vol. 194, no. 6 the american naturalist december 2019

E-Article

Climate Warming, Resource Availability, and the Metabolic Meltdown of Ectotherms

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Submitted December 30, 2018; Accepted June 5, 2019; Electronically published September 18, 2019

abstract: Climate warming may lower environmental resource levels, growth, and fitness of many ectotherms. In a classic experiment, Brett and colleagues documented that growth rates of salmon depended strikingly on both temperature and food levels. Here we develop a simple bioenergetic model that explores how fixed temperatures and food jointly alter the thermal sensitivity of net energy gain. The model incorporates differing thermal sensitivities of energy intake and metabolism. In qualitative agreement with Brett's results, it predicts that decreased food intake reduces growth rates, lowers optimal temperatures for growth, and lowers the highest temperatures sustaining growth (upper thermal limit). Consequently, ectotherms facing reduced food intake in warm environments should restrict activity to times when low body temperatures are biophysically feasible, but—in a warming world—that will force ectotherms to shorten activity times and thus further reduce food intake. This "metabolic meltdown" is a consequence of declining energy intake coupled with accelerating metabolic costs at high temperatures and with warming-imposed restrictions on activity. Next, we extend the model to explore how increasing mean environmental temperatures alter the thermal sensitivity of growth: when food intake is reduced, optimal temperatures and upper thermal limits for growth are lowered. We discuss our model's key assumptions and caveats as well as its relationship to a recent model for phytoplankton. Both models illustrate that the deleterious impacts of climate warming on ectotherms will be amplified if food intake is also reduced, either because warming reduces standing food resources or because it restricts foraging time.

Keywords: climate warming, energetics, resource availability, growth, metabolism, temperature.

Introduction

Net energy gain influences an organism's growth and reproduction—and ultimately its fitness. An ectotherm's net energy gain depends primarily on its body temperature (T_b) and its intake of available food resources. Climate warming could potentially affect net energy gain by altering T_b distributions, by restricting foraging opportunities, or by reducing the availability of food in the environment (Dunham 1993; Kearney et al. 2009; Sinervo et al. 2010; Sears et al. 2016; Lister and Garcia 2018).

Here we develop a basic bioenergetic model that examines how the combined effects of climate warming, T_b, and food intake alter the energetics and thermoregulatory strategies of ectotherms. Our project was inspired by J. R. Brett and colleagues (Brett et al. 1969; Brett 1971), who discovered that the thermal sensitivity of growth rates of young salmon depended strikingly on temperature and food ration (fig. 1, redrawn from data in Brett et al. [1969] and Brett [1971]). When Brett provided food in excess, salmon grew fastest at an intermediate temperature (~13°C) but began to lose mass at ~24°C, which thus represented the upper thermal limit for growth. But when Brett restricted food, (1) growth rate declined at all temperatures, roughly in proportion to level of food restriction; (2) the upper thermal limit for growth dropped; and (3) the optimum temperature (T_{opt}) for growth also dropped. In effect, growth rate became less heat tolerant under restricted food. Similar patterns were later documented for other ectotherms (e.g., Elliott 1976; Gerard 1997; Peck et al. 2003; McLeod et al. 2013; Thomas et al. 2017) and suggests that the negative effects of climate warming will be amplified if warming results in reduced food intake (McLeod et al. 2013; Thomas et al. 2017).

The thermal sensitivity of growth physiology (fig. 2*A*, 2*C*) provides a conceptual basis for the patterns in figure 1. Food consumption (gross energy intake) under unlimited food typically increases with temperature up to an optimum temperature and then drops precipitously (fig. 2*A*; Waldschmidt et al. 1986; Koskela et al. 1997). In contrast, total metabolic expenses (maintenance, foraging, and digestion) typically increase exponentially with temperature but ultimately drop at stressfully high T_b (Lighton and Turner 2004; Marshall and McQuaid 2011). Net energy gain (consumption gain minus metabolic expenses) thus is maximal at an intermediate but relatively warm temperature (see fig. 2*B*, 2*D*). Using this logic, Hainsworth and Wolf (1978; their fig. 2) and Huey (1982; his

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Am. Nat. 2019. Vol. 194, pp. E000–E000.
DOI: 10.1086/705679

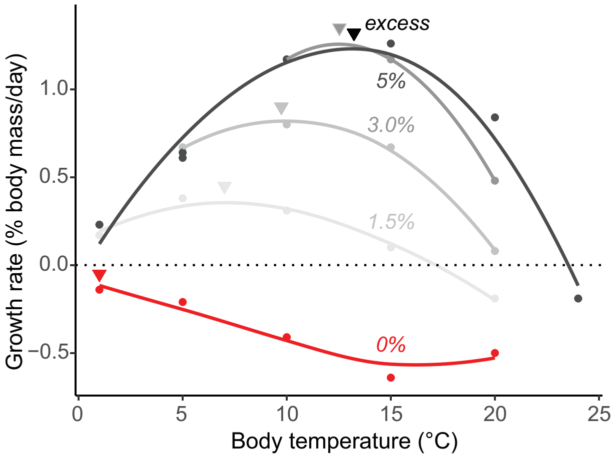

Figure 1: Growth rate of fingerling salmon at fixed temperatures and food rations (from 0% [starvation] to excess; units = % dry weight/day). Inverted triangles indicate estimated T_{opt} for each food ration level. Both T_{opt} and the upper threshold temperature for growth decline with decreasing food ration. Curves are loess smoothers. Redrawn from data in Brett et al. (1969) and Brett (1971).

fig. 5) developed graphic models suggesting that lowered food rations will not merely reduce net energy gain (thus growth) but will also reduce T_{opt} for growth, consistent with Brett's findings (Brett et al. 1969; Brett 1971).

We begin by building a simple energy balance model that formalizes the graphical models of Hainsworth and Wolf (1978) and of Huey (1982). Our basic model mimics Brett's experiment design—and thus assumes fixed T_b and food ration—but also adds comparisons involving thermal generalists versus specialists as well as for metabolic rate curves with different steepness (Q_{10}; fig. 2). However, because ectotherms in nature have variable (not fixed) T_b, we next recast the model to allow for T_b distributions that can have different means and variances. We can thereby determine the T_b distribution that maximizes net energy gain under different food intake levels: in effect, this approach explores how the combined effects of climate change and food level alter the mean net energy gain.

Net energy gain will of course decline if climate warming forces ectotherms to be active at T_b above optimal physiological levels (fig. 2*B*, 2*D*). But if food intake is simultaneously reduced, then net energy gain and growth are now maximized at low T_b. In other words, a warming environment may push ectotherms toward accepting activity at high T_b, but energetics would push ectotherms to try to be active at low T_b. Thus, the selective forces are in opposite directions. In the discussion section, we will argue that declining food intake is in fact a likely consequence of climate warming, at least in environments that are already warm or hot. Thus, warming plus the associated food restriction could potentially amplify negative effects of climate warming, effectively lead to a "metabolic meltdown," and thereby accentuate any negative energetic consequences of warming (see also Thomas et al. 2017).

Growth Rates in Constant Thermal Environments: Basic Model

We use a basic bioenergetic model (Kitchell et al. 1977; Hainsworth and Wolf 1978; Huey 1982), where the growth rate G of an organism is determined by its energy flux balance:

$$G = (A \cdot f \cdot C) - R. \qquad (1)$$

In this model, C is the rate of energy intake of ingested food (ingestion rate), R is the rate of energy expenditure associated with metabolism and digestion (metabolic rate), A is the conversion efficiency of ingested food, and f is the food level (see below). In general, C, R, and A will all depend on body temperature, T_b. For simplicity, we will assume that conversion efficiency A is constant (Brett 1971; Kingsolver and Woods 1997; Angilletta 2009; see "Discussion").

The temperature dependence of ingestion rate ($C(T_b)$) and of metabolic rate ($R(T_b)$) have been examined in many ectotherms (Irlich et al. 2009; Dell et al. 2011). A thermal performance curve (TPC; Huey and Kingsolver 1989) for ingestion rate and other aspects of organism performance has a characteristic asymmetric shape (figs. 1, 2) in which performance is maximal at some intermediate to warm "optimal" temperature (T_{opt}) and declines more rapidly at higher than at lower temperatures (Gilchrist 1995; Dell et al. 2011). Here we model the TPC for ingestion rate (and gross energy intake rate = $A \times C$) as a Gaussian multiplied by a Gompertz function (eq. [2]), with parameters T_{opt}, ρ, and σ, where σ determines the steepness of the left portion of the TPC and ρ determines the steepness of the right portion (for details, see Frazier et al. 2006):

$$C = C_{max} \exp(-\exp((\rho(T_b - T_{opt})) - 6) - \rho(T_b - T_{opt})^2). \qquad (2)$$

In contrast, metabolic rate typically increases exponentially over a wide range of temperatures (Savage 2004) until very high T_b (Lighton and Turner 2004; Marshall and McQuaid 2011). Consequently, we used an exponential equation to quantify the thermal dependence of metabolic rate for three typical Q_{10} values (2.0, 2.5, 3.0) and assume that R is independent of food intake (but see "Discussion"). The net rate of growth (or net energy gain) then is the difference between gross energy gain and metabolic rate (eqq. [1], [2]; fig. 2*C*, 2*E*). All analyses were performed using the R statistical environment (ver. 3.5.3; R Core Team 2019).

How might food limitation alter the thermal sensitivity of ingestion and net energy gain? We will explore another

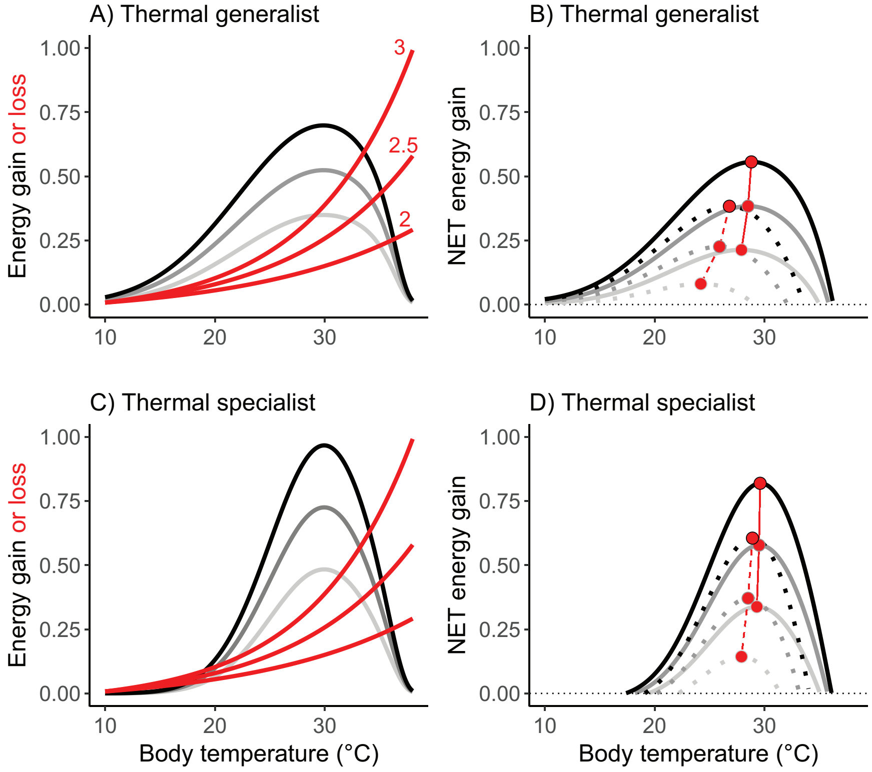

Figure 2: When T_b and food intake are held constant, thermal dependence of net energy gain is sensitive to the breadth of the thermal performance curve for energy intake (generalists, specialists) as well as to the steepness (Q_{10}, or the factorial increase in metabolic rate over +10°C shift) of the metabolic-temperature curve. *A*, *C*, Gross energy gain (declining from black to gray) under three food levels and metabolic losses (red) at three Q_{10} values (2, 2.5, 3) for a thermal generalist (*A*) and for a thermal specialist (*C*). *B*, *D*, Net energy gain for a generalist (*B*) and a specialist (*D*) under three food levels and with a Q_{10} of 2 (solid lines) or 3 (dotted lines). T_{opt} for each (red dots) and the upper temperature threshold for growth both decline with food ration, especially for generalists with steep Q_{10}.

scenario below, but the simplest approach is to allow food level to be altered proportionately at all temperatures: that is, that ingestion rate $= f \cdot C$, where f is the proportional food level relative to unlimited food, when $f = 1$. In this case reductions in food will basically flatten the intake curve (e.g., fig. 2*A* vs. 2*B*). Importantly, reduced food intake not only reduces maximum growth but also reduces both T_{opt} and the maximum T_b for positive growth, especially for steep Q_{10}'s (fig. 2*B*, 2*D*). This simple model, which formalizes prior graphical models (Hainsworth and Wolf 1978; Huey 1982), generates results that qualitatively match those of Brett's experiments (Brett et al. 1969; Brett 1971; fig. 1).

The quantitative effects of food limitation on net growth are also influenced by the shape of the TPC for ingestion ($C(T_b)$) and of the thermal sensitivity of metabolic rate ($R(T_b)$). To illustrate this, we modeled two hypothetical cases: a thermal generalist with a broad performance breadth ($\rho = 0.9$, $\sigma = 0.008$; fig. 2*A*, 2*B*) and a thermal specialist with a narrow performance breadth ("thermal specialist"; $\rho = 0.9$, $\sigma = 0.02$; fig. 2*C*, 2*D*). We set T_{opt} to 30°C for both cases and incorporate a generalist-specialist trade-off where the area under the TPC for energy ingestion is the same for the two cases (Levins 1968; Huey and Slatkin 1976; Gilchrist 1995), resulting in a lower maximum energy gain for the generalist than the specialist (cf. fig. 2*B*, 2*C*). We also consider two levels (3.0, 2.0) of Q_{10} (fig. 2*B*, 2*C*).

The basic patterns (fig. 1) in Brett et al. (1969) and Brett (1971) hold qualitatively for each of these variations (fig. 2). Specifically, reduced food levels reduce T_{opt} as well as the maximum temperature, allowing positive net growth of both generalists and specialists. However, reduced food lowers both traits more for generalists than for specialists (fig. 2), and a steep Q_{10} also accentuates the drops in these traits.

Mean Growth Rates in Variable Thermal Environments

The model described above quantifies ingestion, metabolic, and net growth rate for a given (fixed) temperature T_b and a fixed food level *f*, thus matching Brett's (1971) experimental conditions. However, natural thermal environments vary in both time and space (Waldschmidt and Tracy 1983; Grant and Dunham 1990; Potter et al. 2013; Sears et al. 2016), and so ectotherms generally experience a range of environmental and body temperatures. Our model can predict mean growth rate during some time interval or life stage by integrating over the distribution of body temperatures experienced during the interval or stage ($p(T_b)$; Huey and Slatkin 1976; Deutsch et al. 2008; Vasseur et al. 2014). Body temperature distributions of active ectotherms are typically left skewed and unimodal and can be broad or narrow (Huey and Pianka 2017). We arbitrarily selected activity T_b of two desert lizards (*Pedioplanus lineoocellata*, from the Kalahari Desert; *Phrynosoma playrhinos*, from northern US deserts) as exemplars of T_b distributions (Huey and Pianka 2017) of ectotherms with a relatively narrow versus broad distribution, respectively. We fit a skewed normal distribution (R package fGarch; Wuertz et al. 2017) to field T_b data for each species. Skewness was similar for both species (0.53 and 0.41, respectively), but their standard deviations differed (2.1°C and 3.7°C, respectively). In our simulations, we set skewness $= 0.5$ for both and set standard deviations of 2°C and 4°C, respectively. For simplicity, in our simulations the skew and standard deviation do not change with mean environmental temperature θ. We then calculate mean growth rate $\bar{G}$ for a temperature distribution $p(T_b)$:

$$\bar{G} = \int G(T_b)p(T_b)\,dT_b. \tag{3}$$

Equation (3) shows that mean growth rate will depend on the distribution of body temperatures, the thermal sensitivities of ingestion and metabolic rates, and the food level (see eq. [1]). For simplicity, suppose environmental temperatures directly determine the T_b of an ectotherm (a "thermoconformer"; see "Discussion"). As mean environmental temperature θ (and thus T_b) increases during climate warming, mean growth rate will also change. In the simplest case (food level remains constant and high during climate warming), mean growth rate declines rapidly at high mean environmental temperatures because ingestion declines while metabolic rate accelerates (see fig. 2*A*, 2*C*).

Climate change may also have direct or indirect effects on the food resources available to ectotherms. As described in the discussion section, global warming or other aspects of anthropogenic environmental change may decrease available food levels (Deutsch et al. 2008; Hallmann et al. 2017; Bestion et al. 2018; Lister and Garcia 2018) as well as reduce opportunities to forage (Dunham 1993; Sinervo et al. 2010; Sears et al. 2011), at least at high temperatures (Levy et al. 2017). We consider two cases: (1) reduced food levels that are independent of mean environmental temperatures (fig. 3, solid lines) and (2) food levels that decline as mean environmental temperature increases (fig. 3, dashed line), which might occur if resources decline with climate warming or if foraging becomes restricted at high environmental temperatures (but see Levy et al. 2017). We characterize this decline in food level f using a sigmoid function (Borchers 2018):

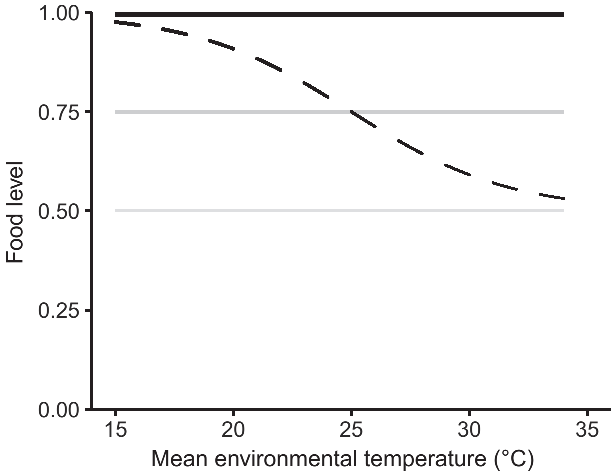

Figure 3: Food levels at different environmental temperatures. Case 1: food level is independent of temperature, and solid lines indicate constant food levels of 1.0 (black), 0.75 (darker gray), and 0.5 (lighter gray). Case 2: food level declines with increasing mean environmental temperatures (dashed black line; $a = 0.3$). Line thickness is scaled to food level.

$$f = f_{\max} - \frac{f_{\max} - f_{\min}}{1 + \exp(-a(\theta - \theta_{\mathrm{mid}}))}, \tag{4}$$

where $f_{\max}$ and $f_{\min}$ are the maximum and minimum food levels, respectively; θ_{mid} is the midpoint environmental temperature at which food level is midway between $f_{\max}$ and $f_{\min}$; and a determines the slope of the decline in food level. Food level f varies between 0 and 1, where $f = 1$ indicates the case of unlimited food (see above). Note that at $\theta = \theta_{\mathrm{mid}}$, the slope of equation (4) is $df/d\theta = -a(f_{\max} - f_{\min})/4$ (see fig. 3).

Effects on growth rates of various levels of food ration and of mean environmental temperature show that Brett's basic results (fig. 1) hold for shifting temperature distributions (fig. 4) as well as at fixed temperatures (fig. 2*B*, 2*D*). When food declines proportionately at all temperatures (solid black or gray lines in fig. 4), growth declines, T_{opt} shifts to lower temperatures, and the highest temperature permitting growth declines, and they all do so more strongly for thermal generalists (fig. 4*A*, 4*B* vs. 4*C*, 4*D*). When food declines (fig. 3) mainly at high environmental temperature (θ), T_{opt} drops dramatically (fig. 4, dashed black lines). In this case, the growth curve converges on that of excess food at low θ but on that of restricted food at high θ. Increasing

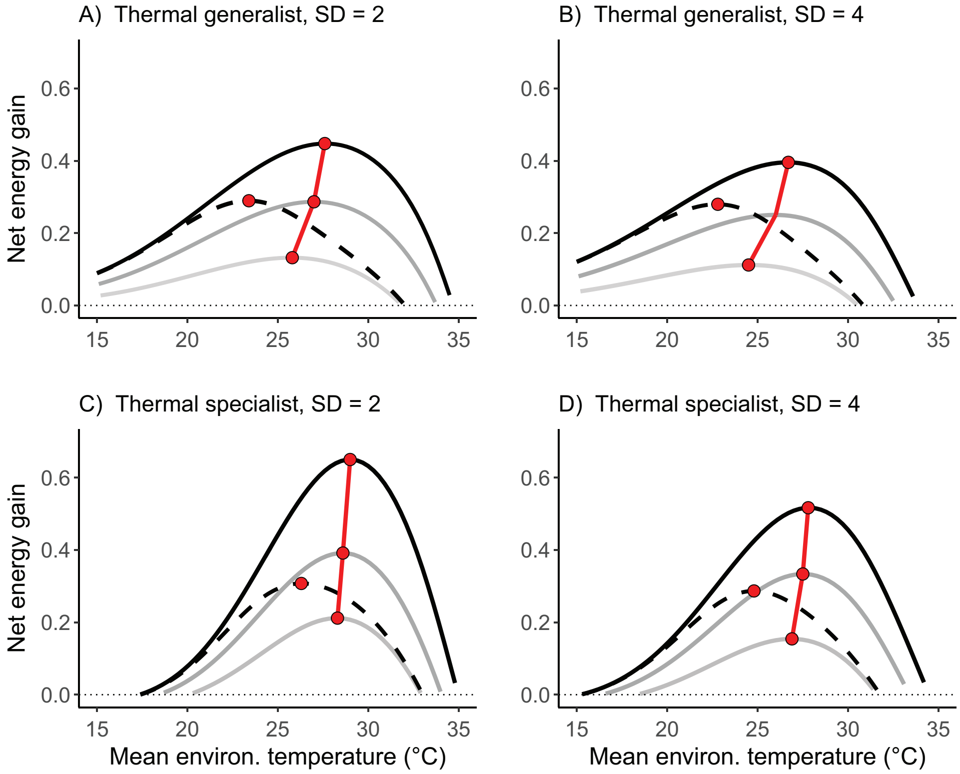

Figure 4: Net energy gain as a function of mean environmental temperature (θ) for thermal generalists (*A*, *B*) and specialists (*C*, *D*) during climate warming. Two levels of thermal environmental variation are considered: SD = 2°C (*A*, *C*) and SD = 4°C (*B*, *D*). The solid black lines indicate net energy gain under excess food, and solid gray lines indicate food levels of 0.75 (darker) or 0.5 (lighter). The dashed black line indicates a sigmoidal decline in food with temperature (1.0 to 0.5). Solid red circles indicate T_{opt} for different food levels.

the magnitude of thermal environmental variation (standard deviation in the temperature distribution $p(T_b)$) generally decreases maximum mean growth rates but causes only a modest increase (<0.5°C) in the magnitude of the response to (uniformly) decreased food intake (compare left and right columns in fig. 4). Changing the midpoint temperature (θ_{mid}) or slope (a) of the relationship between food level and environmental temperature (eq. [4]; fig. 3) does not qualitatively alter these effects. Thus, declining resources will amplify the negative consequences of climate warming for mean growth and will lower the environmental temperatures at which climate warming will start to have negative impacts on growth rate.

Discussion

Climate warming can have disruptive effects on the performance and fitness of organisms, and these effects will be mediated in part on physiological processes such as food consumption and metabolism as well as by behavioral thermoregulation (Kearney et al. 2009). For ectotherms, high environmental temperatures can lead to reduced rates of growth, at least if T_b's are elevated above optimal levels. But if food resources are declining simultaneously, either directly as a result of warming or other concurrent environmental changes or indirectly as a result of behavioral restrictions on activity time during warm periods (Stevenson 1985; Dunham 1993; Sinervo et al. 2010), then maximal growth rates will decline, the highest temperature permitting growth will decline, and the optimal temperature for growth will also decline. Thus, although climate warming can itself be energetically deleterious, warming plus reduced food will be multiplicatively deleterious: ectotherms will become energetically less heat tolerant while living in a warming environment, a phenomenon we call metabolic meltdown. Below we discuss the biological justification underlying key assumptions of our simple model and also consider some implications of metabolic meltdown.

Will T_b Increase with Warming?

Our model assumes that T_b will increase one to one with changes in environmental temperatures (θ). Thus, our model is most appropriate for thermoconformers, which typically have limited mobility or live in thermally homogeneous environments and thus have limited opportunity for behavioral adjustments (Huey 1974; Willmer 1982; Helmuth et al. 2002; Chown and Nicholson 2004). However, our model should still be relevant for thermoregulators, even though their T_b do not change as fast as T_e (Huey 1974; Kearney et al. 2009). Lizards that are careful thermoregulators typically have elevated T_b in warm seasons (Huey et al. 1977; Christian et al. 1983; Gunderson and Leal 2012), and some even stay active at very high T_b during hot times (McGinnis and Dickson 1967; Grant and Dunham 1988; Gunderson and Leal 2012). Thus, $p(T_b)$—especially that of thermoconformers—is likely to increase as climates warm.

Importantly, the primary behavioral adjustments used by thermoregulators often involve restricting activity and foraging time (i.e., by withdrawing to a thermal retreat during hot periods; Porter et al. 1973; Stevenson 1985; Kearney et al. 2009) or restricting space use (i.e., to cool microenvironments; Stevenson 1985; Gunderson and Leal 2015; Sears et al. 2016): both adjustments should effectively reduce food consumption and reproduction (Dunham 1993; Sinervo et al. 2010) even if environmental food levels are unchanged. In effect, the optimal behavioral solution (activity only at lower T_b) will further reduce net energy gain by restricting foraging. Therefore, thermoregulators may be able to reduce metabolic meltdown in warming environments (Kearney et al. 2009; Huey et al. 2012), but they cannot escape it.

Will Food Availability Decline with Warming?

The effects of climate change on primary productivity and resource levels will vary across geographic regions and ecosystems, but recent analyses suggest that warming temperatures and climate change will negatively impact resources in many temperate and tropical systems. For example, decreasing mean and increased variability in precipitation can reduce primary productivity in grassland ecosystems (Pan et al. 2017). Phytoplankton productivity may decline in response to climate change in many marine ecosystems, particularly in tropical shelf and upwelling areas (Blanchard et al. 2012; Thomas et al. 2017).

Warming temperatures potentially reduce standing food levels in several ways. Warming can reduce primary productivity, thereby reducing the food base for herbivores and higher trophic levels (Hallmann et al. 2017; Lister and Garcia 2018). Warming plus drought can cause plant dieback (Ciais et al. 2005), which will reduce not only the food base (for herbivores) but also habitat shading, increasing operative temperatures and thus either increasing T_b or reducing foraging time and opportunity (or both).

Warming temperatures can also alter rates of population growth (fitness) of organisms serving as competitors or as prey for higher trophic levels (Buckley 2013; Bestion et al. 2018). In cold environments, of course, warming may accelerate prey population growth, but in warm environments warming may depress rates of population growth (Vasseur and McCann 2005; Deutsch et al. 2008; Kingsolver et al. 2011). In particular, climate change is predicted to reduce reproductive rates and survival of insects in tropical and many temperate regions (Vasseur and McCann 2005; Deutsch et al. 2008; Kingsolver et al. 2011). In addition, increasing mean temperatures can reduce population carrying capacity (Savage et al. 2004; Vasseur and McCann 2005; Woodworth-Jefcoats et al. 2017; Bernhardt et al. 2018*a*, 2018*b*). For example, a recent experimental study showed that increasing temperature reduced mean cell size, carrying capacity, and total biomass of a mobile phytoplankton (Bernhardt et al. 2018*a*, 2018*b*). These results suggest that climate warming—at least in already-warm environments—may reduce the density of resources available for many ectothermic predators and herbivores.

Field studies confirm that food levels have declined in recent decades in some terrestrial ecosystems. For example, abundances of arthropods have declined markedly over several decades in Puerto Rico and Mexico, with apparent repercussions on higher trophic levels: climate warming is the likely cause (Lister and Garcia 2018). Declines in insect pollinators can potentially reduce plant reproduction and also food supply to predators of pollinators (Biesmeijer et al. 2006). Of course, food can decline for reasons other than climate warming (Zhao and Running 2010; Hallmann et al. 2017). For example, the biomass of flying insects in protected sites in Germany has declined 75% in 27 years, but this decline shows no obvious imprint of climate change (Hallmann et al. 2017). In any case, what matters is whether food is declining in parallel with climate warming, not whether climate warming is the driving factor. Interestingly, diverse ectotherms lower their preferred body temperatures under reduced (or fasting) food regimes (reviewed in Angilletta 2009, pp. 102–105), but lowered preferred temperatures will constrain activity time in warm environments, further reducing energy gain (Dunham 1993; Sinervo et al. 2010). Alternatively, ectotherms could reduce metabolic rates in response to warming (Marshall and McQuaid 2011), which will reduce metabolic meltdown but likely slow growth and reproduction.

Our discussion has focused on the consequences of warming in already-warm environments. However, many ectotherms routinely experience low suboptimal temperatures—especially in seasonal environments (fig. 6*b* in Huey et al. 2012). For them, warming may enhance growth rates (Deutsch et al. 2008; Kingsolver et al. 2013), but that enhancement will be blunted under reduced food ration (fig. 4). Nevertheless, metabolic meltdown is mainly a high-temperature effect.

Can Other Mechanisms Lead to Meltdown?

The predictions from our model emerge from three basic elements: maximal ingestion rate varies with temperature, where ingestion rate is maximal at some intermediate (optimal) temperature; ingestion rate at any given temperature increases with food level; and metabolic rate accelerates with increasing temperature. Our simple model assumes that ingestion rate is linearly related to food level, but nonlinear relationships between ingestion (intake) and food level (nutrient concentration) are widespread. In particular, individual or population growth rate is a saturating (decelerating) function of the availability of a limiting resource in many bacteria, plankton, and animals (Monod 1949; Holling 1959; Eppley et al. 1969; Thomas et al. 2017).

Thomas et al. (2017) recently modeled interactions between temperature and nutrient concentration in phytoplankton. In their model, population growth rate is a function of both temperature (where population growth rate is maximal at some intermediate [optimal] temperature) and of nutrient concentration (where population growth rate is a decelerating function of concentration that saturates at some maximal growth rate). This model predicts that declining nutrient concentrations will reduce maximal (population) growth rate, the optimal temperature, and the upper thermal limit (the temperature at which the population growth rate is zero). Thus, predictions from our energetic model of metabolic meltdown qualitatively match those from a population one (Thomas et al. 2017). Laboratory experiments with a marine diatom confirm that the optimal temperature for population growth declines with declining nutrient (phosphate and nitrate) concentrations; the decline in optimal temperatures is particularly pronounced at very low nutrient concentrations (Thomas et al. 2017). Note that their model does not explicitly consider metabolic or respiration rates (which are incorporated via their effects on population growth rates), nor does it consider behavioral responses to warming.

Mathematically, the similar qualitative predictions from these two models emerge from the decelerating function relating growth rate to resource concentration (Thomas et al. 2017) versus the accelerating function relating respiration rate to temperature (the current model; fig. 2). More generally, suppose that net performance or fitness results from the difference between two functions of temperature: a decelerating “gain” function and an accelerating “loss” function (eqq. [1], [2]). Reductions in resources (or other environment factors) that reduce gains or magnify losses will have similar effects on shifting optimal and maximal temperatures, as described here. In particular, the effects of resource levels on birth and death functions could also alter the thermal dependence of fitness in ectotherms (Amarasekare and Savage 2012). These considerations suggest that there are multiple mechanisms by which temperature and resources may interact to exacerbate the negative consequences of climate changes for ectothermic organisms (Thomas et al. 2017).

Caveats

Our model is intentionally simple and summarizes key factors involving food, temperature, and energetics that are universal for ectotherm growth. In the future, more complex models (e.g., incorporating nutrients, energetics, biophysical models of heat exchange; Kooijman 2010; Clissold and Simpson 2015; Sears et al. 2016; Thomas et al. 2017; Malishev et al. 2018) can explore fine-scaled aspects of metabolic meltdown. Here we highlight a few known complications.

First, our model belongs to a family of models (e.g., Huey and Slatkin 1976; Vasseur et al. 2014) that integrate performance or fitness over a distribution of T_b (eq. [2]). However, physiologists have long appreciated that the effect of T_b on performance or fitness can change with acclimation (Bernard 1865; Fry and Hart 1948), ontogeny (Brett 1970), and time at temperature (Wilhoft 1958; Kingsolver and Woods 2016). Such effects—when major—will alter the conclusions, especially at high temperatures (Brakefield and Kesbeke 1996; Schulte et al. 2011; Niehaus et al. 2012; Colinet et al. 2014; Kingsolver and Woods 2016; Sinclair et al. 2016; Kremer et al. 2018; Bernhardt et al. 2018*a*, 2018*b*).

Second, we assumed that metabolic rate is independent of food intake. However, many ectotherms (and even humans) reduce metabolic rate under reduced food (Secor and Diamond 2000; Auer et al. 2015). Reduced metabolic rate under low food intake should reduce—but not eliminate—the declines in T_{opt} and in the highest temperature for growth (compare results for the two Q_{10}’s in fig. 2*B*, 2*D*).

Third, our model assumes that the distribution of T_b is unimodal and left skewed: this is valid for ectotherms such as diurnal desert lizards when active (Huey and Pianka 2017). However, growth is sensitive to T_b over 24 h, not just during activity. When compiled over 24 h (or longer), T_b distributions typically have relatively broad distributions, at least at low T_b, and sometimes they are even bimodal (Stevenson et al. 1985). However, our simulations with two breadth levels (standard deviations) suggest that the breadth of the T_b distribution will have limited effect on the magnitude of the drop in T_{opt} caused by food restriction. For example, the drops are 1.8°C and 2.2°C, respectively, for the two generalist cases (fig. 4*A*, 4*B*) and 0.7°C and 0.9°C, respectively, for the specialist cases (fig. 4*C*, 4*D*).

To explore in brief the impact of bimodal T_b distribution, we ran the model with two modes set at +4°C and −4°C of the mean T_b (standard deviations of 1 and 2, respectively). The resultant growth curves (not shown) are very similar qualitatively to those of the unimodal cases in figure 4 but have reduced growth (reflecting time at low T_b) and slightly left-shifted T_{opt} and upper threshold temperatures. Also, differences in maximum growth rates between generalists and specialists are reduced relative to the unimodal cases.

Fourth, ectotherms live in communities, and the associated exploitative competition and predation can result in reduced food intake (Huey and Slatkin 1976; Gilman et al. 2010; Thakur et al. 2017). Moreover, microenvironments are often heterogeneous such that individuals may differ in exposure to food intake and to heat stress, even on a local scale (Denny et al. 2011; Sears et al. 2011; Potter et al. 2013). Modeling such complexities will be challenging, given that the responses of interacting ectotherms to climate change may be species specific and context dependent.

Fifth, our model considers the effects of food (resource) quantity on ingestion and net growth rates but assumes that resource quality (as reflected in assimilation efficiency; see eq. [1]) is constant and independent of environmental conditions. However, climate change can reduce resource quality. For example, increasing atmospheric CO_2 reduces protein content and protein-to-carbohydrate ratios and increases concentrations of secondary defense chemicals in leaves of most terrestrial plants (Mooney 1972; Chapin 1980). Numerous studies demonstrate that these effects reduce rates of growth, development, and fitness in insect and other herbivores as well as alter plant defenses against insect herbivores (Lincoln et al. 1993). In addition, increasing temperatures during development reduces final (adult) body size in most ectotherms, and reductions in mean body size during climate warming during recent decades has been widely (but not universally) reported (Atkinson 1994; Kingsolver and Huey 2008; Daufresne et al. 2009; Gardner et al. 2011) in ectotherms. If smaller prey size reduces the efficiency of search, handling, or assimilation by predators, this will decrease net energy gain. Reductions in food quality or conversion efficiency with climate warming should have similar consequences for the thermal dependence of growth, as modeled here for declining food levels (see eq. [1]).

Sixth, we assumed a Gompertz × Gaussian function to describe the thermal growth curve (eq. [2]) and a simple exponential for metabolic rate versus temperature. Other functional relationships are reasonable (Izem and Kingsolver 2005; Angilletta 2006; Sheth and Angert 2014); substitution of biologically reasonable functional forms is unlikely to change the qualitative patterns described here.

In summary, our conceptual extensions of Brett's pioneering experiments (Brett et al. 1969; Brett 1971) and a recent model of Thomas et al. (2017) suggest that the combination of climate warming plus food decline will exaggerate the negative consequences of climate change alone or of food decline alone—at least in areas that are already warm. If only the environment warms, ectotherms may need to accept activity at supraoptimal T_b to maintain sufficient activity time, potentially at a cost of stress. If only food levels decline, ectotherms should accept active at suboptimal T_b, which are energetically favorable but reduce maximal growth. But if both occur together, ectotherms face antagonistic thermoregulatory pressures and thus will be in an ecological double bind or catch-22. Accepting high T_b will maintain activity time but greatly reduce net energetic gain. Accepting low T_b will be energetically advantageous but will greatly reduce activity time, further lowering food intake and further lowering growth.

Acknowledgments

Our article honors the late J. R. Brett, who was a pioneer of fish physiological ecology, in the 50th anniversary year of his seminal 1969 paper. We thank L. Buckley, M. Denny, D. Miles, B. Sinervo, D. Vasseur, and an anonymous reviewer for constructive discussions and suggestions. The Whiteley Center provided an ideal environment for collaborating on model simulations and for drafting the manuscript. We thank the National Science Foundation for support (IOS 1038016 to R.B.H.; IOS 152767 to J.G.K.).

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Associate Editor: David Vasseur
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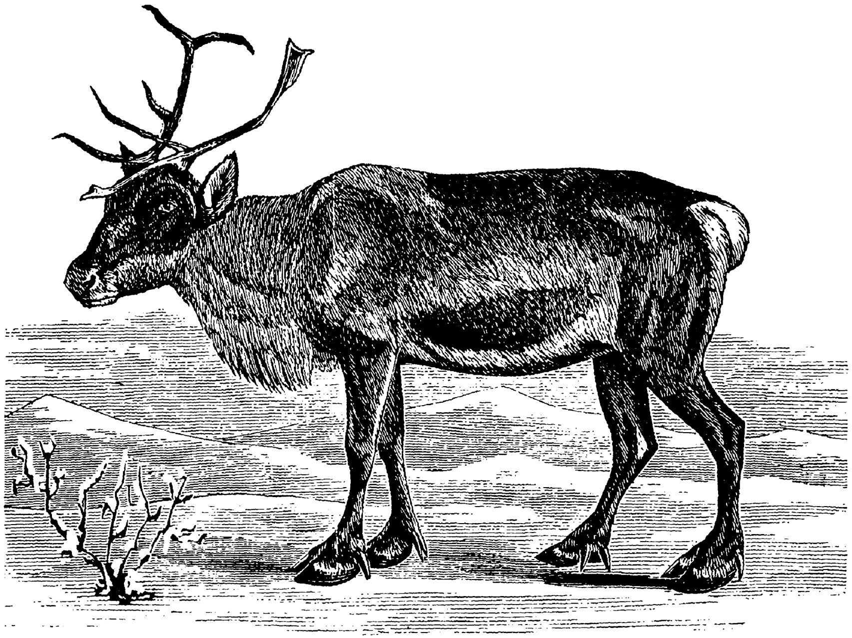

“But of the reindeer and Scandinavian elk our author speaks with the interest and decision of an expert, and his opinion on the specific relations of these animals with our caribou and moose should receive due consideration.” From the review of Caton’s *Summer in Norway* (*The American Naturalist*, 1876, 10:39–42).