

Crossing regimes of temperature dependence in animal movement

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Abstract

A pressing challenge in ecology is to understand the effects of changing global temperatures on food web structure and dynamics. The stability of these complex ecological networks largely depends on how predator–prey interactions may respond to temperature changes. Because predators and prey rely on their velocities to catch food or avoid being eaten, understanding how temperatures may affect animal movement is central to this quest. Despite our efforts, we still lack a mechanistic understanding of how the effect of temperature on metabolic processes scales up to animal movement and beyond. Here, we merge a biomechanical approach, the Metabolic Theory of Ecology and empirical data to show that animal movement displays multiple regimes of temperature dependence. We also show that crossing these regimes has important consequences for population dynamics and stability, which depend on the parameters controlling predator–prey interactions. We argue that this dependence upon interaction parameters may help explain why experimental work on the temperature dependence of interaction strengths has so far yielded conflicting results. More importantly, these changes in the temperature dependence of animal movement can have consequences that go well beyond ecological interactions and affect, for example, animal communication, mating, sensory detection, and any behavioral modality dependent on the movement of limbs. Finally, by not taking into account the changes in temperature dependence reported here we might not be able to properly forecast the impact of global warming on ecological processes and propose appropriate mitigation action when needed.

Keywords: activation energy, animal movement, biomechanics, interaction strengths, metabolic theory, temperature sensitivity, warming

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Introduction

Greenhouse gas emissions and land use change are major contributors to global climate change (Houghton *et al.*, 1996). As a result, global average temperatures have increased by 0.75 °C in the past 100 years and, if current warming trends are maintained, may increase by at least 3 °C in the next 50 years (Stocker *et al.*, 2013). This global increase in mean temperature is expected to have broad ecological impacts, affecting ecosystem processes (Pimm, 2009) and altering species distributions and zonation (Gedan & Bertness, 2009; Lurgi *et al.*, 2012). Thus, an urgent goal of ecology is to understand and predict the effect of temperature changes on biological processes.

By and large, ecologists have been quite successful at assessing how temperature may influence biological processes (Angilletta, 2009). At the organismal level, temperature can affect the behavior of ectotherms (Davis, 1989; Turner *et al.*, 1993; Long *et al.*, 2012) and

alter the body size and body condition of both ectotherms and endotherms (Atkinson, 1994; DeLong, 2012). Changes in body size and condition due to temperature can dramatically affect population dynamics (Vasseur & McCann, 2005; Ims *et al.*, 2008; Johnson *et al.*, 2010; Amarasekare, 2015) by altering per-capita growth rates (Frazier *et al.*, 2006; Jandricic *et al.*, 2010; Amarasekare & Savage, 2012) and genetic diversity (Pauls *et al.*, 2013), leading to an increase in extinction risk (Clements *et al.*, 2014). Additionally, changes in temperature can result in changes in the structure and stability of entire communities (Brose *et al.*, 2012) through their effects on interaction strengths (Rall *et al.*, 2010) and food web body size structure (Albouy *et al.*, 2014; Gibert & DeLong, 2014). Finally, temperature can alter succession rates (Anderson-Teixeira *et al.*, 2008) and ecosystem processes (Saxe *et al.*, 2001; Jeppesen *et al.*, 2010; Yvon-Durocher *et al.*, 2012). To put simply, temperature plays a major role in setting rates and patterns across all levels of biological organization.

Warmer temperatures are also well known to increase organism metabolism through the temperature dependence of biochemical kinetics (West *et al.*, 1999; Gillooly *et al.*, 2001; Brown *et al.*, 2004). Hence, it is

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commonly assumed that increased temperatures should also lead to increased activity (Taylor, 1963; Joern *et al.*, 2006) and velocity in ectotherms (Turner *et al.*, 1985; Hurlbert *et al.*, 2008). Velocities play a paramount role at setting interaction strengths between predators and their prey, as faster speeds can lead to higher encounter rates (Aljetlawi, 2004; Pawar *et al.*, 2012; Dell *et al.*, 2014). Interaction strengths are in turn responsible for population dynamics and the persistence of species within food webs (May, 1972; McCann *et al.*, 1998; Gilbert *et al.*, 2014). Thus, warmer temperatures could increase predator–prey interaction strengths through increased velocities, thus having negative effects for the persistence of species in complex food webs (Brose *et al.*, 2012), especially whenever asymmetrical responses to temperature are expected between predators and their prey (Dell *et al.*, 2014).

Studies assessing the effect of rising temperatures on interaction strengths, however, do not consistently support these predictions. In fact, interaction strengths may increase with temperature (Barton *et al.*, 2009; O'Connor, 2009; Rall *et al.*, 2010), decrease with temperature (Johnson *et al.*, 2010), or be temperature-independent (Novich *et al.*, 2014). Together, these results imply that we only have a very partial understanding of how increased cellular metabolism due to the temperature dependence of biochemical kinetics translates to an increase in the mechanical motion that actually determines velocity, and through that, attack rates and interaction strengths, as others have also suggested (Knies & Kingsolver, 2010; Englund *et al.*, 2011). It is thus crucial to elucidate how animal movement is affected by temperature in a mechanistic way, and how this process in turn affects predator–prey dynamics.

Here, we aim to fill this gap using an integrative approach that merges simple biomechanical models, the Metabolic Theory of Ecology, a classic consumer–resource model, and empirical data. We show that animal movements are indeed temperature-dependent but can be subject to qualitative shifts in their temperature dependence. These shifts are measured as an abrupt change in the activation energy of the process at a threshold temperature. Comparable changes in activation energies have been shown to occur in both chemical and biochemical systems (Truhlar & Kohen, 2001), but, to the best of our knowledge, have not yet been incorporated into theoretical models of species interactions (Pawar *et al.*, 2016). In fact, activation energies have thus far not only been considered constant by ecologists, but also highly conserved across systems and taxa (Gillooly *et al.*, 2001; Brown *et al.*, 2004). We argue that this may not be the case at all, as has also been recently suggested (Dell *et al.*, 2011, 2014; Pawar *et al.*, 2016). On the contrary, these regime changes in

temperature dependence may be common, arising from the additive effect of activation energies across levels of organization (Anderson-Teixeira *et al.*, 2008). Moreover, we show that crossing regimes of temperature dependence in animal movement can significantly alter the stability and dynamics of predator–prey interactions, thus having important consequences for animals living in a world where average temperatures are on the rise.

Materials and methods

To understand how temperature affects animal velocities, we: (i) use biomechanics to derive mathematical expressions for the temperature dependence of the frequency at which animals can move their limbs, (ii) test these models against empirical data and show the existence of changes in the temperature dependence of animal movement, and (iii) explore potential implications of these changes for the stability of predator–prey dynamics.

Cursorial movement

Generalities and assumptions. Animal velocities depend on the product of stride frequency (which depends on the frequency at which an animal can move its limbs) and stride length, both of which are quantities that can be temperature-dependent (Hurlbert *et al.*, 2008). To be conservative, we assumed that stride length remains constant across temperatures and only assessed the effect of temperature on the frequency at which an animal can move any limb. An in-depth depiction of all possible biomechanical models for animal movement is beyond the scope of this paper (but see Alexander, 1983, 2005). We will thus focus on one possible approach: dynamic similarity.

Dynamic similarity has been used extensively to model the movement of animals (Alexander, 1983) and has received empirical support over the years (Christiansen, 2002). It assumes that all forces and times associated with any mechanical movement are geometrically similar across linear dimensions. As a consequence, larger animals are assumed to be under the same physical constraints as smaller animals, the same way that a small physical pendulum can be modeled using the same mathematical approach as a large pendulum.

Assuming dynamic similarity, we focused on two main models of animal cursorial locomotion: the inverted-pendulum model and the spring-mass model. The inverted-pendulum model assumes that the motion of a limb is physically analogous to that of an inverted pendulum, where the mass of the pendulum is concentrated near the body, the limb itself is a mass-less, non-compliant rod, and the pivot of the system is the point of contact of the body with the ground or surface (Alexander, 1983). The spring-mass model assumes that limbs are compliant mass-less springs, thus able to store some kinetic energy in the form of elastic potential energy and to release this energy later on to aid in movement (Alexander, 1983). No animal follows perfectly either one of these mod-

els, but rather a mixture of them depending on their gait and specific limb configuration (Alexander, 1983, 2003; Biewener, 2003). Nonetheless, these models allow us to derive general expressions for limb movement frequency and its temperature dependence. In what follows, we first present the expressions derived from the inverted-pendulum model and then those derived from the spring-mass model.

The inverted-pendulum model. For the inverted-pendulum model, the limb movement frequency is:

$$f = \frac{1}{2\pi} \sqrt{\frac{g}{L}}, \quad (1)$$

where L is the length of the limb and g is the gravitational acceleration (9.83 m s^{-2}) (e.g., Alexander, 1983; Hurlbert *et al.*, 2008). For geometrically similar animals, the mass of the animal scales with the cube of its linear dimensions ($M \propto L^3$, see Derivation S1 for derivation). We can incorporate this assumption into (1) to get:

$$f \propto \frac{1}{2\pi} \sqrt{\frac{g}{M^{1/3}}}. \quad (2)$$

Next, we use results from the Metabolic Theory of Ecology that relates how basal metabolic rate (B) is a function of body mass (M) and temperature (T) as:

$$B = b_0 M^\theta e^{-\frac{E_a}{k_{\text{bol}} T}}, \quad (3)$$

in which B is the basal metabolic rate of an organism, b_0 is a taxon-specific constant, M is its body mass, θ is a taxon-specific scaling exponent typically found to vary between $2/3$ and 1 (DeLong *et al.*, 2010), E_a is the activation energy of the metabolic pathways considered (eV), k_{bol} is the Boltzmann constant ($8.62 \times 10^{-5} \text{ eV K}^{-1}$) and T is body temperature ($^\circ\text{K}$) (West *et al.*, 1999; Gillooly *et al.*, 2001; Brown *et al.*, 2004). Solving for mass in Eqn (3) and assuming $\theta = 3/4$, a common value for θ in nature (e.g., Gillooly *et al.*, 2001) we get

$$M = \left(\frac{B}{b_0}\right)^{\frac{4}{3}} e^{\frac{4 E_a}{3 k_{\text{bol}} T}}, \quad (4)$$

and combining (2) and (4) we obtain:

$$f \propto \frac{1}{2\pi} \sqrt{g} \left(\frac{B}{b_0}\right)^{-\frac{2}{9}} e^{\frac{2 E_a}{9 k_{\text{bol}} T}}. \quad (5)$$

Equation (5) predicts how limb movement frequency explicitly depends on temperature through its effect on metabolic rate for an animal moving according to the inverse-pendulum model.

The spring-mass model. In the spring-mass model, the resonant frequency is:

$$f = \frac{1}{2\pi} \sqrt{\frac{k}{M}}, \quad (6)$$

where k is the spring (or elastic) constant of the limb and M is the mass of the organism. Using (4) and (6) we get:

$$f = \frac{1}{2\pi} \sqrt{k} \left(\frac{B}{b_0}\right)^{-\frac{2}{3}} e^{\frac{2 E_a}{3 k_{\text{bol}} T}}. \quad (7)$$

Equation (7) predicts how limb movement frequency depends on temperature for an animal moving according to the mass-spring model.

Other types of movement

Generalities and assumptions. It is also possible to extend our approach to other types of movement. In what follows, we use dimensional analysis to derive expressions of how the frequency of limb motion depends on temperature for a number of movements for which the pendulum and spring-mass models do not apply (e.g., wings flapping, tongue flicking, rattlesnake rattling, etc.). While these types of movement may not always be directly related to cursorial motion and velocities, they are fueled by the same metabolic processes as stride frequency and they play important ecological roles. As such, their temperature dependence is of great interest. We derived expressions for three different types of movement: surfaces flapped against a medium for propulsion (e.g., wing beats), flicking elastic appendages (e.g., tails, tongues, cilia), and appendages rubbed against each other to produce sound (e.g., cricket fore wings producing chirps).

Flapped appendages for propulsion. Using dimensional analysis, it has been shown that wingbeat frequency depends on wingspan, wing area, the mass of the animal as well as gravitational acceleration and air density (Pennycuik, 1990). Building upon Pennycuik (1990), Eqn (4), and assuming geometric similarity, we rewrote the expression for wingbeat frequency as a function of temperature (see Derivation S2 for a complete derivation):

$$f \propto \frac{\sqrt{g}}{\sqrt[3]{\rho}} \left(\frac{B}{b_0}\right)^{-\frac{2}{9}} e^{\frac{2 E_a}{9 k_{\text{bol}} T}}, \quad (8)$$

where ρ is the density of the air and all other parameters follow from previous equations.

Motion of elastic appendages. Another type of movement involves the motion of compliant but elastic appendages such as tongues or tails. In these cases, the appendage stores a fraction of the kinetic energy as elastic potential energy and releases it later on, but the movement of the appendage also depends on its mass and moment of inertia. In these cases, dimensional analysis suggests that the frequency of the movement of the limb depends on the elastic constant of the appendage (k), the density of the medium in which the movement occurs (ρ), gravitational acceleration, as well as the moment of inertia of the appendage (I), and its total length (see Derivation S3 for a derivation). Assuming dynamic similarity and imposing as a condition that the effect of gravitational acceleration and medium density is the same as in Pennycuik's analysis (1990), we obtain the same expression as for flapped wings (i.e., Eqn (8), see Derivation S3).

Rubbed appendages. Last, in the case of two appendages rubbed against each other, the frequency depends on the length of the appendages, the force exerted by the muscles controlling the movement (F), and the moment of inertia of the appendages. Using (4) and geometric similarity, we find (see Derivation S4 for a derivation):

$$f \propto \sqrt{\bar{a}} \left(\frac{B}{b_0}\right)^{-\frac{2}{9}} e^{-\frac{2E_a}{9k_{\text{bol}}T}}, \quad (9)$$

where \bar{a} is the acceleration exerted by the muscle controlling the movement on the appendage being moved.

Fitting the models

By taking logarithms, we can rearrange Eqns (5), (7), (8), and (9) to simplify the task of fitting the models to empirical data. We get

$$\log(f) \propto \phi - \gamma \frac{E_a}{k_{\text{bol}}T}, \quad (10)$$

where $\phi = \log(\sqrt{g}/2\pi(B/b_0)^{2/9})$ for the pendulum model, $\phi = \log(\sqrt{k}/2\pi(B/b_0)^{2/3})$ for the spring-mass model, $\phi = \log(\sqrt{g}/\sqrt[3]{\rho}(B/b_0)^{2/9})$ for wingbeats and beats of elastic appendages, and $\phi = \log(\sqrt{\bar{a}}(B/b_0)^{2/9})$ for appendages rubbed against each other. For the pendulum model and the other types of movement analyzed, $\gamma = -2/9$, and for the spring-mass model, $\gamma = -2/3$. When $\log(f)$ is plotted against $1/kT$ (i.e., an Arrhenius plot), (10) becomes linear with a negative slope equal to $-2E_a/9$ or $-2E_a/3$ depending on the model. It is thus possible to estimate the activation energy of mechanical movements by fitting the models to appropriate data (i.e., using the model for rubbing appendages for data on chirping crickets, inverted-pendulum model, and spring-mass model for running or walking animals, etc.). The models were fitted to the data using simple linear regressions and breakpoint regressions, which allowed for a change in activation energies (slope). We used R^2 values as a measure of goodness-of-fit to assess whether breakpoint regressions were a better model than simple linear regressions.

The data

To fit our models, we collected published data on empirical estimates of the change in frequency of movement of animal limbs with temperature. When sources only reported animal velocities, we used the physical relationship between frequency, velocity, and length ($f = v/d$) to estimate limb movement frequency by dividing the reported velocities by the body-length (snout-vent or acron-telson length) of the animal. The data encompass vertebrate and invertebrate ectothermic taxa, organisms with different locomotion modes (cursorial, jumping, arboreal, flying, and swimming) and span major evolutionary transitions (unicellular and multicellular) (Tables 1 and 2). Not all of the datasets considered involve locomotion and thus not all of them contribute to our understanding of interaction strengths. However, the inclusion of datasets on

other types of movements not necessarily related to animal locomotion shows that our results may have consequences for other important processes beyond predator-prey interactions (e.g., intraspecific communication and mating).

To assess whether our results could be affected by the heterogeneous nature of our data, we tested whether there were any differences in limb movement frequency among groups before conducting our analyses. While there were some expected differences between species, we detected no significant differences between vertebrates and invertebrates, locomotion modes, and major evolutionary transitions (data not shown).

Consequences for population dynamics

Generalities. To assess how scaling the effect of temperature from cellular metabolism to animal movement can affect the stability of exploitative interactions, we used a classic Rosenzweig-MacArthur model (Rosenzweig & MacArthur, 1963), nowadays considered standard in population ecology (e.g., Abrams, 2000):

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - \frac{\alpha RC}{1 + \alpha\eta R}, \\ \frac{dC}{dt} &= \varepsilon \frac{\alpha RC}{1 + \alpha\eta R} - dC \end{aligned} \quad (11)$$

where R and C are the densities of prey and predators, respectively at a time t , r is the per-capita growth rate of the prey, K is the carrying capacity of the prey, ε is a conversion efficiency parameter that indicates the number of new predators produced per prey eaten, d is the background mortality rate for predators, α is their attack rate and η is their handling time. Finally, the time derivative of R and C represent the rate of change of prey and predator densities, respectively, through time.

In (11), the attack rate, α , affects the rate at which predator foraging rate increases with prey density when prey density is low. It can be written as a function of the relative speeds of predators and prey: $\alpha = A_d \sqrt{v_R^2 + v_C^2}$, where A_d is the predator's area of detection, v_R is the velocity of the prey, and v_C the velocity of the predator (Aljetlawi, 2004; Pawar *et al.*, 2012; Dell *et al.*, 2014; DeLong, 2014). Because the velocity of an animal is the product of the frequency at which the animal can move its limbs and its stride length, we can rewrite the attack rate as a function of temperature using either (5) or (7):

$$\alpha(T) = A_d \sqrt{v_R^2 + \varphi^2 \left(\frac{B}{b_0}\right)^{-2\gamma}} e^{-2\gamma \frac{E_a}{k_{\text{bol}}T}}, \quad (12)$$

where $\varphi = s \frac{1}{2\pi} \sqrt{g}$ and $\gamma = -2/9$ for the pendulum model, or $\varphi = s \frac{1}{2\pi} \sqrt{k}$ and $\gamma = -2/3$ for the spring-mass model. The parameter s comes from assuming dynamic similarity (see Derivation S1) in Eqn (2), and also takes into account the stride length of the animal. Because prey velocities are expected to be under stronger selection than predator velocities (life-dinner principle), they are generally assumed not to be as sensitive to changes in temperature as predator velocities. This assumption has been corroborated empirically (Dell *et al.*, 2011). We thus assumed that only the velocity of the

Table 1 Datasets for cursorial movements used separated by: species, zoological group, locomotion mode, and original variable. The order of the datasets matches the order of taxa in Fig. 1

Common name	Species	Group	Locomotion mode	Original variable	Reference
Viviparous lizard	<i>Zootoca vivipara</i>	Vertebrate	Cursorial	Speed (Snout-vent lengths s ⁻¹)	Avery & Bond (1989)
Fiddler crab	<i>Uca pugilator</i>	Invertebrate	Cursorial	Sprint speed (cm s ⁻¹)	Allen <i>et al.</i> (2012)
American alligator	<i>Alligator mississippiensis</i>	Vertebrate	Cursorial/ Swimming	Burst speed (m s ⁻¹)	Turner <i>et al.</i> (1985)
Dolichorinid ant	<i>Liometopum apiculatum</i>	Invertebrate	Cursorial	Speed (mm s ⁻¹)	Crozier (1924)
Green day gecko	<i>Phelsuma dubia</i>	Vertebrate	Cursorial/ Arboreal	Max speed (m s ⁻¹)	Bergmann & Irschick (2006)
Fence lizard	<i>Sceloporus occidentalis</i>	Vertebrate	Cursorial	Speed (m s ⁻¹)	Marsh & Bennett (1986)
House cricket	<i>Acheta domesticus</i>	Invertebrate	Cursorial/ Jumping	Running speed (mm s ⁻¹)	Lachenicht <i>et al.</i> (2010)
House fly	<i>Musca domestica</i>	Invertebrate	Cursorial/ Flying	Walking speed (mm s ⁻¹)	Schmalhofer & Casey (1999)
Desert iguana	<i>Dipsosaurus dorsalis</i>	Vertebrate	Cursorial	Running speed (m s ⁻¹)	Bennett (1990)
Desert night lizard	<i>Xantusia vigilis</i>	Vertebrate	Cursorial	Running speed (cm s ⁻¹)	Bennett (1990)
Blue-tailed skink	<i>Eumeces elegans</i>	Vertebrate	Cursorial	Running speed (cm s ⁻¹)	Du <i>et al.</i> (2000)
Ornate Box turtle	<i>Terrapene carolina</i>	Vertebrate	Cursorial	Stride frequency (Hz)	Claussen <i>et al.</i> (2002)

Table 2 Datasets for all other types of movement considered separated by species, locomotion mode, zoological group, evolutionary transition, and original variable. The order of the datasets matches the order of taxa in Fig. 2

Common name	Species	Group	Locomotion mode	Evolutionary transition	Original variable	Reference
Fruit fly	<i>Drosophila montana</i>	Invertebrate	Cursorial/Flying	Multicellular	Wing beats s ⁻¹	Ritchie <i>et al.</i> (2001)
Chirping cricket	<i>Gryllus bimaculatus</i>	Invertebrate	Cursorial/ Jumping	Multicellular	Chirp period (ms, i.e. 1/ frequency)	Doherty (1985)
Calopterygid damselfly	<i>Mnais costalis</i>	Invertebrate	Flying	Multicellular	Wing beats s ⁻¹	Tsubaki <i>et al.</i> (2010)
Garter snake	<i>Thamnophis elegans</i>	Vertebrate	Limbless	Multicellular	Flicks s ⁻¹	Stevenson <i>et al.</i> (1985)
Predatory protist	<i>Stentor polymorphus</i>	Protist	Swimming	Unicellular	Cilia beat s ⁻¹	Sleigh (1956)
Rattlesnake	<i>Crotalus atrox</i>	Vertebrate	Limbless	Multicellular	Rattles min ⁻¹	Martin & Bagby (1972)

predator changes with temperature, setting v_R constant. Also, this assumption makes attack rates less sensitive to temperature and our conclusions more conservative. In addition, stride length is also known to increase with temperature (Claussen *et al.*, 2002), so the temperature effects should be larger in magnitude in nature than those shown by this model.

Effects of temperature on dynamics. We assessed how a change in temperature affected the stability of the system in (11) and (12) in two different ways. First, we assessed how a monotonic change in average temperature can affect the stability of the system. Second, we explored how seasonality can affect the stability of the system by imposing temperature fluctuations around 22 °C (as observed in our data for the average threshold temperature at which regimes of temperature dependence change) as a sinusoidal function ($A \sin(\rho 2\pi t) + T_{\text{ref}}$, where A is the amplitude of the wave (2 °C), $\rho 2\pi$ is its period in radians ($\rho = 0.09$), t is time, and $T_{\text{ref}} = 22$ °C, Fig. 4e).

We assessed stability using local stability analysis, which determines the propensity of a system to return to equilibrium after a small perturbation (see Derivation S5 for details on local stability analysis). To do this, we calculated the matrix of derivatives with respect to both R and C of the differential equations in (11) (i.e., Jacobian matrix). We evaluated the Jacobian matrix at the equilibrium and then calculated its eigenvalues. In a model with two species, the Jacobian matrix will only have two eigenvalues. If the real part of the dominant eigenvalue (largest one) of the system is negative, the system is stable (i.e., the system would return to equilibrium after a small perturbation) and unstable otherwise (i.e., the system would go away from equilibrium after a small perturbation).

Parameterization. Parameter values vary wildly in nature, even within species. For example, attack rates range from 0.04 to 14 and handling time does so from 3.64×10^{-14} to 0.01 for the protist *Didinium nasutum* preying on *Paramecium caudatum*

(DeLong & Vasseur, 2013). Per-capita growth rates (r) can range from 0.78 to 0.85 (DeLong *et al.*, 2014) and have been empirically observed to be as large as 7.54 in some protists (DeLong *et al.*, 2015). The conversion efficiency (ϵ) can range from 0.87 to 5.78 (DeLong *et al.*, 2015) as well, and the carrying capacity can assume virtually any positive value depending on the system. Model parameters can thus span several orders of magnitude even within species. Choosing parameter values is therefore a nontrivial task and should be done in the light of the goals of each study. Here, we only aim to illustrate theoretically the potential consequences of crossing regimes of temperature dependence of animal movement on predator–prey stability. In doing so, we are not showing proof that these consequences occur in nature, but that these may occur in some systems. To achieve our goal, we chose a combination of parameters that would ensure the coexistence of both predators and prey, following previous theoretical work (DeLong *et al.*, 2014, 2015; Gibert & Brassil, 2014; Gibert & DeLong, 2015), but in such a way that parameters would fall within biologically feasible ranges (i.e. $r = 2$, $\epsilon = 0.5$, $d = 0.1$, $A_d = 0.02$, $s^2 = 1000$, $B/b_0 = 1$, $v_R = 1 \text{ m s}^{-1}$). Many other parameter combinations are also possible and lead to qualitatively similar results.

Results

Temperature and frequency

Equations (5), (7), (8), and (9) predict that movement frequency increases monotonically with temperature because its derivative with respect to temperature is always positive (i.e., $\partial f/\partial T \propto E_a \sqrt{g}/[9\pi k_{\text{bol}} T^2 e^{2E_a/9k_{\text{bol}} T} (B/b_0)^{2/9}]$ for the pendulum model, $\partial f/\partial T \propto E_a \sqrt{k}/[3\pi k_{\text{bol}} T^2 e^{2E_a/3k_{\text{bol}} T} (B/b_0)^{2/3}]$ for the spring-mass model, $\partial f/\partial T \propto 2E_a \sqrt{g}/[9\sqrt{\rho} k_{\text{bol}} T^2 e^{2E_a/9k_{\text{bol}} T} (B/b_0)^{2/9}]$ for wingbeat frequency, and the movement of elastic appendages, and $\partial f/\partial T \propto 2E_a \sqrt{a}/[9k_{\text{bol}} T^2 e^{2E_a/9k_{\text{bol}} T} (B/b_0)^{2/9}]$ for two appendages being rubbed against each other). Our theoretical prediction is consistent with the data in the temperature range considered, since movement frequency increased monotonically with temperature in all cursorial locomotion datasets (Fig. 1) as well as those considering other types of movement (Fig. 2).

Activation energies

In most cases, the data were better described by a breakpoint regression than by a linear regression (Figs 1 and 2, Table 3, Derivation S6), indicating that activation energies change abruptly with temperature. The temperature at which activation energies change ranged from 10.5 °C (the lizard *Zootoca vivipara* – formerly *Lacerta vivipara*, Fig. 1a) to 31 °C (the ornate box turtle *Terrapene carolina*, Fig. 1l) with a mean of 22 °C \pm 0.2 SE. In three cases (the house fly *Musca*

domestica, Fig. 1h; the fruit fly *Drosophila montana*, Fig. 2a; and the damselfly *Mnais costalis*, Fig. 2c), the regressions do not support a breakpoint. In one case (the green day gecko – *Phelsuma dubia*, Fig. 1e), there was no difference between the model with a breakpoint and the model without one (Table 3). Colder temperatures were characterized by higher activation energies and lower limb movement frequencies due to the combined effect of a steeper slope and a higher intercept (Figs 1 and 2). Warmer temperatures showed lower activation energies with greater limb movement frequencies (Figs 1 and 2).

Regardless of the model considered, the activation energies estimated through a breakpoint regression at colder temperatures (i.e., postbreaking point) were much higher than previously reported (Fig. 3) and significantly higher than those at warmer temperatures (i.e., pre breaking point) (estimate = 3.7 eV \pm 1 SE, two-sample $t = 3.54$, $df = 28$, $P = 0.001$, Fig. SI-a; and estimate = 1.3 eV \pm 0.4 SE, two-sample $t = 3.8$, $df = 28$, $P < 0.0001$, Fig. SI-b). Overall, the pendulum model yielded activation energies three times larger than the spring-mass model when only analyzing cursorial motion.

Consequences for population dynamics

We found that changes in activation energy can have important consequences for population stability (Fig. 4). When only a monotonic increase in average temperature was considered, temperature had a much larger effect on stability in the range of temperatures associated with lower activation energies (i.e., warmer temperature, Fig. 4a–d). This effect was much stronger when a change in activation energy was taken into account (Fig. 4a–d, black line, right inset), than when it was not (Fig. 4a–d gray line, left inset). Because of the discrete nature of the change in temperature dependence, the effect of temperature on consumer–resource stability was discrete and important in magnitude (Fig. 4a–d).

The direction of this effect was dependent on the parameters controlling the consumer–resource interaction. For example, all else being equal, systems with a high prey carrying capacity seemed to be destabilized by increasing temperature when changes in activation energy were included (Fig. 4a, c). Conversely, the stability of systems where the prey had a lower carrying capacity increased with temperature when regime shifts were included, even though predator velocity, and thus attack rates were still increasing (Fig. 4b, d). The effect of temperature on the stability of the dynamics was much stronger when the pendulum model was used (Fig. 4, first row) than when the spring-mass

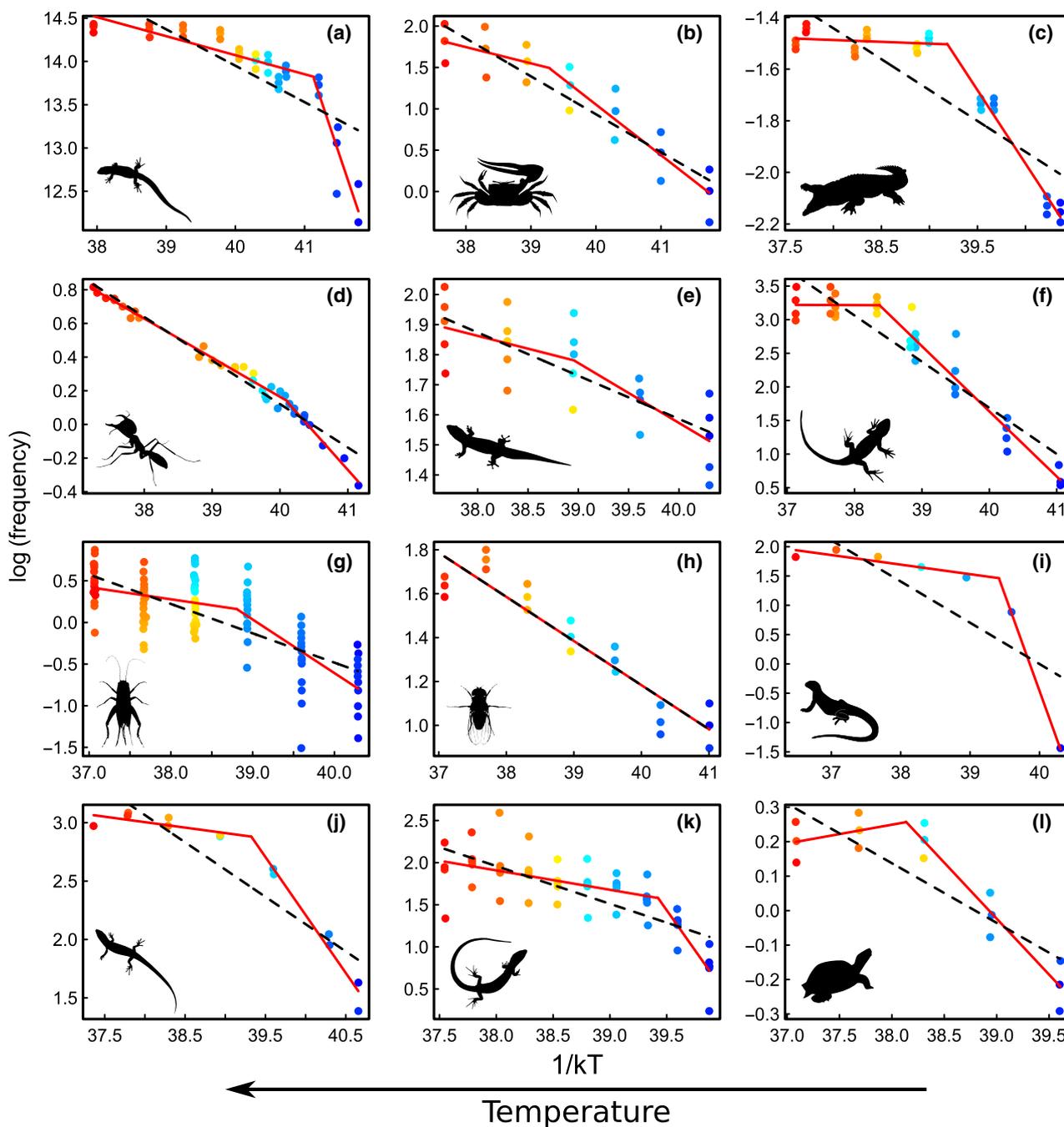


Fig. 1 Effect of temperature on limb movement frequency for all datasets on cursorial movements. Temperature increases from right to left. Datapoint color matches that increase of temperature (blue = lower temperatures; red = warmer temperatures). Equations (5) or (7) fits are shown in black-dashed lines, and fits with changing activation energies (breakpoint regression of Eqn (5) or (7)) are shown as solid red lines. (a) viviparous lizard, (b) fiddler crab, (c) american alligator, (d) dolichorinid ant, (e) green day gecko, (f) fence lizard, (g) house cricket, (h) house fly, (i) desert iguana, (j) desert night lizard, (k) blue-tailed skink, (l) ornate box turtle.

model was used (Fig 4, second row). Finally, when seasonality was taken into account (Fig. 4e), temperature led to fluctuations in stability whenever a change in activation energy was considered (Fig. 4f, black), but almost no change in stability when activation energy was constant (Fig. 4f, gray).

Discussion

Here, we merge a mechanistic biomechanical approach, the Metabolic Theory of Ecology, and empirical data to show that although animal movement is highly temperature-dependent, this temperature dependence occurs

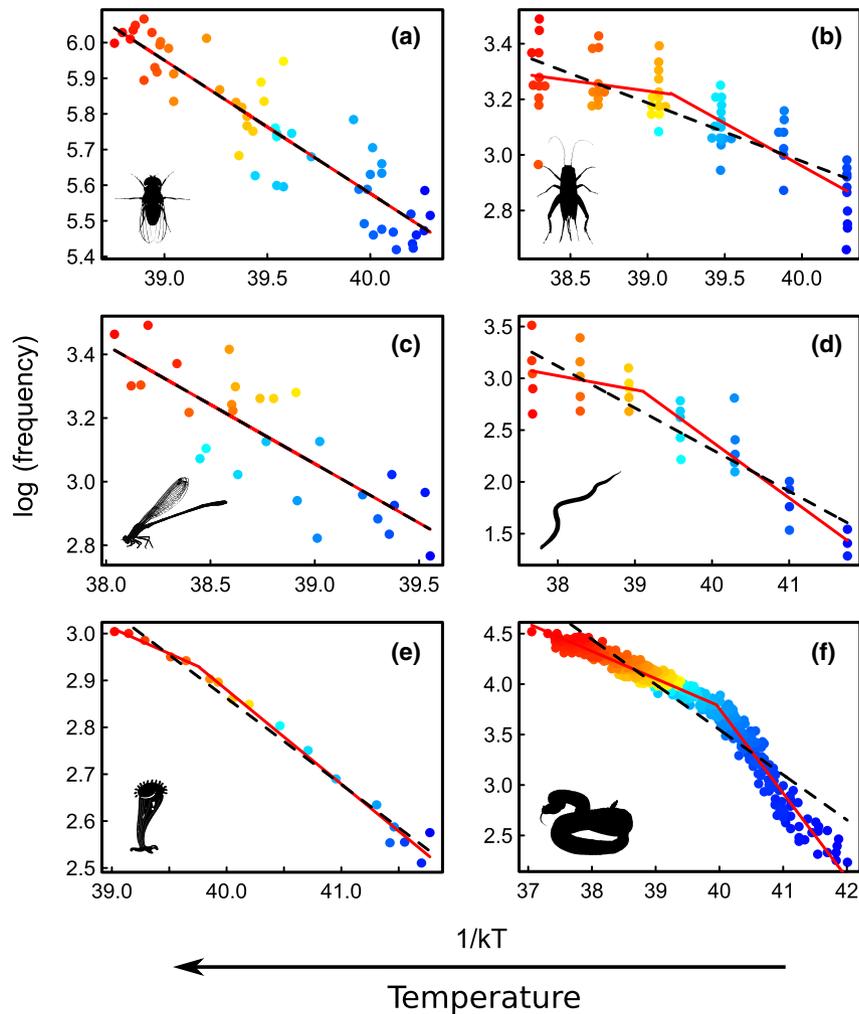


Fig. 2 Effect of temperature on all other types of limb movement. Color code as in Figure 1. (a) fruit fly, (b) chirping cricket, (c) calopterygid damselfly, (d) garter snake, (e) predatory protist, (f) rattlesnake.

in at least two qualitatively different regimes. Moreover, the existence of these regimes of temperature dependence has important consequences for predator–prey interactions both in seasonal environments and in scenarios where temperature may increase monotonically (such as for animals that live only for a season). While our results suggest a monotonic increase of the frequency at which animals can move limbs with temperature, this reflects: (i) the fact that our models consider an Arrhenius equation rather than a unimodal function of temperature (Englund *et al.*, 2011; Amarasekare & Savage, 2012; Amarasekare & Coutinho, 2014) and (ii) the fact that our data were collected in the rising portion of the curve only and thus do not show the dropping portion of the curve. In nature, however, this response should be expected to be unimodal rather than monotonic (Angilletta, 2009; Knies & Kingsolver, 2010; Dell *et al.*, 2014).

Changes in activation energy and its potential causes

The observed change in activation energy with temperature leads to at least two distinct regimes of temperature dependence in animal movement. Crossing regimes of temperature dependence is common in chemical and biochemical reactions (Kohen *et al.*, 1999; Truhlar & Kohen, 2001), as activation energies have been observed to decrease with temperature (Hurlbert *et al.*, 2008). A recent study quantifying activation energies across systems and taxa noticed a pattern in the residuals of Arrhenius plots (Dell *et al.*, 2011) that we think may be due to larger changes in activation energies that went unnoticed. A recent work by the same authors, however, explicitly shows ways to consider the existence of these changes in temperature dependence as well as how ordinary least square estimates (OLS) can under- or overestimate activation energies at

Table 3 Goodness-of-fit of the linear and breakpoint regression fits of the models of cursorial movement and all other types of movement with the best model in bold (regardless of biomechanical model considered). The data for the domestic fly, the fruit fly, and the damselfly did not accept a breakpoint and thus a breakpoint model could not be fitted. The order matches that of Table 1 and 2 as well as Figs 1 and 2

Common name	Linear R ²	Breakpoint R ²	Movement	Model type
Viviparous lizard	0.62	0.96	Cursorial	Pendulum/Spring-Mass
Fiddler crab	0.84	0.88	Cursorial	Pendulum/Spring-Mass
American alligator	0.76	0.98	Cursorial	Pendulum/Spring-Mass
Dolichorinid ant	0.97	0.99	Cursorial	Pendulum/Spring-Mass
Green day gecko	0.61	0.61	Cursorial	Pendulum/Spring-Mass
Fence lizard	0.85	0.94	Cursorial	Pendulum/Spring-Mass
House cricket	0.53	0.59	Cursorial	Pendulum/Spring-Mass
House fly	0.87	–	Cursorial	Pendulum/Spring-Mass
Desert iguana	0.65	0.99	Cursorial	Pendulum/Spring-Mass
Desert night lizard	0.83	0.98	Cursorial	Pendulum/Spring-Mass
Blue-tailed skink	0.54	0.70	Cursorial	Pendulum/Spring-Mass
Ornate Box turtle	0.73	0.92	Cursorial	Pendulum/Spring-Mass
Fruit fly	0.83	–	Wingbeats	Flapped wings
Chirping cricket	0.62	0.68	Rubbed limbs	Rubbed limbs
Calopterygid damselfly	0.65	–	Wingbeats	Flapped wings
Garter snake	0.81	0.85	Tongue flicks	Elastic appendages
Predatory protist	0.98	0.99	Cilia beats	Elastic appendages
Rattlesnake	0.87	0.97	Rattling	Elastic appendages

different temperature ranges (Pawar *et al.*, 2016). While our own results show a difference between OLS and breakpoint regression (Figs 2 and 3), our results further suggest that differences in activation energies may arise from underlying models as well. For example, when animal locomotion was modeled as an inverted pendulum, activation energies were lower than those reported previously (Fig. 3a), but they were equal to average values reported when animal locomotion was modeled using the spring-mass model (Fig. 3b). Together, these results contribute to the broader understanding of the temperature dependence of animal locomotion and suggest that movement temperature sensitivity can change wildly in nature both across temperatures and taxa.

Understanding the causes of these changes may be crucial for predicting the effects of global climate change in natural ecosystems. The pattern we described here could be explained by a number of nonmutually exclusive mechanisms. First, activation energies can change with temperature for a number of reasons. In purely chemical systems, activation energies can decrease with temperature (as observed here) when the distribution of reaction energies is narrower than that of reactant energies (Truhlar & Kohen, 2001). For example, enzymatic reactions generally show a decrease in activation energy with temperature, mainly due to conformation changes in the reactants that increase their reactivity (Truhlar & Kohen, 2001). It has been suggested that the reactivity of enzymes may be under

strong selection, leading to more efficient biochemical reactions at the temperature at which the organism lives (Massey *et al.*, 1966; Truhlar & Kohen, 2001). This range of temperatures that lead to optimal reaction rates has often been referred to as the Physiological Temperature Range (Martin & Huey, 2008; Pawar *et al.*, 2016). Indeed, animal movement has been shown to be more efficient within the PTR, which usually coincides with that at which lower activation energies were observed in our study and in others (Pawar *et al.*, 2016). Changes in temperature dependence in animal movement may thus be adaptive, as selection imposed by predators and mate searching, among others, favor low energetic costs of locomotion and smaller temperature sensitivity (e.g., life-dinner principle).

Alternatively, chemical reactions with multiple steps can have additive activation energies (Anderson-Teixeira *et al.*, 2008). The transformation of biochemical energy from oxidative metabolic pathways to biomechanical movement not only has multiple chemical steps, but also involves added layers of complexity: from the generation of energy to fuel the movement of the macromolecules involved in muscle contraction, to the actual mechanical movement of the limb. Movement requires a change in the shape and size of muscle cells, as well as, overcoming limb inertia, joint friction, and the drag force exerted on the limb by the fluid in which the movement occurs (e.g., water or air). Overcoming each of these steps requires energy input, and the temperature dependence of these inputs may thus

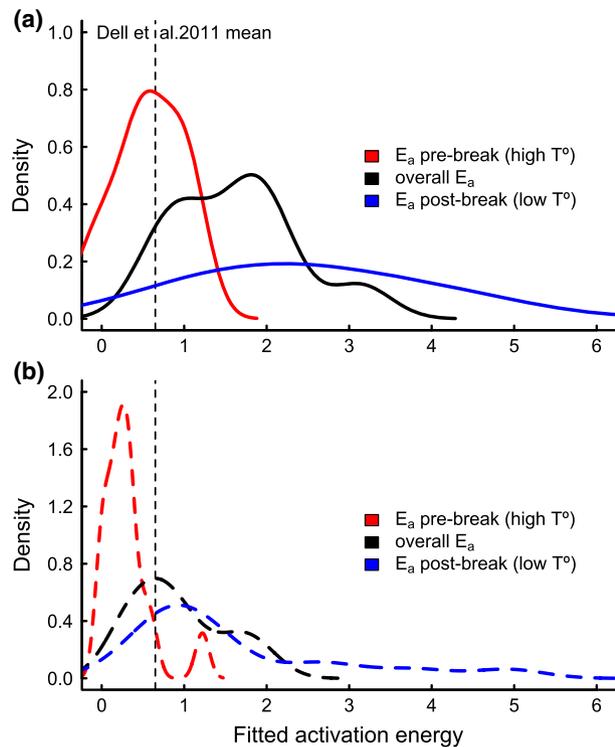


Fig. 3 Estimated density curves for the activation energies (E_a) across all datasets reported for: (i) the fitted models with constant E_a (black), and (ii) the fitted model with shifting E_a : activation energies prebreak (high T° , red) and activation energies postbreak (low T° , blue). For comparison, we also report the mean activation energies across taxa and levels of biological organization reported in the literature (Dell *et al.*, 2011) as a vertical dashed line. (a): activation energies as estimated using the inverted-pendulum model for cursorial types of movement only. (b): activation energies as estimated using the spring-mass model for cursorial types of movement only.

stack up. After some critical temperature, the energy required for some or many of these steps might be greatly diminished, causing a steep change in the observed overall activation energy (e.g., fluidity of synovial liquid increases nonlinearly with temperature, so joint friction decreases with temperature, Barnett (1958); cell membrane fluidity also increases, facilitating cell shape change, Heimburg, 2007).

An important prediction of this explanation in terms of additive activation energies is that the activation energy of a biological process should increase with the complexity of the process. For example, single-step biochemical reactions should have lower activation energies than multistep reactions. These should in turn have lower activation energies than more complex processes such as animal movement, and these should have lower activation energies than upper level processes, such as population growth rates. There is strong support for this prediction, with biochemical and indi-

vidual activation energies being much smaller than population or community level activation energies (Dell *et al.*, 2011). Some ecosystem processes such as respiration rate, however, do not follow this prediction (Yvon-Durocher *et al.*, 2012), probably because they are simply summations of cellular level processes across individuals and activation energies thus may not be additive in this case.

Importantly, this additive effect can be derived from first principles, and has been invoked, for example, as an explanation to why activation energies increase throughout the entire successional process on cooling lava flows at Mauna Loa, Hawaii (Anderson-Teixeira *et al.*, 2008). In that case, the complexity of the system and its associated processes increase over time and so do the estimated activation energies of several processes, which is consistent with our explanation. Together, these results suggest that the change in temperature dependence reported here might be due to the additive effect of activation energies accumulating across levels of biological organization.

Universality

Our results suggest that changes in regimes of temperature dependence may be common. Even in two of the cases where no breakpoint was observed (the fruit fly *Drosophila montana*, Fig. 2a; and the damselfly *Mnais costalis*, Fig. 2c), the range of temperature reported in the original dataset was much smaller than in most other datasets. On average, the reported range of temperature across our datasets was 23 °C, while the fruit fly dataset only reported a 14 °C range and the damselfly reported an 11 °C range. It is therefore possible that the location of the change in activation energy in those datasets was not included in the original experimental ranges considered. Alternatively, these species or groups may not show a change in activation energy. Indeed, no breakpoint was found for the house fly *Musca domestica* walking (Fig. 1h) even though the temperature range collected originally was large (10–40 °C). Regimes of temperature dependence in animal movement may thus not necessarily be universal, but they appear widespread, as also suggested by other recent work (Pawar *et al.*, 2016).

Ecological consequences of crossing regimes of temperature dependence

The consequences of increased temperatures for population dynamics are being studied intensively and important steps toward understanding these are currently being taken (Vasseur & McCann, 2005; Englund *et al.*, 2011; Amarasekare, 2015). We know that

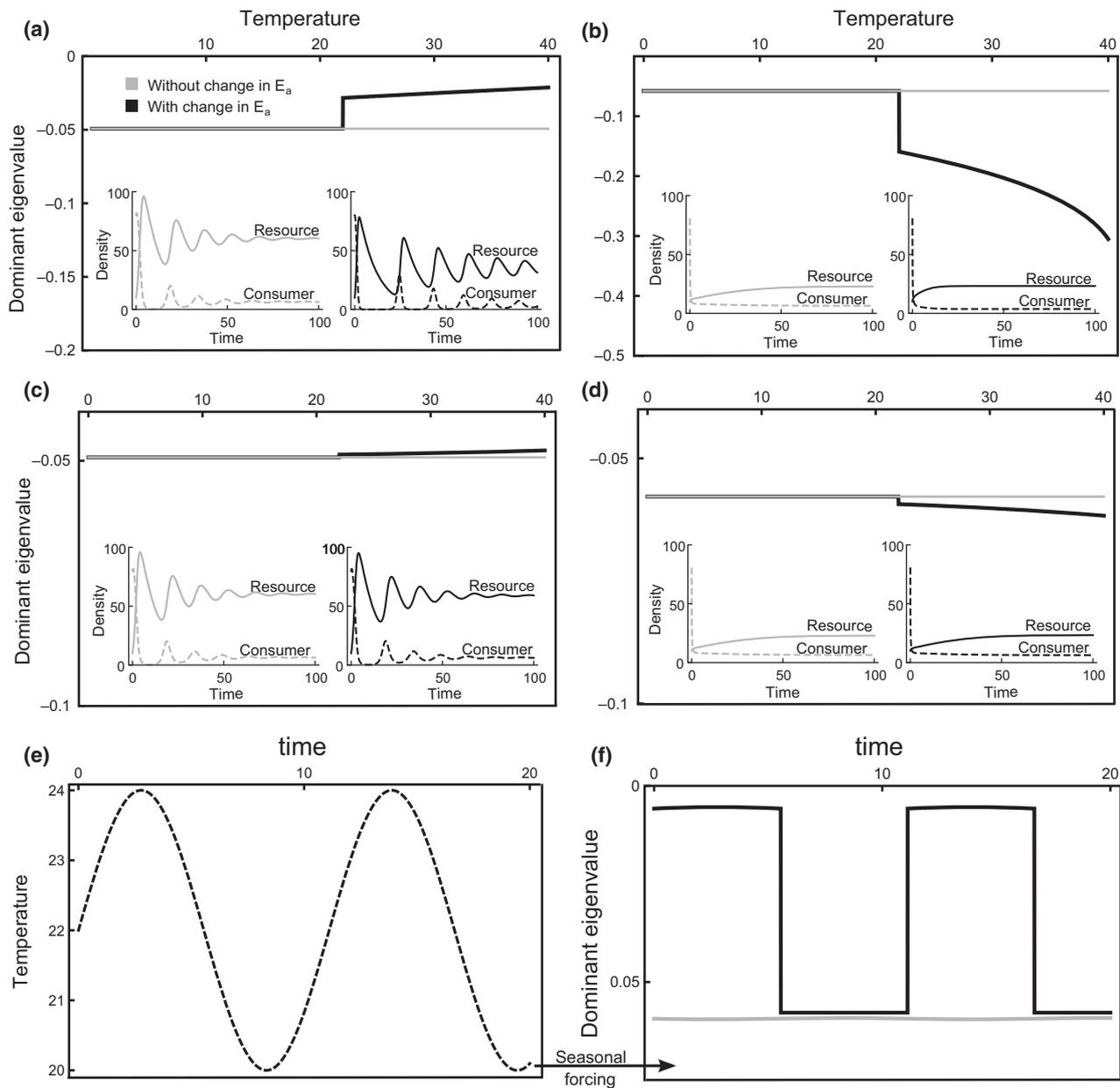


Fig. 4 Plot of how consumer–resource model stability, given by the dominant eigenvalue, changes with temperature. As the dominant eigenvalue gets more negative, stability increases, and stability decreases as the dominant eigenvalue gets positive. In gray, we plot the effect of temperature on the stability of the model when the change in activation energies is not taken into account (i.e., the average slope across datasets for the simple regression model: $E_a = 1.63$ eV for the pendulum model and $E_a = 0.93$ eV for the spring-mass model). In black, we plot the effect of temperature on the stability of the model that includes a shift in activation energies at $T = 22$ °C (i.e., average slopes of the breakpoint regressions: from $E_a = 4.27$ eV to $E_a = 0.57$ eV for the pendulum model, and from $E_a = 1.68$ eV to $E_a = 0.31$ eV for the spring-mass model). The insets show the actual population dynamics for predators and prey for the model considered (Eqns 11 and 12) with (black) and without activation energy shifts (gray). Importantly, the temperature effect on stability is much stronger when the reported change in activation energies is taken into account (black). However, the direction of this effect can change with the parameters of the model. At high resource carrying capacity ($K = 100$), temperature can decrease stability (a and c), while at low resource carrying capacity ($K = 10$), temperature can have the opposite effect (b and d). We chose parameters values to ensure coexistence: $r = 2$, $\epsilon = 0.5$, $d = 0.1$, $A_d = 0.02$, $s^2 = 1000$, $B/b_0 = 1$, $v_R = 1$ m s⁻¹. (e) Plot of the imposed seasonally fluctuating temperatures. (f) How stability is affected by these fluctuations considering changes in E_a (black) or not (gray).

temperature can affect multiple parameters of consumer–resource interactions simultaneously, with important consequences for population dynamics. For example, a unimodal growth rate response to temperature can lead to consumer–resource dynamics that are qualitatively different from those expected from a monotonic response (Amarasekare & Coutinho, 2014; Amarasekare, 2015). However, our understanding of these effects relies to some extent on the assumption that animal movement may respond smoothly to temperature changes throughout the entire range of possible temperatures.

Here, we show that this assumption may be largely incorrect, since the activation energy associated with animal movement decreases with temperature in a step-wise fashion. This change thus needs to be taken into account in future studies on the ecological consequences of warming. By exploring some simple implications of crossing these regimes of temperature dependence, we showed that predator–prey stability can be qualitatively different over different temperature ranges, and that this effect can be even stronger when seasonality is considered (Fig. 4). We have also shown that the sign of the effect observed strongly depends on the other parameters controlling the interaction, leading to situations where an increase in temperature can either increase or decrease consumer–resource stability (Fig. 4), as also suggested by other recent work (Gilbert *et al.*, 2014).

Because unstable dynamics are usually determined by stronger interaction strengths and stable dynamics by weaker interaction strengths (e.g., McCann *et al.*, 1998) the changes in activation energy described here may be an important explanation for the seemingly opposite effects that temperature can have on interaction strengths (e.g. O'Connor, 2009; Johnson *et al.*, 2010; Novich *et al.*, 2014). However, our explanation does not preclude the occurrence of other mechanisms explaining the diverse effects of temperature on interaction strengths, such as, for example, variation in foraging mode (Novich *et al.*, 2014). In fact, these mechanisms may not be independent at all, and the changes in temperature dependence reported here might be linked to changes in foraging mode leading to different resulting interaction strengths. Altogether, these results suggest that the effect of temperature may be system-specific, and predictions may only be possible if based on a solid understanding of the natural history of the system considered.

Our results have implications that go well beyond consumer–resource interactions, extending potentially to any type of animal interaction that relies on locomotion or simply on the movement of limbs. As such, communication, mating, sensory detection, and any behavioral modality dependent on the movement of

limbs may be strongly affected by environmental changes in temperature. Regarding courtship, for example, female fruit flies (*Drosophila montana*) choose mates based on the frequency of wing movement, which increases with temperature (Ritchie *et al.*, 2001). Similar effects are found in the stridulating calls of crickets (Doherty, 1985; Pires & Hoy, 1992a,b; Hedrick *et al.*, 2002), the head-bob displays of lizards (Phillips, 1995) and the leg-tapping courtship of spiders (Shimizu & Barth, 1996; Jiao *et al.*, 2009). In all of these cases, how male courtship responds to changes in temperature (linearly or with changes in regimes of temperature dependence) can have important effects on his ability to attract a mate.

Understanding how animal movement responds to changes in temperature is likely to be crucial to understanding animal behaviors. Indeed, animals may actively avoid, or at least counter the potential effects of temperature changes through their behavior and physiology. Behavioral plasticity may allow animals to overcome the effects of changes in temperature dependence when avoiding suboptimal temperatures is not an option (e.g., multiple reptiles switch their defensive strategy from active fleeing to aggressive ground-standing or thanatosis in colder temperatures, Hertz *et al.* 1982; Citadini & Navas, 2013, but see Gerald, 2008 for an inversed pattern). On the other hand, some animals may be able to avoid or minimize the effects of temperature change by limiting their activities. Animals with intense courtship or contest displays, for example, may limit their reproductive activity to a short season or to very specific environmental conditions to optimize their energetic expenditure (see the contest behavior of the sun-basking wood-speckled butterfly *Pararge aegeria*, where male body temperature is an important predictor of male success, Hardy, 1998, Stutt & Willmer, 1998). In areas where temperature variation is moderate, such as the tropics, animals may minimize the effects of changes in temperature by migrating to different habitats or microhabitats during the colder months of the year (e.g., arachnids aggregating in caves during the winter months, Chelini *et al.*, 2011). Long-range migratory ectotherms may also avoid these changes by following their temperature of lowest activation energy along the year. Indeed, migratory fish such as the fall chinook salmon (*Oncorhynchus tshawytscha*) are adopting longer migratory routes in order to avoid excessively warm, suboptimal waters (Goniaea *et al.*, 2006). These examples also highlight the fact that, for many species, what happens to locomotor activity once the temperature exceeds the optimal range and becomes too warm is largely unknown. As such, understanding the potentially complex effects of changes in the temperature dependence of animal movement is therefore

crucial to predict, and address, the effects of global climate change on the behavior and reproduction of ectotherms.

Conclusions

We merged simple biomechanical models and the Metabolic Theory of Ecology to generate a mechanistic description of the temperature dependence of animal movement. Using empirical data, we showed that animal movement can cross regimes of temperature dependence potentially associated with a more efficient use of energy at higher temperatures. These changes in temperature dependence may occur as a consequence of additive activation energies stacking up across levels of biological organization, but most importantly, suggest that activation energies are far from fixed and conserved in nature. Lastly, we showed that by not taking these changes into account, we may be limiting our understanding of consumer–resource responses to temperature, thus failing to predict accurately the consequences of environmental change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Derivation S1. Geometric similarity and the $M \propto L^3$ relationship.

Derivation S2. Temperature dependence of frequency for flapped wings.

Derivation S3. Temperature dependence of frequency for elastic appendages.

Derivation S4. Temperature dependence of frequency for rubbed appendages.

Derivation S5. Local stability analysis of consumer-resource model.

Derivation S6. Cutoff temperatures and estimated activation energies.

Table S1. Activation energy estimates and temperature cutoff values for all cursorial movements.

Table S2. Activation energy estimates and temperature cutoff values for all other movements and appropriate models (see Table 3 in the main text).

Fig. S1. Fitted activation energies before breakpoint (low Temp, blue), and after the breakpoint (warm Temp, red), for the inverted-pendulum model (a), and the spring-mass model (b).