A Phylogenetic Approach to Total Evaporative Water Loss in Mammals

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ABSTRACT

Maintaining appropriate water balance is a constant challenge for terrestrial mammals, and this problem can be exacerbated in desiccating environments. It has been proposed that natural selection has provided desert-dwelling mammals physiological mechanisms to reduce rates of total evaporative water loss. In this study, we evaluated the relationship between total evaporative water loss and body mass in mammals by using a recent phylogenetic hypothesis. We compared total evaporative water loss in 80 species of arid-zone mammals to that in 56 species that inhabit mesic regions, ranging in size from 4 g to 3,500 kg, to test the hypothesis that mammals from arid environments have lower rates of total evaporative water loss than mammals from mesic environments once phylogeny is taken into account. We found that arid species had lower rates of total evaporative water loss than mesic species when using a dichotomous variable to describe habitat (arid or mesic). We also found that total evaporative water loss was negatively correlated with the average maximum and minimum environmental temperature as well as the maximum vapor pressure deficit of the environment. Annual precipitation and the variable Q (a measure of habitat aridity) were positively correlated with total evaporative water loss. These results support the hypothesis that desert-dwelling mammals have lower rates of total evaporative water loss than mesic species after controlling for body mass and evolutionary relatedness regardless of whether categorical or continuous variables are used to describe habitat.

Introduction

Ever since they invaded land, terrestrial organisms have faced the challenge of reducing rates of water loss to their environment by minimizing evaporation from their respiratory passages (respiratory water loss [RWL]) and/or across their skin (cutaneous water loss [CWL]). Total evaporative water loss (TEWL), the sum of RWL and CWL, exceeds water loss in feces or urine by as much as five times, especially in small species (Chew 1951; MacMillen 1983; Lillywhite 2004). Endotherms have high mass-specific metabolic rates and, as a consequence, high rates of respiration, which results in high RWL. As mammals exhale air, they lose considerable quantities of water from the saturated air in the lungs and respiratory passages. Mammals also lose water through their skin, with rates of CWL being driven by the water vapor gradient between the animal's skin and its environment (Stoutjesdijk and Barkman 1992; Walsberg 2000).

Animals living in deserts face especially desiccating conditions due to high ambient temperatures, low ambient humidity, and scarcity of drinking water (Schmidt-Nielsen 1964; Williams and Tieleman 2000). In these regions, some animals rely on preformed water in their food and on metabolic water production to meet their water needs (Schmidt-Nielsen and Schmidt-Nielsen 1951). Most mammals typically maintain core body temperatures (T_b) of 37°–38°C, but this is particularly difficult in deserts where conditions usually produce environmental temperatures higher than T_b. When environmental temperatures exceed T_b, mammals must either seek more favorable microclimates or evaporate water from their skin or respiratory passages to thermoregulate (Schmidt-Nielsen and Schmidt-Nielsen 1950*a*; Chew 1951).

Several studies have investigated whether species of arid mammals have reduced rates of TEWL compared with those of mesic species (Schmidt-Nielsen and Schmidt-Nielsen 1950*b*; Chew 1965; Hinds and MacMillen 1985, 1986; Williams et al. 2004; Withers et al. 2006). These studies provide evidence that mammals in arid habitats have lower rates of TEWL than species in mesic habitats. More than 40 years ago, Chew (1965)

published an allometric equation for TEWL for 49 species of mammals that has been used to predict evaporative water losses in mammals for decades (Glenn 1970; Studier 1970; Hinds and MacMillen 1985, 1986; Anderson et al. 1997; Williams et al. 2001, 2004). Chew also compared rates of water loss for seven mammals that live in arid environments with rates for 42 mesic species and found that arid species had significantly lower rates of TEWL. Chew's (1965) allometric equation has been widely cited in comparative studies (Glenn 1970; Hinds and Mac-Millen 1985, 1986; Williams et al. 2002, 2004). However, there are aspects of Chew's study that could potentially lead to errors in interpretation. The sample size of arid species was small. Many more studies have been published since Chew's article, and addition of new data, particularly from arid species, could potentially alter his findings. Defining habitat as a categorical variable assumes that all habitats are identical within a given classification. However, within "arid" habitats there are numerous gradations of aridity, with the least arid approaching the least mesic of "mesic" habitats. For this reason the use of a continuous variable to characterize the environmental conditions could potentially reduce ambiguity over placing species into habitat categories (Muñoz-Garcia and Williams 2005). Chew's data set was confounded because it included measurements of animals collected over a wide range of ambient temperatures (T_a) and included some species that were lactating; both of these factors can influence TEWL. Furthermore, methods to account for phylogenetic relatedness of species (Felsenstein 1985) were not available at the time of Chew's (1965) study. Incorporation of more recent phylogenetic statistical models may improve our understanding of TEWL relative to body size. For these reasons we have revisited the relationship between TEWL and body mass in mammals.

In this study, we evaluated the relationship between TEWL and body mass in mammals for 136 species of mammals ranging in body size from 4 g to 3,500 kg. We also examined the relationship between TEWL and habitat to test the hypothesis that species from more arid environments have reduced rates of TEWL, as has been demonstrated in other taxa (Schmidt-Nielsen and Schmidt-Nielsen 1950b; Chew 1965; Hinds and MacMillen 1985, 1986; Williams et al. 2004; Withers et al. 2006). In phylogenetic comparative analyses, our results suggested that TEWL was related to body mass with a slope of 0.69, significantly less than originally reported by Chew. Species from more arid environments had reduced rates of TEWL when body size and phylogenetic relationships were taken into account.

Material and Methods

Data Collection

We obtained values for TEWL (g H_2O/d) measured directly (either gravimetrically or hygrometrically) and mass (g) for 136 species of adult mammals (app. C in the online edition of *Physiological and Biochemical Zoology*). We used values of TEWL deemed to be standard rates of TEWL by the authors when stated; alternatively, we used values of TEWL collected at temperatures closest to the lower critical temperature. Mass

was not reported for one species, *Myotis lucifugus*; we obtained the data for mass from Whitaker (2000). We included data for 10 species that were in laboratory colonies, but we excluded domesticated species. We classified animals as postabsorptive or as not postabsorptive, if stated by the authors. We classified animals in the latter group if authors did not mention feeding regime. Although most mammals are nocturnal, we found data for 18 diurnal species. We excluded data for pregnant animals or for animals that were water deprived. When we found multiple sources of data that met our criteria for a species, we averaged values.

We used two approaches to test whether TEWL of mammals was related to habitat aridity. On one hand, we classified species of mammals in our data set into two discrete categories, arid or mesic species. On the other hand, we used continuous environmental variables to define climate and used these variables as predictors of TEWL. Classifying whether a species is arid or mesic can be problematic because environmental aridity is based on a combination of factors, including temperature, wind, and rainfall (Noy-Meir 1973; Williams 1996; Williams and Tieleman 2000). We adopted the assignments of authors for a species' habitat type and verified these assignments by overlaying range maps with arid areas of the world using McGinnies et al. (1968). On the basis of these assignments, we had 80 species from arid environments and 56 species from mesic habitats. Data on climate were collected from the International Water Management Institute's World Water and Climate Atlas (2012), WeatherReports.com (2012), and WorldClimate.com (2012). We acquired climate data for a location that was as close as possible to the collection site of animals in the original water-loss studies. Collection sites were not reported for 14 species, so we used data on climate from the geographical midpoints of their ranges (see app. C). In the case of laboratory-reared and captive animals, we used climate data from the area where the stock population was collected. We used several independent variables to characterize habitat, including annual precipitation (P; mm), mean maximum temperature of the hottest month of the year (T_{max}; °C), mean minimum temperature of the coldest month of the year (T_{min}; °C), mean yearly temperature (T_{mean}; °C), rainfall variability (RV; coefficient of variation of annual rainfall, calculated as SD divided by the mean of the monthly average precipitation), mean saturation vapor pressure deficit of the driest month of the year (VPD_{max}; mbar), mean saturation vapor pressure deficit of the wettest month of the year (VPD_{min}; mbar), yearly average vapor pressure deficit (VPD_{mean}; mbar), and the variable Q. Developed by Emberger (1955), Q measures primary productivity in arid and semiarid habitats. Primary productivity and aridity are directly related, so Q has been used as a proxy for aridity (Tieleman et al. 2003). Q is calculated by the equation

$$Q = \frac{P}{[(T_{max} + T_{min})(T_{max} - T_{min})] \times 1{,}000}, \qquad (1)$$

where P (mm), T_{max} (°C), and T_{min} (°C) are as described above. The index Q decreases with increasing aridity.

Table 1: Predictors of $\log_{10}$ total evaporative water loss (g/d) determined using the Ornstein-Uhlenbeck transformation (RegOU) model

Model	Coefficient	SE	F	p value	ln ML	AICc	d	ln ML ratio test statistic	
								RegOU vs. OLS	RegOU vs. PGLS
Intercept:	−.721	.064	126.42	<.001	−12.03	32.37	.168	4.42	60.96
$\log_{10}$ mass	.693	.029	588.53	<.001					
Intercept:	−.619	.067	84.21	<.001	−6.88	24.23	.132	5.1	60.5
$\log_{10}$ mass	.682	.027	631.02	<.001					
HABITAT	−.150	.046	10.42	.002					
Intercept:	−.765	.066	135.76	<.001	−9.99	30.45	.133	3.94	63.12
$\log_{10}$ mass	.688	.028	616.70	<.001					
P	.00009	.00004	3.99	.048					
Intercept:	−.450	.130	11.93	.001	−9.50	29.45	.253	9.3	44.02
$\log_{10}$ mass	.694	.030	537.89	<.001					
T_{max}	−.009	.003	6.48	.012					
Intercept:	−.698	.072	94.48	<.001	−9.91	30.28	.280	8.66	47.8
$\log_{10}$ mass	.699	.03	543.27	<.001					
T_{min}	−.005	.002	5.72	.019					
Intercept:	−.667	.083	63.99	<.001	−11.53	33.52	.200	5.34	55.58
$\log_{10}$ mass	.695	.029	571.62	<.001					
T_{mean}	−.003	.003	1.21	.274					
Intercept:	−.620	.079	61.27	<.001	−8.88	28.22	.261	10.48	46.5
$\log_{10}$ mass	.690	.030	544.29	<.001					
VPD_{max}	−.006	.002	7.41	.008					
Intercept:	−.737	.075	95.61	<.001	−11.93	34.32	.156	3.04	60.9
$\log_{10}$ mass	.692	.028	592.24	<.001					
VPD_{min}	.003	.008	.18	.672					
Intercept:	−.660	.079	69.65	<.001	−11.05	32.56	.215	6.22	52.3
$\log_{10}$ mass	.692	.029	558.67	<.001					
VPD_{mean}	−.006	.004	2.30	.132					
Intercept:	−.663	.076	76.22	<.001	−11.09	32.64	.153	3.14	61.66
$\log_{10}$ mass	.694	.029	603.06	<.001					
RV	−.072	.054	1.80	1.83					
Intercept:	−.923	.112	67.54	<.001	−7.72	25.91	.182	5.38	56.92
$\log_{10}$ mass	.688	.028	602.53	<.001					
$\log_{10} Q$	.081	.035	5.36	.023					

Note. $\log_{10}$ mass is $\log_{10}$-transformed body mass (g), HABITAT is coded as 0 for mesic and 1 for arid, P is annual precipitation (mm), T_{max} is the mean maximum temperature of the hottest month of the year (°C), T_{min} is the mean minimum temperature of the coldest month of the year (°C), T_{mean} is the mean yearly temperature (°C), VPD_{max} is the mean saturation vapor pressure deficit of the driest month of the year (mbar), VPD_{min} is the mean saturation vapor pressure deficit of the wettest month of the year (mbar), VPD_{mean} is the yearly average vapor pressure deficit (mbar), RV is rainfall variability calculated as the coefficient of variation of annual rainfall, and $\log_{10} Q$ is the $\log_{10}$-transformed values of the variable Q (measure of aridity). The RegOU models were significantly better than the ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) models in every model except those containing VPD_{min} and RV, evidenced by the ln maximum likelihood (ML) ratio tests at $p < 0.05$ (critical value for a χ^2 distribution with 1 df = 3.841).

Construction of Phylogenetic Tree

We used the phylogenetic supertree published by Bininda-Emonds et al. (2007) to describe phylogenetic relationships and divergence times of the species of mammals in our data set. We pruned the tree to remove all the taxa for which we had no data. Five taxa in our data set were not represented in Bininda-Emonds et al.'s (2007) tree, two distinct populations of *Vulpes vulpes* (one montane and one desert dwelling), *Molossus coibensis*, *Eothenomys miletus*, and *Micoureus paraguayanus*. We treated the two populations of *V. vulpes* as sep-

arate species, assuming they diverged similarly; we used the program Mesquite (Maddison and Maddison 2006) to split the branch of *V. vulpes* in Bininda-Emonds et al. (2007) at the midpoint, generating two branches of equal length (Oufiero et al. 2011). Although *M. coibensis*, *E. miletus*, and *M. paraguayanus* were not included in the supertree (Bininda-Emonds et al. 2007), the authors considered other species in these genera. Therefore, we merged the genus into one species and used that branch length for our species. We also used the taxonomic names used by Bininda-Emonds et al. (2007), and so some of
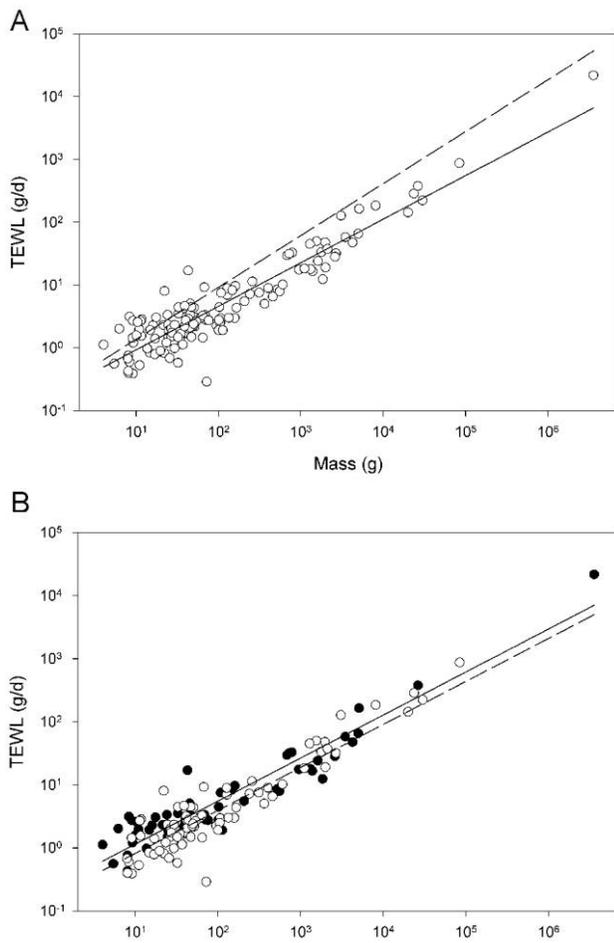
Figure 1. Allometric relationship of total evaporative water loss (TEWL). *A*, The solid line represents the regression generated from our data using the Ornstein-Uhlenbeck transformation (RegOU) model: $\log_{10}$ TEWL $= -0.721 + (0.693 \pm 0.03) \times \log_{10}$ mass ($R^2 = 0.815$, $F_{1,108} = 590.32$, $p < 0.001$). The dashed line represents the regression generated by Chew (1965). *B*, Allometric relationship of TEWL for all mammals separated by habitat using the RegOU model: $\log_{10}$ TEWL $= -0.619 + (0.682 \pm 0.03) \times \log_{10}$ mass $- (0.150 \pm 0.05) \times$ HABITAT ($R^2 = 0.833$, $F_{2,107} = 331.70$, $p < 0.001$). The closed circles and solid line represent mesic species; the open circles and dashed line represent arid species.

the species names we use differ from those used in the original publications.

Some species were included as polytomies since we had incomplete phylogenetic information. All of the polytomies in our tree were considered "soft," and so degrees of freedom for hypothesis testing was determined by the more conservative method (df = no. of nodes − 1) proposed by Purvis and Garland (1993).

Statistical Analysis

When analyzing data from interspecific comparative studies, it can be important to incorporate information about the evo-

lutionary relationships of the species (Garland et al. 1992, 2005). Early on in the discussion about the importance of correcting for phylogeny, some authors warned about complete reliance on statistical methods, such as phylogenetic generalized least squares (PGLS), purported to control for phylogenetic relationships and advocated for using both phylogenetically informed models and non–phylogenetically informed models, such as ordinary least squares (OLS), to understand how natural selection has modified physiological attributes of organisms (Westoby et al. 1995; Price 1997; Muñoz-Garcia and Williams 2005), while Freckleton (2009) encouraged authors to determine which model is most appropriate for their study and only report those results. Here we use both PGLS and OLS and expand our comparison to include an additional phylogenetic hypothesis using an Ornstein-Uhlenbeck transformation (RegOU; see Lavin et al. 2008), which transforms the branch lengths of the starting phylogenetic tree to allow for the simultaneous estimation of the residual error structure with the regression model parameters in which the residual error is modeled by a process similar to stabilizing selection (Hansen 1997). Thus, we have three models of evolution that range in their hierarchical structure of the residual error: OLS, which exhibits no hierarchal structure (a "star" phylogeny); PGLS, which exhibits a hierarchical structure that evolves according to a Brownian motion of evolution; and RegOU, which models the residuals similar to stabilizing selection. The best-fit model can be determined by a comparison of Akaike Information Criterion (AIC) values and log likelihoods (see below) to determine whether the incorporation of phylogenetic information improves the fit of the model.

We used the MATLAB program Regressionv2.m to create linear statistical models using OLS regression, PGLS, and the RegOU model. The RegOU model alters the branch lengths of the phylogenetic tree, pulling the internal nodes either toward the tips or toward the root, using an additional parameter, *d*. When $d = 1$ the tree is equal to the starting PGLS model, whereas when $d = 0$ the tree is equal to the OLS model. The RegOU model simultaneously estimates the phylogenetic signal in the residual error with the regression coefficients. Therefore, *d* provides an indicator of the amount of phylogenetic signal in the residuals of the dependent variable (Blomberg et al. 2003; Lavin et al. 2008). Furthermore, because the RegOU model contains an additional parameter, its fit can be compared with the OLS or PGLS models with a likelihood ratio test, where twice the difference in the log likelihood is assumed to be distributed as a χ^2 with 1 df. The critical value of $\alpha = 0.05$ in this distribution is 3.841 (Oufiero et al. 2011). If the RegOU model exhibits $\chi^2 > 3.841$ compared with the OLS model, then the residual variation in the dependent variable exhibits statistically significant phylogenetic signal.

All data for TEWL and mass were $\log_{10}$ transformed before analysis to correct for deviations in normality. Habitat was coded as 0 for mesic and 1 for arid, referred to hereafter as HABITAT. The variable *Q* is driven by precipitation and rapidly increases as habitats become more mesic, so we used $\log_{10}$-transformed *Q* to avoid biasing data from mesic environments

(Tieleman et al. 2003). We included models with raw values for annual precipitation as well as $\log_{10}$-transformed values. We tested various models using each independent variable listed above (HABITAT, P, T_{max}, T_{min}, T_{mean}, RV, VPD_{max}, VPD_{min}, VPD_{mean}, and $\log_{10} Q$) to determine which was best correlated with TEWL after accounting for body mass. We tested each of these models using the three models of evolution listed above (OLS [star phylogeny], PGLS, and RegOU). We used maximum likelihood ratio tests to determine which model best fit the data, as described above.

Results

We initially determined that activity time (nocturnal or diurnal), TEWL measurement method (gravimetric or hygrometric), lab status, and postabsorptive state were not significant covariates in predicting TEWL and so included data for all animals in our analyses. The RegOU model had a better fit to the data than the OLS or PGLS models, on the basis of maximum likelihood ratio tests (likelihood ratio test > 3.8414, two-tailed $p < 0.05$; table 1), in all cases except for the models containing VPD_{min} and RV. These models were not significantly different (table 1), and VPD_{min} was not a significant predictor of TEWL in any of the three models tested. Therefore, we will focus on results obtained from the RegOU evolutionary models; see appendixes A and B in the online edition of *Physiological and Biochemical Zoology* for full results of the OLS and PGLS models. Regression coefficients are presented with SEs.

The equation that described our data on TEWL among mammals using the RegOU model was $\log_{10}$ TEWL $= -0.721 + (0.693 \pm 0.03) \times \log_{10}$ mass ($R^2 = 0.815$, $F_{1,108} = 590.32$, $p < 0.001$; table 1; fig. 1A). The slope of this model was not significantly different from the OLS model (0.696; $t(268) = 0.09$, $p = 0.927$) but was significantly smaller than the slope that Chew (1965) reported (0.826; $t(181) = 4.13$, $p < 0.001$). When we included HABITAT, the regression equation between TEWL and mass was $\log_{10}$ TEWL $= -0.619 + (0.682 \pm 0.03) \times \log_{10}$ mass $- (0.150 \pm 0.05) \times$ HABITAT ($R^2 = 0.833$, $F_{2,107} = 331.70$, $p < 0.001$; table 1; fig. 1B). The partial regression coefficient for HABITAT was significantly different from 0 and negative ($F = 10.42$, $p = 0.002$), indicating that species living in arid habitats have significantly lower rates of TEWL after accounting for differences in mass.

When we used a continuous variable to describe aridity, we found that the composite variable $\log_{10} Q$ along with all of its components (T_{max}, T_{min}, and P) were significant predictors of TEWL (table 1; fig. 2). VPD_{max} also showed a significant negative relationship with TEWL and was significantly correlated with $\log_{10} Q$ ($r(134) = -0.45$, $p < 0.001$). The relationships between all of these environmental variables and TEWL indicate that TEWL decreases with increasing habitat aridity. The best model predicting TEWL from environmental variables based on AIC for small sample sizes (AICc; Burnham and Anderson 2002) was the model using habitat categorized as mesic or arid. $\log_{10} Q$ was the best continuous variable predicting TEWL, described by the equation $\log_{10}$ TEWL $= -0.923 + (0.688 \pm 0.03) \times \log_{10}$
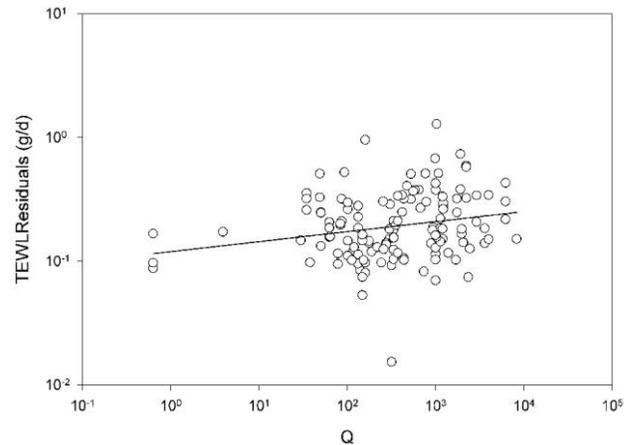

Figure 2. Relationship between total evaporative water loss (TEWL) residuals and Q determined using the Ornstein-Uhlenbeck transformation model: $\log_{10}$ TEWL $= -0.923 + (0.688 \pm 0.03) \times \log_{10}$ mass $+ (0.081 \pm 0.04) \times \log_{10} Q$ ($R^2 = 0.821$, $F_{2,107} = 305.01$, $p < 0.001$). The data indicate that rates of TEWL increase as habitats become increasingly mesic.

mass $+ (0.081 \pm 0.04) \times \log_{10} Q$ ($R^2 = 0.821$, $F_{2,107} = 305.01$, $p < 0.001$; table 1; fig. 2).

Discussion

For nearly 40 years, Chew's allometric equation has been the most inclusive model available for predictions of TEWL based on body mass. These predictions are important for conservation biologists as well as for modelers interested in the impact of climate change on water relations and, therefore, distribution patterns of extant animals. Here we provide an allometric equation for TEWL from body mass based on data from 129 species of mammals with more stringent selection criteria than those used by Chew and incorporation of phylogenetic relationships. Much of the data for TEWL that we included in our model were collected from relatively small mammals. More than 80% of the mammals in our analysis had a body mass of less than 1 kg. The only animal in our data set that was more than 100 kg was the Asian elephant, and the next largest was the Arabian oryx at 84 kg. The differences in mass distribution between our data set and that of Chew are reflected in the predictions provided by the allometric equations. Chew's equation tends to provide higher estimates of TEWL than our equation. The average rate of TEWL for a 100–200-g mammal (using values from our data set, $n = 14$) is 4.9 g/d. Our allometric equation predicts the TEWL of a mammal with a mass of 100 g to be 4.6 g/d, while Chew's equation predicts 9.3 g/d for the same animal. By our equation, a 20-kg mammal has a predicted rate of TEWL of 182.2 g/d, whereas Chew's equation predicts 735 g/d. The equation that we have supplied should provide researchers a valuable tool in physiological research. The incorporation of phylogenetic information did not substantially change the scaling of TEWL with mass (see "Results").

It has long been thought that species living in extreme habitats should have adaptations to reduce rates of water loss (Schmidt-Nielsen 1964). Several studies have investigated whether species of mammals from arid regions have lower rates of TEWL than mesic species (Schmidt-Nielsen and Schmidt-Nielsen 1950b; Chew 1965; Hinds and MacMillen 1985, 1986; Williams et al. 2004; Withers et al. 2006). Using our more inclusive data set, we were able to provide further evidence for the relationship between TEWL and habitat while incorporating phylogenetic relationships and using a continuous variable to describe habitat aridity.

The variable Q was originally developed as an estimate of primary productivity in arid and semiarid environments (Emberger 1955) and has since been used as an estimate of aridity based on the logic that aridity is directly related to primary productivity (Tieleman et al. 2003; Oufiero et al. 2011). Deserts are characterized by hot, dry conditions, and Q is calculated using both temperature and annual precipitation (see eq. [1]). We found that Q and all of its components were significant predictors of TEWL. We also found maximum vapor pressure deficit to be a significant predictor of TEWL, and, based on the physical model of evaporation, vapor pressure deficit should be the major factor determining rates of evaporative water loss (Stoutjesdijk and Barkman 1992; Walsberg 2000). Maximum vapor pressure deficit and Q are highly correlated, and both seem to be good descriptors of habitat aridity. Withers et al. (2006) suggested that it may be advantageous for animals living in areas with unpredictable and variable rainfall to conserve water by lowering TEWL and showed that rates of TEWL were negatively correlated with the variability of rainfall; however, our data did not support this result.

Using continuous variables to describe habitat allows slight gradations in aridity rather than simply grouping animals by habitat type. However, describing habitats as simply mesic or arid provided the best model for predicting TEWL based on AICc (table 1). There are many environmental factors that make a habitat arid, and it appears that the sum of their influence is more important in influencing TEWL than any single variable that we tested. In conclusion, we found that TEWL of species that live in arid environments is significantly lower than that of species that live in mesic environments after accounting for body mass and phylogeny.

Acknowledgments

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