

# Patterns of Thermal Constraint on Ectotherm Activity

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**ABSTRACT:** Thermal activity constraints play a major role in many aspects of ectotherm ecology, including vulnerability to climate change. Therefore, there is strong interest in developing general models of the temperature dependence of activity. Several models have been put forth (explicitly or implicitly) to describe such constraints; nonetheless, tests of the predictive abilities of these models are lacking. In addition, most models consider activity as a threshold trait instead of considering continuous changes in the vigor of activity among individuals. Using field data for a tropical lizard (*Anolis cristatellus*) and simulations parameterized by our observations, we determine how well various threshold and continuous-activity models match observed activity patterns. No models accurately predicted activity under all of the thermal conditions that we considered. In addition, simulations showed that the performance of threshold models decreased as temperatures increased, which is a troubling finding given the threat of global climate change. We also find that activity rates are more sensitive to temperature than are the physiological traits often used as a proxy for fitness. We present a model of thermal constraint on activity that integrates aspects of both the threshold model and the continuous-activity model, the general features of which are supported by activity data from other species. Overall, our results demonstrate that greater attention should be given to fine-scale patterns of thermal constraint on activity.

**Keywords:** activity budget, thermal constraints, ectotherm, climate change, *Anolis*.

## Introduction

Activity budgets play a major role in many aspects of ectotherm biology, influencing energetics, reproductive output, and survival. Temperature is one of the main environmental factors that affect activity, and as such, the temperature dependence of activity has become a major component of investigations into the potential effects of climate warming on populations (Kearney et al. 2009; Sinervo et al. 2010;

Sears et al. 2011; Buckley and Kingsolver 2012). One of the most common methods of assessing thermal constraints on activity is to estimate the thermal thresholds above and below which activity cannot occur, with animals categorized as active if they are out of a nest or some other refuge (e.g., Porter et al. 1973; Fraser et al. 1993; Jayatilaka et al. 2011; Sears et al. 2011). By combining these thresholds with environmental thermal data, one can estimate activity budgets in terms of time available for activity, as well as other important metrics, such as energetic budgets (e.g., Angilletta 2001). Thermal thresholds for activity are often used to predict the consequences of climate change (Kearney et al. 2009; Sinervo et al. 2010; Caruso et al. 2014). For example, a global analysis of vulnerability to climate warming in reptiles projected that activity budgets of many populations would decrease as temperatures increased, leading to energetic imbalance and population collapse (Sinervo et al. 2010). However, the effects of warming on activity are not always projected to be negative, because populations in cooler high latitudes or high-elevation regions may experience an increase in the amount of time that temperatures are within their activity thresholds (Buckley and Kingsolver 2012).

Thermal activity thresholds are not known for most organisms and may be difficult to estimate observationally for species that live in thermally permissive habitats. It would be beneficial to develop general predictors of temperature-dependent activity so that the consequences of thermal change can be calculated for species in which direct observations are limited. In the literature, a number of different thermal thresholds have been assumed to predict activity budgets. In some cases, physiological thermal tolerance limits are assumed to bound activity (Buckley and Roughgarden 2005), whereas in others they are bounded by minimum and maximum body temperature ( $T_b$ ) measured in the field (Porter et al. 1973; Bennie et al. 2013; Caruso et al. 2014). In other cases, thresholds have been based around the preferred temperature ( $T_p$ ; e.g., Brattstrom 1965; DeWitt 1967; Adolph and Porter 1993; Ward and Seely 1996; Sinervo et al. 2010), which was originally developed within the context of behavioral thermoregulation (Hertz et al. 1993) and describes the temperature(s) that or-

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ganisms seek out within a thermally heterogeneous environment (May 1979; Lagerspetz and Vainio 2006; Anderson et al. 2007; Martin and Huey 2008). Activity has been assumed to occur only within the  $T_p$  range (e.g., Adolph and Porter 1993); in a more recent example, it was assumed that activity occurs below, but not above,  $T_p$  (Sinervo et al. 2010).

Threshold models of activity have provided significant insights into the influence of temperature on the ecology of ectotherms. Nonetheless, there are aspects of temperature-dependent activity that these models do not capture. In particular, threshold models do not incorporate variation in how vigorous the activity of individuals will be at different temperatures. Given that physiological processes are temperature sensitive, including the neuromuscular processes that underlie most behaviors, one might expect that individual activity rates will respond to thermal variation in a continuous manner within the activity thresholds. For example, the calling rates of frogs (Gerhardt 1978) and crickets (Olvido and Mousseau 1995) increase with increases in temperature. Moreover, the number of individuals that are out of refuges or engaged in a particular activity often changes in a continuous manner with thermal conditions (Kingsolver 1983; Fraser et al. 1993; Andrew et al. 2013). If the vigor with which individuals engage in activity changes with temperature, then all activity that occurs within the activity thresholds cannot be considered equal. This variation could have implications for many of the factors that threshold models attempt to estimate, including energetic expenditures, contact rates between potential mates, and contact rates between predators and prey.

Here, we compare observed temperature-dependent activity with predictions based on various models of thermal constraint in the tropical lizard *Anolis cristatellus*, a classic system in behavioral and thermal ecology (Huey 1974; Huey and Webster 1976; Hertz 1992a, 1992b; Hertz et al. 1993; Huey et al. 2003; Gunderson and Leal 2012; Leal and Gunderson 2012). We consider temperature-dependent activity a continuous trait by measuring activity rates of individuals, and we use these data to assess both threshold and continuous models of activity constraint. Our goals were threefold: first, to document the temperature range over which activity occurs in the field and determine whether it matches activity thresholds assumed in the literature; second, to evaluate the extent to which the vigor of individual activity changes with temperature and the consequences of assuming that it does not in terms of predicted activity rates; and third, to test whether the vigor with which individuals engage in activity is correlated with the temperature dependence of underlying physiological traits, particularly locomotor performance.

We compared three thermal threshold models that assume varying levels of thermal constraint with the goal of assessing how estimates of activity rates are affected by

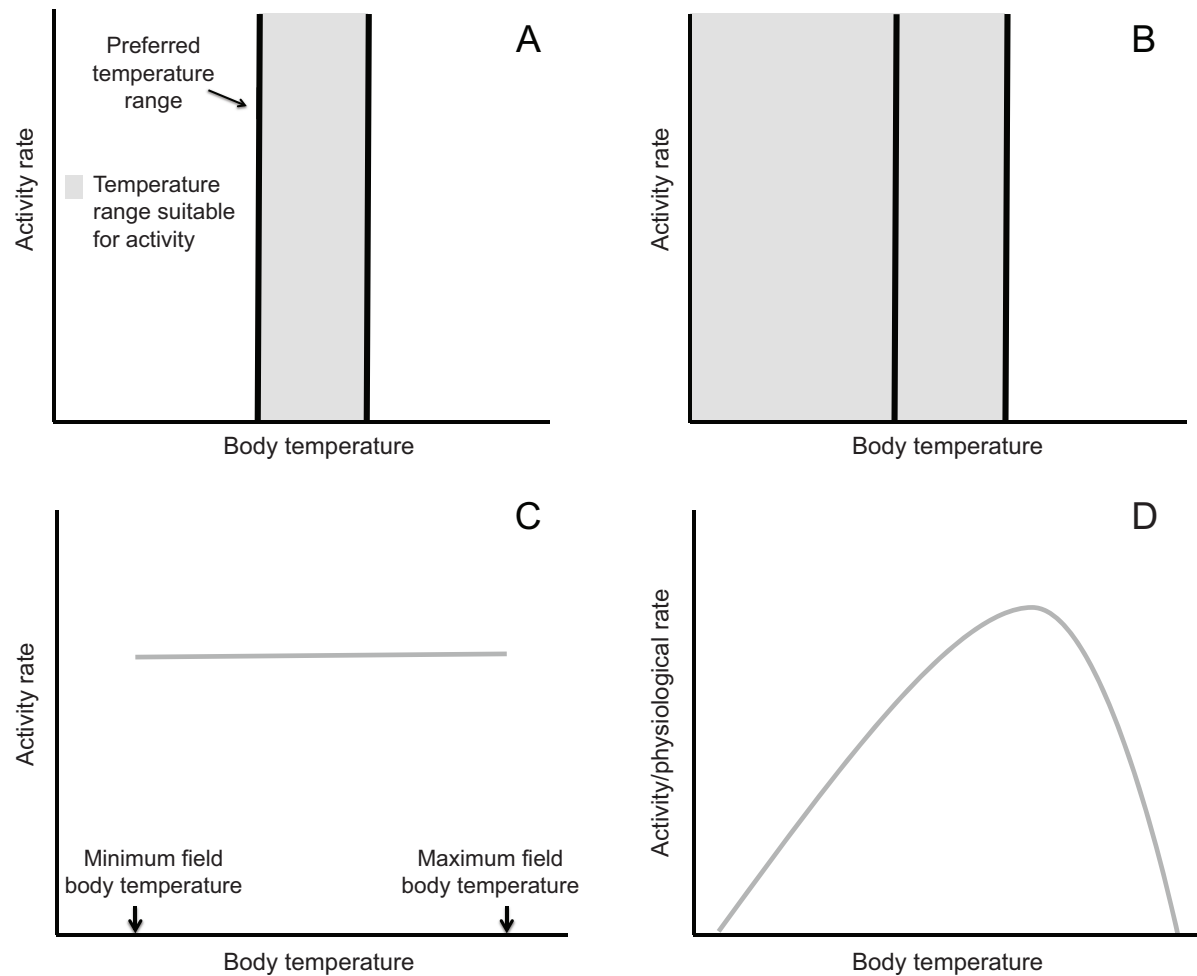
assuming different activity limits. The two most constraining models were constructed around estimates of the  $T_p$ . The first and most limiting model that we consider is based on analyses that assume activity occurs only within a relatively narrow thermal window (e.g., Adolph and Porter 1993; Kearney et al. 2009). Following Adolph and Porter (1993), we assume that that thermal window is the  $T_p$  range (fig. 1A). We refer to this as the “high constraint” model. The next model is based on the methods used by Sinervo et al. (2010), in which we assume that activity does not occur above the  $T_p$  range (fig. 1B). We refer to this as the “medium constraint” model. The third model assumes that animals can be active over a wide range of temperatures (Buckley and Roughgarden 2005; Kearney et al. 2009), delimited by observed minimum and maximum field  $T_b$ , but assuming mean activity rate remains constant with  $T_b$  (fig. 1C). This model assesses the consequence of considering activity rates as constant across the thermal activity window. We refer to this as the “low constraint” model. The final model we test assumes individual activity rates change in a continuous manner with temperature (Peterson and Anderson 1969; Kingsolver 1983; Marsh 1985; Grant and Dunham 1988; Buckley and Kingsolver 2012), driven by thermal effects on physiological rates. Given that most behavioral traits are driven by neuromuscular processes, we use locomotor performance (in this case, sprint speed) as the physiological trait for comparison (fig. 1D). We refer to this as the “organismal performance” model.

We collected data on the activity and  $T_b$  of free-ranging *A. cristatellus* on the island of Puerto Rico during the peak of the breeding season in 2010 (Gorman and Licht 1974). Two separate approaches were used to evaluate the high-, medium-, and low-activity constraint threshold models. In the first approach, we compared observed activity patterns with data sets that we generated by transforming our field data according to the assumptions of each model. In the second approach, we simulated activity rates of *A. cristatellus* with higher  $T_b$  to explore whether the performance of activity models changed under warmer conditions. For the physiological performance model, we tested for an association between activity rate and the estimated sprint performance capacity.

## Material and Methods

### *Behavioral Observations*

*Anolis cristatellus* is a small-to-medium-sized arboreal lizard endemic to the islands of the Greater Puerto Rican Bank (Rand 1964; Heatwole 1976; Hertz 1992b). We conducted focal observations on a total of 299 individuals split between two different habitat types: mesic ( $n = 158$ ) and xeric ( $n = 141$ ) forest (data available from the Dryad Dig-



**Figure 1:** Overview of the various models of temperature-dependent activity that we tested: high constraint (A), medium constraint (B), low constraint (C), and physiological performance (D). See text for details.

ital Repository, <http://dx.doi.org/10.5061/dryad.48vb7>; Gunderson and Leal 2015). The mesic forest has a high, relatively closed canopy, whereas the xeric forest is dominated by scrubby trees and has a more open canopy. Data collection in the mesic habitat occurred from July 26 to August 4, 2010, at Bosque Estatal de Cambalache (18°26'998"N, 66°35'642"W; elevation, 10 m; 81 males and 77 females), whereas data collection in the xeric habitat occurred from July 13 to July 24, 2010, at Bosque Estatal de Guánica (17°58'246"N, 66°52'236"W; elevation, 5 m; 71 males and 70 females). One lizard from Guánica was recorded as having an unusually high activity rate and elevated  $T_b$  and was removed from analyses as an outlier. At both sites, focal observations were conducted from 0730 to 1730 hours each day, excluding periods of rain. Our goal was to follow each focal lizard for 15 min, but lizards occasionally disappeared

from view before an observation was finished. As a result, the mean duration of focal observations was 13.7 min (the minimum observation time was approximately 3 min) with a total of 68.4 h of sampling.

Focal lizards were located by walking slowly through the forest along transect lines that followed randomly generated compass directions and starting in a different haphazard location every day. This method made it extremely unlikely that a given individual was observed more than once, and it allowed us to sample large areas of each forest. Focal lizards were observed at a distance of 3–4 m, and their behaviors were recorded using a PalmPilot running Noldus Observer XT software (Noldus Information Technology, Leesburg, VA). We collected time-stamped activity data, which included agonistic encounters, feeding events, mating, and signaling displays (i.e., production of head-

bobs, push-ups, and dewlap flashes; Jenssen 1977). Following classical methods in animal behavior (Lehner 1998), an activity rate was then estimated for each lizard, calculated as the proportion of the total observation time that the lizard was engaged in the neuromuscular activities described above. In doing so, we differentiate between different components of temperature-dependent activity: because they were not in refuges, all animals in this study would be considered active by traditional definitions that consider activity a threshold trait.

The  $T_b$  of each lizard was subsequently estimated with a copper lizard model placed at the location where the lizard was perched for the majority of the observation. The copper models were constructed using a mold of *A. cristatellus* and have been used in several studies of *A. cristatellus* thermal ecology (see Hertz 1992a, 1992b, for a detailed description of the models). The models are designed to have a low specific heat capacity, and thus their temperature rapidly reaches equilibrium under field conditions (Hertz 1992b). In an earlier study conducted at the same sites sampled here, we paired measurements of lizard  $T_b$  with measurements of copper models placed at random locations near the lizards (Gunderson and Leal 2012). Copper model temperature and lizard  $T_b$  were highly correlated when the model had the same basking status as the lizard (Pearson product-moment correlation,  $r = 0.95$ ; degrees of freedom [df] = 137;  $P < .001$ ), as was the case in this study. Therefore, the copper models provide a robust estimate of lizard  $T_b$  in both habitat types under diverse conditions.

#### *Evaluation of Temperature-Dependent Activity*

We tested for factors that affect activity rates using a type II sum of squares ANOVA model. Activity data were log +0.01 transformed to adhere to assumptions of normality. We began by including the following factors: habitat, sex, and  $T_p$  status (i.e., was the lizard within the  $T_p$  range?), and all possible interactions. Nonsignificant terms were removed in a stepwise manner, beginning with interaction terms. None of the interactions were significant. Because of the unbalanced nature of our design, we constructed a series of models with the first-order terms entered in different orders to determine whether the significance of terms changed at  $\alpha = 0.05$ . We found that order did not affect the significance of any terms. To evaluate the form of the relationship between individual activity rate and  $T_b$ , we fit a restricted cubic spline to the data.

#### *Evaluation of Temperature-Dependent Activity Models*

The threshold activity models were tested by producing three additional data sets, each one generated by transforming our observed activity data to meet the assump-

tions of each of the models. For high constraint, a lizard's activity rate was set to zero if its  $T_b$  was outside of the  $T_p$  range (Adolph and Porter 1993). For medium constraint, a lizard's activity rate was set to zero if its  $T_b$  was above the upper bound of the  $T_p$  range. This is a conservative application of the model employed by Sinervo et al. (2010), because they use point estimates of  $T_p$  as the activity boundary, which are typically lower than the upper bound of the  $T_p$  range. For low constraint, we assigned new activity rates to lizards whose  $T_b$  was outside of the  $T_p$  range. New activity rates were drawn, with replacement, from the pool of activity rates of lizards that were within the  $T_p$  range. This model allows activity across all  $T_b$  values measured in the field but without assuming a continuous change in activity rate with  $T_b$ . We assumed activity within the  $T_p$  range because, under current conditions, many organisms are able to maintain  $T_b$  at or near this range for most hours of the day as a result of behavioral thermoregulation (Bogert 1949). We estimated 95% confidence intervals for the mean activity rates of the observed and transformed data sets by implementing basic bootstrap resampling with replacement ( $n = 1,000$ ) using the boot package in the R statistical programming language, version 2.15.0 (R Development Core Team 2012).

To investigate the performance of threshold activity models under warmer conditions, we conducted individual-based simulations that combined our temperature-dependent activity data from 2010 with  $T_b$  data that we collected at the same two sites in the slightly warmer year of 2009 (Gunderson and Leal 2012). The mean  $T_b$  at the mesic site in 2009 was very similar to that measured in 2010 ( $\bar{X}_{2009} = 29.2^\circ\text{C}$ ,  $\bar{X}_{2010} = 28.8^\circ\text{C}$ ), as was the  $T_b$  range ( $T_b$  range,  $26.4^\circ\text{--}31.1^\circ\text{C}$  in 2009 and  $25.7^\circ\text{--}31.9^\circ\text{C}$  in 2010). However, the mean  $T_b$  at the xeric site was  $2.2^\circ\text{C}$  warmer in 2009 than in 2010 ( $\bar{X}_{2009} = 32.4^\circ\text{C}$ ,  $\bar{X}_{2010} = 30.2^\circ\text{C}$ ), although the range of  $T_b$  values measured was very similar ( $T_b$  range,  $26.2^\circ\text{--}35.5^\circ\text{C}$  in 2009 and  $25.8^\circ\text{--}34.9^\circ\text{C}$  in 2010).

Simulated individuals were tracked through an 11-h day broken into 44 blocks of 15 min each. For each 15-min block, a  $T_b$  was chosen at random from the pool of  $T_b$  values measured in 2009 during the appropriate time period from the same habitat type. Next, the  $T_b$  was converted into an absolute deviation ( $d$ ) from the  $T_p$  range, following Hertz et al. (1993). Under this transformation, if a  $T_b$  falls within the  $T_p$  range, it has a  $d$  value of 0. If a  $T_b$  is  $1^\circ\text{C}$  from the  $T_p$  range (either above or below), it has a  $d$  value of 1, and so on.

We binned our 2010 activity rate data according to the absolute  $d$  value of the focal lizard to create pools of activity rates from which to draw for our simulated lizards. The activity rates were binned as follows:  $d = 0$ ;  $0 < d \leq 1$ ;  $1 < d < 2$ ;  $d \geq 2$ . For example, if a simulated lizard had a  $d$  value of 0 for a particular time block, its activity rate for



that block was drawn from the pool of activity rates measured for lizards with a  $d$  of 0. If a simulated lizard had a  $d$  value of 1.5 for a particular block, its activity rate for that block was drawn from the pool of activity rates measured for lizards with a  $d$  value of  $>1$  but  $\leq 2$ .

To assess the continuous organismal performance model, we first estimated the relative sprint performance capacity of each lizard that we observed. To do so, we entered each lizard's  $T_b$  into a previously published function describing the temperature dependence of maximum sprint speed in *A. cristatellus* (see Gunderson and Leal 2012 for details). We then modeled the association between activity rate and sprint capacity using the Spearman rank-order correlation test (Whitlock and Schluter 2009). All statistical analyses were conducted using the R statistical programming language (R Development Core Team 2012).

## Results

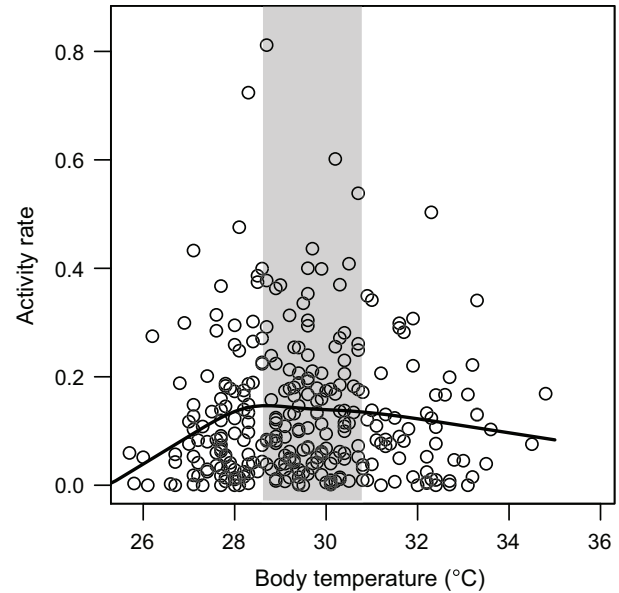
Lizards from mesic and xeric habitats did not differ in mean activity rate ( $F_{1,295} = 2.327$ ,  $P = .128$ ; see table 1 for ANOVA model summary). However, females had lower activity rates than males ( $F_{1,295} = 3.983$ ,  $P = .047$ ) and individuals with  $T_b$  values within the  $T_p$  range had higher activity rates than those with  $T_b$  values outside the  $T_p$  range ( $F_{1,295} = 4.343$ ,  $P = .038$ ; fig. 2). Daily patterns of activity did differ between habitats: mesic habitat lizards had depressed activity early and late in the day, when  $T_b$  values are typically below the  $T_p$  range, whereas xeric habitat lizards had depressed activity during the middle hours of the day, when  $T_b$  values are typically above the  $T_p$  range (see observed data in fig. 3A, 3C).

How well do the threshold activity models predict the observed activity levels of *Anolis cristatellus*? In the mesic habitat, the activity levels predicted by the medium- and low-constraint models were very similar to what we observed. Both models allowed predicted grand mean activity rates within 4% of the measured grand mean (fig. 3A, 3B). In contrast, assuming the high-constraint model would underestimate the grand mean activity rate by 40% (fig. 3A,

**Table 1:** ANOVA table summarizing factors that affect activity rate in *Anolis cristatellus* on the island of Puerto Rico

Variable	df	MS	F	P
Habitat	1	2.524	2.327	.128
Sex	1	4.320	3.983	<b>.047</b>
$T_p$	1	4.711	4.343	<b>.038</b>
Residuals	295	1.085	...	

Note: Boldface type indicates statistical significance. df = degrees of freedom; MS = mean squares;  $T_p$  = whether the lizard was within the preferred temperature range.

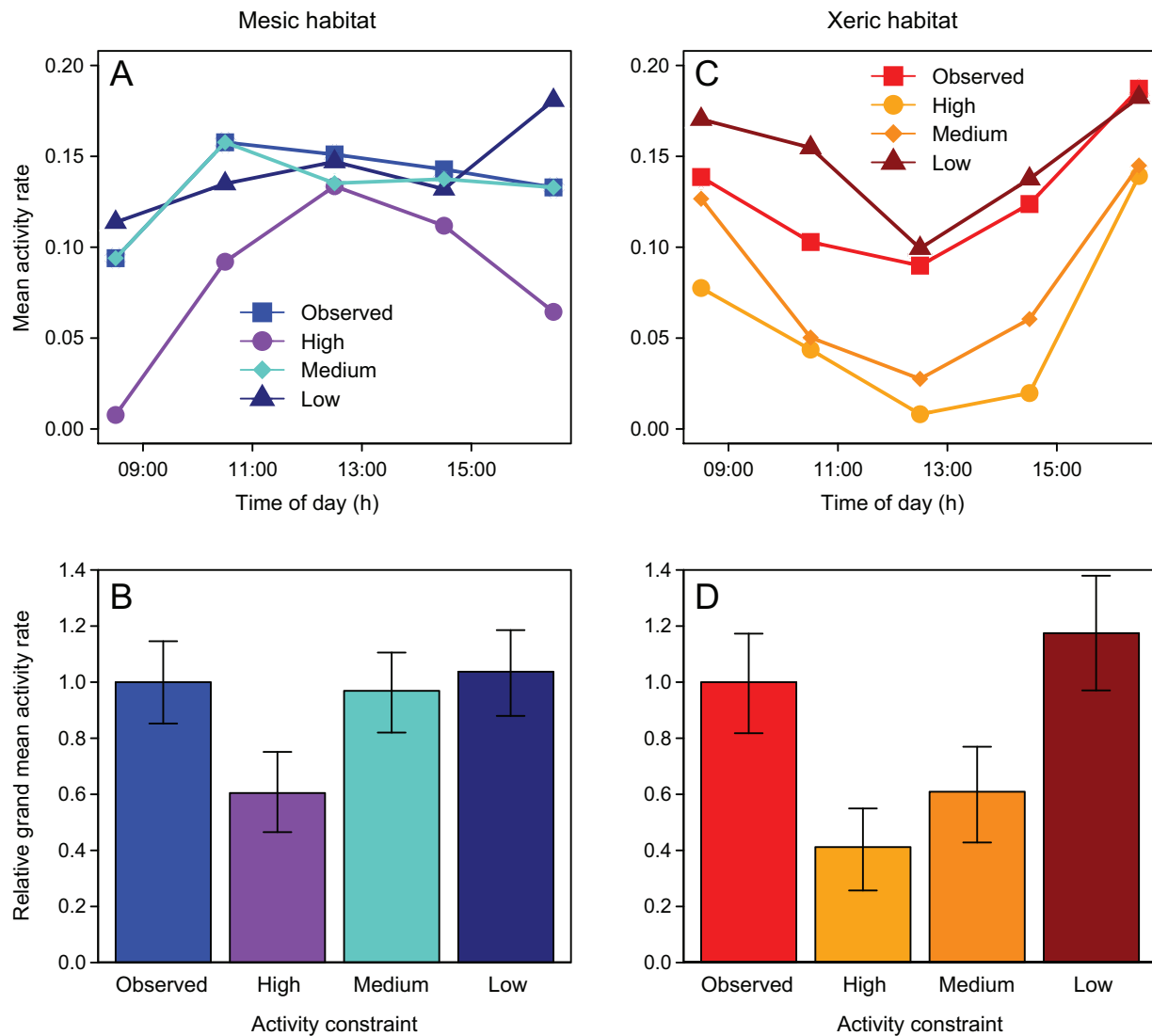


**Figure 2:** Temperature-dependent individual activity rates of *Anolis cristatellus* with a restricted cubic spline curve fit to the data. The activity of lizards from mesic and xeric habitats are combined. The preferred temperature range is indicated by the gray box.

3B). In the xeric habitat, both the high-constraint and medium-constraint models would lead to underestimated activity rates, with grand means 59% and 39% lower than the measured value, respectively (fig. 3C, 3D). Conversely, the low-constraint model would overestimate the grand mean activity rate in the xeric habitat by 17% (fig. 3C, 3D).

How do the threshold activity models perform under the slightly warmer  $T_b$  values we measured in 2009? According to our simulations, in the mesic habitat, the medium-constraint model would underestimate the expected grand mean activity rate by only 2%, whereas the low-constraint model would overestimate the expected grand mean by 12% (fig. 4). In the mesic habitat, the high-constraint model was the worst predictor of the expected result, underestimating expected activity by 39% (fig. 4A, 4B). In the xeric habitat, the high-constraint and medium-constraint models would underestimate the expected grand mean activity rate by 73% and 70%, respectively, whereas the low-constraint model would overestimate the expected grand mean by 30% (fig. 4C, 4D).

Individual activity rates did not correlate with locomotor performance (i.e., sprint speed capacity;  $df = 296$ ,  $r = 0.057$ ,  $P = .324$ ; fig. 5A). When looking at the temperature dependence of activity and locomotor performance in relative terms (i.e., with the maximum rate,  $T_{opt}$ , set to 1), it can be seen that activity rate has a narrower temperature-dependent curve than locomotor performance (fig. 5B).



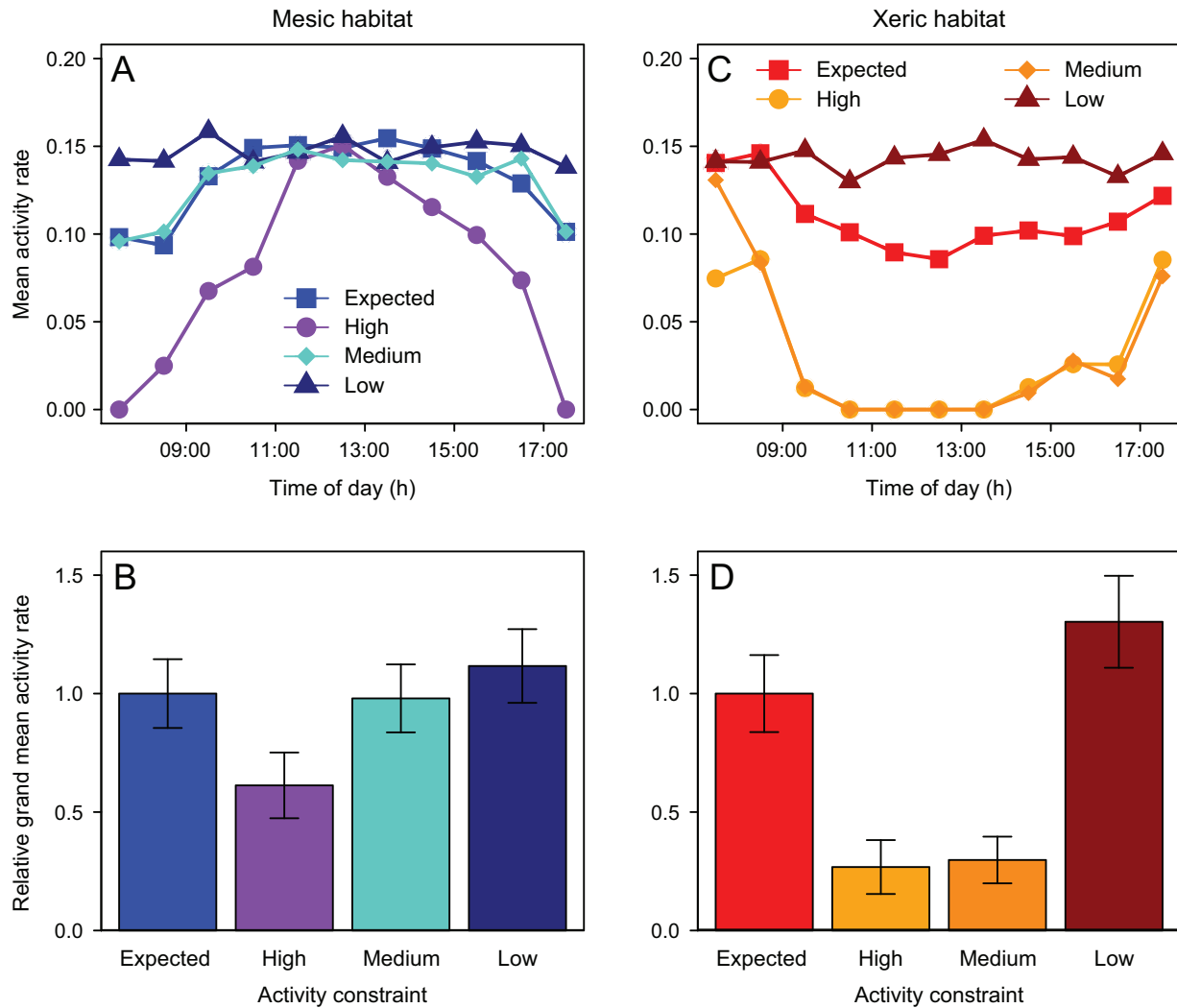
**Figure 3:** Summary of observed and model-transformed activity data for *Anolis cristatellus* in mesic (A, B) and xeric (C, D) habitats. A and C depict mean activity rate binned by time of day. B and D depict grand mean activity rates of models relative to the observed grand activity rate (i.e., grand mean model activity rate divided by grand mean observed activity rate). Error bars indicate bootstrapped 95% confidence intervals.

This indicates that activity is more sensitive than locomotion to thermal variation. In addition, the  $T_{opt}$  for activity is several degrees lower than the  $T_{opt}$  for locomotor performance (fig. 5B).

### Discussion

Thermal constraints on activity have long been recognized as a central component of thermal ecology (Porter et al. 1973; Kingsolver 1983). Nonetheless, our understanding of such thermal constraints is surprisingly limited. We con-

ducted a fine-grained analysis of the relationship between  $T_b$  and activity in free-ranging *Anolis cristatellus* and compared our results with those expected under various models of thermal activity constraint. All of the models that we considered had significant shortcomings and either overestimated or underestimated activity rates, depending on thermal conditions. Our findings demonstrate that fine-scale thermal variation can result in fine-scale variation in activity budgets that threshold models are unlikely to capture. More generally, our findings have important implications for understanding how changes in activity under



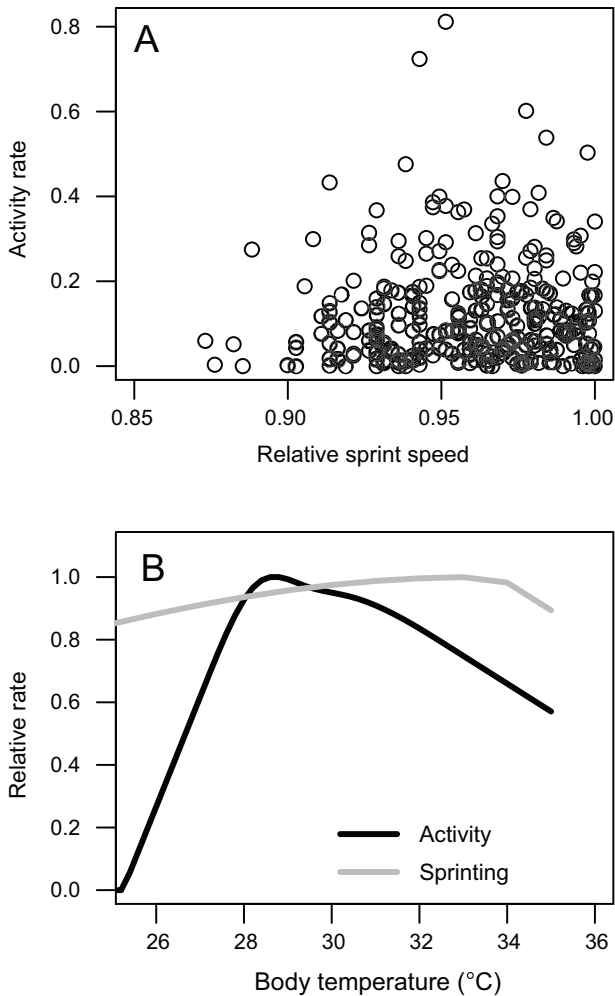
**Figure 4:** Summary of simulated activity data using 2009 body temperature data for *Anolis cristatellus* from mesic (A, B) and xeric (C, D) habitats. A and C depict mean activity rate binned by time of day. B and D depict grand mean activity rates of models relative to the expected grand mean activity rate (i.e., grand mean model activity rate divided by grand mean expected activity rate). Error bars indicate SD.

future conditions will influence the vulnerability of ectotherms to global climate change.

The threshold models tended to do a poor job of predicting activity. The high-constraint model underestimated lizard activity in both the mesic and xeric habitats (fig. 3), because *A. cristatellus* frequently remained active both above and below the  $T_p$  range. The medium-constraint model was a poor representation of lizard activity in the xeric habitat but not in the mesic habitat (fig. 3). This discrepancy can be attributed to the fact that xeric habitat lizards often had  $T_b$ s above the  $T_p$  range (40% of xeric observations), whereas mesic habitat lizards rarely had  $T_b$ s above that range (3% of mesic observations). The low-constraint model was the only model that performed reasonably well in both habi-

tats, overestimating grand mean activity rates by 4% and 17% in the mesic and xeric habitats, respectively (fig. 3).

When we simulated the activity of *A. cristatellus* under warmer  $T_b$  values, the results were qualitatively similar to the transformed results from 2010 (fig. 4). The high-constraint model was a poor predictor of the expected result in both habitats, and the medium-constraint model was a good predictor of the expected result in the mesic but not the xeric habitat. In addition, the low-constraint model performed well in the mesic habitat but less well in the xeric habitat (fig. 4). Despite the qualitative similarity, the activity models performed quantitatively worse in the xeric habitat simulations: the simulated high-constraint and medium-constraint models underestimated the ex-



**Figure 5:** A, Individual activity rates of *Anolis cristatellus* plotted against predicted maximum relative sprint performance. B, Relative activity rate curve (i.e., the cubic spline from figure 2 with the maximum rate set to 1) and the relative sprint performance curve for *A. cristatellus* from Gunderson and Leal (2012).

pected mean activity rate by over 70%, whereas the low-constraint model overestimated the expected mean activity rate by over 30% (fig. 4).

The combined results of the empirical data and the simulations indicate that the choice of activity threshold is extremely important and may dramatically change predictions for the activity levels of populations. For example, the “medium constraint” model, which was recently used to predict impacts of warming for lizards across the globe (Sinervo et al. 2010), clearly underestimates upper activity thresholds and is likely to overestimate the negative impacts of warming. Our data demonstrate that activity should be assumed to occur at least 2°–3°C above and below the  $T_p$  range. Conversely, the results from the “low constraint”

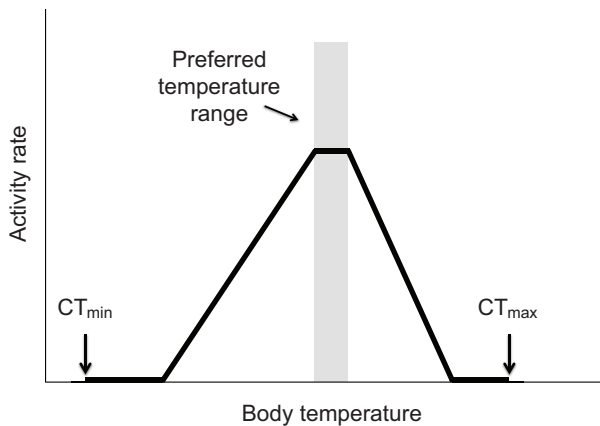
model clearly indicate that assuming constant activity rates across the range of field  $T_b$  values does not represent the reality of temperature-dependent activity.

We found that individual activity rates change with  $T_b$  in a continuous, unimodal pattern (fig. 2). However, we also found that activity rates are not coupled to locomotor performance (fig. 5), despite the fact that activity vigor is driven by neuromuscular processes. In particular, it appears that activity rate is much more sensitive to temperature than is locomotion: lizards often had depressed activity rates at temperatures at which sprint performance remained high (fig. 4B). This finding indicates that warming may affect some aspects of behavior more severely than the whole-organism physiological traits that are often assumed to be a proxy for fitness (e.g., Deutsch et al. 2008). This observation is unexpected and further suggests that we should be explicitly considering fine-scale thermal effects on activity when attempting to understand the effects of climate change on ectotherm populations.

It seems likely that some temperature-dependent physiological traits contribute to the temperature dependence of activity, but we can only speculate as to what those traits are. Locomotor endurance is certainly a candidate. For example, differences in mean activity rates among species (often related to foraging strategy) tend to correlate with endurance (Garland 1999). Unfortunately, species-level differences in endurance are not particularly informative in the present case, because they do not provide data on how activity rates of individuals change as a result of thermal effects on endurance capacity. Furthermore, endurance tends to have a broad thermal performance curve, similar to sprinting (Angilletta et al. 2002). Temperature-dependent physiological traits associated with energetic payoffs of activity, such as the rate at which energy can be assimilated, might also influence individual activity rates. These traits have been shown to be more sensitive than locomotor performance to temperature (Angilletta 2001), consistent with the pattern we observed for *A. cristatellus* activity.

Our analyses lead us to propose a general model of temperature-dependent ectotherm activity that combines characteristics of the threshold and continuous models that we tested (fig. 6). As in the high- and medium-constraint threshold models, the framework is built around estimates of the  $T_p$  range. However, unlike in those models, activity is not bounded by the  $T_p$  range. Instead, we expect activity rates to be maximized within the  $T_p$  range and for those rates to decrease in a continuous manner as  $T_b$  values become warmer or colder. At present, the model does not predict how quickly activity rates will change as  $T_b$  values move away from the  $T_p$  range. (The rarity of temperature-dependent fine-scale behavioral activity data precludes us from developing those components of the model.) However, as with most behavioral or physiological processes,





**Figure 6:** A graphical model of thermal constraint on activity.  $CT_{max}$  = critical thermal maximum;  $CT_{min}$  = critical thermal minimum.

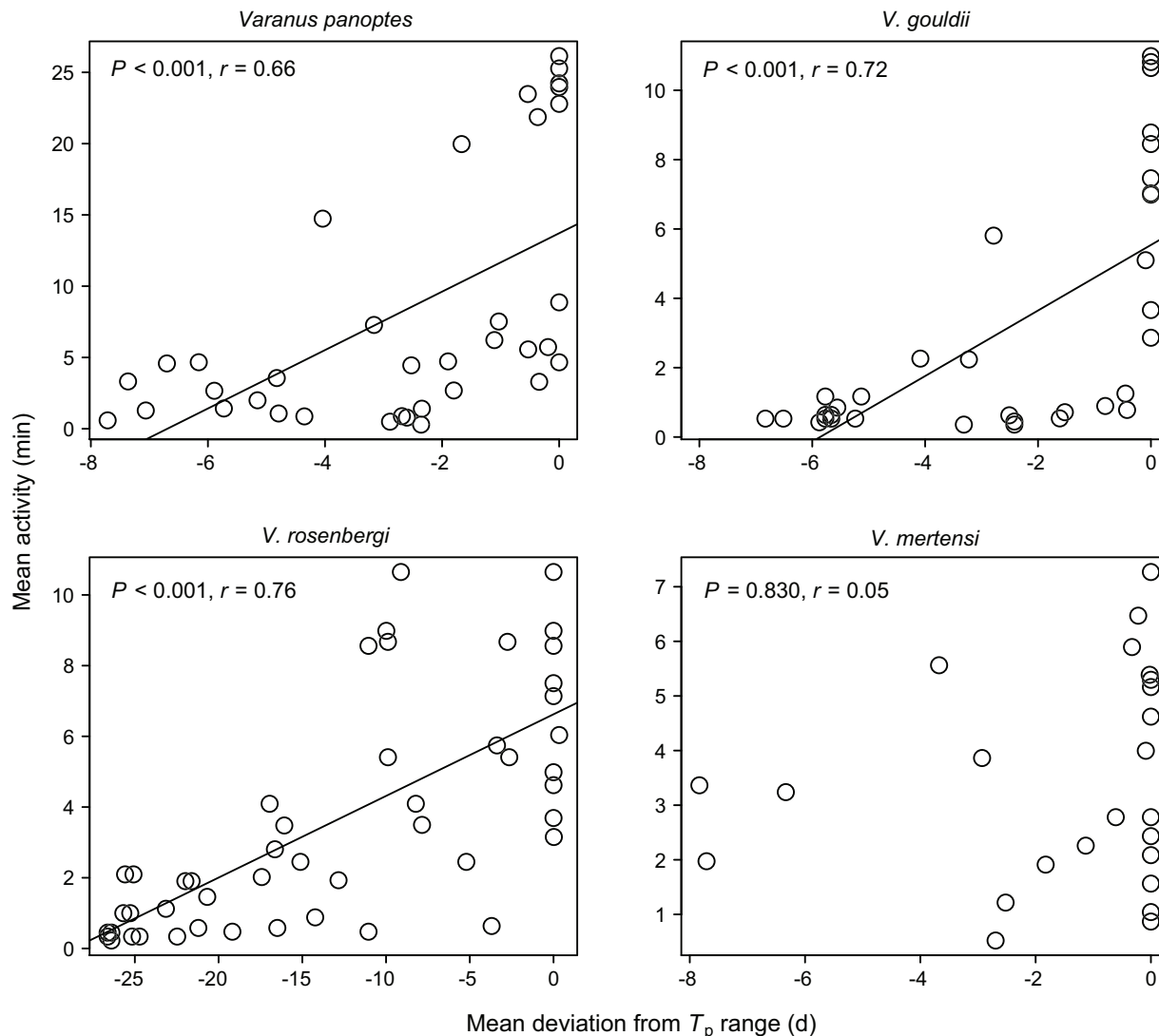
parameter values will almost certainly vary among taxa, and estimating them will require the collection of fine-scale behavioral data across a diverse set of species.

The cornerstone of our model is that activity rates should change continuously with temperature and reach their highest level within the  $T_p$  range. An immediate question that arises is whether this model describes activity in systems outside of *A. cristatellus*. Graded behavioral responses to temperature have been documented for a variety of species, primarily under laboratory conditions. For example, feeding rates of cabbage white caterpillars (*Pieris rapae*; Kingsolver 2000) and courtship display rates in red-sided garter snakes (*Thamnophis sirtalis parietalis*) change with temperature (Hawley and Aleksyuk 1975). At present, very few studies have collected fine-scale data on individual activity rates and  $T_b$  values under natural conditions (but see Gerhardt 1978). Instead, several studies involving insects and reptiles have measured activity rate in the field as a count of the number of individuals observed within a given temporal window under given thermal conditions. If we used the assumption that number of individuals is a proxy of activity, these studies generally demonstrate continuous changes in the number of individuals observed with temperature (Watt 1968; Huey and Pianka 1977; Hertz 1981; Kingsolver 1983) and thus suggest that activity is changing in a continuous manner. However, activity rates estimated from counts of individuals do not provide a direct test of our model, because they contain no information about the intensity of activity for each individual.

Perhaps the most detailed analysis of the direct effect of  $T_b$  on field activity rate outside of the present study was conducted by Christian and Weavers (1996) on four species of Varanid lizard from Australia. They used radio te-

lemetry to simultaneously measure  $T_b$  and activity rates of individuals, and they coupled those data with laboratory measurements of the  $T_p$  ranges for the same species. To determine whether the patterns of activity observed for the four Varanids support the model we have presented, we extracted data on mean activity rate and mean  $T_b$  for each species during their respective breeding seasons from the figures of Christian and Weavers (1996), using the free online software PlotDigitizer. These lizards are effective thermoregulators that rarely experienced  $T_b$  values above their  $T_p$  range. Thus, this analysis is a partial test of our model, pertaining only to  $T_b$  values within and below  $T_p$ . We tested for a correlation between activity and  $T_b$  (after converting  $T_b$  to  $d$ ) using the Spearman rank-order correlation test. In three of the four species, activity rate correlated positively with  $T_b$  ( $P < .05$ ) and peaked within the  $T_p$  range, matching the predictions of our model (fig. 7). It is worth noting that Varanids are a classic example of an active forager, in contrast to *A. cristatellus*, which are sit-and-wait predators and use the typical foraging strategy of most species of Iguanian. Despite these inherent differences in foraging strategy and, thus, in overall activity rate (Perry and Pianka 1997), both of these groups demonstrate patterns of temperature-dependent activity consistent with our model. The lack of temperature association in one of the Varanid species may speak to the fact that multiple factors can influence activity rates and that these factors might overwhelm underlying thermal effects. Such factors may include the presence of predators, prey availability, or the spatial distribution of available thermal microhabitats (Grant 1990).

The model we present has important implications for understanding the current thermal ecology of ectothermic species and for assessing the vulnerability of ectotherms to climate warming. Demographic parameters, such as growth and reproductive rates, are heavily influenced by the activity budgets of populations (Dunham et al. 1989; Adolph and Porter 1993). Our results indicate that current activity models may be too constraining and can thus greatly underestimate the activity budgets of ectotherms under current and especially future conditions. We also find that considering activity as a threshold variable is too simplistic, because the rate, or intensity, of activity is not constant across  $T_b$  values. Ignoring this aspect of activity may lead to overestimates of activity budgets when conditions are frequently outside the  $T_p$  range. Based on our observations, we suggest that calculating realistic activity budgets under current and future thermal conditions requires weighting the amount of time that activity can occur by the distribution of expected  $T_b$  values. Thermal variation in activity rates also has implications for estimating the indirect effects of climate warming via species interactions. For example, encounter rates between interacting species, such as com-



**Figure 7:** Mean activity rates versus mean body temperature, scaled to mean deviation from the preferred temperature ( $T_p$ ) range,  $d$ , for four species of Australian Varanid lizards measured by Christian and Weaver (1996) during the breeding season.

petitors and predators, may be influenced by changes in the intensity of activity as  $T_b$  values increase (Gilman et al. 2010; Vucic-Pestic et al. 2011; Pincebourde et al. 2012; Dell et al. 2014).

Forecasts of biological responses to climate change that are based on species traits can only be as robust as our estimates of those traits (Buckley et al. 2010, 2011; Kearney et al. 2010). Empirical studies of thermal constraints on activity should be a focus of future work, because our current understanding of the temperature dependence of activity is extremely limited. Our model provides a step toward filling this gap by proposing a revised framework for how rates of activities might respond to changes in environmental temperatures, potentially facilitating robust predic-

tions about how individuals, populations, and ultimately communities of interacting species will be affected by climate warming.

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A crested anole (*Anolis cristatellus*). Photo credit: Manuel Leal.