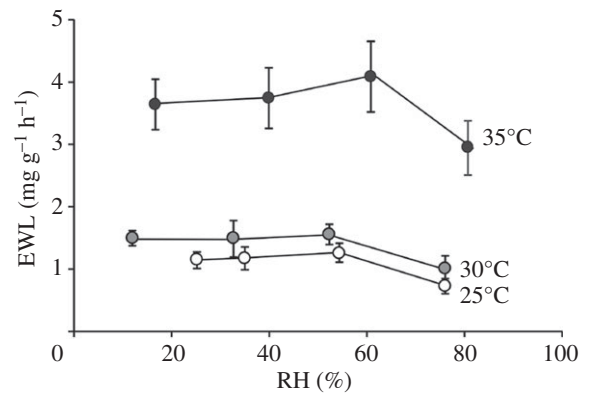


Figure 1. Evaporative water loss (EWL) of little red kalutas (*Dasykaluta rosamondae*), over a range of ambient relative humidities (RHs), measured at ambient temperatures of 25°C, 30°C and 35°C. Values are mean \pm s.e., $N = 8$.

combination (measured in random order) until O_2 , CO_2 and RH were stable and minimal for at least 20 min (see [15]). VO_2 , VCO_2 and EWL were calculated after [18] using a custom-written analysis program (VISUAL BASIC v. 6). Respiratory exchange ratio (RER) was calculated as VCO_2/VO_2 . Metabolic heat production (MHP) was calculated from MR using the measured RER after [2], and evaporative heat loss (EHL) was calculated from EWL using $2.4 J mg^{-1} H_2O$ [3]. Wet thermal conductance (C_{wet} ; $J g^{-1} h^{-1} ^\circ C^{-1}$) was calculated as $MR/(T_b - T_a)$ and dry thermal conductance (C_{dry} ; $J g^{-1} h^{-1} ^\circ C^{-1}$) as $(MHP - EHL)/(T_b - T_a)$, for $(T_b - T_a) > 1^\circ C$.

EWL was also corrected for Δwvp , which was calculated as the difference between saturation wvp and ambient wvp at the measured RH and T_a . It is customary to calculate Δwvp as the difference between wvp at 100% RH and ambient T_a and wvp at ambient RH and T_a [7,14,20]. Skin temperature is more appropriate than T_a to calculate Δwvp [16], but its measurement is more difficult, so ambient temperature is generally used as a proxy. The Δwvp will be similar, particularly at low ambient wvp, unless there is a very large difference between T_a and T_{skin} .

(c) Statistics

Values are presented as mean \pm standard error, with N the number of individuals and n the number of measurements. Multivariate repeated measures ANOVA (mRMANOVA) with two levels of within-individual repeat (T_a and RH) and *a priori* polynomial contrasts were used to analyse the repeated measurements of individuals. Statistical analyses were conducted using a custom-written EXCEL spreadsheet [21] and SPSS (v. 21 for Windows).

3. Results

Mean body mass of kalutas was 33 ± 0.6 g over all experiments ($N = 8$, $n = 84$). Kalutas rested quietly in the chamber, at all T_a and RH combinations. There was no significant difference in body mass with either T_a or RH treatments.

(a) Effects of T_a and relative humidity on evaporative water loss

There was a significant effect of T_a on EWL ($F_{2,5} = 20.5$, $p = 0.004$), but no significant overall effect of RH ($F_{3,4} = 6.03$; $p = 0.058$) by mRMANOVA (figure 1). However, a significant quadratic contrast for EWL ($p = 0.045$) over all RH treatments, combined with a very insignificant mRMANOVA

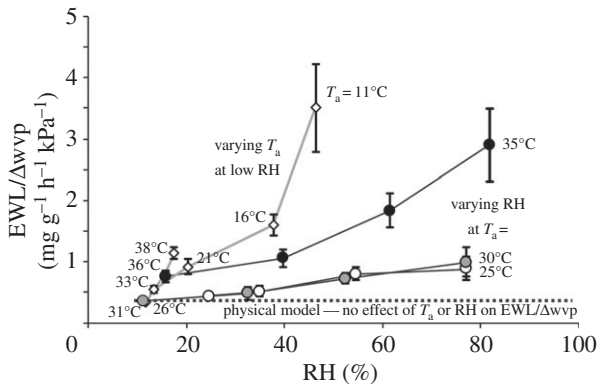


Figure 2. Evaporative water loss (EWL) relative to water vapour pressure deficit, of little red kalutas (*Dasykaluta rosamondae*), over a range of ambient humidities (RHs) and different ambient temperatures (T_a ; values in figure). Values from this study (circles) are for four RH at three T_a ; values from Withers & Cooper [17] (diamonds) are for T_a from 11°C to 38°C, at low RH. A simple physical model of evaporation predicts no effect of T_a or RH on EWL/ Δwvp (see text).

effect ($F_{2,3} = 0.059$; $p = 0.943$), and no significant polynomial contrasts ($p > 0.678$) for the three lowest RH treatments (RH = 78% removed from the model) indicate that EWL was significantly lower at the highest RH but did not differ between the three lower RHs. The insignificant interaction between T_a and RH ($F_{6,1} = 5.23$; $p = 0.317$) suggests the patterns in EWL with RH were consistent for each T_a .

When EWL was expressed per Δwvp (EWL/ Δwvp ; figure 2), there was a significant effect of T_a ($F_{2,5} = 15.5$; $p = 0.007$) and RH ($F_{3,4} = 10.5$; $p = 0.023$) by mRMANOVA. A significant contrast ($p = 0.012$) indicated that EWL/ Δwvp was significantly higher at elevated RH. A significant $T_a \times$ RH interaction term ($p = 0.011$) suggests that the EWL/ Δwvp pattern with RH was different for the three T_a s. EWL/ Δwvp values for kalutas at low RH, from $T_a = 11$ –38°C [17] are included in figure 2.

(b) Effects of T_a and relative humidity on other physiological variables

There were significant T_a effects for T_b ($F_{2,5} = 93.3$, $p < 0.001$), VO_2 and VCO_2 ($F_{2,5} \geq 33.4$, $p \leq 0.007$) and C_{wet} and C_{dry} ($F_{1,6} \geq 13.3$, $p \leq 0.011$). We did not determine C_{wet} or C_{dry} at $T_a = 35^\circ\text{C}$, because $(T_b - T_a)$ was less than 1. There were no overall RH effects for T_b ($F_{3,4} = 2.50$, $p = 0.198$), VO_2 and VCO_2 ($F_{3,4} \leq 3.39$, $p \geq 0.134$) or C_{wet} and C_{dry} ($F_{3,4} \leq 2.34$; $p \geq 0.215$). For all RH data, there was a weak linear effect ($p = 0.020$) of RH on T_b , with higher T_b at the higher RH. There was no significant effect of RH on T_b ($p = 0.173$) when the highest RH data were excluded, indicating that there was no effect of RH on T_b , except at the highest RH where T_b increased slightly.

4. Discussion

Previous studies have shown that EWL changes with T_a , RH and Δwvp in a complex manner [5–14]. Our findings for kalutas of considerable independence of EWL from RH, suggest physiological control. T_a influences on EWL also differ from biophysical predictions. Furthermore, re-examination of effects of RH and Δwvp on EWL data from previous studies

suggests that our results for kalutas are not unusual among small endotherms. Maintaining constancy of EWL at low RH not only conserves water, but also affects thermal and metabolic physiology.

(a) Effect of T_a on evaporative water loss

Above the thermoneutral zone (TNZ), EWL of endotherms typically increases more rapidly than predicted from T_a alone, reflecting augmented EHL for thermoregulation when $T_b > T_a$ [2,3,22,23]. This physiological response is also apparent for kalutas; at T_a above thermoneutrality, EWL is enhanced, with a successively higher EWL/ Δwvp between 31°C and 38°C [17, fig. 2] and a higher EWL/ Δwvp at 35°C compared with 25°C and 30°C (this study; figure 2).

At T_a below TNZ, EWL of endotherms is often constant or even decreases with increasing T_a [24,25], rather than increasing exponentially with T_a as would be predicted (by the physical effect). Kaluta are no exception. EWL is relatively constant at T_a in and below thermoneutrality (30°C; [17]), so EWL/ Δwvp decreases as T_a increases from 11°C to 31°C (figure 2); this pattern differs from the physical model that EWL is proportional to Δwvp . This non-exponential effect of T_a on EWL below thermoneutrality is generally attributed to the counteracting effects of T_a on respiratory and cutaneous EWL. Thermoregulatory adjustments in MR increase respiratory ventilation and EWL at low T_a , which counterbalances the expected decrease in cutaneous EWL [24,25]. In the light of our findings for EWL constancy at low RH, an alternative interpretation of this EWL constancy at low T_a is that EWL is acutely regulated over this T_a range. Whatever the explanation for this EWL constancy below the TNZ, marked deviations in EWL from the simple physical effects of T_a indicate some form of physiological regulation, for thermoregulation via proportionally increased MHP or water conservation by direct regulation of EWL.

(b) Effect of relative humidity on evaporative water loss

Just as deviations of EWL from the physical effects of T_a reflect regulatory processes, comparison of EWL responses with variation in RH at a constant T_a with a biophysical model also provides evidence of physiological regulation of EWL. Various studies have reported that EWL changes inversely with RH and wvp (or linearly with Δwvp) for small endotherms [5–13], consistent with a simple physical model. However, some studies have reported a lower or no relationship between EWL and RH or Δwvp , generally at low or moderate T_a [12–14]. EWL is independent of wvp at 20°C for rock pigeons; adjustments in respiratory ventilation or expired air temperature might account for this [12]. For heterothermic male and post-lactating female little brown bats, there was no wvp effect on EWL at T_a of 28°C or 33°C [13], suggesting that EWL is a controlled rather than a physical process, and there was an unexpected linear relationship between EWL and wvp at $T_a = 37^\circ\text{C}$. We [14] previously reported that EWL of brushtail possums was constant at low RH, at a thermoneutral T_a (25°C); we attributed this EWL constancy at low RH to postural changes and a body core to extremity thermal gradient. Our data for kalutas, showing an unexpected constancy of EWL under environmental conditions that would be expected to perturb water balance, suggest that EWL was under active physiological regulation, reducing their EWL at low RH (high Δwvp).

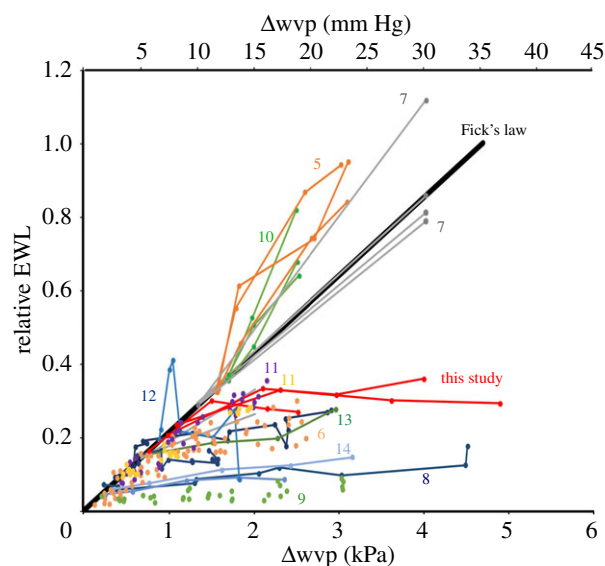


Figure 3. Conceptual model (thick black line) for the expected physical relationship between evaporative water loss (EWL) and water vapour pressure deficit (Δwvp), based on diffusion (Fick's law), compared with the relative EWL for various endotherms from the literature (numbers indicate source). The Δwvp is calculated as $((100 - \text{ambient RH})/100) \times \text{saturation water vapour pressure at the ambient temperature}$. EWL is scaled for each species, so that the EWL for the lowest measured Δwvp fits on the expected physical model line. Data that fall below the expected physical line are consistent with a regulated decrease in EWL (i.e. water conservation), whereas data that fall above the expected physical line are consistent with an increased EWL at higher Δwvp (i.e. enhanced water loss).

Only these few species have been reported to deviate from the expected physical EWL–RH– Δwvp model, whereas most others apparently conform to it. However, we have re-analysed data from other studies examining the effect of RH, wvp or Δwvp , on EWL to evaluate how well those data fit the expectation of a linear physical effect of Δwvp on EWL. We found that the expected linear relationship between Δwvp and EWL is less universal than first thought.

(c) Biophysical model for evaporative water loss and relative humidity

We use here a simple conceptual framework for the biophysical relationship between EWL and Δwvp (at T_a s at or below 35°C) to assess how EWL data from published studies conform to this model. According to the simple Fickian model for diffusion, we would expect a positive linear relationship between EWL and Δwvp that passes through the origin (no EWL when there is no Δwvp). To compare data from these disparate studies, we normalized the data, so that EWL at the lowest Δwvp would fit on an arbitrary 'relative EWL' line; data from higher Δwvp should then also fit on the line if the relationship was Fickian. We found that results from some studies conform to the Fickian model, but many results do not (figure 3). In particular, for many species, the relative EWL decreases substantially below the expected linear relationship at high Δwvp . The potential significance of these deviations from the simple Fickian model has not previously been evaluated in a conceptual framework and was often not even recognized in the original studies. Our re-evaluation of previous data for mammals and birds shows that a lesser dependence of EWL on Δwvp is more

common than previously thought. Our interpretation is that physiological independence of EWL of Δwvp is not just an unusual capacity of a few species, such as the little kaluta, but is a more general capability of many mammals and birds.

Decreasing curvilinear relationships for EWL– Δwvp are of particular interest, because they suggest physiological regulation of EWL at low RH. That EWL is plastic and under physiological control over periods of weeks to months in response to developmental and/or acclimatory changes in water requirements has been demonstrated for birds and mammals [26–29]. However, active regulation of EWL over a period of only 6 h has not, to our knowledge, been previously considered. Although mechanisms that acutely enhance EWL for thermoregulatory purposes at high T_a or high RH are well documented, e.g. salivation, sweating, panting [2–3], mechanisms that could acutely modify EWL in and below thermoneutrality are not. Potential mechanisms for decreasing EWL at high Δwvp will depend on the relative partitioning of cutaneous and respiratory avenues of EWL, and may include decreased cutaneous EWL, e.g. by modification of skin lipids [30–32], and/or reduced respiratory EWL, e.g. by lowered expired air temperature by nasal counter-current heat and water exchange [25,33–36].

We propose that our description of acute deviation of EWL from the expected physical model for EWL at moderate and low T_a is evidence for acute physiological regulation, e.g. over a few hours. This EWL regulation at low RH is presumably an adaptation to conserve body water when EHL is not required for thermoregulation. This probably has considerable adaptive significance, particularly for species with limited access to free water such as the arid-habitat kaluta. A conservative estimate of the water savings for kalutas (calculated by assuming a linear relationship between EWL values at the highest RH, and EWL = 0 at RH = 100%, and extrapolating this relationship to the lowest measured RH then subtracting the observed EWL) indicates that the EWL of kalutas at about 20% RH is only about 40–50% of that predicted if EWL increased as expected biophysically, saving the kaluta at least 1.0–4.6 mg H₂O g^{−1} h^{−1}, depending on T_a .

(d) Other physiological implications of evaporative water loss–relative humidity effects

There is a paucity of data for endotherms that examine the effects of RH on other physiological variables that impact homeostatic thermoregulation, such as T_b , MR and C. If RH had the expected biophysical effect on EWL, then we would expect compensatory thermoregulatory changes in MR, or impacts of changes in EHL on T_b . For example, wvp may affect T_b for kangaroo rats, particularly at high T_a [37]. For brushtail possums [14], there was a significant RH effect on MR at $T_a = 30^\circ\text{C}$, sufficient to maintain a constant T_b when EWL (and thus EHL) was reduced at higher RH. However, RH does not affect T_b or MR for some rodents [6,7,38]. For kalutas, T_b increased significantly only at the highest RH, where EWL (and thus EHL) were significantly reduced; at lower RH, EWL as well as T_b , MR and C were independent of RH. Kalutas did not adjust MR or C to maintain constant T_b at the high RH, reflecting their general thermolability [17].

This observation highlights another important consequence of EWL constancy with varying RH/wvp/ Δwvp . Constancy of EWL avoids thermoregulatory impacts that

would occur as a result of changing EHL. Constant EWL (and thus EHL) at differing RH keeps T_b constant without the need for compensatory changes in MR and/or C .

Experimental work was approved by the Animal Ethics Committee of the University of Western Australia, and animals were held under licence from the West Australian Department of Environment and Conservation.

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