Diminishing returns limit energetic costs of climate change

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Abstract. Changes in the time available for organisms to maintain physiologically preferred temperatures (thermal opportunity) is a primary mechanism by which climate change impacts the fitness and population dynamics of organisms. Yet, it is unclear whether losses or gains in thermal opportunity result in proportional changes in rates of energy procurement and use. We experimentally quantified lizard food consumption and energy assimilation at different durations of thermal opportunity. We incorporated these data in an individual-based model of foraging and digestion in lizards to explore the implications of nonlinear responses to shifts in thermal opportunity across a wide geographic range. Our model predicts that shifts in thermal opportunities resulting from climate change alter energy intake primarily through digestion rather than feeding, because simulated lizards were able to fill their gut faster than they can digest their food. Moreover, since rates of energy assimilation decelerate with increasing thermal opportunity, shifts in daily energetic assimilation would depend on the previous opportunity for thermoregulation. In particular, the same changes in thermal opportunity will have little impact on lizards from warm locations, while having a large impact on lizards from cold locations where thermoregulation is possible for only a few hours each day. Energy expenditure followed spatial patterns in thermal opportunity, with greater annual energy expenditure occurring at warmer locations. Our model predicts that lizards will spend more energy under climate change by maintaining higher body temperatures and remaining active longer. However, the predicted changes in energy assimilation following climate change greatly exceeded the predicted increases in energy expenditure. Simple models, which assume constant rates of energy gain during activity, will potentially mislead efforts to understand and predict the biological impacts of climate change.

Key words: assimilation; climate; digestion; foraging; lizards; Sceloporus; *temperature.*

INTRODUCTION

Because climate change has shifted the distributions (Parmesan 2007) and phenologies (Root et al. 2003) of species, biologists have become increasingly concerned with predicting future responses (Kearney and Porter 2009, Buckley et al. 2010). By quantifying the times when animals can thermoregulate accurately, one can predict the potential to forage, digest, grow, and reproduce (Buckley et al. 2010, Kearney 2011, Gunderson and Leal 2016). Under climate change, a warmer environment may limit the amount of time at optimal temperatures (thermal opportunity) for growth and reproduction (Sinervo et al. 2010, Kearney 2013). Sinervo et al. (2010), for example, suggested that global warming decreases thermal opportunities for lizards around the globe, leading to reduced food intake and reproductive success, eventually leading to local extinctions. On the other hand, warming may offer more opportunities for thermoregulation in colder environments, increasing the fitness of species at high latitudes (Buckley 2008, Kearney 2013, Gunderson

and Leal 2016, Levy et al. 2016*b*) or altitudes (Huang et al. 2013, 2014).

To understand and predict shifts in energetics and phenology, we must consider how climate constrains the time and energy available for reproduction (Levy et al. 2016*b*). This task is easier said than done, because many physiological and ecological processes scale nonlinearly with the time or energy available to organisms. Consequently, the benefits or costs of shifts in thermal opportunity differ among populations that currently experience different climates. Energy intake, through foraging and digestion, is an excellent example of a process that depends nonlinearly on temperature and time (Angilletta 2001*a*). At low body temperatures, a small degree of warming would confer a substantially greater rate of energy gain. By contrast, at high body temperature, the same degree of warming would confer little increase or even decrease the rate of energy gain. Even if an animal were to remain at its optimal temperature indefinitely, the rate of energy gain would decrease over time. For example, an animal that forages for twice as long, does not necessarily gain twice the energy, since the animal might spend more time searching for food as its density decreases (Stephens and Krebs 1986). In such cases, a decrease in the time available for foraging might impose only a marginal cost. Similarly, the rate of energy assimilation also decreases with

the time. Most of the ingested food is assimilated in the first few hours of digestion because the sequential processes of digestion, absorption, and excretion create a physiological bottleneck (Grant and Porter 1992). This phenomenon causes diminishing energetic returns on the time invested in thermoregulation and activity. For example, lizards grew faster when allowed to thermoregulate for 10 h d^{-1} instead of 6 h d^{-1}, but no faster when allowed to thermoregulate for 14 h d^{-1} (Adolph and Porter 1993, Sinervo and Adolph 1994). Hence, an animal with a moderate period of thermoregulation will do nearly as well as one with a longer period.

Because foraging and digestion occur only at certain body temperatures, energy balance requires opportunities to thermoregulate, without paying costs that exceed the benefit (e.g., energy loss or predation risk). As climates warm, thermal opportunity for temperate species should expand (Deutsch et al. 2008, Levy et al. 2016b), enabling ectotherms to spend more time at preferred body temperatures. Whether extended thermal opportunity will enhance the energy budget of an organism depends on its current thermal opportunities. If an animal currently spends only a few hours per day at its preferred temperature, a little warming would confer a large energetic benefit. However, if a species currently spends many hours at its preferred temperature each day, a little warming would either confer a small energetic benefit or impose a small energetic loss (Dillon et al. 2010). For widespread species, these impacts should vary systematically along a latitudinal or altitudinal cline; animals at higher latitudes or altitudes should be more likely to benefit energetically from extended hours at preferred temperatures in a warming climate. Importantly, impacts of climate change will also depend on other factors that vary regionally, such as densities of vegetation and prey.

Using an individual-based model, we explored the impacts of projected changes in climate on the energy budgets of lizards throughout a wide geographic range. First, we experimentally quantified food consumption and energy assimilation at different durations at preferred body temperatures. Then, we used the data to parameterize our model and simulate foraging and assimilation in past and future climates. We show that shifts in thermal opportunities may alter their energy intake primarily through energy assimilation, and less by shifts in food consumption, since lizards need only a few hours of foraging to fill their gut, but may benefit from long periods of energy assimilation. Climate change will limit opportunities for foraging in warm places while expanding opportunities in cold places, but diminishing energetic returns from digestion will weaken effects on energy assimilation.

METHODS

Modeling energy gain

We modeled the relationships between time budgets and energetics, and how shifts in time budgets due to climate change may affect feeding and assimilation rates in North American lizards. We developed an individual-based model of an adult lizard (snout-vent length = 63 mm, mass = 8.9 g) based on a *Sceloporus* model, developed by Buckley (2008) and expanded by Levy et al. (2015, 2016b). We used a published set of hourly microclimates (Levy et al. 2016a) to calculate the operative temperatures of lizards (i.e., the steady state temperature in a particular microclimate, Bakken 1992) on surfaces ranging from 0 to 100% shade. The microclimates represent 11,407 locations across the United States and Mexico with a spatial resolution of 36 × 36 km for the past (1980–2000) and the future (2080–2100, assuming a radiative forcing of +8.5 W m^{-2} at year 2100, RCP 8.5 scenario). At each location, the dataset includes thermal conditions at various heights above and below the ground, and under different levels of shade. In natural habitats, distances between these microhabitats are often a few meters, enabling animals to shuttle between sun and shade. Every hour in the dataset, we tracked the feeding and digestion of the lizard based on potential body temperatures (T_b). Hourly air temperatures, radiative loads, and wind speeds were used to calculate the lizard's operative temperature in each microhabitat and whether this temperature enabled foraging and digestion. We calculated these body temperatures as

$$T_{b,t} = T_{b,t-1} + \Delta T_b, \tag{1}$$

by solving heat-exchange equations in Fei et al. (2012). The parameters and equations used are described in Appendix S1: Table S1. We selected a small value for Δt (120 s) to yield small values of ΔT_b, which enhanced the stability of the model. In the model, the lizard is able to forage and assimilate energy whenever it can attain a body temperature between 29.4° and 36.3°C (central 80% of field body temperature; Angilletta 2001a). For simplicity, we use the term *thermal opportunity* to refer to the number of hours that a lizard could attain a body temperature in this range. During the period of thermal opportunity, we assumed that a lizard maintains its preferred temperature (33.1°C; Angilletta 2001a) by shuttling between exposed and shaded microclimates. Outside of the period of thermal opportunity, we assigned the lizard the closest available temperature to its preferred temperature. During the night, we assumed that lizards rest on the ground surface or under full cover (Personal observations, M. J. Angilletta, unpublished). During winter, if activity was not possible for more than two weeks, we assumed that lizards retreated to a 12-cm burrow.

For each location in our domain, we calculated (1) time budgets as the number of foraging and assimilation hours, and (2) the amount of energy a lizard could ingest and assimilate (kJ h^{-1}). In each location, we also compared between current and future climates, by calculating the difference in the mean near-surface (3-cm above ground, 50% shade cover) temperature during 1980–2000 and 2080–2100.

Lizards were assumed to forage when their body temperature allowed activity. To determine the feeding rates for each hour of foraging, we first calculated the maximal velocity (v, m s^{-1}) of the lizard as

$$\log_{10}(v) = 0.044 + 0.2 \cdot \log_{10}(M_b), \quad (2)$$

based on published observations where M_b equaled the mass of a lizard (Van Damme and Vanhooydonck 2001). Then, assuming lizards forage at 70% of their maximal velocity (Irschick and Losos 1998), we calculated the distance traveled (d, m) in one second as $0.7 \times v \times 1$ s. As in Buckley's analysis (Buckley 2008), we assumed that the energy content of an insect equals 30.12 J, the rate of insect encounter assuming foraging along a line equals 0.005 insects m^{-1} s^{-1} (Jones et al. 1987, Niewiarowski and Roosenburg 1993), 50% of insects encountered are captured by a foraging lizard, and lizards assimilate 76% of ingested energy (Angilletta 2001a). Hence, at each hour, the energy intake ($e_{i,h}$) was

$$e_{i,h}(\text{J h}^{-1}) = 30.12(\text{J insect}^{-1}) \cdot 0.005(\text{insect m}^{-1}\text{s}^{-1})$$
$$\cdot 0.5 \cdot 0.76 \cdot d(\text{m}) \cdot 3600(\text{s h}^{-1}). \quad (3)$$

As the lizards feed, we modeled how feeding filled the gut, reducing the available space ($J_{\text{available}}$, kJ):

$$J_{\text{available}} = C_{\text{max}} - J_{\text{daily max}}, \quad (4)$$

where C_{max} (kJ) is the maximal gut space (2.55 kJ d^{-1}, based on our laboratory measurements) and $J_{\text{daily max}}$ (kJ) is the amount of energy consumed that day.

Lizards assimilated energy whenever they had food in their gut and body temperature was between 29.4° and 36.3°C. This range corresponds to the central 80% of field body temperatures, because digestion proceeds slowly at higher or lower temperatures (Angilletta 2001a). Each day in the simulation, the rate of energy assimilation was derived from our statistical analysis (see results for more details), suggesting that the rate of energy assimilation (E) depended on the interaction of maximal consumption and time budget:

$$E(\text{kJ}) = a \cdot C_{\text{max}} \cdot \log(t_d + 1), \quad (5)$$

where a is a constant fitted to our empirical data, t_d is the duration of assimilation since the first feeding event of that day. Assimilation rates did not exceed the energetic content of the gut:

$$E_{\text{assim}}(\text{kJ}) = \begin{cases} E & \text{when} \quad E \le J_{\text{gut}} \\ J_{\text{gut}} & \text{when} \quad E > J_{\text{gut}} \end{cases} \quad (6)$$

where J_{gut} is the amount of energy (kJ) in the gut.

We estimated energy expenditure from experimental studies of metabolic rate. Resting metabolic rate (RMR, J s^{-1}) was modeled according to Angilletta (2001b):

$$\ln(\text{RMR}) = -10.0 + 0.51 \cdot \log(M_b) + 0.12 \cdot T_b. \quad (7)$$

We multiplied RMR by 1.5 to yield the resting metabolic rate of a digesting lizard (Roe et al. 2005) and then multiplied this rate by 2 to yield the metabolic rate of a foraging lizard (Bennett 1982). To calculate the energy balance of lizards, we subtracted the estimates of energy expenditure from the energy assimilated.

Parameterizing the assimilation model

To parameterize the function relating thermal opportunity to energy assimilation, we conducted experiments with lizards from three population of the *Sceloporus undulatus* complex (Leache 2009): *Sceloporus tristichus* from Pinal County, Arizona (33.308117, −111.049417) and Grand County, Utah (38.26044, 109.6962); and *Sceloporus consobrinus* from Ogallala and *Keith Counties,* Nebraska (41.336767, −102.008993). Lizards were collected in the spring of 2011 and transferred to an animal care facility at Arizona State University. Each lizard was housed in a plastic terrarium partially heated by Flexwatt$^{\text{TM}}$ heat tape (Calorique, West Wareham, MA, USA), allowing lizards to freely thermoregulate. Prior to our experiment, lizards had unlimited access to water and were fed crickets (*Acheta domestica*) three times per week.

Our experiment controlled the duration at which lizards experienced their preferred body temperature. We placed lizards in incubators with diel cycles of temperature and light that simulated three levels of thermal opportunity (6L:18D [$n = 25$], 10L:14D [$n = 21$], and 14L:10D [$n = 19$] light cycles). The temperature during the light phase (33.1°C) was chosen to match the body temperature of lizards during thermoregulation in natural environments and thermal gradients (Buckley et al. 2015). This temperature also maximized the rate of energy assimilation by *S. undulatus* when food is plentiful (Angilletta 2001a). The temperature during dark phase (20°C) was chosen to severely limit the rate of energy assimilation. In a fourth treatment, lizards ($n = 17$) were exposed to the preferred temperature for 24 h d^{-1} and a 14L:10D light cycle. We used a stratified design to randomly assign each lizard to a thermal treatment. In all treatments, lizards were kept in plastic terraria (32 cm × 38 cm × 63 cm) at 70% humidity. Feeding occurred about 2 h after the start of each light phase.

We measured rates of feeding and assimilation during the experiment. First, lizards were fasted for 48 h. Then, each lizard was offered a cricket that was injected with a non-digestible, fluorescent dye (Scientific Marking Materials, Seattle, WA, USA). We used this dye to mark the initial passing of fecal matter from the cricket consumed at the beginning of the trial. We inspected feces daily until this dye was observed. At that point, we began collecting all feces and urates. The trial lasted for 7 d, during which we fed lizards as many crickets as they would consume within 2 h of each morning. More frequent feeding would likely have resulted in a similar

energy intake, because these lizards required about 48 h to digest a single cricket and consume multiple crickets when feeding (Angilletta 2001*a*). In fact, a previous experiment reported a similar rate of consumption by the same species in less than an hour per day for feeding (Angilletta 2001*a*). Water was provided daily by misting the sides of the terraria.

After 7 d, lizards were fed a second cricket marked with fluorescent dye (a different color than the first dye). Because all crickets were weighed to the nearest 0.1 mg, we could calculate the total mass of food consumed between the two marked crickets. Feces were checked daily until the second marker appeared. Feces and urates collected between the two markers resulted from the known mass of food ingested during the trial. Lizards that refused to eat for several days or failed to eat one of the marked crickets were removed from the study.

We used bomb calorimetry to estimate the energy consumed and excreted by each lizard during the trial. A sample of 29 crickets was dried and combusted in a Parr 1425 semimicro bomb calorimeter to determine their caloric density. We then used the mean water content (25%) and the mean energetic density (22.187 kJ g^{-1}) to convert the wet mass consumed to the equivalent number of Joules. We also determined energetic content of the feces and urates produced by each lizard. For each lizard, we calculated feeding rates (kJ d^{-1}) as the energy consumed as crickets, and assimilation rates (kJ d^{-1}) as the difference between the feeding rates and the energy excreted as feces and urates.

Analysis of assimilation data

We used our experimental data to estimate two functions in the individual-based model. The first function related the body length (snout-vent length) of a lizard to its maximal daily consumption of food. Food consumption was the dependent variable and body length was a continuous independent variable. This model was fitted to estimates of food consumption by lizards exposed to their preferred temperature for 24 h d^{-1}, because this treatment enabled the fastest digestion and hence the most consumption (but see Whelan and Brown 2005 for a discussion of factors that affect gut constraints). We used a log link function and a gamma distribution of residual variation.

The second function related the hours of thermal opportunity to the rate of energy assimilation. Energy assimilation was the dependent variable, population of lizards was a categorical predictor, and the log[(h d^{-1}) + 1] was a continuous predictor (see Eq. 5). We forced the intercept of the model to equal zero, because lizards should assimilate little or no energy without access to preferred temperatures. We used an identity link function and a gamma distribution of residual variation. Based on Akaike Information Criterion (Burnham and Anderson 2002), we removed the population factor since it didn't contribute to the fit of the model

(ΔAIC = 3.74). All data analysis was done in R version 3.2.3 (R Development Core Team 2011) using the *glm* function of the *nlme* library (Pinheiro et al. 2011). Descriptive statistics are means and standard deviation estimated from the final model.

Sensitivity analysis

To explore how predictions of our model depend on our assumptions, we altered the values of three parameters and quantified the effect on dependent variables. Specifically, we quantified how time budgets and rates of energy intake may differ when (1) decreasing the density of food by 50%, and when (2) assimilation rates (E in Eq. 5) are assumed to either be constant over time (estimated as $E(t_d = 24)/24 \cdot t_d$) or decelerating faster than in our observations (estimated as $E(t_d = 24) \cdot (1 - e^{-0.3 \cdot t_d})$). Moreover, we quantified how energy expenditure and energy balance may differ when increasing the costs of activity by 50% to account for possible costs of foraging and thermoregulation (three times the RMR). Although all of these assumptions potentially vary among locations, such sensitivity analyses can help understand the effects of such assumptions at different conditions. Moreover, although Bennett and Dawson (1976) reported a maximal five-fold increase between standard metabolic rates and active metabolic rates, these rates were measured during induced activity in the laboratory and spontaneous activity in the field should be significantly lower. Unless otherwise noted, we report each prediction of the model as the mean of values among locations, plus or minus the standard deviation.

RESULTS

Our experiment confirmed the expected diminishing relationship between thermal opportunity and energy assimilation. Lizards that spent more hours per day at their preferred temperature assimilated more energy, but this effect diminished as access to the preferred temperature approached 24 h per day (Fig. 1). The most likely statistical model resulted in the following relationship among thermal opportunity (t_d), maximal gut size (C_{max}, kJ d^{-1}), and energy assimilation (E, kJ d^{-1}): $E = 0.115 \cdot C_{max} \cdot \log(t_d + 1)$. Variation in body size within and among populations contributed indirectly to energy assimilation, because maximal gut size increased exponentially with body length (snout-vent length, SVL, mm): $\ln(C_{max}) = -2.23 + 0.05*SVL$ (Fig. 1). These functions were used to model the impacts of climate on energy gain in past and future climates.

Our simulations characterized a latitudinal gradient in thermal opportunity, where lizards from lower latitudes could spend more time at their preferred temperature and assimilate more energy each year (Appendix S1: Fig. S1). However, simulated lizards spent much less time foraging than digesting (Appendix S1: Fig. S2). Hence, time spent at the preferred temperature did not
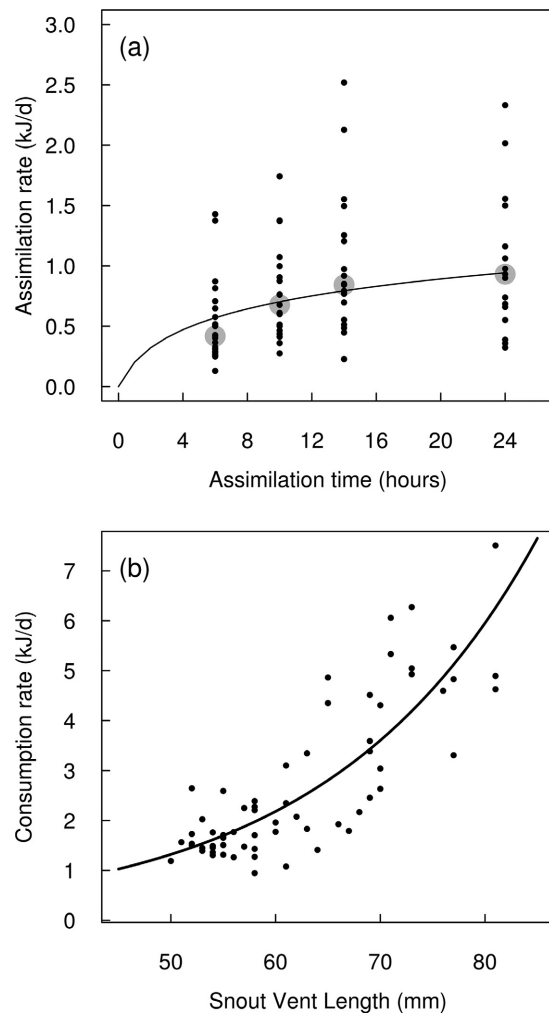
Fig. 1. Our empirical observations (black points) support the hypothesis of diminishing assimilation rates as the daily duration of time suitable for assimilation increases (panel a, $n = 82$). Bigger lizards assimilated more energy per day. We show the relationship between Snout-Vent length and daily assimilation rates for lizards exposed to 24-h of their preferred temperature (panel b, $n = 65$). In panel a, grey circles represent the median of the observations for each assimilation time. In both panels, the line is the fitted curve used in the bio-energetic model.

directly translate to animals eating more each day. In particular, a lizard needed only 2.3 h each day ($\pm$ 0.1 h d^{-1}) to fill its gut, regardless of the climate at its location (Fig. 2). When we halved the density of food, a lizard in any location needed to forage only one more hour per day (0.93 ± 0.05 h) to fill its gut (Appendix S1: Figs. S3, S4). Thus, foraging time was nearly independent of climate, at least in the range of conditions that we explored with our model.

In contrast to foraging, energy assimilation through digestion and absorption proceeded slowly, such that every additional hour of thermal opportunity contributed to energy assimilation when animals had ingested food.

In the past climate (1980–2000), lizards from warm locations could attain preferred temperatures up to 348 d per year for as many as 6.2 h per day (Fig. 3; Appendix S1: Fig. S2). When switching to the climate projected for 2080–2100 (RCP 8.5), a lizard either gained or lost thermal opportunity (Fig. 3a, b), depending on its current climate. The number of days with at least one hour of thermal opportunity increased by 21.1 d per year ($\pm$ 9.0 d yr^{-1}) at 99% of locations. At the remaining locations, the number of days decreased by 0.7 d per year ($\pm$ 1.1 d yr^{-1}). The daily duration of thermal opportunity increased in 86% of the locations, by 0.8 h per day ($\pm$ 0.4 h d^{-1}); these locations were relatively cool in the past climate, having a mean annual temperature of 10.0°C ($\pm$ 9.0°C). At the remaining locations, with a mean annual temperature of 14.6°C ($\pm$ 4.5°C), thermal opportunity decreased by 0.3 h per day ($\pm$ 0.2 h d^{-1}). Thus, simulated climate change enabled phenological shifts in activity, with lizards gaining energy on more days during the summer at cold locations or more days during the winter at warm locations (Fig. 3a, b).

Given the decelerating relationship between thermal opportunity and energy assimilation, additional time at the preferred temperature would benefit lizards in cold locations more than lizards in warm locations, which had more time for digestion each day in the past climate (Fig. 4). Although lizards in the hottest locations spent less time at their preferred temperatures throughout the year, they still had time to digest most of the food in their gut each day. For example, in warm locations (mean temperature above 20°C), a decrease in thermal opportunity of 5 h per day reduces energy assimilation by 0.23 kJ per day ($\pm$ 0.01 kJ yr^{-1}). By contrast, 5 additional hours of thermal opportunity for digestion increased energy assimilation in cold locations (mean temperature below 15°C) by 0.39 kJ per day ($\pm$ 0.03 kJ yr^{-1}) (Figs. 3c, 4). This asymmetry between the impacts of warming depended on the rate at which energy assimilation decelerated with thermal opportunity (Appendix S1: Figs. S6, S7) and disappeared when energy assimilation increased linearly with thermal opportunity (Appendix S1: Figs. S8, S9).

Energy expenditure followed spatial patterns in thermal opportunity, with greater annual energy expenditure occurring at warmer locations. Annual energy expenditure increased under the scenarios of climate change, because lizards maintained higher body temperatures and engaged in more activity (Appendix S1: Fig. S10); overall, energy expenditure increased by 3.56 kJ per year ($\pm$ 0.74 kJ yr^{-1}) when switching from the past climate to the future climate (Appendix S1: Fig. S10). Greater energetic demands occurred mostly as a response to the phenological changes in thermoregulatory behavior based on shifts in thermal opportunity (Fig. 3d). Energy expenditure increased mostly in colder regions during summer and in warmer regions during winter.

The predicted increase in energy assimilation following climate change greatly exceeded the predicted increase in
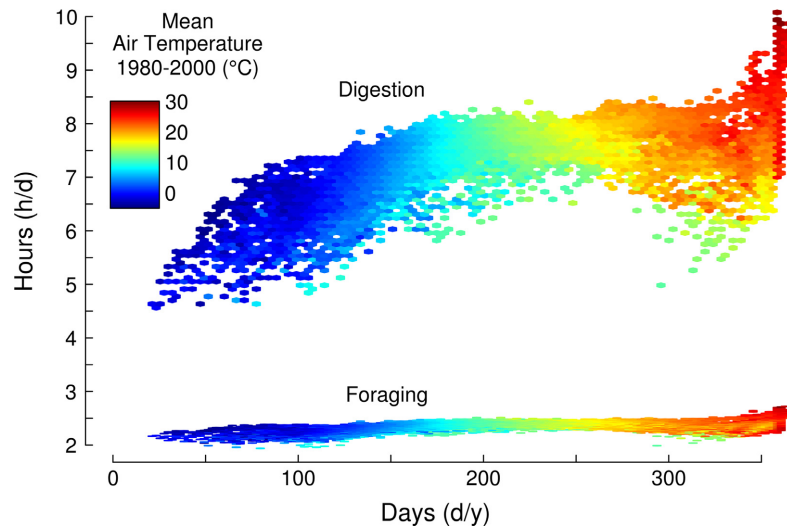
Fig. 2. Thermal opportunity is strongly affected by climate, especially across days. Within each day, thermal opportunity for foraging is not affected by climate since lizards can fill their gut within 2–2.5 h of feeding. Climate significantly affects the daily thermal opportunities for digestion, however, since digestion is a relatively long process. The color of the each point indicates the mean air temperature at one or more locations. See Appendix S1: Fig. S4 for predictions when the abundance of insects is smaller than in our initial parameterization.

energy expenditure (Fig. 3; Appendix S1: Fig. S10). With our initial parametrization, annual energy expenditure was only 21% of annual energy assimilation (± 5%) (Appendix S1: Fig. S11a, b). When we imposed a greater cost of activity (+50%), energy expenditure was still only 23% of energy assimilation (± 5%) (Appendix S1: Fig. S11c, d). Thus, energy balance in past or future climates was dominated by thermal effects on energy assimilation (Fig. 3e; Appendix S1: Fig. S10). Consequently, daily shifts in energy balance of lizards reflected the decelerating relationship between thermal opportunity and energy assimilation (Fig. 4). The high correlation between energy balance and energy assimilation persisted when we simulated lizards with a greater cost of activity (Appendix S1: Figs. S6, S7).

DISCUSSION

Time is an ecological resource that enables animals to feed, grow, and reproduce. Based on our model, climate change will limit opportunities for such activities in warm places while expanding opportunities in cold places. The model sheds light on the mechanisms by which phenological shifts might affect energy gain by animals, and hence influence the dynamics of populations and communities. In particular, diminishing returns during digestion affect changes in energy assimilation as the climate warms. Animals require more time at preferred temperatures to digest and absorb food than to consume it, regardless of body temperature (Angilletta 2001a). Thus, energy assimilation strongly depends on the opportunity to thermoregulate after feeding (reviewed by Huey 1982, Waldschmidt et al. 1987).

Our model considers a scenario in which foraging depends only on body temperature and food density. However, foraging costs and benefits depend on other factors (e.g., water costs, competition, and predation risk) that reduce feeding (Dunham 1980, Lima and Dill 1990, Brown et al. 1999, Levy et al. 2016c), as well as prey density that may differ across locations and seasons with natural variations in temperature, rainfall, and vegetation. Incorporating such factors in future models should enhance our ability to predict impacts of climate change. For example, the marginal value of water may increase during a drought, causing lizards to forage during cooler hours of the day. Such responses were modeled in lizards (Kearney et al. 2013) and observed in other animals (Kotler et al. 1998, Hochman and Kotler 2006, Shrader et al. 2008, Levy et al. 2016c). Moreover, although *Sceloporus* lizards are sit-and-wait predators, different modes of foraging (e.g., active-searching) may incur different exposures to competition and predation as well as different energetic and hydric costs. Thus, factors that affect foraging may vary across ecological communities and shift under global change (Mack et al. 2000, Tylianakis et al. 2008, Hobbs et al. 2009), bringing further complexity to an energy balance model. Alternatively, the low energy demands of ectotherms may enable them to survive with only short bursts of foraging (e.g., Lagarde et al. 2003). Therefore, the time required for reptiles to digest food far exceeds the time required to forage, such that a digestive bottleneck limits feeding more than opportunities to forage (Congdon 1989). In our simulations, lizards needed only a few hours of foraging to fill their gut, and could do so even when warming restricted foraging time or halved prey density. For
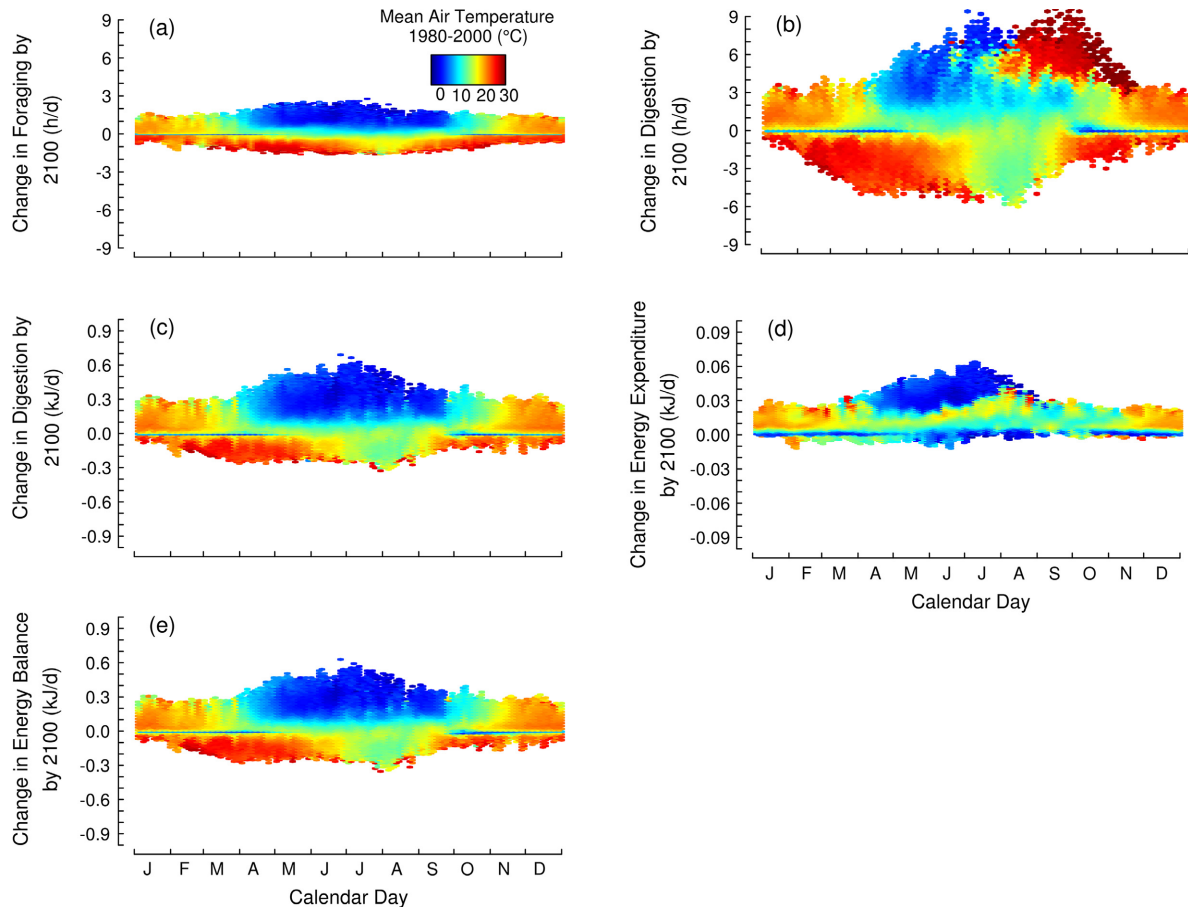
Fig. 3. Phenological impacts of climate change on opportunities for energy intake. The effect of warming on energy intake depends on the current temperature and the time of year. At cool locations, lizards will have more time for foraging (a) and digestion (b) during summer in future climate than in the past climate. At warm locations, however, lizards will have more opportunities for foraging (a) and digestion (b) in winter, but less in the spring and summer and fall. Climate change may offer more opportunity for digestion in the fall at few warm locations, where night temperatures may enable digestion. The effect of warming on energy assimilation matches the effect on the thermal opportunities for digestion (c). Given the deceleration of assimilation rates with thermal opportunity, the daily decreases in assimilation rates at warm locations are relatively small compared to the daily increases in assimilation rates that result from the phenological shifts. Daily energy expenditure of lizards will increase throughout the year, according to phenological increases in activity (d). Although metabolism proceeds more rapidly in a warmer climate, phenological shifts in energy balance will mostly resemble shifts in energy assimilation (e). The color of the each point indicates the mean air temperature at one or more locations. See Appendix S1: Fig. S5 for changes in foraging time budgets when the abundance of insects is smaller than in our initial parameterization. See Appendix S1: Figs. S7 and S9 for shifts in daily assimilation rates when lizards have faster rates of decelerating returns than in our initial parameterization, or have constant rate of assimilation, respectively.

these reasons, we think the major patterns described by our model would hold up under a wider range of conditions that we have considered.

Significant ecological patterns could emerge when the rate of energy assimilation decelerates with increasing thermal opportunity. Although lizards assimilated substantial energy when warmed for just a few hours per day, the rate of energy assimilation decelerated when lizards warmed for longer periods. Previous experiments have shown that lizards require more than 20 h of continuous exposure to their preferred temperature to pass a single item of food (Beaupre et al. 1993, Angilletta 2001*a*). The longest period of exposure would be 10 and

14 h per day in past and future climates, respectively. Therefore, feeding could occur multiple times per day but food remains in the gut for multiple days. Consequently, the annual energy budget in our simulations depended more on the number of days that lizards could feed and digest than on the number of hours per day. Thermoregulation depends on access to preferred microclimates (Porter et al. 1973, Grant and Dunham 1988, Bashey and Dunham 1997, Basson et al. *in press*), and just a few hours of effective thermoregulation during the day enables an individual to acquire enough energy to meet its energetic demands for maintenance. After a few hours, when the marginal value of thermoregulating
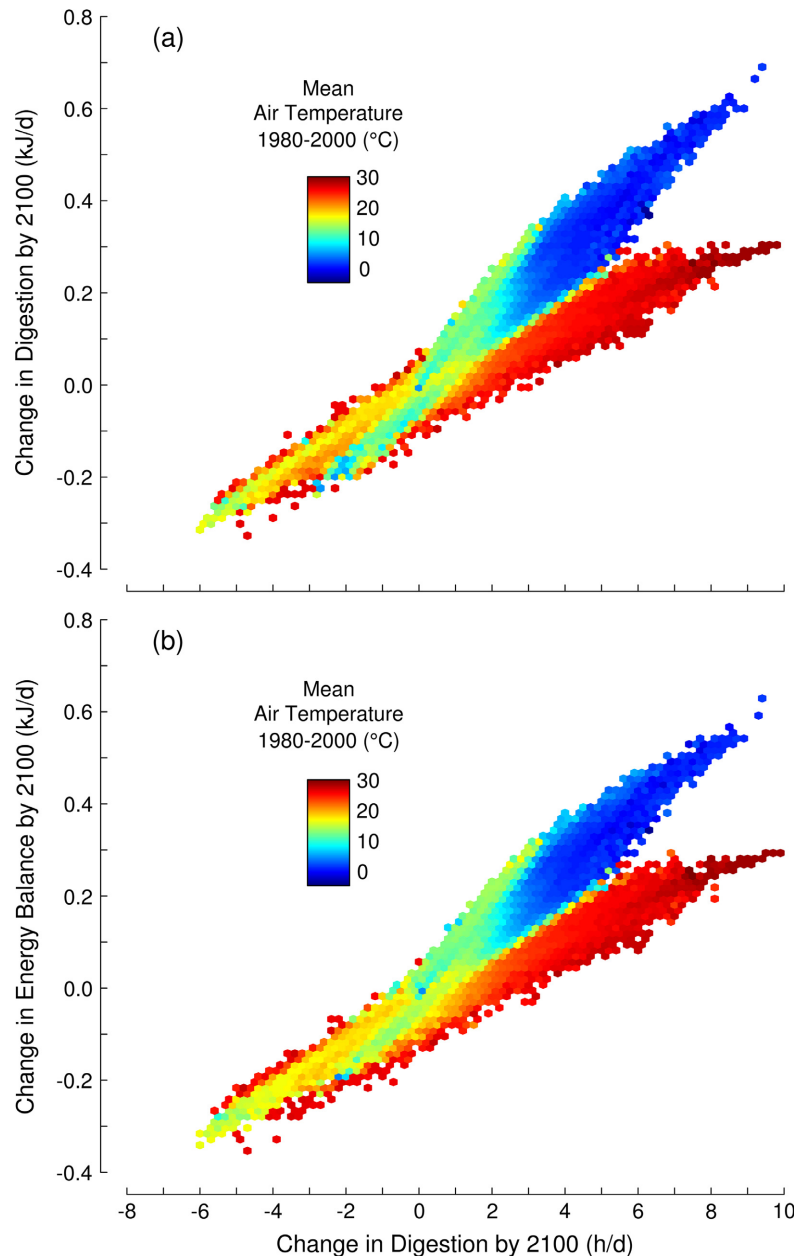
Fɪɢ. 4. Impacts of climate change on daily assimilation rates (a) and energy balances (b) will depend on the current temperature. Given the deceleration of assimilation rates with thermal opportunity, the impact of shifts in thermal opportunity for digestion will pose a lesser effect on daily assimilation rates at warm locations compared to cold locations. The color of the each point indicates the mean air temperature at one or more locations. See Appendix S1: Figs. S6 and S8 for shifts in daily assimilation rates when lizards have faster rates of decelerating returns than in our initial parameterization, or have constant rate of assimilation, respectively.

decreases, lizards can either choose to abandon thermoregulation and seek shelter, perhaps to save energy or avoid predators, or continue to thermoregulate and gain more energy. Although we assumed that lizards only thermoregulate on the ground, heterotherms can climb or burrow to access additional microclimates above or below the ground (Norris and Kavanau 1966, Jacob and Painter 1980). The tradeoffs among energy gain, predation risk, and metabolic costs have been captured by foraging models, in which rates of energy gain decelerate as foraging depletes patches. Foraging theory also predicts that animals will quit foraging earlier when the cost of foraging or the risk of predation increases (Brown 1988, Mitchell et al. 1990).

The diminishing return on thermal opportunity also determines how populations respond to a changing climate. As an environment warms, the energetic benefit of additional time to thermoregulate depends on the previous opportunity for thermoregulation. In particular, the marginal benefit of thermal opportunity was great for lizards that currently have only a few hours of thermal opportunity each day and miniscule for lizards that currently have many hours of thermal opportunity throughout the day. Previous models, in which the rate of energy assimilation was assumed to increase linearly with increasing thermal opportunity (Buckley 2008, Sinervo et al. 2010, Kearney 2013), either under- or over-estimated the energetic consequences of climate change by failing to consider diminishing energetic returns on activity. In particular, a linear function would underestimate the energetic benefit of climate change at cold locations (by 7.1 ± 4.6 kJ at 26% of locations; Appendix S1: Fig. S9) and overestimate the energetic loss due to climate change at warm locations (by 17 ± 9 kJ yr^{-1} at 74% of locations; Appendix S1: Fig. S9). Global warming has already caused species of lizards to go extinct in tropical and subtropical regions (Sinervo et al. 2010), and tropical ectotherms in general seem especially vulnerable to further warming (Huey et al. 2012). Importantly, our model suggests that losing opportunities to forage on warm days might not drive such extinctions if lizards can feed during cooler times of the day and assimilate most of their food in 6 to 10 h of digestion. On the other hand, warmer summers may decrease feeding and digestion while increasing energetic demands (Fig. 3), reducing the probability of survival (Bestion et al. 2015, Levy et al. 2016b). Researchers should account for diminishing returns on thermoregulation when predicting energetics, growth, and reproduction of animals in future climates.

A disadvantage of mechanistic models, relative to climate-envelope models, is that one must define relationships between environmental variables and organismal performance, such as the function relating body temperature to energy assimilation. Any mathematical model is just a series of such functions, and many functions are linearized to make a model easier to analyze and interpret. For example, linear approximations were chosen to relate the duration of thermoregulation to the energetics (e.g., Porter et al. 1973, Kearney et al. 2009a, b), survival (Adolph and Porter 1993), phenology (Kearney et al. 2010), or life history (Adolph and Porter 1993, 1996). More complex models explicitly calculate an energy balance to predict food and water requirements (Kearney and Porter 2004), optimal behavior (Grant and Porter 1992), life history (Kearney 2011), reproduction (Grant and Porter 1992, Adolph and Porter 1993, Kearney 2011), or population growth (Buckley et al. 2010, Kearney 2011). Even in these models, thermoregulatory activity is translated to energy gain by assuming that assimilation rates are linear (but see Adolph and Porter 1993). In contrast to this simplifying assumption,

we have shown that rates of energy assimilation diminish with increasing thermal opportunity in two species of *Sceloporus* lizards. Our observations agree with hypothetical arguments (Adolph and Porter 1993), as well as empirical rates of somatic growth in other *Sceloporus* lizards, which also decelerate with increasing thermal opportunity (Sinervo and Adolph 1989, Sinervo 1990, Avery 1994). Thus, our study provides a potential mechanism for the deceleration of somatic growth during previous experiments. But more importantly, we show that accounting for such nonlinear relationships in mechanistic models can be crucial for understanding potential impacts of climate change on energy and water budgets, life histories, and population dynamics.

The ecological significance of future shifts in assimilation rates may differ between currently cold and warm locations. In previous studies, we found that climate change will enable lizards to remain active for wider spans of days (Levy et al. 2015, 2016b). At cold locations, where daily rates of assimilation increase substantially (as in Fig. 3c), females could reproduce more or store fat for use in winter. At warm locations, however, high mortality of offspring produced during the summer would favor females that avoid reproducing at this time, leading to a bimodal distribution of reproduction throughout the year (Levy et al. 2016b). The decrease in energy gain during summer would reinforce bimodal reproduction, since females that lay eggs during summer would not only put embryos at risk of overheating but also have less energy for reproduction later in the year. By contrast, lizards in colder locations might reproduce continuously throughout the year, because climate change would enhance energy assimilation (Fig. 3c) and offspring survival (Levy et al. 2016b).

Shifts in the availability of time for activity may also incur ecological consequences on populations and communities. With fewer hours of activity, for example, the trade-offs among feeding, mating, and defending a territory may become severe (Dunbar et al. 2009). For territorial animals, more or less time available for defending a territory may in turn increase or decrease territory sizes, respectively (Stiles 1971, Pyke 1979, Davies 1980). During days with little thermal opportunity, organisms would have more difficulty partitioning their activities throughout the day, intensifying competition for space and potentially raising predation risk (Kronfeld-Schor and Dayan 2003). If temporal shifts in activity increase competition or predation, climate change can indirectly reduce survival rates as well as energy gains. At colder locations, on the other hand, an increase in thermal opportunities will not only enable more time for foraging and digestion, but could also promote temporal partitioning to avoid competition and predation (Kronfeld-Schor and Dayan 2003).

The relationship between thermal opportunity and energy gain will vary among species because of body mass, diet quality, handling time, and gut bacteria (Munn and Dawson 2006, Rall et al. 2012). For example,

herbivorous species may be more sensitive to decreased foraging and digestion times than carnivorous species are. Herbivores consume food with high concentrations of indigestible fiber and secondary metabolites and low concentrations of protein (Clauss et al. 2013). To increase assimilation rate, herbivores consume large volumes and carry a microbiome that digests cellulose, hemicellulose, and pectin (Clauss et al. 2013). Rates of assimilation for herbivores might be constant or even accelerate with time, because they can absorb glucose faster after breaking down cellulose. Hence, herbivory may impose selection for longer periods of thermoregulation to speed energy assimilation. If climate change reduces opportunities for thermoregulation in herbivorous species, a shift in physiology, microbiome, or diet might be necessary to offset the loss of thermal opportunity (Hirakawa 1997). By contrast, herbivores at cold locations may experience a significant increase in energy assimilation if thermal opportunity will enable a substantial increase in cellulose breakdown. The diversity of physiological responses among species requires careful analysis of each species to determine the relationship between thermal opportunity and energy gain. Simple models, which assume constant rates of energy gain during activity, will potentially mislead efforts to understand and predict the biological impacts of climate change.

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