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A Random Walk in the Park: An Individual-Based Null Model for Behavioral Thermoregulation

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ABSTRACT: Behavioral thermoregulators leverage environmental temperature to control their body temperature. Habitat thermal quality therefore dictates the difficulty and necessity of precise thermoregulation, and the quality of behavioral thermoregulation in turn impacts organism fitness via the thermal dependence of performance. Comparing the body temperature of a thermoregulator with a null (non-thermoregulating) model allows us to estimate habitat thermal quality and the effect of behavioral thermoregulation on body temperature. We define a null model for behavioral thermoregulation that is a random walk in a temporally and spatially explicit thermal landscape. Predicted body temperature is also integrated through time, so recent body temperature history, environmental temperature, and movement influence current body temperature; there is no particular reliance on an organism's equilibrium temperature. We develop a metric called thermal benefit that equates body temperature to thermally dependent performance as a proxy for fitness. We measure thermal quality of two distinct tropical habitats as a temporally dynamic distribution that is an ergodic property of many random walks, and we compare it with the thermal benefit of real lizards in both habitats. Our simple model focuses on transient body temperature; as such, using it we observe such subtleties as shifts in the thermoregulatory effort and investment of lizards throughout the day, from thermoregulators to thermoconformers.

Keywords: ectotherm, reptile, temperature, thermal performance, heterogeneity.

Introduction

Measuring the costs and benefits of behavioral thermoregulation in a meaningful way is difficult. Disentangling the effects of thermoregulatory and non-thermoregulatory behavior on body temperature and determining associated costs of these behaviors have been topics of study in ectotherm biology and ecology for decades (Hertz et al. 1993; Vickers et al. 2011; Sears and Angilletta 2015). Null models have their great-

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est utility when experiments cannot easily be used to isolate the mechanism underlying a pattern or process (Pianka 1986; Gotelli and Graves 1996). Here, we develop a null model for behavioral thermoregulation that measures the benefit and effort of behavioral thermoregulation as well as describing habitat thermal quality as a function of thermally dependent performance.

Originally, the occurrence of behavioral thermoregulation was determined by comparing the body temperatures of ectotherms with local environmental (air) temperatures, and differences observed were ascribed to behavioral thermoregulation (Cowles and Bogert 1944). In essence, the sample of environmental temperatures was used as a null model for the behavioral process: an expected set of temperatures that the organism should achieve in the absence of behavioral thermoregulation. Null models need to be updated as assumptions are discarded, however. For example, Heath (1964) demonstrated that if thermal mass is left unaccounted, any object—in this case, a can of beer—can appear to thermoregulate. Eventually, Hertz et al. (1993) accounted for thermal mass and included the notion that the organism has a thermal goal (set point temperature) and is not simply striving to be different from the environment. The Hertz et al. (1993) null model requires knowledge of the set point temperature, field body temperature, and operative environmental temperature, which is the thermal equilibrium temperature for a non-thermoregulating organism at that site. Typically, operative environmental temperatures are measured by physical thermal models and considered without reference to temporal or spatial structure, and the indices used to compare values are absolute deviations of body or environmental temperature from the set point.

The Hertz et al. (1993) null model has several important limiting assumptions. First, the effect of using absolute deviations is that overheating and overcooling are equally costly in this model (Hertz et al. 1993), which is not the case for real organisms (Vickers et al. 2011).

Also, using random samples of available environmental temperatures and ignoring their spatial and temporal structure ignores autocorrelation of temperatures, disregarding some important phenomena, for example, that the middle of the day is often warmer than the start or end. Temporal and spatial structure of temperatures may be important for behavioral thermoregulation. Indeed, reptile activity often peaks in the morning and afternoon at intermediate temperatures; similarly, the spatial distribution of temperature influences the spatial distribution of ectotherms (Dillon et al. 2012), indicating the importance of including autocorrelation and structure of the thermal environment in a null model for behavioral thermoregulation. Further, using equilibrium temperatures reached by physical thermal models may not be an appropriate description of body temperatures for organisms that do not attain equilibrium at each site they encounter (Seebacher and Shine 2004). As real organisms move through the habitat, they experience a series of body temperatures that are transient between recent body and current environmental temperature and may in fact never reach equilibrium temperature for any given microsite.

We present a null model for behavioral thermoregulation that uses spatially and temporally realistic environmental temperatures sampled in a random order or by taking a random walk through a realistic thermal landscape (fig. 1A, 1B). Such a null model was predicted by Hertz et al. (1993), and a similar model was implemented by Seebacher et al. (2003). Seebacher et al.'s (2003) model focuses on equilibrium temperature reached by large organisms with nontrivial or significant thermal capacity, determining whether observed body temperature could be achieved by randomly exposing more or less body surface to solar radiation. Importantly, our model generates a temporally integrated prediction of body temperature, such that the body temperature of the null model is the result of a continuous walk (fig. 1C), rather than the equilibrium temperature of any particular site. While continuous, this null model body temperature is comparable to any given observed real body temperature, because real lizard temperature is an instantaneous measurement, which has not necessarily equilibrated to the environment.

We have created a novel index—thermal benefit—which is determined relative to body temperature, using the thermal performance curve; body temperature (fig. 1*D*, *x*-axis) is used to predict performance on a scale from 0 (at critical thermal [CT] limits) to 1 (at the thermal optimum). As such, deviations in body temperature below the thermal optimum (cooler) result in less lost performance than the same deviation above (hotter). Thermal benefit can be calculated for null model temperature to describe the thermal quality of the environment, where a score close to 1 implies a thermal environment near optimum, and 0 is lethal. Similarly, thermal benefit can be calculated from field body and used to assess the quality of thermoregulation, where 1 is the temperature for maximum performance, and 0 implies that CT limits have been exceeded. Our use of the null model and the thermal performance curve is ultimately analogous to Hertz et al.'s (1993) calculations of the deviations of the body temperature of the organism and the environment from set point temperatures ($d_{\rm b}$ and $d_{\rm e}$, respectively), with the important exception that thermal benefit inherently accounts for the asymmetric costs of overheating relative to overcooling (fig. 1D). Thermal benefit is deliberately tied to the thermal performance curve, which can be the curve for any thermally dependent process, for example, metabolism, sprint speed, or digestive rate. Maintaining body temperature near the thermal optimum can maximize performance in many traits (Huey 1982; Angilletta et al. 2002) and, in the field, can improve performance and survivability (Hertz et al. 1993) and, by extension, fitness, though there is mixed support for insects (Dillon et al. 2009). In this way, thermal benefit can be an ecologically relevant and fitness-based measure of the habitat and an individual's performance in it.

Comparison of the thermal benefit of the habitat with the thermal benefit of the inhabitant illustrates ecological interactions, including strategic shifts in behavior. Where the two are equal, the organism is thermoconforming, or at least investing very little effort into thermoregulation. Where the organism maintains a thermal benefit above that of the null model, it indicates that thermoregulation is important and that effort is being invested in controlling body temperature. On the other hand, the case where the organism scores lower than the null model should occur only in habitats that are, on average, not thermally threatening: habitats where the risk of death from overheating or overcooling is low. In this case, it may be that environmental temperature distribution is leptokurtic-making precise thermoregulation difficultor that the relative importance of thermoregulation is lower than that of some other behavior. For example, a dominant conspecific might force a submissive individual into suboptimal habitat; in some cases, foraging, territory defense, or mate acquisition may be more important than thermoregulation (Grant and Dunham 1988; Downes and Shine 1998).

Here, we use effort to describe deliberate behavioral input into thermoregulation. The form effort takes is dependent on the context and organism but may include, for example, increased movement, deliberate nonrandom movement, the retention of a thermal map, capacity to predict the thermal environment, the capacity to learn from previous experience in the same or similar habitat or similar season, or precise sensing of the thermal environment and the flexibility to respond quickly and appropriately. Effort always entails some kind of cost: cognition and strategy require brain development and maintenance, developing and maintaining thermoreception is presumably evolutionarily costly, and so on. We posit that precise, deliberate, behavioral thermoregulation has fitness costs that may be difficult to measure but can be im-



Figure 1: *A*, Temperature was measured in each cell on a toroidal *xy* plane at 2-min intervals (time on the *z*-axis). A random walk was then conducted through the temperature matrix, according to the flow chart in *B*, and used to sample available environmental temperature as a non-thermoregulating lizard might. *C*, Environmental temperature (solid line) was integrated through time according to movement rate and lizard size to estimate body temperature of a lizard (dashed line) using equation (1). *D*, A generalized additive model estimated theoretical thermal performance curve, such that maximum thermal benefit = 1 in the range of optimal or selected body temperature (T_{sel}), and at the critical limits, thermal benefit = 0. The asymmetry of the effects of overly warm body temperatures versus overly cool body temperatures was accounted for by thermal benefit: a given deviation *d* of T_b below T_{sel} ($T_{sel} - d$; cold) scored a higher thermal benefit than the same deviation above ($T_{sel} + d$; hot).

plied by the effort invested in thermoregulation in a given habitat.

Methods

Study Site and Species

To demonstrate this null model for behavioral thermoregulation, we used two ground-dwelling rainbow skink species, *Carlia sexdentata* (Macleay 1877) and *Carlia jarnoldae*, from two very different tropical habitats in Australia. Closed-litter rainbow skinks (*C. sexdentata*) were from Pormpuraaw in Queensland, Australia (14°53′34.23″S, 141°37′25.36″E), and live in the grassland near the edge of low (8 m) vine forest. Pormpuraaw is monsoonal, though we collected data in only the dry season, June 2011. The dry season is remarkably stable in its weather conditions—uniformly sunny, humid, and hot—and thus 1 day of data is highly representative of the environment in winter in general (mean air temperature \pm SD = 23.5° \pm 5.6°C). Lined rainbow skinks (*C. jarnoldae*) were from Townsville, Queensland, Australia (19.2564°S, 146.8183°E), and live in a dry creek bed during the dry season, in a shady, *Melaleuca*-dominated woodland (mean air temperature \pm SD = 24.5° \pm 2.9°C; Bureau of Meteorology 2013). Temperatures we reported appear high because the study areas selected were particularly hot, medium-latitude tropics.

In each location, a 100-m^2 landscape was mapped using 100 calibrated Thermochron iButton data loggers wrapped in neutral beige cloth and placed on the ground, recording temperature $\pm 0.5^{\circ}$ C every 2 min (video A1, available online). At Pormpuraaw, 1 day of data was collected, while at Townsville, 12 days of data were collected in a rocky creek bed.

Body temperature (T_b) of hand-captured active *C. sex*dentata (n = 36) and *C. jarnoldae* (n = 78) were recorded throughout the day, using a calibrated Digitech QM-7223 infrared thermometer within 10 s of capture. Temperature of the dorsal surface between the hind legs was read from a distance of 3 cm from the aperture, which had a distance: spot ratio of 8:1. All recorded T_b were measured within 30 s of sighting the lizard. In addition, at Pormpuraaw, an experienced observer conducted a continuous survey of lizard activity in lizards/min from 0600 until 1800 hours for comparison with thermal benefit of the null model.

T_{sel} and the Thermal Performance Curve

 T_{sel} of *C. sexdentata* from Pormpuraaw was estimated in a thermal gradient in 2012. The gradient was an aluminium slab (2 m × 0.15 m × 0.018 m), heated at one end and cooled at the other by Peltier plates. Temperature was allowed to stabilize for at least 1 h, creating a thermal gradient ranging from 20° to 45°C, at 12.5°C/m. A skink was introduced to the gradient and allowed to habituate for 40 min, and then T_b (cloacal temperature) was measured every 20 min using a quickreading digital thermocouple for a total of 10 times (3 h and 20 min). T_{sel} was defined as the central 50% of T_b determined under these conditions, which was 31.4°–33.8°C. T_{sel} for *C. jarnoldae* was estimated in a photothermal gradient in laboratory conditions, using the same technique as described by Vickers et al. (2011). The central 50% of T_b were used to estimate T_{seb} which was 25.0°–28.9°C.

For both species, thermal performance curves were fitted using generalized additive models (GAMs), with the *y* value for T_{sel} optimized, such that the maximum value of the thermal performance curve was equal to 1 ± 0.000001 . The CT_{min} and CT_{max} for *C. sexdentata* were at 11.4° and 44.5°C, respectively, taken from Greer (1980) as representative of *Carlia* CT limits, while for *C. jarnoldae* they were at 8.1° and 42.8°C (A. Pintor, unpublished data). The GAMs had the expected shape of published thermal performance curves (fig. A1; figs. A1, A2 available online).

Model

The null model was a random walk through a three-dimensional matrix of temperature. Space was represented on the *xy* plane and time on the *z*-axis. The model was given a random start location on the *xy* plane and started at 0 on the *z*-axis. Time incremented every second, such that $z_{(t+1)} = z_{(t)} + 1$, environmental temperature was recorded every second, and body temperature of the null model was calculated every second. With every time increment (*t*), the lizard stayed still or moved one step into one of the eight surrounding cells in

the *xy* plane with probability Pr—where Pr was 0, 0.5, 0.25, 0.125, 0.0625, 0.03125, 0.015625, 0.007813, 0.003906, or 0.001953—to assess the effect of movement rate on the null model. This equated to one step every 0 (stationary), 2, 4, 8, 16, 32, 64, 128, 256, and 512 s. The *xy* plane of the matrix was calculated as a torus: both the *x*- and *y*-axes wrapped around, such that there was no out of bounds.

The model sampled the environmental temperature at every step, so once per second. This environmental temperature was converted to body temperature for the null model using a heat-transfer equation from Vickers (2014; fig. A1; eq. [1]), yielding a distribution of null model body temperatures with a strict temporal structure. The environmental temperatures used in the model were recorded by iButtons and therefore were the result of an accumulation of all thermal influences at the location. Calculation of null model $T_{\rm b}$ was based on a model predicting lizard body temperature from the iButton recorded temperature under similar circumstances, optimized by Vickers (2014; fig. A2). However, temperature from any appropriate physical model could be used. We recommend avoiding equilibrium temperature models for motile organisms that do not necessarily equilibrate at each site (e.g., Seebacher et al. 2003; Seebacher and Shine 2004). Even without regular equilibration, the environment at both sites-but especially at Pormpuraaw-was sufficiently hot that the null model would attain $T_{\rm b}$ in excess of its $\rm CT_{max}$. In such a case, a real lizard should be dead. In the case of the null model, it scored a thermal benefit of 0 but continued its walk.

Null model body temperature was used to predict thermal benefit using thermal performance curve GAMs, yielding thermal benefit, which is reported here. Similarly, real observed field-active body temperature for our species was used as the predictor in the thermal performance curve GAMs, yielding thermal benefit of the thermoregulators. The R script and data are available in the Dryad Digital Repository: http://dx.doi.org /10.5061/dryad.dd571. The equation for body temperature at time *i* is

$$T_{b(i)} = T_{e(i)} + (T_{b(i-1)} - T_{e(i)})\exp(-Kt),$$
(1)

where $T_{e(i)}$ is environmental temperature at time *i* and *K* is the body size parameter, determined experimentally to be 0.005 for *Carlia* lizards (Vickers 2014).

Statistical Methods

The model was written using the R language (R Development Core Team 2014), using the package plyr (Wickham 2011). The GAM was fit using package mgcv (Wood 2006). Activity probability density was estimated from activity survey data (presence of lizards active per minute) by kde in R, using a Gaussian kernel with bandwidth 2000 (fig. 2*D*, Townsville).



Figure 2: Median thermal benefit, 50% confidence interval (CI; dark grey), and 95% CI (light grey) for null model, and thermal benefit for real lizards (points) for skinks in a very hot tropical environment (*Carlia sexdentata*, Pormpuraaw [left]) and skinks in a more congenial tropical habitat (*Carlia jarnoldae*, Townsville [right]). In each panel, the null model moved with a different probability (i.e., different speed): 0.195% (1 step/512 s; A), 25% (1/4 s; B), 50% (1/2 s; C), and 3.125% (1/32 s, most similar to *Carlia species; D*). *D* for Pormpuraaw (left) includes probability density function of activity (dashed line). Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.dd571 (Vickers and Schwarzkopf 2016).

Results

The Null Model

The null model output converged toward a distribution of thermal benefit for the habitat, which is ultimately a description of its thermal quality. We have plotted the median line with confidence intervals (CIs) for each habitat (fig. 2*D*), and clearly each habitat presented different thermal challenges. For both sites, thermal benefit followed a circadian rhythm. We can expect that behavioral thermoregulation is easiest (required the least effort) at those times when thermal benefit for the null model was close to 1 and, conversely, required most effort when thermal benefit is close to 0. A value of 0 indicated that the null model body temperature exceeded CT limits (in the case of these habitats, because it was too hot; fig. 3), though recall that our null model did not die; instead, it carried on scoring 0 until $T_{\rm b} < {\rm CT}_{\rm max}$. Data suggest that lizards should thermoregulate with the most effort and precision when the habitat is worst (Blouin-Demers and Nadeau 2005), and this was the case at Pormpuraaw during the middle of the day but not for Townsville (fig. 2*D*). Movement speed of the null model had a strong impact on the distribution of thermal benefit in Townsville and a much weaker impact at Pormpuraaw (fig. 2*D*), most likely because of the



Figure 3: Hourly diurnal environmental temperatures (T_e) measured by 100 data loggers over 3 days at Pormpuraaw (dark grey) and Townsville (light grey). Line in boxplots represents the median, box is central 50% of data, whiskers include up to 2 SD with outliers beyond, and horizontal line represents the critical thermal maximum for *Carlia* (44.5°C). Data are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.dd571 (Vickers and Schwarzkopf 2016).

difference in temperature distribution in the two habitats: Townsville had a much more leptokurtic distribution, so sampling outlying temperatures was much more common.

Pormpuraaw and Carlia sexdentata

Estimated $T_{\rm b}$ for every iteration of the null model exceeded the CT_{max} (CT_{max} = 44.5 °C) by 1130 hours on the first day. Thermal benefit at 0600 hours was around 0.5 and increased steadily to near 1 at about 1000 hours. Thermal benefit then dropped to 0 around midday, after which it rose again to near 1 around 1600 hours and decreased to about 0.9 by 1700 hours (fig. 2D). The primary effect of increasing movement rate was an increase in variability of thermal benefit with movement rate (fig. 2D). The faster a model lizard moved, the wider the variety of thermal habitat it sampled.

Real *Carlia sexdentata* achieved high (0.6-1) thermal benefit through the day (fig. 2D). The lowest and most variable thermal benefit occurred in the morning until 1000 hours; during this time, lizard thermal benefit was within the 50% CI of null model thermal benefit. Throughout the middle of the day, when T_e was hottest (fig. 3), the thermal benefit maintained by lizards was uniformly above 0.8. The difference between the thermal benefit obtained by real *C. sexdentata* and the null model increased from morning to midday from ~0 to ~1, indicating increasing investment in thermoregulation.

Carlia sexdentata activity aligned moderately well with periods of high thermal benefit for the null model: highest activity was in the morning around 0830 hours, with another small peak at 1530 hours, when environmental thermal benefit was approximately 0.8, though a secondary activity peak occurred around midday when the environment provided a thermal benefit of only approximately 0.2 (fig. 2*D*). The number of $T_{\rm b}$ readings does not reflect precisely the activity curve, since not all lizards seen were able to be captured.

Townsville and Carlia jarnoldae

Despite some temperatures exceeding CT limits (fig. 3), estimated T_b for the null model rarely exceeded CT limits, the 95% CI for thermal benefit included 0 only for the slowest model lizard (one step per 512 s, 0.195%), and the 50% CI never included 0 (fig. 2*C*). Clearly, Townsville in winter was a more congenial habitat for *C. jarnoldae* than Pormpuraaw was for *C. sexdentata*. In Townsville, environmental thermal benefit started the day near 1, increased to 1 by 1000 hours, and reduced slightly in the afternoon. In comparison to the Pormpuraaw site, increasing movement rate of the model decreased variability in thermal benefit. The majority of environmental temperatures encountered in Townsville were within critical limits, and indeed, most were within a few degrees of T_{sel} (fig. 3); thus, the temperature differential experienced from

one second to the next was shallow, so lizard body temperature changed slowly, and moving quickly among similar temperatures brought the null model body temperature closer to the median. At Pormpuraaw, very high temperatures were much more common and the environmental temperature distribution was more playtkurtic, so that one second to the next often had a very high temperature differential, and so increasing movement rate increased variability in the body temperature estimated by the null model temperature. Additionally, median T_e at Pormpuraaw often approached CT_{max} and even exceeded it in the middle of the day (fig. 3).

Despite the relative congeniality of the Townsville habitat, *C. jarnoldae* achieved a much lower thermal benefit than *C. sexdentata*, possibly due to the relative costs of imprecise thermoregulation in the two habitats: at Pormpuraaw the cost was mortality, at Townsville the cost was only the achievement of very high thermal benefit.

Discussion

Our new null model (1) adds spatial and temporal realism to existing methods for studying behavioral thermoregulation; (2) provides a more realistic, asymmetric account of the cost of imprecise thermoregulation above and below the optimal temperature; and (3) introduces a fitness-based metric by which to assess effort. We estimated body temperature through time at fine resolution; by adjusting movement rate, this null model could be applied to any organism, from active foraging organisms, which do not necessarily equilibrate to every site they use, to ambush predators that spend more time in single locations. Ultimately, our null model generates a continuous expected distribution of T_b for a nonthermoregulator, given an environment, which, when converted to thermal benefit, indicates thermal quality of the habitat and, therefore, the thermoregulatory challenges posed to its inhabitants. Simultaneously, thermal benefit of the real organism (lizard) indicates the quality of thermoregulation. Our null model can be used to examine the importance of transient temperatures of both the organism and the habitat: in the examples we provided, the diel shift in habitat thermal quality in a tropical open woodland (fig. 2) and plasticity in behavioral thermoregulation over short periods (fig. 2) were evident.

In the broadest sense, thermoregulation should occur when it benefits fitness (Huey and Slatkin 1976; Vickers et al. 2011), and there is evidence that thermoregulatory effort should increase as thermal quality declines (Blouin-Demers and Nadeau 2005; Besson and Cree 2010; Vickers et al. 2011). There are two ways to increase the net benefit of thermoregulation: increasing gross benefit or decreasing cost. The intrinsic quality of the thermal environment is estimated by the thermal benefit of the null model. The thermal benefit obtained by real lizards can be estimated if T_b is known, and the difference between the real lizard and null model benefit is the benefit gained from behavioral thermoregulation plus some residual benefit that occurs as a by-product of other behaviors, as in the following equation:

thermal benefit obtained by real lizard = thermal benefit of the habitat + thermal benefit of thermoregulation + residual.

Thermal benefit of thermoregulation is the currency of reward for thermoregulatory effort and is a function of effort invested: more effort invested means more benefit. This framework can be used to study thermoregulatory behavior. Contrasting lizard and null model thermal benefits showed the effort invested in thermoregulation: when the null model achieved low benefit but the real lizard achieves high benefit, effort invested must be high; if they achieve similar thermal benefit, thermoregulatory effort can be low, reducing the energetic cost of thermoregulation. To determine the effort invested when thermal benefit of the lizard is similar to the null model, it may be instructive to compare dispersion or degree of randomness of thermal benefit or body temperature. Importantly, our use of effort is not measured in terms of energetics but implies careful, deliberate, or nonrandom site selection.

The dynamic nature of habitat thermal quality at Pormpuraaw and Townsville was well described by the shift in both the median and the variability of thermal benefit of the null model (fig. 2; video A1). Pormpuraaw is tropical woodland, sometimes considered thermally homogeneous and congenial to reptiles (Hertz 1974; Shine and Madsen 1996), though this was clearly not always the case. There were clear peaks in thermal quality at 1000 and 1600 hours but a long-lasting trough between these times when thermal quality dropped to 9 (fig. 2, Pormpuraaw). On the other hand, the Townsville woodland was indeed thermally congenial, and thermal benefit of the habitat was uniformly high, though more variable than at Pormpuraaw. The lizards responded differently to these habitats, though there were some similarities. At Pormpuraaw, high midday temperatures meant that the cost for failing to thermoregulate precisely was unacceptably high. Accordingly, Carlia sexdentata achieved a thermal benefit of ~0.8, despite the habitat being <0.5, indicating high investment in thermoregulation. At both sites when thermal benefit was high (>0.7), lizards appeared to invest little effort into thermoregulation and scored low thermal benefits, sometimes even lower than the null model. This occurred around 1000 hours at Pormpuraaw and throughout the day in Townsville. For C. sexdentata at Pormpuraaw, this indicated a switch in behavioral strategy from thermoregulator to thermoconformer and back, while Carlia jarnoldae appeared to use both strategies throughout the day. These trends are supported by recent results (Blouin-Demers and Nadeau 2005; Vickers

et al. 2011). Interestingly, rather than observing the typical thermoregulator versus thermoconformer split in behavioral types of species, we observed individual lizards within species switching between strategies in response to their habitat. Although it seems paradoxical, investing little effort when the benefit from the environment is already high may be the best strategy to maximize net thermal benefit or may be the most cost-effective method for the thermal benefit attained. The obvious question is: Why were the lizards scoring a lower thermal benefit than the null model? It may be that the simple low cost of imprecise thermoregulation (in this case, down to 0.6 thermal benefit) is not low enough to be a deterrent; accordingly, lizards prioritize other tasks—for example, for-aging, territory maintenance, or mate acquisition—when habitat thermal quality is relatively high.

Thermal benefit can range from 0 to 1, and at almost all times of the day between 0600 and 1800 hours, there were locations where the thermal benefit associated with available environmental temperature was 1. With careful site selection, it may have been possible for a lizard to attain perfect thermal benefit throughout the day, but real lizards rarely did, if ever. This could have been an artifact of either our sampling of field-active lizards or our assumptions: a few lizards (five) were chased up to 30 s, which may have affected their body temperature, or our estimate of the thermal performance curve may have been too coarse, but these factors were unlikely to be important causes of the patterns we observed. We assumed all lizards strived to reach their thermal optimum at all times, but a benefit of 0.8 may be enough, and there may be a diminishing rate of return with increased effort above 0.8 benefit, especially when the quality of the thermal environment was poor (i.e., the thermal benefit of the null model is very low or very high). Theory suggests that rather than strive to attain perfect thermal benefit, active lizards ought to err, maintaining $T_{\rm b}$ below optimal levels to buffer slight imprecision, accidents, or emergencies (Martin and Huey 2008). Carlia sexdentata activity was highest in the early morning when habitat thermal quality was best (i.e., thermal benefit obtained by the null model was highest), and effort invested in thermoregulation by the lizards at this time was low. In his analysis of thermoregulatory behavior, Stevenson (1985b) predicted that constraints on activity time have the greatest impact on body temperature, and the insights from our model support this. Thus, while additional effort invested in thermoregulation in the morning before 1000 hours was low, simply maximizing activity during periods when thermoregulation is low cost is a cheap and highly effective thermoregulatory behavior. In the middle of the day, C. sexdentata activity declined immediately after habitat thermal quality declined (thermal benefit of the null model decreased) to a minimum activity level at about 1400 hours, with a later smaller peak at about 1600 hours. Many studies have observed that reptile activity peaks in the morning, sometimes with a smaller peak in the afternoon (e.g., Schwarzkopf and Brooks 1985; Bauwens et al. 1996; Firth and Belan 1998). The exact reason for the lack of afternoon activity peaks is unknown in the case of *C. sexdentata*, though it may be due to prey activity time. Curiously, C. sexdentata appeared to have two peaks in morning activity, which may indicate that there is an intersection of bimodal (early and late) and unimodal (middle of the day) activity periods by different individuals in the population. At times when most available environmental temperatures were lethally high, C. sexdentata activity ceased, because the lizards retreated to shelter sites. The small afternoon peak in activity and high habitat thermal quality (thermal benefit obtained by the null model) implies that, at least thermally, there is a window of opportunity available for increased activity in the afternoon for C. sexdentata. If so, we may need to update predictions of lizard (Sinervo et al. 2010) and ectotherm (Deutsch et al. 2008) extinction rates under climate change. Without invoking acclimation, adaptation, or spatial range shift, the afternoon might be a period that could be exploited: a temporal invasion increasing potential activity time, assuming prey is available.

The system in which we tested our new null model for thermoregulation was limited by our small landscape size relative to the distribution of C. sexdentata and C. jarnoldae, our use of discrete rather than continuous landscape, and our relatively coarse estimate of the thermal performance curve. However, our new framework should be applicable to a wide range of systems and scales from coarse grained to completely continuous in both space and time. Choice of spatial and temporal scale will depend on the body size and thermal inertia of each species being examined (Sears et al. 2011; Dillon et al. 2012; Woods et al. 2015). Many models for animal movement use highly sophisticated random walks, altering distance moved, including correlated directionality, perception, attractors, and deterrents (Palmer et al. 2011; Sears and Angilletta 2015). In our case, altering movement probability had a similar effect to altering step size: temperatures of areas crossed in longer steps still influence body temperature at the arrival location. Altering movement probability during the walk to follow a Gaussian or similar distribution produced null model results intermediate between the fast and slow walks shown here. By using different biophysical models, the same landscape temperature data could be used to assess the thermal habitat from the perspective of many organisms, from tiny invertebrates to large vertebrates and even endotherms. Appropriate parameterization of a biophysical model for estimating $T_{\rm b}$ from $T_{\rm e}$ accounts for thermal inertia, and while we have used a simple model, other environmental variables may be included as required (e.g., Kearney and Porter 2009).

Our null model provides a framework in which to quantify the relative benefits of thermoregulation and the effort invested in it. The temporal aspect of this model allowed us to see a shift between thermoconforming and effective thermoregulation within individuals at different times of day, and we anticipate using this null model to study thermal niche space. It will be interesting to determine the influence of individual differences in T_{sel} or the shape of thermal performance curves in allowing competing individuals or species to occupy different thermal niches in the same physical space. It will be possible to establish constraints on the model to make it more realistic and more appropriate to describe the likely behavior of a thermoregulator. Systematic removal of such rules could indicate the contribution of each behavior to the benefit of thermoregulation or even identify behaviors that are deleterious to optimum body temperature. The null model is the perfect thermoconformer, and an obvious next step may be to create a perfectly thermoregulating or Panglossian model (R. B. Huey, personal communication): the perfect walk (e.g., Fei et al. 2012). Combined, these models could provide a thermal benefit envelope for our behavioral thermoregulator to predict the likely behavior of real organisms in a changing world.

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