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THE COST–BENEFIT MODEL OF THERMOREGULATION DOES NOT PREDICT LIZARD THERMOREGULATORY BEHAVIOR

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Abstract. Physiological processes are optimized within a narrow range of body temperatures. Reptiles engage in behavioral thermoregulation to achieve the optimal body temperature range. Interestingly, however, thermoregulatory effort varies over time and across species. The cost–benefit model of thermoregulation of R. B. Huey and M. Slatkin is the only conceptual framework that attempts to explain the observed variation. The model postulates that reptiles should engage in thermoregulation when the costs incurred do not outweigh the benefits. The main cost is the thermal quality of the environment: thermoregulation is more costly in habitats of low thermal quality. We used thermal quality of the habitat, measured by the deviations of operative temperatures from the preferred body temperature range, as an indicator of costs and two quantitative indices of thermoregulation as indices of thermoregulatory investment. Regressions of the indices of thermoregulation on thermal quality of the habitat produced no pattern or patterns that were in the opposite direction to the predictions of the cost–benefit model of thermoregulation. These results suggest that the disadvantages of thermoconformity are higher than the costs of thermoregulation in habitats of low thermal quality.

Key words: cost–benefit model; index of thermoregulation; lizard; thermoconformity; thermoregulation.

INTRODUCTION

Physiological processes are strongly temperature-dependent (Huey 1982, Grant 1990, Hutchison and Dupré 1992) and most are optimized within a narrow range of body temperatures (T_b) (Huey 1982, Angilletta et al. 2002). Hence, individuals that can maintain their T_b within the optimal range have higher fitness. Because squamates are ectotherms, they adjust their T_b through behavioral mechanisms such as basking in the sun and modifying their postures (Cowles and Bogert 1944, Huey 1982). Not all squamates thermoregulate to the same extent, however. Some species are predominantly thermoconformers (Ruibal 1961, Hertz et al. 1993, Rummery et al. 1994), while others are precise thermoregulators (Bauwens et al. 1996, Christian 1998, Sartorius et al. 2002). Among thermoregulators, there is variation in the ‘‘precision of thermoregulation,’’ the constancy of T_b over time, and the ‘‘accuracy’’ of thermoregulation, the degree to which preferred body temperatures (T_{set}) are maintained (Hertz et al. 1993). One model exists to explain the observed variation in thermoregulatory behaviors. The cost–benefit model of thermoregulation (Huey and Slatkin 1976) suggests that lizards become thermoconformers when the costs of thermoregulation outweigh the potential benefits.

The obvious costs of thermoregulation are losses of energy and time, because periods of thermoregulation can require travel and can be mutually exclusive with other important activities such as foraging or mate searching (Huey 1974, Grant and Dunham 1988, Adolph and Porter 1993). The cost of thermoregulation depends largely on the thermal quality of the habitat, the degree to which operative environmental temperatures (T_e) differ from the animals' T_{set}. As thermal quality decreases, more energy and time are necessary for effective thermoregulation and it becomes more costly. While the cost–benefit model is widely used (Hertz et al. 1993, Rummery et al. 1994), some squamates thermoregulate actively despite very high costs (Christian 1998, Blouin-Demers and Weatherhead 2001). It has been suggested that the model may not apply to thermally challenging habitats, where the disadvantages of thermoconformity can exceed the costs of thermoregulation (Blouin-Demers and Weatherhead 2001).

Our general goal was to test the cost–benefit model of thermoregulation with published quantitative estimates of thermal quality and of thermoregulation for lizards. If the cost–benefit model is correct, thermoregulation investment should increase as thermal quality increases. The cost–benefit model was designed for a single species and explored how costs of thermoregulation would affect its investment in thermoregulation. Thus, a more rigorous test of the model would require thermoregulation data for individuals under different conditions. Unfortunately, such data are scant and a comparative approach was a necessary first step in testing the model. Blouin-Demers and Weatherhead

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TABLE 1. Definitions of the indices and symbols used in the quantification of thermoregulation.

Index or symbol	Definition
T_b	The body temperatures of a representative sample of free-ranging study animals (typically measured with cloacal probes or with temperature-sensitive radio-telemetry).
T_{set}	The preferred body temperature range or set-point range (typically measured by the bounds of the central 50% of the distribution of body temperatures selected in a laboratory thermal gradient).
T_e	Operative environmental temperatures: the equilibrium body temperatures that non-thermoregulating animals would experience (typically measured by the temperature of copper representations of the study animals placed randomly in the habitat).
d_b	Accuracy of body temperature of Hertz et al. (1993) (measured as the mean of the deviations of field body temperatures from the preferred body temperature range).
d_e	Thermal quality of the habitat of Hertz et al. (1993) (measured as the mean of the deviations of operative environmental temperatures from the preferred body temperature range).
E	Effectiveness of thermoregulation of Hertz et al. (1993). $E = 1 - (d_b/d_e)$.
$d_e - d_b$	Effectiveness of thermoregulation of Blouin-Demers and Weatherhead (2001).
E_x	Thermal exploitation of Christian and Weavers (1996) (calculated as the time in which the body temperatures of the animals were within the preferred body temperature range divided by the time available for the animals to have their body temperatures within the preferred range, as indicated by the operative environmental temperatures).

(2002) did study thermoregulation by black ratsnakes in different habitats and found that snakes invested more in thermoregulation while in more thermally challenging habitats, a result contrary to the predictions of the cost–benefit model of thermoregulation.

Three types of data are required to quantify thermoregulation. First, one needs the body temperatures (T_b) experienced by a representative, free-ranging sample of animals. T_b is typically measured in the field with cloacal probes or with temperature-sensitive radiotelemetry. Second, one needs to document the null distribution of T_b that non-thermoregulating animals would experience: the distribution of operative environmental temperatures (T_e). T_e are typically measured by recording the temperature of copper representations of the animals placed randomly throughout the environment, and thus approximating the T_b of randomly behaving, non-thermoregulating animals. Third, one needs an independently derived measure of the target T_b: the set-point range or preferred body temperature range (T_{set}) of the species. T_{set} is determined by the distribution of T_b selected by the animal in a laboratory thermal gradient. Typically, the central 50% of the distribution is used; we only found three studies that used the central 80%.

Before formally defining indices of thermoregulation, one needs to quantify the accuracy of T_b, the extent to which T_b measured in the field match T_{set}, irrespective of whether the animal is actively thermoregulating. Following Hertz et al. (1993), the accuracy of T_b is typically measured with d_b: the mean of all deviations of T_b (absolute values) from the nearest T_{set} bound. Thus, a high value of d_b indicates low accuracy of T_b because T_b is, on average, distant from T_{set}. Finally, one also needs to quantify the thermal quality of the habitat, or the extent to which T_e match T_{set}. Following Hertz et al. (1993), thermal quality is typically measured with d_e: the mean of all deviations of T_e (absolute values) from the nearest T_{set} bound. Hence, a high value of d_e represents a high cost, low thermal quality environment, since operative temperatures are, on average, distant from T_{set}.

The most frequently used indices of thermoregulation are E, E_x, and $d_e - d_b$ proposed by Hertz et al. (1993), Christian and Weavers (1996), and Blouin-Demers and Weatherhead (2001), respectively (Table 1). E is calculated as $1 - (d_b/d_e)$ (Hertz et al. 1993). Thus, an E value of 1 represents a perfect thermoregulator, while a value of 0 represents a thermoconformer. Conversely, a negative value of E indicates that the animal is actively avoiding thermally favorable microhabitats. E_x is given by the percentage of time when T_b was within T_{set}, relative to the total time during which this could have been possible as indicated by T_e (Christian and Weavers 1996). The higher the E_x value, the more the animal exploits the thermal environment when the environment is permissive. The last index is a rescaling of E as the simple subtraction $d_e - d_b$ (Blouin-Demers and Weatherhead 2001), which measures the departure from perfect thermoconformity. A positive value represents a thermoregulator, a value of 0 represents a thermoconformer, and a negative value indicates an animal actively avoiding thermally favorable microhabitats. For the purpose of testing the cost–benefit model, only the latter two indices were used. E was excluded because of concerns with its validity (see *Discussion* and Blouin-Demers and Weatherhead [2001]) and because it is highly correlated with the other two indices (see *Results*). Hertz et al. (1993) also had proposed to evaluate thermoregulation with reference to curves describing the thermal dependence of performance: one can compare the predicted relative performance of the study animals to that of hypothetical thermoconformers. Although such an index would be closer to the form of the cost–benefit model of thermoregulation (net energy gain as a function of T_b), it suffers from several conceptual (Hertz et al. 1993) and logistical problems that prevented its wide adoption and its use in comparisons.

While the renewed interest in thermoregulation has produced significant conceptual advances, it has also led to the proliferation of thermoregulation indices. The use of multiple indices can be problematic because authors rarely use all, hindering comparisons between studies. Our secondary goal was to calculate correlations between the three major thermoregulation indices to determine their usefulness in concert and to make recommendations regarding their future use.

METHODS

We conducted a literature review with keyword and author searches on BIOSIS Previews (Ovid Technologies, Inc.; *available online*).[2] Because field measurements of thermoregulation became quantitative and more standardized following the seminal paper of Hertz et al. (1993), we considered only studies published thereafter. To ensure comparability, we followed Hertz et al. (1993) and retained only studies where T_{set} was determined in a laboratory thermal gradient and where T_{e} was measured with models. When a suitable article was found, a follow-up search was performed on all its cited references using Web of Science (Thomson ISI; *available online*).[3] A total of 21 publications satisfied the aforementioned criteria, yielding data for 27 species: four snakes, one amphisbaenian, and 22 lizards (see Appendices A and C). From these articles, we extracted data on thermal quality of the habitat (d_{e}) and on thermoregulatory investment (E_x, E, and $d_{\mathrm{e}} - d_{\mathrm{b}}$) by the animal.

In six studies, d_{e} and d_{b} were not found within the text, but it was possible to calculate these values using data available in figures. In these cases, numerical values for T_{e} and T_{b} were extracted with the software DigitizeIt 1.5 (ShareIt, Cologne, Germany), which enables the user to obtain data in spreadsheet format from a scanned graph. In four cases, extrapolation was necessary to estimate midday values of T_{e} when these extended above the plot area. Because T_{e} profiles are typically bell-shaped curves, available T_{e} values were used to generate a best-fit second-degree polynomial equation. Missing data points were approximated using the equation of the polynomial curve.

We conducted the comparative analyses of thermoregulatory investment as a function of thermal quality of the habitat with lizards only because the cost–benefit model of Huey and Slatkin (1976) only considered lizards. We also excluded two nocturnal geckos because they have few opportunities for thermoregulation during their active period. Thus, we had data for 20 species of diurnal lizards for those analyses. We used phylogenetically independent contrasts (PIC) to correct for the lack of statistical independence arising when comparing related species (Felsenstein 1985). Although it is uncommon to perform PIC analysis on characters that are not morphological, as was the case for thermoregulatory investment, several studies have calculated contrasts on habitat characteristics such as water depth or range size (Stillman and Somero 2000, Thompson and Ceriani 2003). We performed analyses on PIC on the basis that thermoregulatory investment represents a behavioral phenotype. To establish the phylogeny of study species necessary for PIC analysis, data were combined from many sources obtained by a separate literature review (see Appendix B). The phylogenetic tree was constructed with TREEVIEW 1.6 (Page 1996). Because molecular phylogenies were not available for all species, branch lengths in units of expected variance were unavailable. Therefore, we set branch values arbitrarily to 1 because only relative branch lengths affect PIC analysis. We did not use alternative topological approaches to set arbitrary branch lengths because these approaches have been shown to increase Type I error rate (Ackerly 2000). PIC were generated with PHYLIP (Felsenstein 1989). For comparative purposes, analyses were performed both on contrasts and on raw data. In the case of contrasts, regressions were forced through the origin because contrasts have an inherent expectation of zero (Felsenstein 1985).

In all statistical analyses, means were calculated for d_{b}, d_{e}, T_{set}, E, and E_x such that each species was represented by a single data point, regardless of the spatial and temporal variation recorded in the original study. To examine how thermoregulation varied as a function of the thermal quality of the habitat, we used linear regressions of thermal exploitation (E_x) versus thermal quality (d_{e}). A negative slope would indicate that thermal exploitation decreases when the thermal environment becomes more challenging, as predicted by the cost–benefit model of thermoregulation. When conducting analyses with the index of thermoregulatory effectiveness $d_{\mathrm{e}} - d_{\mathrm{b}}$, the above method was modified to circumvent the problem of regressing $d_{\mathrm{e}} - d_{\mathrm{b}}$ on d_{e}, where d_{e} would be found on both axes. Therefore, we regressed d_{b} on d_{e}. It can be shown mathematically that testing the null hypothesis of $m = 0$ with ($d_{\mathrm{e}} - d_{\mathrm{b}} = m \times d_{\mathrm{e}} + b$) is equivalent to testing the null hypothesis of $m = 1$ with ($d_{\mathrm{b}} = m \times d_{\mathrm{e}} - \mathrm{b}$). The expected results of this regression with regards to the cost–benefit model are presented in Fig. 1. A slope >1 would indicate that thermoregulatory investment ($d_{\mathrm{e}} - d_{\mathrm{b}}$) decreases as thermal quality decreases, as predicted by the cost–benefit model of thermoregulation. Hence, we used *t* tests to determine if slopes differed from 1. In all regressions, we used the mass of the species as a covariate because a given value of d_{e} has different implications for large and small animals since they have different heating rates. Mass was never a significant covariate, however, and we thus only present reduced models. To examine the correlation between all three thermoreg-

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[3] ⟨http://www.isinet.com/products/citation/wos/⟩

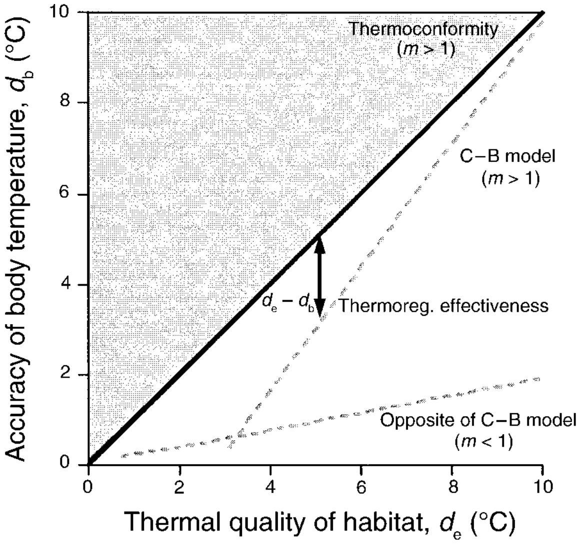

FIG. 1. Accuracy of body temperature (d_b) as a function of the thermal quality of the habitat (d_e), showing the line of thermoconformity ($m = 1$). The index of thermoregulation effectiveness ($d_e - d_b$) is the vertical distance between the line of thermoconformity and the data point for a species. The prediction of the cost–benefit (C–B) model of thermoregulation is that the effectiveness of thermoregulation should be higher (high $d_e - d_b$) in habitats of high thermal quality (low d_e) ($m > 1$). The shaded area represents negative thermoregulation where animals thermoregulate less effectively than randomly placed models.

ulatory indices, we generated a matrix of correlations. We used JMP 5.0 (SAS 2002) to perform our statistical analyses.

RESULTS

A slope <0 in a regression of thermal exploitation (E_x) on thermal quality (d_e) would indicate that thermal exploitation decreases when the thermal environment becomes more challenging, as predicted by the cost–benefit model of thermoregulation. Without correcting for phylogenetic affinities, we found no relationship between thermal exploitation and thermal quality (Fig. 2). Although the slope of the regression of E_x on d_e was negative ($m = -2.666$), it did not differ significantly from 0 ($R^2 = 0.07$, $n = 14$, $t = 0.94$, $P = 0.368$). When we analyzed PIC rather than raw data, the variance explained by the models increased, but the relationships remained nonsignificant (Fig. 2). The slope of the regression was negative ($m = -4.654$), but did not differ significantly from 0 ($R^2 = 0.20$, $n = 13$, $t = 1.73$, $P = 0.109$). Therefore, thermal exploitation was not higher when the thermal quality of the environment was high and the prediction of the cost–benefit model was not supported.

A slope >1 in a regression of precision of T_b (d_b) on thermal quality (d_e) would indicate that thermoregulatory investment ($d_e - d_b$) decreases when the thermal environment becomes more challenging (Fig. 1), as predicted by the cost–benefit model of thermoregulation. Without correcting for phylogenetic affinities, we found a strong relationship between the effectiveness of thermoregulation and thermal quality (Fig. 3). The slope of the regression of d_b on d_e ($m = -0.030$) was significantly smaller than 1 ($R^2 = 0.94$, $n = 20$, $t = 9.28$, $P < 0.001$). When we analyzed PIC rather than raw data, the relationship remained the same qualitatively (Fig. 3). The slope of the regression ($m = 0.172$) was significantly smaller than 1 ($R^2 = 0.76$, $n = 19$, $t = 7.53$, $P < 0.001$). Therefore, the effectiveness of thermoregulation decreased with increasing thermal quality of the habitat, a pattern contrary to the prediction of the cost–benefit model.

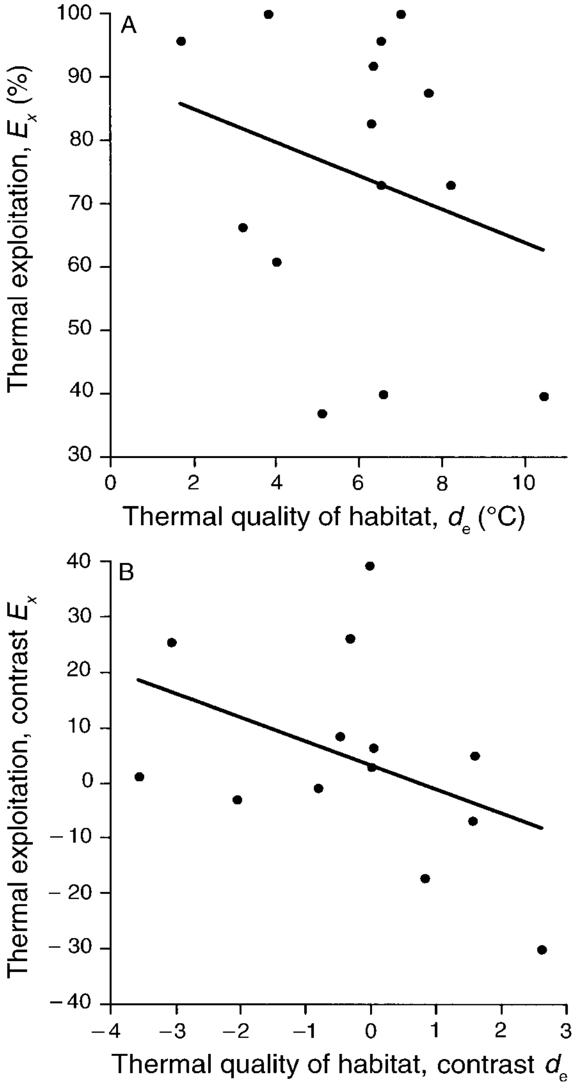

FIG. 2. Consistent with the prediction of the cost–benefit model of thermoregulation, thermal exploitation by lizards is higher (high E_x) when the thermal quality of the habitat is high (low d_e) based on (A) raw data and (B) contrasts, but the regressions were not statistically significant. The regression was forced through the origin in the case of contrasts.

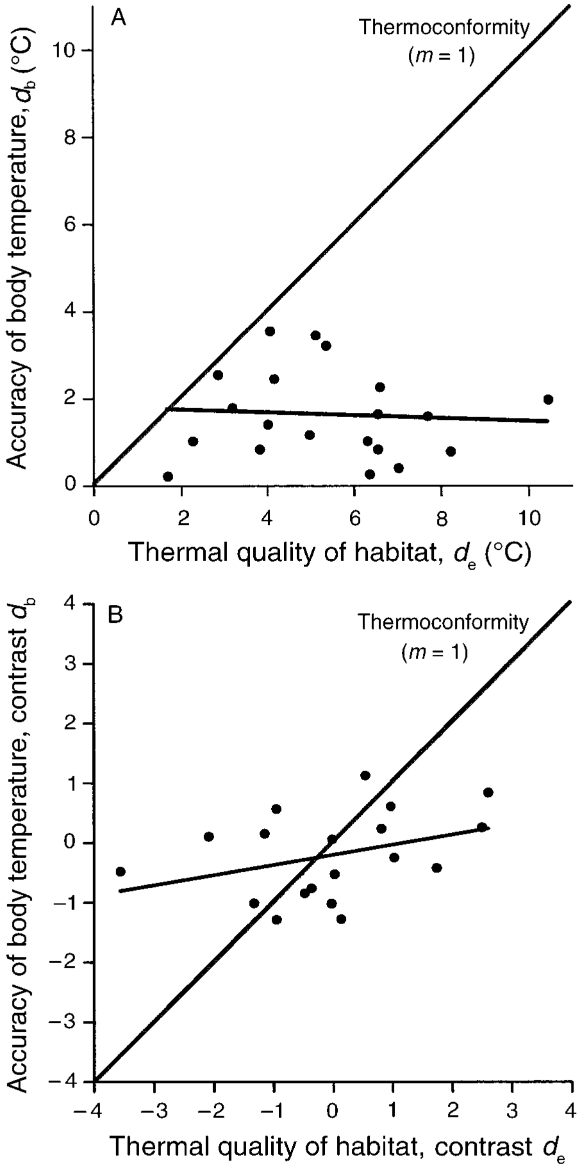

FIG. 3. Contrary to the prediction of the cost–benefit model of thermoregulation, lizards thermoregulate more effectively (are farther from thermoconformity, high $d_e - d_b$) when the thermal quality of the habitat is low (high d_e). This is indicated by slopes significantly <1 in regressions of the accuracy of body temperature (d_b) as a function of thermal quality of the habitat (d_e) based on (A) raw data and (B) contrasts. The regression was forced through the origin in the case of contrasts.

E was highly correlated with both E_x and $d_e - d_b$ ($r = 0.72$ and $r = 0.76$, respectively, Fig. 4). The high correlation between E and $d_e - d_b$ was expected because both indices share the variable d_e. E_x and $d_e - d_b$ were less correlated ($r = 0.33$, Fig. 4).

DISCUSSION

We used arbitrary branch lengths as a proxy for actual branch lengths in units of expected variance to derive our PIC. Additionally, there is debate over the phylogeny of amphisbaenians, geckos, and snakes (see Appendix D) that could affect the topology or our tree and, consequently, our PIC. Because the use of PIC instead of raw data did not change our results qualitatively, however, we are confident that our findings are valid.

Thermal exploitation by lizards, as measured by E_x, did not vary as a function of thermal quality of their habitat. Although the slopes were negative and, thus, in the direction predicted by the cost–benefit model, the relationships were not significant. In contrast, the effectiveness of thermoregulation by lizards, as measured by $d_e - d_b$, varied with the thermal quality of their habitat. Instead of thermoregulation increasing in low-cost habitats, however, thermoregulation decreased in low-cost, high thermal quality habitats, a result contrary to the predictions of the cost–benefit model of thermoregulation (Huey and Slatkin 1976). It is interesting, but in retrospect unsurprising, that we obtained different results regarding the relationship between thermoregulation and thermal quality depending on the index we used (E_x or $d_e - d_b$). The weak correlation between the two indices indicates that they measure different aspects of thermoregulatory investment. By definition, E_x is only calculated for the time periods when T_e indicates that T_b within T_{set} can be attained, should the animal select the appropriate microhabitat. Consequently, E_x does not take into account time periods when the habitat is most thermally challenging, despite active thermoregulation potentially occurring during these periods. Thus, it is unsurprising that E_x does not vary with thermal quality because it is only measured when thermal quality is relatively high.

In the cost–benefit model of thermoregulation (Huey and Slatkin 1976), the cost of thermoregulation is believed to increase monotonically with the magnitude of the difference between the T_b to be achieved (T_{set} for field-active ectotherms) and environmental temperatures. Environmental temperatures have been replaced by T_e, a more accurate estimate of available T_b. Therefore, we can state that as T_e is further from T_{set} (denoted by a high d_e, indicative of low thermal quality), the cost of thermoregulation increases. The central prediction of this model relating the cost of thermoregulation to the extent of thermoregulation is that ‘‘For all reasonable forms for c (cost curve) and b (benefit curve), we would predict that a lower value of k (increased thermoregulation) would be optimal in the habitat with the lower cost’’ (Huey and Slatkin 1976:371). Although it seems reasonable to assume that the optimal amount of thermoregulation for an ectotherm is determined by some trade-off between costs and benefits, our results suggest that the main cost of thermoregulation identified in the original model is insufficient to explain the extent of thermoregulation in lizards for which quantitative thermoregulation data

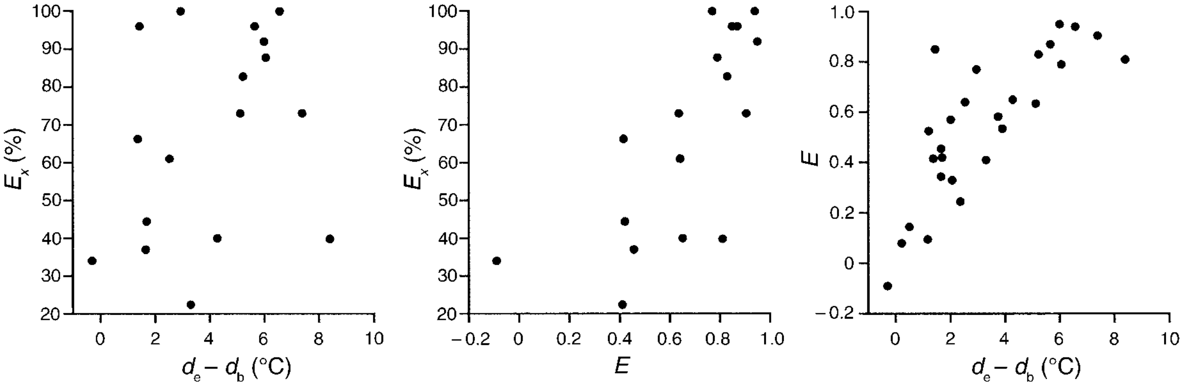

FIG. 4. For all squamates for which quantitative thermoregulation data were available, the index of thermoregulation effectiveness E is strongly and positively correlated to the index of thermal exploitation E_x (middle panel) and to the index of thermoregulation effectiveness $d_e - d_b$ (right panel). The index of thermal exploitation E_x is positively correlated to the index of thermoregulation effectiveness $d_e - d_b$, but the correlation is weak (left panel).

were available. We reiterate that a more rigorous test of this within-species cost–benefit model would require data on thermoregulation by individuals while faced with different costs, but such data are scant (but see Blouin-Demers and Weatherhead (2002) for an exception) and we used a comparative approach as an initial test. An explanation for the pattern we found is that the physiological disadvantages of thermoconformity are very low when the thermal environment is benign (low d_e), because even without thermoregulation, T_b is close to T_{set} (Huey 1982, Blouin-Demers and Weatherhead 2001). Huey and Slatkin (1976) recognized that the advantages of thermoregulation decrease in low-cost habitats (and hence one can infer that the disadvantages of thermoconformity also decrease in these habitats and increase as the thermal quality of the habitat decreases): on page 372 they state ''Note also that the relative advantage of thermoregulation in 'low-cost' habitats is reduced as environmental temperatures approach x_0 (the optimal body temperature).'' Nonetheless, their model puts more emphasis on the premise that the cost of thermoregulation increases as the thermal quality of the habitat decreases. The disadvantages of thermoconformity, however, might be more important than heretofore recognized and might force species or individuals in more challenging habitats to thermoregulate more carefully than species or individuals in benign habitats. For example, in a very high-d_e habitat, a lizard that would not start thermoregulating more carefully than it did in a low-d_e habitat would perform so poorly that it would not survive: to survive the lizard would have to thermoregulate more carefully in the very high-d_e habitat, despite the high costs. Another problem with the model is that in nature the costs and benefits of thermoregulation are not always independent. For example, when the benefit of thermoregulation is high because the habitat is of poor thermal quality (non-thermoregulating animals experience low T_b and poor performance), the cost of thermoregulation is also high because a lot of time and movement are necessary to locate the few available thermoregulatory opportunities. Laboratory experiments similar to the one of Withers and Campbell (1985) will be necessary to decouple the costs and benefits of thermoregulation to assess their influence on thermoregulatory behavior both singly and in concert.

Blouin-Demers and Weatherhead (2001) already suggested abandoning E as an index of thermoregulatory effectiveness because (1) it is not defined when the thermal environment is perfect ($d_e = 0$) (Hertz et al. 1993), (2) it is impossible to interpret without considering the respective magnitude of d_b and d_e (Hertz et al. 1993), and (3) it can give spurious representations of the thermal ecology of a species because it uses a ratio. The fact that E is highly correlated to both E_x and $d_e - d_b$ reinforces the suggestion to abandon it: E is not only problematic, but is also superfluous. Following Hertz et al. (1993), (1) d_e should be used to quantify the thermal quality of the habitat and (2) d_b should be used to determine the accuracy of T_b. Following Blouin-Demers and Weatherhead (2001), we reiterate that (3) $d_e - d_b$ should be used to quantify the extent of departure from thermoconformity and as the primary index of the effectiveness of thermoregulation and (4) E_x (Christian and Weavers 1996) should be used to determine the extent to which species exploit the available opportunities for behavioral thermoregulation, keeping in mind its limitations because of the disregard for times when the environment is thermally challenging.

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APPENDIX A

A table showing information on species for which quantitative thermoregulatory data were available to test the cost–benefit model of thermoregulation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-029-A1.

APPENDIX B

A list of references used in the construction of the phylogenetic tree of study species (Appendix D) necessary for the calculation of phylogenetically independent contrasts used to test the cost–benefit model of thermoregulation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-029-A2.

APPENDIX C

A figure showing world distribution of locations where thermoregulation was studied quantitatively, allowing a test of the cost–benefit model of thermoregulation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-029-A3.

APPENDIX D

A phylogenetic tree of study species generated from references in Appendix B and used to derive phylogenetically independent contrasts testing the cost–benefit model of thermoregulation is available in ESA's Electronic Data Archive: *Ecological Archives* E086-029-A4.