CLIMATE CHANGE

Climate change and the cost-of-living squeeze in desert lizards

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Climate warming can induce a cost-of-living "squeeze" in ectotherms by increasing energetic expenditures while reducing foraging gains. We used biophysical models (validated by 2685 field observations) to test this hypothesis for 10 ecologically diverse lizards in African and Australian deserts. Historical warming (1950–2020) has been more intense in Africa than in Australia, translating to an energetic squeeze for African diurnal species. Although no net impact on Australian diurnal species was observed, warming generated an energetic "relief" (by increasing foraging time) for nocturnal species. Future warming impacts will be more severe in Africa than in Australia, requiring increased rates of food intake (+10% per hour active for diurnal species). The effects of climate warming on desert lizard energy budgets will thus be species-specific but potentially predictable.

T he year 2023 was the hottest since global temperature records began (*1*). Existing and projected biodiversity impacts of such warming are generally considered broad and negative, but predicting the nature, direction, and magnitude of species-specific responses remains challenging (*2–5*).

The impacts of climate change on species result from extreme events (pulses) on a background of chronic change (press) (*6*). Research has focused on the potential exposure of ectotherms to pulses of extremely high body temperatures (*7–10*), but ectotherms can often use behavioral thermoregulation to buffer thermal extremes (*11, 12*). How climate warming affects the press of sustained increases in costs of living is potentially a more pervasive problem for ectotherms than is occasional exposure to extreme heat.

For ectotherms, the cost of living is dominated by the near-exponential effect of temperature on metabolic expenses, which are incurred whether active or resting (*12, 13*). Metabolic expenses of ectotherms will increase with warming temperatures, requiring more food (i.e., income) to counter rising costs (*14–16*). The ability of an ectotherm to find food is also temperature-sensitive because activity is limited by body temperature (*2, 17*). The joint influences of temperature on metabolic rate and potential foraging time lead to a required baseline feeding rate per hour of activity—the metabolic equivalent of a "minimum viable income"—that must be met to survive, with additional energy allocated for reproduction and growth. Depending on how species' potential foraging times, metabolic demands, and prey availability respond to warming, some scenarios with modest temperature increases could trap ectotherms in a cost-of-living "squeeze" (Fig. 1D), potentially reducing population densities and stabilities (*2, 14, 16*).

Quantifying the cost of living

How climate warming changes the cost of living depends not only on the magnitude of warming across space and time (*15, 17*) but also on species-specific biology (*9, 18–20*). Previous efforts to quantify such costs were correlative, using maximum air temperature to predict activity restriction, and did not explicitly quantify species-specific energy requirements (*2, 21, 22*). However, quantitative models of biophysical ecology, based on first principles from physics and physiology (*23*), quantify how ecology (microhabitat), behavior (foraging), and physiology (metabolic rates) interact via body temperature to affect the energetic impacts of warming.

Desert ectotherms are vulnerable to the cost-of-living squeeze because food and cool refuges are scarce in arid habitats, especially in summer (*24*). In this work, we applied biophysical models to address cost-of-living budgets under past and future climates for 10 species of desert lizards from two continents, focusing on the Kgalagadi Desert (Kalahari Desert) in Southern Africa (*24–26*) and the Great Victoria Desert in Australia (*24, 27*) (Fig. 1). We chose these sites so that we could ground-truth our predictions with long-term datasets (2685 observations) that span more than 40 years (fig. S1 and table S1) and include local ambient temperature, field body temperature, activity patterns, and microhabitat use (*24*) (e.g., Fig. 1 and table S2).

Model evaluation

Using the ERA5 [European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis v5] reanalysis weather dataset (*28*) to drive a microclimate model (*29*), we accurately predicted historical air temperatures (T_a) that were originally measured directly at our remote sites (biases as measured by mean prediction differences from observed temperatures of ±1°C, deviation as measured by root mean squared error of ~2.5°C; figs. S2 and S3, table S3, and data S1). Microclimate outputs were further evaluated by extracting daily minimum and maximum air temperatures for comparison with local weather station observations, yielding similar accuracy and precision (data S2). Using microclimate model outputs to drive an ectotherm heat exchange model (*30*), we predicted body temperature measurements (T_b) with biases within 1°C and an average deviation from observations of 3.1°C (figs. S2 and S3, table S4, and data S1).

We compared the predicted metabolic rates with observed field metabolic rates (doubly labeled water) for a Kgalagadi Desert diurnal species [*Pedioplanis* (previously *Eremias*) *lineoocellata*] (*26*). The observed field metabolic rate [739 ± 68 (SD) J day^{-1}] was nearly identical to the biophysical model prediction [735 ± 79 (SD) J day^{-1}] for the same location and sample period (see supplementary materials for calculations, November 1981, Af_L; fig. S1). Next, we compared predicted feeding rates with observed rates for the Australian ant specialist *Moloch horridus* (*31*). Our feeding rate prediction of 837 ants per day (see supplementary materials) aligns with the observed field range of 750 to 1500 ants per day (*Iridomyrmex* spp.).

The precision and accuracy of our predictions are high given the coarseness of the ERA5 forcing data (horizontal resolution ~30 km), the variability of lizard behavior and microhabitats, and the measurement error of field body temperatures. Thus, our biophysical models should enable reliable estimates of the cost-of-living consequences of past and future warming.

Historical warming patterns

Having validated our modeling approach, we assessed how foraging time constraints, energy demands, and thus the cost of living have varied among continents, seasons, and species in the recent past (1950–2020) and into the future [+2° and +4°C, TerraClimate database (*32*)] (Fig. 1). We considered summer and winter separately to bracket yearly extremes and included spring to capture the energetically critical reproductive period (*2, 24*).

Consistent with coarser global analyses (*33–35*), we found that arid regions have undergone more severe warming over the past seven decades (1950–2020) in southern Africa than in western Australia. Air temperatures increased by 1.19°C in the Kgalagadi Desert (0.17°C decade^{-1}) but only by 0.49°C (0.07°C decade^{-1}) in the Great Victoria Desert (Fig. 2, A and B). Warming in the Kgalagadi Desert was strongest in

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summer and weakest in winter, and this pattern was reversed in the Great Victoria Desert (Fig. 2, A and B). These between-continent differences arise from regional variation in atmospheric circulation patterns that drive spatial heterogeneity in temperature and influence local soil moisture and vegetation characteristics (34, 35).
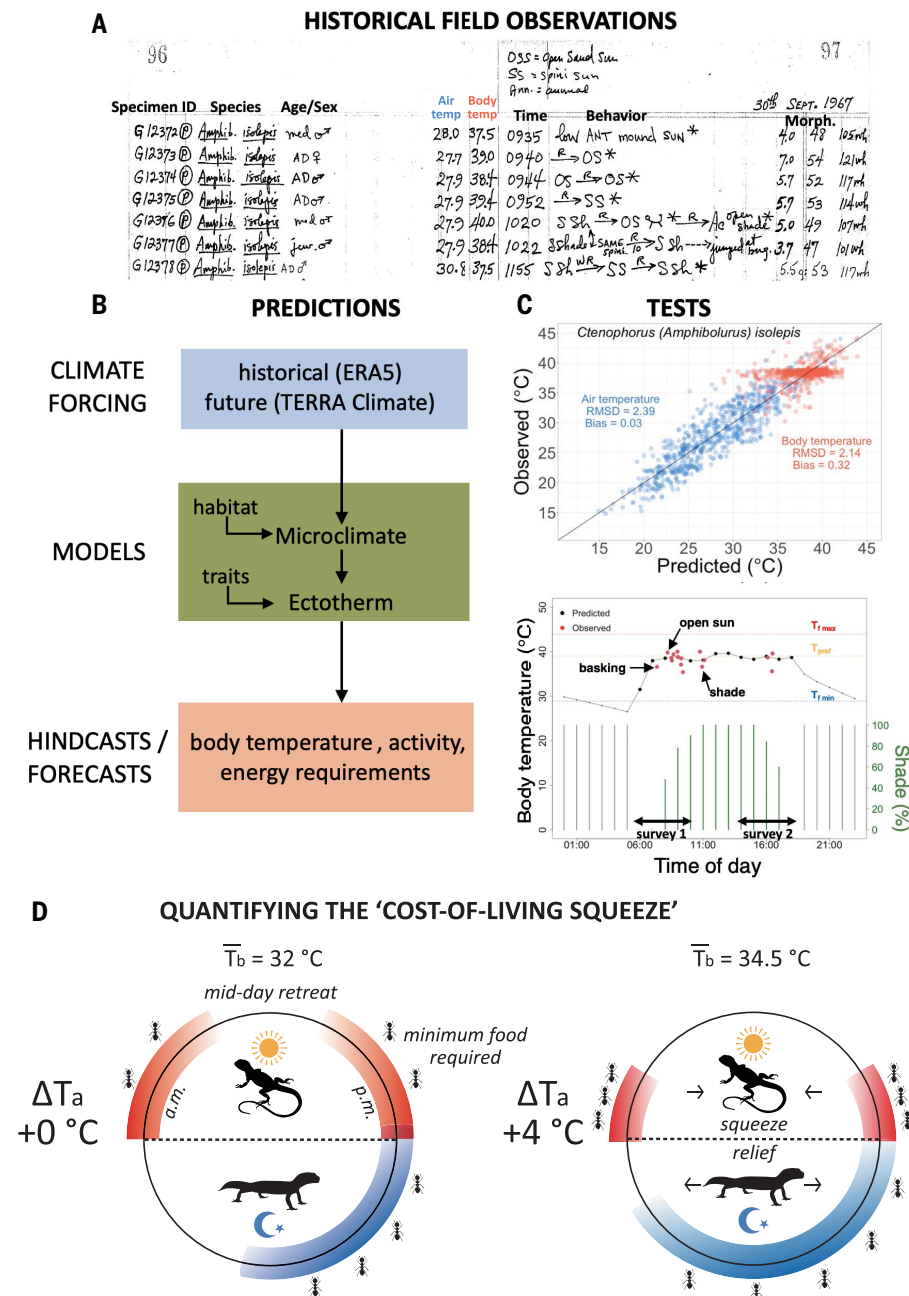

Fig. 1. Schema used for combining historical datasets (1966–2010) with biophysical models to test how environmental, physiological, and behavioral processes can change through time. (**A** to **C**) Detailed historical field notes (A) were used to test how well microclimate and ectotherm simulations (B) predict air temperature [(C), top], body temperature [(C), top], and behaviors [(C), bottom] across all seasons using the example of *Ctenophorus isolepis* in the Great Victorian Desert. Field observations of behaviors [arrows in (C), bottom] are shown in relation to body temperature and predicted shade (green). Thermal preference (T_{pref} in orange) and foraging thresholds ($T_{f,min}$ in blue, $T_{f,max}$ in red) are shown for reference [(C), bottom]. RMSD, root mean square deviation. (**D**) Models validated with field data were run across 70 years (1950–2020) and for two future warming climate scenarios (+2° and +4°C). Differences in the cost-of-living squeeze were compared between diurnal and nocturnal species under different climate scenarios. Colored traces on the edge of the circles indicate available foraging times in relation to food (red, diurnal; blue, nocturnal) and how squeeze can change under present conditions (left) and +4°C warming (right).

Historical body temperature responses

The continental divergence in historical thermal trends led to different responses in lizard body temperatures that were continent and species specific (Fig. 2) when the biophysical models were tuned for species-specific ecological traits (diurnality, shade seeking, retreating underground, climbing) (figs. S4 and S5 and data S1). In the Kgalagadi Desert, historical warming was predicted to have increased all body temperature estimates (minimum, mean, maximum) regardless of the lizard species or season (Fig. 2A). In the Great Victoria Desert, however, the relatively modest historical warming led to relatively small increases in body temperatures (Fig. 2B). Moreover, in the Great Victoria Desert, body temperatures were predicted to have increased in winter, but not in summer. In the spring, in the Great Victoria Desert, four of five species saw no change in mean body temperature.

Increased air temperature mapped to body temperature in nonadditive ways that varied by species and with the specific air temperature metric used, indicating that body temperature predictions derived from biophysical models cannot be uniformly scaled on air temperature (Fig. 2). This underscores the importance of species-specific models, because even small differences in natural history or behavior can result in markedly different thermal responses. For example, mean air temperature warming of 0.17°C decade^{-1} in the Kgalagadi Desert translated to a change in mean body temperature of only ~0.11°C decade^{-1} for all five species considered. The more substantial change in maximum air temperature of 0.29°C decade^{-1} translated to only ~0.10°C decade^{-1} in maximum body temperature. This smaller change in maximum body temperature resulted from behavioral thermoregulation, because the model allows the lizards to seek shade, climb, or retreat below ground to avoid high temperatures. Additionally, significant warming during spring in the Great Victoria Desert led to significant increases in body temperature for only two of the five species, whereas in summer, there was no directional change in either air or body temperature. This illustrates how the complex relationship between air temperature and body temperature is driven by species-specific behavioral strategies in response to regional warming and seasonal variations. Thus, thermoregulatory behavior can buffer temperature extremes during the day (36) and over decadal-scale climate warming (11, 12), but behavioral buffering can also reduce selection for geographic variation (37).

Historical activity responses

Lizards can become inactive and seek cooler retreats when ambient temperatures are excessively high (2, 38). In the Kgalagadi Desert, net
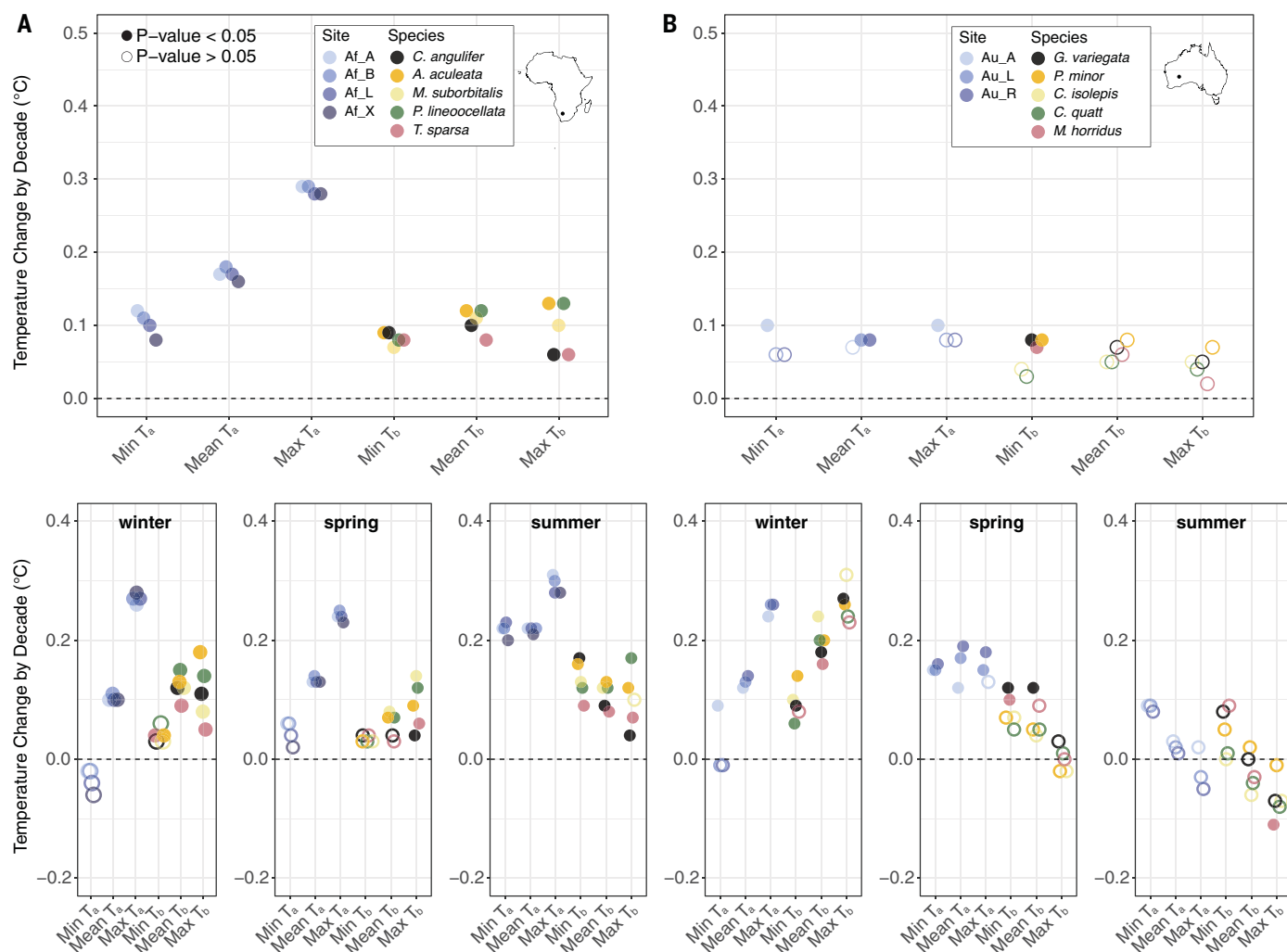
Fig. 2. Historical decadal changes in calculated air temperature and body temperature of lizards at field locations based on historical climate data.
(**A** and **B**) Historical decadal changes in calculated air temperature (T_a) and calculated body temperature of lizards (T_b) at field locations in the Kgalagadi Desert (A) and the Great Victorian Desert (B) based on historical climate data (ERA5) between 1950 and 2020. Filled points indicate statistically significant ($P < 0.05$) linear regressions with time. T_a and T_b data (minimum, mean, maximum) were summarized by day and then by year (top panels) or by season (bottom panels). Points are jittered for visual clarity. Values above the dashed line indicate an overall increase in the response variable with time and vice versa. *A. aculeata, Agama aculeata; C. angulifer, Chondrodactylus angulifer; C. isolepis, Ctenophorus isolepis; C. quatt, Ctenotus quattuordecimlineatus; G. variegata, Gehyra variegata; M. horridus, Moloch horridus; M. suborbitalis, Meroles suborbitalis; P. lineoocellata, Pedioplanis lineoocellata; P. minor, Pogona minor; T. sparsa, Trachylepis sparsa.*

foraging time decreased by only 2.9 hours decade^{-1} between 1950 and 2020 (Fig. 3A). The most extreme decline in foraging time occurred in summer (7.4 hours decade^{-1}) but was nearly balanced by activity gains in winter (5.1 hours decade^{-1}) (Fig. 3A). In the Great Victoria Desert, net foraging time increased by 12.4 hours decade^{-1} (Fig. 3A) between 1950 and 2020, where activity gains in cool seasons were greater than losses in the summer (Fig. 3A). Notably, the largest differences in net foraging times were between nocturnal (+19.7 hours decade^{-1}; black circles in Fig. 3A) and diurnal species (+1 hour decade^{-1}).

Spring and summer are the biologically critical seasons (*2, 24*) when energetic demands for reproduction are acute for desert lizards (*39*). Foraging time was reduced during this window for many of the species (Fig. 3A). However, these differences range only from –7 to +6 min of change per month. These small shifts in activity times predicted by our biophysical models are consistent with the magnitude of shifts predicted by a previous correlative model (fig. S6) (*2*). The latter model was used to argue that historical climate warming of this magnitude has tipped the total hours of restricted activity over thresholds sufficient to cause widespread extinctions (*2*). Our analyses allow for lizards to use behavior to exploit thermal heterogeneity and thus buffer thermal environments (*40, 41*), but this only affects the total hours available and not the historical change in hours of restriction (fig. S6). Together, these analyses of activity constraints demonstrate that recent warming, on the order of <0.2°C decade^{-1}, has had only a modest impact on the potential for activity and that this varies from positive to negative depending on season and on species' activity patterns (diurnal or nocturnal).

Historical energetic responses

Even though warming should cause only minor reductions in activity durations, it could still cause an energetic squeeze if metabolic rates increase because of elevated body temperature (*14*). Mass-specific metabolic rate (J g^{-1} decade^{-1}) increased in four of five Kgalagadi Desert species
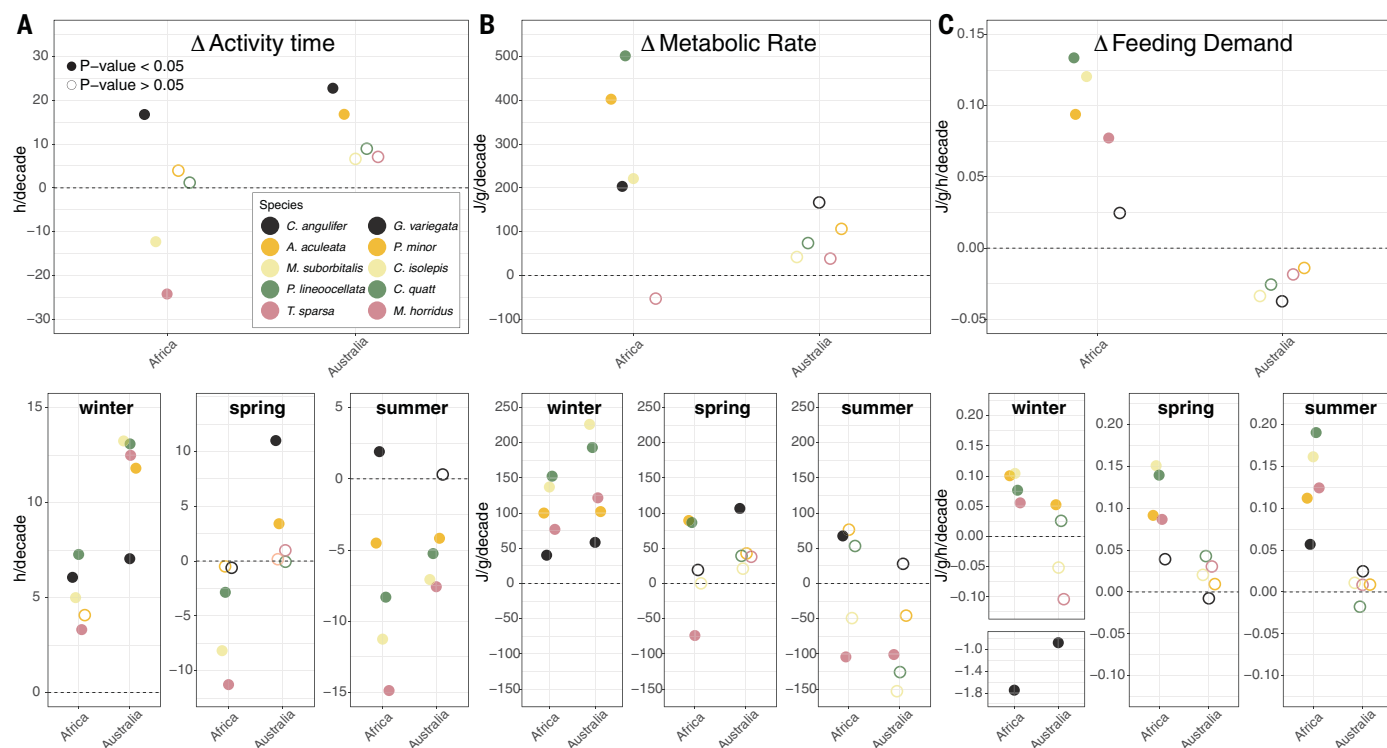
Fig. 3. Historical decadal changes in foraging activity, metabolic rate, and feeding demand. (**A** to **C**) Historical decadal changes in foraging activity (A), metabolic rate (B), and feeding demand (C) for lizards at field locations in the Kgalagadi Desert and the Great Victorian Desert. Data are based on historical climate data (ERA5) between 1950 and 2020. Filled points indicate statistically significant ($P < 0.05$) linear regressions with time. Response variables were summed for each year (top panels) or per season (bottom panels). Feeding demand was derived by taking the annual sum of metabolic rate (J g^{-1}) and dividing it by the sum of foraging time (hours). Values above the dashed line indicate an overall increase in the response variable with time and vice versa.

(Fig. 3B). Between 1950 and 2020, the increase in mean net metabolic rate for Kgalagadi Desert species was 2.9 times higher than that for Australian species. This difference was primarily driven by increased metabolic costs for Kgalagadi Desert diurnal species (Fig. 3B). The net metabolic rate of the Great Victoria Desert species did not increase significantly between 1950 and 2020 (Fig. 3B). Metabolic rate trended upward during winter on both continents (~121 J $decade^{-1}$) but varied by species in other seasons (Fig. 3B). The metabolic rate of nocturnal species on both continents (black circles in Fig. 3) increased significantly only during seasons when mean T_b had increased significantly (Fig. 2).

Feeding demand (J g^{-1} $hour^{-1}$) was calculated by taking the annual or seasonal total metabolic rate (J g^{-1}) and dividing it by the total foraging time (hours). For example, in January 2010, the thermal conditions allowed the Australian ant specialist, *M. horridus*, to forage for a total of 262 hours. Within this period, an individual (39 g) must consume enough food to meet its monthly maintenance energy costs (4.2 kJ g^{-1}). This translates to a foraging requirement of approximately 16 J g^{-1} $hour^{-1}$ or 153 ants per active hour, closely resembling field metabolic rate and feeding rates observed in natural settings (*31*).

Feeding demand differed markedly for species between continents (Fig. 3C). For diurnal species in the Kgalagadi Desert, the increase in mean net feeding demand between 1950 and 2020 was 5.0 times higher than that of diurnal species in the Great Victoria Desert (Fig. 3C). Higher feeding demands for diurnal species in the Kgalagadi Desert can be attributed to decreases in foraging times (Fig. 3A) with concurrent increases in metabolic demands (Fig. 3B). Seasonal feeding demand significantly increased for all diurnal species in the Kgalagadi Desert, but seasonal changes were minimal for diurnal species in the Great Victoria Desert (Fig. 3C). Net feeding demand did not change for nocturnal species on either continent (black circles in Fig. 3C) and decreased during winter seasons because warmer temperatures enabled nocturnal species to forage for longer periods (Fig. 3A).

Future warming scenario

Under the two climate change scenarios (+2° and +4°C global mean), warming of both air temperature and body temperature was greater in the Kgalagadi Desert than in the Great Victoria Desert (Fig. 4, A and B). We collapsed species into nocturnal versus diurnal foraging categories for future warming comparisons because the impact of warming on activity, metabolic rate,

and feeding demand was dominated by this circadian difference (fig. S7). Regardless of the scenario or continent, warming was predicted to escalate metabolic costs (J g^{-1} $year^{-1}$) for diurnal and nocturnal species, but increased foraging times acted to offset feeding demand for nocturnal species (Fig. 5). Although behavioral adjustments allow diurnal species to avoid dangerously high body temperatures in extreme conditions (Fig. 4), constrained foraging times will further intensify feeding demand for diurnal species (Fig. 5, A and C).

The cumulative impact of climate warming on feeding demand is particularly critical when considering the time of day at which species can feed, the regions in which they are found, and the number of prey items they require. For example, a projected 4°C increase in global air temperature will result in a 21% rise in hourly feeding demand for Kgalagadi Desert diurnal species and a 10% rise for Great Victoria Desert diurnal species (table S5). Furthermore, these pressures should be most acute during the spring reproductive periods for diurnal species in both deserts (*2, 24*) (table S6). By contrast, for nocturnal species, climate warming reduces feeding demand under the +2°C scenario; under the +4°C scenario, feeding demand remains largely unchanged overall (table S5)
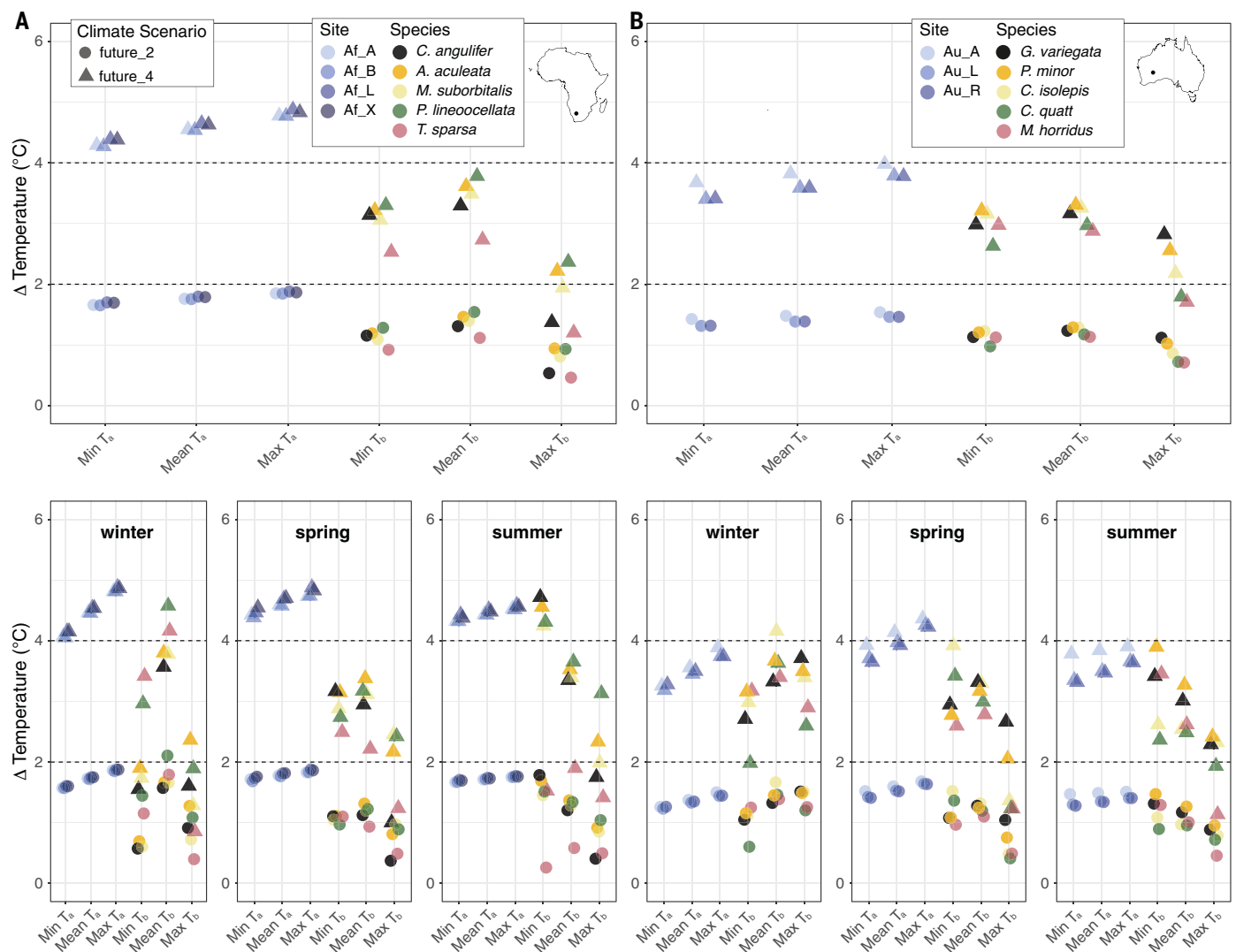
Fig. 4. Comparisons of the effects of global climate change scenarios on the magnitude of changes in air temperature and thermoregulating lizard body temperature. (**A** and **B**) Comparisons of the effects of global climate change scenarios (+2° and +4°C) on the magnitude of changes in air temperature and thermoregulating lizard body temperature at field locations in the Kgalagadi Desert (A) and the Great Victorian Desert (B). Climate warming scenarios (circles, +2°C; triangles, +4°C) were imposed on recent ERA5 reanalysis weather data (1985 to 2015), which were used as the baseline for comparison. Dashed lines serve as a reference for a 1:1 translation of global +2° and +4°C warming to regional air temperature and lizard body temperature.

but does increase during summer seasons, when foraging times become restricted (Fig. 5A). Thus, climate warming may incur a cost-of-living relief that is season-specific for nocturnal species by reducing feeding demands under moderate warming while imposing a rather continuous cost-of-living squeeze for diurnal species, especially in the Kgalagadi Desert (Fig. 5D and tables S5 to S9).

Implications of a cost-of-living squeeze

Contrary to a prior study (*2*), our analyses show that recent warming has caused only modest reductions in foraging times and net energy gains. Continued warming will increasingly constrict the energetic expenditures, posing substantial sustainability challenges for ecto-

therm populations depending on their activity windows and the habitats they use. Historical analyses of the frequency of empty guts of lizards at our sites suggest that diurnal species "run on empty" only ~5 to 10% of the time and nocturnal species ~25% of the time (*42*). Yet a temperate Australian grassland lizard required 40% more energy to offset increased metabolic demands and reduced activity as a result of climate warming (*22*), indicating that species in desert environments may need even greater energy compensation where thermal refugia and prey items are limited. Moderate warming scenarios (+2°C) may thus pose energetic challenges for many diurnal species, but warming may benefit nocturnal species (*19, 43*). Under a +4°C global warming scenario, even nocturnal

species may need to contend with rapidly increasing metabolic demands (Fig. 5D).

We emphasize that our analyses are conservative. The deleterious effects of warming on energy budgets will be compounded by other factors associated with climate change, including temporal mismatches between activity and food availability (especially during breeding seasons) (*44, 45*), as well as increased water requirements (due to enhanced evaporation) in arid environments (*46*). Importantly, we show that energy budget pressures are greatest in spring and summer (Figs. 3 and 5), which is the reproductive window for most species (*2, 24, 27*). Global declines in insect abundance have been attributed to climate change (*47*), which could compound the effects of reduced
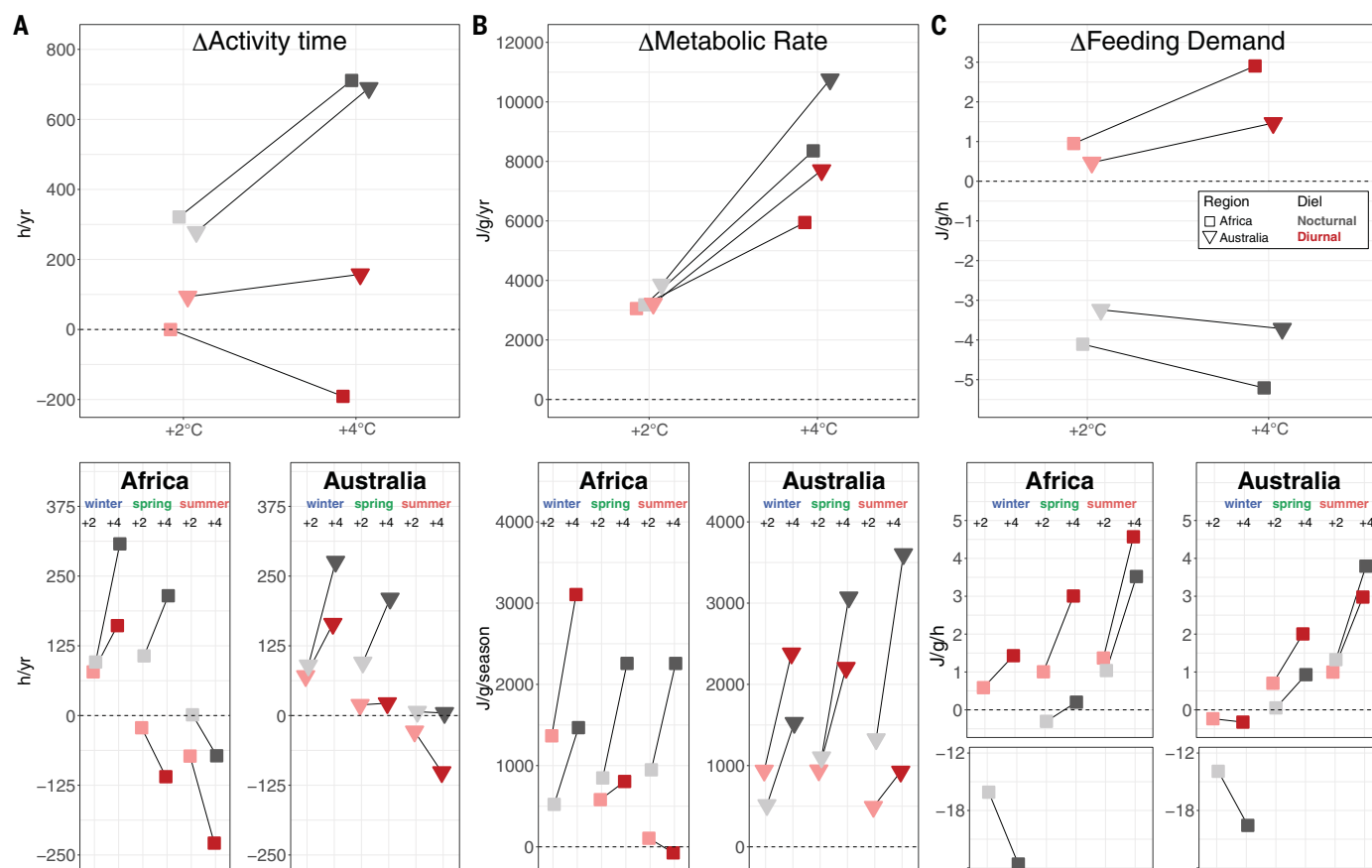
Fig. 5. Foraging activity, metabolic rate, and feeding demand change when comparing future climate scenarios for nocturnal and diurnal ectotherms.
(**A** to **C**) Foraging activity (A), metabolic rate (B), and feeding demand (C) change when comparing future climate scenarios (+2° and +4°C) for nocturnal (gray) and diurnal (red) ectotherms in the Kgalagadi Desert and the Great Victorian Desert. Responses to climate warming of +2° and +4°C were simulated using TerraClimate

data from 1985 to 2015. The change in response variables was derived from the overall average difference between predictions under recent conditions and under each future climate scenario for each species. Feeding demand was estimated as described in Fig. 3. These data were then averaged for each activity category (nocturnal or diurnal) across species. Values above the dashed line indicate an overall increase in the response variable with time and vice versa.

foraging times in diurnal lizards, especially during reproductive seasons. Species might reduce their preferred body temperature (T_{pref}) (*48*) or decrease metabolism to conserve energy under low-food conditions (*16*). Should energy gains fall below the minimum viable income, the cost-of-living squeeze will tighten and result in population declines that will increase the risk of local extirpation.

Our results suggest that the direction and magnitude of climate warming impacts on ectotherms will vary by continent and local environmental conditions, implying that risks will differ across biomes. Tropical species, for instance, are highly vulnerable because many species operate at body temperatures near their thermal limits (*14, 49*); slight temperature increases are thus potentially detrimental to their energy budgets. Temperate ectotherms might initially benefit from moderate warming because of broader thermal safety margins, but this advantage will diminish if extreme temperatures become more frequent (*15, 22*).

Species found across steep elevational gradients are expected to shift ranges to higher elevations with warming, which will present new challenges as available up-slope habitats shrink (*49*).

The cost-of-living squeeze under both historical and projected warming represents a press stress on energy budgets. Regional heat waves are predicted to increase in intensity, frequency, and duration (*50*), and such pulse events will further contribute to the cost of living for ectotherms (*6, 14, 16*). Our calculations suggest that diurnal species are likely to be vulnerable to these pulse heat wave events because of the high metabolic burden and increased activity required to meet feeding demands or costs associated with thermoregulatory behaviors, rather than direct exposure to extreme heat.

Overall, our analyses illustrate how the direct impacts of climate warming on desert lizards—and potentially many other ectotherms—could lead to cost-of-living pressures, primarily be-

cause of reduced energy budgets rather than reduced activity times (*2*). However, the impact of warming, whether harmful or beneficial, will vary owing to the extent of local temperature increases and the specific behaviors and ecology of each species (*24*). The potential for biophysical models to infer such diverse responses (*23*) is supported by our findings that model predictions are highly congruent with historical field observations of empirical metabolic rate, feeding rate, and body temperatures, and, thus, such approaches should be implemented in future conservation planning.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S9
Tables S1 to S10
References (51–71)
MDAR Reproducibility Checklist
Data S1 and S2

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