



The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming

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Increasing concern about the impacts of global warming on biodiversity has stimulated extensive discussion, but methods to translate broad-scale shifts in climate into direct impacts on living animals remain simplistic. A key missing element from models of climatic change impacts on animals is the buffering influence of behavioral thermoregulation. Here, we show how behavioral and mass/energy balance models can be combined with spatial data on climate, topography, and vegetation to predict impacts of increased air temperature on thermoregulating ectotherms such as reptiles and insects (a large portion of global biodiversity). We show that for most “cold-blooded” terrestrial animals, the primary thermal challenge is not to attain high body temperatures (although this is important in temperate environments) but to stay cool (particularly in tropical and desert areas, where ectotherm biodiversity is greatest). The impact of climate warming on thermoregulating ectotherms will depend critically on how changes in vegetation cover alter the availability of shade as well as the animals’ capacities to alter their seasonal timing of activity and reproduction. Warmer environments also may increase maintenance energy costs while simultaneously constraining activity time, putting pressure on mass and energy budgets. Energy- and mass-balance models provide a general method to integrate the complexity of these direct interactions between organisms and climate into spatial predictions of the impact of climate change on biodiversity. This methodology allows quantitative organism- and habitat-specific assessments of climate change impacts.

Australia | biophysical model | climate change | terrestrial ectotherm | GIS

The response of organisms to climate warming will have implications for conservation, pest management, and the spread of disease. To respond effectively to these changes, we must be able to predict how changes in climate, especially air temperature, will affect biodiversity (1, 2). Current approaches to predicting these impacts are largely based on statistical correlations between a species’ observed distribution and coarse-scale macroclimatic data (3–5). Correlative approaches provide little insight into the mechanisms by which species respond to climate (6–8), particularly the potential for behavioral, plastic, or genetic adaptation. For example, most organisms are ectotherms, and many of them can exploit complex microclimatic mosaics to regulate their body temperatures behaviorally (9, 10). For a complete understanding of their response to climate change, we need to consider not only the physiological sensitivity of ectotherms to temperature but their capacity to buffer the impact of climate change through behavior, morphology, and physiology (11–14).

Recent research suggests that the physiological sensitivity of tropical ectotherms may render them more vulnerable to a given magnitude of climate warming than are temperate species (15), under the assumption that body temperature is equal to ambient air temperature. As the authors of that study point out, the actual impact will depend on the capacity of ectotherms to buffer air temperature rises through acclimation, adaptation, dispersal, and behavioral thermoregulation. The methods of biophysical ecology

provide a way to incorporate such buffering traits of organisms into predictions of climate change impacts (12, 13, 16–18). This is achieved by estimating microclimatic conditions (air and surface temperatures, radiation, wind speed, and humidity) available to an organism as a function of Geographic Information System (GIS) data sets on macroclimate, terrain, soil, and vegetation. Coupled energy- and mass-balance equations can then be solved to predict body temperature, metabolic rate, and water exchange as a function of available microclimates, the properties of the animal (e.g., reflectance, size, shape), and its behavioral repertoire.

Here, we apply a biophysical approach to assess the present thermoregulatory priorities of diurnal terrestrial ectotherms (i.e., the relative importance of staying cool vs. becoming warm) and how this balance may be affected by increases in air temperature. We consider diurnal species because they are more likely to encounter stressfully high body temperatures during their active period than are nocturnal species (7). We focus on Australia as an example because it encompasses a broad latitudinal range and the required climatic data (air temperature, humidity, cloud cover, and wind speed) are available at fine spatial resolution. Australia is also a center of diversity for terrestrial vertebrate ectotherms. We generalize our results to a global scale using the Worldclim air temperature data set (19).

Results and Discussion

Site-Specific Analyses. Our biophysical model accurately predicted fine-scale variation in the temperature of a small lizard-sized object under complex natural conditions [supporting information (SI) *Methods*, Figs. S1 and S2 and Table S1]. It also provides good correspondence with empirical data on potential and actual lizard body temperatures and activity patterns in tropical and temperate environments across different seasons (SI *Methods*, Fig. S3). We used this model to examine the frequency distributions of expected daytime body temperatures of a small (5 g) ectotherm throughout the year at 3 climatically distinct sites within Australia: a coastal tropical site (Darwin), an arid continental site (Alice Springs), and a coastal temperate site (Melbourne) (Fig. 1). The consequences of 3 different behavioral scenarios are illustrated: (i) sitting passively on the surface in full sun, (ii) sitting passively on the surface in deep (90%) shade, or (iii) actively thermoregulating from 20–40 °C (targeting a preferred temperature of 33 °C whenever possible) by moving in and out of shade or retreating below ground as a last resort (Fig. 1). This approach provides a means to determine the

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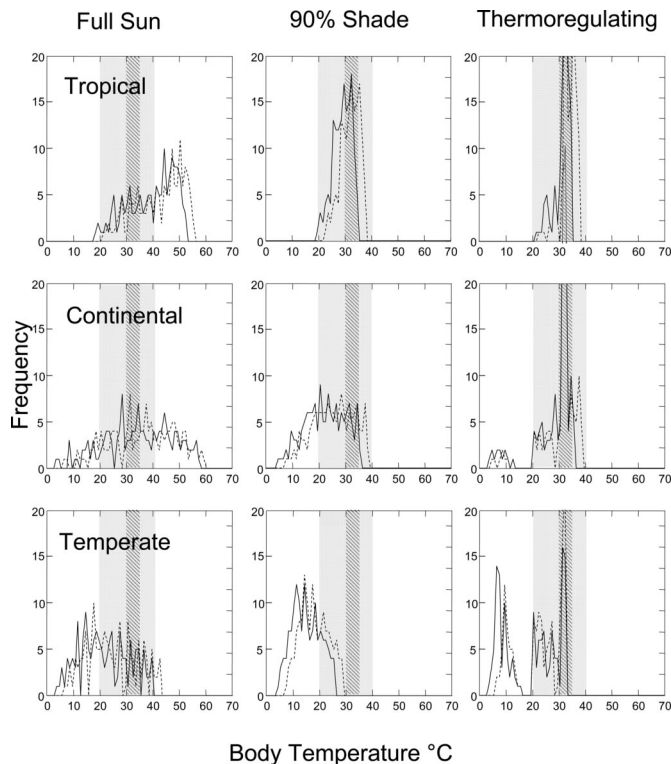


Fig. 1. Annual daytime body temperature distributions for ectotherms under current climatic conditions (solid line) and with a air temperature increase of 3.0 °C (dotted line) at 3 sites: Darwin (tropical), Alice Springs (continental), and Melbourne (temperate). Thermal distributions are shown for animals sitting passively in full sun or deep (90%) shade and for animals actively thermoregulating (target of 33.0 °C) by shuttling between sun and shade or by moving underground (inactive) as a last resort. The gray bar indicates a typical physiologically suitable temperature range for dry-skinned ectotherms (20–40 °C), whereas the hatched bar represents optimal temperatures (30–35 °C).

impact of thermoregulatory behavior (20) (for alternative approaches, see refs. 21 and 22).

It is useful to interpret these figures with respect to physiologically relevant reference points. The thermal performance curve of an ectotherm is typically skewed such that it drops sharply as temperature rises above the optimal value, but it drops more gradually as temperature shifts below the optimal value (23). Thus, ectotherms often operate at body temperatures close to their upper thermal limits. For many terrestrial ectotherms, performance is greatest at core temperatures above 20 °C, peaking at around 30–35 °C, and the vast majority will experience heat stress at temperatures above 40 °C (15, 24–28). For example, the mean critical thermal maximum (loss of righting response) for Australian skinks is 40.4 °C (28). Using these as general reference points, we observe that under current climatic conditions (Fig. 1, solid lines, and Fig. S4), ectotherms at the temperate site would not reach dangerously high core temperatures in open environments and would not reach optimal (30–35 °C) core temperatures in heavily shaded environments. Thus, behavioral thermoregulation at the temperate site largely would involve maintaining a position in the sun. In stark contrast, ectotherms at the tropical and continental sites would exceed stressfully high temperatures in open sunny environments 53% and 38% of the time, respectively, and would be at core temperatures from 30–35 °C only 42% and 19% of the time, respectively, in heavily shaded environments. Behavioral thermoregulation at these sites requires shuttling between sun and shade and significantly increases the time spent within optimal limits for species with high (>30 °C) thermal optima. (Although we have here

considered particular thermal thresholds that we consider to be representative of many ectotherms, the reader can easily envisage the consequences of different thresholds imposed on Fig. 1.)

How would an increase in air temperature affect these patterns? Under a moderate climate warming of 3.0 °C (Fig. 1, dashed lines), the potential for a passively behaving ectotherm in the open to overheat becomes considerably higher at the tropical (63% of time >40 °C) and continental (40% of time >40 °C) sites, with some risk for overheating also at the temperate site (5% of time >40 °C). Shaded environments remain suboptimal for the temperate site (0% of time at 30–35 °C, 38% of time at 20–40 °C) but are largely within optimal limits at the continental (19% of time at 30–35 °C, 73% of time at 20–40 °C) and tropical (48% of time at 30–35 °C, ca. 100% of time at 20–40 °C) sites. Thus, behavioral thermoregulation would require maintenance of a position in the shade at the tropical site and shuttling between sun and shade at the temperate and continental sites. Although a moderate warming would confer a considerable advantage at the temperate site (in terms of time spent within optimal limits, Fig. S3), the advantage is much less at the continental site and nonexistent at the tropical site. These conclusions parallel those of Deutsch et al. (15), yet are based on a very different analysis.

Continent-Wide Analyses. The availability of relevant climate data for Australia (monthly maximum and minimum values for air temperature, wind speed, and cloud cover) allowed us to extend these point estimates to assess the effects of climate warming on ectotherm body temperatures to the continental scale. We calculated the percentage of daylight hours a small ectotherm would spend below 30 °C in the sun (cold stress) and above 40 °C in the shade (heat stress) across Australia (Fig. 2A–F). Under the current climate, cold stress would only be an issue for a fraction of the continent, with ectotherms basking in full sun spending significant time (>3/4 of the daylight hours) below 30 °C at 2.3% of the locations sampled (Fig. 2A). This percentage would be reduced to only 0.8% under an increase in air temperature of 3.0 °C (Fig. 2D), suggesting a positive influence of climate warming.

The potential benefits of reduced cold stress must, however, be considered against the costs imposed by heat stress. Our analysis suggests that under the current climate, ectotherms in deep shade would experience core body temperatures above 40 °C across only 1% of the continent, in the arid northwest (Fig. 2B). However, the cost of failing to seek shade is high across most of the continent and can be quantified by the mean degrees deviation outside a threshold target temperature range of a passively behaving ectotherm (d_c) (21). Using a threshold of 40 °C, mean d_c in the sun is greater than 1 °C for over 80% of the Australian continent and reaches almost 6 °C in the northwest of the continent (Fig. 2C). Thus, the thermoregulatory priority for most Australian ectotherms under present climatic conditions, particularly in open sunny habitats, is staying cool. They must seek low temperatures during the day by seeking shade, going deep below ground, climbing into higher wind speeds (and lower air temperatures), or entering water (note that going below ground is a form of shade seeking, but it also exploits the buffering effect of the soil and restricts foraging ability). This situation would be considerably exacerbated by increases in air temperature; with an increase of 3.0 °C, core temperatures would rise above 40 °C in deep shade at some time of the year across 37% of Australia (Fig. 2E). Correspondingly, the percentage of the continent where d_c in the sun is more than 1 °C increases to over 90% of the continent and would approach 7 °C in some areas (Fig. 2F). Extreme weather events, which are not considered in our analysis, would exacerbate these risks (29).

Global Analyses. We extended our analyses to the global scale using the Worldclim estimates of monthly maximum and minimum air temperatures (19) (Fig. 3). These results are more tentative, because it was necessary to assume uniform

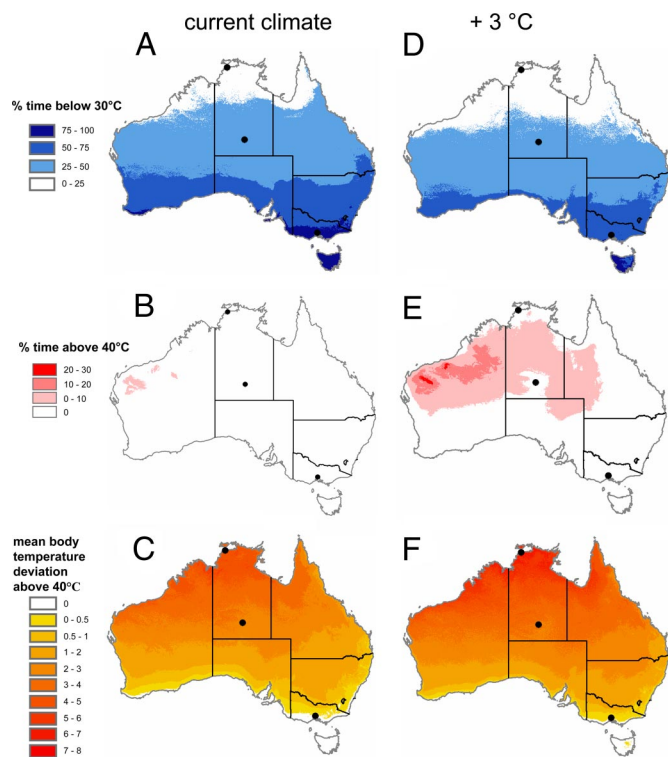


Fig. 2. Australia-wide calculations of the percent of total daylight hours that small terrestrial ectotherms are predicted to spend below 30 °C body temperature in the sun (A, D) and above 40 °C body temperature in the shade (B, E) under current climate and with an air temperature increase of 3.0 °C. (C, F) Also shown is the d_e above 40 °C of an ectotherm staying in full sun. A–C represents current climate and D–F represents a 3 °C warming. The locations of the 3 sites used for the single-site analyses (tropical, Darwin; continental, Alice Springs; and temperate, Melbourne) are indicated by black dots.

wind speeds and cloud cover across the globe in the absence of appropriate spatial data. Moreover, we found the Worldclim air temperatures to be biased upward compared with the Australia-specific data set (0.4 °C on average and up to 4.6 °C in January). Nonetheless, the results are broadly similar, and the global analysis suggests that for a very large portion of the planet, the thermoregulatory priority for terrestrial diurnal ectotherms is to avoid overheating. For example, mean d_e in the sun would rise above 1 °C for 66% of the globe (Fig. 3C). Although body temperature in deep shade would rise above 40 °C for only 1.6% of the globe, especially in northwest Africa and the Middle East (Fig. 3B), an air temperature rise of 3 °C would increase this to 18% of the globe (Fig. S5). As the word “cold-blooded” reflects, there is often a tendency to focus on the challenges that ectotherms face in attaining relatively high body temperatures, perhaps reflecting a bias in thermoregulatory studies toward cold-environment taxa (30). Yet, the much higher species diversity of ectotherms in tropical-zone than in temperate-zone habitats means that for most taxa, the primary thermoregulatory challenge is staying cool.

Seasonal Constraints, Shade Requirements, and Metabolic Costs. Although ectotherms such as reptiles can buffer changes in air temperature through behavioral thermoregulation, their capacity to do so is constrained by life cycle and habitat requirements as well as energy budgets. A major mechanism of behavioral thermoregulation in ectotherms is an altered daily and seasonal timing of activity (31, 32). Constraints on seasonal activity times for a thermoregulating ectotherm with the thermal activity range of the generic ectotherm considered in all previous analyses (20–40 °C)

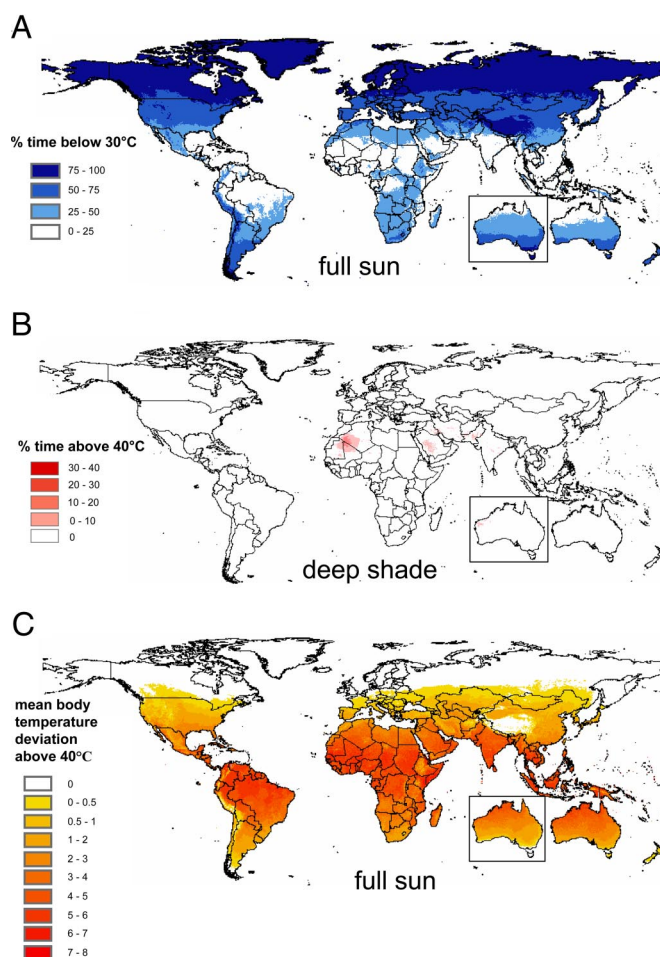


Fig. 3. Global calculations of the percent of total daylight hours that small terrestrial ectotherms are predicted to spend below 30 °C body temperature in the sun (A) and above 40 °C body temperature in the shade (B) under current air temperatures. (C) Also shown is the d_e above 40 °C of an ectotherm staying in full sun. These calculations assumed uniform daily cycles in wind speed (1.0–4.0 ms^{-1}) and uniform cloud cover (50%). The equivalent simulation based on Australia-specific data for air temperature, wind speed, and cloud cover is also shown (Inset).

are illustrated in Fig. 4A–C for each of the 3 Australian localities under the current climate and with a 3.0 °C increase in air temperature. For such an ectotherm, activity constraints largely reflect seasonal variations in day length for the tropical and continental sites under current climate, with winter activity significantly curtailed by temperature only at the temperate site (Fig. 4C, see also Fig. S3a and b). Under the climate warming scenario, potential activity over the cooler months is extended at the temperate site (Fig. 4C) and there is only minimal impact at the continental and tropical sites (Fig. 4A and B).

Tropical ectotherms often have narrower thermal sensitivities (15, 24), and a very different picture emerges for activity patterns if we consider a narrower activity range (28–33 °C) (Fig. 4D–F). Such an organism would also experience a longer activity season under the warming scenario at the temperate site (Fig. 4F). Yet, at the continental site, it would have to reduce activity considerably during the middle of the day in the summer months (Fig. 4E). Most dramatically, under the warming scenario at the tropical site, a “tropical” physiology would restrict much of its activity to the cooler months of the year (Fig. 4D), which is the dry season in this part of Australia. Depending on the breeding cycle of the animal, such changes in seasonal timing of activity may require concomitant changes in life history (33).

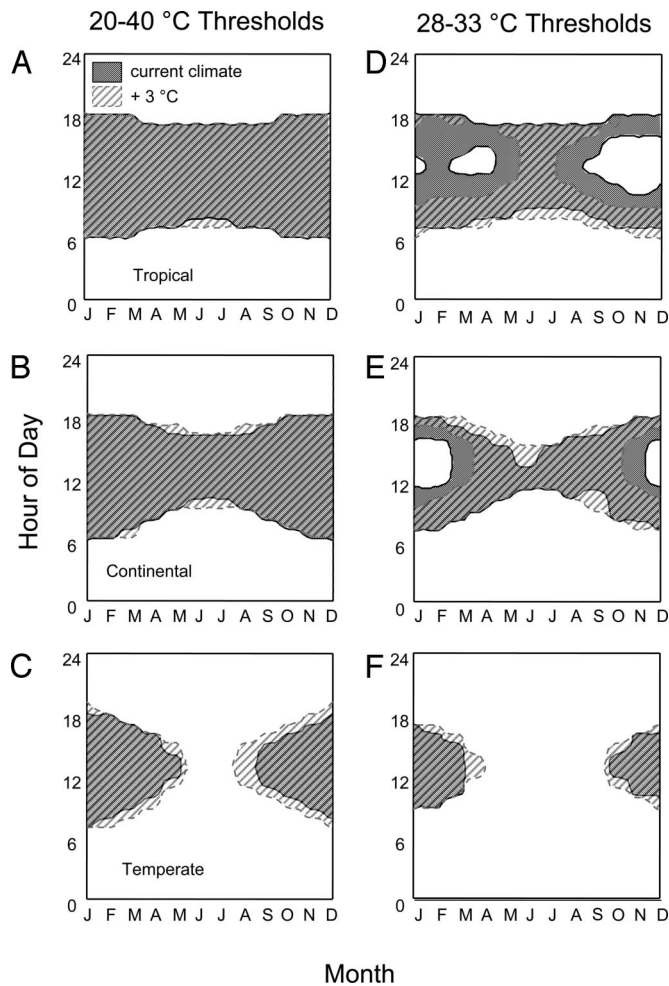


Fig. 4. Seasonal and daily activity constraints for behaviorally thermoregulating diurnal ectotherms with broad (20–40 °C) activity thresholds typical of temperate species (A–C) and narrow (28–33 °C) thresholds representative of some tropical species (D–F). Calculations are shown for 3 climatically distinct sites (tropical, Darwin; continental, Alice Springs; and temperate, Melbourne) under current climate and with an air temperature increase of 3.0 °C. Shaded regions indicate suitable times of day and months of the year for activity. Note that these calculations are for the Southern Hemisphere, with months ordered from January through December.

A second constraint is that an ectotherm’s ability to buffer increases in air temperature behaviorally depends on the availability of shade (or other cool environments or water). Fig. 5 indicates seasonal changes in the percentage of overhead shade required (i.e., behaviorally selected) for thermoregulation by our temperate-physiology ectotherm under the 2 climate scenarios for each of the 3 sites. Only moderate levels of shade are required for thermoregulation at the temperate site under either climate scenario (Fig. 5 C and F), but deep shade is needed at the continental (Fig. 5 B and E) and tropical (Fig. 5 A and D) sites if ectotherms are to maintain the same daily and seasonal patterns of activity under climate change (see also Fig. S3c).

Calculations of mean annual shade requirements for an ectotherm thermoregulating between 20 and 40 °C are shown for the globe in Fig. 6, in comparison to the availability of vegetation cover (mean annual normalized difference vegetation index), which provides a coarse index of shade availability (see Fig. S6 for seasonal patterns). From these figures, it is clear that there are some regions of mismatch between required and available shade, such as the deserts of northern Australia and northern Africa (insufficient

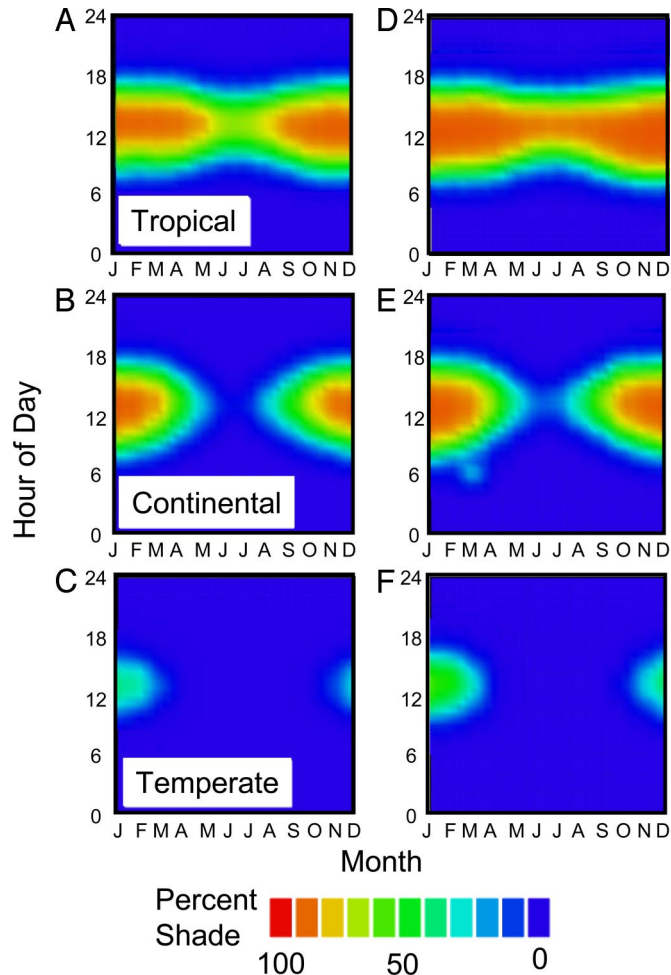


Fig. 5. Seasonal shade requirements for a behaviorally thermoregulating diurnal ectotherm active with a body temperatures from 20–40 °C and targeting a body temperature of 33 °C. Simulations initially assumed that the animal was in the open, and if body temperature exceeded 40 °C, shade was incremented in 1% steps until a suitable core body temperature was found. Calculations are shown for 3 climatically distinct sites (tropical, Darwin; continental, Alice Springs; and temperate, Melbourne) under current climate (A–C) and with an air temperature increase of 3.0 °C (D–F). Note that these calculations are for the Southern Hemisphere, with months ordered from January through December.

shade) and temperate Australia, North America, and Europe (too much shade). The costs of thermoregulation in terms of constraints on the times and places suitable for activity are likely to be very high in such areas. In contrast, heavy vegetation cover in many tropical areas would reduce the need for overt behavioral thermoregulation in many taxa (e.g., ref. 30). Human activities such as deforestation are dramatically altering the degree of shading available for thermoregulating ectotherms in tropical regions. Climate change will also alter vegetation cover through processes such as increased carbon dioxide (which encourages plant growth) and changed fire frequency, with potentially complex feedback loops (34). Thus, a full assessment of the extent to which ectotherms can buffer climate change through behavioral means requires knowledge not only of their life history constraints but of how climate change will affect habitat structure.

Finally, altered seasonal activity and shade availability under climate warming also may interact across a landscape to affect rates of energy acquisition. Although ectotherms can avoid overheating by reducing activity during warm periods of the year, their resting body temperatures, and hence metabolic rates, may be unavoidably high. Thus, thermal constrictions on potential foraging time under

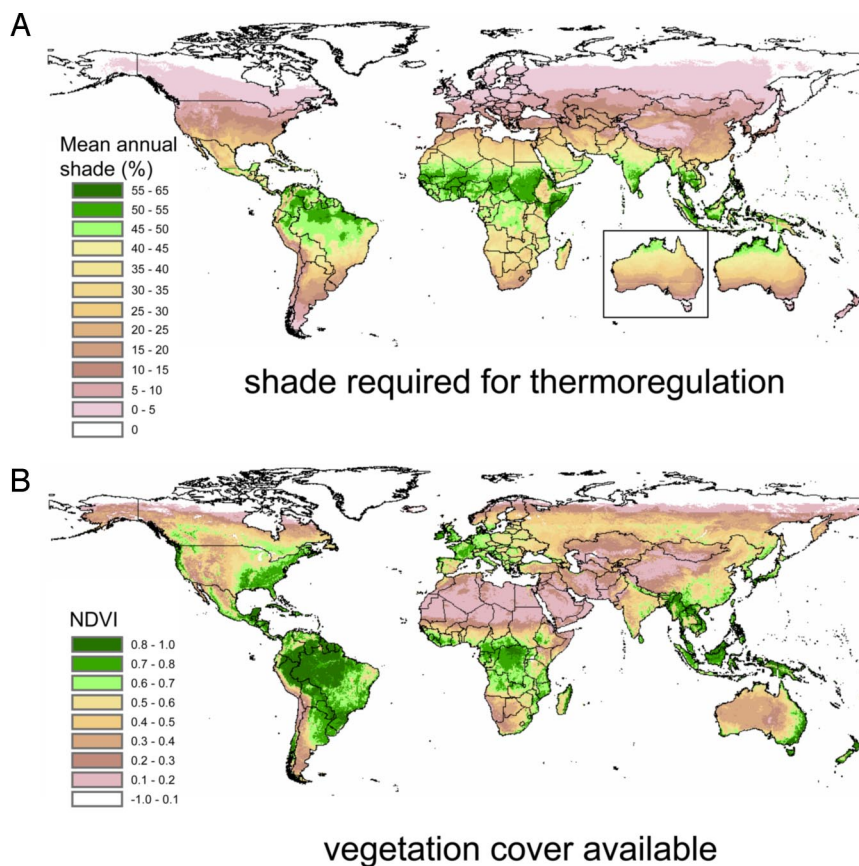


Fig. 6. Global shade requirements (i.e., behaviorally selected) during daylight hours averaged over the year for a small terrestrial ectotherm thermoregulating during the day between core body temperatures of 20 and 40 °C and targeting a body temperature of 33 °C (A) in comparison to the mean annual vegetation cover across the globe as represented by the normalized difference vegetation index (NDVI) (B). Simulations initially assumed that the animal was in the open, and if body temperature exceeded 40 °C, shade was incremented in 10% steps until a suitable core body temperature was found. Monthly comparisons can be found in Fig. S5.

climate warming may have an adverse impact on an ectotherm's energy budget. The magnitude of this impact will depend, in part, on the thermal performance curves underlying foraging success. As an illustration, we have considered the consequences of a warming of 3 °C on the required foraging rate (food requirements per distance traveled) of the monitor lizard, *Varanus rosenbergi*, in its native temperate range and in a tropical site (Table 1 and Table S2). We converted thermally imposed metabolic cost into grams of food (insects) (7) and divided this by the potential annual distance traveled as a function of core body temperature (see *SI Methods* for more details). At the temperate site, although climate warming increased annual food requirements because of the effect of increased body temperatures on metabolic demand, the required foraging rate changed little because of increased opportunities for

activity (Table 1). At the tropical site, consequences were more complex and varied with the availability of shade. A reduction in shade availability (from a maximum of 100% to 50% shade) lowered annual energy requirements, because animals were forced to retreat to burrows at midday in the warmer months. However, the resulting constriction on potential foraging distance caused an increase in required rates of food acquisition per distance traveled. For both shade scenarios, an increase in air temperature of 3 °C increased the required foraging rate, but this effect was more severe when shade availability was limited (Table 1).

Conclusions

Most species of terrestrial ectotherms live in tropical or desert areas, where thermoregulatory priorities are keeping cool rather than

Table 1. The effect of an air temperature rise of 3.0°C on the minimum required feeding rate needed to meet maintenance metabolic costs for a lizard (*Varanus rosenbergi*)

Maximum shade	Site	Current climate			Plus 3°C			Foraging rate, % change
		Food needed, kg/yr ⁻¹	Distance traveled, km/yr ⁻¹	Foraging rate, grams of food per km ⁻¹	Food needed, kg/yr ⁻¹	Distance traveled, km/yr ⁻¹	Foraging rate, grams of food per km ⁻¹	
100%	Temperate	3.7	318	11.6	5.1	427	11.9	103%
	Tropical	12.4	760	16.4	15.1	790	19.1	116%
50%	Temperate	3.7	318	11.6	5.1	427	11.9	103%
	Tropical	10.9	417	26.2	10.0	323	31.0	119%

Annual maintenance energy requirements are based on hourly core temperatures experienced, whereas annual distance moved is based on thermal constraints on activity. See *SI Methods* and Table S2 for further details.

staying warm. The efficacy of behavioral thermoregulation is tied strongly to the availability of shade, and hence to the nature and extent of vegetation cover. Although ectotherms in temperate areas often require low-shade environments for basking, ectotherms in tropical and temperate areas require high levels of shade to maintain above-ground activity. In temperate environments, climate warming may indeed increase potential activity time for many ectotherms. For tropical and desert taxa, however, potential activity may often be reduced and the potential for behavioral thermoregulation to buffer the impacts of climate warming on potential above-ground activity will be strongly contingent on the availability of shade. Indeed, depending on their thermal sensitivities, some tropical taxa may be vulnerable to heat stress even in deep shade under climate warming (15).

Although many of the impacts of global climate change on biodiversity will occur through altered interactions between species, those impacts will be driven fundamentally by the kinds of direct effects we have described. We must therefore incorporate information about mechanistic (cause-and-effect) pathways to predict the impact of climate change on organisms more accurately. Biophysical models achieve this aim by incorporating realistic levels of complexity in thermal environments as well as in behavioral, morphological, and physiological attributes that can modify the link between “ambient” temperature and ectotherm body temperature. Although we have considered terrestrial ectothermic animals only, biophysical analyses can readily be extended to endotherms, plants, and marine organisms (18, 35–37).

An important advantage of a mechanistic approach is that it identifies key traits that limit a species’ direct response to climate change, and hence may be under pressure to alter through plasticity or through evolutionary change. For example, our analysis emphasizes that the seasonal timing of activity (including reproductive activity) can be an important determinant of a species’ ability to tolerate climate change (38). If the phenology

of a species is labile, it can simply modify the times of onset and cessation of specific annual activities to accommodate to climate change. Without such lability, the feasible options to maintain population viability are greatly limited and likely will require substantial evolutionary shifts (33).

Our study also highlights the need for appropriate spatial data sets for biophysical analyses to be developed on a global scale. Key data currently absent or difficult to obtain include monthly variation in cloud cover and wind speed. For fine-scale analyses, monthly variation in vegetation cover and surface albedo are also of value. Such data sets, when coupled with biophysical models, will significantly improve our ability to predict and quantify climate warming impacts on biodiversity.

Materials and Methods

The biophysical models, collectively called Niche Mapper, include a microclimate model and an animal model (39). The microclimate model uses monthly macroclimatic data as well as topographic and location data to reconstruct hourly microclimatic conditions above and below ground under different levels of shade (7, 31, 39). These include hourly changes in solar and infrared radiation, humidity, surface temperatures, and subsoil temperatures as well as air temperature and wind speed profiles above ground. The animal model solves coupled energy and mass balance equations to find suitable core temperatures within the available microclimates as a function of empirically determined behavior, morphology, and physiology (39). This approach thus defines the fundamental niches of organisms from a thermal perspective and allows the niche to be mapped to a landscape (7, 18, 40).

The body temperature of terrestrial dry-skinned ectotherms largely reflects radiative and convective heat exchange, although conduction and evaporation can also be important. Ectotherms exposed to solar radiation can be tens of degrees above ambient air temperature, and tests of our biophysical model showed that it accurately (within 1 °C, on average) predicted such differentials at a fine temporal scale under a range of weather conditions (see *SI Methods*, *Table S1*, and *Figs. S1 and S2* for more details).

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